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Out-of-Africa origin and dispersal-mediated diversification of the butterfly genus *Junonia* (Nymphalidae: Nymphalinae)

U. KODANDARAMAIAH* & N. WAHLBERG*†

*Department of Zoology, Stockholm University, Stockholm, Sweden
†Laboratory of Genetics, Department of Biology, University of Turku, Turku, Finland

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Abstract

The relative importance of dispersal and vicariance in the diversification of taxa has been much debated. Within butterflies, a few studies published so far have demonstrated vicariant patterns at the global level. We studied the historical biogeography of the genus *Junonia* (Nymphalidae: Nymphalinae) at the intercontinental level based on a molecular phylogeny. The genus is distributed over all major biogeographical regions of the world except the Palaearctic. We found dispersal to be the dominant process in the diversification of the genus. The genus originated and started diversifying in Africa about 20 Ma and soon after dispersed into Asia possibly through the Arabian Peninsula. From Asia, there were dispersals into Africa and Australasia, all around 5 Ma. The origin of the New World species is ambiguous; the ancestral may have dispersed from Asia via the Beringian Strait or from Africa over the Atlantic, about 3 Ma. We found no evidence for vicariance at the intercontinental scale. We argue that dispersal is as important as vicariance, if not more, in the global diversification of butterflies.

Introduction

Understanding the evolutionary history of life on earth is a field of endeavour that has attracted a number of researchers. This research has proliferated during the past couple of decades, with rapid advances in the other fields of study on which historical biogeography is based on. The lack of informative phylogenies to resolve the systematic positions and illuminate speciation patterns within different groups of organisms has been the most crucial impediment in the quest to understand the evolutionary history from a geographical standpoint (Wahlberg & Freitas, 2007). This problem has been alleviated to a great extent with developments in computing, molecular technology to sequence DNA and advances in phylogenetic methodology. Concordant refinements in molecular dating estimation methods and the rapid increase in knowledge about the geological past of the earth are other important factors in the development of historical biogeography. Armed with these powerful tools, historical biogeography has blossomed into a well-established area of study that is beginning to contribute immensely to our understanding of the evolution of life on earth.

Historical biogeography has provided us with great insights into the evolution of well-known groups such as birds (e.g. Cracraft, 2001; Filardi & Moyle, 2005), amphibians (e.g. Feller & Hedges, 1998; Roelants & Bossuyt, 2005), mammals (e.g. Karanth *et al.*, 2005; Nilsson *et al.*, 2005) and flowering plants (e.g. Manos & Stanford, 2001; Conti *et al.*, 2002). However, the evolutionary histories of most groups of organisms, particularly among the invertebrates, are still poorly understood. Butterflies are one such group. Despite their charismatic nature and popularity both within and outside the scientific community, their past is quite obscure (Boggs *et al.*, 2003; Vane-Wright, 2003) and there is little general consensus among the studies that have been published so far (de Jong, 2003; Braby *et al.*, 2005). As such we are far from a good understanding of their evolution and it is clear that a concerted effort to tackle different groups of butterflies with modern historical biogeographical methods would go a long way in filling in this existing lacuna in knowledge. Though studies encompassing subgroups within butterflies may not answer the question of the

Correspondence: Ullasa Kodandaramaiah, Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden.
Tel.: +46 8 164 398; fax: +46 8 167 715;
e-mail: ullasa.kodandaramaiah@zoologi.su.se

origins of butterflies as a whole, they are of utmost importance to understand the various historical processes that have given rise to present-day distributions.

The relative roles of dispersal and vicariance in the evolution of distributions of organisms have been a subject of much debate (Zink *et al.*, 2000; Brooks & McLennan, 2001; Ebach & Humphries, 2003). Before plate tectonic theory was accepted, the dispersal school of thought enjoyed a period of little dissent among the biogeographers' community (Udvardy, 1969). Disjunct intercontinental distributions of many taxa were explained by long-distance dispersals. However, the acceptance of the theory of plate tectonics influenced the debate in favour of vicariance (Wiley, 1988). The idea of long-distance intercontinental dispersals on an unchanging earth gradually gave way to explanations of vicariant events caused by a dynamic earth. A more or less concomitant development was the decline of phenetics, which was replaced by phylogenetic systematics (Hennig, 1966). Phylogenetics provided a powerful tool to understand relatedness between different areas for a given taxon and together with the theory of plate tectonics gave rise to a new paradigm in historical biogeographical analyses – vicariance biogeography (Nelson & Platnick, 1981). The essence of vicariance biogeography can be stated thus – vicariance is to be preferred over dispersal in an explanation of disjunct distributions (Wiley, 1988). Dispersal is invoked largely as a second-order explanation when vicariance cannot explain the pattern.

However, the distributions of many organisms have not been effected by vicariant events at the global scale. Young groups that have evolved after the Miocene, for instance, have had a geologically relatively stable earth to contend with. Their distributions are thus not so much affected by continental movements as they are by other factors such as changing climate. In other groups with high dispersive powers, the effects of vicariant events are likely to have been obscured by subsequent dispersals.

