PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2009) **276**, 1957–1964
doi:10.1098/rspb.2009.0088

Matrilocal residence is ancestral in Austronesian societies

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The nature of social life in human prehistory is elusive, yet knowing how kinship systems evolve is critical for understanding population history and cultural diversity. Post-marital residence rules specify sex-specific dispersal and kin association, influencing the pattern of genetic markers across populations. Cultural phylogenetics allows us to practise 'virtual archaeology' on these aspects of social life that leave no trace in the archaeological record. Here we show that early Austronesian societies practised matrilocal post-marital residence. Using a Markov-chain Monte Carlo comparative method implemented in a Bayesian phylogenetic framework, we estimated the type of residence at each ancestral node in a sample of Austronesian language trees spanning 135 Pacific societies. Matrilocal residence has been hypothesized for proto-Oceanic society (*ca* 3500 BP), but we find strong evidence that matrilocality was predominant in earlier Austronesian societies *ca* 5000–4500 BP, at the root of the language family and its early branches. Our results illuminate the divergent patterns of mtDNA and Y-chromosome markers seen in the Pacific. The analysis of present-day cross-cultural data in this way allows us to directly address cultural evolutionary and life-history processes in prehistory.

Keywords: anthropology; kinship; cultural phylogenetics; ancestral states; matrilocality

1. INTRODUCTION

Kinship organization, like other aspects of our social phenotype, has evolved (Cronk & Gerkey 2007). Across the world, kinship systems are organized in a restricted set of all the combinatorial possibilities available (e.g. Nerlove & Romney 1967), suggesting that selection acts to produce a limited number of optimal solutions in this domain (Jones 2003). Social behaviours do not fossilize, so speculations about the evolution of human kinship structure have concentrated on the recent timespan of the historical record, especially hunter–gatherer groups (e.g. Marlowe 2004), or the distant timespan of comparison with non-human primates and our hominid ancestors (Foley & Lee 1989; Gowlett 2008). By contrast, to understand the adaptive social dynamics of the past 10 000 years, we require large-scale analyses of cross-cultural variation that control for shared evolutionary history. Until recently, appropriate theoretical and methodological frameworks have been lacking. A cultural phylogenetic approach that combines linguistic trees as models of population history with the rich ethnographic literature on kinship provides the best solution (Mace & Holden 2005; Gray *et al.* 2007). In this way, 'virtual archaeology' lets us infer the ancestral states of human social structure.

A growing literature attests to the successful use of these methods to test coevolutionary hypotheses and ancestral state reconstruction in anthropology (e.g. Mace *et al.* 2005; Lipo *et al.* 2006). By Darwinising culture, the adaptive nature of human social organization can be understood in an evolutionary context. For example, Holden & Mace (2003) demonstrated that patriliny coevolved with the adoption of pastoralism in Bantu societies, with matrilineal societies first acquiring cattle and then switching to patriliny. In Indo-European societies, Fortunato *et al.* (2006) showed dowry combined with monogamy was the likely ancestral state, and that wealth transfer and marriage systems were coevolving (Fortunato & Mace in press).

Knowledge of ancestral social organization is critical for interpreting genetic findings, especially when mtDNA and Y-chromosome patterns conflict (Oota *et al.* 2001; Wilkins & Marlowe 2006). The most important factor is sex-specific dispersal, which in human societies is regulated by post-marital residence rules. Patrilocal residence—where the wife lives with the husband's kin—is the most common pattern worldwide, occurring in approximately 70 per cent of societies (Levinson & Malone 1980). Other common patterns are matrilocality, where the husband lives with the wife's kin, and ambilocality, where the couple choose which set of kin they will reside with (Holy 1996). Although residence rules covary with descent rules in predictable ways, they are not strictly determined by descent systems (Murdock 1949; Levinson & Malone 1980), and are therefore the primary set of kinship norms that regulate human dispersal.

(a) *Kinship in Austronesian societies*

Worldwide, regions such as Eurasia show predominantly patrilocal residence, while Africa has mostly strict patrilocal or matrilocal systems (Murdock 1949; Goody 1976). By contrast, the Austronesian-speaking societies of

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2009.0088 or via http://rspb.royalsocietypublishing.org.

