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Historical biogeography and the evolution of the latitudinal gradient of species richness in the Papionini (Primata: Cercopithecidae)

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We apply historical biogeography techniques to the macaques, baboons and their relatives (Primata: Papionini) and relate the inferred history of range shifts, and associated evolutionary events, to the latitudinal distribution of extant species, which is strongly tropical. The results of reversible parsimony, weighted ancestral area and dispersal-vicariance analyses all agree that Central Africa was part of the range of the ancestor of the tribe. Tropical regions with high current species richness (Central Africa, South-east Asia, Indonesia) have: (1) had a relatively long history of occupation, (2) experienced both a greater number and a greater average rate of speciation events and (3) given rise to more dispersal events to other regions. However, nested sister-taxon comparisons across the tribe show no overall association between differences in latitude and differences in rates of cladogenesis. Our historical reconstructions are largely consistent with previous hypotheses and fossil data, and suggest that both the passage of time since colonization and rates of cladogenesis have enhanced tropical species richness. Historical biogeography may thus considerably aid understanding of this and other spatial problems in macroecology. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 235–246.

ADDITIONAL KEYWORDS: adaptive radiation – macroevolution – origination – primates – speciation – tropical diversity.

INTRODUCTION

In recent years, the revolutionary advances in cladistic and molecular analyses have made phylogenetic information on living species available as never before. This information provides a potential window on the past that is, to an extent, independent of that provided by the fossil record, and has made it possible to infer the history of evolutionary changes in taxa where it was previously impossible to do so (see Harvey *et al.*, 1996; Pagel, 1999).

One type of data that may be combined with phylogenetic information is the spatial location of extant species. Given appropriate techniques, known collectively by the term ‘historical biogeography’ (Morrone & Crisci, 1995), past geographical distributions can be inferred, together with the processes that have created them, such as the different forms of speciation, extinction and dispersal events (see Croizat, 1958; Nelson & Platnick, 1981; Humphries & Parenti, 1986; Myers & Giller, 1988; Wiley, 1988; Morrone & Crisci, 1995; Avise, 2000). Information on such processes is also useful for macroecologists attempting to understand large-scale spatial patterns such as latitudinal gradients in species richness, body size and geographical range (see Brown, 1995; Gaston & Blackburn, 2000). In this paper we attempt to use such information to uncover the origins of a macroecological pattern; the latitudinal gradient in species richness in the tribe Papionini (Primata: Cercopithecidae).

Although historical biogeography has been established as a discipline for more than 180 years (Morrone & Crisci, 1995), few studies have attempted to relate the results of such analyses to major macroecological patterns (see Gaston & Blackburn, 2000). A recent study by Bleiweiss (1998) investigated the his-

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*Corresponding author. E-mail: pjm19@york.ac.uk tory of range change in hummingbirds using parsimony reconstruction, but only related reconstructions to species richness patterns in a descriptive *post hoc* fashion. Furthermore, although some macroecologists have attempted to document the historical and evolutionary processes underlying spatial patterns (see Stehli, Douglas & Kafescioglu, 1972; Jablonski, 1993; Flessa & Jablonski, 1996; Gaston & Blackburn, 1996; Cardillo, 1999; Sepkoski, 1999; Proches, 2001; Stuart-Fox & Owens, 2003), none to our knowledge have done so using methods of historical biogeography.

We set out to assess the potential of historical biogeography in helping to understand one of the prominent spatial macroecological patterns. As a case study we searched for a group that (1) has a well-resolved and complete species-level phylogeny, (2) has range data for all species and (3) displays a prominent macroecological pattern. Primates are possibly the most completely studied substantial clade phylogenetically, and, because they are known to be a largely tropical group, were likely to display the classical latitudinal gradient in species richness. From the primates, we chose the best resolved part of the tree that contains a large number of species (>20): the old world monkey tribe Papionini, containing the gelada, baboons, the drill, the mandrill, mangabeys and macaques (Table 1). Their distributions are also reasonably well known.

Previous scenarios, based on fossils and current distributions, suggest a sub-Saharan African origin for the clade. Following this, an African radiation of baboons and relatives occurred, whilst the macaques dispersed into Eurasia and radiated in South-east Asia (see Szalay & Delson, 1979; Abegg & Thierry, 2002; Jablonski, 2002). We wished to observe whether historical biogeography would confirm this hypothesis.

In addition, we wished to use the historical reconstructions to identify the processes responsible for the current tropical distribution of species. There are three major potential causes of tropical species richness: (1) latitudinally biased dispersal (e.g. Gaston & Blackburn, 1996; Bleiweiss, 1998), such that there is less dispersal away from tropical regions or differential invasion of the tropics by temperate species; (2) a long history of occupation and hence longer time for diversification (e.g. Jablonski, 1993; Bleiweiss, 1998; Proches, 2001); (3) higher tropical net rates of cladogenesis (e.g. Cardillo, 1999).

METHODS

DATA

Species definitions of Corbet & Hill (1991) matching those in the phylogeny (Purvis, 1995) were used in the analysis. Purvis (1995) provides a supertree of all living primate species based on a large sample of previous phylogenetic studies and constructed using matrix representation with parsimony. The tree has been widely used for comparative evolutionary studies. Geographical distributions came from the UNEP World Conservation Monitoring Centre database (http://www.wcmc.org.uk), refined to the nearest degree latitude and longitude using Honacki, Kinman & Koeppl (1982) and Nowak & Walker (1999). The resulting species richness gradient is illustrated in Figure 1.

BIOGEOGRAPHICAL RECONSTRUCTION

To estimate the history of range change we used three recently developed methods with contrasting assumptions. Reversible parsimony analysis of ancestral areas as described in Ronquist (1994) was implemented in MacClade 4 (Maddison & Maddison, 2000). This method minimizes changes in distribution across the phylogeny, and favours dispersal over vicariance scenarios because they require fewer steps.