In the case of butterflies, there is continuing strong debate as to whether they are old enough to have been affected by the break-up of Gondwana (de Jong, 2003). The majority of the few studies so far have indicated that vicariance has been the more important factor in their evolution at the intercontinental scale (Viloria, 2003; Braby *et al.*, 2005; Braby & Pierce, 2007). Evidence for vicariance has been construed to be strong enough to be used as geological calibration points to obtain molecular dating estimates of lineage splits (Zakharov *et al.*, 2004; Braby *et al.*, 2005). However, it is clear that more studies are needed to ascertain the importance of dispersal in butterfly biogeography.

Here we address one important group of butterflies, belonging to the genus *Junonia* Hübner (1819). The butterflies of the genus, much as other members of the family Nymphalidae, have been contributing to our understanding of evolutionary biology and ecology (e.g. Bowers, 1984; Pereyra & Bowers, 1988; Klockars *et al.*, 1993; Camara, 1997; Haddad, 1999, 2000). They have been used as model organisms in studies on eye spot evolution (e.g. Nijhout, 1980; Brakefield & Larsen, 1984; Rountree & Nijhout, 1995). Commonly referred to as the pansies and buck-eyes, they are also some of the most charismatic insects. The extant members of the genus are predominantly of tropical affinity, with 29 of the 30 species confined to tropical latitudes. One species is distributed in the Nearctic region (North America) and four in the Neotropics (South and Central America). The genus is best represented in the Old World with the Afrotropical region accounting for 17 (15 endemic) species, the Oriental region 10 (eight endemic) species and the Australasian region chipping in with three species.

Using a phylogeny of *Junonia*, we show that the genus began its evolution on a northwards drifting Africa. Dispersal has been a dominant component in the history of this group. The distribution has been shaped by a complex series of intercontinental dispersal events. We find little evidence for vicariance at the intercontinental scale. We argue that the role of dispersal in butterfly evolution has been quite underrated, especially in groups with medium to high dispersal abilities.

Materials and methods

Laboratory protocols

Samples of 22 of the 30 species of *Junonia* representing all the major biogeographical regions were collected. Outgroup species were sampled from seven genera based on Wahlberg *et al.* (2005b). All genera in the tribe Junoniini (*Precis*, *Hypolimnas*, *Yoma*, *Salamis*, *Protogoniomorpha*) were included along with *Kallimoides* and *Anartia* (Victorinini). Sequences for some samples were taken from Wahlberg *et al.* (2005b). The *Junonia* specimens sampled for the study and their respective collection localities are listed in the online supplement. Once collected, either by the authors or by collaborators, the DNA was preserved by placing two legs in alcohol or by freezing the samples.

DNA was extracted from two legs using the DNEasy extraction kit (QIAgen, Hilden, Germany). Six published primer pairs were used to amplify three gene regions amounting to a total of 3090 base pairs (bp). Primer pairs LCO-HCO and Jerry-Pat (Wahlberg & Zimmermann, 2000) were used for the mitochondrial gene COI (cytochrome oxidase subunit I) which yielded 1450 bp. 1240 bp of elongation factor 1-α, a nuclear gene, was amplified using primers (Starsky-Luke, Cho-Verdi and EF 51.9- EfrcM4) from Peña *et al.* (2006). A 400-bp segment of another nuclear gene, *wingless*, was amplified with the primer pair LepWing1-LepWing2 published in Brower & DeSalle (1998). PCR reactions were performed in a 20 μL reaction volume. The thermal cycling profile for all primer pairs except Starsky-Luke was as follows: 95 °C for 7 min, 40 cycles of 95 °C for 30 s, 50 °C for 30 s and

72 °C for 1 min followed by a final extension period of 72 °C for 10 min. The profile for Starsky-Luke differed in that the annealing temperature was set at 55 °C. Sequencing was done using the same primers in a Beckmann-Coulter (Fullerton, CA, USA) CEQ8000 8-capillary automated sequencer. BioEdit v7.0.5.3 (Hall, 1999) was used to visualize and align the sequences. Aligning was straightforward and thus made by eye.

Phylogenetic analyses

The final data set consisting of 3090 bp was analysed using the maximum parsimony criterion with the software TNT 1.1 (Goloboff *et al.*, 2004). Heuristic searches were performed on 1000 random addition replicates. The heuristic searches consisted of both traditional searches such as TBR branch-swapping routines and new technology searches – Tree-Drifting, Sectorial searches and Tree-fusing. Parameters of the new technology searches were left unchanged from the default values. The same search strategy was used to analyse individual gene data sets.

Support for individual clades was estimated using two indices – bootstrap support values (Felsenstein, 1985) and Bremer support (BS) values (Bremer, 1988). Estimation of bootstrap support was made using 1000 random pseudoreplicates with 10 replicates each. We also calculated Partitioned Bremer Support (PBS) (Baker & DeSalle, 1997; Baker *et al.*, 1998) values to assess the degree of agreement between the different gene partitions. We estimated PBS values for the clades recovered in the strict consensus tree of the parsimony analysis, using a script written for TNT (see Peña *et al.*, 2006).

