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Expanding Southwest Pacific mitochondrial haplogroups P and Q

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Abstract

Modern humans have occupied New Guinea and the nearby Bismarck and Solomon archipelagos of Island Melanesia for at least 40,000 years. Previous mitochondrial DNA (mtDNA) studies indicated that two common lineages in this region, haplogroups P and Q, were particularly diverse, with the coalescence for P considered significantly older than that for Q.

In this study, we expand the definition of haplogroup Q so that it includes three major branches, each separated by multiple mutational distinctions (Q1, equivalent to the earlier definition of Q, plus Q2 and Q3). We report three whole mtDNA genomes that establish Q2 as a major Q branch. In addition, we describe 314 control region sequences that belong to the expanded haplogroups P and Q from our Southwest Pacific collection. The coalescence dates for the largest P and Q branches (P1 and Q1) are similar to each other (~ 50,000 years old), and considerably older than prior estimates. Newly identified Q2, which was found in Island Melanesian samples just to the east, is somewhat younger, by more than 10,000 years. Our coalescence estimates should be more reliable than prior ones because they were based on significantly larger samples, as well as complete mtDNA coding region sequencing. Our estimates are roughly in accord with current suggested dates for the first settlement of New Guinea/Sahul.

The phylogeography of P and Q indicates almost total (female) isolation of ancient New Guinea/Island Melanesia from Australia that may have existed from the time of first settlement. While Q subsequently diversified extensively in New Guinea/Island Melanesia, it has not been found in Australia. The only shared mtDNA haplogroup between Australia and New Guinea identified to date remains one minor branch of P.

Introduction

This paper on variation in two major mtDNA haplogroups that are restricted to Southwest Pacific populations is pertinent to three questions on the prehistory of Sahul (the ancient continent that encompassed Australia and New Guinea) and Island Melanesia. First, are there any clear signatures in these data reflecting differences in population dynamics across the region (i.e., in ancient population expansions or dispersals)? Second, how limited has contact been between populations in New Guinea/Island Melanesia and Australia during the Holocene and Upper Pleistocene? Finally, are there any indications that the initial settlers of northern and southern Sahul were part of a single population, or instead were composed of multiple founding groups?

The current dates from excavated habitation sites could be interpreted to suggest the Australian section of Sahul was settled first. While there have been claims for settlement dates >100,000 BP, the earliest generally accepted dates from Australia fall into the 50,000 to 60,000 year range and are based on thermoluminescence dating (O'Connor and Chappell 2003). However, some maintain that the dates before 42-45,000 BP are not well supported there (O'Connell and Allen 2004). The proposed entry point for any southern voyaging was via the Nusa Tenggara island chain through Timor, as first suggested by Birdsell (1967). The earliest accepted dates for the occupation of New Guinea/Island Melanesia, where no deposits amenable to thermoluminscence dating have been identified, are at the limits of radiocarbon reliability ~ 40,000 BP for both the Huon Peninsula in eastern New Guinea (Groube 1986) and New Ireland (Leavesley et al. 2002), with dates from the Moluccas being no earlier (Bellwood et al. 1998). This temporal framework suggests that a second contemporaneous settlement route originating in

the Moluccas and progressing eastward along the ancient New Guinea north coast into the Bismarck Archipelago is very likely (Allen 2003; Yen 1995).

Subsequent to initial settlement, populations appear to have followed different resource exploitation strategies in the two regions (more terrestrial in Australia vs. mixed maritime and terrestrial in Melanesia - Leavesley et al. 2002) and to have experienced different expansion rates (more numerous sites in Pleistocene Australia - Chappell 2000). By 20,000 years ago, a number of novel cultural developments are detectable, particularly in the Island Melanesian record (Allen 2003), and this pattern of episodic change intensifies in the Holocene (Green 2003). There are competing colonization scenarios for Pleistocene Australia (Bowdler 1993; Flannery 1994; Horton 1999; O'Connell and Allen 1998), with some indication of more fluid population movements in the interior (O'Connor and Chappell 2003).

Relevant to more recent times, historical linguists have not found any connections between Aboriginal Australian and New Guinea/Island Melanesian languages, implying little to no significant contact occurred during the Holocene. In New Guinea/Island Melanesia, one language family (a branch of Austronesian) was introduced from the west only ~3,500 years ago (Kirch 1997; Pawley 2003; Spriggs 1997). The hundreds of other heterogeneous languages spoken there are referred to as non-Austronesian or Papuan, and fall into more than 20 different families which are not demonstrably related (Dunn, Terrill and Reesink 2002; Ross 2001, in press). The largest of these is the Trans New Guinea Phylum, which has been reconstructed for all the languages of the central cordillera of New Guinea, or approximately 70% of the languages of the interior. It is thought to be at least 8 - 12,000 years old (Pawley in press). The diverse languages in north New Guinea and the interiors of Island Melanesia suggest the presence of even older linguistic strata (Pawley in press). The Aboriginal Australian languages are less

diverse. The one major family, Pama-Nyungan, that may be derived from a single proto-language spoken ~10,000 years ago (Bowern and Koch 2004), includes all the Australian languages outside the northwest, and one speculation associated it with the spread of the Small-Tool Tradition (Evans and Jones 1997). In sum, the linguistic and archaeological data suggest little to no contact between the two regions subsequent to their initial settlement, with considerably more inland mobility in Australia than within New Guinea.

Past genetic surveys, particularly those involving the HLA and α-globin loci, indicated simple isolation by distance relationships across the region, with some weak associations reported between Australian Aborigines and highland New Guinea populations (Gao and Serjeantson 1991; Kirk 1989; Roberts-Thomson et al. 1996; Tsintsof et al. 1990). Pertinent mtDNA data have been equivocal in this regard (Forster et al. 2001; Huoponen et al. 2001; Ingman and Gyllensten 2003; Ingman et al. 2000; Redd and Stoneking 1999; Redd et al. 1995; Stoneking et al. 1990). Haplogroups P and Q (as defined by Forster et al. 2001) were especially common in New Guinea/Island Melanesia, and other variants that belong to P were also found in Australia (B^, H^, and I^ of Huoponen et al. 2001; 1b, 1c, and 1d of Ingman and Gyllensten 2003). Previous estimates of their coalescence times and ages of expansion have not been consistent, although haplogroup P appeared to be considerably older than Q as then defined.

Here we report complementary analyses of these two mtDNA haplogroups from our large Southwest Pacific sample set, which clarify their definitions, distributions and ancient expansions. The first is a phylogenetic study of the two haplogroups based on whole mtDNA genome sequences (from published data plus three of our own) that clarifies and modifies published reports on P and expands the definition of Q. The second covers the phylogeography of these P and Q branches (from the total of 886 matrilineages identified in our Southwest

Pacific samples) on the basis of mtDNA hypervariable segment 1 and 2 sequences (HVS1 and HVS2, from np 16000 to 408). The results of these analyses show that haplogroup Q in its expanded definition is complex, with at least two major star-like branches and occurs primarily in populations in New Guinea/Island Melanesia. It has not been found in Australia. P1 and Q1, which have their greatest diversities in New Guinea, have approximately the same coalescence times, while that of the Island Melanesian branch Q2 is smaller (younger).

