Evolution, 58(9), 2004, pp. 1984–2001

EVOLUTIONARY RATES IN THE ADAPTIVE RADIATION OF BEETLES ON PLANTS*

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Abstract.—Herbivorous insects and other small consumers are often specialized both in use of particular host taxa and in use of particular host tissues. Such consumers also often seem to show consistent differences in the rates of evolution of these two dimensions of host use, implying common processes, but this has been little studied. Here we quantify these rates of change in host use evolution in a major radiation of herbivorous insects, the Chrysomeloidea, whose diversity has been attributed to their use of flowering plants. We find a significant difference in the rates of evolutionary change in these two dimensions of host use, with host taxon associations most labile. There are apparently similar differences in rates of host use evolution in other parasite groups, suggesting the generality of this pattern. Divergences in parasite form associated with use of different host tissues may facilitate resource partitioning among successive adaptive radiations on particular host taxa.

Key words.—Bruchidae, Cerambycidae, Chrysomelidae, herbivory, insect-plant interactions, parasite-host interactions, phylogeny.

Received July 30, 2003. Accepted July 2, 2004.

Consistently different rates of evolutionary change in different kinds of characters are phenomena as common to adaptive radiation as to molecular evolution. Rate regularity may reflect differences in selection intensities (Hartl and Clark 1997) or in genetic/developmental constraints (Williams 1992; Knoll and Carroll 1999). In the context of the evolution of resource use, different aspects of host use appear to evolve at different rates and evolutionary changes in host-choice behaviors are widely accorded a creative role in fostering adaptive radiations (Wcislo 1989; West-Eberhard 1989; Blomberg et al. 2003; but see Huey et al. 2003).

In such small consumers as parasitic or herbivorous invertebrates, major changes in host taxa preferences (e.g., preferences for use of different families, orders, classes, or phyla of host) are generally thought relatively rare (e.g., as compared to shifts in use of different species of closely related hosts). Specializations on particular host taxa therefore often characterize (and by extension are thought to result in) higher taxonomic groups of consumers, although many instances of dramatic host shifts are known (Ehrlich and Raven 1964; Farrell and Mitter 1993; Powell et al. 1998; Schoonhoven et al. 1998). Less well studied are rates of change in the ways hosts are consumed, which can range from attachment outside the host body and grazing on external tissues as in many beetles, caterpillars, or fleas; to boring inside particular host tissues such as seeds, stems, roots or skin, or other internal organs. Such differences in the variability of feeding mode versus host taxa used have long been part of the accepted lore on parasites of all kinds (Mayr 1963). Indeed, the proliferation of parasite species across a wide array of hosts, apparently spurred by a new mode of feeding, is a classic observation under the adaptive radiation hypothesis (Schluter 2000). For example, among the platyhelminth vertebrate parasites, a specialized haptor permits different monogenean trematodes to cling to the epidermis of their various fish, frog, or lizard hosts (Kearn et al. 2001; Desdevises et al. 2002), whereas the cestodes use an adhering scolex and absorptive integument for life in the lower intestine. Similar patterns of taxon and tissue specificity occur in nearly every kingdom, ranging from the smut fungal genus *Tilletia* (specific to seeds of different grass genera), and the Trichomycetes (restricted to the guts of mandibulate arthropods, Mirsa and Lichtwardt 2000) to the *Plasmodium* malarias of birds and mammals that occur in the liver and circulatory system. Even human and bovine parainfluenza viruses, specialized for different host taxa, retain specificity to the respiratory epithelium from their common ancestor (Taber and Pease 1990).

Specificity in host tissues and taxa are also well known in plant-feeding insects, particularly in the diverse orders Lepidoptera (Powell 1980; Powell et al. 1998), Coleoptera (Farrell 1998), and Hymenoptera (Shaw 1988; Belshaw and Quicke 2002), although most ecological or phylogenetic studies have focused on use of host taxa rather than particular tissues, per se. For example, the importance of behavior and physiology in insect specialization on particular host-plant species is widely accepted (Bernays 2001; Via 2001), and trade-offs in performance (and enemy avoidance) are thought their primary explanation (Futuyma and Moreno 1988; Jaenike 1990). Phylogenetic studies of evolutionary shifts among host-plant taxa reveal that host shifts are often very conservative, showing strong correlation with host taxonomy (Farrell and Mitter 1990, 1993; Futuyma et al. 1995; Farrell 1998, 2001; Marvaldi et al. 2002) or correlation with host growth form or habitat (Mardulyn et al. 1997; Janz and Nylin 1998).

Comparable studies of the evolution of host tissue specializations in insects are few (but see Ronquist and Liljeblad 2001; Cook et al. 2002). For the rest of this paper we will refer to larval feeding preferences only, because adults generally either feed on the leaves of the same larval plants, or subsist on nectar or pollen to fuel their comparatively brief life of mating and oviposition as in Lepidoptera and sym-

*We dedicate this paper to Ernst Mayr, Professor Emeritus in the Museum of Comparative Zoology at Harvard University, on the occasion of his 100th birthday, July 5, 2004.

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phytan Hymenoptera, and frequently in the beetle families Cerambycidae and Chrysomelidae discussed here.

Taken together, these different aspects of host use in herbivorous insects provide a context in which to evaluate the postulate that rates of evolution of host taxon choices are generally more rapid than tissue use in an adaptive radiation of insects on plants. We have therefore compared rates calculated from a phylogeny estimate for a diverse group of insect herbivores, the beetle superfamily Chrysomeloidea, that comprises a significant element of the adaptive radiations of phytophagous insects (Farrell 1998; Mitter et al. 1988) and shows substantial variation in both dimensions of host use.

The Chrysomeloidea consists of the Cerambycidae longhorned beetles, and the three families of leaf beetles, Chrysomelidae, Orsodacnidae, and Megalopodidae. Together with their Curculionoidea weevil sister group, these families show a positive correlation between use of angiosperms and higher diversification rates, regardless of whether the shifts are from gymnosperms to angiosperms or the reverse (Farrell 1998; Farrell et al. 2001). These beetle families collectively display an array of larval habits across host tissues that range from roots to seeds (Fig. 1a–g), and across taxa from cycads and conifers to monocots and dicots (Farrell 1998; Farrell et al. 2001; Marvaldi et al. 2002). The Chrysomeloidea includes some 25,000 species in the almost entirely dicot and conifer stem mining Cerambycidae (Fig. 1a), including the invasive Chinese maple borer (*Anoplophora glabripennis*), pine sawyers (genus *Monochamus*), and other invasive forest tree borers. The Chrysomeloidea also includes some 40,000 species of Chrysomelidae whose hosts are principally herbaceous. Indeed, these beetles are among the most destructive invasive species around the world, causing billions of dollars in annual losses of agricultural crops. Notorious Chrysomelidae include the seed-consuming subfamily Bruchinae (Fig. 1b) such as the cowpea weevil (*Callosobruchus maculatus*); the several thousand external leaf chewers in the subfamilies Chrysomelinae (Fig. 1j), which includes the Colorado potato beetle (*Leptinotarsa decimlineata*) and willow leaf beetles (genera *Chrysomela* and *Plagiodera*); and Criocerinae (Fig. 1k), which includes the cereal leaf beetle (*Oulema*), asparagus beetles (*Crioceris*), and lily leaf beetles (*Lilioceris*). Other subfamilies that contain tribes with external feeding larvae are the Galerucinae, which includes the *Xanthogaleruca* elm leaf beetles (Fig. 1i) and the Hispinae, which contains the rolled-leaf hispines in the genera *Cephaloleia* and *Chelobasis* (Fig. 1l). Root feeding characterizes all Eumolpinae (e.g., the dogbane beetle *Chryochus auratus* and relatives; Fig. 1f; Dobler and Farrell 1999), the Galerucinae tribe Luperini such as the *Scutellaria* specialist *Phyllobrotica*; (Fig. 1g, Farrell and Mitter 1990), and several groups of flea beetles as well. In general, the internal-feeding chrysomeloid beetles (Fig. 1a–h) have highly reduced or vestigial legs and light-sensing ocelli as well as thin cuticle and flattened or curved bodies, while external feeders are much more robust (Fig. 1i–m). Similar differences characterize internal versus external feeding Lepidoptera and Hymenoptera, and no doubt have analogues in other tissue specialist groups.

In this paper, in order to estimate phylogeny, we combine new sequence data with previously published 18S ribosomal subunit data sets and perform new alignments. Additionally, morphological characters of both adults and larva were scored for representatives of 73 genera in 24 subfamilies of Chrysomeloidea with each species scored for host taxa and larval habits. We then calculate trait-transition probabilities to test if host taxon use is more rapidly evolving than host tissue use.