We weighted changes according to the minimum overland distance between the centre of regions (see Fig. 1), hence minimizing actual dispersal distance. This is a logical progression on Ronquist's method that acknowledges that some dispersal events are more likely to occur than others by virtue of geographical proximity. Distances were obtained from map measurements of the shortest overland distance between

Table 1. List of the genera analysed, their ecology and distributions. Taxonomy is taken from Corbet & Hill (1991)

Genus	Species	Common names	Description	Distribution
Cercocebus	4	mangabeys	medium sized arboreal forest monkeys	Central Africa
Macaca	16	macaques	heavily built, partly terrestrial monkeys	North Africa to Japan and Indonesia
Mandrillus	2	drill, mandrill	large terrestrial forest monkeys	Central Africa
Papio	5	baboons	robust terrestrial monkeys of open habitats	Arabia to Southern Africa
Theropithecus	1	gelada	large terrestrial grazer of high altitude grasslands	Ethiopia

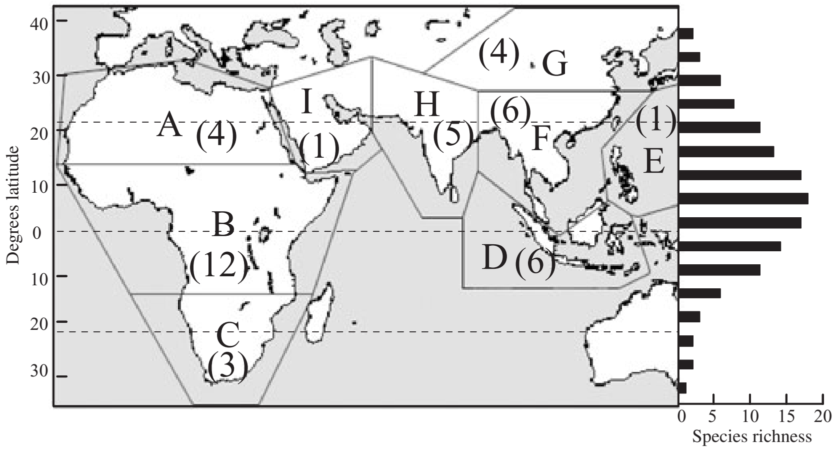

Figure 1. Regional divisions used in historical biogeography analyses. Numbers in parentheses indicate number of Papionini species found in each area. The equator and the tropics are shown as dashed lines. Species richness per 5 degree latitudinal band is shown at the right.

the midpoint of one region (means of the maximum and minimum longitudes and latitudes) and the midpoint of another (mm on a 1: 4×10^7 constant-distance scale map of the globe), assuming initially that the Philippines were colonized via the shortest overseas route from Indonesia, and Indonesia from Singapore. Because the time scale involved is geologically very short (< 10 Myr), there are no major problems in assuming a static regional distribution.

The second method was weighted ancestral area analysis (WAAA) (Hausdorf, 1998), implemented with MacClade 4. The output is a probability index (PI) for each node that each area is ancestral to that node, and is calculated from the ratio of number of range changes required, first assuming that an area was not ancestral and then assuming that it was. The method uses a weighting procedure such that ranges of species which branch close to the root of the tree are more likely to be estimated as ancestral.

The third method was dispersal-vicariance analysis (DVA), implemented in DIVA 1.1 (Ronquist, 1996). In DVA, optimum ancestral distributions are inferred by minimizing the number of dispersal and extinction events (Ronquist, 1997). As a result, this type of analysis puts high emphasis on vicariance events. Two trichotomies in the tree (see Fig. 2) were resolved by running the analysis on all possible (nine) fully bifurcating trees. These resolutions all gave very similar results.

Although initially unrestricted, the maximum number of areas an ancestor can inhabit was later restricted to two. The amount of dispersal required when no limit is placed on the number of ancestral regions gives an indication of the importance of dispersal in generating present-day distributions (see Zink, Blackwell-Rago & Ronquist, 2000). Restriction allows the identification of a more local centre of origin, and also delimits the possible area ranges of descendant lineages. This conforms to the assumption that new species first become established within restricted local populations from which they may then spread into larger areas over time (see Barton, 1994; Zink *et al*., 2000). When DVA returned several equally optimal solutions, we made a *post hoc* inspection to examine their plausibility. Solutions were considered more plausible if ancestral areas were less disjunct (i.e. adjacent).

All the above analyses required us to code distributions into discrete regions (Fig. 1). Regions were chosen in order to represent areas of endemism (areas with many species and species not found elsewhere), to provide different latitudes for later analyses, and to maximize the discriminatory power of the reconstructions (having few areas in total). The regions were: North (A), Central (B), and Southern Africa (C), Indonesia (D), the Philippines (E), South-east Asia (F), Northern Asia (G), the Indo-Afghan region (H), and Arabia (I). Because the sister clade to the group of interest (the Cercopithecini; Purvis, 1995) is entirely Central African, that was taken as the outgroup state (Fig. 1) for DVA and reversible parsimony (WAAA does not use outgroup information).