The data set was also analysed using Bayesian Inference using MRBAYES 3.1 (Ronquist & Huelsenbeck, 2003). The combined data set was partitioned by gene and codon position to yield a total of nine partitions. The General Time Reversible model with a gamma correction for rate variation among sites was imposed on each of the nine partitions. The parameters for the different partitions were unlinked. Two runs of four chains each were run for 3 000 000 generations on an AMD 64 dualcore-twin processor system using the LAM/MPI technology for parallel computing (Altekar *et al.*, 2004). The chains were sampled every 100 generations. The convergence of the two runs was confirmed using the average standard deviation of split frequencies, which was at 0.007 at the final generation. The first 500 trees were discarded as burnin.

Biogeographical analysis

Analytical methods based on the paradigm of vicariance biogeography have developed rapidly. The first formal method was described by Platnick & Nelson (1978). Since then a number of methods have been described (Brooks, 1981; Nelson & Platnick, 1981; Ronquist, 1997; Wojcicki & Brooks, 2005). Currently the most popular method for analysing single taxon data sets is dispersal-vicariance analysis (DIVA) (Ronquist, 1997). This has been used in a number of recent studies (Voelker, 2002; Biswas & Pawar, 2006; Bremer & Janssen, 2006; Braby & Pierce, 2007; Wahlberg & Freitas, 2007).

The program DIVA 1.1 was used to infer the relative roles of dispersal and vicariance using dispersal–vicariance optimization (Ronquist, 1997). Unresolved nodes were resolved into all possible sister groupings in successive analyses. Though the tree used in each analysis was fully resolved, no inferences were made on the nodes that were unresolved in the consensus tree. DIVA assumes a cost of 1 for dispersal and extinction and a 0 cost for vicariance and sympatric (within-area) speciation. The ancestral state reconstruction with the least cost is deemed to be the best ancestral reconstruction (Ronquist, 1997). The following regions were defined: New World, Afrotropical, Oriental and Australasian.

Molecular dating

The tree with the highest log-likelihood score in the Bayesian run was used for molecular dating analyses using the Penalized Likelihood method in r8s 1.71 (Sanderson, 2002). We were unable to use any fossil calibration point, because there are no known fossils of *Junonia*. Instead, the age of Junoniini was constrained at 35.5 Ma, based on the results of Wahlberg (2006). This approach was similar to that used by Wahlberg & Freitas (2007). A cross-validation run was initially performed to estimate the optimal smoothing parameter 's'. The final analysis was carried out using the thus estimated value of 's'. As the calibration point was external, we decided to use the upper and lower limits of the Junoniini divergence estimate in Wahlberg (2006) (25.5–48.5 Ma) to get an estimate of the error. For this exercise, we used the topology with the highest likelihood score in the Bayesian MCMC runs.

Results

Characteristics of the data set and congruence between different analyses

The complete data set of the three genes consisted of 3090 bp. Of these, 691 were parsimony informative. Parsimony analysis of the combined data set resulted in 791 equally parsimonious trees. The strict consensus is shown in Fig. 1. The tree topology was broadly congruent with the Bayesian topology (Fig. 2), with the Bayesian tree being more resolved at a few nodes. *Junonia* was recovered as a monophyletic unit in all the analyses. All species except *J. orithya* and *J. hierta* were monophyletic. The topologies resulting from analyses of the individual nuclear gene data sets (not shown) did

