Molecular Phylogenetics and Evolution 89 (2015) 91–103

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Evolution of *Spermophagus* seed beetles (Coleoptera, Bruchinae, Amblycerini) indicates both synchronous and delayed colonizations of host plants ☆

Gael J. Kergoat [a,*], Bruno P. Le Ru [b,c,d], Seyed E. Sadeghi [e], Midori Tuda [f,g], Chris A.M. Reid [h], Zoltán György [i], Gwenaëlle Genson [a], Cibele S. Ribeiro-Costa [j], Alex Delobel [k]

[a] INRA, UMR 1062 CBGP (INRA, IRD, CIRAD, Montpellier SupAgro), 755 Avenue du campus Agropolis, 34988 Montferrier/Lez, France
[b] IRD/CNRS, Laboratoire Evolution Génomes Spéciation, Avenue de la terrasse, BP1, 91198 Gif-sur-Yvette, France
[c] Université Paris-Sud 11, 91405 Orsay, France
[d] Unité de Recherche IRD 072, African Insect Science for Food and Health (ICIPE), PO Box 30772-00100, Nairobi, Kenya
[e] Research Institute of Forests and Rangelands of Iran, PO Box 13185-116, Tehran, Iran
[f] Institute of Biological Control, Faculty of Agriculture, Kyushu University, 812-8581 Fukuoka, Japan
[g] Laboratory of Insect Natural Enemies, Division of Agricultural Bioresource Sciences, Department of Bioresource Sciences, Faculty of Agriculture, Kyushu University, 812-8581 Fukuoka, Japan
[h] Department of Entomology, Australian Museum, 6 College Street, Sydney, NSW 2010, Australia
[i] Department of Zoology, Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13, Hungary
[j] Laboratório de Sistemática e Bioecologia de Coleoptera, Departamento de Zoologia, Universidade Federal do Paraná, Caixa Postal 19020, 81531-980 Curitiba, Paraná, Brazil
[k] Muséum National d'Histoire Naturelle, 45 rue Buffon, 75005 Paris, France

ARTICLE INFO

Article history:
Received 5 February 2015
Revised 10 April 2015
Accepted 18 April 2015
Available online 24 April 2015

Keywords:
Bruchinae
Convolvulaceae
Historical biogeography
Host-plant associations
Malvoideae
Spermophagus

ABSTRACT

Seed beetles are a group of specialized chrysomelid beetles, which are mostly associated with plants of the legume family (Fabaceae). In the legume-feeding species, a marked trend of phylogenetic conservatism of host use has been highlighted by several molecular phylogenetics studies. Yet, little is known about the evolutionary patterns of association of species feeding outside the legume family. Here, we investigate the evolution of host use in *Spermophagus*, a species-rich seed beetle genus that is specialized on two non-legume host-plant groups: morning glories (Convolvulaceae) and mallows (Malvaceae: Malvoideae). *Spermophagus* species are widespread in the Old World, especially in the Afrotropical, Indomalaya and Palearctic regions. In this study we rely on eight gene regions to provide the first phylogenetic framework for the genus, along with reconstructions of host use evolution, estimates of divergence times and historical biogeography analyses. Like the legume-feeding species, a marked trend toward conservatism of host use is revealed, with one clade specializing on Convolvulaceae and the other on Malvoideae. Comparisons of plants' and insects' estimates of divergence times yield a contrasted pattern: on one hand a quite congruent temporal framework was recovered for morning-glories and their seed-predators; on the other hand the diversification of *Spermophagus* species associated with mallows apparently lagged far behind the diversification of their hosts. We hypothesize that this delayed colonization of Malvoideae can be accounted for by the respective biogeographic histories of the two groups.

1. Introduction

Seed beetles (Coleoptera, Chrysomelidae, Bruchinae) are a group of specialized seed predators, which encompasses about 1700 species (Johnson et al., 2004). Almost all bruchine species have a narrow host range and are associated with a small set of related host plant species, which generally belong to one genus or botanical tribe (Janzen, 1980; Johnson, 1981, 1989; Delobel and Delobel, 2003, 2006; Jermy and Szentesi, 2003; Kingsolver, 2004). Of the ca. 35 plant families attacked by bruchines (Johnson and Romero, 2004), the family Fabaceae (legumes) is the main target, as about 84% of bruchine species are strictly associated with seeds of legume plants (Borowiec, 1987). The remaining species are mostly associated with Arecaceae (4.5%), Convolvulaceae (4.5%) or Malvaceae (2%) (Borowiec, 1987).

☆ This paper has been recommended for acceptance by Alfried Vogler.

* Corresponding author. Fax: +33 499 623 345.
E-mail addresses: kergoat@supagro.inra.fr (G.J. Kergoat), bleru@icipe.org (B.P. Le Ru), ebrasadeghi@gmail.com (S.E. Sadeghi), tuda@grt.kyushu-u.ac.jp (M. Tuda), Chris.Reid@austmus.gov.au (C.A.M. Reid), gyorgy@zoo.nhmus.hu (Z. György), cibele.ribeirocosta@gmail.com (C.S. Ribeiro-Costa), delobel.alex@aliceadsl.fr (A. Delobel).

http://dx.doi.org/10.1016/j.ympev.2015.04.014
1055-7903/

Molecular phylogenetic studies on legume-feeding seed beetles have highlighted a marked trend toward taxonomic conservatism in host use, in which species that are phylogenetically related tend to feed on phylogenetically related host plants (Kergoat et al., 2004, 2005a, 2007b,c, 2008, 2011; Tuda et al., 2006; Tuda, 2007). This pattern is not uncommon for phytophagous insects in which long-term plant-insect associations are potentially mediated by plant chemical similarities (Futuyma and Moreno, 1988; Becerra, 1997; Kelley and Farrell, 1998; Abrahamson et al., 2003; Kergoat et al., 2005b). While plant secondary chemistry is considered a major constraint on the evolution of host use, numerous studies have suggested that other factors (e.g. morphological features and type of growth form, phenology, plant-associated parasitoids and predators, geographical distribution, habitat) may also be important for determining host use in phytophagous insects (see the review of Nyman, 2010). For example, habitat and climate are significant in the adaptation of *Callosobruchus* Pic to dry beans (Tuda et al., 2005, 2006; Tuda, 2011), and oviposition behavior is important in shaping the host-plant association patterns in several groups, such as *Mimosestes* Bridwell (Kato et al., 2010) and *Stator* Bridwell (Morse, 2003; Morse and Farrell, 2005).

The specificity of Bruchinae to their host plants is useful for investigating variation in evolutionary patterns of host-plant use. Thus far, molecular studies on seed beetles have only focused on species associated with legume plants, and only a few species of bruchines feeding outside the Fabaceae have been sequenced (e.g. a few species of *Acanthoscelides* Schilsky in Kergoat et al., 2005a and Álvarez et al., 2006). The precise timing of colonization of various plant groups by seed beetles is not known in detail but a recent study has indicated that the diversification of some legume-feeding species in the genus *Conicobruchus* Decelle might have closely followed those of their host-plants (Kergoat et al., 2011). Evidence for similar patterns in other phytophagous insect groups remains elusive, as most studies have recovered patterns of delayed colonizations (e.g. Sequeira et al., 2000; Lopez-Vaamonde et al., 2006; Gómez-Zurita et al., 2007; Hunt et al., 2007; McKenna et al., 2009; McLeish et al., 2013; but see Farrell, 2001; Becerra, 2003; Brändle et al., 2005; Cruaud et al., 2012).

Here we focus on the evolutionary history and pattern of host use in a non-legume feeder seed beetle group, the genus *Spermophagus* Schoenherr. With 118 valid species (see Table S1 for a detailed list) the genus *Spermophagus* is one of the most species-rich genera of seed beetles. It belongs to the tribe Amblycerini, which also encompasses the genera *Amblycerus* Thunberg and *Zabrotes* Horn. A fourth genus, *Pygospermophagus* Pic, only consists of a poorly described species whose type is lost, and the species is probably invalid (Kingsolver, 1970; Borowiec, 1991). Morphologically, *Amblycerus*, *Spermophagus* and *Zabrotes* are quite distinctive from other seed beetles: they exhibit two conspicuous long apical metatibial spurs and a distinct lateral pronotal carina. *Spermophagus* is morphologically most similar to *Zabrotes* as both genera share the following combination of character states: deeply emarginated eyes, triangular scutellum, abbreviated prosternal process with partly reduced parasutural rows; externally they only differ by the supracoxal carina (present in *Spermophagus*, absent in *Zabrotes*) and the tenth elytral stria (complete in *Spermophagus*, abbreviated in *Zabrotes*). While *Spermophagus* species are rather uniform in their external morphology, they exhibit distinctive male genitalic structures that have allowed the definition of informal species groups (Borowiec, 1991; Anton, 1996, 1999b) for a majority of the extant species (87 out of 118; see Table S1). These species-groups are referred to by the names of typical species of each group (e.g. *S. hottentotus* Fåhraeus for the *S. hottentotus* species-group: Borowiec, 1991). In contrast with the New World genera *Amblycerus* and *Zabrotes*, species in the genus *Spermophagus* are only found in the Old World: 51 species are distributed in the Afrotropical region, 46 in the Indomalaya region and 19 in the Palearctic region (Table S1). Only three species are distributed into more than one biogeographic region: *S. perpastus* (Lea) in Indomalaya and Australasia (Anton, 1999a; Reid and Beatson, 2013), *S. pygopubens* Pic in Afrotropical and Palearctic (Borowiec, 1991) and *S. sophorae* Fåhraeus in Afrotropic and Indomalaya (Borowiec, 1991). Two fossil taxa (from the Eocene Florissant formation of Colorado) have been tentatively assigned to the genus *Spermophagus* (Scudder, 1876; Wickham, 1914) but their assignations seem questionable because of the lack of diagnostic characters at the genus level and the fact that extant *Spermophagus* species are not distributed in the Western hemisphere. Though it may be hypothesized that these fossils can be assigned to the tribe Amblycerini because of indications of the presence of two metatibial spurs (Scudder, 1876: 82; Wickham, 1914: 480), we also cannot exclude the hypothesis that these fossils correspond to a distinct and extinct seed beetle lineage.

