

Prehistoric inter-archipelago trading of Polynesian tree snails leaves a conservation legacy

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Inter-archipelago exchange networks were an important aspect of prehistoric Polynesian societies. We report here a novel genetic characterization of a prehistoric exchange network involving an endemic Pacific island tree snail, *Partula hyalina*. It occurs in the Society (Tahiti only), Austral and Southern Cook Islands. Our genetic data, based on museum, captive and wild-caught samples, establish Tahiti as the source island. The source lineage is polymorphic in shell coloration and contains a second nominal species, the dark-shelled *Partula clara*, in addition to the white-shelled *P. hyalina*. Prehistoric inter-island introductions were non-random: they involved white-shelled snails only and were exclusively inter-archipelago in scope. Partulid shells were commonly used in regional Polynesian jewellery, and we propose that the white-shelled *P. hyalina*, originally restricted to Tahiti, had aesthetic value throughout these archipelagoes. Demand within the Society Islands could be best met by trading dead shells, but a low rate of inter-archipelago exchange may have prompted the establishment of multiple founder populations in the Australs and Southern Cooks. The alien carnivorous land snail *Euglandina rosea* has recently devastated populations of all 61 endemic species of Society Island partulid snails. Southern Cooks and Australs *P. hyalina* now represent the only unscathed wild populations remaining of this once spectacular land snail radiation.

Keywords: *Partula*; Oceania; prehistoric exchange network; molecular phylogeny; conservation biology

1. INTRODUCTION

The epic settlement of Remote Oceania by Austronesian-speaking peoples, commencing approximately 3100 BP, represents one of the most notable episodes of long-distance colonization in human history (Kirch 2000). It has long attracted intense scholarly interest and is being studied using a collective multidisciplinary approach that encompasses archaeological, palaeoecological, ethnographic, linguistic and genetic lines of evidence (Hurles *et al.* 2003). Recent genetic analyses have focused not only on Polynesian human populations (Gibbons 2001; Pierson *et al.* 2006) but also on synanthropic/commensal biota, including plants (Clarke *et al.* 2006), animals (Matisoo-Smith & Robins 2004; Storey *et al.* 2007) and bacteria (Falush *et al.* 2003).

Commensal models are now widely, and successfully, used in the study of prehistoric Polynesia. Recent genetic studies (including archaeological samples) of the Pacific rat (*Rattus exulans*; Matisoo-Smith & Robins 2004) and the domesticated chicken (*Gallus gallus*; Storey *et al.* 2007) have, respectively, tested hypotheses of initial human expansion into Remote Oceania and of pre-Columbian contact with the New World. However, all of the commensal taxa studied to date are exotic introductions

to Remote Oceania and therefore lack a robust, within-basin, phylogeographic signature. This acts to undermine their utility for inferring geographically fine-scale prehistoric connections, e.g. it is not possible to identify source islands/archipelagoes for the introduced New World *G. gallus* lineage (Storey *et al.* 2007). Although *R. exulans* genetic variation has been used to infer broadscale prehistoric Polynesian interactions (Matisoo-Smith *et al.* 1998), its predominant mitochondrial (mt) haplotype (no. 9) in Remote Oceania has a basin-wide distribution (Matisoo-Smith & Robins 2004), implying that additional sampling could significantly alter specific inferences of inter-island and inter-archipelago connectivity.

Regular inter-island and inter-archipelago exchange networks are thought to have been a critical aspect of prehistoric Polynesian societies (Hage & Harary 1991; Irwin 1992). Empirical evidence for such prehistoric exchange networks requires that a putatively translocated item, encountered in an exotic and dated context, be attributable with confidence to a source island/archipelago, e.g. traded stone tools may be geographically sourced using geochemical analyses (Weisler 1998). Endemic Pacific island organisms are more likely to possess a within-basin phylogeographic structure, and it may therefore be possible to use molecular genealogies to identify source islands/archipelagoes for endemic taxa putatively translocated by prehistoric Polynesians, e.g. the lorikeet (*Vini kuhlii*; Watling 1995), the fruit bat (*Pteropus tonganus*; Weisler *et al.* 2006) and the land snail

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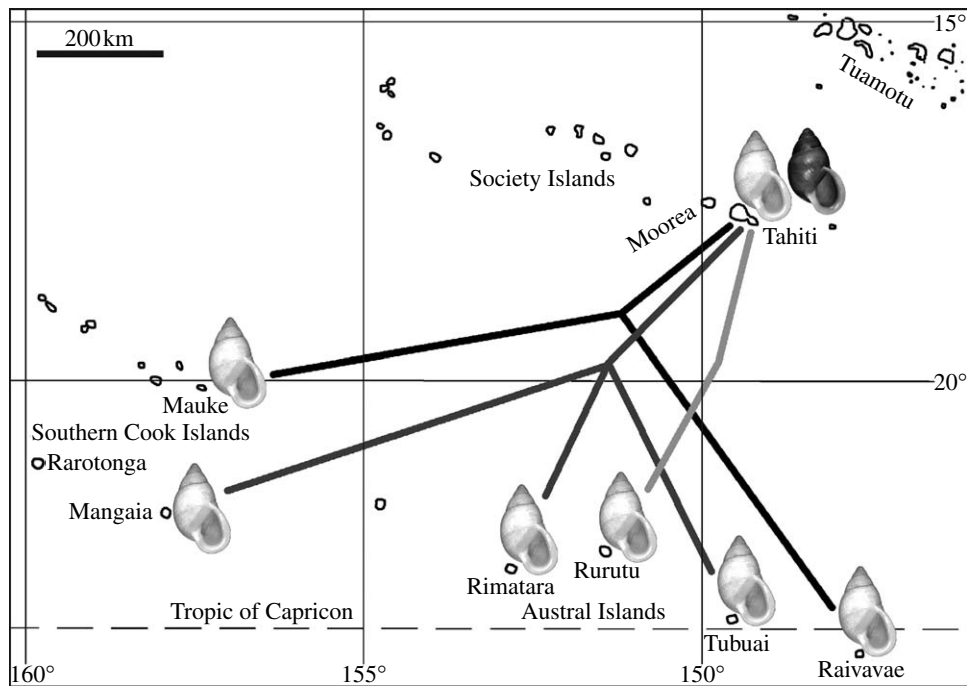