STATISTICAL ANALYSES

Using the events implied by the historical reconstructions, we tested for associations across geographical regions using the nine regions in Figure 1. In particular we wished to know whether any of their features (size, average latitude, time since first occupation) might explain the frequency of evolutionary events and current species richness. This was done using cor-

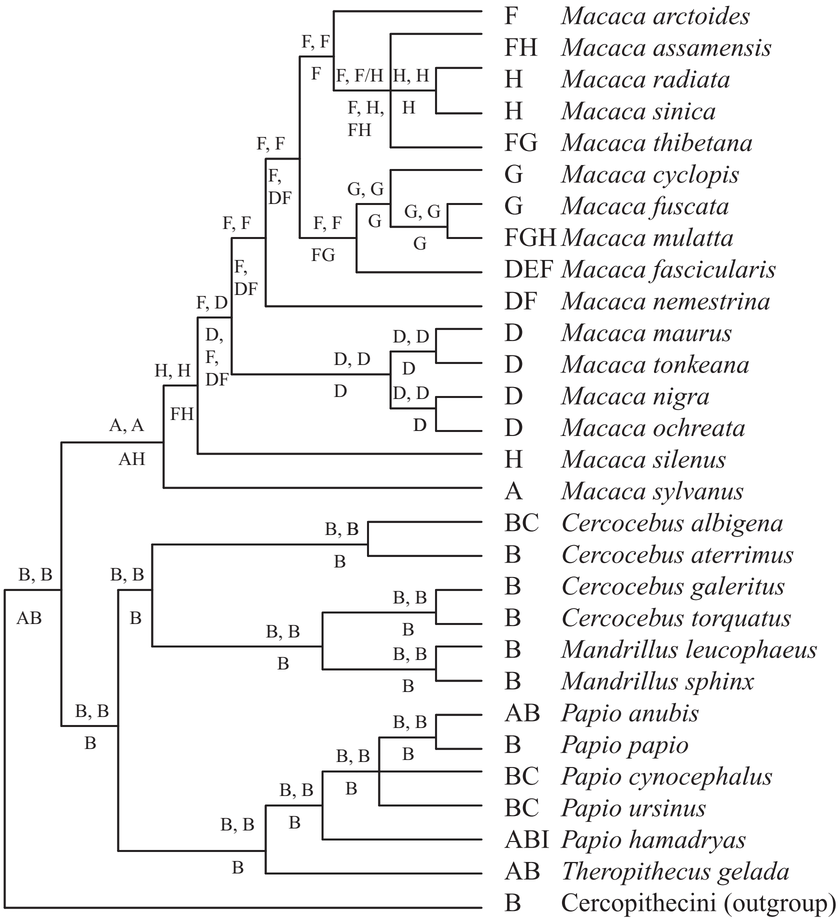

Figure 2. Phylogenetic topology used in the study. Letters refer to the areas in Fig. 1, and indicate range data used in the analysis (for terminal species) and optimal reconstructions to the left of each node. Letters above branches are from reversible parsimony, WAAA, below branches from DVA (preferred solutions when maximum areas is restricted to two). For DVA there were several equally optimal solutions at some nodes, and for WAAA one trichotomy gave two alternative results depending on how it was resolved. (A) North Africa, (B) Central Africa, (C) Southern Africa, (D) Indonesia, (E) Philippines, (F) South-east Asia, (G) Northern Asia, (H) Indo-Afghan, (I) Arabia.

relation, treating each region as an independent replicate. Because land area varied considerably between regions, we investigated the effect of controlling for it using partial regression. We debate the implications of this approach in the Discussion.

These analyses involve a considerable number of comparisons between variables, raising the overall probability of a Type I error. Therefore, sequential Bonferroni correction was carried out on the significance levels (Rice, 1989). The value of such correction is still debated in the ecological and evolutionary literature (e.g. Moran, 2003; Neuhäuser, 2004). In general, we do not believe that Type I errors represent a problem for our analyses for two reasons: (1) some tests remain significant even after such correction, showing that we can reject the overall null hypothesis of no associations in the data; (2) we always find many more significant results before correction than predicted by the Type I error rate. Significance values are therefore reported both before and after correction.

The relationship between latitude and rates of diversification was tested using a standard comparative technique that is independent of the historical biogeography analyses (see below). However, we also wished to use the reconstructions described above to allow greater comparability with the other analyses. To do this, we first totalled for each region the number of speciation events implied from each reconstruction (for DVA this included both vicariance and sympatric speciation). We then controlled for the area of each region by regressing the number of speciation events against land area and taking residuals as our relative measure of the number of events.

Regions with high residual values had experienced much speciation relative to their land area, whilst those with low residual values had experienced little.

These residuals were then divided by the time since a region was first occupied, giving a relative measure of the average rate of species creation. Finally, we investigated the relationship between this relative rate and the midlatitude of a region using correlation. This approach is, again, evaluated in the Discussion.

We also investigated whether differences in latitude are related to diversification rate using nested sister-taxon comparisons implemented in MacroCAIC (Agapow & Isaac, 2002). Measures of clade richness are regressed (through the origin) against contrasts in the predictor variable, in this case latitudinal change. The relative rate difference (RRD), also known as LnCladeRatio (Agapow & Isaac, 2002), is the statistically most robust measure of clade richness when nodal ages are known (see Isaac *et al*., 2003). The RRD is the natural logarithm of the ratio of the clade size with high latitudinal values (i.e further away from the equator) to the clade size with low latitudinal values.

We initially used untransformed latitudinal data (degrees) for ease of subsequent interpretation. Species were assigned the mean of their northern and southern range margins. Latitudes were however, subsequently square-root transformed to conform to statistical assumptions. Branch lengths were coded in units of time from the phylogeny as recommended (Isaac *et al*., 2003). Solely to remove negative branch lengths resulting from conflicting estimates of the age of the node, we designated the age of *Macaca silenus* as 3 Myr, and the age of the common ancestor of baboons, mangabeys, mandrills and geladas as 6.73 Myr. For our initial analysis we used absolute latitudinal values (i.e. regardless of sign) as our species data. This tests the null hypothesis that diversification will be independent of raw distance (in degrees) from the equator. To estimate precise ancestral latitudes however, the sign of the latitudinal values was used.

