letters to nature

aluminum foil) and light bottles (28–33 μmol photons m^{-2} s^{-1}) and incubated them for 24 h at 3 °C. We isolated individual ciliates from each light and dark replicate, washed them three times with sterile media (10 ml) and transferred ten washed cells into a scintillation vial. During the 2–3 h isolation period we maintained the samples in the dark on ice. We prepared the samples for liquid scintillation counting as described[28]. We calculated rates of photosynthesis by subtracting average ^{14}C fixation in the dark from fixation in the light. For the determination of *M. rubrum* chlorophyll, we isolated and washed ten cells before transferring them into vials containing cold 90% acetone and incubating them at −20 °C overnight for extraction. We measured chlorophyll *a* using a 10-AU Turner fluorometer.

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Language trees support the express-train sequence of Austronesian expansion

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Languages, like molecules, document evolutionary history. Darwin[1] observed that evolutionary change in languages greatly resembled the processes of biological evolution: inheritance from a common ancestor and convergent evolution operate in both. Despite many suggestions[2–4], few attempts have been made to apply the phylogenetic methods used in biology to linguistic data. Here we report a parsimony analysis of a large language data set. We use this analysis to test competing hypotheses—the "express-train"[5] and the "entangled-bank"[6,7] models—for the colonization of the Pacific by Austronesian-speaking peoples. The parsimony analysis of a matrix of 77 Austronesian languages with 5,185 lexical items produced a single most-parsimonious tree. The express-train model was converted into an ordered geographical character and mapped onto the language tree. We found that the topology of the language tree was highly compatible with the express-train model.

There are many parallels between the processes of biological and linguistic evolution and the methods used to analyse them[4]. Despite these parallels, however, historical linguists have not used the quantitative phylogenetic methods that have revolutionized evolutionary biology in the past 20 years[8]. So, although linguists routinely use the "comparative method"[9] to construct language family trees from discrete lexical, morphological and phonological data, they do not use an explicit optimality criterion to select the best tree, nor do they typically use an efficient computer algorithm to search for the best tree from the discrete data. This is surprising given that the task of finding the best tree is inherently a combinatorial optimization problem of considerable computational difficulty[10]. One potential problem with a quantitative phylogenetic approach to linguistic evolution arises from the more reticulate nature of cultural evolution. Some authors[11,12] have claimed that reticulate processes in linguistic evolution overshadow those of descent, leading them to reject the appropriateness of the family-tree model. We believe that this is an empirical claim, which can be evaluated using phylogenetic methods. If the data fit well on the tree and there is little systematic conflicting signal, then the family-tree model is supported. If the data fit poorly, then alternative phylogenetic methods that do not assume a tree model, such as spectral analysis or split decomposition, should be investigated. A critical part of phylogenetic inference involves testing for congruence between independent lines of evidence. Here we test a model of the colonization of the Pacific that is derived from predominantly archaeological data by quantitatively examining its fit with a parsimony tree of Austronesian languages.

Prehistoric human colonization in the Pacific happened in two phases. Initially, Pleistocene hunter–gatherer expansions from Island Southeast Asia through New Guinea reached the Bismarck archipelago by 33,000 BP and the Papuan-speaking descendants of these people are dispersed throughout New Guinea and parts of Island Melanesia[13]. The second colonization wave of Austronesian language speakers involved a diaspora of Neolithic farming peoples out of south China and Taiwan around 6,000 BP[13–15]. According to the 'express train to Polynesia' model, the Austronesian expansion from Taiwan was extremely rapid, taking roughly 2,100 years to reach the edges of western Polynesia—a distance of 10,000 kilometres.

