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ORIGINAL ARTICLE

Biogeography and diversification of colletid bees (Hymenoptera: Colletidae): emerging patterns from the southern end of the world

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ABSTRACT

Aim The evolutionary history of bees is presumed to extend back in time to the Early Cretaceous. Among all major clades of bees, Colletidae has been a prime example of an ancient group whose Gondwanan origin probably precedes the complete break-up of Africa, Antarctica, Australia and South America, because modern lineages of this family occur primarily in southern continents. In this paper, we aim to study the temporal and spatial diversification of colletid bees to better understand the processes that have resulted in the present southern disjunctions.

Location Southern continents.

Methods We assembled a dataset comprising four nuclear genes of a broad sample of Colletidae. We used Bayesian inference analyses to estimate the phylogenetic tree topology and divergence times. Biogeographical relationships were investigated using event-based analytical methods: a Bayesian approach to dispersal–vicariance analysis, a likelihood-based dispersal–extinction–cladogenesis model and a Bayesian model. We also used lineage through time analyses to explore the tempo of radiations of Colletidae and their context in the biogeographical history of these bees.

Results Initial diversification of Colletidae took place at the Late Cretaceous (≥ 70 Ma). Several (6–14) lineage exchanges between Australia and South America via Antarctica during the Late Cretaceous and Eocene epochs could explain the disjunctions observed between colletid lineages today. All biogeographical methods consistently indicated that there were multiple lineage exchanges between South America and Australia, and these approaches were valuable in exploring the degree of uncertainty inherent in the ancestral reconstructions. Biogeographical and dating results preclude an explanation of Scrapterinae in Africa as a result of vicariance, so one dispersal event is assumed to explain the disjunction in relation to Euryglossinae. The net diversification rate was found to be highest in the recent history of colletid evolution.

Main conclusions The biogeography and macroevolutionary history of colletid bees can be explained by a combination of Cenozoic vicariance and palaeoclimatic changes during the Neogene. The austral connection and posterior break-up of South America, Antarctica and Australia resulted in a pattern of disjunct sister lineages. Increased biome aridification coupled with floristic diversification in the southern continents during the Neogene may have contributed to the high rates of cladogenesis in these bees in the last 25–30 million years.

Keywords

Antarctica, Apoidea, Australia, event-based methods, Gondwana, historical biogeography, macroevolution, palaeoclimatology, South America.

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INTRODUCTION

The set of events that resulted in the complete break-up of the supercontinent Gondwana took place between 160 and 30 million years ago (Ma), and resulted in the separation of Africa, Antarctica, Australia, India, Madagascar, New Zealand and South America. Proper understanding of the sequence and timing of geological events associated with the break-up of the southern continents (e.g. Scotese *et al.*, 1988; Lawver *et al.*, 1992; Briggs, 1995; McLoughlin, 2001; Scotese, 2001; Jokat *et al.*, 2003) is crucial for interpreting biogeographical histories of biological taxa (e.g. Sanmartín & Ronquist, 2004). Sister taxa occurring in Africa and South America are potentially older than those only occurring in Australia and South America because the connection between the former was interrupted during the mid-Cretaceous (e.g. Tarling, 1971; Jardine & McKenzie, 1972; Scotese *et al.*, 1988; Lawver *et al.*, 1992; McLoughlin, 2001; Jokat *et al.*, 2003), whereas the connection between Australia and South America via Antarctica allowed biotic interchanges until the late Eocene (McLoughlin, 2001). Overall, the geological history of Gondwana is viewed as complex and still insufficiently understood in some respects (reviewed by McCarthy *et al.*, 2007; Upchurch, 2008), but it is widely accepted that geological events related to the break-up of Gondwana added geographical barriers in a stepwise manner (e.g. Cracraft, 2001; Sequeira & Farrell, 2001; Upchurch *et al.*, 2002; Sanmartín & Ronquist, 2004).

Several animal and plant taxa exhibit distributional patterns indicating that their biogeography and diversification were influenced by Gondwanan fragmentation (e.g. Croizat, 1962; Brundin, 1966; Raven & Axelrod, 1974; Schlinger, 1974; Cracraft, 1975; Crisci *et al.*, 1991; Sequeira & Farrell, 2001; Sanmartín & Ronquist, 2004). The plant family Proteaceae has related genera in South America and Africa that probably diverged prior to the separation of the two continents during the Late Cretaceous (Barker *et al.*, 2007). Other groups of Proteaceae occur in South America but have their closest relatives in Australia, indicating the importance of the Antarctic connection between Australia and South America during the Cretaceous and continuing through the Eocene (Barker *et al.*, 2007). Based on phylogenetic evidence, Cracraft (2001) proposed that various bird lineages originated in the southern continents either before the initial stages of Gondwanan break-up (early diverging lineages, such as ratite birds), or before the full separation of Antarctica, Australia and South America (more derived lineages such as the Passeriformes).

The plant genus *Nothofagus* (Nothofagaceae), the southern beeches, constitutes a prime example of diversification on southern continents during the period when Antarctica was connected to Australia and South America and the average temperatures were warm even in high latitudes (e.g. Schlinger, 1974). Antarctica was covered with a lush subtropical–temperate rain forest, of which the southern beeches were a dominant component (Hill & Scriven, 1995; Iglesias *et al.*, 2011), similar to some of the forests found in Patagonia, Tasmania and New Zealand at the present time (Thorne, 1986; Swenson *et al.*, 2001). Another classic biogeographical case of austral distributions is the distribution of midges or chironomid flies (Brundin, 1966). These insects occur in southern Africa, South America, New Zealand, Australia and nearby islands. The phylogenetic study of Chironomidae allowed further investigation of the vicariant history for the group in southern continents, which dates back to at least the Cretaceous. Brundin's research was pivotal for explaining the relevance of Southern Hemisphere biogeographical patterns (e.g. Brundin, 1966). These biogeographical connections are made even more interesting by the fact that insects (e.g. Schlinger, 1974; Sequeira & Farrell, 2001) and fungi (Peterson *et al.*, 2010) are associated with groups of plants typical of southern continents (e.g. *Nothofagus* and the conifer genus *Araucaria*) and possibly had congruent biogeographical histories with them.

The land bridge formed by Antarctica connecting South America to Australia affected the histories of a number of taxa, whose species were distributed throughout a southern temperate biogeographical province (denominated the 'Weddellian Province' by Case, 1989), and later fragmented by the separation of these continents. Darlington (1965) made a formidable attempt to systematize and promote case studies that exemplify patterns found in the 'southern end of the world' – as he referred to this biogeographical province. These concordant distributional patterns have been identified by a number of biogeographers (e.g. trans-Antarctic patterns; Cracraft, 2001). Congruent patterns of ocean-wide disjunctions strongly suggest common palaeogeological causes, but biogeographical studies can illuminate whether they ultimately share common causal mechanisms.

Bees, a major clade within Hymenoptera with almost 20,000 described species, are presumed to have arisen during the Early to mid-Cretaceous coincident with the fragmentation of the southern continents (Michener, 1979, 2007; Engel, 2001a, 2004; Poinar & Danforth, 2006; Brady *et al.*, 2009). Two groups of bees share an early biogeographical history associated with the break-up of Africa and South America in the mid-Cretaceous – Halictidae (particularly the Rophitinae; Danforth *et al.*, 2004) and Megachilidae (particularly the Fideliini; Litman *et al.*, 2011). Two other bee families show a close association with just one of the southern continents: Andrenidae with South America and Melittidae with Africa (e.g. Ascher, 2004; Michener, 2007; Michez *et al.*, 2010).

The bee family Colletidae is represented by a clade of approximately 2500 species distributed world-wide, but with a distinct pattern of endemism and greatest diversity in southern continents. Colletid bees have long been thought to be a 'Gondwanan' group because the centres of subfamily diversity are all in the southern continents: the Australian region, southern Africa and southern South America. There are only two widespread genera, *Colletes* (Colletinae) and *Hylaeus* (Hylaeinae), and in both cases it is quite clear that their current distribution is secondary as they are closely related to lineages in the southern continents (Michener, 1979; Kuhlmann *et al.*, 2009; P. Kayaalp & M. Schwarz, pers. comm.). There are only two known fossils of Colletidae, both belonging to the subfamily Xeromelissinae and relatively recent in age (from late Oligocene–early Miocene Dominican amber; Michener & Poinar, 1996; Engel, 1999). Neither the past distribution of colletid bees nor the ages of their subfamilies can be reliably inferred from the fossil record for this family alone (Engel, 1999).

The current distribution of Colletidae appears to reflect the break-up of Gondwana 110 Ma or later, because this is the approximate time when Africa, Australia, South America were last connected. No endemic colletid genus currently inhabits India and Madagascar, nor is there any fossil evidence that they did so in the past. This indicates that the biogeographical history of Colletidae is probably better explained by a more recent scenario than the rifting of the Indian plate away from East Gondwana during the Jurassic (*c.* 165–150 Ma; Scotese *et al.*, 1988).