The evolutionary history of *Spermophagus* species is of particular interest because the genus constitutes one of the most successful radiations of bruchine beetles outside the Fabaceae. Indeed, all *Spermophagus* species for which unambiguous host records are known are associated with morning glories (Convolvulaceae) and mallows (Malvaceae: Malvoideae). Some records indicate that *Spermophagus* species may feed outside these two groups, but most of them correspond to adult catches rather than actual rearing records (Delobel, 2010; Delobel and Anton, 2011). This is exemplified by the case of *S. albosparsus* Gyllenhal, which supposedly feeds on both legumes and mallows (Udayagiri and Wadhi, 1989). Examination of the records shows that reared specimens were only from Malvoideae (Arora, 1977; Borowiec, 1991); the record on the legume *Albizia* Durazz by Zacher (1952) is unlikely to be correct because this source is well known for doubtful and inaccurate host records (Kingsolver and Johnson, 1978; Southgate, 1979; Romero et al., 1996; Romero and Johnson, 2003; Delobel et al., 2004; Kergoat et al., 2007a). Though the host-plant associations of numerous species remain unknown or only partially known; recent investigations in South-East Asia (Delobel, 2008; Delobel and Anton, 2011), Western Asia (Delobel and Sadeghi, 2013) and Africa (Le Ru, pers. obs.) are progressively filling gaps in our knowledge of host use in the genus. Reliable host records are now available for 48 of the 118 valid species (Table S1), indicating that a majority of the species for which host records are available (i.e. 37 species) are associated with Convolvulaceae belonging to ten genera in tribes Cardiochlamyeae (*Poranopsis* Roberty), Convolvuleae (*Calystegia* R. Br. and *Convolvulus* Linnaeus), Dichondreae (*Porana* Burm. f.), Ipomoeeae (*Astripomoea* A. Meeuse, *Ipomoea* Linnaeus and *Lepistemon* Blume) and Merremieae (*Hewittia* Wight and Arn., *Merremia* Dennst. ex. Endl. and *Xenostegia* D.F. Austin and Staples). The remaining 11 species are associated with Malvoideae belonging to four genera in tribes Hibisceae (*Abelmoschus* Medik., *Hibiscus* Linnaeus and *Urena* Linnaeus) and Malveae (*Sida* Linnaeus). Recent studies have revised the origin and timing of diversification of Convolvulaceae and Malvoideae. For Convolvulaceae, whole plastome sequences and fossil calibrations (Eserman et al., 2014) provide a robust temporal context for diversification of morning glories, with estimated origin of Convolvulaceae at ca. 55.3 million years old (Ma); this estimate is consistent with the age of 54.1 Ma from the study of Zanne et al. (2014) on angiosperms, which relies on seven molecular markers and fossil calibrations. Convolvulaceae have a likely origin in the Old World, as attested by their fossil record and biogeographic hypotheses based on the fragmentation of Gondwana (Olmstead, 2013). Regarding the Malvoideae, Carvalho et al. (2011) recently documented the oldest known fossil from the middle Paleocene (58–60 Ma) of Colombia, which predates previous molecular clock estimates (Koopman and Baum, 2008; Zanne

et al., 2014) by more than 30 million years (Myr); they also claimed that a Neotropical origin for Malvoideae is highly plausible given their current distribution and fossil record. It is thus possible to investigate the question of the timing of the colonization of *Spermophagus* seed beetles.

To determine the evolutionary relationships and evolution of *Spermophagus* seed beetles we conducted molecular phylogenetic analyses on a representative sample of 77 bruchine species, including 37 *Spermophagus* species. The first objective of the study was to assess the respective positions of the three genera belonging to the tribe Amblycerini and to provide a phylogenetic framework for the genus *Spermophagus*. The second objective was to estimate the history of colonization of *Spermophagus* seed beetles on their host-plants. Our final objective was to infer a temporal framework for the genus using Bayesian relaxed clock (BRC) methods. The resulting timelines allow us to implement historical biogeography analyses and to compare the timing of *Spermophagus* diversification with those of their host-plants.

2. Materials and methods

2.1. Taxon sampling and molecular methods

Most *Spermophagus* specimens were obtained through various field missions conducted in 16 countries (see Table S2 for details). Techniques used for sample collection and seed beetles rearing were similar to those described earlier (Delobel and Delobel, 2003, 2006; Jermy and Szentesi, 2003; Johnson and Romero, 2004). By rearing adults from fruits and seeds, we can report new host-plant records for 14 *Spermophagus* species (Table S2). A few sampled *Spermophagus* specimens were collected from unidentified hosts (see Table S2). Identification of most specimens was done by Alex Delobel, who is a recognized authority in bruchine taxonomy. Specimens from 78 species were included in the molecular analyses (see Table S3). 37 *Spermophagus* species were sampled, including members of 15 of the 20 recognized *Spermophagus* species groups (where possible we have included the species for which these groups are named). To assess phylogenetic relationships within Amblycerini, we included two representatives of *Amblycerus* and five representatives of *Zabrotes*. 33 other seed beetles species were also included in the sampling: 29 species from the tribe Bruchini (belonging to eight distinct genera), three species from the tribe Kytorhinini and one species from the tribe Pachymerini. We were not able to include specimens from the two remaining bruchine tribes (Eubaptini and Rhaebini), which encompass a handful of very rare species. To root the tree we used a representative of a distinct chrysomelid subfamily, *Crioceris duodecimpunctata* (Linnaeus) (Chrysomelidae, Criocerinae).

Non-destructive DNA extractions of whole specimens were conducted using Qiagen DNAeasy tissue kits (Qiagen, Hilden, Germany). Polymerase chain reaction (PCR) amplifications were conducted for four mitochondrial gene fragments: cytochrome oxidase I (COI), cytochrome b (Cytb), ribosomal 12S RNA (12S), and ribosomal 16S RNA (16S) (see Table S4 for the list of primers). Four nuclear gene regions were also sequenced: 28S ribosomal DNA domain D2-D3 (28S-D2D3), 28S ribosomal DNA domain D4-D5 (28S-D4D5), 28S ribosomal DNA domain D6-D7 (28S-D6D7), and 18S ribosomal DNA (18S) (see Table S4 for the list of primers). For the 28S-D6D7 domain, we used the settings detailed in Ceotto et al. (2008). For the 18S gene, three overlapping regions were sequenced following Kergoat et al. (2014b). For all remaining genes, we used the settings detailed in Kergoat et al. (2011). Newly generated PCR products were processed by Eurofins MWG Synthesis GmbH (Ebersberg, Germany). Both strands were sequenced for all specimens to minimize PCR artefacts and ambiguities. Sequences of complementary strands were edited and reconciled using Geneious v5.1 software (available at: www.geneious.com/). All the sequences generated in this study were deposited in GenBank (see Table S5 for the accession numbers). Unlike the sequences of coding genes (COI and Cytb), the sequences of ribosomal genes were variable in length. Their alignment was accomplished using MAFFT 7 (Katoh and Standley, 2013) with default settings. For all protein-coding genes, we used Mesquite 3.0 (available at: www.mesquiteproject.org) to check the coding frame for possible errors or stop codons. The combination of the eight gene fragments resulted in a combined matrix of 78 specimens and 6852 aligned characters.

2.2. Phylogenetic analyses

Phylogenetic analyses were conducted using Maximum likelihood (ML) and Bayesian inference (BI). For both methods we carried out partitioned analyses to improve phylogenetic accuracy (Nylander et al., 2004). Partitions and substitution models were determined using PartitionFinder v1.1.1 (Lanfear et al., 2012). The corrected Akaike information criterion (AICc; Posada and Buckley, 2004) was used as a metric for ML analyses whereas the Bayesian information criterion (BIC) was used for BI analyses.

Maximum Likelihood analyses were performed using RAxML v8 (Stamatakis, 2014). Based on the AICc results we used 12 partitions with either a General time reversible (GTR) + G + I model or a GTR + G model (see Table S4). The best ML tree was obtained using a heuristic search implementing 100 random-addition replicates. Clade support was then assessed using a non-parametric bootstrap procedure (1,000 replicates were used). Nodes supported by bootstrap values (BV) $\geqslant$ 70% were considered strongly supported following Hillis and Bull (1993).

Bayesian inference analyses were carried out using MrBayes 3.2.3 (Ronquist et al., 2012). Based on the BIC results we used ten partitions (see Table S6) but instead of using a specific model for each partition we used the mixed model option. The latter allows for sampling across the substitution model space in the Bayesian Markov Chains Monte Carlo (MCMC) analysis itself, removing the need for a priori model testing (Huelsenbeck et al., 2004). We conducted two independent runs with four MCMC (one cold and three incrementally heated) that ran for 50 million generations, with trees sampled every 1000 generations. A conservative burn-in of 25% was then applied after checking for stability on the log-likelihood curves and the split-frequencies of the runs. Support of nodes for MrBayes analyses was provided by clade posterior probabilities (PP) as directly estimated from the majority-rule consensus topology. Nodes supported by PP $\geqslant$ 0.95 were considered strongly supported following Erixon et al. (2003). Whenever a group of interest was recovered in paraphyly, we used Bayes factors (B_F) to assess whether there was statistical support for their non-monophyly. To do so, specific analyses (in which taxa of interest are constrained to be monophyletic) were carried out using MrBayes.

2.3. Character optimizations

Host plant associations of sampled bruchine species were determined based on a critical review of the extant literature (Udayagiri and Wadhi, 1989; Borowiec, 1991, 1995; Anton and Delobel, 2003; Delobel and Delobel, 2003, 2006; Jermy and Szentesi, 2003; Kergoat et al., 2007a; Delobel, 2008; Delobel and Anton, 2011; Delobel and Sadeghi, 2013; Le Ru et al., 2014), or directly compiled from data obtained during field collecting trips. Outside the genus *Spermophagus*, all sampled bruchine species are associated with Fabaceae except for *Bruchidius biguttatus* (Olivier) (associated with Cistaceae), *B. cinerascens* (Gyllenhal) (associated with Apiaceae) and *Pachymerus cardo* (Fåhraeus) (associated with Arecaceae).

Finally, the only sampled Criocerinae, *Crioceris duodecimpunctata* (Linnaeus), is associated with Liliaceae (Schmitt, 1988). We thus used the following optimization scheme with seven possible character states: (1) associated with Arecaceae; (2) associated with Apiaceae; (3) associated with Cistaceae; (4) associated with Convolvulaceae; (5) associated with Malvoideae; (6) associated with Fabaceae; (7) associated with Liliaceae. As a guide tree we used the best ML tree obtained through the RAxML analyses. This tree was modified under Mesquite, by pruning the only taxon for which no host record was available (i.e. *Spermophagus* sp. BRU.GK544). Ancestral character state estimations were further carried out under ML using a one-parameter Markov k-state model with symmetrical rates (Lewis, 2001), as implemented in Mesquite. The support of one state over another (at a given node) was considered as significant if the difference between their log-likelihoods was greater than or equal to 2.0 (Schluter et al., 1997).

2.4. Dating analyses

We used the BRC approach implemented in BEAST v1.8.1 (Drummond et al., 2012). Two age constraints were enforced to provide a more precise estimation of divergence times. For the first constraint we relied on the age of *Mesopachymerus antiqua* Poinar Jr. (Pachymerini), the oldest known fossil bruchine (Poinar, 2005), to set a minimum age for the seed beetle crown group. This fossil was found in amber sediments belonging to the Judith River Formation (Grassy Lake, Alberta, Canada), which were radiometrically dated at 79.0 Ma by Eberth and Hambin (1993). To limit the risk of age overestimations we also used as an upper bound the minimum age associated with the stem age of Chrysomelidae (152.0 Ma), which corresponds to the oldest known occurrence of a member of the superfamily Chrysomeloidea (see Kergoat et al., 2014a for more details). This fossil constraint was enforced using either a lognormal statistical distribution or an exponential statistical distribution following the recommendations of Ho and Phillips (2009). 95% of the prior distribution was set between 79.0 to 152.0 Myrs using the following settings: (i) for the exponential prior: *mean* = 24.8; *offset* = 77.72; (ii) for the lognormal prior: *mean* = 1.002; *stdev* = 2.0; *offset* = 78.90. Second, we relied on *Spermophagus lindbergorum* Decelle, a species endemic to the Canary archipelago, to set a geological constraint. Given that the magmatic event represented by the Canary Islands started 24.0 Ma (Fernández-Palacios et al., 2011), we used a uniform distribution to set an age comprised between 0.0 and 24.0 Myr (24.0 Myr corresponds to the age of the two oldest islands) for the node corresponding to the most recent common ancestor (MRCA) of *S. lindbergorum* and its sister-taxa. Because accurate fossil assignation is critical for dating procedures (Sauquet et al., 2012), we also chose not to rely on the two questionable *Spermophagus* fossils. BEAST analyses were further implemented with a birth–death tree speciation prior to account for the fact that our trees describe inter-specific relationships. To limit the number of parameters to estimate: (i) we only used two clock models (one for the mitochondrial genes and one for the nuclear genes); and (ii) we used a guide tree that corresponds to the topology inferred with MrBayes. Supplementary analyses were also conducted with one clock model per gene in order to estimate their rates of evolution.