RESULTS

BIOGEOGRAPHICAL RECONSTRUCTIONS

Estimates of ancestral geographical ranges are given in Figure 2. All three methods agree that Central Africa was part of the range of the common ancestor of the Papionini. Under reversible parsimony, the next most parsimonious ancestral areas after Central Africa were North Africa, Arabia and Southern Africa (Table 2); the least parsimonious ancestral area was the Philippines.

Under WAAA, Central Africa is the optimal ancestral area, although North Africa is another likely possibility (Table 2). Other areas are comparatively unlikely ancestral locations and the Philippines is the least optimal. Under DVA, when the number of ancestral areas was unlimited, 17 dispersal events were required and the ancestral area was optimized as ABDFH or ABDEFGH, i.e as of trans-Afro-Asian origin. When the number of areas was constrained to two or less (three is the maximum in extant taxa and one is the mode), the number of equally optimal solutions was quite large at the root, with AB, BD, BF or BH being the ancestral area. Of these, only AB is plausible since other area combinations are not geographically adjacent.

All methods also agree on a Central African origin for all lineages of *Theropithecus*, *Papio*, *Mandrillus* and *Cercocebus* (Fig. 2). Ancestral ranges are more equivocal in the genus *Macaca*, but there are some areas of agreement where lineages are estimated by all methods to have radiated in one region, such as the Indonesian radiation (*M. maurus* + *M. tonkeana* + *M. nigra* + *M. ochreata*), the North Asian radiation (*M. cyclopis* + *M. fuscata* + *M. mulatta*) and one Indo-Afghan speciation (*M. radiata* + *M. sinica*) (Fig. 2).

Table 2. Results of the WAAA and reversible parsimony analysis for the root of the Papionini. *Abbreviations:* WGS, weighted gain steps; WLS, weighted loss steps; PI, probability index (= WGS/WLS; see Hausdorf, 1998); S, number of steps; RP, relative probability (= S_{min}/S_i; see Ronquist, 1994)

Region		WAAA			Parsimony	
		WGS	WLS	PI	S (km × 10^3)	RP
A	North Africa	1.167	1.25	0.934	54.44	0.946
B	Central Africa	1	1	1	51.52	1
C	Southern Africa	0.5	2.167	0.231	59.80	0.862
D	Indonesia	0.333	2.310	0.144	80.08	0.643
E	Philippines	0.143	2	0.072	86.96	0.592
F	South-east Asia	0.361	2.268	0.159	73.32	0.703
G	Northern Asia	0.268	2	0.134	73.64	0.700
H	Indo-Afghan	0.587	2.125	0.276	65.16	0.791
I	Arabia	0.25	2	0.125	59.60	0.864

RELATIONSHIPS ACROSS REGIONS

The relationship between the size of a region and current species richness was positive but marginally non-significant (Pearson's $r = 0.600$, $P = 0.088$), while that between the absolute mid-latitude of a region and current species richness was non-significantly negative ($r = -0.568$, $P = 0.110$). However, controlling for the size of a region by partial regression, species richness became significantly associated with latitude ($b = -0.201$, $P = 0.011$). Controlling for latitude, species richness became significantly associated with area ($b = 4.84 \times 10^{-7}$, $P = 0.009$). The relationship between the size of an area and its mid-latitude was not significant ($r = 0.145$, $P = 0.709$).

Bivariate relationships between these regional traits and the number of biogeographical events in the historical reconstructions are given in Tables 3–5. Under both reversible parsimony and WAAA, the number of species in a region was positively associated with the length of time since it was initially occupied and the number of speciation events that had occurred (e.g. Fig. 3). Regions that had been occupied for longer tended to be larger, and had experienced more speciation events and gives rise to more dispersal events away from the region (e.g. Fig. 4). Regions that were the source of range extensions tended to be on the receiving end of relatively few. Under DVA the results were similar: more speciation was associated with regions which were both larger and had been occupied for longer. Such regions also gave rise to more dispersal events (Table 5). Latitude was in all cases non-significantly associated with the frequency of evolutionary events. However, there was a trend for regions at low latitudes to have been occupied for longer, experienced more speciation, given rise to more dispersal, and to have received less dispersal (Tables 3–5).

Controlling for the area of a region by partial regression, there was a significant negative association between latitude and (1) time since an area was first colonized, and (2) number of speciation events (Table 6). An exception was in DVA, where the relationship between time since occupation and latitude was not significant, whilst that between dispersal from an area and latitude was.

RATES OF CLADOGENESIS

Using the relative rate of cladogenesis per region calculated from the historical reconstructions was significantly negatively related to latitude in the parsimony analysis ($N = 6$, Spearman's $r = 0.899$, $P = 0.015$), and also in WAAA and DVA (both analyses $N = 6$, Spearman's $r = 0.812$, $P = 0.05$) (Fig. 5). Sample sizes were reduced because three areas were colonized only after the most recent speciation event and a diversification rate cannot be calculated.