Received 19 January 2009
Accepted 5 February 2009

the Pacific are not only more ambilocal, but also have a ‘matricentric orientation’; that is, a theme of matrilineal descent and matrilocal kinship structures (Burton *et al.* 1996). Austronesian societies are a useful regional case to test hypotheses about the evolution of kinship norms (Lane 1961) and the interaction between residence patterns and divergent genetic findings.

Pacific scholars have debated the nature of early Austronesian social organization for many years, usually inferring ancestral kinship patterns from proto-language reconstructions, comparative ethnology and examination of kin terminology (e.g. Van Wouden 1935 [1968]; Murdock 1949; Blust 1980). Little consensus has emerged regarding post-marital residence norms. Previous work has focused on three ancestral speech communities, each associated with distinct archaeological ‘pauses’ (Green 2003) in the Austronesian colonization of the Pacific beginning *ca* 5500 BP (Diamond & Bellwood 2003; Gray *et al.* 2009). The first pause is the proto-Austronesian (PAn) root, the second constitutes the proto-Malayo-Polynesian (PMP) community prior to Austronesian entry into The Philippines *ca* 4–4500 BP (Pawley 2002; Gray *et al.* 2009) and the third is proto-Oceanic (POc), *ca* 3500 BP, associated with the archaeological ‘Lapita Cultural Complex’ and the dispersal of Austronesian peoples into the previously uninhabited regions of Remote Oceania such as Polynesia (Kirch & Green 2001; Green 2003; figure 1).

In two syntheses of the available evidence, Hage (1998) and Hage & Marck (2003) hypothesized that matrilocality and/or matriliny characterized ancestral Oceanic society (i.e. POc). A matri-biased social organization in POc peoples would therefore have restricted female genetic diversity while increasing male diversity as non-Austronesian men married in. Matrilocality is thus consistent with the divergent mtDNA and Y-chromosome patterns seen in the Pacific human genetics (for recent reviews, see Hurles *et al.* 2002, 2003). Kayser *et al.* (2008) stated that ‘the large discrepancy in the estimated Asian and Melanesian contributions to Polynesians for mtDNA versus the Y-chromosome suggests sex-biased genetic admixture … This scenario is supported by suggestions of matrilineal descent and matrilocal residence in the ancestral Polynesian society.’ (p. 197).

Cultural phylogenetics allows us to quantitatively test these hypotheses about Austronesian kinship. Here we use a Bayesian Markov-chain Monte Carlo (MCMC) comparative method on language trees to reconstruct the ancestral states of post-marital residence in Austronesian societies. This approach proceeds by using information about characters in the present-day ‘taxa’ (societies) to infer the ancestral states of those characters in the past along a phylogeny (Pagel 1999). By capitalizing on the powerful model-based aspects of Bayesian phylogenetic inference (Huelsenbeck *et al.* 2001; Lewis 2001), these estimates of ancestral states take into account the uncertainty of both the tree topology and the cultural trait reconstructions.

2. MATERIAL AND METHODS

(a) *Language phylogenies*

Language, especially basic vocabulary, is an excellent proxy for inferring population history (Mace & Pagel 1994; Greenhill *et al.* 2008). It changes on a time scale suitable for investigating cultural evolution, and words may evolve under the twin regimes of conformist bias (Henrich & Boyd 1998; Labov 2007) and certain predictable evolutionary dynamics (Lieberman *et al.* 2007; Pagel *et al.* 2007). We used a sample of 1000 language trees derived from a phylogenetic analysis of the Austronesian Basic Vocabulary Database (ABVD; Greenhill *et al.* 2008; http://language.psy.auckland.ac.nz/austronesian/). The ABVD consists of the cognate sets of a 210-item word list from over 500 Austronesian languages. Cognate words, which can be shown by the linguistic comparative method to share a common ancestor on the basis of systematic sound correspondences, have been coded into a binary matrix showing the presence/absence of cognate terms (Gray *et al.* 2009).