Converging evidence from archaeology and molecular anthropology supports a rapid and relatively encapsulated dispersal of the Austronesian speakers throughout the Pacific[13,16–18] (Fig. 1); however, there is some dispute about the exact degree of interaction with earlier Melanesian settlers, the rate at which the migration occurred and the extent and location of any colonization pauses[19]. In broad terms, most Pacific scholars seem to favour the express-train model, but others have argued that the ancestral Polynesians derive from an older Melanesian "matrix"[7,20]. The latter authors stress that a phylogenetic, colonization-focused perspective obscures the high degree of prehistoric contact and inter-relationships amongst Pacific people; we use Terrell's phrase[6]—the entangled-bank model—to represent this. These two models are not mutually exclusive, but are best characterized as two ends of a continuum of modes of human prehistory, with a pure tree at one end and a maximally connected network at the other. The issues surrounding the settlement of the Pacific are thus a microcosm of the general debate about whether human cultural evolution can be appropriately represented as a tree.

We tested one aspect of the express-train model, the colonization sequence, in the way that biologists test hypotheses about the sequence of events in biological evolution. We constructed a tree and then mapped the trait onto the tree to see whether the inferred sequence of changes fits a particular scheme[21]. Figure 2 shows how a simple colonization scheme can be tested by mapping geography onto an independent tree. We grouped languages according to Diamond's archaeological/geographical stations[5,22]. Using character-state functions in the program MacClade[23], we assigned each station a character state from 0 to 9. The states were ordered in a character-state tree to fit the sequence proposed by the express-train model. For example, in Fig. 1 the Taiwanese languages were grouped as state 1, the Remote Oceanic languages as state 8; this means a change from state 1 to 8 would require five steps (according to the model presented in Fig. 1). By mapping these character states onto the most-parsimonious language tree (Fig. 3), we were able to evaluate the express-train model in a quantitative manner. If the language tree fits the express-train model well, then the character-state tree should fit well onto our obtained tree. The shortest possible tree length required to optimize the character-state tree onto the language tree was nine (that is, the number of character states minus one). When the character-state tree was mapped onto the optimal tree, we obtained a tree length of 13. To assess the statistical significance of the fit, we randomly shuffled the character states between the 77 languages 200 times[23]. This gave us a null distribution of tree lengths with a mean tree length of 48.9 steps (s.d. 1.98, range 43–53). This indicates that the express-train character-state tree fits the language tree with significantly fewer steps than would occur by chance. In fact, the obtained fit was very close to the shortest possible length (nine), indicating that the express-train model fits the language tree exceptionally well.

By definition, an entangled-bank model cannot be represented by a character-state tree; however, we can assess whether the language data support the entangled-bank model by examining the topology
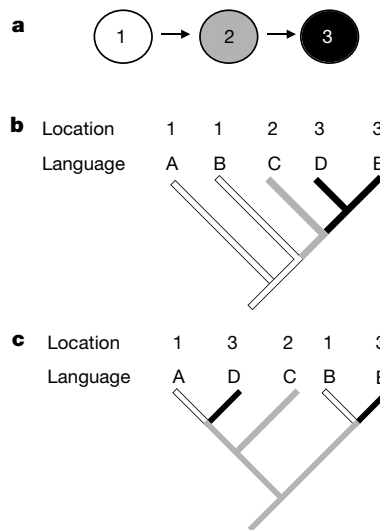