Materials and Methods

Sample Collection

Our core data set derived from more than 1,500 blood samples collected over the last six years from the Bismarck Archipelago (New Britain, New Ireland, New Hanover/Lavongai and Mussau) and Bougainville Island, Papua New Guinea. Information collected on survey subjects included language, residence, and genealogy. The core sample was supplemented with plasmas from older collections belonging to J. S. Friedlaender, L. Weitkamp, B. S. Blumberg, M. Schanfield, R. Deka, B. Zemel, and A. Damon, and with urine samples obtained from R. Yanagihara and V. Nerukar. Details on sample provenience and collection source are given in the Supplementary Materials, table 1. As detailed there, identification of residence and familial relationships were more problematic for individuals in some of these sets, as they came from a variety of locations in New Guinea, Island Melanesia, Polynesia, and Micronesia. The core samples were collected, and all samples were analyzed, with the approval of the appropriate Human Subjects Ethical Committees of Papua New Guinea, the University of Michigan, and Temple University.

Sample Extraction, Amplification and Analysis

DNA was extracted from 100 to 200 microliters of plasma, red cells, buffy coat or urine (depending on the source of the sample) by using either the quanidine-silica based IsoQuick extraction kit (Orca Scientific) or the column-based Qiagen extraction kit (Qiagen, Inc).

The analysis of these mtDNAs occurred in three steps. The first was the sequencing of the HVS1 and HVS2 from the 886 different matrilineages identified from survey records. The HVS1/2 sequences that could not be definitely assigned to known clades were then screened for the two mutations defining macrohaplogroup M (DdeI 10394, AluI 10397), and then, depending on the presence or absence of these sites, were surveyed for additional RFLPs identified in Malaysian Aborigines, Orang Asli and Malays (Ballinger et al. 1992), PNG populations (Stoneking et al. 1990) and Aboriginal Australians (Cann et al. 1987). Finally, sequencing of the coding region was performed on representative samples from each of the major branches identified by PCR-RFLP analysis using the PCR conditions and primer sets of Rieder et al. (1998).

For control region sequencing, DNA was PCR amplified following standard protocols, using primers spanning nucleotide pairs (nps) 15938 to 00429 and Platinum Taq Polymerase (Invitrogen). Successful amplification was verified by electrophoresis on a 1% ethidium bromide stained agarose gels. Samples were prepared for sequencing by an ExoI digest followed by filtration through a Millipore 96-well filter plate (Millipore, Inc) to remove single stranded DNA and unincorporated nucleotides, and then sequenced using BigDye Terminator 3.0 Ready-reaction kits (ABI). The sequences were then purified with Centri-Sep columns (Princeton Separations), and sequence data collected on an ABI 377XL automated sequencer. Sequence alignment on the coding region was accomplished with Sequencher: Forensic Version (GeneCodes Inc), and, for the control region, Sequence Navigator.

Median joining networks were generated from the control region sequences (manually converted to binary format) in Network 4.0 (Bandelt et al. 1995). The measures of haplotype diversities of the star phylogeny networks, their standard errors and associated expansion age estimates were calculated as specified in Saillard et al. (2000), and as modified in the Appendix to cover HVS1 plus HVS2 (nps16090 -16365 and 035 - 315) .

Results

As defined by Forster et al. (2001), haplogroups P and Q form deep branches within the two major mtDNA clades that exist outside Africa, with P being part of the R division of the N clade, and Q being part of the M clade. The accepted schematic relationships of P and Q to the other mtDNA branches of the African root, L3, are shown in figure 1. Earlier studies indicated these two haplogroups constituted approximately 90% of the observed mtDNA haplotypes in New Guinea (Forster et al. 2001; Tommaseo-Ponzetta et al. 2002).

Haplogroup Q

Figure 2 shows the phylogeny of Q based on whole mtDNA genome sequences. This analysis enlarged the prior definition of Q (now equivalent to Q1) by adding a newly identified branch (Q2), and confirming a third branch (Q3) that had been previously reported in this region with different nomenclatures (Ingman et al. 2003; Redd and Stoneking 1999; Tomasseo-Ponzetta et al. 2001). As shown here, all Q branches shared distinctive transitions at the base, including nps 4117, 5843, 8790, 12940, 13500, 16129, and 16241. Each branch also had its own long set of defining mutations. Interestingly, eight of the ten mutations that define Q1 were found in the control region.

Figure 3 shows the median joining network derived from the haplogroup Q control region sequences. In this network, Q1, Q2, and Q3 all had long branch lengths, and both Q1 and Q2 had

clear “star-like” expansion signatures. The internal diversity of Q1 was greater than Q2. Q3 was represented by only nine total samples (five of our own), and therefore remained poorly delineated. Because of the clear separation of the Q branches, the Q mismatch distribution was bimodal, with a large mean (Supplementary Materials, figure 1).

Haplogroup P

The phylogenetic tree for haplogroup P in figure 4 incorporated published whole mtDNA genome sequences (Ingman and Gyllensten 2003; Ingman et al. 2000; Kivisild et al. 2002). The specific internal branching order of P was ambiguous for two reasons. First, there were many apparent parallel mutations in the separate long branches, probably because of their great age and the loss of intermediate states. Second, the major branches of P were only linked together by a single coding region mutation at np 15607. This is not a common mutation, but it has occurred independently in two West Eurasian haplogroups (J and T).

P3 was the only haplogroup that contained both New Guinea and Australian branches (as reported with different methods and terminology in Ingman and Gyllensten 2003 and Huoponen et al. 2001). Ingman and Gyllensten (2003) proposed a second New Guinea-Australian connection (their branch 1d), which corresponds to our P2 plus P5 branches. However, this tie is not convincing since it is based on the single frequently occurring shared transition at np 1438 (which has occurred independently within haplogroups L1a, L1b, D, H, I and R).

The median joining network for P based on control region sequences (in figure 5) was not as clearly resolved as that for Q, as it contained a number of reticulations. Still, the P1 branch had a clear star-like quality suggesting its great age, with long branches and an under populated central node. The pairwise mismatch distribution for P was smooth and unimodal, with a mean of 7.076 (see also Supplementary Materials, figure 1).