For each calibration procedure ('lognormal prior for the fossil constraint' and 'exponential prior for the fossil constraint'), two distinct runs were carried out with 50 million generations and trees sampled every 5000 generations (10,000 trees were sampled for each run). BEAST xml files were modified to implement the path-sampling procedure for B_F estimation following the recommendations of Baele et al. (2013). We used a conservative burn-in-period of 12.5 million generations per run. Post burn-in trees from the two distinct runs (7500 trees for each run) were further combined using the LogCombiner module of BEAST. Convergence of runs was assessed graphically under Tracer v1.5 (available at http://tree.bio.ed.ac.uk/software/tracer/) and by examining the effective sample size (ESS) of parameters. Convergence was indicated by ESS of parameters $\geqslant 200$ for the post burn-in trees. Out of the two calibrations, the calibration procedure with an exponential prior has the best harmonic mean (−56293.84 versus −56303.88 for the procedure with an lognormal prior) and is recovered as the best-fit calibration procedure because of a statistically significant B_F of 20.08 ($B_F > 10$; Kass and Raftery, 1995).

2.5. Historical biogeography

Historical biogeography analyses were carried out using the R package BioGeoBEARS (BioGeography with Bayesian (and likelihood) Evolutionary Analysis of RangeS; Matzke, 2014). This package relies on the LAGRANGE (Ree et al., 2005; Ree and Smith, 2008) dispersal extinction cladogenesis (DEC) model. It also implements a new model called DEC + J model which accounts for founder event speciation (Matzke, 2014). Here we carried out distinct analyses for the DEC and DEC + J models. As a guide tree we used the dated phylogeny corresponding to the best-fit calibration procedure (i.e. with an exponential prior). This tree was further pruned to only include *Spermophagus* species, in order to avoid potential biases resulting from the fact that many of the sampled outgroup taxa are also distributed in the same geographic areas as *Spermophagus* species.

We defined four geographical areas for the BioGeoBEARS analysis after considering the evidence available for historical relationships between relevant geographic areas (Sanmartín et al., 2001; Sanmartín and Ronquist, 2004) and the distribution of *Spermophagus* taxa. These biogeographic regions were as follows: (i) Afrotropical; (ii) Australasian; (iii) Indomalayan; (iv) Palearctic. Species ranges were coded by presence–absence and a maximum number of four areas was set for both DEC and DEC + J analyses. Finally, to account for major periods of geological rearrangements, we used time-stratified biogeographical models, with three distinct time slices (Fig. S1). The first time slice ($t1$) runs from 40.0 to 66.0 Ma: it restricts dispersal between Australasia and all remaining areas and also accounts for the fact that the Afrotropical, Indomalayan and Palearctic regions are not connected but are separated by shallow seas. The second time slice ($t2$) runs from 27.0 to 40.0 Ma and accounts for a greater connectivity between the Afrotropical, the Indomalayan and the Palearctic. The last time slice ($t3$) runs from 0.0 to 27.0 Ma and corresponds to the highest level of connectivity between all considered geographic areas. After running both analyses, we used Likelihood Ratio Tests (LRT) to sort between the two competing models (DEC and DEC + J), as recommended by Matzke (2014).

3. Results

3.1. Phylogenetic analyses

Most of the phylogenetic support is provided by the mitochondrial genes, which account for 70.7% (1323 sites out of 1870) of the variable sites (Table 1). The four mitochondrial gene fragments that are used exhibit similar variability (proportion of variable sites comprised between 45% for the COI and 51.7% for the Cytb. Regarding the nuclear genes, the variability is low for the 18S (7.8%), 28S-D4D5 (8.6%) and 28S-D6D7 (12.1%); by contrast the 28S-D2D3 fragment exhibits a higher level of variability (31.2%). Both ML and BI analyses yield similar topologies (see Fig. 1 for the topology inferred under BI, and Fig. S2 for the best-fit ML tree), as indicated by a high proportion of shared nodes (69 out of 77). Most differences relate to the placement of several bruchine taxa

Table 1
Information on the sequenced gene fragments. For each gene the following information is provided: the length of the aligned fragment, the number of variable sites (#var. sites), the percentage of variable sites (%var. sites), the number of parsimony informative sites with gaps considered as a fifth character (#PI sites), the percentage of PI sites with gaps considered as a fifth character (%PI sites), the number of gaps (#gaps) and the A-T percentage (%A-T).

Gene	Length	#var. sites	%var. sites	#PI sites	%PI sites	#gaps	%A-T
COI	1011	455	45.0	385	38.0	0	67.1
Cytb	778	403	51.7	330	42.4	0	68.9
12S	410	210	51.2	168	40.9	9	76.3
16S	544	255	46.8	210	38.6	9	74.2
28S-D2D3	801	250	31.2	162	20.2	20	40.5
28S-D4D5	703	61	8.6	34	4.8	7	47.4
28S-D6D7	715	87	12.1	43	6.0	9	42.6
18S	1892	149	7.8	34	1.7	12	48.3

that do not belong to Amblycerini, such as members of the *Bruchidius submaculatus* group (*B. cadei* Delobel, *B. pygidiopictus* Delobel and *B. submaculatus* (Fåhraeus)). Clade support is moderate to high on average; if considering the number of nodes that are supported by PP $\geqslant$ 0.95 or BV $\geqslant$ 70%, BI analyses yield a slightly more robust topology (38 well-supported nodes) compared to the ML tree (33 well-supported nodes).

All sampled members of the tribe Bruchini are recovered monophyletic with strong support (PP of 1.0 and BV of 93%; see Figs. 1 and S2), and sister to the representative of the tribe Pachymerini, *Pachymerus cardo* (Fåhraeus). Sister to this clade is one that groups the representatives of Amblycerini and Kytorhinini. Due to the position of Kytorhinini, members of the tribe Amblycerini are paraphyletic in all phylogenetic analyses. Kytorhinini representatives appear sister to *Amblycerus* with moderately high support (PP of 0.94 and BV of 67%) whereas both *Spermophagus* and *Zabrotes* are grouped together with strong support (PP of 1.0 and BV of 98%). Additional analyses carried out under BI clearly support the paraphyly of the tribe Amblycerini: MCMC runs where Amblycerini representatives are constrained to be monophyletic yield a harmonic mean estimate of −52521.72 versus −52493.78 for the MCMC runs where Kytorhinini representatives are grouped with *Amblycerus* spp. Hence the difference corresponds to a statistically significant B_F of 55.80. The genus *Spermophagus* is recovered monophyletic with strong support (PP of 0.99 and BV of 76%). Four major clades can be distinguished: (i) 15 species, mostly from four species groups (species groups *S. hottentotus*, *S. johnsoni*, *S. sericeus* and *S. titivilitius*); (ii) sister to (i), 11 species, including members of seven distinct species groups (species groups *S. albomaculatus*, *S. brevipes*, *S. cederholmi*, *S. latithorax*, *S. posticus*, *S. rufipes* and *S. stemmleri*); (iii) three species from species groups *S. mannarensis* and *S. multipunctatus* form a clade sister to (i) + (ii); eight species, mostly belonging to species groups *S. albosparsus* and *S. niger* form a clade sister to (i) + (ii) + (iii).

3.2. Character optimizations

Character optimizations of host plant associations (Fig. 2) yield a well-supported pattern as the character states of all but two nodes are statistically supported by the likelihood comparisons (log-likelihood difference of one state over another > 2.0). For *Spermophagus* a shift from Fabaceae to Convolvulaceae is recovered as the most likely (relative probability of 62.55%), but without statistical support. A clear pattern with a high level of phylogenetic conservatism in host use is revealed for *Spermophagus* beetles: all Convolvulaceae feeders are grouped together and are sister to a clade that encompasses all Malvoideae feeders. For the MRCA of both clades an ancestral host association with either Convolvulaceae or Malvoideae is statistically significantly supported.

3.3. Dating analyses

Both calibration procedures yield comparable timeframes (see Figs. S3 and S4). Age estimates for the subfamily Bruchinae suggest an origin around 78–81 Ma (median age of 81.3 Ma, 95% HPD: 77.7–92.7 for the exponential-based calibration and median age of 78.1 Ma, 95% HPD: 78.9–96.3 for the lognormal-based calibration). As for *Spermophagus*, dating analyses suggest an origin around 60 Ma (median age of 60.3 Ma, 95% HPD: 52.6–70.2 for the exponential-based calibration and median age of 59.3 Ma, 95% HPD: 52.9–66.5 for the lognormal-based calibration). Regarding the two major clades that are specialized on distinct plant groups, an older origin is inferred for the species associated with Convolvulaceae about 57 Ma (median age of 57.7 Ma, 95% HPD: 50.3–67.1 for the exponential-based calibration and median age of 56.7 Ma, 95% HPD: 50.2–63.4 for the lognormal-based calibration). The clade that diversified on Malvoideae diversified more recently about 42 Ma (median age of 42.7 Ma, 95% HPD: 34.3–52.1 for the exponential-based calibration and median age of 41.9 Ma, 95% HPD: 34.3–50.2 for the lognormal-based calibration). The supplementary analyses relying on eight molecular clocks gave similar estimates (see Figs. S5 and S6): (i) 79–80 Ma for the Bruchinae (median age of 80.6 Ma, 95% HPD: 77.7–113.6 for the exponential-based calibration and median age of 79.7 Ma, 95% HPD: 78.9–102.4 for the lognormal-based calibration); (ii) 55–56 Ma for the genus *Spermophagus* (median age of 56.0 Ma, 95% HPD: 44.3–80.5 for the exponential-based calibration and median age of 55.4 Ma, 95% HPD: 43.4–73.9 for the lognormal-based calibration); (iii) 52–53 Ma for the clade associated with Convolvulaceae (median age of 53.2 Ma, 95% HPD: 40.9–79.9 for the exponential-based calibration and median age of 52.5 Ma, 95% HPD: 41.9–70.5 for the lognormal-based calibration); (iv) 36–37 Ma for the clade associated with Malvoideae (median age of 37.6 Ma, 95% HPD: 25.5–54.2 for the exponential-based calibration and median age of 36.9 Ma, 95% HPD: 24.2–53.5 for the lognormal-based calibration). The estimated rates of evolution for each gene are presented in Table 2. The fastest evolving mitochondrial gene is the Cytb (mean rate of 0.003189 substitution/site/Myr) while the 12S is the slowest (mean rate of 0.001525 substitution/site/Myr). As for the nuclear genes, the fastest evolving gene is the 28S-D2D3 (mean rate of 0.001115 substitution/site/Myr) while the 18S is the slowest (mean rate of 0.000099 substitution/site/Myr).