Table 3. Relationships between the characteristics of geographical areas (Fig. 1) and the frequency of evolutionary events as determined by parsimony analysis (Fig. 2). Numbers are Spearman's rank correlation coefficients (cells above and to the right; $^{*}P < 0.05$, $^{**}P < 0.01$) and associated two-tailed probabilities (cells below and to the left). In all cases $N = 9$. Coefficients remaining significant after sequential Bonferroni correction are in parentheses. By chance alone, 1.8 significant results are expected, and 8 are found

	Species richness	Size[1]	Mid-latitude[2]	Time[3]	Speciation[4]	Transition to[5]	Transition from[6]	Extension to[7]	Extension from[8]
Species richness		0.506	–0.587	0.747*	(0.983**)	0.416	0.627	–0.241	0.632
Size	0.164		0.118	0.848*	0.536	0.219	0.634	–0.246	0.663
Mid-latitude	0.096	0.768		–0.299	–0.609	0.037	–0.301	0.279	–0.195
Time	0.021	0.004	0.434		0.771*	0.464	0.796*	–0.125	0.534
Speciation	0.001	0.137	0.081	0.015		0.420	0.685*	–0.332	0.683*
Transition to	0.265	0.571	0.925	0.208	0.261		0.429	0.342	–0.038
Transition from	0.073	0.067	0.432	0.010	0.042	0.250		–0.098	0.487
Extension to	0.581	0.524	0.467	0.748	0.383	0.368	0.802		–0.710*
Extension from	0.068	0.051	0.616	0.139	0.043	0.923	0.184	0.032	

[1] Current land area of the region ($km^2 \times 10^6$).

[2] Absolute value of the mean of the maximum and minimum latitudes.

[3] Myr since the area was first occupied according to the age of nodes in the reconstruction.

[4] Total number of speciation events in the region according to the optimal reconstruction.

[5–8] Total number of events in which:

[5] a region was newly occupied by a species which did not retain its range in the source area.

[6] a species gave rise to a dispersal event while not retaining presence in the former region.

[7] a region was newly occupied by a species which retained its range in the source area.

[8] a species gave rise to a dispersal event while retaining presence in the former region.

Table 4. Relationships between the characteristics of geographical areas (Fig. 1) and the frequency of evolutionary events as determined by one of the two equally optimal reconstructions under weighted ancestral area analysis (Fig. 2). Numbers are Spearman rank correlation coefficients (cells above and to the right; *$P < 0.05$, **< 0.01) and associated two-tailed probabilities (cells below and to the left). In all cases $N = 9$. Variable definitions as in Table 1. Coefficients remaining significant after sequential Bonferroni correction are in parentheses. By chance alone, 1.8 significant results are expected, but 9 are found

	Species	Size	Mid-latitude	Time	Speciation	Transition to	Transition from	Extension to	Extension from
Species		0.506	−0.587	0.798*	(0.944**)	0.416	0.818**	−0.214	0.632
Size	0.164		0.118	0.695*	0.587	0.219	0.411	−0.246	0.663
Mid-latitude	0.096	0.763		−0.470	−0.506	0.037	−0.562	0.279	−0.195
Time	0.010	0.038	0.202		0.719*	0.464	0.743*	−0.018	0.373
Speciation	0.001	0.096	0.164	0.029		0.350	0.737*	−0.413	0.789*
Transition to	0.265	0.571	0.925	0.208	0.356		0.555	0.342	−0.038
Transition from	0.007	0.272	0.116	0.022	0.024	0.121		0.005	0.380
Extension to	0.581	0.524	0.467	0.964	0.270	0.368	0.990		0.710*
Extension from	0.068	0.051	0.616	0.323	0.011	0.923	0.314	0.032	

Table 5. Relationships between the characteristics of geographical areas (Fig. 1) and the frequency of evolutionary events as determined by one of the preferred reconstructions under dispersal vicariance analysis (Fig. 2). Numbers are Spearman's rank correlation coefficients (cells above and the right; *$P < 0.05$, **$P < 0.01$) and associated two-tailed probabilities (cells below and to the left). In all cases $N = 9$. Variables are as in Table 1 except where stated. Coefficients remaining significant after sequential Bonferroni correction are in parentheses. By chance alone, 1.8 significant results are expected, but 6 are found

	Species	Size	Mid-latitude	Time	Vicariance[1]	Sympatric speciation[2]	Extinction[3]	Dispersal to	Dispersal from[5]
Species		0.506	−0.587	0.763*	0.510	(0.930**)	0.347	−0.053	0.632
Size	0.164		0.118	0.758*	0.596	0.420	−0.411	−0.009	0.733*
Mid-latitude	0.096	0.763		−0.391	−0.197	−0.564	−0.483	0.406	−0.404
Time	0.017	0.018	0.299		0.818*	0.558	0.000	0.150	0.728*
Vicariance	0.161	0.090	0.611	0.007		0.332	−0.306	0.349	0.653
Sympatric speciation	0.001	0.261	0.113	0.118	0.382		0.287	−0.309	0.556
Extinction	0.361	0.272	0.188	1.000	0.423	0.453		0.000	−0. 244
Dispersal to	0.893	0.982	0.278	0.699	0.358	0.418	1.000		−0.237
Dispersal from	0.068	0.025	0.280	0.026	0.056	0.120	0.527	0.540	

Total number of times in which:

[1] a region was involved in a vicariance event.

[2] speciation occurred in a region with both ancestors and descendants retaining the same range.

[3] a region was deleted from a species range.

[4] a region was newly occupied by a species.

[5] a region gave rise to a dispersal event to another region.

Nested sister-taxon comparisons showed no significant association between latitude and net rate of diversification ($F = 0.043$, d.f. = 1, 14, $b = 0.122$, $P = 0.839$) (Fig. 6). The three most negative diversity contrasts were, respectively, those involving *Macaca sylvanus*, *M. silenus* and *Papio hamadryas* (a–c in Fig. 6), all of which are northerly species and the sister group of a more equatorial radiation. The largest positive contrasts involved, respectively, *Theropithecus gelada* and *Macaca nemestrina* (d and e in Fig. 6). Both are the sister groups of radiations that occurred in less equatorial regions in Africa and Asia, respectively. The divergence between the Indonesian and mainland Asian macaques, and between *Macaca fascicularis* and the Northern Asian macaques (f and g in Fig. 6) both involved large changes in latitude without much change in diversification rate. Using raw latitudinal data (with signs attached), the ancestor of Papionini was estimated to have arisen at 7.87°N.