Coalescence Times for P and Q

Table 1 presents the coalescence estimates and associated ages for the "star-like" branches of P and Q. Comparable results from Forster et al. (2001) are paired with them. For expansion age calculations, we had to estimate an average substitution rate per nucleotide per year across both HVS1 and HVS2, which was one per 24,880 years (see the Appendix). The calculated expansion ages for Q1 and P1 from our dataset were large and essentially the same, ~50,000 years. As shown, Forster et al. (2001) reported much smaller coalescence values for their Q1 and P1 equivalents. However, their calculations were based on a set of RFLPs from a very small sample, as opposed to our much larger sample of control region sequences (>4 times greater for P1 and >5 times greater for Q1). Our data also indicated that Q2 expanded ~36,000 years ago, more than 10,000 years later than Q1 and P1.

Geographic Distributions of P and Q

The distributions of P and Q in New Guinea/Island Melanesia are given in table 2 and figure 6 (the much younger haplotype B data are also included but not discussed). The distributions of P and Q do not completely overlap. Q is the more common of the two, and, within New Guinea, the only place that Q has not been found is the South Coast. Haplogroup P is infrequent in the western half of New Guinea (Tommaseo-Ponzetta et al. 2002), and very unevenly distributed through the eastern half of the island. East of New Guinea, P is rare in Island Melanesia except in certain islands of the Louisiade Archipelago off the Papuan Tip.

The Island Melanesian distribution of these two haplogroups is particularly heterogeneous (see table 3 and figure 7). Q2 is found primarily in certain Papuan-speaking groups of New Britain, which indicates its origin lies in this part of Island Melanesia. In New Ireland, P and Q are both very rare, with Q2 present in low frequency in the Madak, who used to

speak a Papuan language. Q1 occurs frequently in most, but not all Papuan-speaking areas reported in table 3.

Further details of the P and Q haplotype subdivisions on the total sample set are given in the Supplementary Materials, tables 1-3. These show that specific haplotypes, especially within Q branches, often have extremely restricted distributions, and sometimes are found only in particular island sections. P haplotypes occur even more sporadically in sections of Island Melanesia than New Guinea, with one subbranch (P1e) being specific to New Britain, while one specific P2 haplotype was found in Fiji, New Caledonia and also Misima Island - all Austronesian-speaking groups. The structured branching implies a relatively undisturbed accumulation of mutational diversity in time and space, with the deepest branches generally being more widely dispersed geographically than the shallower, more recent ones.

Both P and Q were carried further to the southeast (see table 3 and figure 6), to Santa Cruz (Friedlaender et al. 2002), Vanuatu (Cox 2003; Hagelberg et al. 1999; Sykes et al. 1995), and to Fiji (present study), while only Q has been found in Polynesia, in frequencies less than 0.05 (Sykes et al. 1995). Also, both haplogroups have been found in Micronesia to the north in low frequencies. Out of 584 samples tested, ten Q1s and 47 P1s were reported there by Lum and Cann (2000).

To the west of New Guinea, both P and Q are rare. Out of more than 1100 mtDNAs reported from Island Southeast Asia, only seven Qs and three Ps have been identified, all but one of these occurring in central and eastern Indonesia (Ballinger et al. 1992; Cox 2003; Redd and Stoneking 1999; Tajima et al. 2004). We suggest these rare occurrences are most likely the result of a few women moving to those regions from New Guinea, rather than this region of Island Southeast Asia being the ancient homeland of the haplogroups P and Q.

Discussion

These results illustrate a number of problems concerning coalescent statistics and associated age estimates, but also their utility. One issue is that mutation rates vary for different mtDNA regions and nucleotide sites and also among clades (Forster et al. 2002; Macaulay et al. 1999; Parsons et al. 1997). In our study, the proportion of mutations that occurred in the control region was particularly large in the base stem of Q1, compared to other parts of the P and Q trees (compare figures 2 and 4). If, instead, this distortion had happened within Q1, control region sequence and RFLP data would yield divergent coalescence estimates for Q1. Fortunately for our comparisons, this disproportion is not apparent in the expansions within Q1, Q2, and P1 (figures 2 and 4). A second more obvious issue is that reliable coalescence estimates depend on adequate sample sizes as well as clear expansion signatures. The discrepancies between our results and those of Forster et al. (2001) for P1 and Q1 in table 1 suggest that, especially when analyzing more expanded, older networks, very large samples are required.

When considered together, haplogroups P and Q and their coalescence estimates do inform questions on ancient population dynamics, settlement and isolation in this region. The star-like networks of P1 and Q1 independently suggest the same ancient population expansion in New Guinea subsequent to first settlement ~50,000 years ago, followed by the expansion of Q2 in adjacent Island Melanesia somewhat more than 10,000 years later. In addition, the extremely localized distributions of specific haplotypes within the branches of Q and P are consistent with very restricted female movement within the region over the following millennia. The absence of Q in Australia, plus the very separate branch distributions of P in Australia and in New Guinea, indicate an almost complete (female) isolation between the two regions. The single shared haplogroup (P3) only occurs in New Guinea in a restricted southwestern region. Also the New

Guinea branch of P3 is distinctive, suggesting its Australian connection is very old. The first female settlers of Sahul might have effectively been members of the same population, possibly even entering at one place – this cannot be ascertained - but, if that was the case, then they split into two groups shortly afterwards, and remained effectively isolated thereafter.

Specific links of haplogroups P and Q to other branches within macrohaplogroups M and N remain unresolved. The best candidates for close Q relationships are some other Island Melanesian M haplogroups designated "other" in the last two tables and figures (Friedlaender et al. 2002; Friedlaender et al. in press), as well as the very limited M haplotypes reported in Aboriginal Australian populations (Redd and Stoneking 1999; Huoponen et al. 2001; Holst Van Pellekaan et al. 1998; Ingman and Gyllensten 2003). No convincing ties to other particular branches of M or N outside the Southwest Pacific have yet been presented, which means that the ancient Eurasian origins of these peoples remain an open question.

GenBank Accessions. Accession numbers AY956412, AY956413, and AY956414 have been assigned to the whole mtDNA genome Q2 sequences (see figure 2).

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Appendix

An average substitution rate per np per year for HVS1 (more accurately nps 16090-16365) has been estimated as one per np per 20,180 years (Forster et al. 1996), but we extrapolated this substitution rate to include HVS2 (information available on nps 35-315) by comparing known variability in HVS1 to HVS1 plus HVS2. First, we estimated a weighted substitution rate per np across both HVS1 and HVS2 from data in table 2 of Forster et al. (2002) on Eurasian mtDNA trees, giving less or no weight to the most mutable nps. Five hypermutable sites were excluded (nps16189, 16362, 146, 152, and 195) and the 21 sites with three to six independent substitutions were assigned half weights (six substitutions - at nps16129 and 16311; five – nps16093, 16304, 150, and 200; four – nps16126, 16274, 16278, and 228; three – nps 93, 151, 189, 194, 199, 204, 16179, 16234, 16256, 16266, and 16357). The resulting weighted substitution rates per np were calculated as follows: HVS 1 = 0.40; HVS 2 = 0.26; and HVS 1 and 2 combined = 0.353. The ratio of the HVS 1 rate to that for the entire control region is then 1.2329, or ~20% faster. Therefore, as the estimated average substitution rate for HVS 1 (nps16090 -16365) is one per 20,180 years, the average substitution rate for HVS1 plus HVS2 is 1 per 24,880 years.