A phylogenetic hypothesis for the Colletidae on a worldwide basis was not available until recently (Almeida & Danforth, 2009), hampering attempts at inferences about the biogeographical history of these bees. This is the first study to offer a biogeographical scenario for colletid diversification in time and space, aiming to understand the processes that have resulted in the present disjunctions of these bees in the southern continents. This biogeographical investigation is further complemented by a discussion of palaeoclimatic and palaeovegetational data from the late Mesozoic through the Cenozoic of the southern continents in the context of colletid diversification.

MATERIALS AND METHODS

Classification

The classification in this paper follows Almeida (2008a) and Almeida & Danforth (2009), the only difference being the use of the subfamily name Neopasiphaeinae Cockerell, 1930 to refer to all taxa in Paracolletinae Cockerell, 1934, except *Paracolletes* Smith, 1853 (see Appendix 1). According to the classification that we adopt here, Colletidae is subdivided into eight subfamilies: Colletinae s. str., Callomelittinae, Diphaglossinae, Euryglossinae, Hylaeinae, Neopasiphaeinae, Scrapterinae and Xeromelissinae; *Paracolletes* is left as *incertae sedis* within Colletidae, not being assigned to any subfamily (despite its clear proximity to Diphaglossinae).

Phylogenetic and dating analyses

Phylogenetic relationships and divergence time estimation were inferred in a Bayesian framework using BEAST 1.5.4 by employing an uncorrelated lognormal relaxed clock model (Drummond *et al.*, 2006; Drummond & Rambaut, 2007). The molecular dataset comprised 123 species of Colletidae plus 22 outgroup taxa (Andrenidae, Halictidae and Stenotritidae) for 4770 aligned nucleotide characters from four nuclear genes: elongation factor 1 alpha (EF-1α F2), long-wavelength rhodopsin (opsin), wingless and 28S rRNA. Further details on how this dataset was assembled are provided in Appendix S1 in Supporting Information. Substitution and clock models were unlinked among partitions with the underlying trees linked. A Yule speciation process with a random starting tree was used for the tree prior. Lognormal or normal a priori age distributions (in Ma) were assigned to three nodes. Minimum ages for the two lognormal priors are based on stem group calibrations using constituent taxa from the fossil record. The common ancestor of *Xenochilicola mamigna* and *Chilicola* spp., a robust clade within the Neotropical subfamily Xeromelissinae (Almeida *et al.*, 2008; Almeida & Danforth, 2009), was given a lognormal prior of log(mean) = 2.708, log(SD) = 0.421, offset = 15 (equivalent to a minimum bound of 15 Ma, median value of 30 Ma, and a 95% quantile of 45 Ma) based on *Chilicola* (*Hylaeosoma*) *gracilis* Michener & Poinar, 1996 and *Chilicola* (*Hylaeosoma*) *electrodominicana* Engel, 1999 fossils from Dominican amber (Michener & Poinar, 1996; Engel, 1999). The stem group node of Halictini was given a lognormal prior age distribution of log(mean) = 2.565, log(SD) = 0.347, offset = 42 (equivalent to a minimum bound of 42, median value of 55 Ma, and a 95% quantile of 65 Ma) based on the Baltic amber fossil *Electrolictus antiquus* (Engel, 2001a) and the results of divergence dating and biogeographical analyses within Halictidae (Danforth *et al.*, 2004). The crown group node for the family Halictidae was given a normal prior age distribution of mean = 100, SD = 18 (equivalent to a 5% quantile of 70 Ma and a 95% quantile of 130 Ma) based on previous age estimates using independent data from this family and the pattern of multiple lineage exchanges between South America and Africa in its early stages of diversification (Danforth *et al.*, 2004). Initial exploratory analyses that varied the distribution of priors by multiplying the log(SD) by 0.5 or 2 units had little effect on inferred ages, changing date estimates by only 0–4 Ma. Final Markov chain Monte Carlo (MCMC) searches were conducted for 100,000,000 generations with the first 20,000,000 generations discarded as burn-in. Convergence and stationarity were assessed with TRACER 1.5 (Rambaut & Drummond, 2007) using effective sample size (ESS) scores and the consistency of results between multiple runs. The results from two independent runs were combined using the program TREEANNOTATOR 1.5.4 and visualized using FIGTREE 1.3.1.

Diversification analyses

We investigated the tempo of colletid diversification using lineage-through-time (LTT) plots, which are graphical representations of the cumulative number of reconstructed lineages over time based on a chronogram (in this case, the BEAST tree). In particular, we tested whether there is sufficient evidence to reject a diversification scenario in which speciation and extinction rates were constant throughout the history of Colletidae. We compared the inferred tempo of diversification of the family (i.e. the shape of the LTT extracted from the

BEAST trees) with a variety of expected scenarios where the rate of diversification of the family was constant, but the simulated data were subject to a range of potential biases, namely: (1) uncertainty from the process of phylogenetic inference; (2) uncertainty from the stochastic nature of the lineage branching process itself; and (3) biases due to incomplete and non-random taxon sampling of the complete tree.

The shape of a simulated LTT plot depends on the relative magnitude of the speciation and extinction rates (e.g. Nee *et al.*, 1992). In order to generate appropriate LTT confidence intervals, we used the method of Paradis (2003) to combine taxonomic and phylogenetic data to estimate the speciation and extinction rates during colletid diversification. These calculations were made assuming those rates remained constant, using the function 'bd.ext' in APE 2.13.1 (Paradis *et al.*, 2004), and used the relative magnitude of the estimated rates to simulate phylogenies under the assumption of a constant birth–death process using the 'birthdeath.tree' function in GEIGER 1.0 (Harmon *et al.*, 2008). The number of species in each clade considered for the analyses (i.e. genera assumed to be monophyletic or least inclusive suprageneric groups about which monophyly could be assumed) was based on the respective number of described species, as indicated in the Apoidea species guide (Ascher & Pickering, 2010). Second, the shape of the LTT plot is affected by the level of taxon sampling in relation to all extant lineages of the investigated clade; in order to take that effect into account, we computed confidence intervals by simulating a phylogeny with constant speciation and extinction rates (as indicated above) until we reached 2423 species (the number of known colletid species; Ascher & Pickering, 2010). The complete phylogeny was then randomly pruned of 98.8% of its species to represent the approximate proportion of all extant lineages included in the phylogeny by Almeida & Danforth (2009). Because the shape of our final LTT plots is affected by taxon sampling biases (i.e. missing taxa tend to result in a pattern suggestive of a decline in diversification) we generated a LTT plot under a constant speciation and extinction rate and pruned out 98.8% of the taxa, giving us an adjusted null expectation for a constant rate of diversification. Additionally, we simulated the effects of *non*-random sampling of the underlying phylogeny in that it purposefully chooses distantly related taxa (i.e. an over-dispersed sample). For this to be considered, we initially removed the most recently derived species, then removed the second, and so on, thus maximizing the phylogenetic diversity in the sample. Both simulations above were repeated 500 times and the average root age was rescaled to the inferred age to provide a Monte Carlo approach to determine the confidence intervals of the diversification model (Pie & Tschá, 2009).

To assess the effect of phylogenetic uncertainty, we generated a LTT with 1000 randomly selected post-burn-in phylogenies from the BEAST analyses described above. Comparisons among expected LTTs under different scenarios may be difficult due to the high level of stochasticity in the first few events of cladogenesis, even under constant speciation and extinction rates. Therefore, a comparison was made of all scenarios while rescaling them to coincide at the point where the average number of lineages equalled five. Finally, variation in diversification rate among colletid lineages was used to investigate the degree of imbalance in each node of the tree using the method of Slowinski & Guyer (1993).

Historical biogeography

Areas

We defined four biogeographically relevant areas: (A) South America, (B) Australia, (C) the Holarctic and (D) Africa. The choice of large areas as operational units to be used in the analyses can be justified by a geological criterion, as we defined areas of study according to palaeogeographical history (i.e. plate tectonics).

It is well known that the South American continent is not a proper biogeographical unit (Amorim & Pires, 1996), and it should be pointed out that the diversity of colletid bees is not evenly distributed in this continent. Most of the diversity of Colletidae is found in the xeric southern subtropical and temperate regions of the continent, but for the purposes of the biogeographical analyses, this area will also encompass the tropical portion of the continent, as well as Central America and the southern USA. As considered here, South America is in fact the junction of the Neotropical + Neotemperate regions (*sensu* Amorim & Pires, 1996) in addition to a narrow southern portion of the Nearctic region. As for the area named 'Australia', the great majority of the species- and genus-level diversity is restricted to Australia itself, but adjacent islands in the Australian region (including New Zealand and, in some cases, New Guinea) are included in the same area. In Bayes-DIVA analyses (see below), New Zealand and Australia were treated both separately and as a single area to check for any influence on the reconstructions.