Figure 1. Map of the south-central Pacific showing the seven islands inhabited by *P. hyalina* (indicated by the white shell icons). Note that, on Tahiti, the lineage which *P. hyalina* belongs to also contains snails with non-white shell coloration, traditionally classified as *Partula clara* (indicated by the dark shell icon). An area cladogram is superimposed on the map to indicate the respective distributions of three multi-archipelago mitochondrial haplotypes, each found on Tahiti and on a discrete subset of the other islands.

(*Partula hyalina*; Garrett 1880, 1881, 1884; Pilsbry 1909–1910; Crampton 1916, 1932).

The predominantly arboreal land snail family Partulidae is endemic to tropical Pacific islands and ranges over 10 000 km of Oceania from Belau and the Marianas in the northwest to the Marquesas, Austral and Society Islands in the southeast (Cowie 1992). Individual tree snails rarely disperse more than a few metres during their lives (Murray & Clarke 1984) and most species, including 59 of 61 described Society Islands taxa (Pilsbry 1909–1910), are restricted to single islands (Cowie 1992). *Partula hyalina*, a distinctive white-shelled species, is the only partulid with a multi-archipelago distribution (Garrett 1880; Pilsbry 1909–1910; Crampton 1916). It occurs on seven islands distributed among three neighbouring south-central Pacific island groups: the Society (Tahiti only), Austral (Rurutu, Tubuai, Raivavae and Rimatara) and Southern Cook Islands (Mangaia and Mauke; figure 1). In addition to being geographically disjunct, the seven islands inhabited by *P. hyalina* are heterogeneous in terms of geological origin, age and ecology. For instance, Tahiti belongs to a linear volcanic chain (Hildenbrand *et al.* 2004) that is distinct from the Southern Cook–Austral volcanic chain complex (Bonneville *et al.* 2002). Mangaia contains the oldest exposed volcanic rocks, at an estimated 19.3 Ma (Turner & Jarrard 1982), on the Pacific Plate, whereas Tahiti's main shield is dated 0.87–1.4 Ma (Hildenbrand *et al.* 2004). Mangaia, Mauke and Rimatara lack the classic 'high island' rainforest ecosystem that comprises typical partulid habitat (Crampton 1916) and much of their land mass is composed of raised fossilized reef limestone platforms known as *makatea*.

A number of lines of evidence support the attainment of *P. hyalina*'s multi-archipelago distribution prior to European/American contact in the late eighteenth and

early nineteenth centuries. Archaeological studies of prehistoric, human-associated, rockshelter strata have found *P. hyalina* shells on Tahiti (Orliac 1997) and *Partula* spp. shells on Mangaia (Kirch *et al.* 1995). The latter record is significant because *P. hyalina* is the only partulid that occurs on Mangaia (Garrett 1881; Crampton 1916). The earliest Austral Islands record we are aware of is the 1828 collection of *P. hyalina* on Rurutu, its type locality (Broderip 1832; St John 1940).

Partula hyalina's multi-archipelago distribution generated considerable interest and speculation among early Pacific island malacologists and it was variously attributed to convergent evolution (Garrett 1880), a now untenable (Duncan & McDougall 1976) sunken continent hypothesis (Garrett 1880; Pilsbry 1909–1910; Crampton 1916, 1932) and prehistoric human transfer (Pilsbry 1909–1910; Crampton 1916) from 'its headquarters' in the Australs to the other three islands (Crampton 1932). However, recent phylogenetic analysis (Lee *et al.* 2007) has revealed the unambiguous *in situ* genealogical roots of Tahitian *P. hyalina* populations involving a very close evolutionary relationship with the endemic Tahitian nominal species *Partula clara*. This result is unsurprising because Tahiti is the only island where *P. hyalina* co-occurs with congeners (Kondo 1968) and Crampton (1916) could reliably distinguish it from *P. clara* only on the basis of shell coloration.

The goal of our study was to provide a genealogical perspective of *P. hyalina*'s multi-archipelago distribution in order to gain new insights into the genesis of its most unusual biogeography. This required genotyping a comprehensive sampling of *P. hyalina* and *P. clara* genetic diversity in Tahiti, the putative source island, as well as samples of *P. hyalina* from all six putative founder populations in the Cooks and Australs. The former

Table 1. Nominal taxonomic identity of the snails genotyped in this study, together with the number of sampling locations, individuals sequenced and haplotypes recovered per island.