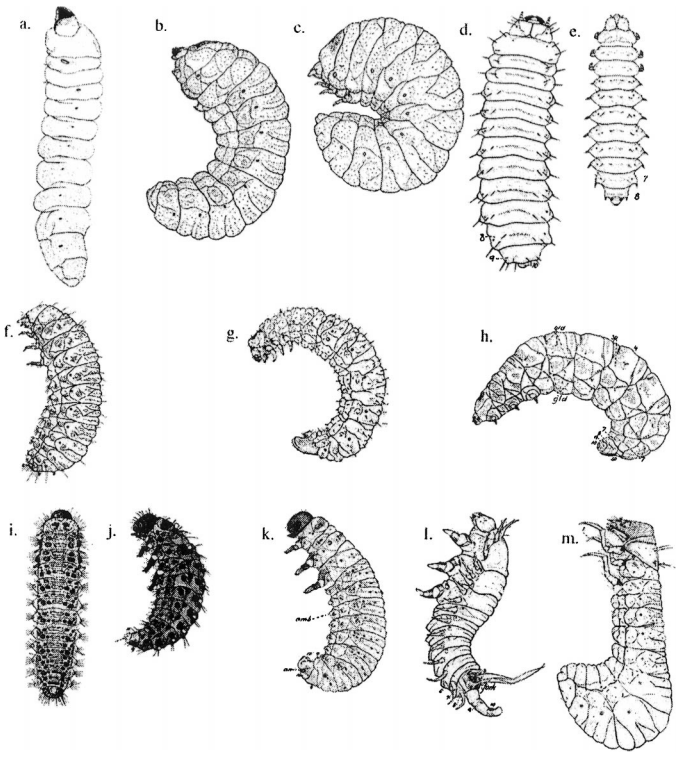

FIG. 1. Illustrations from Böving and Craighead (1931) (unless otherwise indicated). (a–e) internal feeders; a: trunk boring *Arhopalus ferus*, Aseminae, Cerambycidae, lateral view (Duffy 1968); b: seed boring *Pachymerus nucleorum*, Bruchinae, lateral view; c: one stem gall forming *Sagra femorata*, Sagrinae, lateral view; d: leaf mining *Zeugophora scutellaris*, Zeugophorinae, dorsal view; e: leaf-mining *Chalepus ater*, Hispini, Hispinae, dorsal view. (f–h) external protected feeders; f: root-feeding *Chrysochus auratus*, Eumolpinae, lateral view; g: root-feeding *Phyllobrotica quadrimaculata*, Luperini, Galerucinae, lateral view; h: aquatic root/stem feeding *Donacia* sp., Donaciinae, lateral view. (i–m) external exposed feeders: i: leaf chewing *Galerucella* (=*Xanthogaleruca*) *luteola*, Galerucini, Galerucinae, dorsal view; j: leaf chewing *Gastroidea cyanea*, Chrysomelinae, lateral view; k: leaf chewing *Crioceris asparagi*, Criocerinae, lateral view; l: leaf chewing *Cassida nebulosa*, Cassidini, Hispinae, lateral view; m: leaf-chewing (case-bearing) *Clytra quadripunctata*, Cryptocephalinae, lateral view.

METHODS AND MATERIALS

Beetle sequences were compiled from a previous study (Farrell 1998) and 11 new sequences were added corresponding to three new subfamilies and three new tribes (eight new genera total) in the ingroup, plus one new family and one new subfamily (four new genera total) in the outgroup (Marvaldi et al. 2002). Accession numbers and collecting localities are in the Appendix.

A matrix of morphological characters was assembled for the subfamilies of the Chrysomelidae and Cerambycidae us-

TABLE 1. List of morphological larval and adult characters in which the scorings are not as published in Reid (1995a), following Reid (1995b), and Svacha et al. (1997). Character numbers correspond to Reid (2000).

Character number and name	Original state coding	Modifications included by Reid 1995b, 2000; Svacha et al. 1997.
4. Ligula	single (0), bilobed (1)	for Megalopodinae changed from 0 to 1 (Reid 1995b, 2000)
8. Interantennal space	broad without groves (0); narrow, with median groove (1); narrow with X groves (2)	Omitted state 3 in Reid 2000 (separate with a quadrate depression between) so Orsodacnidae and Aulacoscelidae from 3 to 2, Donaciinae from 0 & 1 to 0, and Criocerinae from 2 to 1.
18. Cubito-anal cells	2 cells present (1); at most one elongate basal cell present (1). Reid 1995a, 2000 Second cubitoanal cell present or absent (Svacha et al. 1997).	Spondyliniae = Aseminae, from ? to 0. (Svacha et al. 1997)
22. CuA1+MP4/ MP3+4	forked (0), both free (1), reduced to one vein (2)	Aulacoscelidae from 2 to 1; Cryptocephalinae from 2 to 1; Bruchinae from 1 to 0; Criocerinae, Hispinae, Chrysomelinae, and Galerucinae from 2 to 1. (Reid 2000)
39. Lobes of testes	2+2(0), 1+1(1), or fused together as one (2)	for Orsodacnidae from ? to 1 (Reid 2000)
40. Accessory gland	Far from testis (0), adjacent to testis (1)	for Orsodacnidae from ? to 0 (Reid 2000)
41. Accessory gland number on each vas deferens	One (0), more than one (1)	for Orsodacnidae from ? to 0 (Reid 2000)
56. Antenna	Three segmented (0), two segmented (1), one segmented (2).	Aulacoscelidae from ? to 1, Eumolpini from 2 to 1, and Megascelidini from 2 to 1. (Reid 2000)
57. Number of stemmata	Six (0), five (1), four (2), three (3), two (4), one (5), or zero (6).	Spondylinae = Aseminae from 0 to 1
58. Labium and thorax separation	Gula present (0), absent (1)	Svacha et al. 1997 state that ''gula is almost universally absent in all Phytophaga, except for the Cerambycidae,'' thus Megalopodidae, Orsodacnidae, and Chrysomelidae from 0 to 1
59. Occipital foramen	Not divided, 0; divided, 1; intermediate, 2 (state added in Svacha et al. 1997)	Spondylinae = Aseminae from 1 to 2, and change in Lepturinae from 1 to 0, and Lamiinae 2 (Svacha et al. 1997)
64. Dorsal ampullae	absent (0), present (1)	Zeugophorinae, from 0 to 1 (Reid 2000)

ing the recent reviews of Reid (1995a,b, 2000) and Svacha et al. (1997), respectively. To promote consistency in continued phylogenetic studies of these beetles we follow the numbering system for chrysomelid morphological characters introduced by Reid (1995a). All changes to the matrix published by Reid (1995a) are listed in Table 1. We included as outgroups seven genera from three basal weevil families, Nemonychidae, Anthribidae, and Belidae (Crowson 1946; Farrell 1998; Marvaldi et al. 2002).

Polymerase chain reaction and cycle sequencing were used to obtain partial sequences of 18S following methods described by Farrell (1998) and Marvaldi et al. (2002) with primers used for amplification and sequencing listed in Sequeira et al. (2000).

All sequences were compiled using Sequencher 4 (Gene Codes, Ann Arbor, MI). Ribosomal sequences have insertion-deletion differences, and were aligned using Clustal X (Thompson et al. 1999) with a range of default gap openings and gap extension costs combinations. Ambiguous regions of the alignment were identified and excluded. The parsimony analysis included few gap-bearing regions where gaps were treated as missing data. However, character partitions were defined for hypervariable regions and those were included in Bayesian searches (see below). The aligned matrix is available from the authors.

Phylogenetic Analysis

Phylogenetic analysis was performed using maximum parsimony with version 4.0b8a of PAUP* (Swofford 1999). Although the best estimate in this study will most likely be from the combined analysis, separate phylogenetic analyses of the data sets (molecular and morphological) were performed for comparative purposes. Each dataset was analyzed separately and then combined in a total evidence matrix (1854 molecular and 56 included morphological characters—see below). Topologies were compared from unweighted and weighted morphological analyses and the molecular analysis. Weighting schemes, irreversibility, and character exclusion for morphological characters were implemented following (Reid 2000) for both the individual and combined analyses for comparative purposes. Characters 10, 13, 25, 31, and 55 were excluded in all of Reid's previous analysis (Reid 1995a) due to scoring problems or high variability. Ten invariable characters were also listed by Reid (2000) because of frequent citation in early works, but not included in the analysis. We also list these characters because of the possibility of usefulness in subsequent studies at lower taxonomic levels than considered here. The remaining weighting scheme developed by Reid (2000) is as follows. Losses and reductions in complex characters (e.g., in number of larval antennal segments)

were coded as irreversible (characters 19, 27, 34, 36, 53, 54, 56, 57, and 71), whereas striking morphological novelties (e.g., unusually formed defensive glands: characters 12, 14, 16, 29, 30, 42, 45, and 66) were given double weight (see analysis viii in Reid 2000).

Heuristic searches used 100 random-addition-sequence starting trees and started from random trees with a no max trees limit, and tree bisection and reconnection (TBR) branch swapping on best trees only. These same character exclusion and weighting schemes were used with an implementation of the parsimony ratchet procedure (courtesy of Paul Lewis and Derek Sikes, Department of Ecology and Evolution, University of Connecticut, Storrs, CT, based on Nixon (1999)), with 200 replicates and 15% weighting (procedure repeated five times with different proportions of weighted characters in each search). For bootstrapping analyses, 1000 pseudoreplicates were generated with 20 random taxon additions.

To create the constraint trees for the nodes from the individual analysis and from the combined most parsimonious (MP) tree and to calculate decay indexes (Bremer 1994), we used Autodecay 4.0 (Eriksson 1998). TreeRot 3.0 (Sorenson 1999) was used to calculate the partitioned Bremer support indices for each dataset (Baker and DeSalle 1997; Baker et al. 1998). Decay indexes (Bremer 1994) were calculated from the runs performed in PAUP* using heuristic searches with 100 random addition sequences.

We performed searches for each separate dataset (weighted and unweighted for morphology) and a combined dataset (weighted morphology and molecules, see below). The argument for using the combined topology for character mapping and rate calculations is based on observations that combining data generally increases phylogenetic accuracy due to the larger number of characters (Bull et al. 1993; Chippindale and Wiens 1994). It has also been proposed that simultaneous analysis of combined data can allow emergence of hidden phylogenetic signal (Olmstead and Sweere 1994). The application of Reid's (1995a) weighting scheme to the morphological data in the combined analysis is evaluated as to effect on congruence between topologies of independent analyses (molecular vs. morphological).