Phylogenetic analysis was conducted in *BayesPhylogenies* (Pagel & Meade 2004). The posterior distribution of trees was inferred using Bayesian MCMC methods under a model of evolution where cognates were gained or lost at the same rate but sites could vary according to a two-state (fast/slow) covarion. These languages ($n=400$), the trees and their properties are described more fully in Gray *et al.* (2009). We have used a sample of 1000 trees from the post-burn-in posterior distribution as the prior on trees for the comparative analyses, retaining those taxa for which we have corresponding cultural data ($n=135$). Old Chinese and Buyang, non-Austronesian languages used to root the 400-taxa tree, are not included in the cultural analyses; however, all Austronesian languages formed a single clade (posterior probability$=$100). A single consensus tree summarizes the results visually, but the comparative analyses were performed over all 1000 trees.

(b) *Coding residence data*

We matched languages from the ABVD to ethnographic data on post-marital residence using the geographical and descriptive information on societies in the anthropological literature. Murdock’s (1967) *Ethnographic Atlas* (EA; the updated SPSS database by Gray 1999) supplied 94 matches. Ethnographic encyclopaedias (LeBar 1975; Levinson 1990) provided data for 27 matches. Additionally, we targeted societies in sparsely described regions such as West New Guinea and parts of Near Oceania to round out the sample coverage; in 14 cases, we identified relevant ethnographic literature or contacted fieldworkers for information on social structure and kinship (table S1 in the electronic supplementary material). The locations of the 135 societies are shown coloured by residence pattern on the map of the Pacific area (figure 1).

We coded societies in the EA according to the variables specifying marital residence with kin (table S1 in the electronic supplementary material). Other societies were coded according to the residence pattern that was designated the most common, or the sole pattern if that were the case, in the ethnographic description. States used were: patrilocal (including virilocal) ‘P’, $n=66$; matrilocal (including uxorilocal and avunculocal) ‘M’, $n=37$; and ambilocal (by assignment of a dual state) ‘MP’, $n=32$). The ambilocal class included nine societies with neolocal or no common residence. These were coded as missing in a separate analysis, without any effect on the results.

(c) *Estimation of ancestral states*

A continuous-time Markov model of trait evolution, implemented in the program *BayesTraits* (Pagel *et al.* 2004;

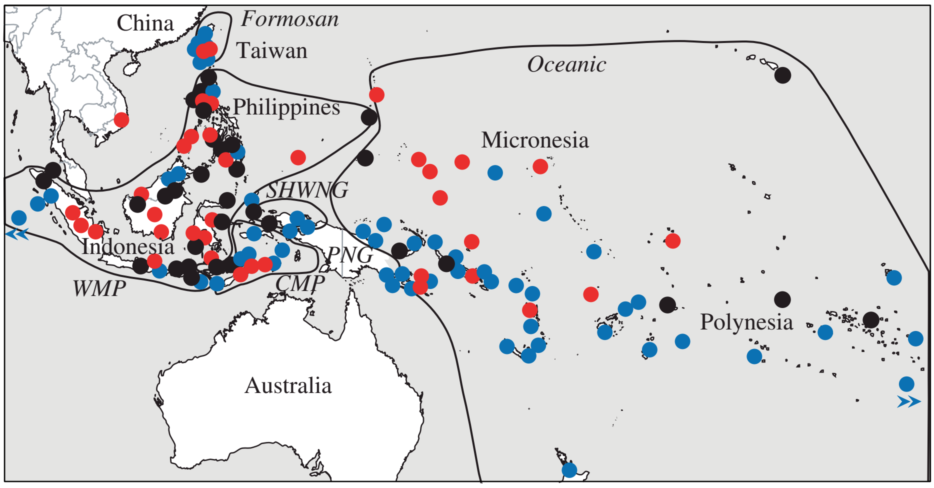

Figure 1. Map of the Pacific depicting locations of 135 Austronesian ethno-linguistic groups, colour-coded by their main residence pattern (blue circles, patrilocal; red circles, matrilocal; black circles, ambilocal). Outlines show the distribution of five high-order language subgroups, corresponding to groups indicated on phylogeny in figure 3.