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Figure Legends

Figure 1. Schematic mtDNA phylogeny for Eurasia. The African L3 root splits into the Eurasian N and Asian M branches. Haplogroups P and Q are ancient subdivisions of each major branch.

Figure 2. Haplogroup Q branching from the African L3 root, based on whole mtDNA sequencing. Note the deep stem from M, the long primary branch lengths, and the short terminal branches. No Qs have been found in Australia. Q as defined by Forster et al. (2001) is boxed as the "Original definition." Provenience abbreviations at the top are as follows: New Guniea (NG); New Britain (NB); New Ireland (NI); and Nasioi (of Bougainville). GenBank accession numbers are listed with the AY and AF prefixes. Other designations are from Redd and Stoneking (1999), Stoneking et al. (1990), Ingman and Gyllensten (2003) or the current series (UV). PNG C89 was previously identified as a Q by Kivisild et al. (2002). Sub-branches of Q refer to those shown in table 2. Control region mutations are in bold, transversions have a base suffix, recurrent mutations in the same tree are underlined, back mutations are italicized, and 16519 is ignored.

Figure 3. A haplogroup Q median network phylogeny, based on control region sequences of the 210 Q samples from the current study. The major Q1 and Q2 branches are star-like in their configurations, with the majority of samples outside the centers, suggesting ancient population expansion(s). Node sizes are proportional to the number of haplotypes contained within each. Nucleotide pair (np) numbers are transitions from the CRS, with bases noted for transversions. The star indicates the branching from ancestral M.

Figure 4. Haplogroup P branching from the African root L3, based on whole genome sequencing. In contrast to Q, the different branches of P share only one defining mutation

(15607), the terminal branches are generally very long, and only P1 from Melanesia has extensive internal branching. Abbreviations follow figure 2, with the addition of Australian Aboriginals (AUS). H35, H6, and C80 were previously identified as Ps by Kivisild et al. (2002). Half the sequences are Australian, and only P3 occurs there and New Guinea.

Figure 5. Haplogroup P median network phylogeny, based on control region sequences on the 104 P samples from the current study. Only P1 (from New Guinea) has a star-like array, although its core is almost empty, consistent with its great age. Other branches are indeterminate in part because relatively few control region mutations distinguish them. The star indicates the origin from R.

Figure 6. Population locations and frequencies of P and Q haplotypes in the Southwest Pacific. Numbers are given in table 2.

Figure 7. Population locations and frequencies of P and Q haplotypes in the Bismarck Archipelago and Bougainville Island. Numbers are given in table 3. Underlined names are the Papuan-speaking locations.

Table 1. **Coalescence Estimates for the main P and Q branches**

Haplogroup	ρ[a]	ρ (Years)	σ	σ (years)	*n*	Source
Q1	2.0214	49,856[b]	0.4353	10,832	192	This study
"Q"[c]	0.7027	15,300[d]	0.1622	3,500	37	Forster et al. 2001
Q2	1.4839	36,599	0.4977	11,617	87	This study
P1	2.0806	51,316	0.3861	9,827	90	This study
"P/p94"	1.5263	33,300	0.3722	8,100	19	Forster et al. 2001

Total P and Q Mean Pairwise Differences[e]

Q	7.936
P	7.076

[a] As defined in Saillard et al. (2000), ρ is the mean mutational distance from the haplogroup node of interest (i.e. its center), and σ is its standard error. The value of σ does not include uncertainty concerning mutation rates.
[b] Based on one mutation per 24,880 years across HVS1 and 2 (see Appendix for the rate estimation).
[c] Quotation marks denote equivalent haplogroup and estimates from high resolution RFLP analysis (Forster et al. 2001).
[d] Based on one mutation per 21,800 for coding region RFLP data from (Forster et al. 2001, Table 2).
[e] From mismatch distributions presented in Supplemental Materials Figure 1, after the method of Rogers and Harpending (1992).

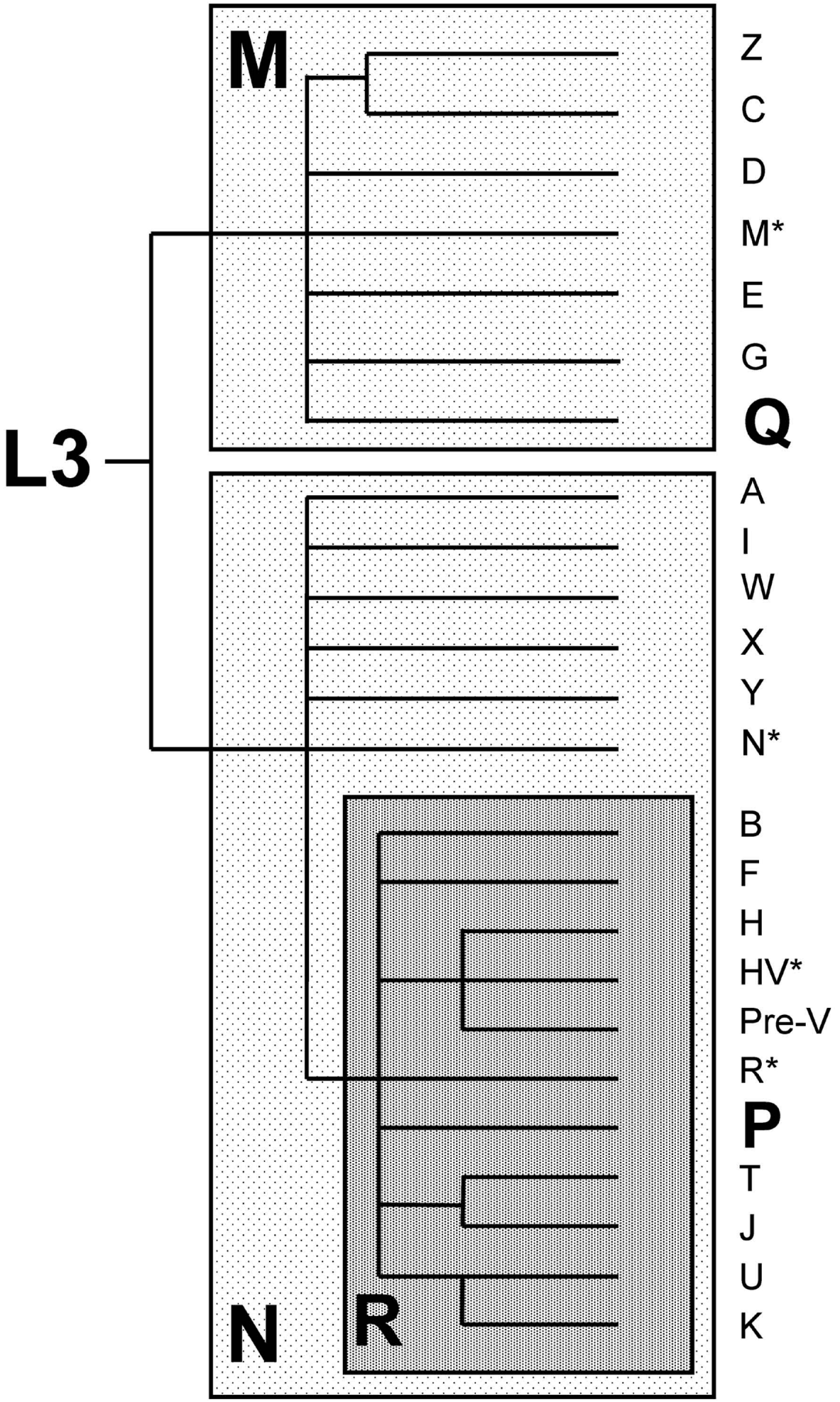
Table 2. Distribution of Control Region Samples from Haplogroups P and Q in the Southwest Pacific