We also evaluated, via parametric bootstrapping, the effect of constraining the monophyly of groups suggested by Reid's (1995a) morphological analysis but not present in our own combined analyses. We constrained as monophyletic those nodes that were present in only one of the separate analyses and performed these searches on the dataset that did not show the node (Table 2). Sequences were simulated on a constraint tree for a given hypothesis constructed with PAUP* using maximum-likelihood distances with parameter estimates derived from the ModelTest (Posada and Crandall 1998) analysis. Simulated sequences (100 datasets) were generated in Seqgen (Rambaut and Grassly 1997) using the same model of sequence evolution and parameter estimates as were used to construct the hypothesis tree. The resulting distribution of differences was then compared with the tree length differences for the empirical constraint and nonconstraint trees. All tree searches were performed in PAUP* 4.0 with 100 random addition sequences and TBR with no max trees limit (Table 2).

Molecular Data Analysis Using Bayesian Inference

ModelTest (Posada and Crandall 1998) was used to select the most likely model of evolution for the 18S dataset. This test performs a likelihood-ratio test (LRT) between increasingly complex models (i.e., a hierarchical LRT) and selects the least complex model in the class of best-fitting models. The selected model was incorporated in Bayesian searches for estimation of phylogenetic relationships. All searches were performed in Mr. Bayes 2.01 (Huelsenbeck and Ronquist 2001). Bayesian searches were run with four simultaneous chains for 1,000,000 generations, sampling every 100 generations and applying temperatures of 1, 0.5, and 0.3, which influence the rate of switching between chains. The burning or stationarity generation was determined by plotting generations versus ln-likelihoods (Ln L); all trees below the stationarity level were discarded. The selected model was a general time reversible model (GTR), estimating the proportion of invariable sites and the shape of the gamma parameter. A second set of runs was performed under a site specific model and therefore did not exclude any of the hypervariable regions. Posterior probabilities were also determined for some groupings not supported by some of the analyses but proposed from previous studies (Table 2).

Scoring Larval Habits

Scoring biological attributes inevitably involves a degree of arbitrariness and avoidance of bias is the highest priority. Because host use is the object of study we scored two summary host consumption traits for each species rather than particular morphological traits per se, as detailed below. In the present case, the scorings of host use traits follows independently recognizable resource types (taxa and host organs) that represent a balance in resolution and uniformity in scorability of beetle subfamilies. Thus, to maximize the inclusiveness of scoring of host taxon used (and thus representativeness of the species sampled for the history they are meant to represent), host taxon was characterized as corresponding to one of three major taxa: gymnosperms (0: conifers plus cycads) or angiosperm subclass (1: monocots; 2: eudicots). Larval habit was scored as follows.

First we scored each species as a two-state character: feeding internally (0: in roots, stems, leaves, or reproductive parts) or externally (1: external feeding on leaves). Because it is conceivable that differences in exposure (e.g., to parasitic insects) are more important than are structural differences among tissue types (e.g., Bernays and Graham 1988; Hawkins 1994), we also scored habits as a three state character where external feeding is specified as either protected when under soil or water (1: external protected) or exposed (2: external exposed).

Finally, we scored larval feeding habits for each species from the plant perspective, scoring insects by plant organ as follows. Feeding on reproductive tissues (0: strobili or seed; Palophaginae, Bruchinae, Nemonychidae); feeding on leaves (1: chewing—Criocerinae, Chrysomelinae, Cryptocephalinae, Lamprosomatinae, Chlamisinae, Clytrinae, part Hispinae, part Galerucinae, part Alticinae, plus the leaf mining Zeugophorinae and part of Hispinae), or feeding on vascular tissue (2: stem, twig, trunk, or roots; Cerambycidae, Sagrinae,

Eumolpinae, part Galerucinae, part Alticinae, Donaciinae). Two subfamily scorings require special note. First, there are two ways to score larval habits for the subfamily Donaciinae, the only aquatic larvae in the Chrysomelidae, which feed on the roots, stems, and underwater leaf surfaces of waterlily hosts. These unusual habits have been reported as external leaf feeding (Reid 2000), and as root feeding (and therefore internal or protected feeding, Jolivet 1988). We performed analyses with alternative scorings for states, and differences are reported in the results if significant. Second, the larvae of the subfamily Aulacoscelidinae have only recently been described (Cox and Windsor 1999) from hatchlings reared from eggs laid by a captive female. Because the adult *Aulacoscelis* are well known associates of cycads, the larvae are inferred to be internal (hence cryptic) feeders on these plants. All larval host use states were scored for each beetle species (representing nearly every currently recognized subfamily) and are listed in Appendix 1.

These larval character states were mapped onto the combined topology using parsimony and maximum likelihood (Pagel 1999). Under parsimony, both accelerated and delayed transformations were applied as implemented in MacClade (Maddison and Maddison 2000). We are unaware of a parsimony method that would provide empirical values for comparing instantaneous rates of change, other than the number of steps for each character. Moreover, parsimony has been characterized as not incorporating potentially useful information from branch lengths, which may be underestimated in long branches (Pagel 1999), and do not usually incorporate error in the calculation of ancestral states (Mooers and Schluter 1999). However, recent theoretical studies of ancestral state estimation indicate that the parsimony algorithm can benefit from increased sampling of terminal taxa and the use of tree topology (Salisbury and Kim 2001). The robustness of ancestral state reconstructions can also be estimated with Bayesian analysis (Huelsenbeck and Bollback 2001) and calculated for parsimony reconstructions (Ree and Donoghue 1998).

However, our focus is not inferring ancestral states of any nodes in particular, but rather comparing the overall transition rate for the larval host use character states. Therefore, likelihood approaches seem especially appropriate as these incorporate uncertainty in ancestral state reconstructions and branch lengths for the estimations of instantaneous rates of transitions among states (Pagel 1999). To calculate and compare rates of evolution between larval characters we performed log likelihood comparisons using Discrete and Multistate (Pagel 1994). Employing a continuous Markov model of character evolution we used Discrete to analyze binary characters and Multistate for characters with three or more character states.

Larval characters were mapped onto a pruned combined parsimony topology where the taxa with at least one unknown larval character were excluded (71 taxa included, see Fig. 4a). Because bifurcating nodes are required for rate calculations, analyses were performed on the majority rule consensus topology of the combined analysis and rate variation assessed among all 50 equally parsimonious trees (Fig. 4a). Branch lengths are likelihood optimized for the molecular data alone on the pruned topology with the model selected by ModelTest without imposing a molecular clock. Although not clocklike, branch lengths provide some idea of operational time and recent documentation of correlation between rates of molecular and morphological evolution justifies further inquiry (Omland 1997).

All three character-scorings are three-state models that would estimate six parameters (changes between states). A simplified model is also applicable, in which we restrict certain rates to be equal to each other, retaining the flexibility of many states but reducing the number of parameters. Assigning characters to a simpler forward/backward model when character states refer to qualitatively different traits can be arbitrary, so we simplified each model to a single parameter (restricted model A from six parameters to one parameter and restricted model B from two parameters to one parameter). The simplified model is first compared to the full model by a likelihood ratio test (LRT) to determine its applicability (Cook et al. 2002). If the simplified model does not differ significantly from the full model, its application will provide one overall rate for changes between states in each character (host, tissue, and habit) that summarizes the information of all changes between states for that character. To compare those overall rates between characters the likelihood estimates around the rates estimated for each simplified model were examined to construct 95% confidence intervals around that value. Differences between rates were explored by examining the likelihood values, restricting rates to values obtained for the other two characters, and using two log likelihood units as a significant difference (Cook et al. 2002).

Results

Parsimony and Bayesian Estimation of Phylogenetic Relationships with 18S Sequences

From the 1994 bp of the 18S Clustal alignment; 140 bases (7%) were excluded because they could not be unambiguously aligned, producing a final matrix of 1854 characters with 208 parsimony-informative sites. The few included gaps were treated as missing data in the five Paup Rat runs (each 200 replicates) and the 100 random addition sequences analysis performed on the unweighted molecular data. Both analyses recovered 294 MP trees (L = 1141, majority rule consensus in Fig. 2a). Both bootstrap and decay indexes support the monophyly of two of the seven included cerambycid subfamilies: Lepturinae and Aseminae; and four of the 14 chrysomelid subfamilies: Bruchinae, Sagrinae, Cryptocephalinae (including *Imatidium*) and Galerucinae (not including Alticinae). Other well-supported relationships include the grouping of all Hispinae except *Imatidium*, and of Chrysomelinae except *Labidomera*. Other relationships resolved in this analysis are the respective monophyly of subfamilies Lamiinae, Donaciinae, and Alticinae, the grouping of Chrysomelinae (except *Labidomera*) with Galerucinae and Alticinae and the sister group relationship of Bruchinae and Sagrinae. This analysis suggests paraphyly for families Cerambycidae, Megalopodidae, Orsodacnidae, although imposing these groupings as constraints on the molecular data does not result in significantly longer trees (Table 2), indicating a lack of signal rather than conflicting signal between datasets (see below).