Pagel & Meade 2005), was used to estimate the ancestral states of residence across the sample of 1000 trees. The instantaneous rate of change between two traits is given by transition-rate parameters. These transition rates are then used to define the probability of changes between these two states along the branches of the tree(s). In the Bayesian context, a Markov chain is used to sample values of the rate parameters periodically across the posterior tree distribution (Pagel *et al.* 2004). The ancestral state at each node can then be characterized by a posterior probability for matrilocality and patrilocality, derived by combining the probability of the state at the node with the probability that the node exists. For example, for a given node, *BayesTraits* may return a posterior probability distribution with a mean of 0.8 for patrilocality; this is denoted $p(P|\text{node})$. If the node is present in all trees, i.e. $p(\text{node})=1.00$, we accept the 0.8 value as the posterior probability of patrilocality at that node. However, if the node is only present in 70 per cent of the trees, i.e. $p(\text{node})=0.70$, we report the 'combined probability' for patrilocality, $p(P)=p(P|\text{node})\times p(\text{node})=0.7\times0.8=0.56$. A value of 0.7 for the combined posterior probabilities was taken as the threshold value of certainty for an ancestral state at a node (M. Pagel 2006, personal communication).

The maximum-likelihood values of the rate parameters indicated that the residence data could be described well by a wide range of rate coefficients. Therefore, in order to characterize the likelihoods, we used a gamma-distributed prior (a two-parameter, right-skewed probability distribution) to estimate these parameters. We used a hyperprior approach to estimate the gamma-shape prior from the data by seeding from a flat prior (mean range 0–50, variance range 0–25) and allowed rates to vary across the tree using a covarion (Pagel *et al.* 2004).

The MCMC simulation started with a random tree from the tree distribution and the parameters were sampled from the chain every 10 000 iterations, ensuring each sample was independent and autocorrelation was minimized. Over the course of the analysis, each tree was repeatedly visited and different combinations of rate parameters were proposed. Each chain was run nine times for at least 10^9 iterations each to check that harmonic means were converging on the same value. Posterior probabilities of the parameters, likelihoods and estimates of ancestral states ($n=10\,000$) at each internal node were taken from a final post-convergence portion of the run with the median likelihood.

We were interested in four nodes corresponding to points in Austronesian prehistory where coherent speech communities have been suggested: PAn; PMP; proto-Central-Eastern Malayo-Polynesian (PCEMP); and POc. We show the posterior distribution for the separate probabilities of matrilocality and patrilocality as the ancestral state at these four nodes in the graphs (figure 2*a*). We also calculated the 95 per cent highest posterior density (HPD) intervals of the parameters using *Tracer* (Rambaut & Drummond 2007) to describe the range within which 95 per cent of the posterior probability is contained.

3. RESULTS

(a) *Phylogeny*

The posterior distribution of phylogenetic trees is summarized by a consensus tree in figure 3. Gray *et al.* (2009) show that this posterior tree distribution is strikingly concordant with the topology suggested by Austronesian linguists (Blust in press), with 26 out of the 34 major subgroups found with high posterior probabilities. When branch lengths are proportional to time (Gray *et al.* 2009) and/or amount of linguistic change (figure S1 in the electronic supplementary material), the internal branch lengths of PMP are significantly longer than others in the tree, suggesting that this node especially represents a coherent ancestral linguistic population. We are confident that our tree sample thus captures the important aspects of Austronesian population history.