Scrapterinae is the only colletid lineage endemic to Africa. With the exception of one species of this subfamily, *Scrapter nitidus* (Friese), distributed from Kenya to South Africa, all others are restricted to southern Africa (Davies *et al.*, 2005). No endemic genus of Colletidae occurs in the Nearctic, Oriental and Palaearctic regions, which have relatively depauperate colletid faunas (in terms of higher taxa). The genus *Colletes* is distributed in all continents except Australia and Antarctica, and it most certainly had its initial diversification in southern South America (Michener, 1979; Kuhlmann *et al.*, 2009). Hylaeinae is most diverse morphologically in the Australian region, but one genus of this subfamily, *Hylaeus*, is widely distributed and comprises a large number of species world-wide, even in several oceanic islands (Michener, 1965). All evidence indicates that *Hylaeus* expanded its range from Australia to reach its current wide-ranging distribution (Michener, 1979; P. Kayaalp & M. Schwarz, pers. comm.). For the purposes of the analyses using dispersal–extinction–cladogenesis (DEC) models (see below), all geographical occurrences that could be safely assumed to be secondary were considered biogeographically uninformative. These occurrences include the two widespread genera *Colletes* and *Hylaeus*, as well as the diphaglossine genera *Caupolicana* and *Ptiloglossa* and the neopasiphaeine genus *Eulonchopria*, which reach the south of the Nearctic region.

Biogeographical inference

We aimed to propose a hypothesis for the biogeographical history of Colletidae that could be extracted from the phylogenetic and distributional data of these bees. Event-based methods were used to explore possible biogeographical scenarios of colletid diversification across time and space by means of reconstructing events in a given phylogeny without prior assumptions about the area relationships (Ronquist, 1997). We chose to use a combination of analytical approaches and verified their ability to extract a historical biogeographical signal from the data (Ree & Sanmartín, 2009; Buerki *et al.*, 2011). These included parsimony-based DIVA (dispersal–vicariance analysis; Ronquist, 1997), a likelihood-based DEC model (Ree *et al.*, 2005; Ree & Smith, 2008) and a Bayesian model for biogeographical reconstruction (Sanmartín *et al.*, 2008).

Dispersal–vicariance analysis

DIVA is a parsimony-based method that optimizes ancestral areas onto the phylogenetic nodes by minimizing the number of dispersal and extinction events in relation to vicariance events (Ronquist, 1997). More recently, Nylander *et al.* (2008) proposed a modified approach to DIVA and referred to this as Bayes-DIVA because it integrates biogeographical reconstructions from DIVA over the posterior distribution of a Bayesian MCMC sample of tree topologies. This approach allows an estimation of marginal probabilities of ancestral ranges for a given node while integrating over the uncertainty in the rest of the tree topology. It has been argued that accounting for the uncertainty in phylogenetic relationships may sometimes reduce the uncertainty in the biogeographical reconstruction itself (Nylander *et al.*, 2008). In addition to the topological uncertainty, DIVA often outputs multiple, equally parsimonious, biogeographical scenarios for a given phylogeny and there are no quantifiable means of selecting among these possibilities. Both types of uncertainty can be accounted for in the Bayes-DIVA approach when ancestral distributions are plotted as marginal distributions (probabilities) on nodes in the tree (Nylander *et al.*, 2008; Yu *et al.*, 2010, 2011).

We ran Bayes-DIVA analyses using rasp (Reconstruct Ancestral State in Phylogenies) version 2, also referred to as S-DIVA (statistical dispersal–vicariance analysis; Yu *et al.*, 2010, 2011). Most parsimonious biogeographical scenarios were sought with the number of ancestral areas unrestricted. We inferred the geographical distribution for the ancestors by integrating (marginalizing) over all 1000 tree topologies in the sample drawn from the Bayesian MCMC beast analysis. Each tree was weighted according to its posterior probability (relative frequency in the sample). Biogeographical results were summarized on the majority rule consensus of the beast analysis, which is fully bifurcating. The sister group of Colletidae, the endemic Australian lineage Stenotritidae (Danforth *et al.*, 2006; Almeida & Danforth, 2009) and the two more distantly related outgroups (Andrenidae and Halictidae) were included in the analyses. rasp imposes a restriction of a maximum number of 127 taxa; therefore, analyses were run using slightly pruned trees, in which each clade of outgroups was thinned to a single lineage. Halictidae was considered to be distributed in South America + Africa, or in South America + Africa + the Nearctic (the resulting DIVA reconstruction obtained by Danforth *et al.*, 2004) and Andrenidae was considered to be from the Nearctic + South America (as in the reconstruction obtained by Ascher, 2004).

The DEC model

The DEC continuous-time model for geographical range evolution (the DEC model: Ree *et al.*, 2005; Ree & Smith, 2008) is implemented in the package Lagrange 2 (Likelihood Analysis of Geographic RANGe Evolution). Maximum likelihood (ML) parameters are estimated for rates of migratory events between areas (range expansions) and local extinctions within areas (range contraction). DEC models take advantage of the time-scale provided by the chronogram to estimate the probability of changes between ancestral states along a given branch (Ree *et al.*, 2005; Ree & Smith, 2008; Ree & Sanmartín, 2009). Given a tree topology, branch lengths and present distributions of species, this method finds the value of the biogeographical parameters that maximize the probability of observing the data. Since all alternative reconstructions are evaluated in estimating the relative probabilities of ancestral states, ML analyses incorporate uncertainty in ancestral state reconstruction.

The DEC model resembles a character-state reconstruction approach (Ree & Smith, 2008) but differs markedly from this class of methods in its treatment of cladogenesis events. Unlike character states, which are assumed to be inherited identically by daughter lineages, geographical ranges can potentially be inherited in a non-identical manner, as a consequence of spatial subdivision of the ancestral range (Ree & Sanmartín, 2009). This is the most serious drawback of a character-state optimization method because it represents an a priori dismissal of vicariance as a relevant event in the course of the spatial history of a lineage (Ronquist, 1994; Ree & Smith, 2008). Models such as DIVA and DEC are much better suited to exploring the three most relevant processes of the biogeographical history of a lineage, namely vicariance, dispersal and extinction, because all are simultaneously considered as relevant explanatory events, although these two approaches are radically distinct in their methodological implementations.

A desirable property of Lagrange is the possibility of specifying instantaneous transition rates between geographical ranges according to user needs (Ree *et al.*, 2005; Ree & Smith, 2008; Ree & Sanmartín, 2009). In the first scenario we tested, movement between areas at any time was unconstrained.

Under this model, all areas are treated as equiprobable ancestral ranges. DEC models can also incorporate information on past geological events, particularly connectivity among areas. We divided our model into four time slices (TS) to reflect the main palaeogeographical periods of the history of Colletidae: (1) between 105 and 123 Ma; (2) between 105 and 40 Ma; (3) between 41 and 31 Ma; and (4) between 31 Ma and the present day. Range evolution along phylogenetic branches (internodes) is governed by a *Q* matrix of instantaneous transition rates (Ree & Smith, 2008). This stratified scenario (here termed DEC-strat) also enabled a hypothesis test to be performed: while leaving all dispersal parameters fixed, connection between South America and Australia was downweighted from 1.0 to 0.1 during the time layer between 41 and 31 Ma. According to some authors (e.g. Briggs, 1995; Woodburne & Case, 1996), the trans-Antarctic biotic connection was significantly reduced after *c.* 40 Ma. Differences in the global likelihood score associated with biogeographical reconstructions greater than two log-likelihood units can be considered significant (Ree *et al.*, 2005).

The BEAST chronogram (Fig. 1) was used for all LAGRANGE calculations and the root node of the tree was calibrated to 123 Ma, the point estimate age of the most recent ancestor of all terminal taxa considered. In all analyses, ancestral ranges were assumed to include no more than three areas.

Bayesian biogeographical reconstruction

Bayesian approaches to ancestral state reconstruction have recently been applied to biogeographical inference (Olsson *et al.*, 2006; Sanmartín *et al.*, 2008). This approach models dispersal among areas as a stochastic process represented by a Markov chain, involving the transition between two or more discrete states with different rates or probabilities. Here, we estimated the geographical range evolution of Colletidae over time applying the model F81 + Γ (with transition and among site variation parameters empirically estimated). This is the most general and complex model implemented in RASP, with properties expected to yield maximum realism to reconstructions of this kind (Sanmartín *et al.*, 2008). Using this framework, we performed a biogeographical analysis on a sample of 1000 trees in RASP (Yu *et al.*, 2011).

RESULTS

A time scale of colletid evolution and diversification

The phylogenetic relationships among major colletid lineages inferred with BEAST (Fig. 1) matched those established using MrBayes by a previous study (Almeida & Danforth, 2009). We have expanded upon the previous phylogeny with the addition of *Nesocolletes fulvescens*, as representative of Neopasiphaeinae from New Zealand. This species was resolved within the largest clade of Australian Neopasiphaeinae (Fig. 1, Clade 3), close to three species of *Leioproctus*: *Leioproctus irroratus*, *Leioproctus plumosus* and *Leioproctus platycephalus*.

The inferred divergence dates indicate that the diversification of Colletidae began in the Late Cretaceous 71 ± 14 Ma (Fig. 1, Table 1). This result closely matches a previous dating estimate for the stem node of colletid bees (mean age of 69.6 Ma) based on analyses of ribosomal DNA from Aculeata (Brady *et al.*, 2009). Most colletid lineages currently recognized as subfamilies began to diverge during this initial time period and the differentiation of these major lineages occurred in a time span of only about 7 Myr.