taxon	archipelago	island	no. of locations sampled	no. of snails sequenced	no. of haplotypes obtained
<i>Partula clara</i> Pease 1864	Society Islands	Tahiti	18	67	14
<i>Partula hyalina</i>	Society Islands	Tahiti	17	64	16
<i>Broderip</i> 1832	Austral Islands	Rurutu	4	4	3
		Tubuai	1	1	1
		Raivavae	2	3	1
	Cook Islands	Rimatara	1	5	2
		Mauke	2	4	1
		Mangaia	5	6	1

objective has been complicated by the recent mass extirpation of Society Island tree snail populations following the deliberate introduction of the alien carnivorous land snail *Euglandina rosea* (Clarke *et al.* 1984; Cowie 1992; Coote & Loève 2003). Scattered remnant populations of *P. hyalina* and *P. clara* persist in some Tahitian valleys (Coote 2007), a few captive lineages have been established (Pearce-Kelly *et al.* 1997) and a historical museum collection of Tahitian tree snail tissues is available that pre-dates introduction of the predator (Lee *et al.* 2007). Combining museum, captive and relict wild samples enabled us to genotype a total of 131 *P. hyalina* and *P. clara* snails collectively sourced from 30 Tahitian valley populations over a 36-year period. Although this falls short of a comprehensive sampling of historical Tahitian populations (Crampton 1916 recorded *P. hyalina* from 51 Tahitian valleys), it is sufficient to look meaningfully for the genetic signature of putative anthropogenic introduction from Tahiti to the Cooks and Australs. Genetic diversity in the recipient islands should represent a subsampling of Tahitian diversity and at least some of the Cook and Austral snails should exhibit genotypes identical to those of Tahitian snails.

2. MATERIAL AND METHODS

(a) Sampling

Summary sampling data are presented in table 1 showing the nominal taxonomic identity of the snails genotyped, the numbers of sampling locations, individuals sequenced and haplotypes recovered per island. A more detailed sampling table is provided in the electronic supplementary material (table 1 in the electronic supplementary material) which shows specific location data for each snail and haplotype.

(i) Tahiti

From June to August 1970, collections of *P. hyalina* (50 individuals) and *P. clara* (53 individuals) were made at 20 sampling stations, incorporating a total of 16 valleys in both Tahiti-Nui and Tahiti-Iti, by J.B.B. and associates (table 1 in the electronic supplementary material). Specimens were identified in the field using Crampton (1916) taxonomic descriptions. They were airmailed alive to the University of Michigan Museum of Zoology (UMMZ), where they were dissected, their foot tissues individually lyophilized and the shells retained as vouchers (table 1 in the electronic supplementary material). The lyophilized samples have been stored at the UMMZ since 1970 at -20°C and we genotyped all of them.

Captive Tahitian *P. hyalina* (four individuals) and *P. clara* (eight individuals), supplied by the International Partulid Conservation Programme, were also genotyped (table 1 in the electronic supplementary material). These specimens were descendants of snails captured in 1995 from remnant Tahitian populations: two locations for *P. clara* and one for *P. hyalina*. They had died in captivity at London Zoo and had been preserved in 95% alcohol.

A total of 10 *P. hyalina* and 6 *P. clara* remnant wild snails were sampled by one of the authors (T.C.), between September 2004 and January 2006, from scattered remnant surviving populations in 13 Tahitian valleys (table 1 in the electronic supplementary material). Non-lethal biopsies of posterior foot tissue (Thacker & Hadfield 2000) from these snails were preserved in 95% ethanol and airmailed to the UMMZ for genotyping.

(ii) Cook and Austral Islands

Over a 5-year period, specimens of *P. hyalina* from the Austral and Cook Islands were sampled, preserved in ethanol and airmailed to the UMMZ for genotyping (table 1; see table 1 in the electronic supplementary material for details).

(b) Molecular methods

Total genomic DNA was isolated using a DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) according to the manufacturer's instructions. A 655 nucleotide (nt) mt cytochrome *c* oxidase subunit I (*COI*) target fragment was amplified with GoTaq DNA Polymerase (Promega, Madison, WI, USA) using the 'universal' (Folmer *et al.* 1994) primer pair LCO1490/HCO2198 and a negative control (no template) was included in each amplification run. After 2 min denaturation at 95°C , an initial annealing temperature of 53°C was decreased by 1°C per cycle (30 s denaturing at 95°C , 40 s annealing and 1 min extension at 72°C) until the final annealing temperature (45°C) was reached and subsequently maintained for an additional 30 cycles. Double-stranded products were isolated on 1% agarose gel, excised over UV light and extracted using a QIAquick Gel Extraction Kit (Qiagen). Both strands of the amplified fragments were directly cycle sequenced, using the PCR primers, by the University of Michigan's Sequencing Core Facility.

(c) Phylogenetic analyses

The resulting chromatograms were edited by comparing both strands using SEQUENCE NAVIGATOR v. 1.0.1 (Applied Biosystems, Foster City, CA, USA). *COI* sequences were aligned easily due to the absence of indels. Maximum-likelihood (ML) analyses were performed using PAUP*

v. 4.0b10 (Swofford 2003) under the K81uf+I model of sequence evolution, the best-fit model selected by the Akaike information criterion implemented in MODELTEST v. 3.7 (Posada & Crandall 1998). Maximum parsimony trees were first heuristically searched (100 random stepwise additions and tree bisection–reconnection (TBR) branch swapping), and using one of the MP trees as a starting tree, heuristic ML searches were executed with TBR branch swapping and all parameter values estimated. Bootstrap support values (Felsenstein 1985) were generated using a fast heuristic search with 100 replicates. Using PAUP*, ML-corrected pairwise distances among all haplotypes were calculated, with the same set of parameter values used above, to estimate sequence divergence rate.