Bayesian runs performed at different temperatures pre-

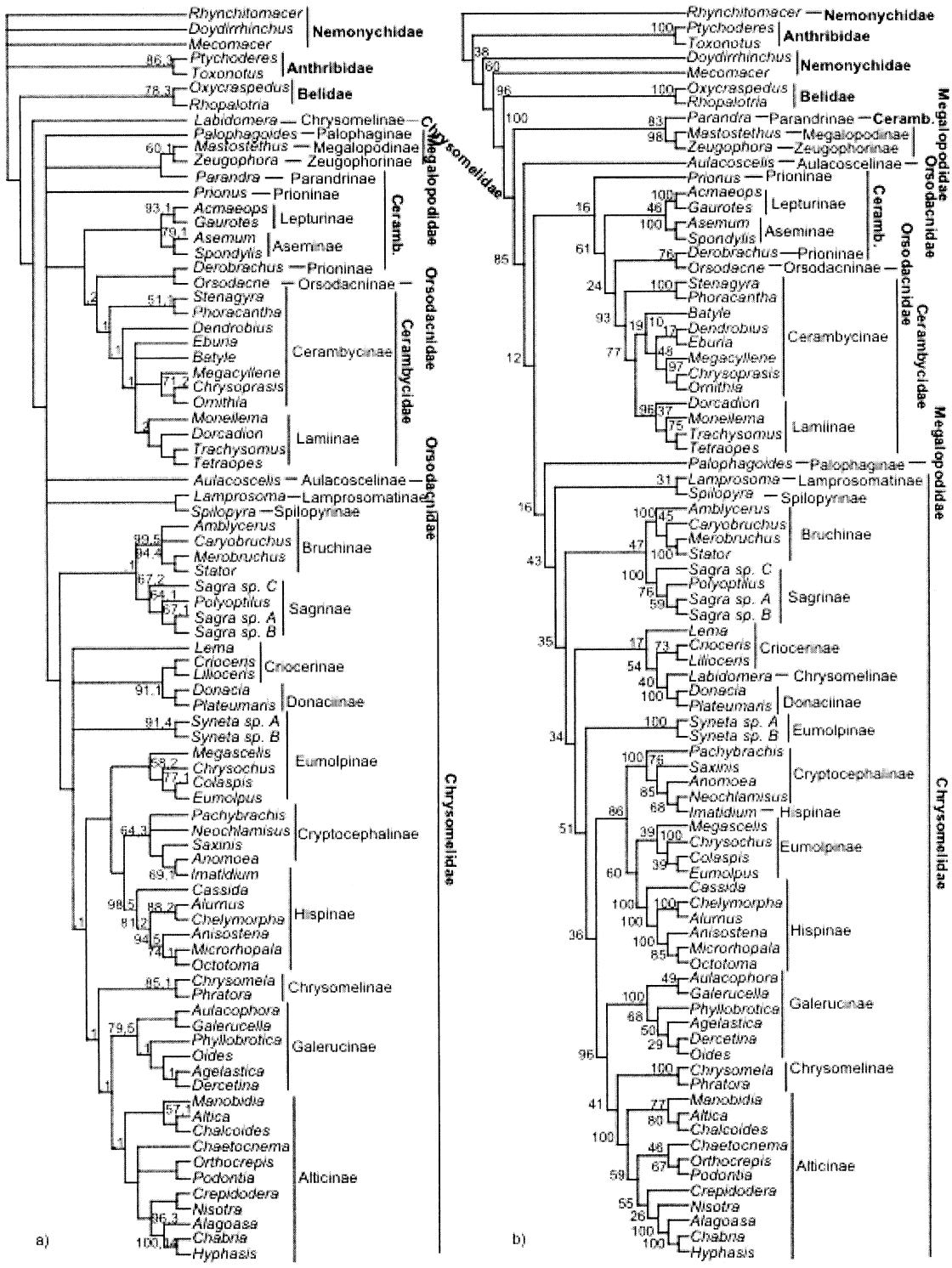

FIG. 2. (a) Majority rule consensus of the 294 maximum parsimony trees obtained from the parsimony analysis of the molecular data only (L = 1141, Ci = 0.596, Ri = 0.556, Hi = 0.404). Numbers above the internal branches indicate bootstrap support and Bremer support for the node to the right. For specific epithets see Appendix. Bars beside taxon names indicate subfamily classification after (Reid 1995a, 2000). (b) Bayesian majority rule consensus, (7992 trees, one million generations, burnin = 200, four chains, T = 0.5). Numbers above the branches or to the right of nodes indicate posterior probabilities expressed as percentages.

TABLE 2. Number of synapomorphies supporting each group on the combined topology, Figure 3b (#T), in parentheses the number of synapomorphies contributed by each of the datasets (morphology, molecules), and in each of the separate analyses (morphology and molecules). Brackets in those columns indicate the number of extra steps with respect to the length of the optimal tree when imposing the group as a constraint. Under the heading PB are the probability values under parametric bootstrapping for those groupings not present in the molecular only analysis. Post prob. lists the posterior probabilities of those same groupings.

Group	#T	Morph	Mol.	PB	Post prob.
Cerambycidae	10(10,0)	[1]	[2]	$0.05 < P < 0.06$	<0.0001
(Prioninae + Parandrinae)	8(6,2)	7	[2]	$0.05 < P < 0.06$	<0.0001
(Cerambycinae + Lamiinae)	5(3,2)	3	2		0.93
(Lepturinae + Aseminae + Cerambycinae + Lamiinae)	2(1,1)	8	[5]	$0.06 < P < 0.07$	<0.0001
(Lepturinae + Aseminae)	1(0,1)	[1]	1	—	0.46
Aseminae	12(1,11)	1	11	—	1
Lepturinae	6(0,6)	[1]	6	—	0.99
Lamiinae	4(0,4)	[1]	4	—	0.95
Megalopodidae	12(8,4)	7	[2]	$0.06 < P < 0.07$	0.071
Orsodacnidae	15(15,0)	20	[3]	$0.48 < P < 0.49$	0.0004
Chrysomelidae	12(9,3)	[1]	[1]	$0.2 < P < 0.21$	0.42
(Eumolpinae + *Megascelis*)	12(9,3)	9	[1]	$0.12 < P < 0.13$	0.39
(Eumolpinae + *Megascelis* + Synetini)	11(8,3)	9	[3]	$0.39 < P < 0.4$	<0.0001
(Lamprosomatinae + Cryptocephalinae)	10(9,1)	10	[9]	$0.05 < P < 0.06$	<0.0001
(Spilopyrinae + Lamprosomtinae + Cryptocephalinae + Eumolpinae)	6(4,2)	13	[15]	$0.01 < P < 0.02$	<0.0001
(Bruchinae + Sagrinae)	7(5,2)	12	2	—	0.47
Galerucinae	7(0,7)	[1]	8	—	1
Chrysomelinae	9(4,5)	4	[4]	$0.42 < P < 0.43$	<0.0001
Alticine	7(0,7)	[1]	3	—	1
Hispinae	11(6,5)	6	[10]	$0.04 < P < 0.05$	<0.0001
Sagrinae	34(5,29)	5	29	—	1
Donaciinae	11(2,9)	6	7	—	1
Bruchinae	19(7,12)	7	12	—	1
(Criocerinae + Hispinae)	[39]	[15]	[20]	<0.01	<0.0001
(Spilopyrinae + Eumolpinae)	[7]	[7]	[2]	$0.05 < P < 0.06$	<0.0001

sented consistent and correlated posterior probability values ($R^2 = 0.976$ and $R^2 = 0.945$). Bayesian estimation of phylogenetic relationships (identical topology obtained from GTR and site specific models; Fig. 2b, $T = 0.5$) displays many similarities and few disagreements with the parsimony analysis. Relationships with high posterior probabilities in the Bayesian topology include: the monophyly of Alticinae (Alticini after Reid (1995a)) and the grouping of Hispinae, and Eumolpinae (in part). Relationships with high posteriors and not present in the parsimony analysis include the grouping of Cryptocephalinae, Hispinae, and Eumolpinae. Enigmatic groupings repeated in the parsimony analysis are: the inclusion of *Imatidium* (Hispinae) with the cryptocephalines, the grouping of the primitive prionine *Derobrachus* with *Orsodacne* and the exclusion of *Labidomera* from the well supported Chrysomelinae grouping.

Parsimony Morphological Analysis

The 100 random addition analysis and Pauprat runs recovered 167 MP trees ($L = 250$, majority rule consensus in Fig. 3a). In these analyses the monophyly of the Cerambycidae is resolved but not well supported: three groups are formed, one comprised by subfamilies Prioninae and Parandrinae (68% bootstrap, one decay), a grouping of the Aseminae and Lepturinae subfamilies (57% bootstrap, one decay), and another comprising all remaining cerambycid subfamilies. Within the leaf beetles, well-supported relationships between subfamilies are between Bruchinae and Sagrinae, Chrysomelinae and Galerucinae + Alticinae, and Lamprosomatinae and Cryptocephalinae. Other well-supported relationships include the monophyly of each of the subfamilies Bruchinae, Sagrinae, Donaciinae, Criocerinae, Hispinae, and Chrysomelinae. Unweighted morphological analysis of the included characters differs from the weighted analysis in that the resulting consensus topology shows no grouping of the cerambycid subfamilies except for Prioninae and Parandrinae and no evidence of a sister group relationship between Bruchinae and Sagrinae. Both relationships are consistently recovered in the molecular analysis (MP and Bayesian, Fig. 2a,b).