The reconstructed LTT and its confidence interval, taking into account uncertainty in the estimation of divergence times, are shown in Fig. 2 together with the expected LTTs following different diversification scenarios. When clade diversification with constant speciation is pruned to the level of taxon sampling of the empirical dataset, a sudden change in slope is unexpected when pruning is either random (Fig. 2a) or phylogenetically overdispersed (Fig. 2b), even when considering the variability inherent in pure-birth processes. The reconstructed LTT showed an unusual shape, with a sudden increase in slope in the last third of the plot (Fig. 2c). When the LTTs shown in Fig. 2(a,c) are overlapped (Fig. 2d), the shift in the slope of the empirical curve becomes evident, suggesting that the early diversification had already begun to asymptote and would stabilize at a level much lower than the observed diversity. Rescaling the LTTs to the timeframe of the colletid chronogram indicated that the presumed acceleration of the rate of cladogenesis began around 30 Ma, in the mid Oligocene (Fig. 3).

Based on the method of Slowinski & Guyer (1993), the largest asymmetries involved the contrast between (1) the genus *Colletes* and its closest related genera that compose Colletinae and (2) the bulk of Hylaeinae (including the genus *Hylaeus*) and its sister lineage, *Hyleoides* (Fig. 2). These two lineages are the two most widely distributed genera of Colletidae, occurring in all continents except Antarctica (and in the case of *Colletes*, Australia) and a number of oceanic islands. The approximate temporal coincidence of early diversification of these two clades and the beginning of the period when colletid diversification rates were inferred to have risen is striking (Fig. 2; the crown age of the *Colletes* is 24 ± 6 Ma and that of *Hylaeus* is 29 ± 7 Ma). There may be a relationship between the overall acceleration of the rate of cladogenesis in Colletidae and shifts occurred in particular branches, particularly those of *Colletes* and *Hylaeus*, for the reasons explained above. However, for this to be properly inferred, more refined phylogenetic information within each colletid lineage will be necessary.

Colletid biogeography

All biogeographical analyses provide strong evidence of multiple lineage interchanges between Australia and South America. Despite differences in approach, the DEC model of LAGRANGE (Fig. 4b) and the Bayes-DIVA and Bayesian reconstructions of RASP (Fig. 4b) converged in the main results, which are summarized in Fig. 4(c). The epoch of the

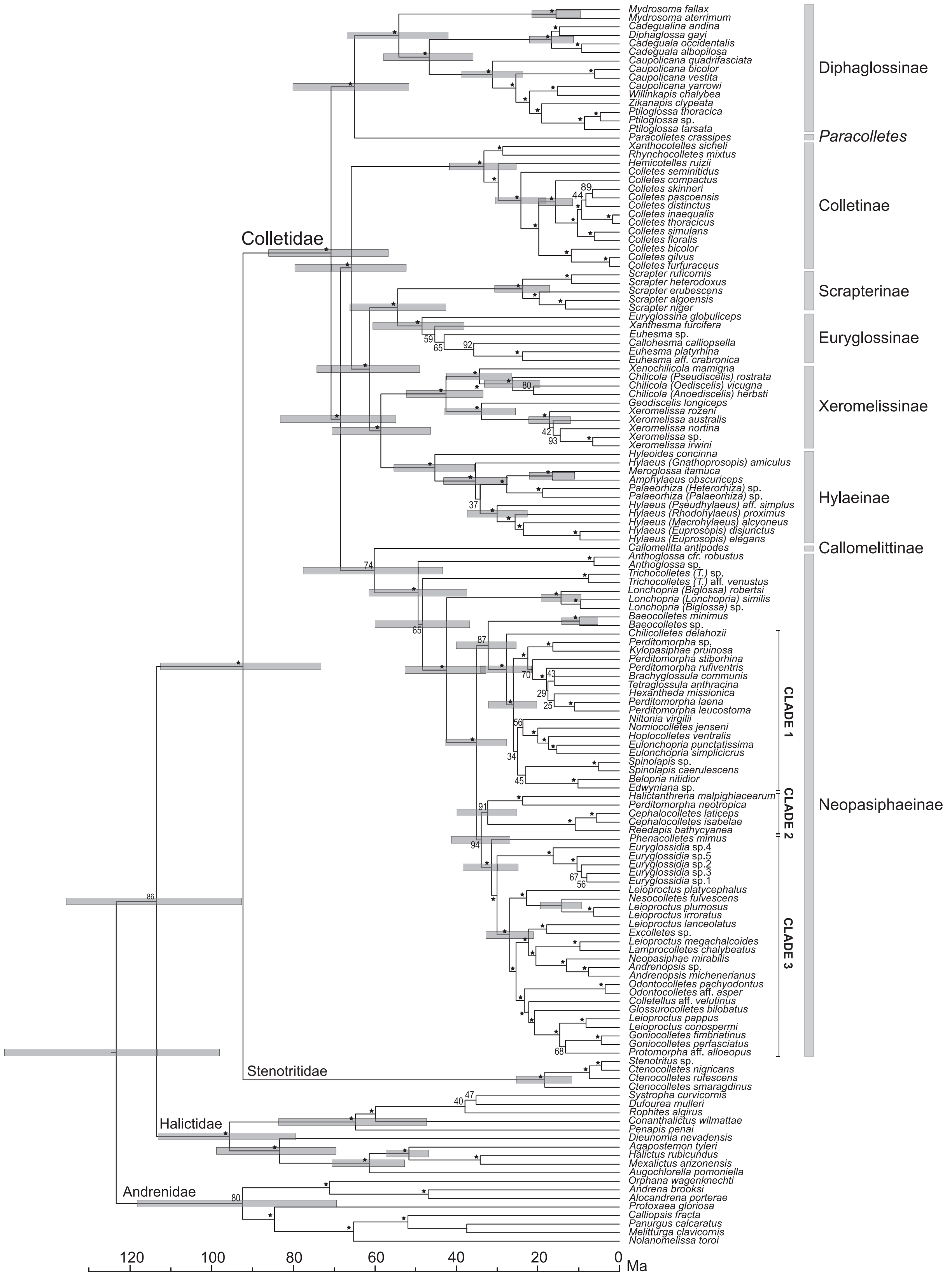

Figure 1 Chronogram for Colletidae derived from a Bayesian analysis employing a relaxed molecular clock (bottom). Stars above branches indicate posterior probabilities ≥ 0.95. Probabilities lower than 0.95 (converted to scores 0–95) are shown next to the corresponding nodes. Branch lengths are drawn proportional to time and 95% intervals for the ages of select nodes are indicated by horizontal grey bars. The horizontal scale bar measures time in millions of years.

Table 1 Age estimates (in Myr) for major lineages of colletid bees. Values in parentheses are 95% credibility intervals. Note that stem ages for sister groups refer to the same node by definition.

Clade	Crown age	Stem age
Colletidae	71 (57, 86)	92 (73, 112)
Diphaglossinae	54 (42, 67)	65 (52, 80)
Diphaglossinae + *Paracolletes*	65 (52, 80)	71 (57, 86)
Colletinae	33 (25, 42)	66 (52, 79)
Scrapterinae	24 (17, 31)	54 (42, 66)
Euryglossinae	48 (38, 60)	54 (42, 66)
Euryglossinae + Scrapterinae	54 (42, 66)	61 (49, 74)
Xeromelissinae	42 (33, 52)	58 (46, 70)
Hylaeinae	45 (35, 55)	58 (46, 70)
Hylaeinae excluding *Hyleoides*	35 (27, 43)	45 (35, 55)
Hylaeinae + Xeromelissinae	58 (46, 70)	61 (49, 74)
Neopasiphaeinae + Callomelittinae	60 (43, 77)	68 (55, 83)
Neopasiphaeinae	49 (37, 61)	60 (43, 77)
Neopasiphaeinae excluding *Anthoglossa*, *Trichocolletes* and *Lonchopria*	35 (28, 42)	42 (33, 52)
Colletes	24 (18, 30)	30 (23, 37)
Chilicola	26 (19, 33)	34 (26, 42)
Lonchopria	14 (9, 19)	42 (33, 52)
Hylaeus	30 (23, 37)	35 (27, 43)
Xeromelissa	17 (12, 23)	34 (25, 43)

biogeographical scenario is consistent with a geological reconstruction of close connections between Antarctica and Australia, and South America and Antarctica (Fig. 4d). Antarctica is not explicitly shown in the biogeographical hypotheses given by the analytical results (Fig. 4a,b) because it is not part of any extant species distribution, but it is implied by the joint occurrence of Australia and South America in several reconstructions.

The hypothesis of range evolution of the DEC model shows the joint occurrence of Australia and South America (A–B) in six lineages of the tree as the most likely geographical range for those ancestors (Fig. 4a). If we consider that 'Australia + South America' is the second most likely reconstruction for four lineages reconstructed as having differentiated in Australia, the number of lineages thought to have inhabited this austral supercontinent rises to 10. The results shown in Fig. 4(a) consider the simplest model of LAGRANGE that does not include stratification. In addition to the unconstrained model, when we tested several stratified models that served as representations of geological connections and disjunctions of areas through time, we did not observe significantly different results in comparison to the simple DEC model. Moreover, the difference in likelihood between a stratified model that presupposed lower trans-Antarctic range expansions during the period from 41 to 31 Ma was not significant ($\Delta \ln L_{\mathrm{DECstr1-DECstr2}} = 0.54$; only $\Delta \geq 2.0$ could be considered significant).