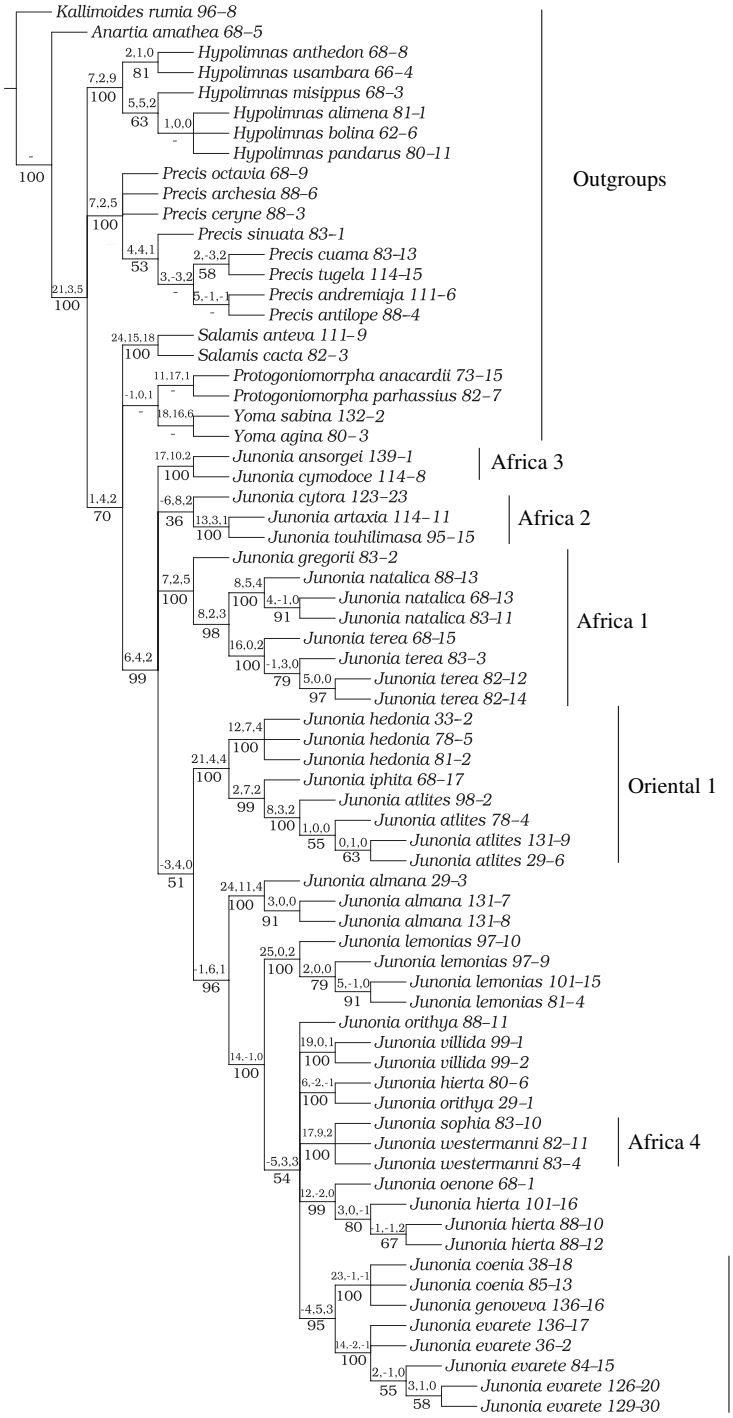

Fig. 1 Summary of strict consensus of the 791 equally parsimony trees derived from the analysis of the combined data set (L = 3517, RI = 0.67, CI = 0.38). Numbers above are partitioned Bremer support values for cytochrome oxidase subunit I, elongation factor 1-α and wingless respectively. Numbers below are bootstrap support values.

not differ substantially from the phylogeny in Fig. 2, i.e. the combined Bayesian analysis. The COI gene tree differed in some respects from the nuclear genes and thus from the combined data set topology. However, the PBS values for the COI partition indicate positive support for most nodes in the combined analysis (Fig. 1). PBS values are an indication of the relative support of the different data partitions to the combined analysis, and a positive value indicates that COI supports those groupings when combined with other data, a case of 'Hidden Bremer Support' (Gatesy *et al.*, 1999; Wahlberg *et al.*, 2005a).