Figure 2 A phylogenetic approach to testing a colonization sequence. **a**, Model for the colonization of three areas, in which an ancestral population moves from area one to area two and then to area three. **b**, Tree that fits perfectly with the colonization model in **a** (fit = 2 steps). **c**, A tree that fits poorly with the colonization sequence (fit = 4 steps).
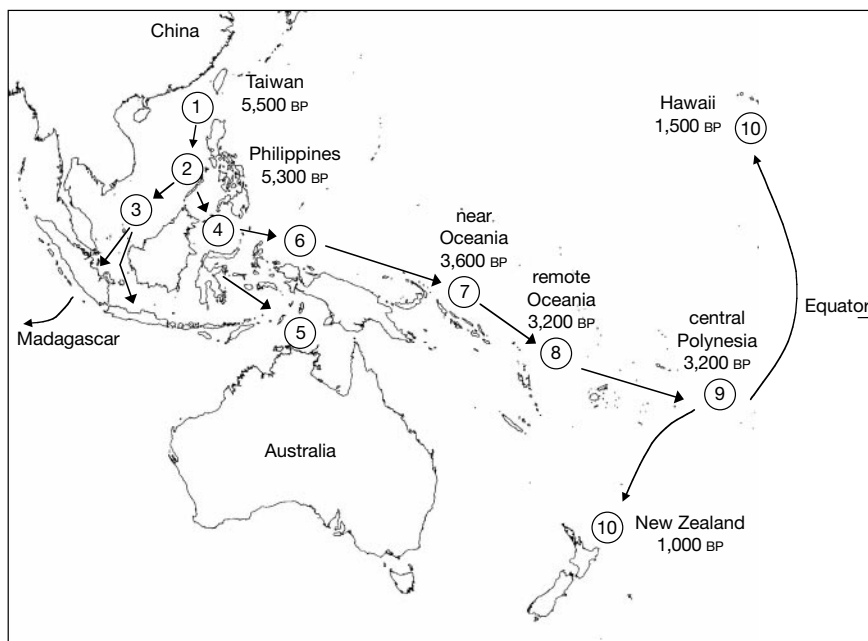

Figure 1 The express train to Polynesia model of the Austronesian colonization of the Pacific (adapted from refs 5 and 22). Approximate archaeological dates of settlement are indicated[13,22]. Each 'station' is a separate character state: 1, Taiwan; 2, Philippines, Chamorro, Palau; 3, Borneo, Indonesia, Malay; 4, Sulawesi; 5, central Malayo-Polynesian; 6, south Halmahera/west New Guinea; 7, near Oceania; 8, remote Oceania; 9, central Polynesia; 10, east Polynesia.

of the tree. While advocates of this model make no predictions about the likely shape of a language tree under an entangled-bank conception, they argue that large-scale migration patterns in languages are obscured by culture contact[7]. Consequently, they might predict a layered, 'candelabra-like' tree that emphasizes regional contact. In contrast, an (archaeologically) quick colonizing wave from Island Southeast Asia through the Pacific to Polynesia should produce a tree topology that is 'chain-like' (see Fig. 3). Proponents of the entangled-bank model argue that culture, language and biology 'combine and recombine' in such complex interactions that patterns of language relationships may tell us very little about the history of language speakers[7]. In this case, the tree should merely reflect geographical proximity. Our tree, however, shows several cases where the relationships fit the historical sequences implied by the express-train model but conflict with geographical proximity (see Fig. 3).