According to the Bayes-DIVA reconstruction, six nodes have South America + Australia as the most probable ancestral reconstruction, which can be interpreted as at least six interchanges/vicariance events (involving these two continents, as well as Antarctica) to explain the current distribution of colletid lineages (Fig. 4c). Considering all possible reconstructions given by Bayes-DIVA, as many as 12 trans-Antarctic interchange events may be necessary to explain the current distribution of colletid bees. The Bayesian reconstruction conducted in RASP yielded results that were overall similar to the DIVA scenarios, but two striking differences must be highlighted: (1) 'South America + Australia' was one of the scenarios presented as a possible reconstruction in every node of the tree; (2) none of the nodes showed 'South America + Australia' as the most probable ancestral distribution.

It has been reported that DIVA (or Bayes-DIVA, in our case) often gives biogeographical reconstructions congruent to the

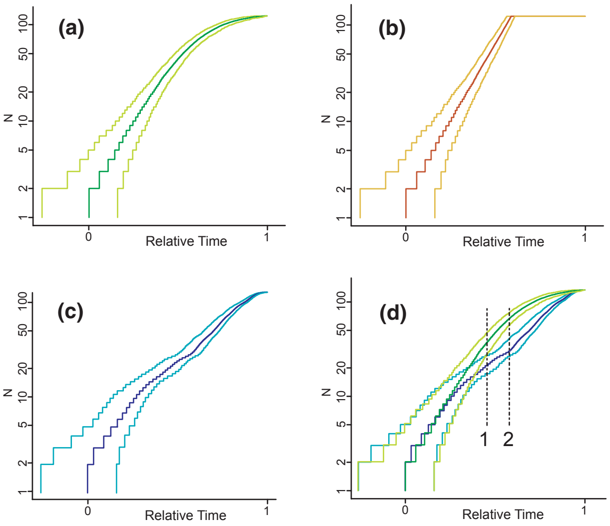

Figure 2 Simulated and empirical lineage-though-time (LTT) plot reconstructions of the diversification process of Colletidae. (a) Constant Yule process starting with one species and generating 2423 lineages, followed by pruning of 2289 tips from the trees to simulate random sampling (i.e. expected LTT of a constant-rate diversification of Colletidae with the corresponding level of taxon sampling). Sampling was repeated 1000 times to calculate the 95% confidence interval (light green lines). (b) Constant Yule process generating 2423 lineages as in (a), followed by pruning of 2289 tips from the trees to simulate *non*-random sampling (i.e. most distantly related taxa are purposefully chosen to be retained). Sampling was repeated 1000 times to calculate the 95% confidence interval (orange lines). (c) Observed LTT obtained from the phylogeny inferred for Colletidae (dark blue line) and confidence interval (light blue lines) given by a random sample of 1000 post-burn-in BEAST trees to account for the uncertainty from the method of phylogenetic inference and the level of phylogenetic signal in the dataset. (d) Superposition of LTT plots (a) and (c). Dashed line '1' indicates the beginning of a period when the observed LTT deviated significantly from the simulated constant-rate LTT; dashed line '2' indicates a positive shift of the diversification rate in the empirical LTT (slope of empirical curve bent at a clearly higher angle than simulated LTTs).

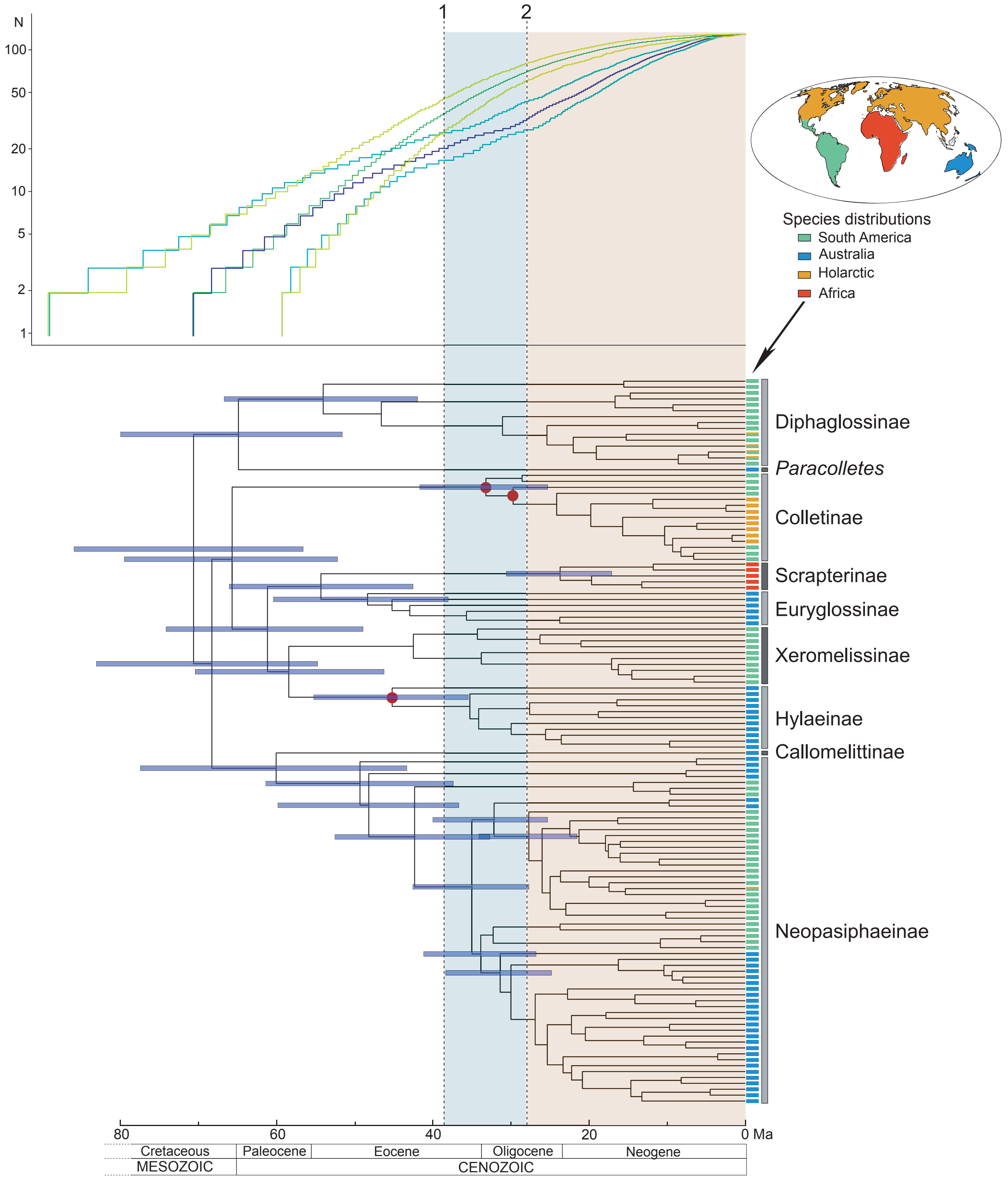

Figure 3 Chronogram for Colletidae derived from a Bayesian analysis employing a relaxed molecular clock as given by the time-scale on the bottom. Branch lengths are drawn proportional to time and 95% intervals for the ages of select nodes are indicated by horizontal blue bars; terminal species names are omitted, but their arrangement is identical to that in Fig. 1. Red circles represent statistically significant ($P < 0.01$) cases of species-diversity asymmetries between sister lineages based on the Slowinski–Guyer test. Lineage-through-time (LTT; top graph) plots represent observed LTTs obtained from the phylogeny inferred for Colletidae and simulated LTTs corresponding to the expected constant-rate diversifying process. The red shaded region (right of the line marked '2') represents the approximate period when Colletidae went through a hypothesized accelerated rate of cladogenesis; the blue shaded region (right of the line marked '1') represents the approximate period when the Colletidae diversification rate started deviating from an expected constant rate of cladogenesis (see Fig. 2d and text for details).