Major Region	Region	Population	Haplogroups							
			P		Q			B	Other	Total
			P1	P2	Q1	Q2	Q3			
New Guinea	West Papua	Southwest Riverine	7	6	19			1		33
		Lowland Riverine	3		22				1	26
	PNG	PNG	2		4		1	7	5	19
	PNG Highlands	West Highlands	10	1	6				1	18
		Fringe Highlands	3		2		2		8	15
		East Highlands	2		1				1	4
		Morobe Highlnds	5	1	1			7	6	20
	PNG Coastal	Sepik	5		4		2	4		15
		Markham	9	5	12	10		22	9	67
		South Coast	1					10	2	13
	PNG islands	Misima	4	2					1	7
		Rossel	3						2	5
Island Melanesia	New Britain	West New Britain			11	14		17	60	102
		East New Britain	3		9	21		12	87	132
	Mussau	Mussau				1		1		2
	New Ireland	New Ireland	1			5		72	13	91
	Bougainville	North Bougainville	4		38			17	16	75
		South Bougainville						24	7	31
	Solomon Is.	Solomon Islands	1					18	7	26
		Santa Cruz	5		12	7		23	22	69
	Vanuatu	Vanuatu	3			2		8	9	22
	New Caledonia	New Caledonia	2	8		1		6	14	31
	Fiji	Fiji		1	2	1		9	3	16
Micronesia		Kiribati						4	2	6
		Ontong Java						16	8	24
Polynesia		Samoa						4		4
		Tonga						3		3
		Wallis						2		2
Totals			74	30	143	62	5	286	290	878

Table 3. Distribution of haplogroups P and Q in populations from the Bismarck Archipelago and Bougainville Island.

Island	Island section	Population	Haplogroups					
			P1	Q1	Q2	B	Other	Total
New Britain	West New Britain	Ata (Uasilau)[f]			5		12	17
		Ata (Lugei)		1	3		12	16
		Kol		7	6	14	35	62
		Mengen (Pomio)		3		3	1	7
	East New Britain	Baining (Marabu)	2	1	21		34	58
		Baining (Malasait)					19	19
		Sulka (Ganai)		3		2	5	10
		Sulka (Watwat)		2		2	6	10
		Tolai (Kabakada)		3		1	8	12
		Tolai (Vunairoto)				4	3	7
		Tolai (Matupit)	1			1	3	5
		Tolai				2	9	11
Mussau		Kapugu			1	1		2
New Ireland		Kavieng	1			1		2
		Kuot (Lamalaua)				9		9
		Kuot (Kabil)				38	3	41
		Kuot				9		9
		Madak			5	15	10	30
Bougainville	North Bougainville	Aita	4	31		1	2	38
		Rotokas		5			6	11
		Eivo		2		13	4	19
		Simeku				3	4	7
	South Bougainville	Nasioi				1	6	7
		Torau				4	1	5
		Nagovisi				15		15
		Siwai				4		4
Totals			8	58	41	143	170	433