3. RESULTS

Figure 2 graphically represents a genealogical assessment of the Cook and Austral *P. hyalina* relative to museum, captive and remnant wild Tahitian *P. hyalina* and *P. clara* samples. Note that multiple mt haplotypes, in all primary network domains, were shared by *P. hyalina* and *P. clara* snails, indicating that these two nominal species represent a discrete polymorphic lineage (Lee *et al.* 2007). Of the 23 Cooks and Australs *P. hyalina* genotyped, 19, collectively distributed among all 6 putative founder island populations (Mauke, Mangaia, Rimatara, Rurutu, Tubuai and Raivavae), exhibited genotypic identity with one of three Tahitian *P. hyalina/clara* haplotypes (figure 2). In all the three cases, co-clustering one- to two-step mutational derivatives were exclusively Tahitian (figure 2), a result consistent with a Tahitian origin for each multi-archipelago haplotype. These data strongly corroborate Tahiti as the source island and the Cook and Austral *P. hyalina* populations as founders.

Not all founder island population *P. hyalina* samples displayed genetic identity with Tahitian reference sequences. One snail from Rimatara and three from Rurutu yielded three haplotypes that lacked close mutational derivatives among snails sampled not only in Tahiti but also in Rimatara, Rurutu and the other four islands. These three haplotypes did not form a discrete clade and positioned topologically within the Tahitian network. We therefore assume that they stem from Tahitian source populations that are not represented in our necessarily incomplete sampling of that island's historical diversity.

With the exception of Rurutu, snails in each founder island shared a multi-archipelago haplotype with at least one other founder population, in addition to the Tahitian source, e.g. Mangaia + Rimatara + Tubuai, Mauke + Raivavae (figures 1 and 2). This raises the possibility of secondary introductions of *P. hyalina* among these recipient island sets. However, an exclusive secondary introduction involving Mauke and Raiavave seems unlikely on grounds of geographical remoteness (figure 1), and we cannot rule out other explanations such as independent introductions from the same Tahitian source population, inadequate sampling and/or differential lineage sorting among previously homogeneous founder island populations.

Our molecular data (figure 2) reveal that Tahitian *P. hyalina* lineages established founder populations on each of the six Cook and Austral Islands within the time

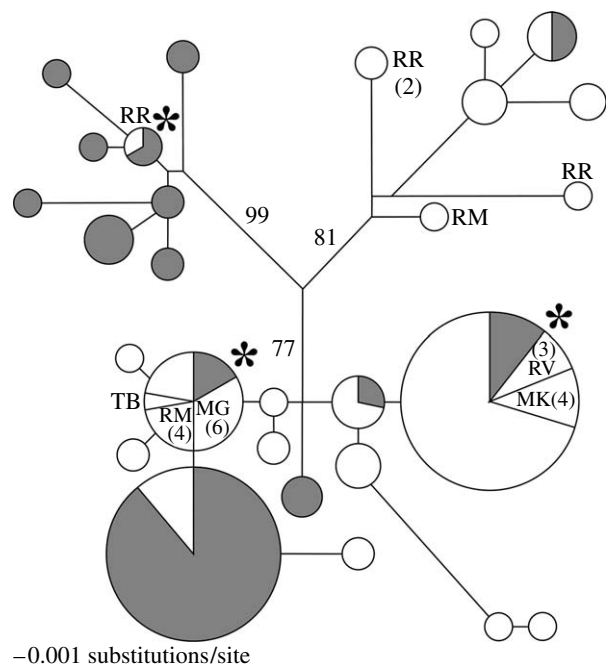


Figure 2. Unrooted maximum-likelihood network of 28 mitochondrial *COI* haplotypes (655 nt) obtained from 154 *P. hyalina* and *P. clara* snails genotyped for this study. Each terminal circle represents a single haplotype, sized according to its relative abundance and shaded to reflect the shell coloration of the snail(s) bearing that haplotype: dark for *P. clara* individuals (present in Tahiti only) and white for *P. hyalina* individuals (present on all seven islands). Haplotypes of non-Tahitian snails are labelled with island-specific abbreviations: RR, Rurutu; RM, Rimatara; RV, Raivavae; MK, Mauke; TB, Tubuai; MG, Mangaia. Haplotypes of Tahitian snails, which make up the large majority, are unlabelled. Three multi-archipelago haplotypes, present on Tahiti and at least one of the other islands, are each indicated with an asterisk. Numbers on internal branches indicate ML bootstrap values. See electronic supplementary materials for sampling locality and voucher information of each haplotype.

frame of a single mutational substitution of our mt gene marker. The oldest known rocks on Tahiti dated 1.4 Ma (Hildenbrand *et al.* 2004) and *P. hyalina* and *P. clara* collectively form a discrete colonizing Tahitian lineage (Lee *et al.* 2007) with sister lineages on Moorea (Goodacre & Wade 2001). ML-corrected pairwise distances among Tahitian *P. hyalina* and *P. clara* mt genotypes range up to 46 inferred substitutions (7% divergence). Assuming that this represents up to 1.4 Ma of accumulated genetic change, it yields a mean estimate of 30 kyr per substitution (5% divergence per Ma), a high but plausible rate for land snail mt genes (Davison 2002). Our genetic data therefore indicate that Tahitian *P. hyalina* snails successfully colonized Mauke, Mangaia, Rimatara, Rurutu, Tubuai and Raivavae at some point(s) in time within the past 30 000 years.