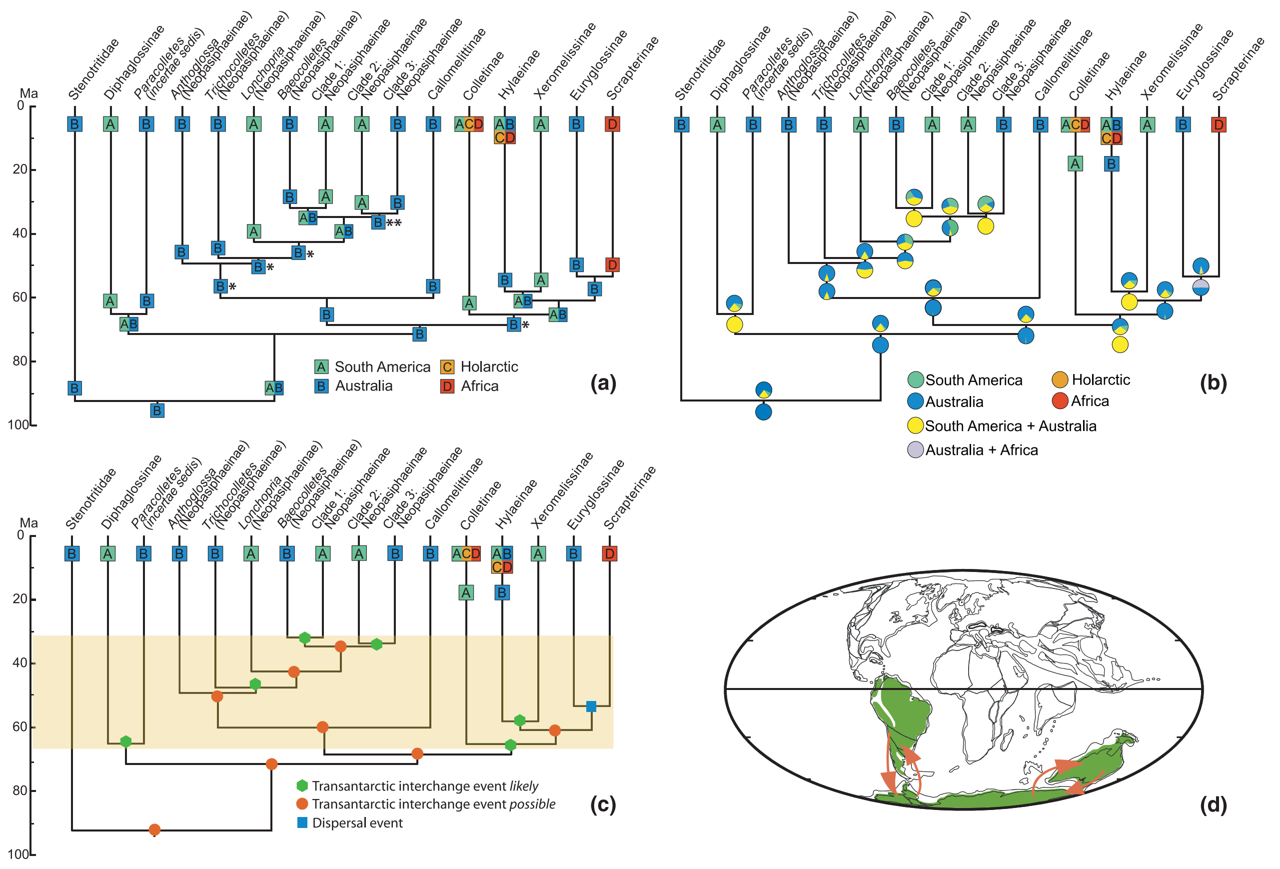

Figure 4 Simplified chronogram of Colletidae derived from a Bayesian analysis employing a flexible molecular clock (time-scale on left). (a) Maximum likelihood reconstruction of geographical range evolution under the unconstrained dispersal–extinction–cladogenesis (DEC) model ($\ln L = 76.58$). The second most likely scenario for reconstructions marked with an asterisk were 'Australia + South America' (i.e. areas AB); as for the lineage marked with two asterisks, South America (area A) was a reconstruction equally as likely as Australia. (b) Pie charts show optimization (as proportional to the posterior probabilities of the Bayesian tree) at nodes indicating ancestral ranges considered as biogeographical hypotheses. The bottom charts depict dispersal–vicariance analysis (Bayes-DIVA) most parsimonious reconstructions, whereas the upper charts show the result of the Bayesian method of biogeographical reconstruction. (c) The shaded bar represents the time range over which lineage-interchanges probably occurred between Australia and South America, but this period may have extended further back into the past (orange circles). Circles represent nodes at which these hypothesized lineage-interchange events may have occurred; square represents dispersal event required to explain the current distribution of Scrapterinae in Africa. (d) Hypothetical reconstruction of the relative positions of the continents on the globe during the Palaeocene (60 Ma), showing the probable route of trans-Antarctic interchanges between Australia and South America (map adapted from Scotese, 2001).

model-based likelihood of the DEC model of Lagrange (Ree *et al.*, 2005; Ree & Smith, 2008; Buerki *et al.*, 2011). Whereas DEC models do not take into account uncertainty, Bayes-DIVA does not (explicitly) take into account divergence times of lineages (Ree & Sanmartín, 2009). Unlike DIVA, which calculates the number of dispersal and extinction events and tries to minimize them, Lagrange calculates the relative likelihood of each possible ancestral range at each node, given a particular probability of dispersal and extinction (Ree *et al.*, 2005). In recent methodological comparisons between Bayes-DIVA and DEC models, it has been observed that these two methods often converge on the inferred biogeographical scenarios (e.g. Buerki *et al.*, 2011). This kind of consistency was observed in the analyses herein. Despite differences in the representation of the outcome of the hypothesis by the three methods (Fig. 4a,b), their interpretation converges on a scenario of multiple trans-Antarctic exchanges (Fig. 4c). In all cases, uncertainty was an important factor to be considered and the exact number of exchanges cannot be determined; we can only hypothesize that it was greater than or equal to six, but not greater than 14 (Fig. 4c).

Some biogeographical reconstructions indicate Australia as the most likely ancestral distribution of Colletidae, as well as of the clade formed by Colletidae and Stenotritidae (Fig. 4b). These results must be interpreted with caution, however, because the diversification of Colletidae and Stenotritidae took place while Australia was not an isolated land mass. It was connected to Antarctica and, therefore, did not represent an individualized geographical component as it is today. The sister lineage of Colletidae consists of only 21 species in the endemic Australian family Stenotritidae, which possibly originated in eastern Gondwana and never expanded its range westward.

In addition to the recurrent interchanges between Australia and South America, one dispersal event to Africa is invoked to explain the occurrence of Scrapterinae in Africa. Scrapterinae, the endemic African subfamily of Colletidae, is nested well within the colletid clade, and is sister to the Australian Euryglossinae. Dispersal could have occurred from Australia (all methods considered this possibility), Australia + South America or South America (Bayesian reconstruction). There is no scenario in which the present distribution of Scrapterinae in Africa is explained by vicariance (e.g. ancestral reconstruction of ancestor of Scrapterinae in South America + Africa), given the unparsimonious nature of this alternative hypothesis in view of the phylogenetic topology. The differentiation of *Scrapter* probably occurred in the Eocene (54 ± 12 Ma), a time when Africa had already diverged considerably from Australia, Antarctica and South America.

Another dispersal event needed to complete the biogeographical scenario (not shown in Fig. 4, but tested with Bayes-DIVA) is the dispersal of a lineage the ancestor of *Nesocolletes fulvescens* from Australia to New Zealand. The stem age of *Nesocolletes* is only 14 ± 6 Ma, which effectively excludes a scenario of vicariance involving Australia or any other Gondwanan land mass.

DISCUSSION

Bees presumably arose in concert with the rise of flowering plants sometime during the Cretaceous, approximately 120 Ma, possibly in western Gondwana (Michener, 1979; Engel, 2004; Poinar & Danforth, 2006; Brady *et al.*, 2009). It is therefore expected that at least the earliest lineages of bees have disjunct, austral distributions, reflecting the fragmentation of Gondwana. Colletidae has been the prime example among bee taxa of an ancient group whose origin in Gondwana precedes the complete break-up of this supercontinent, with endemic groups present in three prime southern regions: Australia, South America and southern Africa.

Historical biogeographical analyses presented in this paper strongly support an austral origin of this family. However, colletid bee distribution, relationships and divergence dates all suggest a pattern of diversification that occurred in the southern continents *after* the break-up of Africa from South America. The time range of these events estimated with dating methods is remarkably congruent with the geological timing of connections among Antarctica, Australia and South America, which remained associated until the end of the Eocene.

The biogeographical results imply that Antarctica served as an important setting for colletid bees in the past, as this continent is presumed to have connected Australia and South America until the end of the Eocene (Lawver *et al.*, 1992). Throughout the evolution of Colletidae, a minimum of six lineage exchange events are inferred between Australia and South America across Antarctica in a period between the Late Cretaceous and the late Oligocene or earlier (Fig. 4). We thus conclude that migratory movements of taxa between Antarctica and South America and between the Australian region and Antarctica allowed range expansions, or 'geodispersal' (*sensu* Upchurch, 2008), of a number of colletid lineages. Subsequent to the isolation of Antarctica, colletid taxa appear to have differentiated and further diversified in South America (e.g. Xeromelissinae, Diphaglossinae, three clades of Neopasiphaeinae) and in Australia (e.g. Euryglossinae, *Paracolletes*, four clades of Neopasiphaeinae).