3.4. Historical biogeography

Model selections through LRT significantly support the DEC + J model ($L = -53.59$) over the DEC model ($L = -74.1$) as the best-fit model for the BioGeoBEARS historical biogeography analyses. The corresponding inference of ancestral areas evolution (Fig. 3) suggests an origin in Indomalaya for *Spermophagus* during the Paleocene, followed by multiple independent colonizations of the Palearctic and Afrotropic during the Eocene. During the Oligocene, several lineages also reached the Afrotropic from the Palearctic. Colonization of Australasia from Indomalaya occurred more recently, likely during the Miocene. Analyses with a DEC model also recover a very similar pattern (Fig. S7), and mostly differ by a higher number of inferred vicariance events: one vicariance event was inferred by the BioGeoBEARS analysis with a DEC + J model (in the clade i: between the group consisting of *S. cornutus* Delobel and *S. insularis* Delobel and the group that encompasses members of the *S. sericeus* species group) whereas four vicariance events were inferred for the analysis with a DEC model (Fig. S7).

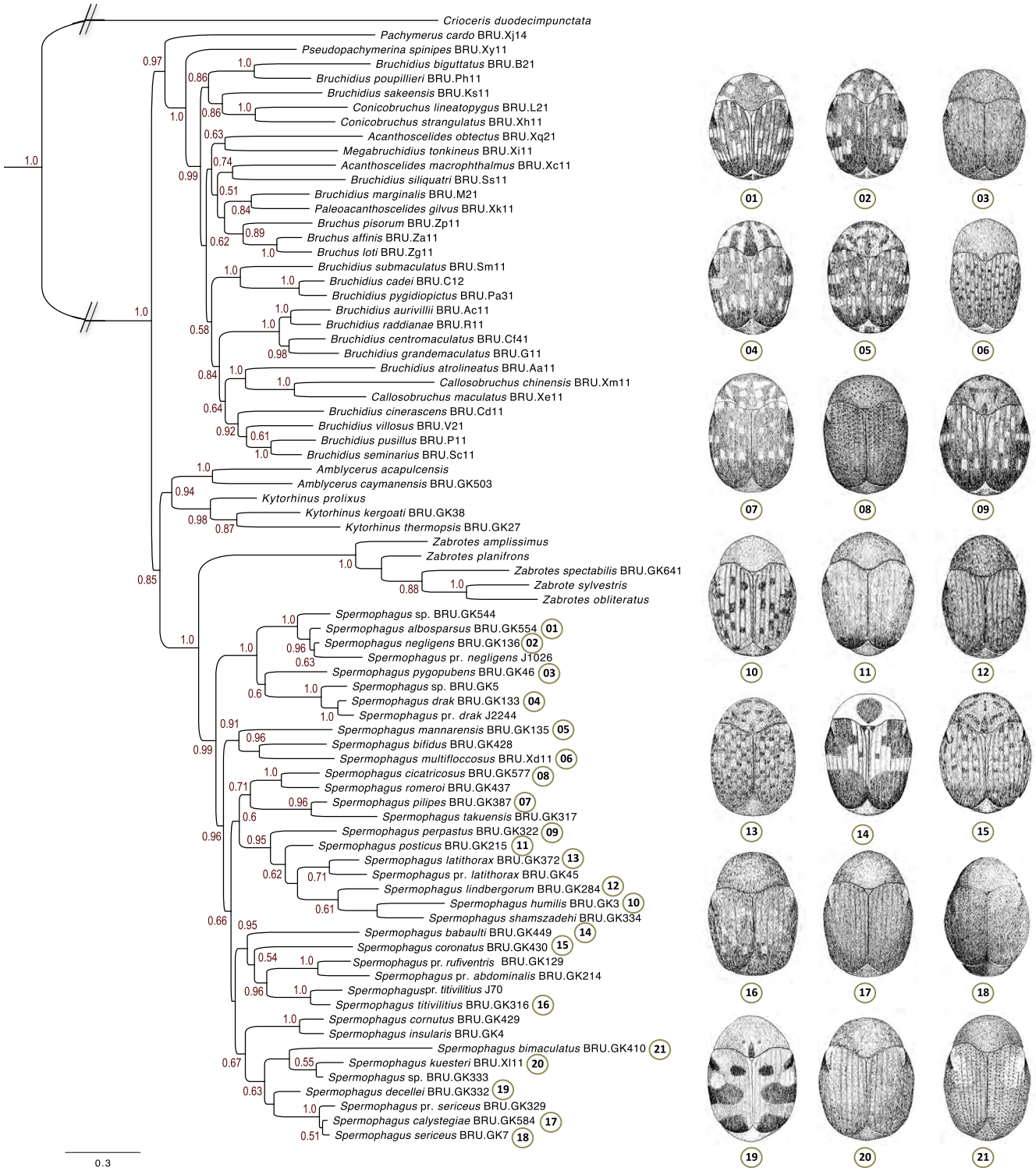

Fig. 1. Majority-rule consensus topology from Bayesian inference analyses. Support values are provided on nodes (only PP $\geqslant$ 50% are shown). On the right side, drawings of 21 *Spermophagus* species are figured for illustrative purpose (drawings were reproduced with the kind authorization of Lech Borowiec).

4. Discussion

4.1. Phylogenetic analyses

Our analyses provide novel insights on amblycerine phylogenetic relationships and clearly support the paraphyly of the tribe Amblycerini. While *Spermophagus* and *Zabrotes* form a monophyletic group, the tribe Kytorhinini is recovered sister to the genus *Amblycerus* with a strong support. Interestingly the paraphyly of the tribe Amblycerini was also recovered in the study of Morse (2003), who analyzed a two-gene dataset of 88 seed beetle taxa with a more limited sampling for Amblycerini and Kytorhinini (i.e. five *Amblycerus*, one *Spermophagus*, three *Zabrotes* and one *Kytorhinus* species). In the corresponding study, the paraphyly of the tribe Amblycerini was recovered in all analyses, though the sister-relationship of *Amblycerus* with Kytorhinini was only found

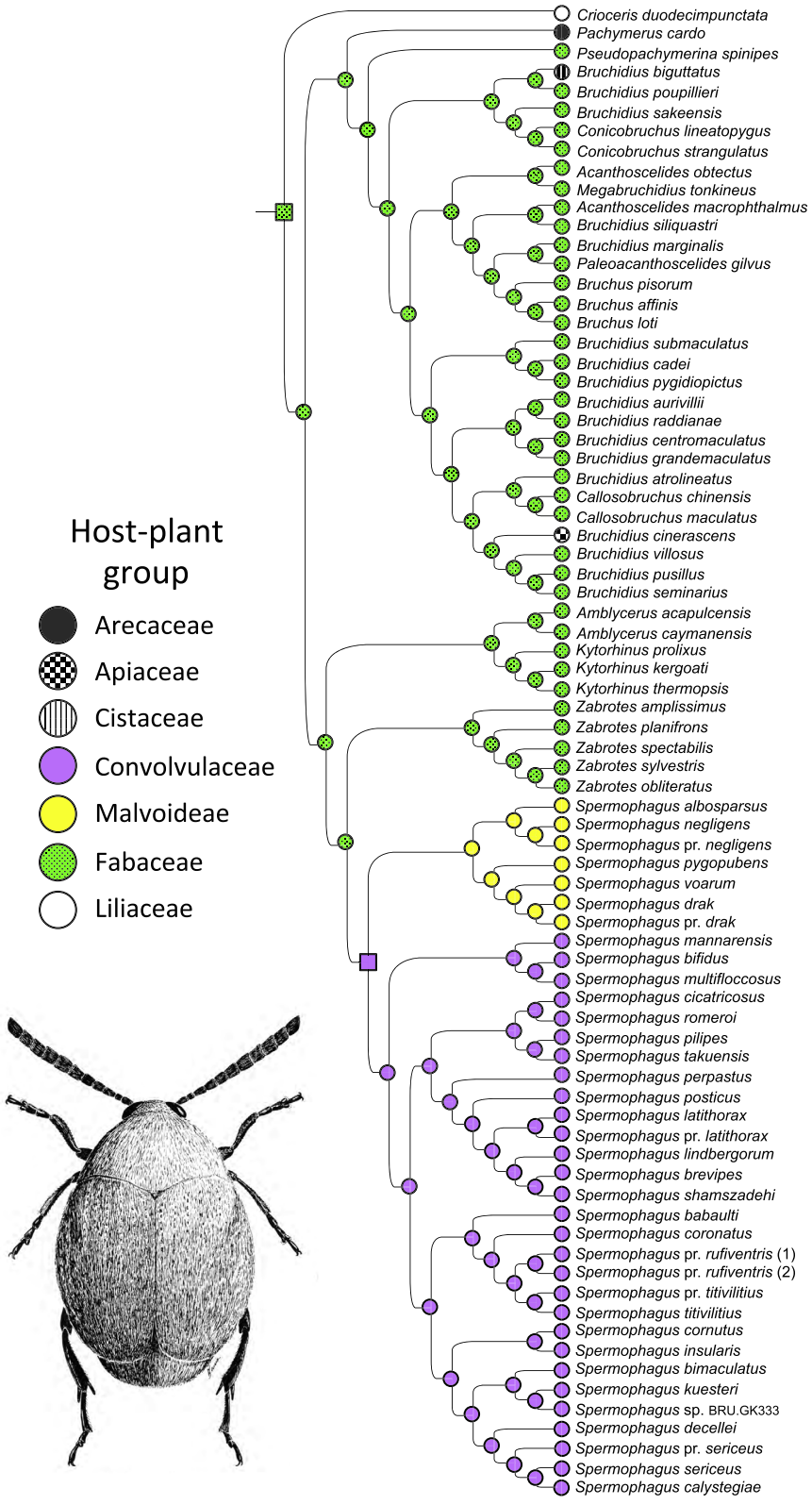

Fig. 2. Result of the character optimizations of host-plant associations. Host-plant groups of each species are figured on the tip of the tree. Ancestral host associations are figured using either colored circles or squares: circles indicate statistically supported ancestral character traits whereas squares indicate that the corresponding host association is the most likely but not statistically supported. On the bottom left, a drawing of *Spermophagus sericeus* is figured for illustrative purpose; the paired metatibial spurs can be seen when looking at the posterior legs (drawing was reproduced with the kind authorization of Lech Borowiec). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Estimated rates of evolution (substitution/site/Myr) for the eight genes used in this study. Rate statistics are based on the results of the BEAST analyses with an exponential prior for the fossil constraint and one molecular clock per gene. Average rates are also presented for mitochondrial (mtDNA) and nuclear DNA (nucDNA); they correspond to the results of the BEAST analyses with an exponential prior for the fossil constraint and two molecular clocks (one for the combined mitochondrial genes, one for the combined nuclear genes).