Combined Phylogenetic Analyses

The parsimony searches (100 random addition sequences) starting with random trees and 200 Pauprat repetitions resulted in the same 63 MP trees, of length =1419 (Fig. 3b). The partitioned Bremer support values suggest comparable contributions of morphological and molecular data to the combined topology (Fig. 3b; near-equal negative decay values for both sources of data indicate similar costs for imposing nodes on that topology), as do the number of nodes/relationships from each of the separate analyses that are not recovered in the total evidence consensus tree.

The phylogeny estimate is in broad agreement with Reid (1995a), Farrell (1998), and the latest combined Chrysomeloidea phylogeny (Duckett et al. 2003) with some exceptions. As in these earlier studies, the combined analysis provides evidence for the monophyly of Cerambycidae, Megalopodidae, Orsodacnidae, and Chrysomelidae. The combined analysis also provides evidence (although not strong support) for the previously proposed close relationship between Megascelidini and Eumolpinae and the close relationship between Synetini and Eumolpinae (Mann and Crowson 1981; Reid 2000).

Other previously proposed relationships well supported in this analysis are (Lamprosomatinae + Cryptocephalinae) and (Chrysomelinae + Galerucinae and Alticinae). However, with the dataset and taxon sampling in this study we do not find evidence to support the hypothesis of Alticinae nested within the Galerucinae (Lingafelter and Konstantinov 1999) nor for a paraphyletic Alticini (Alticinae) with respect to Galerucinae (Duckett et al. 2003). Moreover, both subfamilies are very well-supported groupings (97% and 100% bootstrap levels) and their sister group relationship is also reasonably well supported (67% bootstrap level). All individual (MP and Bayesian) and combined analysis supports a sister group relationship between Sagrinae and Bruchinae as has been previously proposed from larval and adult data (Crowson 1946; Reid 1995a). All of these groupings are also supported when performing the combined analysis while not applying the weighting scheme on the morphological dataset. However, the unweighted analysis shows two main topological differences: a common origin for the Donaciinae and Criocerinae as a sister group to the Bruchinae-Sagrinae clade basal to the remaining Chrysomelidae (circle 1 Fig. 4a) and a derived position of Hispinae in the Eumolpinae-Criptocephalinae-Hispinae clade with *Imatidium* closely related to the Cryptocephalinae (circles 2, 3, and 4 Fig. 4a).

Results of parametric bootstrap tests of the monophyly of groups suggested by previous morphological studies, or present in the combined or morphological analysis but absent from molecular analysis, are listed in Table 2. Most of the tests fail to reject nodes present in only one data set and imposed as constraints in the other (Table 2), again indicating little significant signal conflict between the two datasets.

Evolution of Larval Life Histories: Comparing Rates of Change in Larval Feeding Strategies

A parsimony approach to the evolution of larval traits (Fig. 4a) indicates that changes in host association are mostly restricted to the base of recognized subfamily groups. Use of monocots appears characteristic of basal lineages in the Chrysomelidae: subfamilies Donaciinae, Criocerinae, and some members of Bruchinae and Hispinae. The most parsimonious reconstruction of tissue use in chrysomeloid beetles indicates one origin of leaf feeding encompassing several chrysomelid subfamilies with further change in the Alticinae + Galerucinae and Hispinae. The proposed single origin of leaf feeding is maintained in the combined unweighted analysis, however, the prevalence of monocot feeding on the basal groups could be interpreted as shifts to monocots from conifers (Donaciinae) and reversals from Eudicot feeding (some Bruchinae and Hispinae).

Likelihood evaluations of instantaneous rates of change among larval character states are presented in Table 3. The models are named according to the transition parameters used, ''multistate'' if the full six-parameter model was used, ''restricted A'' if the data were fitted to a model with only one transition rate, ''binary'' if only two states were used in

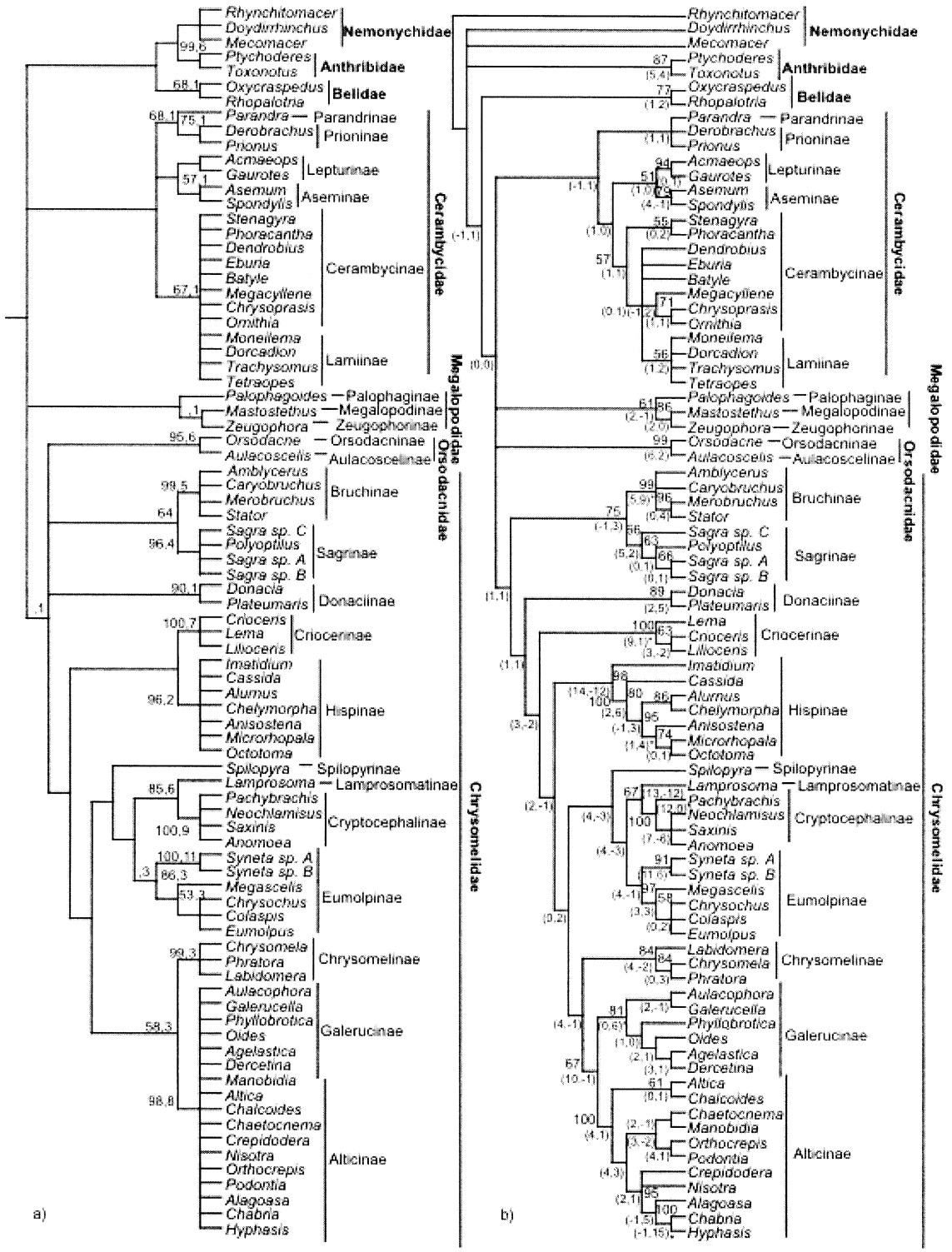

FIG. 3. (a) Majority rule consensus of the 167 maximum parsimony (MP) trees obtained from the parsimony analysis of the morphological data only (L = 250, Ci = 0.352, Ri = 0.895, Hi = 0.648). Numbers above the internal branches and bars beside taxon names as in Figure 2. (b) Strict consensus of 63 MP trees obtained from the combined analysis of weighted morphological and molecular data (L = 1419, Ci = 0.541, Ri = 0.748, Hi = 0.459). Numbers above the branches and bars as in Figure 2. Numbers in parentheses below the branches indicate partitioned Bremer support from the morphological and molecular data for that node. Asterisks correspond to total Bremer support above the critical values as a function of branch lengths (see DeBry 2001).

a forward/backward model (for habits), and ''restricted B'' if the forward/backward model was restricted to a single-parameter model. The simple one-parameter model was not significantly worse than the full model or the binary model for the three analyzed characters, therefore rates were compared for all three characters using the simple models and 95% confidence intervals. *Thus, the number of rates compared is constant across characters.*

Significant differences between rates for changes in host taxon used (gymnosperms, monocots, eudicots) compared to those for changes in habit (internal, external protected, external exposed) and tissue (reproductive, photosynthetic, structural tissue) are indicated by nonoverlapping confidence intervals and by the significantly worse likelihood (more than two log likelihood units) of models when fitted with their respective rates (Table 3). Rates of changes in habit and tissue are not significantly different from each other. These results are robust with some variation in topology since they remain consistent when exploring rates in all MP topologies and also for the alternative MP topology obtained from a combined analysis with unweighted morphological characters (see solid lines in Fig. 4b). The rates of tissue use and habit overlap with each other but not with the much higher values of rates of host taxon change (Fig. 4b). Moreover, the confidence intervals of the lowest host rate (1.452; Upper Confidence Interval (UCI): 1.62; Lower Confidence Interval (LCI): 0.98; tree 21) and the highest tissue rate (0.368; UCI: 0.43; LCI: 0.12; tree 45) do not overlap. Results were also consistent when performing the analysis excluding the outgroups (on the MP majority rule consensus tree for 66 taxa), frequency of changes between host families were significantly higher (1.07; UCI: 1.43; LCI: 0.86) than those between habits (0.06; UCI: 0.08; LCI: 0.04) and tissues (0.09; UCI: 0.19; LCI: 0.07). All analyses yielded higher estimates for changes in host plant group used than for plant tissue used and even higher still than those for changes in larval habit (either with three or two character states) (Table 3).