Another approach to reconstructing inter-archipelago *P. hyalina* transfers involves placing the three multi-archipelago haplotypes within Tahiti to determine whether they were sourced from the same, neighbouring or disjunct valleys. However, figure 3 reveals that it is not possible to infer Tahitian source valleys with confidence. Two of the three multi-archipelago haplotypes, carried by nominal *P. hyalina* and *P. clara* snails, occurred in multiple,

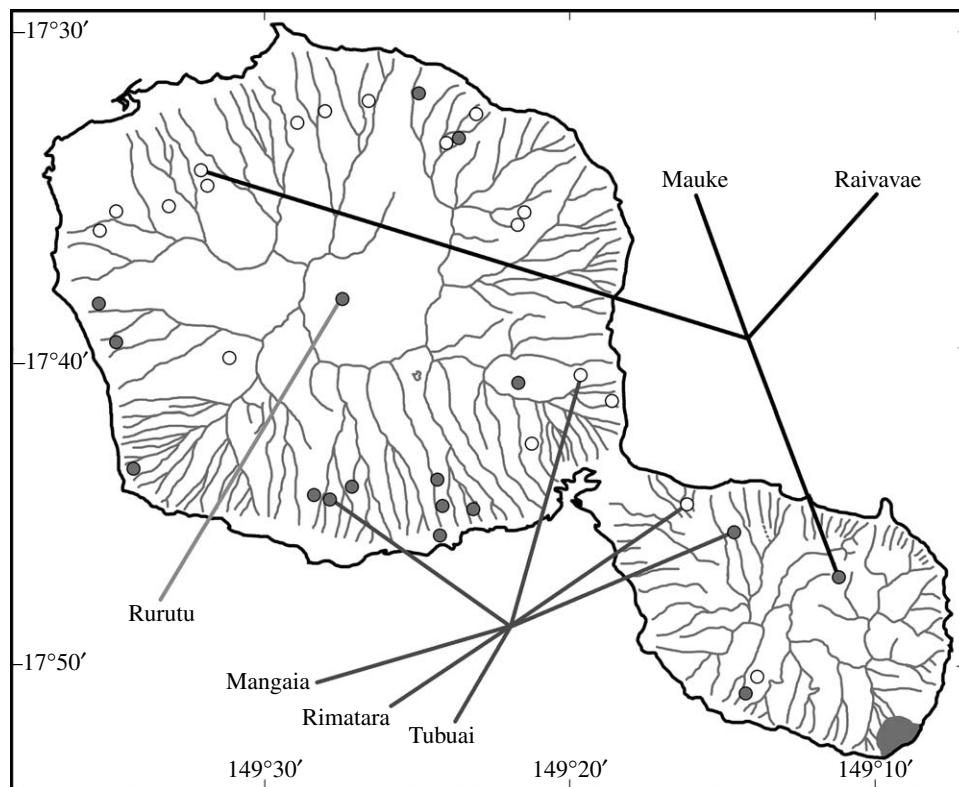


Figure 3. Map of Tahiti showing the valley sampling locations for the *P. hyalina* (white circles) and *P. clara* (dark circles) snails genotyped in this study. Three multi-archipelago haplotypes were detected (figures 1 and 2), and their respective distributions among our Tahitian sampling locations, together with the salient founder island(s) they occur on, are graphically indicated. See electronic supplementary material for details of individual sampling events including valley names and time frame of sample acquisition.

geographically disjunct Tahitian valleys and it is probable that their respective historical distributions encompassed additional valleys. The third multi-archipelago haplotype was present in a *P. clara* population in the remote interior of the island (figure 3), an unlikely source for inter-archipelago introduction.

4. DISCUSSION

Our data provide a number of important new insights into the enigmatic multi-archipelago distribution of *P. hyalina*. They rule out convergent evolution as a possible explanation, establish Tahiti as the source island and the other six as founder islands, and suggest that all six founders received live colonizing snails (directly or indirectly) from Tahiti within the past 30 kyr. These data, in conjunction with archaeological evidence for a prehistoric multi-archipelago distribution (Kirch *et al.* 1995; Orliac 1997), provide a compelling case for the introduction of this snail from Tahiti to the Australs and Cooks by prehistoric Polynesians.

The *P. hyalina* results are important because they provide qualitatively new material evidence of directional interaction among these central Eastern Polynesian archipelagoes. They complement and reinforce earlier material reconstructions of known (Cooks, Societies) or suspected (Cooks, Societies, Australs) regional interaction spheres inferred from geochemically sourced stone tools (Weisler 1998). The Tahiti–Austral linkage is particularly interesting because the latter islands have been relatively understudied archaeologically (Kirch 2000). The presence of *P. hyalina* on four Austral Islands, together

with the evidence of a genetically exclusive Rurutu–Tahiti linkage involving haplotypes from more than one topological domain (figure 2), is consistent with multiple prehistoric episodes of Tahiti–Austral interaction involving directional transfer of live snails.

Although *P. hyalina*'s multi-archipelago distribution is unique among partulids, there are many well-documented cases of synanthropic land snails that became widely distributed among Pacific island archipelagoes during Polynesian prehistory (Kirch & Hunt 1993; Kirch *et al.* 1995; Kirch 1996; Orliac 1997; Preece 1998; Weisler 1999). These other cases differ markedly from *P. hyalina* in that they are all exotic introductions to Remote Oceania, are typically much smaller in body size, occur in association with introduced exotic food plants and have spread extensively throughout a large number of archipelagoes. For instance, *Gastrocopta pediculus* is approximately 3 mm in size, occurs in nearly every inhabited atoll and high island in Oceania (Pilsbry 1909–1910), where it is a constituent of Polynesian archaeological strata (Kirch 1973; Preece 1998; Weisler 1999), and is thought to have been inadvertently introduced in association with cultigen root stock carried by early human colonists (Weisler 1999).