Gene	Mean rate	ucld.mean	ucld.stdev	Coeff. variation	Covariance
COI	0.003063 ± 0.00000831	0.003114 ± 0.00001124	0.4291 ± 0.0038	0.4308 ± 0.0037	0.0504 ± 0.0013
Cytb	0.003189 ± 0.00001119	0.003489 ± 0.00002260	0.8456 ± 0.0071	0.8698 ± 0.0210	−0.0928 ± 0.0040
12S	0.001525 ± 0.00000399	0.001508 ± 0.00000367	0.4827 ± 0.0020	0.4860 ± 0.0018	0.0441 ± 0.0010
16S	0.002121 ± 0.00000605	0.002110 ± 0.00000599	0.4614 ± 0.0022	0.4833 ± 0.0020	0.0758 ± 0.0010
28S-D2D3	0.001115 ± 0.00000269	0.001142 ± 0.00000906	0.9797 ± 0.0059	1.2465 ± 0.0051	0.0715 ± 0.0014
28S-D4D5	0.000261 ± 0.00000068	0.000272 ± 0.00000103	0.8895 ± 0.0044	1.0358 ± 0.0059	−0.0075 ± 0.0007
28S-D6D7	0.001392 ± 0.00000409	0.001438 ± 0.00000457	0.6470 ± 0.0030	0.7034 ± 0.0038	0.0007 ± 0.0008
18S	0.000099 ± 0.00000087	0.000102 ± 0.00000143	1.0493 ± 0.0101	1.3127 ± 0.0124	−0.0015 ± 0.0009
mtDNA	0.002717 ± 0.00000422	0.002707 ± 0.00000516	0.2784 ± 0.0013	0.2808 ± 0.0010	0.0655 ± 0.0012
nucDNA	0.000386 ± 0.00000067	0.000430 ± 0.00000275	0.8713 ± 0.0050	0.9827 ± 0.0036	0.0931 ± 0.0015

under Bayesian inference (and not under parsimony). Taken altogether these results suggest that the morphological characters (presence of paired metatibial spurs and lateral pronotal carina) that have been used to easily define the tribe Amblycerini have either evolved independently in the lineage of *Amblycerus* and the *Spermophagus + Zabrotes* clade, or have been lost in Kytorhinini. Reid (1995) discusses these characters in Chrysomeloidea generally and rejects them as useful for determining higher phylogeny: paired metatibial spurs are certainly a plesiomorphy in the Chrysomelidae (and in beetles generally) and therefore only useful in bruchine classification when lost; the lateral pronotal carina comes and goes, even in a single genus (*Microdonacia* Blackburn; Reid, 1992). So from the outset, the reliance on both characters to define the tribe Amblycerini is questionable. Kytorhinini is a monotypic tribe of about 15 species (Delobel and Legalov, 2009), harboring a combination of apomorphic and plesiomorphic characters (Borowiec, 1987). The external morphology of Kytorhinini is distinctive (Delobel and Legalov, 2009): antennae pectinate or strongly serrate; slender legs; metafemur without a ventral spine; metatibia without a distinct mucro; metatibia with one or without a carina; tergites six [VI] and seven [VII] exposed. Based on external morphology, Kytorhinini do not appear to be related to Amblycerini, especially *Amblycerus.* However, male genitalia in Kytorhinini definitely share more similarities with Amblycerini and especially *Amblycerus*: the internal sac possesses strong hooked sclerites (as in most *Amblycerus* species) and the parameres are almost completely fused (as in *Amblycerus* or *Zabrotes*) (Borowiec, 1987). We can hypothesize that the lack of a more obvious morphological relationship between *Amblycerus* and Kytorhinini may be accounted for by their early divergence within Bruchinae, as indicated by our age estimates from the MRCA of the two groups (median age of 73.2 Ma, 95% HPD: 62.9–86.0 for the exponential-based calibration and median age of 72.2 Ma, 95% HPD: 63.5–80.0 for the lognormal-based calibration). The paraphyly of Amblycerini requires revision of the classification of Bruchinae, by elevating the taxonomic rank of subtribes Amblycerina and Spermophagina *sensu* Borowiec (to Amblycerini and Spermophagini, respectively; see also Bouchard et al., 2011 for more information of the status of Spermophagina), or synonymizing Kytorhinini with Amblycerini, with either having precedence (both were defined by Bridwell, 1932).

The monophyly of *Spermophagus* is strongly supported (BV of 76% and PP of 0.99). Though our sampling only encompasses about one third of *Spermophagus* species it provides some support for several of the species groups that have been defined in the last decades. Species that belong to the same species groups are generally found in the same clade. However, we cannot precisely delimit species-groups within *Spermophagus* from this study as only a fraction of species was sampled and some species were not identified, or are undescribed (the latter indicated by 'pr.', meaning near). Because *Spermophagus* species groups have been defined on the basis of both external and internal (male genitalia) morphological characters we suggest that the majority of the corresponding assignations are correct (i.e. species groups are monophyletic), as has been confirmed in several molecular studies on other seed beetle genera (Kergoat et al., 2004, 2007c, 2008; Delobel et al., 2013; Le Ru et al., 2014).

4.2. Origin of Bruchinae

With respect to the age of Bruchinae, our estimates (78–81 Ma) are congruent with the ages inferred in a comparable study focusing on a distinct seed beetle group (82–85 Ma in Kergoat et al., 2011). Both estimates significantly predate ages of the Bruchinae recovered in other molecular studies (Kergoat et al., 2005a; Gómez-Zurita et al., 2007). This discrepancy may be due to the way the fossil *Mesopachymerus antiqua* was used as a constraint in the present study and in the study of Kergoat et al. (2011). In the study of Kergoat et al. (2005a), the authors did not use *M. antiqua* for their calibrations (the description of *M. antiqua* by Poinar was shortly after the publication of their study); instead they relied on the standard rate estimate by Brower (1994) for mitochondrial DNA evolution in arthropods and estimated an age of 70 Ma for the origin of Bruchinae. In the study of Gómez-Zurita et al. (2007), younger ages (stem ages are comprised between 49 to 69 Ma) were obtained because *M. antiqua* was erroneously considered a sagrine beetle, following the interpretations of older studies (Poinar, 1999; Grimaldi and Engel, 2005), but corrected by Reid (2000: 855). The authors also relied on a younger age estimate (72 Ma) for the age of the fossil (following Grimaldi and Engel, 2005). As a result their estimations of the origin of Chrysomelidae (at 73–79 Ma) and Bruchinae are biased; the discrepancies in dates underline the need for further studies on the timing of chrysomelid diversification. Such studies will also provide more precise estimates for the age of bruchine beetles, through the use of multiple external calibration points (as opposed to the use of only one fossil constraint in our study).

4.3. Origin and diversification of Spermophagus beetles

With an origin estimated at ca. 60 Ma the genus *Spermophagus* is a relatively ancient lineage within Bruchinae, and now occupies all major biogeographic regions in the Old World. Regarding model selection, the fact that a DEC + J model was selected is consistent with the observation of Matzke (2014), who found out that biogeographic studies that treat major landmasses as areas, with most species endemic to a single area, are usually better fitted by the

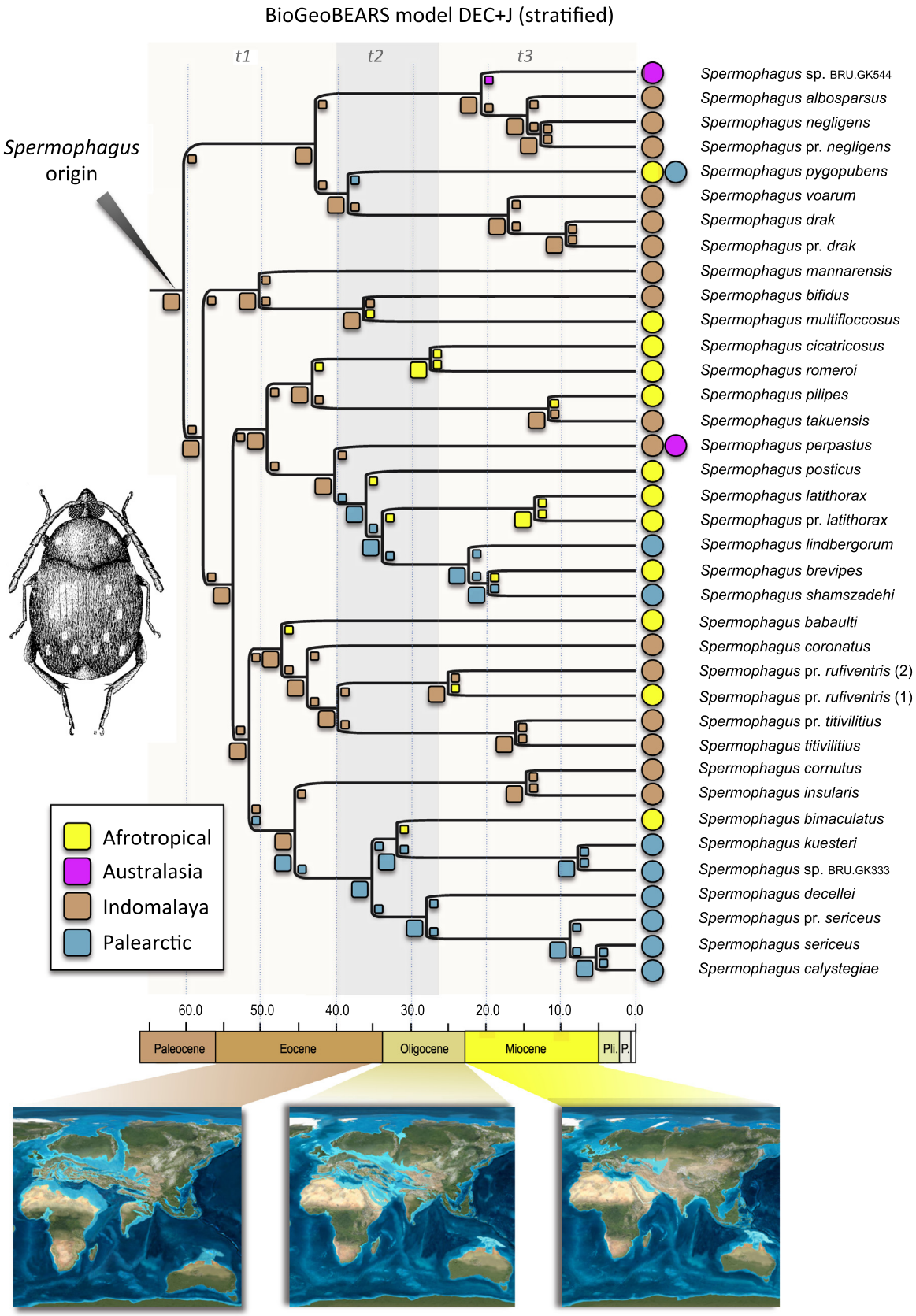

Fig. 3. Historical biogeography of *Spermophagus* as inferred by ancestral area reconstructions carried out by the DEC + J model of BioGeoBEARS with three stratified time slices (*t*1, *t*2 and *t*3). For each node the most likely ancestral geographic range is shown on the left (ranges that correspond to combinations of multiple areas are represented by using several colored squares). Smaller squares on corners represent the ancestral areas just after speciation. On the left side, a drawing of *Spermophagus titivilitius* is figured for illustrative purpose (drawing was reproduced with the kind authorization of Lech Borowiec). The paleomaps on the bottom of the figure are courtesy of Ron Blakey, Colorado Plateau Geosystems. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

DEC + J model. The corresponding biogeographic analysis suggests an origin in the Indomalaya region, which currently constitutes the second most species-rich biogeographic region for the genus (48 known Indomalayan species versus 53 Afrotropical species). From there a quite dynamic pattern is inferred with multiple independent colonizations of the adjacent Palearctic and Afrotropic regions during the Eocene and the Oligocene. The diversification of the two clades that include most of the species in temperate climates coincided with the major cooling event that occurred at the Eocene–Oligocene boundary (Liu et al., 2009). The biogeographic analyses tend to support the hypothesis of a recent colonization of the Australasian from the Indomalaya, but it is not possible to provide more accurate estimates on this point, especially for *S. perpastus* (Lea) whose MRCA is about 40 Ma old. Yet, the fact that only two indigenous species (including apparently new species in Timor) are known from the Australasian region, supports the hypothesis of a late colonization of the Australasian region by multiple derived seed beetle lineages. However at least one isolated and therefore probably old bruchine lineage exists in Australia (Reid and Beatson, 2013), so others may occur there.