(b) *Ancestral state reconstructions*

Austronesian societies showed marked variation in post-marital residence patterns across the phylogeny (figures 1 and 3). Despite the lability in this cultural trait, the comparative method reconstructed the ancestral pattern for 57 nodes with a combined (phylogenetic × trait uncertainty) probability greater than 0.7, including PAn and PMP. Both PAn and PMP are matrilocal (posterior probability = 0.70 and 0.99, respectively),

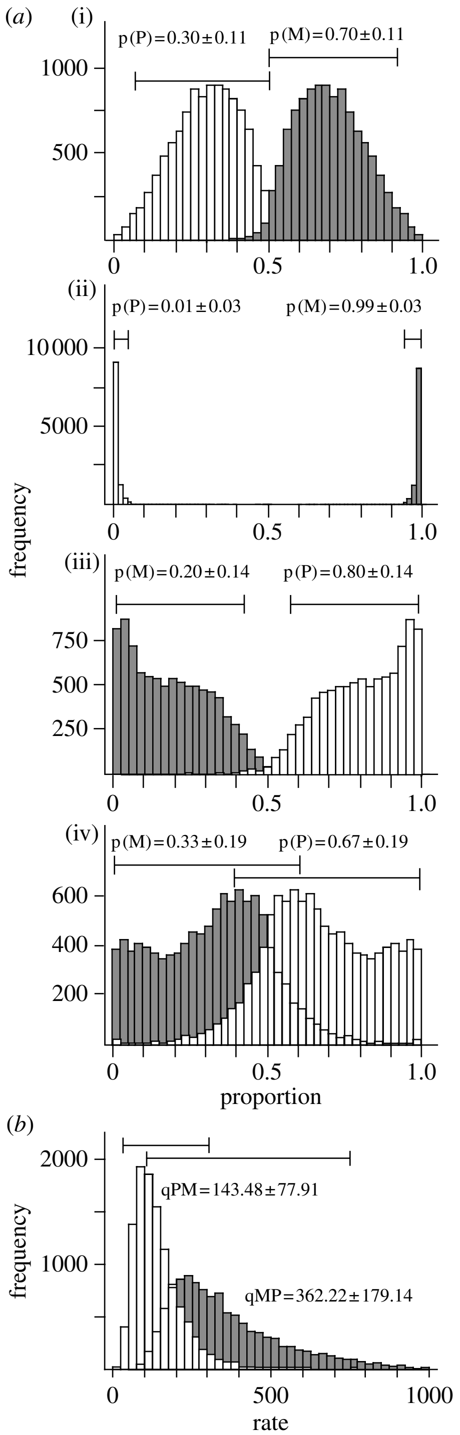

Figure 2. (*a*) Posterior distributions of the probabilities (x-axis) of an ancestral state being matrilocal (grey bars) or patrilocal (white bars) for the four high-level subgroups corresponding in figure 3 ((i) PAN, (ii) PMP, (iii) CEMP, (iv) POc). Values given are the mean ± s.d. for the distribution. Bars represent the 95% highest posterior density. (*b*) Posterior distribution of transition rates showing that transitions from matrilocality to patrilocality (qMP, grey bars) take values twice as high as the reverse (qPM, white bars).

suggesting that early Austronesian societies were predominantly matrilocal, and that patrilocality was a later development in some Formosan (Taiwan) societies and the Austronesian family as a whole. Matrilocality is especially secure in PMP (0.99), and many daughter subgroups and societies (e.g. proto-Philippines, many Sumatran societies) still retain this pattern. More recently, residence switches to patrilocal in many societies surrounding the island of New Guinea (clades A, B and C), although some retain matrilocality. Figure 2*a* demonstrates that patrilocality is reconstructed with 0.80 probability for PCEMP, but as this node is present only in 84 per cent of the tree sample, the combined probability of 0.67 must express the uncertainty associated with this reconstruction. POc reconstructs with 0.67 patrilocality, close to the threshold, but the 95 per cent HPD intervals display a considerable overlap, suggesting that there is a great deal of uncertainty.

(c) *Model comparison*

To directly test the fit of these hypotheses, we constrained the nodes belonging to crucial ancestral societies to be either matrilineal or patrilineal. In *BayesTraits*, we compared two models by fixing ('fossilizing') PAn, PMP and POC (as all were present in 100% of the posterior) alternatively to matrilocality and patrilocality. The mean marginal likelihood across the obtained posterior distribution can be estimated as the harmonic mean of the likelihoods (Suchard 2005). Each analysis was replicated three times and the analysis with the median marginal likelihood was chosen for the further tests. The conditions were the same as those used for the ancestral character state reconstructions (e.g. prior distribution, run length, burn-in period).