Prehistoric Polynesians introduced two broad functional groups of organisms to the islands they settled: targeted organisms of material value, such as food crops and animals, and inadvertently translocated organisms, such as *G. pediculus*, often associated with the former group. Garrett (1881), Pilsbry (1909–1910) and Crampton (1916, 1932) considered only *P. hyalina* as a possible member of the latter category, although they were well

aware of its many exceptions to the typical profile of Pacific island synanthropic land snails in terms of its ecology, body size and geographical distribution. In particular, they puzzled over the contrast between its multi-archipelago range extending over 1000 km and restricted distribution in the Society Islands: present throughout Tahiti and absent from the other Society Islands including Moorea, a mere 17 km away. On the spatial scale of its home archipelago, the Society Islands, *P. hyalina*'s distribution pattern (single-island endemic) is typically partulid. In contrast, on the spatial scale of regional archipelagoes, its distribution pattern is more characteristic of exotic synanthropic land snails.

Polynesian cultures have long used mollusc shells as integral components of traditional jewellery and ornamentation (Neich & Periera 2004) and, prior to the recent mass extinction of Society Island partulids, local Polynesian communities made extensive use of a wide variety of colour morphs present among this archipelago's 61 partulid species for shell *lei* manufacture (Coote & Loève 2003). Apart from an isolated subpopulation of *Partula varia* on Huahine (Goodacre 2002), *P. hyalina* is the only white-shelled member of its genus and it has a distinct aesthetic appearance—Broderip (1832) made a specific mention of its 'elegant' appearance in his four line species description. As recently as 2002, *lei*-containing *P. hyalina* shells were being produced for sale on Rurutu (B. Fontaine & O. Gargominy, personal observation).

We propose a new model of anthropogenic transfer for *P. hyalina* that assumes it to have been deliberately introduced, for its ornamental aesthetic utility, from Tahiti to the Cooks and Australs. Our model assumes that, in early Polynesia, this species was initially restricted to Tahiti but that its shells had aesthetic value throughout a regional interaction sphere incorporating the Society, Austral and Southern Cook Islands. Snail shells are relatively imperishable, and demand outside of Tahiti would be most conveniently met by trading shells, rather than by live snails. We assume that transportation costs increased, and frequency of trading contact decreased, with distance from Tahiti. The cost/value/novelty of traded *P. hyalina* shells would therefore be minimal in Moorea, which engaged in almost daily trading activity with Tahiti (Garrett 1881), intermediate in the rest of the Society Islands and maximal in the distant Austral and Cook Islands. An equivalent geographical gradient would also exist concerning motivation levels for transporting live *P. hyalina* from Tahiti and establishing founder populations. There are parallels here with the modern marketing of 'hot products' (Stock & Balachander 2005), especially so for fashion items for which scarcity often acts to enhance their perceived value (Pesendorfer 1995). Once founder populations were established in the Australs and Cooks, we expect that local production replaced importation of shells from Tahiti and that increased availability acted to erode their novelty-fuelled aesthetic status.

The most attractive aspect of the model is its explanatory power vis-à-vis this snail's paradoxical distribution pattern: absent from the neighbouring islands in the source archipelago and present in multiple islands of distant recipient archipelagoes. It also explains the shell colour bias observed in the founder populations: the polymorphic Tahitian source lineage contains snails with a spectrum of light-to-dark brown shell phenotypes

(*P. clara*) and white shell phenotypes (*P. hyalina*), but the six recipient islands were seeded only with the latter (figures 1 and 2). The assumptions made are largely unproblematic: long-distance trade in prehistoric Polynesia was strongly motivated by the pursuit of 'luxury goods' including shell ornaments (Hage & Harary 1991), and records of *P. hyalina* shells on Rarotonga (where the species does not occur) were attributed by Crampton (1916) to inter-island trading by Polynesians. Although we lack records of inter-island/archipelago trading of live snails, indirect evidence of those is present in the multi-archipelago genealogy (figure 2) and the Tangatatau Rockshelter excavations on Mangaia provide an independent temporal reference point (Kirch *et al.* 1995). Further archaeological work on Mauke, Rimatara, Rurutu, Tubuai and Raivavae may flesh out the temporal sequence of this species' introduction to the recipient islands.

Partula hyalina was but one of a large number of exotic synanthropic species introduced by prehistoric Polynesians to the Austral and Southern Cook Islands. Unlike the majority of these introductions, this snail's status as a Pacific island endemic species gives it a robust regional phylogenetic frame of reference. This feature provides new insights into a prehistoric regional interaction sphere and it also has an important present-day conservation legacy. The alien carnivorous land snail *E. rosea* has recently devastated natural populations of all 61 endemic species of the Society Island partulid snails (Coote & Loève 2003). This rich malacofauna represented approximately 50% of partulid nominal species diversity, a remarkable fraction for one archipelago considering that Partulidae ranges over 10 000 km of Oceania (Cowie 1992). The only unscathed wild populations remaining of this spectacular endemic land snail radiation are the founder island populations of *P. hyalina*, all products of a prehistoric Polynesian exchange network that linked these archipelagoes.