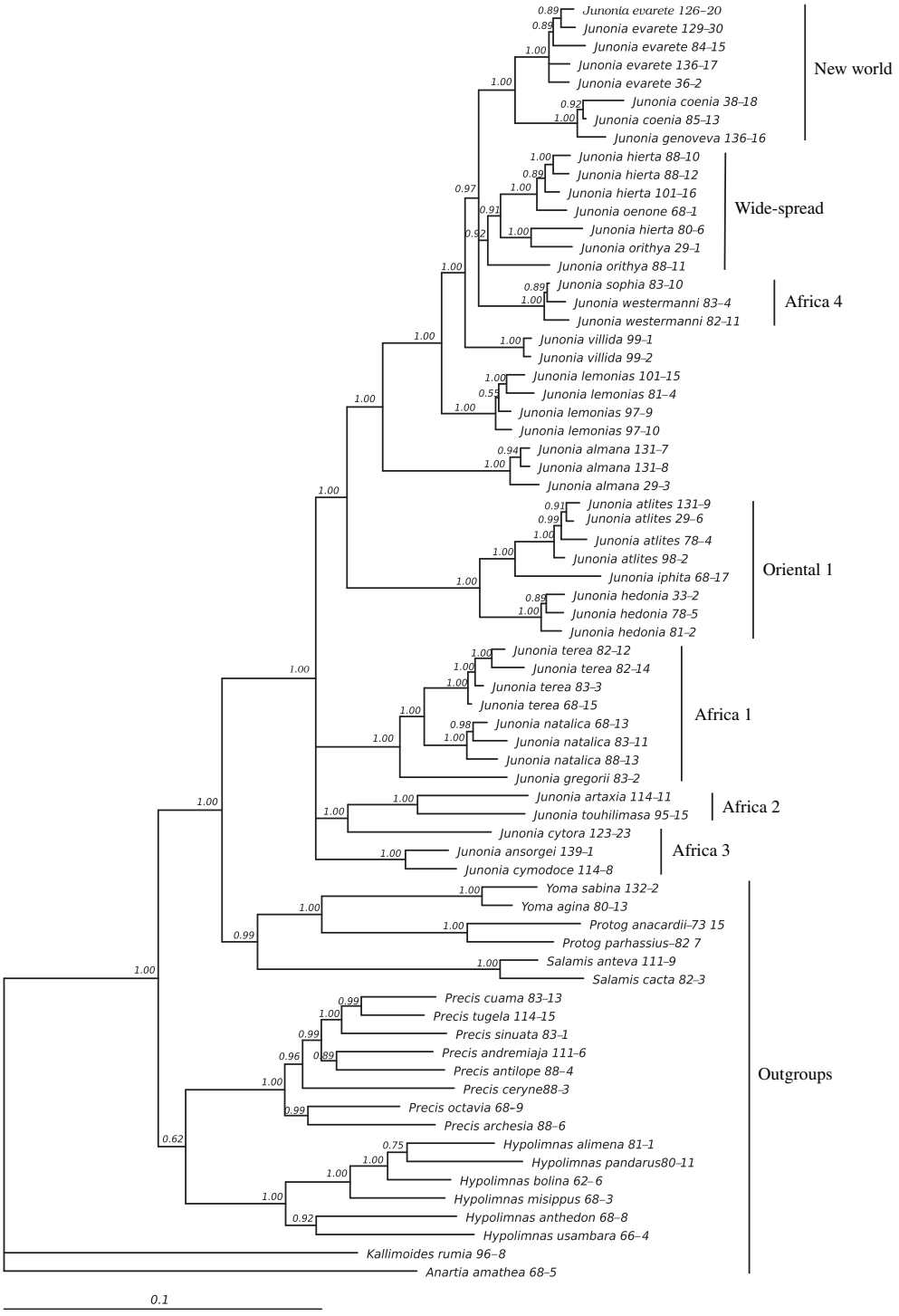

Fig. 2 Phylogeny resulting from the Bayesian inference of the combined data set. The numbers are the posterior probabilities of the respective nodes.

General phylogenetic patterns

Junonia was sister to the clade consisting of *Salamis*, *Protogoniomorpha* and *Yoma*, consistent with Wahlberg *et al.* (2005b). Within *Junonia*, the African endemics were clustered into five distinct clades with good support for their respective monophyly. For the purpose of this study, we assign names to these clades and the same are

labelled in relevant figures as Africa 1, Africa 2, Africa 3 and Africa 4, whereas the fifth clade was formed by a single species *J. oenone*. The affinities of Africa 1, 2 and 3 were not resolved in this study and represent a polytomy along with the clade consisting of the rest of the *Junonia* species. The Oriental endemic species clustered into three clades. The first clade consisted of *J. atlites*, *J. hedonia* and *J. iphita* and is referred to as Oriental 1. *Junonia almana* and *J. lemonias* made up the other two clades. The New World species formed a monophyletic group, which will be referred to as the New-World clade.

The two widespread species *J. hierta* (which ranges from Africa to Asia) and *J. orithya* (Africa through Asia to Australia) are recovered as polyphyletic units in this study. Both species together formed a clade along with *J. oenone* (endemic to Africa). We refer to this clade as 'Wide-Spread'. The Wide-Spread clade formed a higher clade with the New-World clade and the Africa 4 clade (*sophia-westermanni*). This clade was recovered as a polytomy.

Biogeographical patterns

The Bayesian topology was used for further interpretations. The unresolved nodes in the phylogeny posed a few problems for the biogeographical analysis. We considered all sister-group relationships among the groups subtended by the unresolved nodes, and the biogeographical scenario presented here does not conflict with any of these possible relationships.

The best ancestral state optimizations are indicated in Fig. 3. The Africa 1, 2 and 3 clades are depicted as two clades for simplicity, with one of them being sister to the rest of the *Junonia* species. Other possible relationships among these species did not affect our interpretations. The grey ovals indicate uncertain ancestral state reconstructions. Based on the optimal reconstruction of DIVA, we infer events in the evolution of *Junonia* as follows. The ancestor of *Junonia* diverged from the ancestor of *Yoma*, *Protogoniomorpha* and *Salamis* in Africa, thus making Africa the origin of *Junonia*. The species *J. natalica*, *J. gregorii*, *J. terea*, *J. artaxia*, *J. ansorgei*, *J. cymodoce* and *J. touhilimasa* descended from this ancestor through speciation within Africa. One descendant of the ultimate African ancestor of *Junonia* colonized Asia, most probably across the Arabian Peninsula. This ancestor first gave rise to the *atlites-iphita-hedonia* clade within Asia. *Junonia hedonia* later expanded its range into the Australasian region. *Junonia almana* and *J. lemonias* speciated in Asia. *Junonia villida* colonized Australasia from Asia.