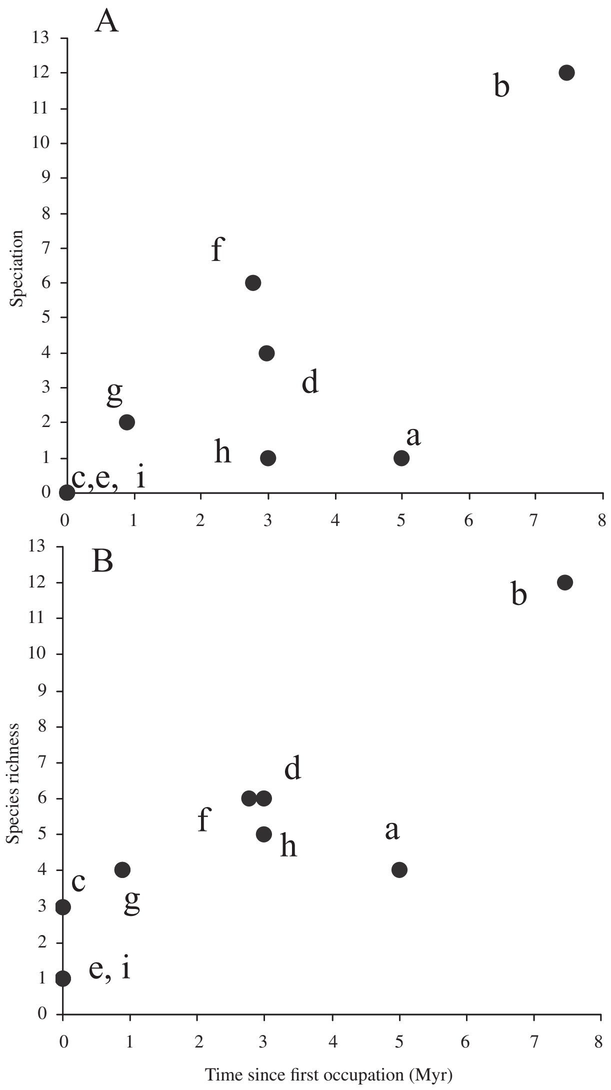

Figure 3. Time since first occupation against (A) the total number of speciation events in that region and (B) current species richness. Time since first occupation and speciation events from one of the optimal reconstructions under WAAA. Letters refer to the regions in Fig. 1.

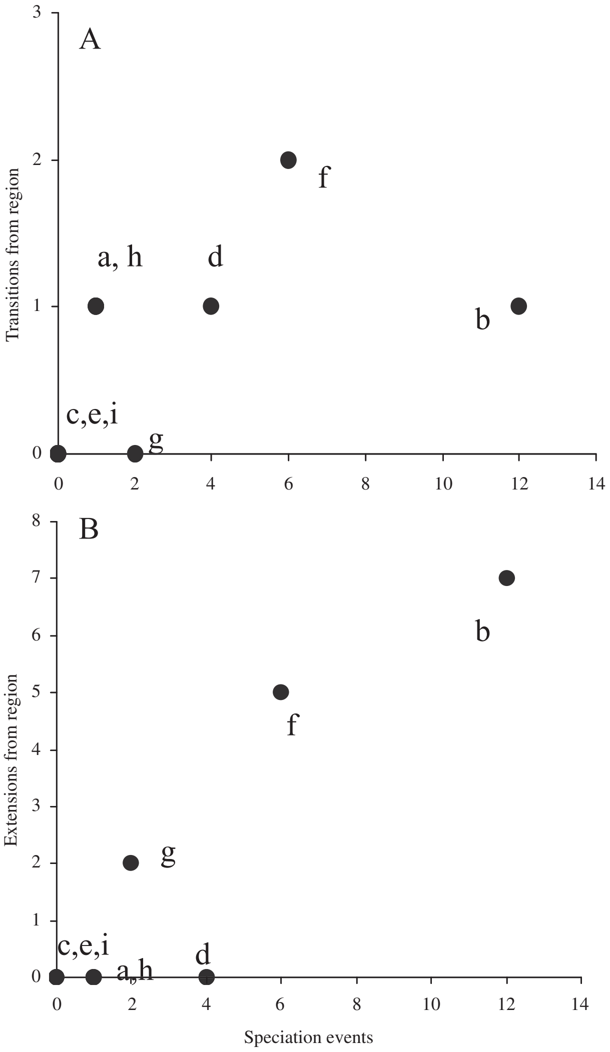

Figure 4. Number of speciation events per region against the number of (A) range transitions and (B) range extensions from that region. Data are from one of the optimal reconstructions under weighted ancestral area analysis. Letters refer to the regions in Fig. 1. A range extension occurs when a species expands to fill a new region while continuing to occupy its previous range. A range transition is when a new region is occupied without retaining the source range.

DISCUSSION

In this study we attempted to apply the techniques of historical biogeography to one of the major macroecological patterns in one taxon, the Papionini. Our analyses suggest that the regions closer to the equator, after controlling for area, have been occupied for longer and have experienced greater rates of cladogenesis, leading to greater species richness. However, they have not received more, or given rise to less, dispersal, and have, if anything, been sources of dispersal to other regions. Historical biogeography therefore supports two of the three hypotheses we set out to test concerning the evolutionary processes underlying the latitudinal gradient in species richness. Nested sister-taxon comparisons, in contrast, fail to support a general relationship between differences in latitude and differences in rate of cladogenesis. Below we put these results in context before discussing their general applicability.