Discussion

Ecological Diversification

The results of our analyses of the rates of host use in chrysomeloid beetles provide support for the postulate that changes in use of host-plant taxa are more rapidly evolving than are changes in use of different plant tissues. Moreover, the differences in rates documented here are probably underestimated because of unsampled variation in host taxon use. For example, we were not able to include some monocot-associated species within the dicot-associated clades (e.g., the grass-feeding *virgata* species-group within the otherwise largely curcurbit- and bean-feeding galerucine chrysomelid genus *Diabrotica*, Eben 1999), or the several reversals to conifer feeding in the Cerambycidae (Linsley and Chemsak 1984). In contrast, we are aware of no unaccounted for variation in larval tissue use within the Chrysomeloidea. Therefore, complete sampling seems likely to reveal even higher rates of host shifts than of changes in tissue use. Although the pattern we document might be taken to show more rapid evolution in behavior than in morphology (Blomberg et al. (2003) but see DeQueiroz and Wimberger (1993)), the morphological traits involved in host tissue use in beetles are most probably acquired long after the initial shifts.

The adaptive radiation of Chrysomeloidea approximates the timing of appearances of their seed plant hosts. Many of the affiliations with the major groups of host-plant taxa are thus still quite strongly conserved across subfamilies, with some instances of associations with gymnosperms apparently persisting through much of the Mesozoic (Farrell 1998). For example, members of the Palophaginae (Kuschel and May 1990) today represent the descendants of the earliest chrysomelids. These and the primitive nemonychid and belid weevils remain associated with the ancient conifer genus *Araucaria* in their disjunct, relictual distributions in the South American (Chile and Argentina) and Australian south temperate regions (Kuschel and May 1990). The ostensibly homologous association with conifer strobili of Palophaginae and the basal weevil families (also represented by Jurassic fossils in beds containing *Araucaria* remains, (Arnoldi'i et al. 1991)) implies that this comparatively protein-rich plant structure was a very early plant resource used by the common ancestor of the Phytophaga (Crowson 1981). Moreover, Jurassic fossils, phylogenetic position, and current associations all suggest that an early Mesozoic community of insect larvae from three major orders of insects (Coleoptera, Lepidoptera, and Hymenoptera) has persisted in feeding inside gymnosperm strobili for over 150 million years (occurring today in conifer strobili in the north and south temperate zones of the Old and New World (Kuschel and May 1990; Howden 1995; Farrell 1998; Powell et al. 1998), an observation that may seem surprising given the generally high incidences of interspecific competition among internally feeding insects (Denno et al. 1995).

Early Jurassic concealed-feeding on gymnosperms was followed by diversification both of insect feeding habits and of angiosperm hosts. A Cretaceous origin of external leaf feeding and shifts onto dicots in the Chrysomelinae and Galerucinae and monocots in the Criocerinae and Hispinae followed the origin of angiosperm feeding, and were followed by Tertiary radiations of leaf-mining, seed-boring, and root feeding. Fossils and phylogenetic proximity of the lineages Donaciinae, Criocerinae, and Hispinae in an intermediate position on the phylogeny estimate suggest common origin(s) of monocot feeding in the Cretaceous (Reid 2000; Wilf et al. 2000), comparable to the origin(s) of monocot feeding in the weevils (Marvaldi et al. 2002). Both beetle groups thus diversified during the mid-Cretaceous expansion of monocots (Bremer 2000).

Phylogenetic evidence and fossils suggest that parasitism of wood-boring insects by wasps began very early (Shaw 1988; Powell et al. 1998; Basibuyuk et al. 1999; Quicke and Belshaw 1999), nevertheless parasitism rates are generally higher today among externally feeding insects and may be responsible for demonstrably lower incidences of competition in this guild (Hairston et al. 1960; Lawton and Strong 1981; Hawkins 1994; Denno et al. 1995). Indeed, external feeding chrysomelids have elaborated an array of glands (and pathways) for secretion of defensive chemicals or developed morphological structures for retaining plant chemical laden fecal material as a shield against parasitoids (Termonia et al. 2001). Other taxonomic groups of external-feeding insect lar-

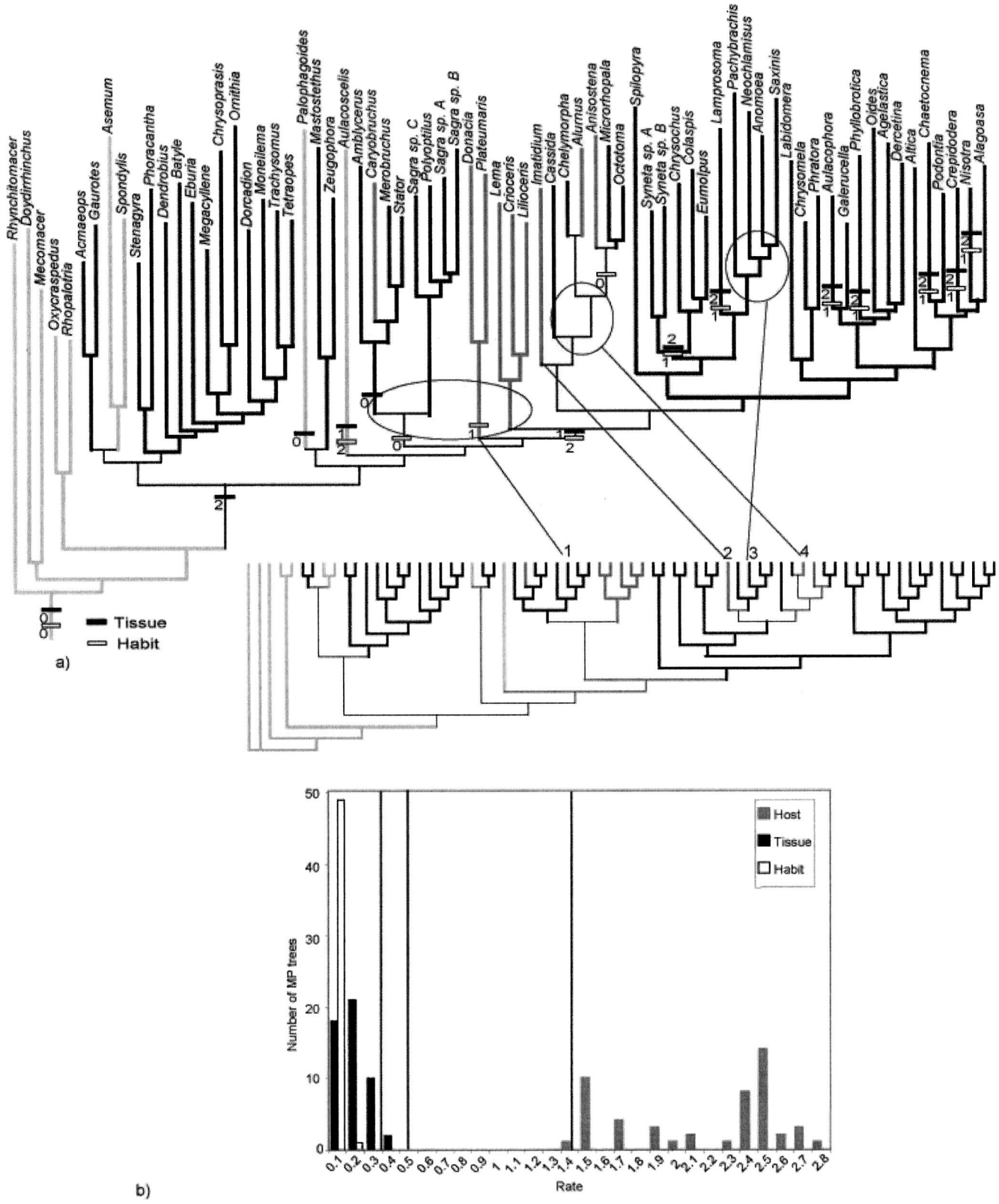

FIG. 4. (a) Majority rule consensus topology from the combined dataset pruned to 71 taxa. Branch lengths are maximum likelihood optimized under GTR + I + Γ, without enforcing a molecular clock. Colors on branches indicate host groups as follows: light gray, gymnosperms (coded as 0 in Appendix); gray, monocots (coded as 1 in Appendix); black, eudicots (coded as 2 in Appendix). Shifts in tissues used and larval exposure are indicated by black or white bars and associated numbers refer to the states. Host tissue used (black bars) comprise the following states: reproductive structures (strobili, seeds: 0); photosynthetic (leaves: 1); and vascular tissues (roots, stems: 2). Shifts in habit of larvae (exposed or concealed: white bars) are between the states internal concealed (stemboring, seedboring,

TABLE 3. Maximum-likelihood rate comparisons between larval characters listed as ''Host, Tissue, and Habit'' (see Methods) on the majority rule pruned combined topology (Fig. 4a). Under ''model,'' the term ''multistate'' corresponds to the six-parameter models and ''binary'' to the two-character, two-parameter model only applicable to habits; ''restricted model A'' corresponds to a simplified model restricted from six parameters to one parameter; and ''restricted model B'' to a simplified model restricted from two parameters, binary model, to one parameter, applicable only to habits. Values in brackets after ''rates'' correspond to 95% confidence intervals. ''LR'' corresponds to significance of likelihood-value differences, through likelihood-ratio test (for restricted models compared to the corresponding complete model) or two log-likelihood units difference (for models fitted with rates from other characters following Cook et al. (2002): from, followed by the name of the character, indicates it was fitted with the rate from the restricted A model for that character, except when fitting other characters with habit rates for which it specifies if fitted from restricted A (from multistate) or B (from binary) models). Nonsignificant differences are marked as ns; significant differences are marked as *.