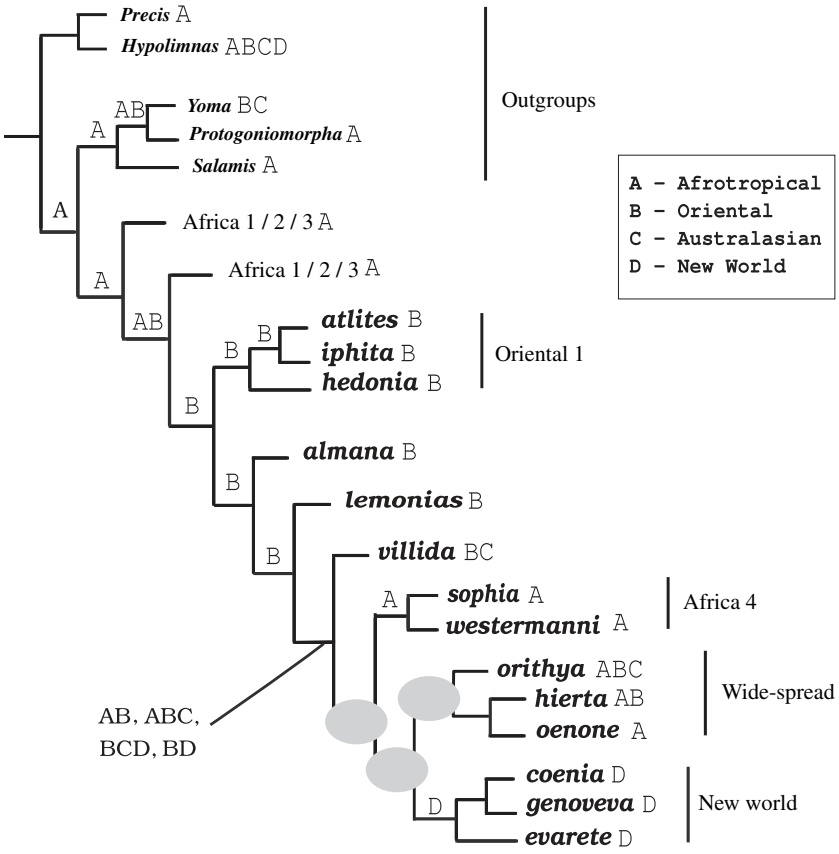

Fig. 3 Best ancestral state reconstruction based on dispersal-vicariance analysis. Shaded areas indicate uncertain ancestral state reconstructions.

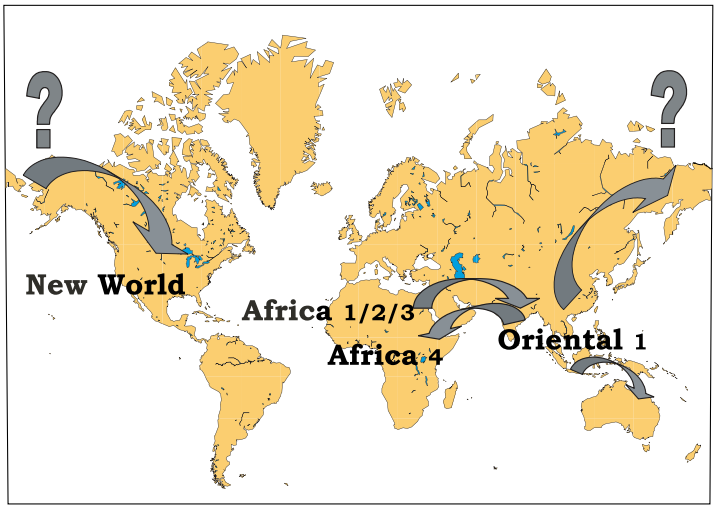

Fig. 4 Major inter-continental routes of dispersal. The colonization route of the New World is ambiguous.

The Africa 4 clade, the New-World clade and the Wide-Spread clade were the eventual result of dispersal events out of Asia. Owing to the unresolved relationships between these clades, DIVA was unable to shed more light on the details of these 'Out-of-Asia' dispersals (Fig. 4).

Molecular dating estimates

The optimal smoothing parameter, as determined by the cross-validation run, was 32. The ultrametric tree from the r8s dating analysis with a smoothing parameter of 32 is shown in Fig. 5. With the divergence of Junoniini constrained at 35.5 Ma, the first divergence in *Junonia* is estimated to have happened about 20 Ma (range 27–15 Myr). The first colonization from Africa to Asia is dated to have occurred about 19 Ma (range 14–26 Myr), for the topology used in the r8s estimate. The back-dispersal event that gave rise to the Africa 4 clade (*sophia-westermanni*) is dated at around 0.8 Ma (range 0.6–1.0 Myr). The colonization of the New World is indicated to have happened around 3.1 Ma (range 2.3–4.2 Myr).

Discussion

Inferences made from a phylogeny are only as good as the phylogeny itself. In our case, although a few nodes are unresolved, the resolved nodes are well supported as indicated by the support values. Thus our inferences have good backing in the phylogeny. The unresolved nodes had short branches leading to them, suggesting that it is a lack of signal in the data rather than conflicting signal that is the cause of the poor resolution. We think this is due to rapid speciation from a single ancestor at different points in the phylogeny. The additional sequences did not improve resolution and this further emphasizes our viewpoint.

This study was focused more on intercontinental biogeography. We did not have enough taxon sampling to refine our analysis to get more information on within-continent speciation. The results clearly indicate that *Junonia* began evolving in Africa. This is not very surprising given the fact that most of the genera of Junoniini occur within Africa. Due to the lack of resolution, we were unable to enquire further into speciation within Africa among lineages that were direct descendants of this ancestor.