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REFERENCES

- Bonneville, A., Le Suavé, R., Audin, L., Clouard, V., Dosso, L., Gillot, P. Y., Janney, P., Jordahl, K. & Maamaatuaiahutapu, K. 2002 Arago seamount: the missing hotspot found in the Austral Islands. *Geology* **30**, 1023–1026. (doi:10.1130/0091-7613(2002)030<1023:ASTMHF>2.0.CO;2)
- Broderip, W. J. 1832 Characters of new species of *Mollusca* and *Conchifera* collected by Mr. Cuming. *Proc. Zool. Soc. Lond.* **2**, 32.
- Clarke, B., Murray, J. & Johnson, M. S. 1984 The extinction of endemic species by a program of biological control. *Pac. Sci.* **38**, 97–104.
- Clarke, A. C., Burtenshaw, M. K., McLenachan, P. A., Erickson, D. L. & Penny, D. 2006 Reconstructing the origins and dispersal of the Polynesian bottle gourd (*Lagenaria siceraria*). *Mol. Biol. Evol.* **23**, 893–900. (doi:10.1093/molbev/msj092)
- Coote, T. 2007 Partulids on Tahiti: differential persistence of a minority of endemic taxa among relict populations. *Am. Malacol. Bull.* **22**, 83–87.

- Coote, T. & Loève, E. 2003 From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. *Oryx* **37**, 91–96. (doi:10.1017/S0030605303000176)
- Cowie, R. H. 1992 Evolution and extinction of partulidae, endemic Pacific island land snails. *Phil. Trans. R. Soc. B* **335**, 167–191. (doi:10.1098/rstb.1992.0017)
- Crampton, H. E. 1916 Studies on the variation, distribution and evolution of the genus *Partula*, the species inhabiting Tahiti. *Carnegie Inst. Wash. Publ.* **228**, 1–311.
- Crampton, H. E. 1932 Studies on the variation, distribution and evolution of the genus *Partula*, the species inhabiting Moorea. *Carnegie Inst. Wash. Publ.* **410**, 1–335.
- Davison, A. 2002 Land snails as a model to understand the role of history and selection in the origins of biodiversity. *Popul. Ecol.* **44**, 129–136. (doi:10.1007/s101440200016)
- Duncan, R. A. & McDougall, I. 1976 Linear volcanism in French polynesia. *J. Volcanol. Geotherm. Res.* **1**, 197–227. (doi:10.1016/0377-0273(76)90008-1)
- Falush, D. et al. 2003 Traces of human migrations in *Helicobacter pylori* populations. *Science* **299**, 1582–1585. (doi:10.1126/science.1080857)
- Felsenstein, J. 1985 Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791. (doi:10.2307/2408678)
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. 1994 DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* **3**, 294–299.
- Garrett, A. 1880 List of land shells inhabiting Rurutu, one of the Austral Islands, with remarks of their synonymy, geographical range, and descriptions of new species. *Proc. Acad. Nat. Sci. Phila.* **31**, 17–30.
- Garrett, A. 1881 The terrestrial Mollusca inhabiting the Cook's or Harvey islands. *J. Acad. Nat. Sci. Phila.* **8**, 381–411.
- Garrett, A. 1884 The terrestrial Mollusca inhabiting the Society Islands. *J. Acad. Nat. Sci. Phila.* **9**, 17–114.
- Gibbons, A. 2001 The peopling of the Pacific. *Science* **291**, 1735–1737. (doi:10.1126/science.291.5509.1735)
- Goodacre, S. L. 2002 Population structure, history and gene flow in a group of closely related land snails: genetic variation in *Partula* from the Society Islands of the Pacific. *Mol. Ecol.* **11**, 55–68. (doi:10.1046/j.0962-1083.2001.01422.x)
- Goodacre, S. L. & Wade, C. M. 2001 Patterns of genetic variation in Pacific island land snails: the distribution of cytochrome *b* lineages among Society Island *Partula*. *Biol. J. Linn. Soc.* **73**, 131–138. (doi:10.1006/bijl.2001.0530)
- Hage, P. & Harary, F. 1991 Exchange in Oceania: a graph theoretic analysis. Oxford, UK: Clarendon Press.
- Hildenbrand, A., Gillot, P.-Y. & Le Roy, I. 2004 Volcano-tectonic and geochemical evolution of an oceanic intra-plate volcano: Tahiti-Nui (French polynesia). *Earth Planet. Sci. Lett.* **217**, 349–365. (doi:10.1016/S0012-821X(03)00599-5)
- Hurles, M. E., Matisoo-Smith, E., Gray, R. D. & Penny, D. 2003 Untangling oceanic settlement: the edge of the knowable. *Trends Ecol. Evol.* **18**, 531–540. (doi:10.1016/S0169-5347(03)00245-3)
- Irwin, G. 1992 *The prehistoric exploration and colonisation of the Pacific*. Cambridge, UK: Cambridge University Press.
- Kirch, P. V. 1973 Prehistoric subsistence patterns in the northern Marquesas Islands, French Polynesia. *Archaeol. Phys. Anthropol. Oceania* **8**, 24–40.
- Kirch, P. V. 1996 Late Holocene human-induced modifications to a central Polynesian island ecosystem. *Proc. Natl Acad. Sci. USA* **93**, 5296–5300. (doi:10.1073/pnas.93.11.5296)
- Kirch, P. V. 2000 *On the road of the winds: an archaeological history of the Pacific Islands before European contact*. Berkeley, CA: University of California.
- Kirch, P. V. & Hunt, T. L. 1993 *The To'aga site: three millennia of polynesian occupation in the Manu'a Islands, American Samoa*. Archaeological Research Facility Contribution, no. 51. Berkeley, CA: University of California.
- Kirch, P. V., Steadman, D. W., Butler, V. L., Hather, J. & Weisler, M. I. 1995 Prehistory and human ecology in eastern Polynesia: excavations at Tangatatau Rockshelter, Mangaia, Cook Islands. *Archaeol. Oceania* **30**, 47–65.
- Kondo, Y. 1968 Partulidae: preview of anatomical revision. *Nautilus* **81**, 73–77.
- Lee, T., Burch, J., Jung, Y., Coote, T., Pearce-Kelly, P. & Ó Foighil, D. 2007 Tahitian tree snail mitochondrial clades survived recent mass-extirpation. *Curr. Biol.* **17**, R502–R503. (doi:10.1016/j.cub.2007.05.006)
- Matisoo-Smith, E. & Robins, J. H. 2004 Origins and dispersals of Pacific peoples: evidence from mtDNA phylogenies of the Pacific rat. *Proc. Natl Acad. Sci. USA* **101**, 9167–9172. (doi:10.1073/pnas.0403120101)
- Matisoo-Smith, E., Roberts, R. M., Irwin, G. J., Allen, J. S., Penny, D. & Lambert, D. M. 1998 Patterns of prehistoric human mobility in Polynesia indicated by mtDNA from the Pacific rat. *Proc. Natl Acad. Sci. USA* **95**, 15 145–15 150. (doi:10.1073/pnas.95.25.15145)
- Murray, J. & Clarke, B. 1984 Movement and gene flow in *Partula taeniata*. *Malacologia* **25**, 343–348.
- Neich, R. & Pereira, F. 2004 *Pacific jewellery and adornment*. Auckland, New Zealand: David Bateman Ltd.
- Orliac, M. 1997 Human occupation and environmental modifications in the Papeno'o Valley. In *Historical ecology in the Pacific Islands* (eds P. V. Kirch & T. L. Hunt), pp. 200–229. New Haven, CT: Yale University Press.
- Pearce-Kelly, P., Clarke, D., Walker, C. & Atkin, P. 1997 A conservation programme for the partulid tree snails of the Pacific region. *Mem. Mus. Victoria* **56**, 431–433.
- Pesendorfer, W. 1995 Design innovation and fashion cycles. *Am. Econ. Rev.* **85**, 771–792.
- Pierson, M. J., Martinez-Arias, R., Holland, B. R., Gemmell, N. J., Hurles, M. E. & Penny, D. 2006 Deciphering past human population movements in Oceania: provably optimal trees of 127 mtDNA genomes. *Mol. Biol. Evol.* **23**, 1966–1975. (doi:10.1093/molbev/msl063)
- Pilsbry, H. A. 1909–1910 Manual of conchology, structural and systematic. Caecilioides, Glessula and Partulidae. *Acad. Nat. Sci. Phila.* **20**, 1–336.
- Posada, D. & Crandall, K. A. 1998 MODELTEST: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818. (doi:10.1093/bioinformatics/14.9.817)
- Preece, R. C. 1998 Impact of early Polynesian occupation on the land snail fauna of Henderson Island. Pitcairn group (South Pacific). *Phil. Trans. R. Soc. B* **353**, 347–368. (doi:10.1098/rstb.1998.0214)
- St John, H. 1940 Itinerary of Hugh Cumming in polynesia. *Occ. Pap. Bern. P. Bish. Mus.* **16**, 81–90.
- Stock, A. & Balachander, S. 2005 The making of a 'hot product': a signaling explanation of marketers' scarcity strategy. *Manage. Sci.* **51**, 1181–1192. (doi:10.1287/mnsc.1050.0381)
- Storey, A. A. et al. 2007 Radiocarbon and DNA evidence for a pre-Columbian introduction of Polynesian chickens to Chile. *Proc. Natl Acad. Sci. USA* **104**, 10 335–10 339. (doi:10.1073/pnas.0703993104)
- Swofford, D. L. 2003 PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4. Sunderland, MA: Sinauer Associates.
- Thacker, R. W. & Hadfield, M. G. 2000 Mitochondrial phylogeny of extant Hawaiian tree snails (*Achatinellinae*). *Mol. Phylogenet. Evol.* **16**, 263–270. (doi:10.1006/mpev.2000.0793)