Character	Model	Rate	L	LR
Host	multistate	—	−40.08	
	restricted A	1.603 [1.90;0.90]	−44.68	0.101 ns
	from tissue		−49.04	*
	from habit A		−49.09	*
	from habit B		−49.98	*
Tissue	multistate	—	−43.51	
	restricted A	0.203 [0.40;0.09]	−48.05	0.107 ns
	from host		−51.76	*
	from habit A		−49.19	ns
	from habit B		−48.12	ns
Habit	multistate	—	−36.98	
	restricted A	0.067 [0.10;0.05]	−39.82	0.34 ns
	from host		−43.93	*
	from tissue		−40.12	ns
	binary	0.06 0.31	−61.04	
	restricted B	0.098 [0.13;0.08]	−62.43	ns
	from host		−66.85	*
	from tissue		−62.67	ns

vae in the Lepidoptera and Hymenoptera have comparable defenses against parasitoids.

Ecological release from competition for resources has been thought to underlie adaptive radiation (Schluter 2000). Thus, these external-feeding beetles are much more diverse than their concealed-feeding sister group (Fig. 1i–m, Fig. 4a: Chrysomelinae + Criocerinae + Cassidini plus several groups of Galerucinae, Alticinae and Hispini = ~10,000 species, excluding species with reversals to concealed feeding vs. their sister group Bruchinae + Sagrine = ~3300 spp.). Although external feeding chrysomelids collectively use a much broader array of host taxa than bruchines and sagrines (largely specialists on palms and legumes), it is not clear whether they shift host species more rapidly per capita than these internal feeders, as may be predicted if natural enemies drive specialization on enemy-free space (Bernays and Graham 1988; Hawkins 1994). Nevertheless, this possibility gains credence from the observation that parasitic insects are also conservative in both host preferences and in the host plants they search (Shaw 1988; Belshaw and Quicke 2002), enabling herbivorous insects to escape via shifts to different taxa or tissues. Although species-level phylogenies for herbivorous insects typically show that closely related species use different host-plant species, external feeders do seem to often use plants in different families (e.g., Dobler et al. 1996; Mardulyn et al. 1997). However, there have been no studies of the possible association between parasitism rates and phylogenetic dispersion of host taxa used in a group of herbivorous insects.

Evolutionary conservatism in shifts among feeding guilds is manifested in various aspects of the present day composition of insects on plants (Claridge and Wilson 1982; Mitter and Brooks 1983; Stork 1987; Labandeira and Sepkoski 1993; Wilf et al. 2001). For example, a sister group relationship between the seed-feeding Bruchinae and the stem gall-inducing Sagrinae suggests progression from the ancestral internal stem feeding to gall inducing and to seed boring in the late Cretaceous. Thus, the seed-boring guild is among the youngest feeding guilds in herbivorous insects, and is dominated by the 3000 bruchine species (Johnson 1967; Johnson et al. 2001). The seed-boring guild has been invaded only very few times among more recent herbivorous insects (e.g., a few tens to several hundred species in the scolytine genus *Coccotrypes* and in the weevil genus *Curculio*, neither of which use the same host taxa as bruchines (Chittenden 1926; Jordal et al. 2000)). Similarly, the Jurassic–Cretaceous lineages of Cerambycidae, Siricidae, and Buprestidae collectively overwhelm the diversity of the later-originating lineages of Scolytinae bark beetles (Whitfield 1998; Alexeev 2000; Farrell et al. 2001; Sequeira and Farrell 2001). The persistence on particular kinds of resources of early colonists for millennia implies a potential role for ecological preemption in adaptive radiation (Schluter 2000).

At the same time, it may seem surprising that not a single cerambycid beetle, for example, has evolved external feeding among some 25,000 species on trees and herbaceous plants, especially because chrysomelids have done so. Nevertheless, shifts to external feeding are also rare in the chrysomeloid sister group Curculionoidea (Marvaldi et al. 2002) and have evolved only once in the plant-feeding sawflies. Such conservatism also characterizes external feeders such as in the Lepidoptera, where the butterflies have never shifted to feeding inside plants although moths have done so (Powell 1980; Powell et al. 1998). Comparable patterns of conservatism in tissue use seem the rule among diverse groups of parasites and pathogens, but may be little noted because most taxonomic groups of interest to particular researchers are invariant in these traits. Evident exceptions to tissue use con-

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and leafmining: 0), external concealed (root feeding, aquatic feeding: 1) and external exposed (leaf-chewing: 2). See Material and Methods. Majority rule consensus topology from the combined dataset but not applying the morphology weighting schemes is shown in the inset, host use is mapped on the branches and circles and lines show the differences with the combined weighted topology explained in the text. (b) Distribution of rate values for all 50 maximum parsimony combined weighted pruned topologies. Vertical lines indicate the rate values calculated on the combined topology not applying weights to the morphological characters.

servatism in insects are notable among gall formers in the wasp family Cynipidae that form structurally similar tissue matrices produced on different host-plant parts (Ronquist and Liljeblad 2001; Cook et al. 2002).

The pattern of greater conservatism in beetles of host tissue affiliations relative to host taxon affiliations seems similar to host use evolution not just in other insects, but also in groups as disparate as nematodes (Subbotin et al. 2001, 2002) and fungi (Pandey et al. 2003), and is an accepted generalization concerning virus host use as well (Knipe and Howley 2001).

Complementary study of the assembly of tissue specific guilds may also be illuminating in these other consumer groups. For example, vertebrates are collectively host to an array of pathogens that are both specific to particular classes and specific to various tissues. Thus, the respiratory epithelium is attacked by paramyxoviruses and by other poxes affiliated with the different vertebrate classes (Taber and Pease 1990; Westover and Hughes 2001), whereas conserved specificity to circulatory systems is characteristic of the many different *Plasmodium* malarias as well as the lentiviruses (Fultz 1989; Hirsch et al. 1995; Charleston and Robertson 2002). Indeed, human infecting viruses are almost invariably closest relatives of viruses infecting the same tissues in other mammal hosts (Munro et al. 1992; Pohlmeyer et al. 1993; Tidona et al. 1999; Mackenzie et al. 2001). Plant viruses also show strong conservatism in host tissue and taxon use (Power 1992). However, as in insect studies relatively little is known of the factors underlying the conservation of tissue specializations (Hotzel and Cheevers 2002; Schmidtke et al. 2003) whereas the much more rapidly evolving use of different host groups receives much attention (Knipe and Howley 2001). Under a model of gradual, stepwise evolution (Mayr 1963), more rapid evolution of host taxon preferences would be expected to reflect lower genetic barriers between alternative host taxa than host tissues. Because the immune systems or other defenses are presumably more similar in different tissues of the same organism than in the same tissues of different organisms, such defenses would then seem not to be the principal barriers to shifts.

This apparently consistent difference in rates of host use evolution in beetles and other consumers may represent a promising opening for experimental research into underlying causes that could, at least for pathogens, inform strategies for managing their evolution. Parasite research emphases understandably tend towards rapidly evolving aspects of interactions, but investigation of more deeply conservative dimensions offers a complementary line of inquiry that may lend special insight into the ecological diversification of small consumers (Antonovics 1987; Williams 1992).

Acknowledgments

We would like to thank S. Boyce, J. Wiens, and two anonymous reviewers for useful reviews and comments.

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APPENDIX

Specimens incorporated in the study with accession numbers, locality, and collector data (when available) and coding of larval characters from the literature (subscripts indicate source).