[f] Papuan speaking groups are underlined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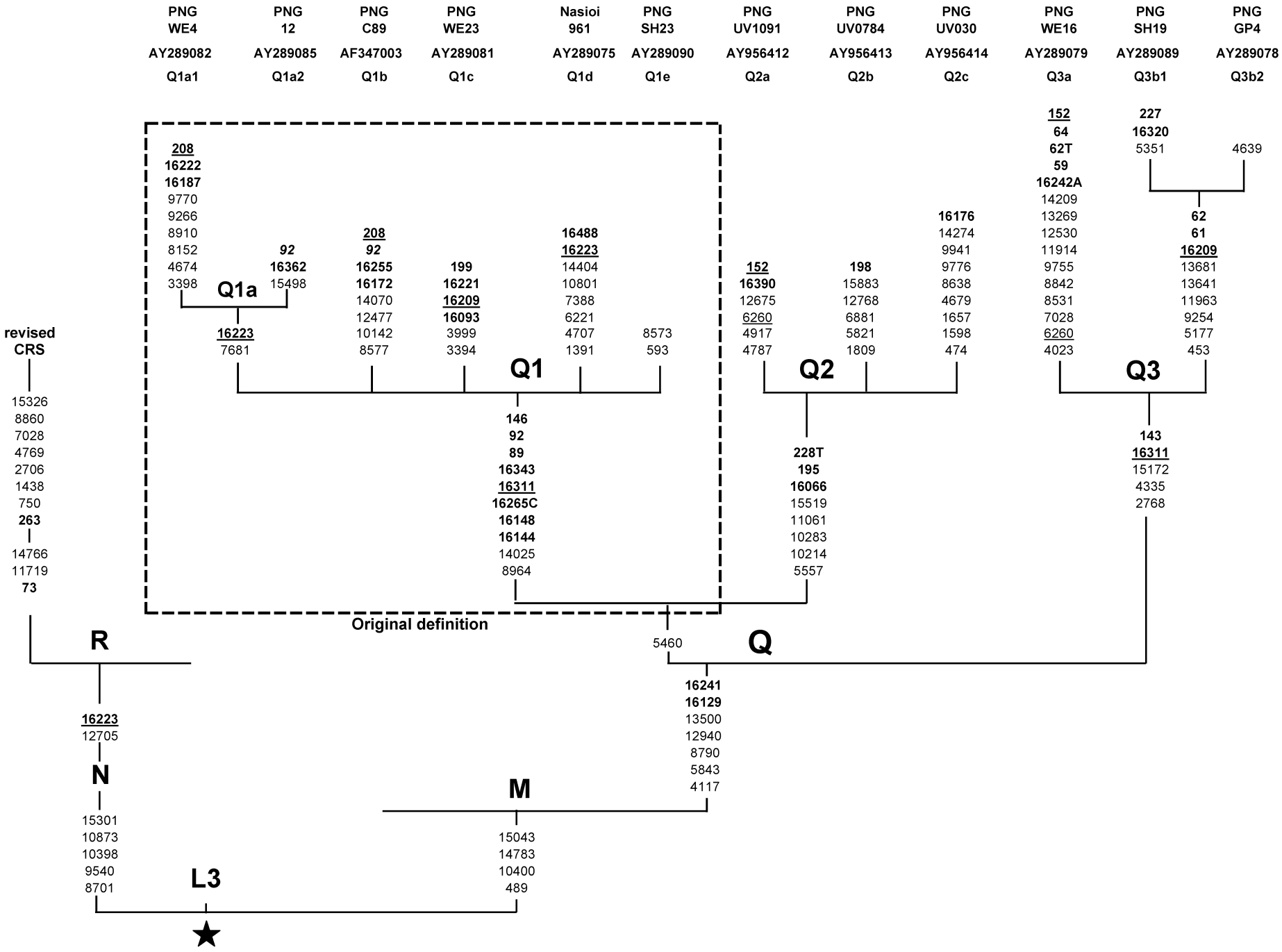
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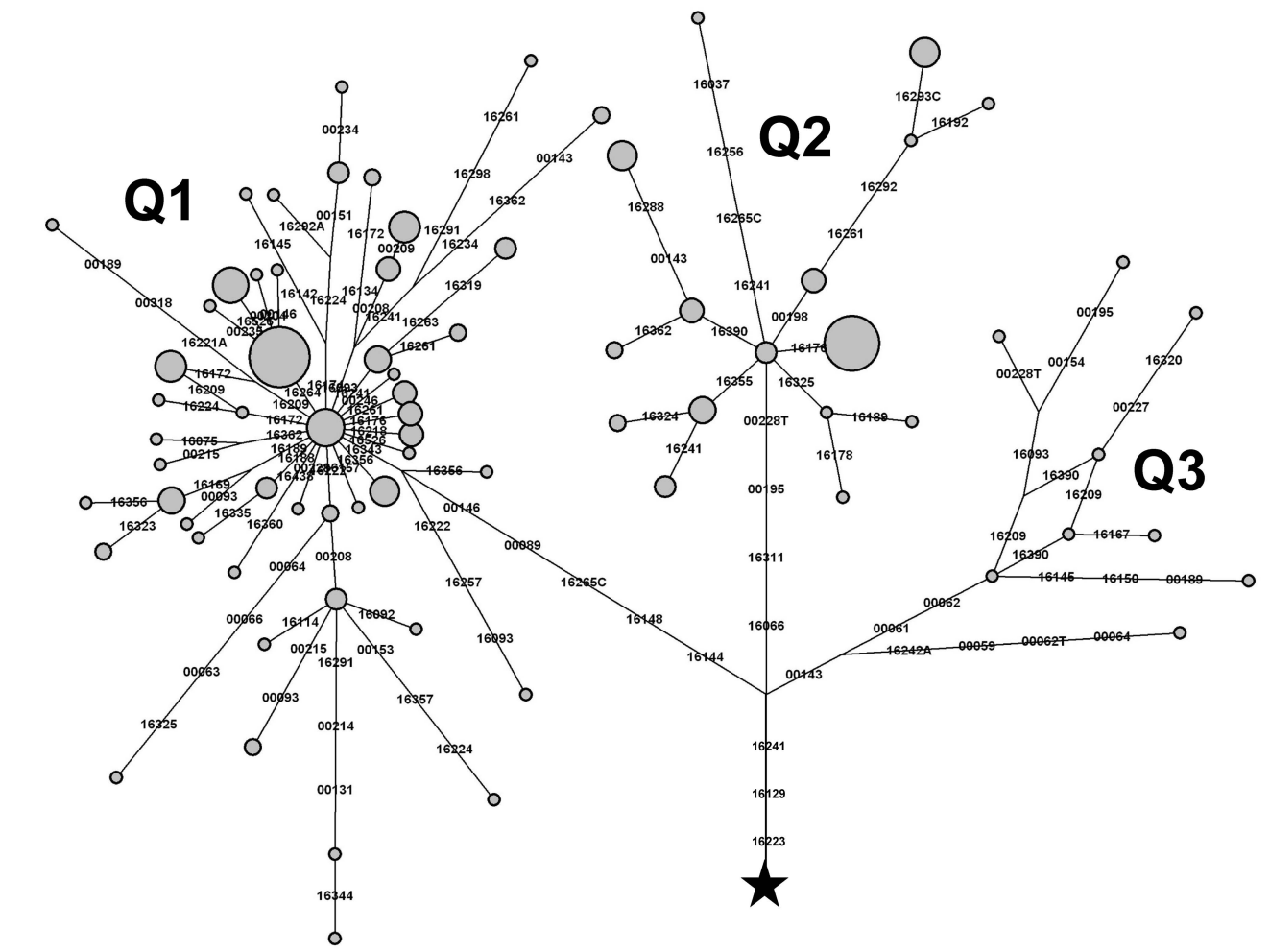