We determined which fossilized state had more support by calculating ln Bayes factors (BF) as twice the difference in the marginal likelihood, following Pagel *et al.* (2004). We interpret BF as a summary of the evidence for one model over another, based on Kass & Raftery's (1995) schema: 0–2, barely worth mentioning; 2–6, positive; 6–10, strong; above 10, very strong. Our results (table 1) show that there is strong evidence in favour of PMP matrilocality, positive evidence for PAn matrilocality and positive evidence for POc patrilocality.

We also examined how residence traits change over time on the trees. The posterior distribution of the transition-rate parameters from matri- to patrilocality and vice versa allowed us to compare the rates of trait switching (figure 2*b*). Changes from matrilocality to patrilocality occurred at more than twice the rate (rate = 362.22 ± 179.14) at which patrilocality changed to matrilocality (rate = 143.48 ± 77.91). A further analysis fixing the transition rates in either direction to be equal fits the data significantly worse (BF = −7.03), providing strong negative evidence against equal rates (row 4).

4. DISCUSSION

Using phylogenetic comparative methods and ethnolinguistic information on 135 societies, we have inferred an important aspect of social structure of peoples who lived over 5000 years ago. We reconstructed the postmarital residence patterns of PAn and PMP societies as matrilocal. This suggests their descent systems may have also had matrilineal aspects, informing a long debate about the presence of land-holding kin groups in early Austronesian societies (Murdock 1949; Goodenough 1955; Lane 1961; Blust 1980; Hage 1998). We examined residence rather than descent for two reasons. Firstly, in a number of Austronesian societies, residence itself

Table 1. Comparing model support with the Bayes factor. (Bayes factors were calculated as follows: BF = 2(ln LhA − ln LhB), where ln Lh*x* is the marginal likelihood (i.e. the harmonic mean of the post-convergence ln likelihoods, allowing us to compare the posterior distributions). BF values indicate evidence in favour of model A: 0–2, barely worth mentioning; 2–6, positive; 6–10, strong; above 10, very strong/decisive (Kass & Raftery 1995). Negative values favour model B. m, matrilocal; p, patrilocal.)

model A	ln Lh	model B	ln Lh	BF	verbal description
PAN-m	−61.36	PAN-p	−62.49	2.26	positive evidence for matrilocality
PMP-m	−60.80	PMP-p	−64.99	8.38	strong evidence for matrilocality
POC-m	−62.79	POC-p	−61.50	−2.58	positive evidence for patrilocality
equal rates	−63.12	default	−59.61	−7.03	strong evidence for unequal rates of character change

determines kin group membership e.g. Ifugao, Kiribati (Goodenough 1955). Secondly, genetic patterns will be mainly influenced by social norms regarding dispersal, rather than norms of association and inheritance. The sex-biased dispersal model of early Austronesian matrilocality fits the predominant pattern seen in the Pacific genetics: restricted Asian-derived maternal lineages and a more diverse set of NRY variants (Hurles *et al.* 2002). Our results do suggest, for instance, that Y-chromosome variants from as far west as Halmahera should not be unexpected in Remote Oceanic populations. Disentangling the interactive effects of residence and migration will be complex, but given the known ethnographic and molecular data, we should now be able to address the issue directly rather than through inference, by modelling different scenarios about kinship structures and their effect on genetic diversity (c.f. Veeramah *et al.* 2008).

Patrilocality was reconstructed for PCEMP and suggested for POc. Our results thus do not support Hage & Marck's (2003) hypothesis that POc was matrilocal (table 1). Their prediction was derived from comparative linguistic analysis of kinship terminology and extrapolation from archaeological and ethnographic distributions (Hage 1998; 1999). While this 'triangulation' approach (Kirch & Green 2001) supports rich inferences about past societies, our methodology allows for explicit, formal testing of these scenarios. In future, our methods could directly examine how kin terms are evolving on the phylogeny. These terms may preserve 'relict' aspects of older kinship systems: for example, a specific term for mother's brother may suggest previous matriliny (Blust 1980; Marck in press).