Our biogeographic reconstructions rely on an incomplete phylogeny, which only encompasses one third of the known *Spermophagus* diversity. Biogeographic reconstructions can be adversely affected by missing taxa (Turner et al., 2009), therefore the inferred biogeographic pattern for *Spermophagus* should only be considered as a first step toward a biogeographic history for the genus. Nonetheless, more complete sampling is likely to yield a comparable result, because the current sampling is already quite representative of the diversity of the genus (species from 15 of the 20 known species groups, most of which are biogeographically

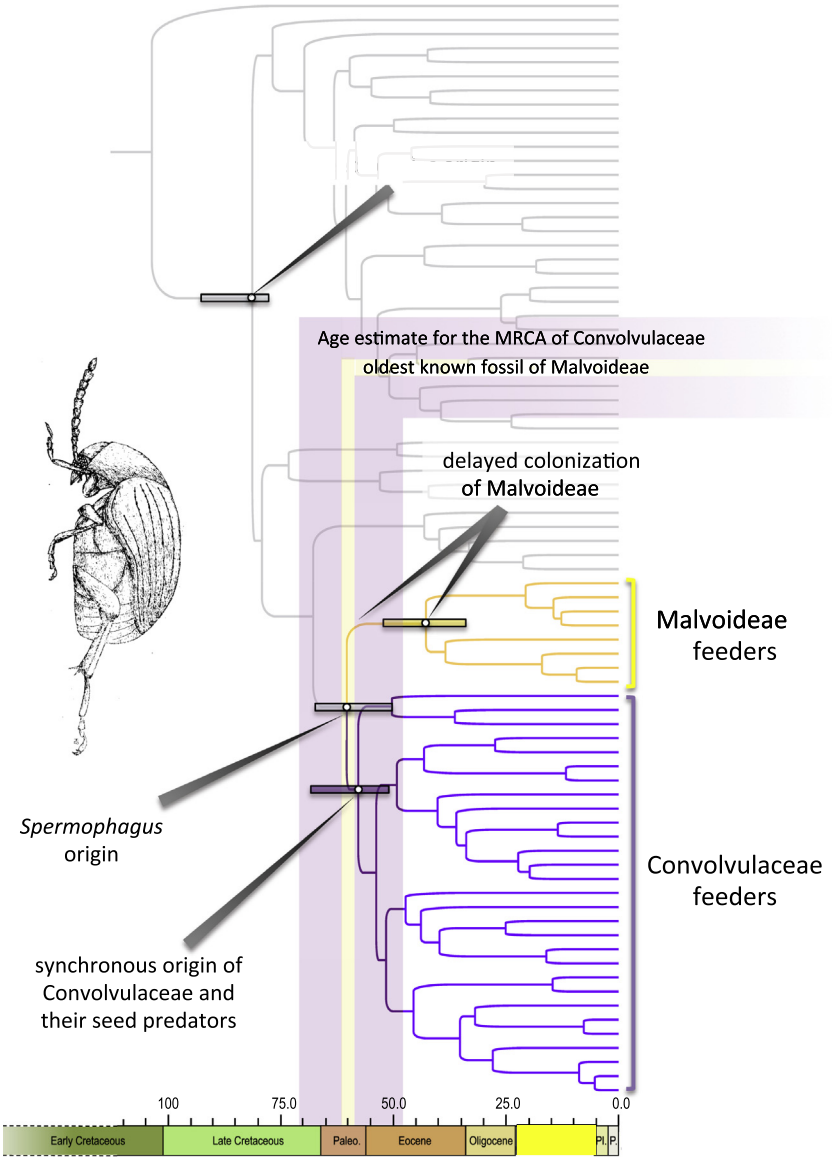

Fig. 4. Timing of diversification of *Spermophagus* seed beetles. The dated phylogeny corresponds to the result of the best-fit calibration procedure that relies on an exponential priori distribution for its fossil constraint. For more clarity, a focus is putted on the respective diversifications of *Spermophagus* feeding on Malvoideae (in yellow) or on *Convolvulaceae* (in purple). An error bar corresponding to the 95% highest probability density is figured at the origin of each *Spermophagus* clade. For comparison purpose we also figure the 95% highest probability density for the age estimate of the MRCA of Convolvulaceae from the study of Eserman et al. (2014), which suggests a synchronous origin of Convolvulaceae and their seed predator. As for Malvoideae, we also provide a conservative minimum bound for the MRCA of the group, which corresponds to the age of the oldest know fossil of the group (Carvalho et al., 2011). The latter suggests a potential delayed colonization of Malvoideae by their specialized seed predators. Finally on the left side is figured a drawing of *Spermophagus* (reproduced with the kind authorization of Lech Borowiec). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

constrained, and balanced sampling of species from all four biogeographic areas) (Table S1).

4.4. Pattern and timing of host colonization

Evolution of host associations in *Spermophagus* is comparable to those inferred in legume-feeding bruchine species: a marked trend toward conservatism of host use with one clade specializing on Convolvulaceae and the other on Malvoideae. However, at the botanical tribe level, *Spermophagus* beetles appear less specialized, contrary to other seed beetle genera such as *Bruchus* or *Conicobruchus* (Kergoat et al., 2007, 2011). Of the 49 species for which host-plants are known, at least nine (18%) (*S. albosparsus*, *S. cornutus, S. latithorax, S. mannarensis, S. perpastus, S. posticus, S. romeroi*, *S. sophorae* and *S. titivilitius*) are able to develop in plants belonging to more than one tribe (Dichondreae and Ipomoeeae, Ipomoeeae and Merremieae or Hibisceae and Malveae). Host records for numerous species are missing or incomplete; therefore 18% is a conservative figure. Additional host-plant records will also allow us to investigate whether specific secondary metabolites are affecting host choice. Chemical specialization probably constitutes a major constraint on the evolution of host use in *Spermophagus* species, especially because both Convolvulaceae and Malvoideae possess a large array of toxic secondary compounds, such as alkaloids or flavonoids (Bohm, 1998; Eich, 2008).

Regarding the timing of host colonization, we recovered two contrasted patterns (Fig. 4). An older origin ca. 56–57 Ma was found for the clade including all the species that are associated with morning-glories. This median age is similar to age estimates for the origin of Convolvulaceae from two recent studies: an age of 54.1 Ma was recovered in the study of Zanne et al. (2014) whereas an age estimate of 55.3 Ma was found in the study of Eserman et al. (2014). The clade of *Spermophagus* that is specialized with Malvoideae diversified more recently, about 42 Ma. In this case, there is a clear discrepancy between the age of the seed beetle group and the minimum age of 58–60 Ma of the oldest known Malvoideae fossil. In addition the minimum age of Malvoideae falls far before the timeframe corresponding to the uncertainty of age estimates for the seed beetle clade (95% HPD of 34.3–52.1 or 34.3–50.2 Ma, depending on calibration settings) (Fig. 4).

To account for the apparent discrepancies in the timing of colonization of *Spermophagus* seed beetles on their host-plants, we postulate for the role of the respective biogeographic histories of insects and plants. *Spermophagus* apparently originated in the Indomalayan region, quickly colonizing all major Old World landmasses except for the Australasian region. The early and almost synchronous shift toward Convolvulaceae was favored by the origin of the latter in the Old World, possibly in the Afrotropical region, where the oldest unambiguous morning-glory fossils can be found (Eserman et al., 2014). In contrast, mallows apparently originated in the Western hemisphere, most likely in the Neotropical region which concentrates most of the early fossils of the group (Carvalho et al., 2011). Our results suggest that the time taken by mallows to reach the Old World may explain the delayed colonization of their associated seed predators.

4.5. Conclusion and perspectives

Through the reconstruction of the evolutionary history of a representative sample of *Spermophagus* species we have been able to highlight a phylogenetically conserved pattern of host use in a group of non-legume feeding seed beetles. Dating analyses indicate an early origin for the group, which nonetheless postdates by more than 20 Ma the diversification of the earliest known lineages of seed beetles at the end of the Mesozoic. Our biogeographic reconstructions suggest a dynamic pattern in the Old World, with an origin in Indomalaya and a late colonization of Australasia. The contrast between synchronicity of speciation of one clade and its hosts and the delayed colonization of hosts by the other clade of *Spermophagus* is best explained by the respective biogeographic histories of the two host-plant groups. Our work provides additional evidence for some phytophagous insect groups being rapidly able to colonize new host-plant groups (Kergoat et al., 2011).

Conflict of interest

No conflicts of interest were discovered.

Acknowledgments

We thank Alfried Vogler, Árpád Szentesi, Jessica Abbate and an anonymous reviewer for numerous comments and corrections on a previous version of the manuscript, Lech Borowiec for the communication of several papers on *Spermophagus* and the authorization to use several of his drawings of *Spermophagus* spp. and Alexandre Dehne Garcia for his help on the CBGP HPC computational platform. We also thank all the collaborators from the project 'Collecting and identifying insect's seed feeder and associated natural enemies in Iran' and the Research Institute of Forest and Rangelands of Iran for the corresponding financial support. Part of the sequencing was supported by the network "Bibliothèque du Vivant" funded by the CNRS, the Muséum National d'Histoire Naturelle, the INRA and the CEA (Centre National de Séquençage). Sequencing of new specimens was supported by the Plant Health and Environment Division of INRA (project INRA-SPE ADA-COM).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2015.04.014.