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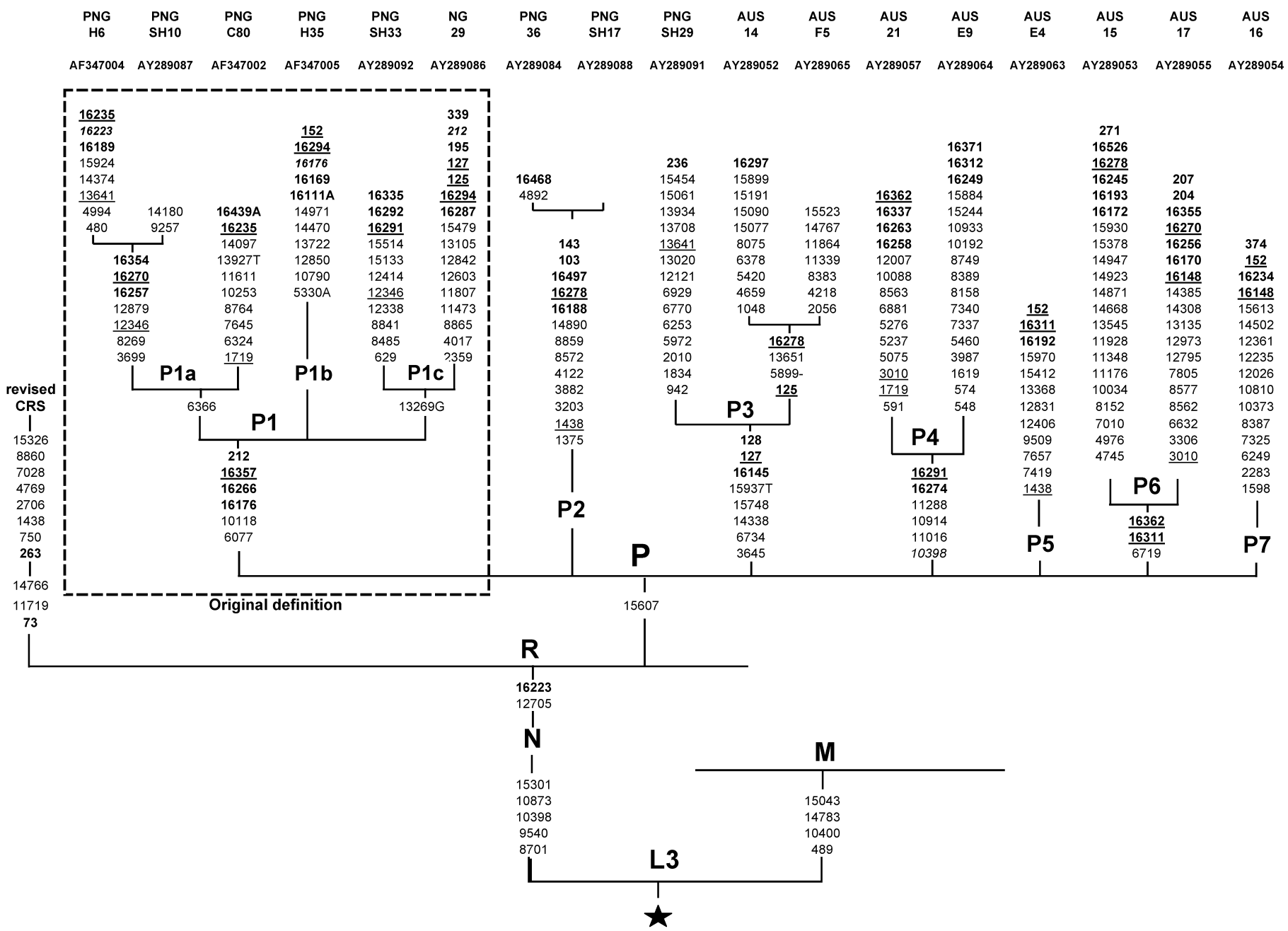
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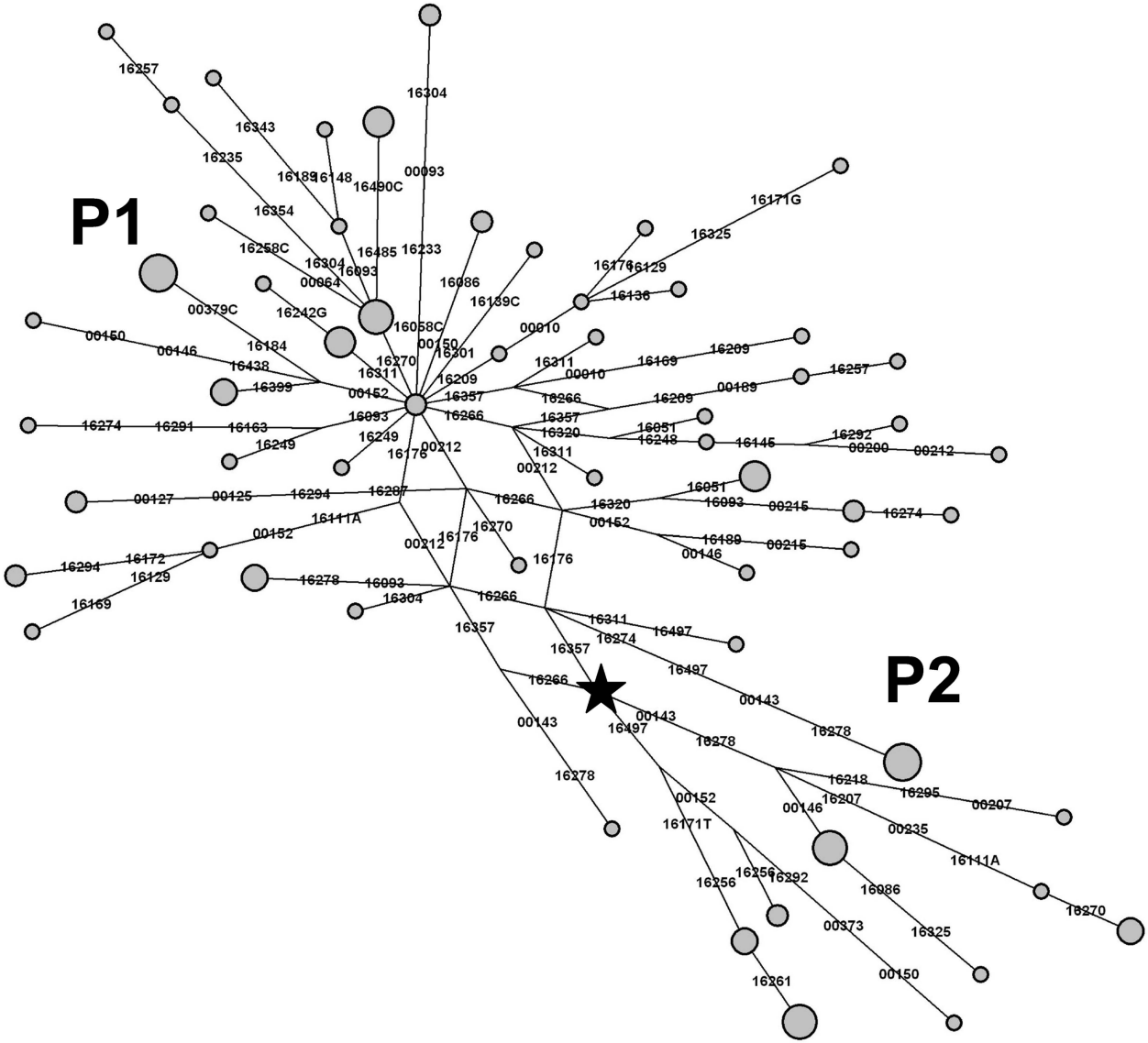