HISTORICAL PATTERNS

All methods agree on an African origin for the Papionini, most probably tropical Africa, a result that is con-

Table 6. Associations between the absolute mid-latitude of a region and evolutionary events in that region, controlling for land area by partial regression. Values are slopes (*$P < 0.05$, **$P < 0.01$). Coefficients significant after Bonferroni correction are in parentheses. By chance alone 0.9 significant results are expected, but 6 are found

	Parsimony	WAAA	DVA
Time	–0.115*	(–0.149**)	–0.121
Vicariance	NA	NA	–0.006
Sympatric speciation	–0.254*	–0.256*	–0.251*
Extinction	NA	NA	–0.015
Transitions to	0.012	0.012	NA
Transitions from	0.013	–0.028	NA
Extensions to	0.031	0.031	NA
Extensions from	–0.105	–0.105	NA
Dispersal to	NA	NA	0.051
Dispersal from	NA	NA	–0.134*

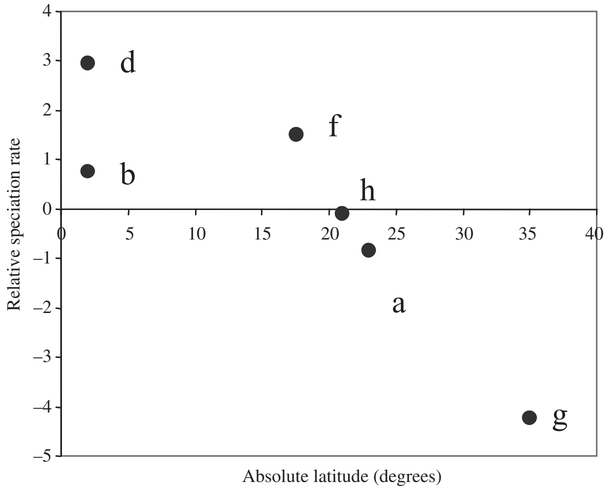

Figure 5. Relative rate of cladogenesis (residual number of speciations per unit land area, divided by time since the region was first occupied) against latitude for the different geographical regions under the parsimony analysis. Letters refer to the regions in Fig. 1. Three regions are excluded because their time since first occupation is estimated as zero.

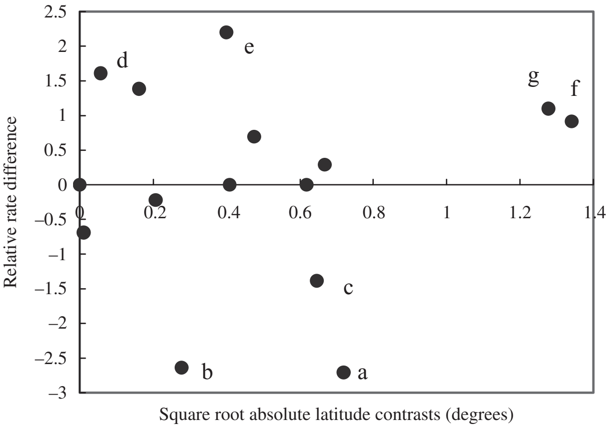

Figure 6. Relationship between diversification rate and latitude using nested sister-taxon comparisons. See text for explanation of letters related to nodes.

sistent with previously published scenarios for the group. The ancestral location may be influential in spatial macroecological patterns, as it is where the clade will have spent the most time. All other things being equal, there may be a tendency for diversity to peak at the site of origin because more time will have been available for the process of diversification. This appears to be true of the Papionini. It is also in line with Jablonski's (1993) finding that first fossils of marine invertebrates are more often found in the tropics than might be expected by chance.

Here we have produced equivalent data, without using fossils, by the use of current distributions and phylogenies. Many taxa have a poor fossil record and for these the only source of data on evolutionary processes may be the kind of analyses we have performed here. To produce an analysis exactly equivalent to Jablonski's (1993) with this new source of data would require repeating our analyses across several taxonomic groups and then comparing the geographical data with a null hypothesis. The prospects for achieving this in the near future are not good, as even with this highly resolved tree there were some ambiguities in our results. However, such an extended analysis may be possible as phylogenetic information improves.

After controlling for the size of a region, we found a significant negative relationship between its latitude and the rate of cladogenesis in all three historical reconstructions. However, this result appears to be contradicted by the nested sister-taxon comparisons, which showed no consistent association between differences in latitude and differences in rate of diversification

Why the discrepancy? The primary difference between the analyses is that data in the former are properties of regions, whilst those in the latter are differences between clades. Given such a difference, there need be no underlying biological contradiction, and in fact both outcomes are intuitive: regions closer to the equator may indeed have given rise to cladogenesis at higher overall rates, but this may not require a consistent decrease in the rate of cladogenesis each time a radiation occurs at a higher latitude, as long as the total radiation rate remains high in species from low latitude regions and low in species from high latitude regions. There are other technical differences between the analyses that may also have been contributory factors: the various rate measures, statistical tests and methods used to estimate ancestral ranges.

In general, our results suggest that some important biology may be missed if only nested sister-taxon comparisons are carried out, a finding that has, arguably, received support from recent work on the effect of body size on species richness (see Orme, Issac & Purvis, 2002). Our results are consistent with those of Stuart-Fox & Owens (2003), who found no consistent relationship using nested sister-taxon comparisons in agamid lizards. Cardillo (1999) found significant relationships for birds and butterflies using non-nested comparisons between taxa with non-overlapping ranges, an analysis we cannot attempt here due to lack of suitable replicates.

Additionally, we found that the regions in which speciation was richest, which tended to be tropical, were also 'source' regions, giving rise to dispersal events into other regions. This is the opposite trend to that expected if biased dispersals were responsible for tropical species richness, but in line with expectations if the tropics are a 'cauldron' of diversity (see Gaston & Blackburn, 1996). Accepting the results at face value therefore provisionally allows us to rule out one and accept two of the three hypotheses we set out to test.