Although we reject the specific features of the entangled-bank
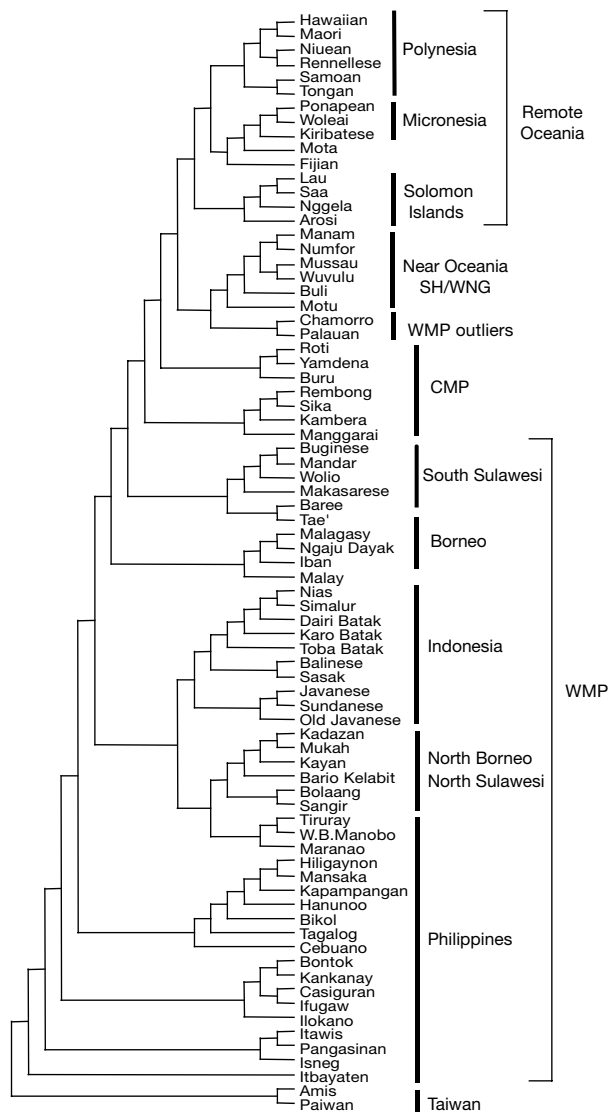
Figure 3 Phylogenetic tree of 77 Austronesian languages. WMP, Western Malayo-Polynesian; CMP, Central Malayo-Polynesian; SH/WNG, South Halmahera/West New Guinea. The topology of the tree shows considerable agreement with traditional linguistic groupings[14,15,28]; these groupings reflect historical relationships, not just geographical proximity. For instance, Malagasy (spoken on Madagascar) is grouped with Ngaju Dayak from western Borneo. Tae′ (from Central Sulawesi) groups within the south Sulawesi languages, whereas the north Sulawesi languages (for example, Bolaang Mongondow (Bolaang)) are more closely related to languages of north Borneo than are other Sulawesi languages.

model, we do not claim that Austronesian cultural history is totally tree-like. The consistency index (a measure of the fit of the lexical data on the tree) is only 0.25. This value is not substantially lower than would be expected for equivalently sized morphological and molecular data sets[24] in which hybridization is uncommon. Although it is probable that much of the poor fit in the lexical data is due to the loss of cultural or linguistic features[15,25], archaeological[26] and genetic[27] evidence do indicate that population interaction and 'borrowing' are likely to have occurred even between far-flung archipelagoes. A way of approaching the issue of borrowing is to examine languages whose placement conflicts with the colonization scheme. For example, Buli and Numfor are grouped inside the Oceanic language group on our tree, whereas the express-train model places these south Halmahera/west New Guinea languages outside the Oceanic group. Similarly, Chamorro and Palau—languages whose closest relationships are most likely with the Philippines[28]—are grouped with the Oceanic languages. In both these cases, borrowing is a likely cause of the incongruence between the express-train model and our tree. More detailed evidence for specific patterns of reticulation is evaluated elsewhere (F.M.J. and R.D.G, manuscript in preparation).

The patterns apparent in linguistic relationships are integrally tied to the movements, contacts and activities of language speakers. Our preliminary investigations have shown that a phylogenetic approach to languages offers the ability to test hypotheses about human prehistory. In biology, phylogenetic methods have become invaluable tools for investigating patterns and processes in evolution. In the future, phylogenetic methods may provide a common methodology and analytic framework to integrate data from ethnography, archaeology, linguistics and genetics. This is an important step towards a unified approach to biological and cultural evolution. □

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Mosaic evolution of brain structure in mammals

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The mammalian brain comprises a number of functionally distinct systems. It might therefore be expected that natural selection on particular behavioural capacities would have caused size changes selectively, in the systems mediating those capacities[1-3]. It has been claimed, however, that developmental constraints limited such mosaic evolution, causing co-ordinated size change among individual brain components[3]. Here we analyse comparative data to demonstrate that mosaic change has been an important factor in brain structure evolution. First, the neocortex shows about a fivefold difference in volume between primates and insectivores even after accounting for its scaling relationship with the rest of the brain. Second, brain structures with major anatomical and functional links evolved together independently of evolutionary change in other structures. This is true at the level of both basic brain subdivisions and more fine-grained functional

systems. Hence, brain evolution in these groups involved complex relationships among individual brain components.