Africa was part of Gondwana and was attached to South America in the west and Antarctica in the south from the time when Gondwana was formed up to about 100 Ma (McLoughlin, 2001; Sanmartín & Ronquist, 2004). The Arabian Peninsula was attached to the north-eastern part of Africa. Africa started drifting away from Antarctica around 100 Ma, at an average rate of 2–3 cm per year (McLoughlin, 2001). Eventually this resulted in the collision of Arabia with Eurasia. Although the final closure of the Neotethys Ocean, which separated the two plates, took place sometime during the early Miocene (23.8–5.3 Ma) (Stonely, 1981), land connections were formed between Arabia and Eurasia earlier (Hessami *et al.*, 2001). The first colonization event into Asia is dated at about 19 Ma. This indicates that colonization occurred across the Arabian Peninsula, through the newly formed land bridges. We stress that the age of Junoniini determined by Wahlberg (2006) was based on fossil evidence, not biogeographical scenarios. However, we have to add a note of caution here that the confidence intervals for our age estimates here are quite high. Apparently the aridification of the Sahara and the Arabian Peninsula, which occurred somewhere around 16–17 Ma (Douady *et al.*, 2003), was a harsh enough barrier to make the colonization of Asia by *Junonia* unlikely. Our results suggest that extant Asian *Junonia* are the progeny of only one colonizing ancestor from Africa.

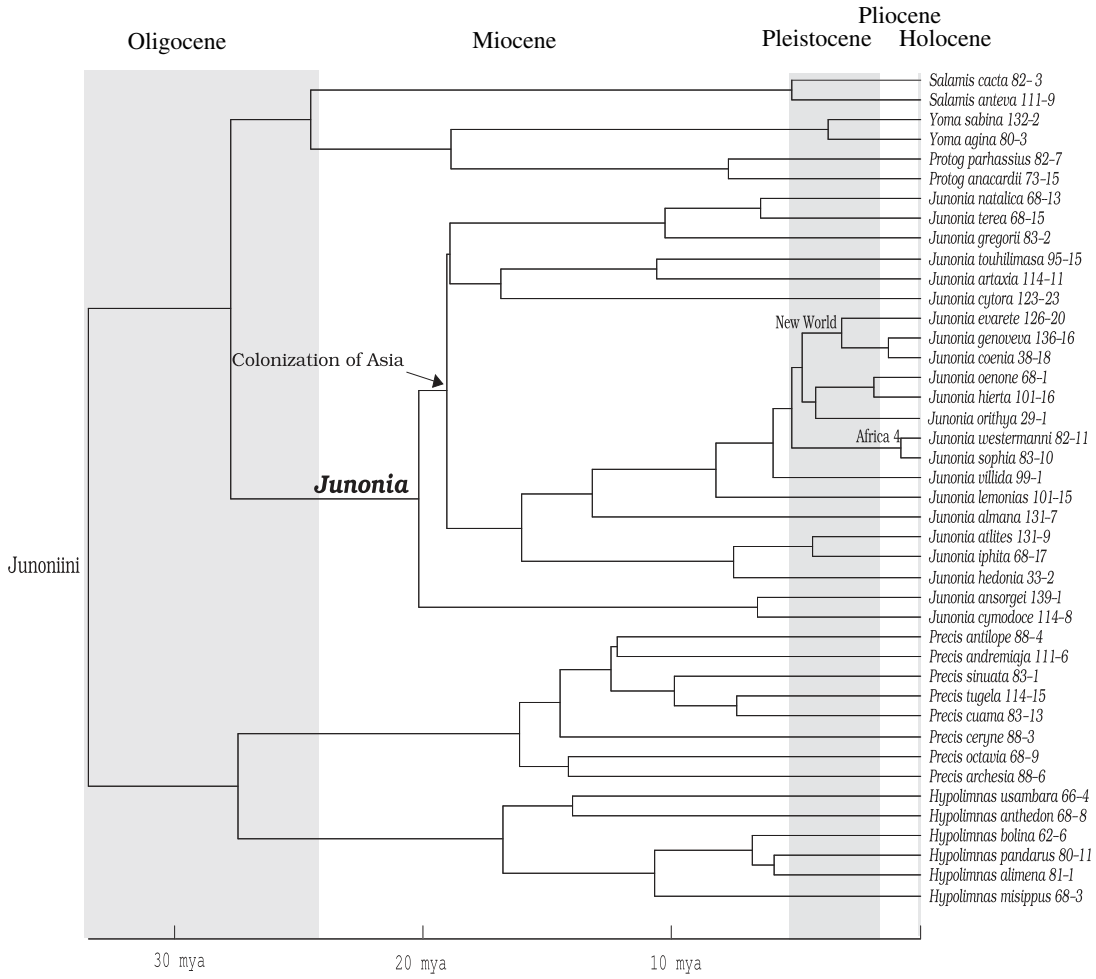

Fig. 5 Estimated divergence times using Penalized Likelihood (using the software r8s) based on the topology with the highest likelihood score in the Bayesian analysis.