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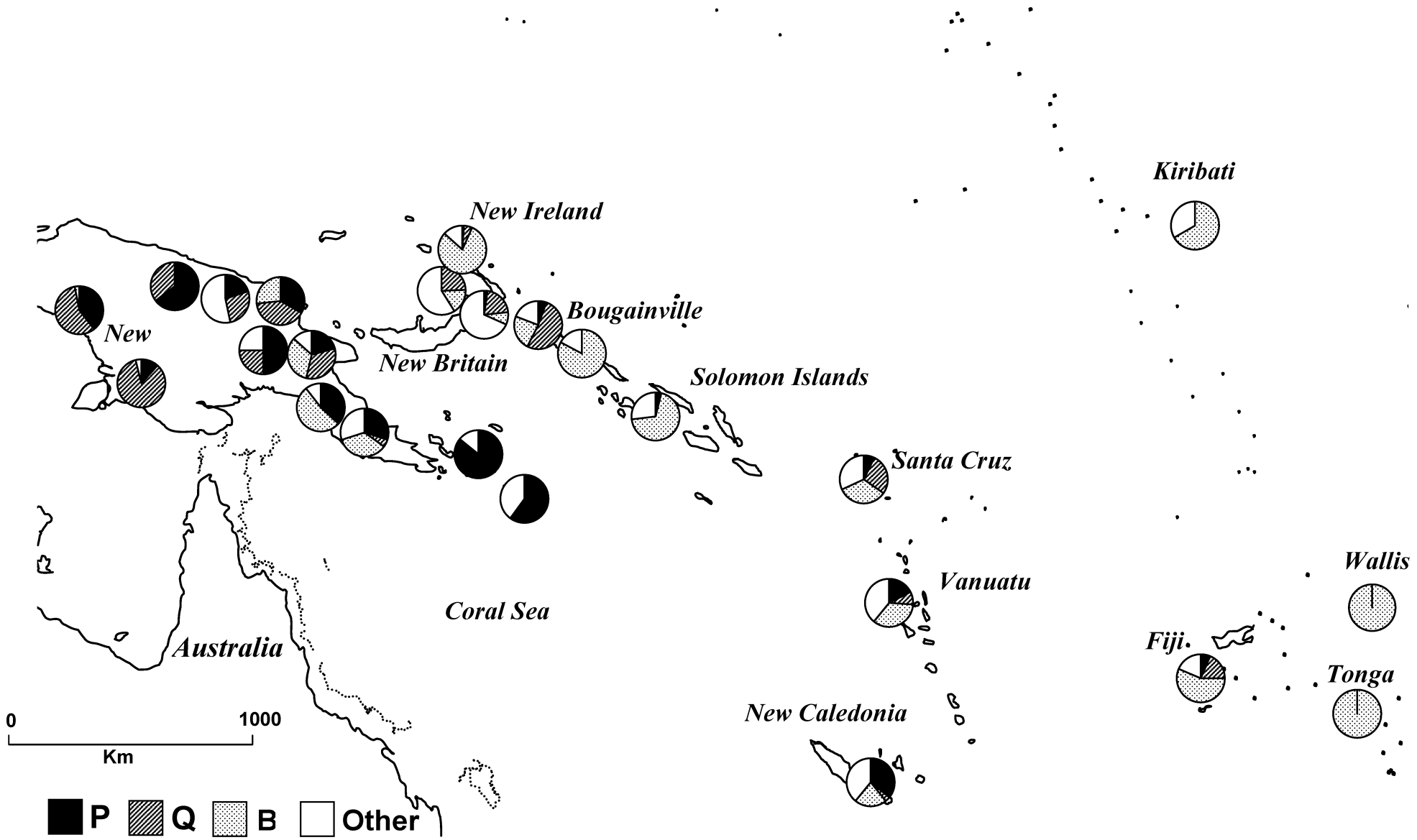
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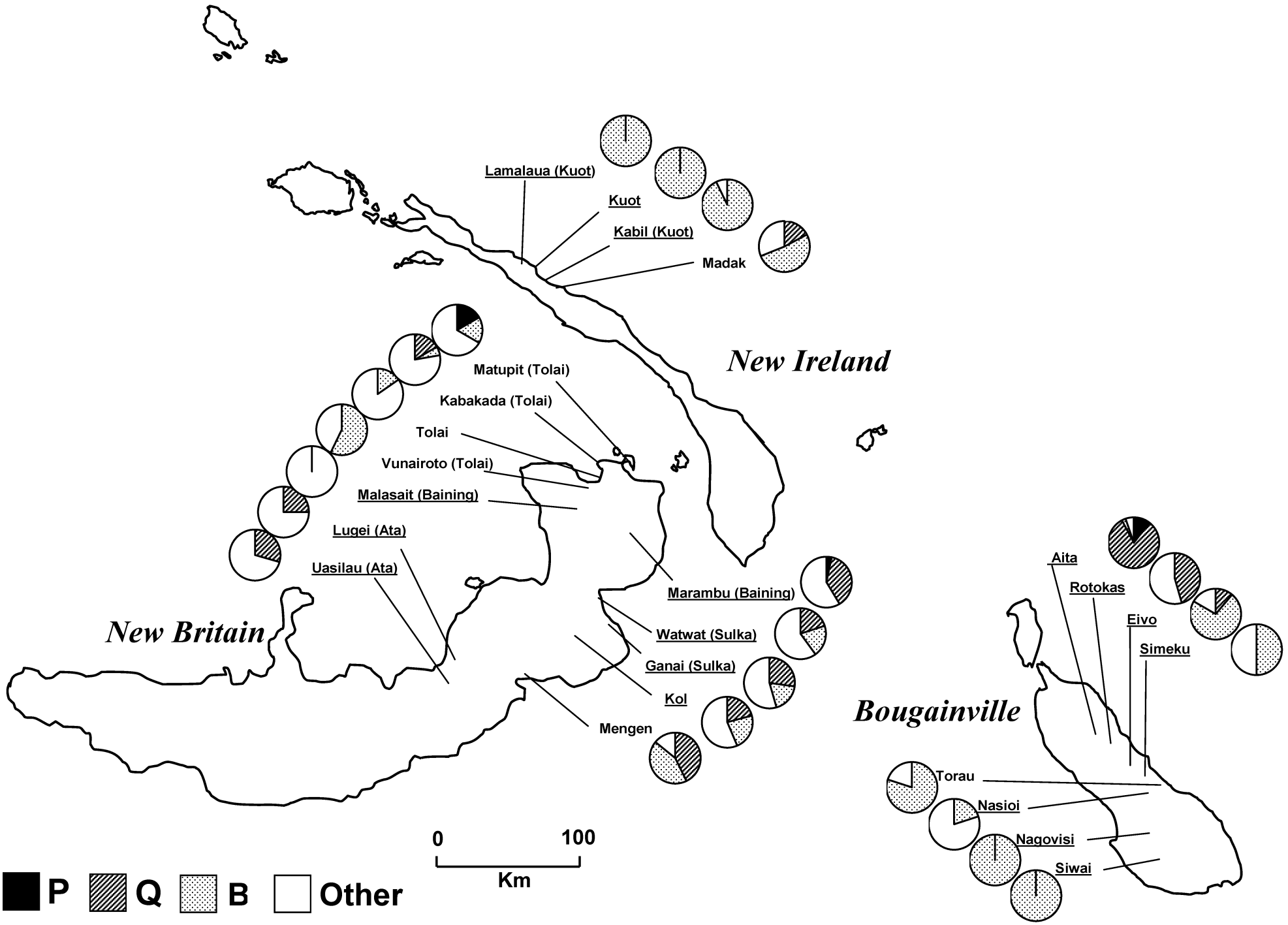
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