Family	Subfamily	Tribe		Accession. #	Locality	Coll.	Host	Habit	Tissue
Nemonychidae	Rhino-rhynchinae	Mecomacerini	*Mecomacer* sp.	AF250069a	AR, Neuquen	AM	0_7	0_7	0_7
		Mecomacerini	*Rhynchitomacerinus kuscheli*	AF389026	CHI, Malleco	WK	0_7	0_7	0_7
		Doydirrhynchini	*Doydirrhinchus austriacus*	AF389025	GER, Freiburg	SD	0_7	0_7	0_7
Anthribidae	Cimberidinae	Ptychoderini	*Ptychoderes nebulosus*	AF389027	PA	COB	—	—	—
	Anthribinae	Platystomini	*Toxonotus cornutus*	AF389028	US, FL	COB	—	—	—
Belidae		Allocorynini	*Rhopalotria* sp.	AF250067	PA	COB	0_7	0_7	0_7
	Oxycoryninae	Oxycorynini	*Oxycraspedus cornutus*	AF250068	CHI, Malleco	AN	0_7	0_7	0_7
Cerambycidae	Parandrinae	Parandrini	*Parandra cribrata*	AF267415	DR	MI	—	—	—
	Prioninae	Prionini	*Prionus laticollis*	AF267413	US, CO	BDF	—	—	—
			Derobrachus sp.	AY676684	US, AZ	DM	—	—	—
	Spondylinae= Aseminae	Asemini	*Asemum striatum*	AF267398	US, MA	DM	0_{12}	0_{12}	2_{12}
		Spondylini	*Spondylis upiformis*	AF267399	US, MT	MI	0_{17}	0_{17}	2_{17}
	Cerambycinae	Clytini	*Megacyllene robiniae*	AF267404	US, NY	BDF	2_{18}	0_{18}	2_{18}
		Dryobiini	*Dendrobias* sp.	AF267403	MO	JC	2_{19}	0_{19}	2_{19}
		Hesperophanini = Eburiini	*Ornithia* sp.	AY676685	ME, Jalisco	CH	2_{11}	0_{11}	2_{11}
			Eburia sp.	AF267402	ME, Jalisco	CH	2_{20}	0_{20}	2_{20}
		Heteropsini	*Chrysoprasis* sp.	AF267405	ME, Jalisco	CH	2_{13}	0_{13}	2_{13}
		Phoracanthini	*Phoracantha semipunctata*	AF267409	AU, Victoria	LH	2_{21}	0_{21}	2_{21}
		Platyarthrini	*Stenagyra* sp.	AF267406	ME, Jalisco	CH	2_9	0_9	2_9
		Purpuricenini	*Batyle suturalis*	AF267407	US, CO	BDF	2_9	0_9	2_9
	Lamiinae	Dorcadionini	*Dorcadion* sp.	AF267412	MO	JC	2_9	0_9	2_9
		Moneilemini	*Moneilema gigas*	AF267408	ME, Pto.Penasco	BDF	2_8	0_8	2_8
		Onciderini	*Trachysomus* sp.	AF267410	PE, Manu	DY	2_8	0_8	2_8
		Tetraopini	*Tetraopes pilosus*	AF267411	USA, KS	BDF	2_9	1_9	2_9
	Lepturinae	Lepturini	*Gaurotes virginea*	AF267401	SW	SD	2	0	2
			Acmaeops collaris	AF267400	FR	SD	2	0	2
Megalopodidae	Palophaginae		*Palophagoides vargasorum*	AF267418	CHI	WK	0_4	0_4	0_4
	Megalopodinae		*Mastotethus* sp.	AF267416	CR	WF	2_4	0_4	2_4
	Zeugophorinae		*Zeugophora scutellaris*	AF267417	US, TX	ER	2_4	0_4	1_4
Orsodacnidae	Aulacosceli-dinae		*Aulacoscelis* sp.	AF267419	CR	LG	0_3	2_3	1_3
	Orsodacninae		*Orsodacne atra*	AF267420	US, UT	TH	—	—	—
Chrysomelidae	Bruchinae	Amblycerini	*Amblycerus robiniae*	AF267422	US,MA	GM	2_{14}	0_{14}	0_{14}
		Acanthoscelidini	*Stator limbatus*	AF267423	US,AZ	DJ	2_{10}	0_{10}	0_{10}
			Merobruchus julianus	AF267424	US,AZ	DJ	2_{10}	0_{10}	0_{10}
		Pachymerini	*Caryobruchus gleditsiae*	AF267421	US,AZ	DJ	1_{10}	0_{10}	0_{10}
	Sagrinae	Sagrini	*Sagra femorata*	AY676690	MA	DF	2_5	0_5	2_5
			Sagra sp.1 (*Sa03*)	AY676691	MA	DL	2_5	0_5	2_5
			Sagra sp.2 (*Sa04*)	AY676692	MA	DL	2_5	0_5	2_5
			Polioptylis sp. 3 (*Sa02*)	AY676693	AU	GM	2_5	0_5	2_5
	Spilopyrinae		*Spilopyra sumptuosa*	AY676689	AU, Qsld.	DC	2_2	2_2	1_2
	Chrysomelinae	Chrysomelini: Doryphorina	*Labidomera clivicollis*	AF267437	US, CO	BDF	2_4	2_4	1_4
		Chrysomelini: Chrysomelina	*Chrysomela scripta*	AF267436	US, CO	BDF	2_4	2_4	1_4
		Chrysomelini: Phyllodectina	*Phratora laticollis*	AF267435	US, UT	TH	2_4	2_4	1_4
	Criocerinae	Criocerini	*Crioceris asparagi*	AF267426	US, NY	BDF	1_4	2_4	1_4
			Lilioceris merdigera	AF267425	BE	SD	1_4	2_4	1_4
		Lemiini	*Lema trilineata*	AY676686	US, NY	BDF	1_4	2_4	1_4

APPENDIX. Continued.

Family	Subfamily	Tribe		Accession. #	Locality	Coll.	Host	Habit	Tissue
	Cryptocepha-linae	Pachybrachini	*Pachybrachis mexicanus*	AF267458	US, TX	ER	2_4	2_4	1_4
		Chlamisini	*Neochlamisus* sp.	AF267455	US, NY	DFu	2_4	2_4	1_4
		Clytrini	*Saxinis saucia*	AF267456	US, Utah	TH	2_4	2_4	1_4
			Anomoea flavolcansiensis	AF267457	UK, KS	BDF	2_4	2_4	1_4
	Donaciinae		*Plateumaris pusilla*	AF267427	CA	IA	1	$1_4/2_2$	$1_2/2_4$
			Donacia distincta	AF267428	CA	IA	1	$1_4/2_2$	$1_2/2_4$
	Eumolpinae	Colaspini	*Colaspis* sp.	AF267461	ME	BDF	2_4	1_4	2_4
		Eumolpini	*Chrysochus auratus*	AF267462	US, MD	BDF	2_4	1_4	2_4
			Eumolpus sp.	AF267460	ME, Chamela	BDF	2_4	1_4	2_4
		Megascelidini	*Megascelis* sp.	AF267463	CR	WF	—	—	—
	Galerucinae	Galerucini	*Galerucella nymphaeae*	AF267443	US, NY	FR	2_{15}	2_{15}	1_{15}
		Luperini	*Phyllobrotica decorata*	AF267441	US, CO	BDF	2_4	1_4	2_4
			Aulacophora palmerstoni	AF267442	AU	DF	2_4	1_4	2_4
		Metacyclini	*Agelastica alni*	AF267440	US, UT	TH	2_4	2_4	1_4
		Oidini	*Oides demipunctata*	AF267438	TH	DF	2	2_2	1_2
			Alagoasa bicolor.	AF267447	PR	CD	2	2_6	1_6
			Dercetina varipennis	AF267439	TH	DF	2	2	1
	Alticinae	Altinici	*Altica pagana*	AF267453	TA	DF	2	2_1	1_1
		Chaetocnemini	*Chaetocnema basalis*	AF267450	TH	DF	2	1	2
			Podontia affinis	AF267444	TH	DF	2_{16}	2_{16}	1_{16}
		Crepidoderini	*Crepidodera rhaetica*	AF267451	SW	SD	2	1	2
			Chalcoides aurata	AF267452	GER	SD	—	—	—
			Orthocrepis hanoiensis	AF267445	CH	DF	—	—	—
			Nisotra orbiculata	AF267446	TH	DF	2	1	2
			Chabria anhulicollis	AF267449	TH	DF	—	—	—
			Manobidia simplicithorax	AF267454	AU, Qld.	DF	—	—	—
			Hyphasis parvula	AF267448	TH	DF	—	—	—
	Hispinae	Hispini	*Alurnus biornata*	AF267430	PE	BDF	1_4	2_4	1_4
			Anisostena nigrita	AF267429	US, UT	TH	1_4	0_4	1_4
			Microrhophala vittata	AF276434	US, UT	TH	2_4	0_4	1_4
			Octotoma scabripennis	AF267431	AU, Qsld.	DF	2_4	0_4	1_4
		Cassidini	*Cassida rubriginosa*	AY676687	SW	SD	2_4	2_4	1_4
			Imatidium sp.	AF267432	PE	BDF	1_4	2_4	1_4
			Chelymorpha cassida	AF267433	US, CO	BDF	2_4	2_4	1_4
	Synetinae		*Syneta pilosa*	AF267464	US, MT	MI	2_4	1_4	2_4
			Syneta adamsi	AY676694	JA	DFu	2_4	1_4	2_4
	Lamprosoma-tinae	Lamprosomatini	*Lamprosoma* sp.	AY676688	PE	BDF/ TLE	2_4	2_4	2_4

Locality: Country abbreviations: AR (Argentina), AU (Australia), BE (Belgium), CHI (Chile), CH (China), CR (Costa Rica), DR (Dominican Republic), FR (France), GER (Germany), JA (Japan), MA (Malaysia), ME (Mexico), MO (Mongolia), PA (Panama), PE (Peru), SW (Switzerland), TA (Taiwan), TH (Thailand), US (USA).

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Hosts: 0, gymnosperms—conifers plus cycads; 1, monocots; 2, eudicots; Habits: 0, inside plant tissue; 1, external protected; 2, external exposed; Tissue: 0, Reproductive structures—strobili or seed; 1, photosynthetic tissue—leaves; 2, structural with vascular tissue—stems, twigs, trunk, or roots.

References: 1, Lee and Furth (2000); 2, Reid (2000); 3, Cox and Windsor (1999); 4, Jolivet (1988); 5, Crowson (1946); 6, Widner et al. (1988); 7, Kuschel (1994); 8, Linsley and Chemsak (1984); 9, Linsley (1961); 10, Johnson (1967); 11, Linsley (1964); 12, Skiles (1978); 13, DiIorio (1994); 14, Johnson et al. (2001); 15, Kouki (1993); 16, Pramanik and Basu (1973); 17, Kondo and Nagai (1982); 18, Boldt (1987); 19, Manley and French (1976); 20, Turnbow and Hovore (1979); 21, Powell (1978).