Various taxonomic groups that have their current distributions intimately associated with southern regions of the globe have long been considered good candidates for having a history of vicariance concordant with the geological history of Gondwanan plate tectonics (Jardine & McKenzie, 1972; reviewed in Cranston, 2005); a number of authors have also re-examined study cases of Southern Hemisphere biogeography (e.g. Croizat, 1962; Brundin, 1966; Thorne, 1986; Crisci *et al.*, 1991; Sequeira & Farrell, 2001; Sanmartín & Ronquist, 2004). Particular cases that have a close relationship with the southern biogeographical province formed by connections between Antarctica, South America and Australia have been recognized by a number of researchers. This southern province has been referred to by a variety of names, as follows: circum-Antarctic track (Moreira-Muñoz, 2007); trans-Antarctic track (e.g. Cranston, 2005); Austral-Antarctic track (Moreira-Muñoz, 2011), Weddellian Province (Case, 1989), South Pacific track (Crisp *et al.*, 1999) and Amphinotic track (Matile, 1990). The same name has frequently been assigned to distributions whose histories date back to the Early Cretaceous or earlier (when many present disjunctions could be attributable to vicariance of Gondwana), or more recent histories only coupled to the vicariant events, which happened after the Late Cretaceous and the Tertiary. Colletid biogeography appears to be part of the second type of history because disjunctions involving taxa now in Africa and New Zealand do not appear to be consistent with vicariance, either based on our fossil-calibrated trees or our biogeographical reconstructions. Rather, these taxa appear to have arrived in Africa and New Zealand via recent dispersal relative to the time of separation of these land masses and those comprising the circum-Antarctic track.

Australia progressively drifted away from Antarctica during the Palaeogene, but remained connected to it until the late Eocene (*c.* 40–35 Ma), when the two continents were separated by the South Tasman Sea (Lawver *et al.*, 1992; Briggs, 1995), which became considerably deep at approximately 32 Ma (Lawver & Gahagan, 2003). South America was separated from western portion of Antarctica with the opening of the Drake Passage north of the Antarctic Peninsula at about 35–30.5 Ma (McLoughlin, 2001; Scotese, 2001; Lawver & Gahagan, 2003). Temperatures during this interval were higher than currently (see below); Antarctica may have remained ice-free until approximately 34 Ma and the continent hosted a subtropical–temperate vegetation (Dingle & Lavelle, 1998;

Thorn & DeConto, 2006; but see Bijl *et al.*, 2009, for an alternative view). Various Antarctic fossils of both animals (e.g. ratite birds, Tambusi *et al.*, 1994; marsupials, Woodburne & Case, 1996) and plants (e.g. *Nothofagus*, Dettmann *et al.*, 1990) document the importance of this trans-Antarctic corridor during much of the Late Cretaceous and the Palaeogene. Briggs (1995) considered the period from about 60–40 Ma as the most important migratory window of opportunity for taxa distributed in those southern areas. LAGRANGE was used to test for a reduction in connectivity between Australia and South America in the period 41–31 Ma (in comparison to previous periods) and no significant reduction in the biogeographical connection could be detected.

The opening of the Tasmanian and Drake Passages and the subsequent development of a South Circum-Polar current were the most likely causes for the rapid cooling of the planet and glaciation of Antarctica after the Eocene–Oligocene boundary (e.g. Lawver *et al.*, 1992; McLoughlin, 2001). Based on the dating results of our study, the most recent events of exchange between South America and Australia took place within the neopasiphaeine clade and were estimated to have occurred during the early Oligocene at 32 ± 7 and 33.8 ± 7 Ma (Figs 1 & 4). Movement among the Southern Hemisphere land masses ended with global cooling and physical separation of these areas. Even if there was a narrow ocean separating Antarctica, Australia and South America during certain periods of the Palaeogene and prior to the complete opening of Drake's Passage and the Tasmanian Sea, this may not have represented an impediment for the migration of members Neopasiphaeinae. Indeed, Michener (1965, p. 302) stated 'the presence of a few species of the genus [*Leioproctus*] in New Zealand and one in New Caledonia indicates an ability to cross rather large water gaps'.

We only included a single species from New Zealand in this study, *Nesocolletes fulvescens*, which was positioned within a clade of Australian *Leioproctus* species. Although *Nesocolletes* is the only supraspecific taxon of Colletidae endemic to New Zealand, Michener (1965, p. 52) had already suspected its close relatedness to Australian *Leioproctus* based on morphological similarities. The isolation of New Zealand occurred before the vicariance between southern South America and Australia (*c.* 75–85 Ma) (Lawver *et al.*, 1992; McLoughlin, 2001), and this contrasts with the stem age obtained for *Nesocolletes* in this study: 14 ± 6 Ma. The native New Zealand bee fauna is quite depauperate, comprising 28 colletids and only 33 species overall, of which 27 are endemic and six are also found in Australia (Donovan, 2007). According to Michener (2007, p. 105), this is the 'smallest [bee] fauna of any substantial land area except for arctic and Antarctic regions; rare over-water dispersal seems to be the only reasonable explanation for its fauna'. Our results provide an important corroboration to Michener's hypothesis that the colletid fauna of New Zealand does not represent an ancient biota but a recently assembled community whose source was the Australian mainland bee fauna. The absence of unusual bees in New Zealand suggests that this land mass did not sustain components of the bee fauna present in East Gondwana when it drifted away from the remaining southern continents.

Scrapterinae

Neither the biogeographical nor the molecular dating results support an origin of Colletidae prior to the separation of Africa and South America. The African endemic colletid lineage, Scrapterinae, is closely related to the Australian endemic Euryglossinae. Africa and South America started drifting away during the Cretaceous and their connections were interrupted 105 Ma or earlier (McLoughlin, 2001). Direct connection between Australia and Africa was interrupted even earlier (*c.* 135 Ma; Sanmartín & Ronquist, 2004). Given this phylogenetic scenario for Colletidae, the explanation of the disjunction between Scrapterinae and its sister group as a result of the break-up of Gondwana would require a number *ad hoc* hypotheses of extinction events of early (basal) African lineages of Colletidae. This is not out of the realm of possibility considering that bees were greatly affected by the Eocene–Oligocene transition (Engel, 2001b) and perhaps by the Cretaceous–Tertiary extinctions as well. However, the history of Colletidae is poorly preserved in the fossil record and extinctions are not the type of event historical biogeography can easily test.

Michener (1979, p. 302) proposed that the presence of Scrapterinae in Africa could be explained by a single over-water dispersal event from Australia. Our results are consistent with Michener's hypothesis, as vicariance is ruled out as the most parsimonious explanation for the presence of Scrapterinae in Africa. Extant representatives of the sister clade of Scrapterinae (i.e. Euryglossinae) are exclusively distributed in the Australian region, but at the time dispersal occurred the propagule that gave rise to *Scrapter* could have departed from Antarctica. A similar hypothesis was conceived to explain disjunctions observed in the distribution of exoneurine bees (Hymenoptera: Apidae: Allodapini), interpreted as resulting from an Eocene dispersal from southern Africa to Australia, perhaps via Antarctica (Chenoweth & Schwarz, 2011).

At least two conceivable scenarios can be envisioned for the dispersal to Africa. First, a stem-nesting ancestor of Scrapterinae could have dispersed overseas from Antarctica or Australia. Stem-nesting is common within the clade comprising Callomelittinae, Colletinae, Euryglossinae, Hylaeinae, Scrapterinae and Xeromelissinae (reviewed in Almeida, 2008b), and it may even be the ancestral state for this character within this clade (but several reversals to ground-nesting are reported). Stem-nesters tend to be very good dispersers among bees, as evidenced by the presence of groups with this nesting habit in oceanic islands (Michener, 2007). The three species of *Scrapter* for which there is available nesting information are ground nesters (Rozen & Michener, 1968). An alternative explanation would rely on a range expansion of the scrapterine ancestor over the Kerguelen Plateau and/or the Crozet Plateau, hypothesized to have functioned as a land bridge connecting Antarctica, Madagascar, India and perhaps continental Africa, from Late or mid Cretaceous until mid Tertiary (McLoughlin, 2001; Wallace *et al.*, 2002; Lawver & Gahagan, 2003). Even if these land masses, and smaller islands nearby, did not form a continuous bridge between Antarctica and continents northward, the reduction in dispersal distance may have favoured biotic exchanges in the region (dispersal barriers abated). Despite the uncertainty regarding the geological basis, formation time and importance as a land bridge (or stepping stone) of the Kerguelen Plateau and Crozet Plateau, these land masses have often been hypothesized to play a role in explaining disjunctions between Australia and Africa and/or India (e.g. Noonan & Chippindale, 2006; Schwarz *et al.*, 2006; but see Ali & Aitchison, 2009, for a critique).

Palaeovegetation through the Late Cretaceous and Cenozoic

The predominant forest ecosystem in Antarctica and most of Australia and southern South America during the Late Cretaceous until the late Eocene was probably similar to a vegetation type that is still prevalent in parts of the world: the *Nothofagus*-dominated temperate rain forests. These ecosystems are currently restricted to southern South America, New Zealand, Tasmania, south-eastern Australia and northern Queensland, New Caledonia, and New Guinea (Thorne, 1986; Swenson *et al.*, 2001). Research conducted in humid temperate areas of southern Chile and Argentina recorded all subfamilies of Colletidae also present in other parts of South America (Spagarino *et al.*, 2001; Vázquez & Simberloff, 2002; Packer, 2004; Smith-Ramírez *et al.*, 2005), but species diversity is extremely low compared with areas further north (particularly in arid temperate and subtropical habitats). Colletid bee diversity in Tasmania, New Zealand and humid areas of Australia, as compared with xeric areas of Australia (Michener, 1965; Hingston, 1999; Donovan, 2007), indicates a similar trend of faunal impoverishment in humid subtropical environments. Moreover, no endemic supraspecific endemic taxa are known from these southernmost regions of South America and Australia. Based on the geographical pattern of diversity of extant species, it is safe to assert that colletid bees are particularly fond of dry temperate and subtropical areas (Michener, 1979, 2007), and it is reasonable to assume biome conservatism in the absence of evidence to the contrary (Crisp *et al.*, 2009). We argue that the habitat found in the subtropical and temperate forests of the Weddellian Province was at best marginal for Colletidae. Initial diversification of Colletidae took place during the Late Cretaceous, but extensive xeric biomes were not present in the southern continents until much later.