References

Abrahamson, W.G., Hunter, M.D., Melika, G., Price, P.W., 2003. Cynipid gall-wasp communities correlate with oak chemistry. J. Chem. Ecol. 29, 209–223.
Álvarez, N., Romero-Napoles, J., Anton, K.-W., Benrey, B., Hossaert-McKey, M., 2006. Phylogenetic relationsPlehips in the Neotropical bruchid genus *Acanthoscelides* (Bruchinae, Bruchidae, Coleoptera). J. Zool. Syst. Evol. Res. 44, 63–74.
Anton, K.-W., 1996. *Spermophagus borowieci* n. sp. from Pakistan (Coleoptera: Bruchidae: Amblycerinae). Genus – Int. J. Invert. Taxon. 7, 481–483.
Anton, K.-W., 1999a. Three new species of *Spermophagus* Schoenherr, 1833 from Thailand, with note on synonymy of *S. perpastus* (Lea) (Coleoptera: Bruchidae: Amblycerinae). Genus – Int. J. Invert. Taxon. 10, 73–80.
Anton, K.-W., 1999b. Description of *Spermophagus montanus* nov. spec. (Coleoptera, Bruchidae, Amblycerinae) from Laos. Linzer Biol. Beitr. 31, 651–654.
Anton, K.-W., Delobel, A., 2003. African species of the *Bruchidius centromaculatus* group with "eyed" female pygidium (Coleoptera: Bruchidae: Bruchinae). Genus – Int. J. Invert. Taxon. 14, 159–190.
Arora, G.L., 1977. Taxonomy of the Bruchidae (Coleoptera) of Northwest India. Orient. Insects, Supplement.
Baele, G., Li, W.L.S., Drummond, A.J., Suchard, M.A., Lemey, P., 2013. Accurate model selection of relaxed clocks in Bayesian phylogenetics. Mol. Biol. Evol. 30, 239–243.
Becerra, J.X., 1997. Insects on plants: macroevolutionary chemical trends in host use. Science 276, 253–256.
Becerra, J.X., 2003. Synchronous coadaptation in an ancient case of herbivory. Proc. Natl. Acad. Sci. USA 100, 12804–12807.
Bohm, B.A., 1998. Introduction to Flavonoids. Harwood Academic Publishers, Amsterdam, The Netherlands.
Borowiec, L., 1987. The genera of seed beetles (Coleoptera, Bruchidae). Polsk. Pismo Entomol. 57, 3–207.
Borowiec, L., 1991. Revision of the genus *Spermophagus* Schoenherr (Coleoptera, Bruchidae, Amblycerinae). Genus – Int. J. Invert. Taxon. (supplement), Wroclaw.
Borowiec, L., 1995. *Spermophagus atrispinus* n. sp. from India and Thailand (Coleoptera: Bruchidae: Amblycerinae). Genus – Int. J. Invert. Taxon. 6, 99–102.
Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Slipinski, S.A., Smith, A.B.T., 2011. Family-group names in Coleoptera (Insecta). ZooKeys 88, 1–972.

Brändle, M., Knoll, S., Eber, S., Stadler, J., Brandl, R., 2005. Flies on thistles: support for synchronous speciation? Biol. J. Linn. Soc. 84, 775–784.
Bridwell, J.C., 1932. The subfamilies of the Bruchidae (Coleoptera). Proc. Entomol. Soc. Wash. 34, 100–106.
Brower, A.V.Z., 1994. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. Proc. Natl. Acad. Sci. USA 91, 6491–6495.
Carvalho, M.R., Herrera, F.A., Jaramillo, C.A., Wing, S.L., Callejas, R., 2011. Paleocene Malvaceae from northern South America and their biogeographical implications. Am. J. Bot. 98, 1337–1355.
Ceotto, P., Kergoat, G.J., Rasplus, J.-Y., Bourgoin, T., 2008. Molecular phylogenetics of cixiid planthoppers (Hemiptera: Fulgoromorpha): New insights from combined analyses of mitochondrial and nuclear genes. Mol. Phylogenet. Evol. 48, 667–678.
Cruaud, A., Rønsted, N., Chantarasuwan, B., Chou, L.S., Clement, W.L., Couloux, A., Cousins, B., Genson, G., Harrison, R.D., Hanson, P.E., Hossaert-McKey, M., Jabbour-Zahab, R., Jousselin, E., Kerdelhué, C., Kjellberg, F., Lopez-Vaamonde, C., Peebles, J., Peng, Y.Q., Pereira, R.A., Schramm, T., Ubaidillah, R., van Noort, S., Weiblen, G.D., Yang, D.R., Yodpinyanee, A., Libeskind-Hadas, R., Cook, J.M., Rasplus, J.-Y., Savolainen, V., 2012. An extreme case of plant-insect codiversification: figs and fig-pollinating wasps. Syst. Biol. 61, 1029–1047.
Delobel, A., 2008. The genus *Spermophagus* in Vietnam: biological data and description of three new species (Coleoptera: Chrysomelidae: Bruchinae: Amblycerini). Genus – Int. J. Invert. Taxon. 19, 201–211.
Delobel, A., 2010. Seed beetles associated with Desmodieae in Vietnam (Coleoptera: Chrysomelidae: Bruchinae). Genus – Int. J. Invert. Taxon. 21, 513–533.
Delobel, A., Anton, K.-W., 2011. New data on *Spermophagus* from Vietnam, with the description of a new species (Coleoptera: Chrysomelidae: Bruchinae: Amblycerini). Genus – Int. J. Invert. Taxon. 22, 261–270.
Delobel, A., Delobel, B., 2003. Les plantes-hôtes des bruches (Coleoptera, Bruchidae) de la faune de France, une analyse critique. Bull. Mens. Soc. Linn. Lyon 72, 199–221.
Delobel, B., Delobel, A., 2006. Dietary specialization in European species groups of seed beetles (Coleoptera: Bruchidae: Bruchinae). Oecologia 149, 428–443.
Delobel, A., Legalov, A., 2009. A new species of *Kytorhinus* Fisch. – Wald. from Western Pamir (Coleoptera: Bruchinae). Genus – Int. J. Invert. Taxon. 20, 71–76.
Delobel, A., Sadeghi, S.E., 2013. Remarks on the *Spermophagus rufipes* species group, with the description of a new species from Iran (Coleoptera: Chrysomelidae: Bruchinae: Amblycerini). Genus – Int. J. Invert. Taxon. 24, 309–314.
Delobel, A., Anton, K.-W., Kergoat, G.J., 2004. New data on European *Astragalus*-feeding *Bruchidius*, with the description of a new species from Southern Italy (Coleoptera: Bruchidae: Bruchinae). Genus – Int. J. Invert. Taxon. 15, 173–185.
Delobel, A., Anton, K.-W., Le Ru, B.P., Kergoat, G.J., 2013. Morphology, biology and phylogeny of African seed beetles belonging to the *Bruchidius ituriensis* species group (Coleoptera: Chrysomelidae: Bruchinae). Genus – Int. J. Invert. Taxon. 24, 39–63.
Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973.
Eberth, D.A., Hambin, A.P., 1993. Tectonic, stratigraphic and sedimentological significance of a regional discontinuity in the Judith River Group (Belly River Wedge) of southern Alberta, Saskatchewan and northern Montana. Can. J. Earth Sci. 30, 174–200.
Eich, E., 2008. Solanaceae and Convolvulaceae: Secondary Metabolites. Springer, Berlin.
Erixon, P., Svennblad, B., Britton, T., Oxelman, B., 2003. Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. Syst. Biol. 52, 665–673.
Eserman, L.A., Tiley, G.P., Jarret, R.L., Leebens-Mack, J.H., Miller, R.E., 2014. Phylogenetics and diversification of morning glories (tribe Ipomeeae, Convolvulaceae) based on whole plastome sequences. Am. J. Bot. 101, 92–103.
Farrell, B.D., 2001. Evolutionary assembly of the milkweed fauna: cytochrome oxidase I and the age of *Tetraopes* beetles. Mol. Phylogenet. Evol. 18, 467–478.
Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., Garcia-del-Rey, E., Arévalo, J.R., Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forest. J. Biogeogr. 38, 226–246.
Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialization. Ann. Rev. Ecol. Syst. 19, 207–233.
Gómez-Zurita, J., Hunt, T., Kopliku, F., Vogler, A., 2007. Recalibrated tree of leaf beetles (Chrysomelidae) indicates independent diversification of angiosperms and their insect herbivores. PLoS ONE 2, e360.
Grimaldi, D., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press.
Hillis, D.M., Bull, J.J., 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst. Biol. 42, 182–192.
Ho, S.Y.W., Phillips, M.J., 2009. Accounting for calibration uncertainties in phylogenetic estimation of evolutionary divergence times. Syst. Biol. 58, 367–380.
Huelsenbeck, J.P., Larget, B., Alfaro, M.E., 2004. Bayesian phylogenetic model selection using reversible jump Markov chain Monte Carlo. Mol. Biol. Evol. 21, 1123–1133.
Hunt, T., Bergsten, J., Levkaničová, Z., Papadopoulou, A., St. John, O., Wild, R., Hammond, P.M., Ahrens, D., Balke, M., Caterino, M.S., Gómez-Zurita, J., Ribera, I., Barraclough, T.G., Bocakova, M., Bocak, L., Vogler, A.P., 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science 318, 1913–1916.
Janzen, D.H., 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. J. Ecol. 68, 929–952.
Jermy, T., Szentesi, Á., 2003. Evolutionary aspects of host plant specialization – a study on bruchids (Coleoptera: Bruchidae). Oikos 101, 196–204.
Johnson, C.D., 1981. Seed beetle host specificity and the systematics of the Leguminosae. In: Polhill, R.M., Raven, P.H. (Eds.), Advances in Legume Systematics. The Royal Botanic Gardens, Kew, pp. 995–1027.
Johnson, C.D., 1989. Adaptive radiation of Acanthoscelides in seeds: examples of legume-bruchid interactions. In: Stirton, I.C.H., Zarucchi, J.L. (Eds.), Advances in Legume Biology, Monograph in Systematic Botany from the Missouri Botanical Garden, St Louis, MO, pp. 747–779.
Johnson, C.D., Romero, J., 2004. A review of evolution of oviposition guilds in the Bruchidae (Coleoptera). Rev. Bras. Entomol. 48, 401–408.
Johnson, C.D., Southgate, B.J., Delobel, A., 2004. A revision of the Caryedontini (Coleoptera: Bruchidae: Pachymerinae) of Africa and the Middle East. Mem. Am. Entomol. Soc. 44, 1–120.
Kass, R.E., Raftery, A.E., 1995. Bayes factors. J. Am. Stat. Assoc. 90, 773–795.
Kato, T., Bonet, A., Yoshitake, H., Romero-Nápoles, J., Jinbo, U., Ito, M., Shimada, M., 2010. Evolution of host utilization patterns in the seed beetle genus *Mimosestes* Bridwell (Coleoptera: Chrysomelidae: Bruchinae). Mol. Phylogenet. Evol. 55, 816–832.
Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30, 772–780.
Kelley, S.T., Farrell, B.D., 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). Evolution 52, 1731–1743.
Kergoat, G.J., Delobel, A., Silvain, J.-F., 2004. Phylogeny and host-specificity of European seed beetles (Coleoptera, Bruchidae), new insights from molecular and ecological data. Mol. Phylogenet. Evol. 32, 855–865.
Kergoat, G.J., Álvarez, N., Hossaert-McKey, M., Faure, N., Silvain, J.-F., 2005a. Parallels in the evolution of the two largest New and Old World seed beetle genera (Coleoptera, Bruchidae). Mol. Ecol. 14, 4003–4021.
Kergoat, G.J., Delobel, A., Fédière, G., Le Ru, B., Silvain, J.-F., 2005b. Both host-plant phylogeny and chemistry have shaped the African seed beetle radiation. Mol. Phylogenet. Evol., 602–611
Kergoat, G.J., Delobel, P., Delobel, A., 2007a. Phylogenetic relationships of a new species of seed beetle infesting *Cercis siliquastrum* L. in China and in Europe (Coleoptera: Chrysomelidae: Bruchinae: Bruchini). Ann. Soc. Entomol. Fr. 43, 265–271.
Kergoat, G.J., Silvain, J.-F., Buranapanichpan, S., Tuda, M., 2007b. When insects help to resolve plant phylogeny: evidence for a paraphyletic genus *Acacia* from the systematics and host-plant range of their seed-predators. Zool. Scr. 36, 143–152.
Kergoat, G.J., Silvain, J.-F., Delobel, A., Tuda, M., Anton, K.-W., 2007c. Defining the limits of taxonomic conservatism in host-plant use for phytophagous insects: molecular systematics and evolution of host-plant associations in the seed beetle genus *Bruchus* Linnaeus (Coleoptera: Chrysomelidae: Bruchinae). Mol. Phylogenet. Evol. 43, 251–269.
Kergoat, G.J., Delobel, A., Le Ru, B., Silvain, J.-F., 2008. Seed beetles in the age of the molecule: recent advances on systematics and host-plant association patterns. In: Jolivet, P., Santiago-Blay, J., Schmitt, M. (Eds.), Research on Chrysomelidae. Brill. 1, 59–96, 376–378.
Kergoat, G.J., Le Ru, B.P., Genson, G., Cruaud, C., Couloux, A., Delobel, A., 2011. Phylogenetics, species boundaries and timing of resource tracking in a highly specialized group of seed beetles (Coleoptera: Chrysomelidae: Bruchinae). Mol. Phylogenet. Evol. 59, 746–760.
Kergoat, G.J., Bouchard, P., Clamens, A.-L., Abbate, J.L., Jourdan, H., Zahab, R., Genson, G., Soldati, L., Condamine, F.L., 2014a. Cretaceous environmental changes led to high turnovers and decreases in diversification rates in a hyperdiverse non-phytophagous beetle family. BMC Evol. Biol. 14, 220.
Kergoat, G.J., Soldati, L., Clamens, A.-L., Jourdan, H., Zahab, R., Genson, G., Bouchard, P., Condamine, F.L., 2014b. Higher-level molecular phylogeny of darkling beetles (Coleoptera, Tenebrionoidea, Tenebrionidae). Syst. Entomol. 39, 486–499.
Kingsolver, J.M., 1970. A synopsis of the subfamily Amblycerinae Bridwell in the West Indies, with descriptions of new species (Coleoptera: Bruchidae). Trans. Amer. Entomol. Soc. 96, 469–497.
Kingsolver, J.M., 2004. Handbook of the Bruchidae of the United States and Canada (Insecta, Coleoptera). Volume 1. United States Department of Agriculture, Agricultural Research Service, Technical Bulletin Number 1912.
Kingsolver, J.M., Johnson, C.D., 1978. Systematics of the genus *Mimosestes* (Coleoptera: Bruchidae). United States Department of Agriculture, Agricultural Research Service, Technical Bulletin, 1590.
Koopman, M.M., Baum, D.A., 2008. Phylogeny and biogeography of tribe Hibisceae (Malvaceae) on Madagascar. Syst. Bot. 33, 364–374.
Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon, S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29, 1695–1701.
Le Ru, B.P., Delobel, A., György, Z., Genson, G., Kergoat, G.J., 2014. Taxonomy, host-plant associations and phylogeny of African Crotalaria-feeding seed beetles (Coleoptera, Chrysomelidae, Bruchinae): the Conicobruchus strangulatus (Fåhraeus) species group. Zootaxa 3895, 238–256.
Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Syst. Biol. 50, 913–925.

Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S.R., Leckie, R.M., Pearson, A., 2009. Global cooling during the Eocene–Oligocene climate transition. Science 323, 1187–1190.
Lopez-Vaamonde, C., Wikström, N., Labandeira, C., Godfray, H.C.J., Goodman, S.J., Cook, J.M., 2006. Fossil-calibrated molecular phylogenies reveal that leaf-mining moths radiated millions of years after their host-plants. J. Mol. Evol. 19, 1314–1326.
Matzke, N., 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. Syst. Biol. 63, 951–970.
McKenna, D.D., Sequeira, A.S., Marvaldi, A.E., Farrell, B.D., 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. Proc. Natl. Acad. Sci. USA 106, 7083–7088.
McLeish, M.J., Miller, J.T., Mound, L.A., 2013. Delayed colonisation of Acacia by thrips and the timing of host-conservatism and behavioural specialisation. BMC Evol. Biol. 13, 188.
Morse, G.E., 2003. Ecological and Evolutionary Diversification in Seed Beetles (Coleoptera: Bruchinae), Ph.D., Harvard University, Cambridge, MA.
Morse, G.E., Farrell, B.D., 2005. Ecological and evolutionary diversification of the seed beetle genus *Stator* (Coleoptera: Chrysomelidae: Bruchinae). Evolution 59, 1315–1333.
Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P., Nieves-Aldrey, J.L., 2004. Bayesian phylogenetic analysis of combined data. Syst. Biol. 53, 47–67.
Nyman, T., 2010. To speciate, or not to speciate? Resource heterogeneity, the subjectivity of similarity, and the macroevolutionary consequences of niche width shifts in plant-feeding insects. Biol. Rev. 85, 393–411.
Olmstead, R.G., 2013. Phylogeny and biogeography in Solanaceae, Verbenaceae and Bignoniaceae: a comparison of continental and intercontinental diversification patterns. Bot. J. Linn. Soc. 171, 80–102.
Poinar Jr., G., 1999. Chrysomelidae in fossilized resin: behavioural inferences. In: Cox, M.L. (Ed.), Advances in Chrysomelidae Biology. Blackhuys Publishers, Leiden, The Netherlands, pp. 1–16.
Poinar Jr., G., 2005. A Cretaceous palm bruchid, *Mesopachymerus antiqua*, n. gen., n. sp. (Coleoptera: Bruchidae: Pachymerini) and biogeographical implications. Proc. Entomol. Soc. Wash. 107, 392–397.
Posada, D., Buckley, T.R., 2004. Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. Syst. Biol. 53, 793–808.
Ree, R.H., Smith, S.A., 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Syst. Biol. 57, 4–14.
Ree, R.H., Moore, B.R., Webb, C.O., Donoghue, M.J., 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Syst. Biol. 59, 2299–2311.
Reid, C.A.M., 1992. The leaf-beetle genus *Microdonacia* Blackburn (Coleoptera: Chrysomelidae: Galerucinae): revision and systematic placement. Syst. Entomol. 17, 359–387.
Reid, C.A.M., 1995. A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu lato (Chrysomeloidea). In: Pakaluk, J., Slipinski, S.A. (Eds.), Biology, phylogeny and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson, Muzeum i Instytut Zoologii PAN, Warszawa, pp. 559–631.
Reid, C.A.M., 2000. Spilopyrinae Chapuis: a new subfamily in the Chrysomelidae and its systematic placement (Coleoptera). Invert. Tax. 14, 837–862.
Reid, C.A.M., Beatson, M., 2013. A new genus and species of Bruchinae, with a key to the genera from Australia (Coleoptera: Chrysomelidae). Zootaxa 3599, 535–548.
Romero, J., Johnson, C.D., 2003. Revision of the genus *Neltumius* Bridwell (Coleoptera: Bruchidae). Coleopt. Bull. 57, 219–236.
Romero, J., Johnson, C.D., Kingsolver, J.M., 1996. Revision of the Genus *Amblycerus* of the United States and Mexico (Coleoptera: Bruchidae: Amblycerinae). United States Department of Agriculture, Agricultural Research Service, Technical Bulletin, 1845.
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542.
Sanmartín, I., Ronquist, F., 2004. Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. Syst. Biol. 53, 216–243.
Sanmartín, I., Enghoff, H., Ronquist, F., 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. 2001. Biol. J. Linn. Soc. 73, 345–390.
Sauquet, H., Ho, S.Y.W., Gandolfo, M.A., Jordan, G.J., Wilf, P., Cantrill, D.J., Bayly, M.J., Bromham, L., Brown, G.K., Carpenter, R.J., Lee, D.M., Murphy, D.J., Sniderman, J.M.K., Udovicic, F., 2012. Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). Syst. Biol. 61, 289–313.
Schluter, D., Price, T., Mooers, A.O., Ludwig, D., 1997. Likelihood of ancestor states in adaptive radiation. Evolution 51, 1699–1711.
Schmitt, M., 1988. The Criocerinae: biology, phylogeny and evolution. In: Jolivet, P., Petitpierre, E., Hsiao, T.H. (Eds.), Biology of the Chrysomelidae. Springer, Netherlands, pp. 475–495.
Scudder, S.H., 1876. Fossil Coleoptera from the Rocky Mountain Tertiaries. Bull. U.S. Geol. Geogr. Surv. Terr. 2, 77–87.
Sequeira, A.S., Normark, B.B., Farrell, B.D., 2000. Evolutionary assembly of the conifer fauna: distinguishing between ancient from recent associations in bark beetles. Philos. Trans. Roy. Soc. B 267, 2359–2366.
Southgate, B.J., 1979. Biology of the bruchidae. Ann. Rev. Entomol. 24, 449–473.
Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312–1313.
Tuda, M., 2007. Applied evolutionary ecology of insects of the subfamily Bruchinae (Coleoptera: Chrysomelidae). Appl. Entomol. Zool. 42, 337–346.
Tuda, M., 2011. Evolutionary diversification of bruchine beetles: climate-dependent traits and development associated with pest status. Bull. Entomol. Res. 101, 415–422.
Tuda, M., Chou, L.-Y., Niyomdham, C., Buranapanichpan, S., Tateishi, Y., 2005. Ecological factors associated with pest status in *Callosobruchus* (Coleoptera: Bruchidae): high host specificity of non-pests to Cajaninae (Fabaceae). J. Stored Prod. Res. 41, 31–45.
Tuda, M., Ronn, J., Buranapanichpan, S., Wasano, N., Arnqvist, G., 2006. Evolutionary diversification of the bean beetle genus *Callosobruchus* (Coleoptera: Bruchidae): traits associated with stored-product pest status. Mol. Ecol. 15, 3541–3551.
Turner, A.H., Smith, N.D., Callery, J.A., 2009. Gauging the effects of sampling failure in biogeographical analysis. J. Biogeogr. 36, 612–625.
Udayagiri, S., Wadhi, S.R., 1989. Catalog of Bruchidae. Mem. Am. Entomol. Inst. 45, 1–301.
Wickham, H.F., 1914. New Miocene Coleoptera from Florissant. Bull. Mus. Comp. Zool. 53, 423–494.
Zacher, F., 1952. Die nährpflanzen der Samenkäfer. liste 1: Verzeichnis der von den einzelnen Bruchiden Arten befallenen nährpflanzen. Zeit. Angew. Entomol. 33, 460–482.
Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G., McGlinn, D.J., O'Meara, B.C., Moles, A.T., Reich, P.B., Royer, D.L., Soltis, D.E., Stevens, P.F., Westoby, M., Wright, I.J., Aarssen, L., Bertin, R.I., Calaminus, A., Govaerts, R., Hemmings, F., Leishman, M.R., Oleksyn, J., Soltis, P.S., Swenson, N.G., Warman, L., Beaulieu, J.M., 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506, 89–92.