Studies of mammalian brain evolution have highlighted the neocortex as a structure associated with intelligence and flexible behaviour, which varies enormously in size between species[4-6]. Large-brained mammals, such as primates, tend to have a neocortex that is disproportionately expanded relative to other structures[3]. The extent to which this size variation can be explained by allometric scaling relative to the rest of the brain, as opposed to size changes independent of other brain structures, remains unclear however[3,7]. Figure 1 indicates clearly that neocortex size varies even after accounting for its scaling relationship with the size of the rest of the brain. The three parallel lines with different intercepts indicate taxonomic differences (grade shifts) in relative neocortex size between primates and insectivores, and, within the primates, between strepsirhine and haplorhine sub-orders. Independent contrasts analysis confirms the presence of significant grade shifts in relative neocortex size. First, the slopes are statistically indistinguishable (haplorhine versus strepsirhine primates: $t = 1.6$, degrees of freedom, d.f. $= 37$, $P = 0.13$; primates versus insectivores: $t = 0.6$, d.f. $= 71$, $P = 0.54$). Second, the absolute values of the contrasts between orders and sub-orders are unusually large and beyond the range of all other contrasts in each data set (haplorhine versus strepsirhine residual $= 2.8$ standard deviations greater than the mean; primate versus insectivore residual $= 5.6$ standard deviations greater than the mean). On the basis of separate regression equations for insectivores and primates (averaging between strepsirhines and haplorhines), a primate with a non-neocortical brain size of $1,000\ \text{mm}^3$ would have a neocortex nearly five times larger than would an insectivore with the same non-neocortical brain size ($881\ \text{mm}^3$ versus $187\ \text{mm}^3$). In some specific cases, we observe an even greater difference in relative size. For example, the common tenrec *Tenrec ecaudatus*, an insectivore, has a non-neocortical brain volume somewhat greater than that of the
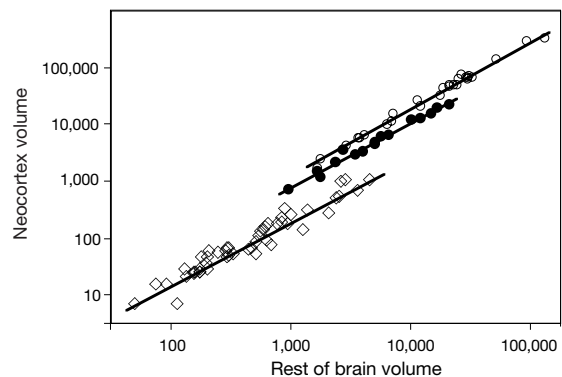

Figure 1 Taxonomic differences in relative neocortex size among primates (strepsirhines and haplorhines) and insectivores. Brain part volumes are in cubic millimetres. Open circles, harplorhine primates; closed circles, strepsirhine primates; diamonds, insectivores. Slopes (and 95% confidence intervals) for insectivores, strepsirhines and haplorhines respectively are 1.11 (1.03–1.20), 1.13 (1.04–1.22) and 1.20 (1.14–1.26).

Table 1 Regression statistics for the scaling of neocortical white and grey matter volume on volume of the rest of the brain

	White matter volume			Grey matter volume		
	Slope	Confidence intervals	r^2	Slope	Confidence intervals	r^2
Insectivores	1.32	1.23–1.41	0.95	1.09	0.94–1.18	0.94
Strepsirhines	1.48	1.32–1.65	0.99	1.06	0.98–1.14	0.99
Haplorhines	1.53	1.37–1.67	0.98	1.12	1.07–1.18	0.99
New World Monkeys	1.40	1.20–1.59	0.98	1.08	0.96–1.21	0.98
Old World monkeys	1.42	0.13–2.71	0.92	0.97	0.45–1.49	0.97