Within Asia, the first species to diverge were *J. atlites*, *J. iphita* and *J. hedonia*, which are morphologically similar to their African ancestors. The next species to diverge from the ancestral Asian *Junonia* were *J. almana*, *J. lemonias* and *J. villida*, which are morphologically different to the more basal species. It is likely that the ancestor of *J. villida*, Wide-Spread clade, Africa 4 clade and the New-World clade had high dispersal abilities, which enabled it to colonize Africa, Australia and the New World from Asia. Eventually, the different clades diverged allopatrically in Africa (the Africa 4 clade) and the New World (New-World clade). DIVA indicates the ancestor of the Wide-spread clade as Africa in all the analyses, which means that *J. hierta* and *J. orithya* expanded their range into Asia through post-speciation dispersal. This is a reasonable explanation as these two species are the most widespread among the extant members of the genus. Within the Wide-Spread clade, the lack of monophyly of *J. hierta* and *J. orithya* could be explained either by hybridization in the past or incomplete lineage sorting in these widespread species which presumably had large ancestral populations.

The route of colonization of the New World is unclear. The ancestor could have colonized the New World directly through the Beringian Strait. In another scenario the dispersal could have occurred through a trans-Atlantic dispersal from Africa, in which case the New-World clade would be sister to either the Africa 4 clade or the Wide-Spread clade.

The singular feature of the biogeography of *Junonia* is the absence of any identifiable vicariant pattern at the intercontinental level. This contrasts with other studies on butterfly biogeography (e.g. Braby *et al.*, 2005; Braby & Pierce, 2007) where vicariant patterns have been indicated to be predominant at similar geographical scales. It could be argued that vicariance was important in the evolution of *Junonia* and that its traces have been obliterated by subsequent dispersals and extinctions. We believe that

invoking such additional events is less parsimonious and thus directly opposed to the principle on which vicariance biogeography *per se* was founded upon.

Thus, the northwards drifting Africa harboured the ancestral Junoniini and perhaps earlier ancestors as well (Wahlberg, 2006). Were these lineages from Gondwana or did they appear in Africa as a result of dispersal across the forming Atlantic Ocean from South America? According to Wahlberg (2006), the common ancestor of the subfamily Nymphalinae (to which Junoniini belongs) diverged around 65 Ma in South America, with a colonization event of Africa soon after. Speciation within Africa eventually gave rise to the ancestor of *Junonia* around 20 Ma. Thus *Junonia* seems to have first started evolving on the rafting African plate. To our knowledge, this is the first study showing such a pattern in butterflies.

The taxon pulse hypothesis of Erwin (1979, 1981) is a model of speciation where both vicariance and dispersal are taken into account. It states that the distributional ranges of taxa expand and contract around a 'stable centre'. Taxon pulses are characterized by dispersal during expansion into suitable habitat when previous barriers break down and this expansion phase may lead to peripheral isolates speciation (Halas *et al.*, 2005). This model fits well with the history of *Junonia*. In the case of *Junonia*, such an expansion phase initially occurred from Africa when the land bridge was formed between Arabia and Asia. Later on, Asia was the 'stable centre' from where further range expansions took place into Australasia, Africa and South America. Similar patterns of diversification have been shown in primates, hyaenas, proboscids and primate parasites using a PACT (Wojcicki & Brooks, 2005) analysis by Folinsbee & Brooks (2007). In all these groups, a first episode of species formation in Africa was followed by 'Out of Africa' dispersal into Europe, Asia and North America. There was a second episode of species formation in Asia, followed by 'Out of Asia' dispersal into Africa, Asia and North America. In particular, the collision of Africa with Asia/Europe is likely to have led to the dispersal of numerous other taxa into Europe and Asia. Such congruent, temporally correlated dispersal patterns have been called geo-dispersals (Lieberman & Eldredge, 1996; Lieberman, 1997, 2000).

We here show that dispersal can leave identifiable patterns, which can be recovered through a phylogeny and a historical biogeographical analysis. We argue that dispersal has played a pivotal role in the diversification of butterflies. For groups such as *Junonia* which have evolved after the break-up of Gondwana, there is little reason to assume that vicariance has been important at the intercontinental level. Taxon pulses and geo-dispersal patterns are much more likely to have been predominant.

Conclusions

Here we show that speciation mediated by dispersal can produce strong and interesting patterns which can be inferred with good confidence, given a robust phylogeny for the group. We provide a good example using the genus *Junonia*, where we infer the intricate series of dispersal events that have shaped its global distribution. We infer that the genus had its origin on the northwards drifting Africa, followed by dispersal to Asia after the collision of the Arabian Peninsula against Asia. There were further dispersals to Australia from Asia. Africa was back-colonized from Asia at least twice, and the New World species were the result of a long-distance dispersal event. The taxon pulse model of Erwin (1979) fits well with the history of *Junonia* and merits more attention within historical biogeography. We argue that the role of dispersal in speciation at the global scale within butterflies has been underestimated. As more and more butterfly groups are investigated biogeographically, we predict that dispersal will be found dominant.

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Supplementary Material

The following supplementary material is available for this article:

Table S1 List of specimens used in the study with their voucher ID and genbank accession numbers for the respective genes.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1420-9101.2007.01425.x.

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