During the Cretaceous to early Tertiary, the Australian and South American floras experienced remarkable diversification, resulting in the origin of endemic families, tribes and genera (Solbrig, 1976; Hopper & Gioia, 2004; Wilf *et al.*, 2005; Ortiz-Jaureguizar & Cladera, 2006; Martin, 2006; Iglesias *et al.*, 2011), as well as of various kinds of biomes, including Australian heathlands (Henderson *et al.*, 2000). During the Palaeogene, xeric habitats were not as geographically extensive as they currently are in South America and Australia. Unequivocal xeromorphic plant fossils date from the late Eocene (41–36 Ma) in south-western Australia, and the early Oligocene (36–28 Ma) in south-eastern Australia (Hill, 2004). After the opening of the Drake Passage and Andes uplift, southern South America experienced drier climates that favoured expansion of xeric biomes (Ortiz-Jaureguizar & Cladera, 2006; Iglesias *et al.*, 2011). Lower temperatures in the Southern Hemisphere, coupled with colder southern sea currents (in the case of both Australia and South America), were important for cooler continental climates and expansion of xeric environments (Dingle & Lavelle, 1998; Martin, 2006; Iglesias *et al.*, 2011). There is an indication of increased colletid diversification within the Australian and the South American lineages beginning in the late Eocene (Fig. 3), coincident with a general trend towards cooler, drier climates in southern continents.

Research on the origins of the Australian flora has shown a significant burst of speciation of Australian plant taxa from late Tertiary to Quaternary (Crisp *et al.*, 2004; Hopper & Gioia, 2004). The potential impacts of this recent floral diversification on bees specialized on those plants wait to be tested, but least one other group of bees seems to have responded to the aridification in Australia during the Miocene. Chenoweth & Schwarz (2011) found evidence for increased diversification of Australian exoneurine bees, which are widespread in arid Australia, around 10 Ma.

Rates of diversification

Initial diversification of Colletidae appears to have occurred between the Late Cretaceous and the early Tertiary. Range expansions (i.e. migration or geodispersal) via Antarctica by South American and Australian species prompted the diversification of clades distinctive enough to be currently classified as subfamilies. Six or more austral lineage interchanges and the origin of all colletid subfamilies (Fig. 4) occurred during a relatively long time-window (*c.* 70–30 Ma). The increased net diversification rate observed in the second half of colletid history took place after the complete break-up of the Austral-Antarctic track (*c.* 28 Ma–present: Fig. 3) and may be explained by a number of hypotheses, as detailed below.

One possible explanation may be the biogeographical success of two lineages that expanded their distributions to become the two most widespread and speciose colletid genera: *Colletes* (*c.* 450 species, *c.* 18% of the known species-level diversity of Colletidae) and *Hylaeus* (*c.* 740 species, *c.* 29% of the known species-level diversity of Colletidae). Unsurprisingly, these large genera are the only two clades for which we could detect a significant imbalance in diversity when compared with their sister lineages using the Slowinski and Guyer test. Alternatively, it could be argued that there has been an extensive extinction event such as the Eocene–Oligocene transition (Engel, 2001b) followed by increased diversification. However, mass extinctions may only seldom leave a signature on LTT plots, as opposed to the evidence left by an accelerated net diversification rate, as demonstrated by Kubo & Iwasa (1995). Moreover, Colletidae is one of the least represented groups of bees in the fossil record (Engel, 2001a), thus making hypotheses of this kind hard to verify.

The most attractive hypothesis to help us understand the evolution of Colletidae is that host-plant specialization (oligolecty) may be related to the tempo of diversification of these bees. Oligolecty has been reported as a characteristic of Colletidae, or at least of a number of groups within this family (e.g. Wcislo & Cane, 1996). Various examples of highly specialized groups of Colletidae are presented by Houston (1983, 1992, 2000), Müller & Kuhlmann (2003), Laroca *et al.* (1989), Carvalho & Schlindwein (2011) and others. Detailed data concerning some colletid taxa are nonetheless insufficient, precluding any inference of general patterns of resource utilization for the family as whole. For the better understood colletid subfamilies (Neopasiphaeinae, Scrapterinae and Xeromelissinae), oligolecty is widespread.

Specialization is not necessarily an evolutionary dead end and, in fact, changes in host preferences may be a dynamic process, which can promote speciation (e.g. Janz *et al.*, 2001; Termonia *et al.*, 2001). Specialist bees show lower levels of genetic diversity than related generalist species living in the same environment (Packer *et al.*, 2005; a similar pattern was found by Kelley *et al.*, 2000, for bark beetles). Patchy resource distribution seems to be associated with this pattern of reduced genetic diversity (Danforth *et al.*, 2003; Zayed *et al.*, 2005) and colletid bees are clearly most diverse in xeric habits, which are often characterized by high floral diversity and by spatial heterogeneity (e.g. Minckley *et al.*, 1999). The expected long-term consequences of this kind of spatial structure of genetic diversity associated with habitat/resource specialization are an increased rate of diversification for a clade of bees fitting such a description.

Differentiation of Australian and South American colletid lineages took place throughout the Cenozoic, and was probably affected by the increasing floristic diversity and associated climatic changes in these continents during the Tertiary (see above). This would also coincide with the expansion of the temperate/subtropical xeric regions in both Australia and South America (Crisp *et al.*, 2004). We can suppose that either the colletid fauna has been a predominantly arid-adapted fauna from its origin or that it simply took advantage of the resources available in the xeric floras evolving on southern continents. Whichever interpretation is preferred, the mode of diversification within Colletidae was likely, at least in part, to have been driven by the expansion of desertic and semi-desertic habitats in the southern continents and their associated floras.

In this paper, we detected higher diversification rates in the later period of colletid history, a period coincident with the epoch when arid biomes in both Australia and South America began their expansion. Further research illuminating fine-scale relationships within each of the colletid clades, coupled with increased knowledge on host-plant relationships of these bees, will allow deeper understanding of the role of floral specialization on the tempo and mode of their macroevolutionary history.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Phylogenetic and dating analyses.

BIOSKETCHES

The authors' research programmes focus on the systematics and evolution of bees and ants, applying phylogenetic methods to investigate biogeography, lineage diversification, phenotypic evolution, social evolution, co-evolution and other evolutionary questions.

Author contributions: all authors conceived the ideas; E.A. and B.N.D. collected the data; E.A., M.R.P. and S.G.B. analysed the data; and E.A. led the writing.

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APPENDIX 1 USAGE OF THE NAME NEOPASIPHAEINAE COCKERELL, INSTEAD OF PARACOLLETINAE COCKERELL

Almeida & Danforth (2009) presented a phylogenetic hypothesis in which Paracolletinae *sensu* Michener was paraphyletic in relation to the remaining colletid subfamilies. *Paracolletes* and Diphaglossinae have been placed as sister groups (Almeida & Danforth, 2009; results in this paper; Fig. 1). All other genera traditionally placed in Paracolletinae were, nonetheless, shown to form a monophyletic group, which did not include *Paracolletes* and was in the meantime referred to as 'Paracolletinae' (see discussion by Almeida, 2008a; and Almeida & Danforth, 2009). However, there is an alternative solution for this nomenclatural problem, which is quite simple because a family-based name exists – Neopasiphaeinae – based on *Neopasiphae* Cockerell, an Australian genus included among the 'Paracolletinae'.

Although Neopasiphaeinae Cockerell, 1930 is a senior synonym of Paracolletinae Cockerell, 1934, Michener (1991) proposed that precedence should be given to the latter name based on the rare usage of Neopasiphaeinae. The ruling of the International Commission on Zoological Nomenclature was favourable to Michener's request and gave precedence to family group names based on *Paracolletes* Smith, 1853, over those based on *Neopasiphae* Perkins, 1912 (Ruling 1b: ICZN, 1993, p. 85; see further comments by Engel, 2005, p. 8). This ruling, however, did not make family-group names based on *Neopasiphae* unavailable, therefore allowing the usage of Neopasiphaeinae for the colletid clade that does not include *Paracolletes* (Figs 1 & 3). Only after further studies are conducted, especially a close morphological investigation of the phylogenetic position of *Paracolletes* in relation to other colletid taxa, will it be possible to revise the subfamilial classification and decide on the most justifiable placement of this genus. Until then, it will be treated as Colletidae *incertae sedis*.

In summary, Neopasiphaeinae is a natural group as well as a valid taxonomic name with the removal of *Paracolletes*.