We suggest an explanation that integrates Hage's descriptive evidence together with the results of our quantitative analyses. The PCEMP and POc nodes represent a rapid period of Austronesian expansion over a short period of time (Green 2003), where extensive contact with non-An-speaking societies on the islands of New Guinea is likely to have occurred. PCEMP, POc and the intervening nodes may have been originally matrilocal (or ambilocal), but over time, the majority of descendant groups may have switched to patrilocality, perhaps due to cultural diffusion or integration into systems of wife exchange. It is possible, given the higher rates of change from matrilocality to patrilocality than the reverse, that patrilocal residence was repeatedly adopted by Austronesian peoples across the Pacific. A switch to patrilocal norms could also occur without culture contact as a catalyst. Residence patterns may have shifted as adaptive responses to new sedentary lifestyles or the reduction of long-distance voyaging, both of which could diminish the 'male absence' factor that may drive the origin and/or maintenance of matrilocality (Keegan & Machlachlan 1989; Hage 1999). We are currently working to address this coevolutionary hypothesis.

From an evolutionary perspective, social norms concerning kinship are likely to be stable for many generations due to the requirement for interlocking and coordinated social exchange between kin groups; furthermore, these norms may track population history themselves if they represent an effective behavioural strategy in a particular environment (Guglielmino *et al.* 1995). Marginal environments and depopulation events may have selected for the maintenance of malleable social structures in Austronesian societies (Lane 1961); a similar rationale is claimed for flexible residence patterns in foragers (Marlowe 2004). It is unsurprising that ambilocal residence is common; here, the most adaptive cultural norms may be those that allow the movement of people and resources without strict proscriptions (Vayda & Rappaport 1963).

A decade ago, reconstructing the social organization of ancestral populations was considered a fanciful enterprise for Pacific scholars (Sutton 1996). The power of a cultural phylogenetic approach is the ability to make robust estimates about prehistoric social life, while avoiding the pitfalls of Galton's problem—the non-independence of societies who share commonalities by descent (Mace & Pagel 1994). Our analysis highlights the complexities involved in reconstructing ancestral social norms and the necessity of examining multiple lines of evidence when undertaking virtual archaeology. Darwinian approaches to social science have stirred a renewed interest in kinship, as predictions can be derived from evolutionary theory about human life history (Jones 2003; Cronk & Gerkey 2007; Allen *et al.* 2008). With this suite of methods that do not rely on a single hypothesis about population history, we can test how kinship traits and other cultural norms evolve.

We thank Robert Blust, John Lynch, Jeff Marck, Cordelia Nickelsen, Malcolm Ross, Laurent Sagart and all contributors to the ABVD for their assistance with lexical data and cognate judgements, and BeSTGRID.org and Andrew Meade, Mark Pagel, and the Centre for Advanced Computing and Emerging Technologies (ACET) at the University of Reading for computational support. Funding was provided by the Arts and Humanities Research Council to F.M.J., the Royal Society of New Zealand Marsden Fund and a Bright Futures doctoral scholarship to S.J.G.