- Turner, D. L. & Jarrard, R. D. 1982 K–Ar dating of the Cook–Austral Island chain: a test of the hot-spot hypothesis. *J. Volcanol. Geotherm. Res.* **12**, 187–220. (doi:10.1016/0377-0273(82)90027-0)
- Watling, D. 1995 Notes on the status of Kuhl's Lorikeet (*Vini kuhlii*) in the Northern Line Islands Kiribati. *Bird Conserv. Int.* **5**, 481–489.
- Weisler, M. I. 1998 Hard evidence for prehistoric interaction in Polynesia. *Curr. Anthropol.* **39**, 521–532. (doi:10.1086/204768)
- Weisler, M. I. 1999 The antiquity of aroid pit agriculture and significance of buried A Horizons on Pacific atolls. *Geoarchaeology* **14**, 621–654. (doi:10.1002/(SICI)1520-6548(199910)14:7<621::AID-GEA2>3.0.CO;2-2)
- Weisler, M. I., Bollt, R. & Findlater, A. 2006 A new eastern limit of the Pacific flying fox. *Pteropus tonganus* (Chiroptera: Pteropodidae), in prehistoric Polynesia: a case of possible human transport and extirpation. *Pac. Sci.* **60**, 403–411. (doi:10.1353/psc.2006.0020)