However, should our results be accepted at face value? There are two issues: (1) are the methods reliable in general; (2) are they reliable in this specific case?

ANALYTICAL ISSUES

Brown (1995: 190) has argued against using historical biogeographical methods to infer macroecological process, but that fossils potentially provide a more secure source of data. He reasons that phylogenetically based methods may give a biased or otherwise inaccurate historical picture in the face of extinction or range change within lineages.

We do not deny these potential problems: they are real possibilities for any analysis that attempts to draw historical inferences using phylogenies of extant species. However, in other areas of phylogenetic ecology we believe progress has been stimulated by use rather than disuse, and the result has been not the abandonment of phylogenetic methods but simply more rigorous use in the light of experience, which we expect to see here also (see Pagel, 1999; Freckleton, Harvey & Pagel, 2002). To deal with the problems identified by Brown, studies are needed that identify the power and validity of the methods used. These might include computer simulation. However, an alternative approach, of which the present study is an example, compares fossil patterns with historical/biogeographical reconstructions to see if they match.

What of this particular study? A major finding from the historical reconstructions was that the most species-rich regions were more ancestral. Perhaps this result is not unexpected given the nature of the methods used, yet we can readily envisage evolutionary scenarios in which the ancestral location is not the most species-rich, and signals in the data would allow this to be detected; for example, if a primitive, species-poor taxon occurred in a different region to a derived, species-rich one. This is the case with our data, where the primitive macaque *M. sylvanus* has a North African range, with the rest of the genus being Asian. As seems sensible, our analyses do suggest a spread from North Africa into Asia.

Might extinction have biased our results? Purvis, Nee & Harvey (1995) have estimated zero extinction in the old world monkeys as a whole from the shape of the phylogeny, suggesting that it is a minor problem in the present context. The fossil record of the Papionini rather contradicts this; for example, there are more extinct than extant genera (Szalay & Delson, 1979). The fossil record of the group does, despite this, confirm the general pattern of our analyses, (see Szalay & Delson, 1979; Jablonski, 2002) suggesting that extinction has not been sufficient to bias them. However, one event that is evident from fossils but absent from our data is the colonization of northern Europe by macaques (probably *M. sylvanus*) during periods of climate warming. The discrepancy occurs because our study did not take into account regions which are currently unoccupied by extant species. This perhaps is a warning against an uncritical acceptance of results from historical biogeography.

There are issues concerning the statistical use of historical data. One problem is spatial autocorrelation, by which regions become less independent when they are close together in space. This generally reduces the significance of any relationships, although it does not affect slopes (Clifford, Richardson & Hemon, 1989). Methods for dealing with the problem have been proposed (see Lennon, 2000; Willis, Kaufmann & Stevens, 2004), but are problematic in the present context given the nature of our data (Fig. 1), which cannot easily be transformed because of the particular demands of the historical biogeography methods. Precise significance levels should therefore be treated with some caution. However, we deliberately used few regional replicates in our samples, and this has the advantage of decreasing the risk of spatial autocorrelation (we are less likely to pseudoreplicate genuinely independent regions), and reducing power (only robust trends are likely to be detected).

In addition, where possible, we have carried out conservative non-parametric tests. We still observed significant findings despite these measures. Furthermore, one recent study has suggested no foundation for the claim that studies that do not take into account spatial autocorrelation are flawed (Diniz, Bini & Hawkins, 2003).

Other issues of independence may also be raised. We have counted evolutionary events in each region as if they were independent. Of course, there is also a phylogenetic component to these events that we, and macroecologists in general, have not attempted to deal with. One component of this phylogenetic non-independence comes from when a single species or event involves two regions. These are real events and so perhaps should *prima facie* be analysed, yet they may also be viewed as a form of pseudoreplication. How these problems can be overcome is not obvious at present.

WIDER PROSPECTS

Although we have attempted to distinguish the various possible historical processes underlying present distributions, this does not mean that they are limiting. We cannot tell if the same current richness pattern would have resulted through some alternative history, for example if the group had had a temperate rather than tropical origin. However, given sufficient similar studies, it might be possible to test this by observing whether different histories give rise to different present day richness patterns across taxa. Proches (2001) suggests that this might have occurred in secondary marine organisms.

Latitude is, of course, just a proxy for other ultimate abiotic variables and we would like to be able to determine these. Once the location of a biogeographical event is known or estimated, variables relating to it can be investigated, in much the same way as extant diversity is correlated with variables such as temperature (see Lennon, Greenwood & Turner, 2000). Current statistical associations involving ultimate variables such as temperature mostly fail to identify proximate events and processes. As we seek to extend our knowledge of both proximate and ultimate influences and the relationships between them, historical biogeography offers one means of generating data on the proximate variables.

In this study we have addressed only the question of spatial patterns in species richness. However, we believe that the methods have a broader applicability in a macroecological context, extending to any large-scale spatial pattern. We believe that once ancestral distributions have been estimated or ascertained, they can potentially be related to any other data that can be mapped onto a phylogeny. This could be body mass (e.g. Taylor & Gotelli, 1994), life history (Cardillo, 2002), or even the extent of geographical range itself.

If the approach we have described is taken up by other workers, it will have serious consequences for the way in which macroecologists will need to address their subject. First, they will need basic data on what species exist and where. Second they will need a good knowledge of the evolutionary relationships of the studied species. Those requirements will initially restrict the taxa that can be studied in a productive way, as for most taxa even a global inventory of species remains a distant prospect. Finally, they will need to involve themselves with and further develop methods to analyse the resulting data. We hope that this paper has shown the initial way forward.

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