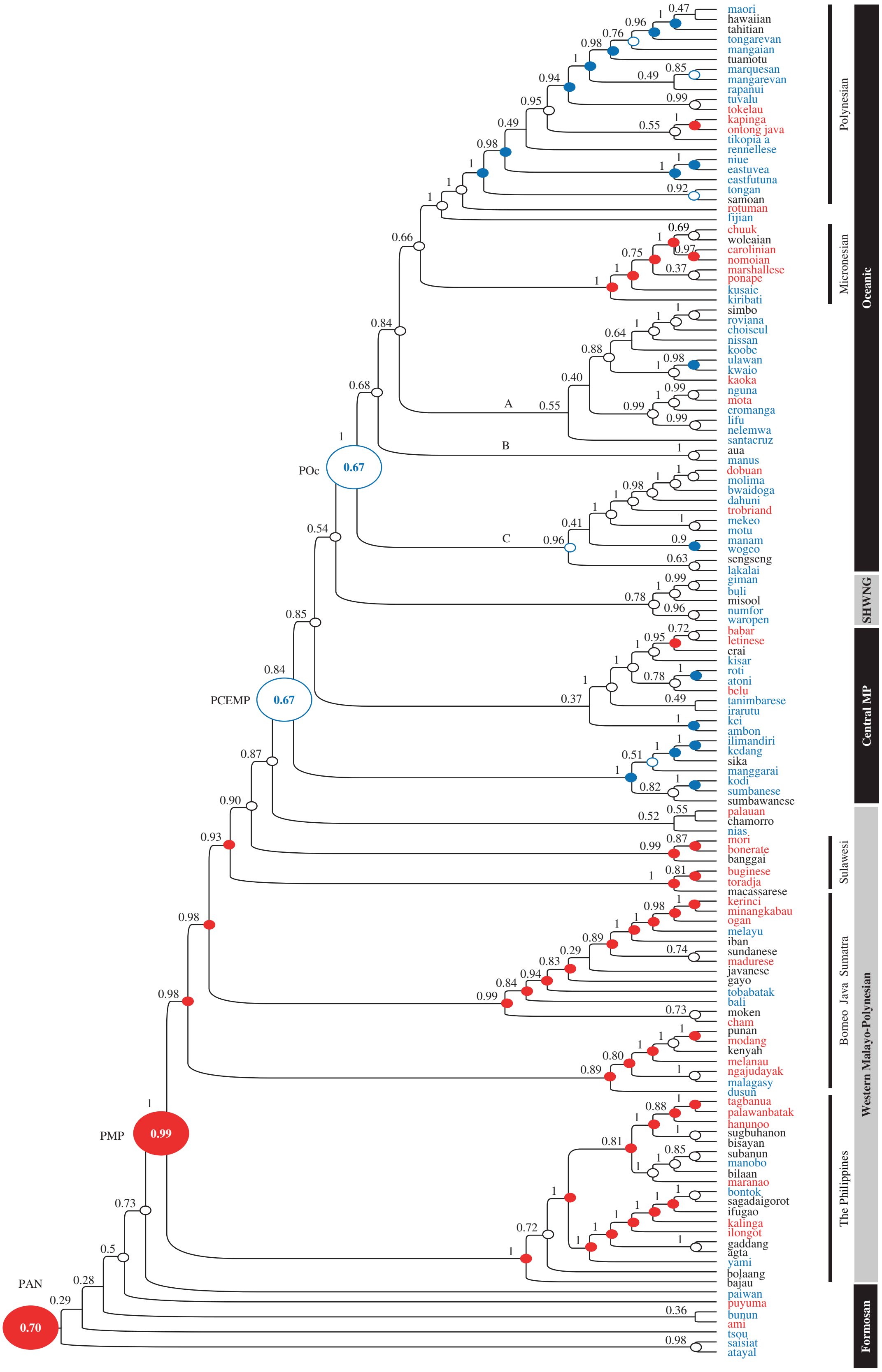

Figure 3. Summary phylogeny of 135 Austronesian languages; this is a 50% majority rule consensus tree of all 1000 trees in the posterior (see §2; branch lengths not to scale). Taxa colour depicts a society's residence pattern (red, matrilocal; blue, patrilocal; black, ambilocal). Subgrouping bars (right) correspond to map in figure 1. Numbers above nodes are Bayesian posterior probabilities for that clade (phylogenetic uncertainty, only those above 0.5 shown). Nodes are colour-coded to reflect ancestral states of residence. Filled circles have probabilities of being matrilocal (red) or patrilocal (blue) above 0.7, taking into account both phylogenetic and trait uncertainty. Open circles are where trait reconstruction was above 0.7 matrilocal/patrilocal but when combined with the clade posterior probabilities were below 0.7. All other nodes are above 0.7 for both clade and trait. The four large nodes correspond to the distributions in figure 2 and show the combined probability for the ancestral state. An, Austronesian; MP, Malayo-Polynesian; Oc, Oceanic; SHWNG, South Halmahera–West New Guinea; W, Western; C, Central; E, Eastern; P, proto.

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