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Name That Rat: Molecular and Morphological Identification of Pacific Rodent Remains

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ABSTRACT Generally, species identification of rodent remains from archaeological sites in the Pacific is made based on the overall size and robusticity of those bones most commonly recovered—mandibles and femora. Molecular identifications of Pacific rat remains suggest that the current method of morphological identification may not be appropriate for species identification. It appears that there is a high degree of size variation in *Rattus exulans* throughout the Pacific, and an overlap in size between *R. exulans* and other rat species present in the region. Our results suggest not only a need to re-examine our current methods for identification of rodent skeletal remains, but also, perhaps, our views on the distribution of various rodent species throughout the Pacific, and the implications of such for the human prehistory of the region. Copyright © 2001 John Wiley & Sons, Ltd.

Key words: Rattus exulans; rodents; mitochondrial DNA; molecular archaeology; Pacific

Introduction

Research conducted over the last 5 years at the University of Auckland has focused on the genetic relationships of Pacific populations of *Rattus exulans*, the Pacific rat. Its ubiquitous distribution and appearance in early, if not the earliest archaeological layers throughout Remote Oceania suggests this species was transported into the region by ancestral Polynesian populations, and later was dispersed throughout the Pacific. Based on this commensal relationship, the identified phylogenies, or family trees of the rat, serve as markers of paths of human colonization and post colonization contacts (Matisoo-Smith, 1994; Matisoo-Smith *et al.*, 1998). Recent reports regarding *R. exulans* remains from natural deposits in New Zealand, which pre-date archaeological evidence of sustained human presence there by at least 1000 years (Holdaway, 1996), suggest that this rat may have also been transported during pre-colonization exploration voyages, or may be a marker of earlier unsuccessful human colonization attempts (but see Anderson 1996 and Smith & Anderson, 1998 for an alternative view). Given the fact that *R. exulans* cannot swim more than a few metres, and are unlikely to have dispersed naturally in an island environment, the arrival of this species on islands in Remote Oceania is one clear indicator of human contact with those islands.

While initial research on *R. exulans* focused on central and east Polynesian populations, the demonstrated value of using this commensal animal as a marker for human mobility has led to an extension of our research focus. We have now begun to expand our regional focus back towards the western Pacific, where the rodent species distribution is much more complex. No longer are we working in a region where there is only one rodent species present during the prehistoric period.

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The Wallace–Huxley Line, which runs between Borneo and Sulawesi, marks a major transition, separating a region with one of the richest vertebrate faunas from a region with one of the worlds poorest. The trend towards faunal impoverishment continues as one moves eastward out into the Pacific. Twenty-four genera of rodents, including 16 species of *Rattus* are indigenous to New Guinea (Taylor *et al.*, 1985; Roberts, 1994). Only three rodent genera and three species of *Rattus*, *R. mordax*, *R. praetor* and *R. exulans*, have been identified from prehistoric sites in New Ireland (Allen *et al.*, 1989). What has been referred to as the 'Thorne–Green Line' (Roberts, 1994), delineating Near and Remote Oceania (Figure 1), represents 'a major cut off point in the natural distribution of animal and plant species' (Pawley & Green, 1973, p. 5), beyond which only bats and commensal mammals are found. In the southern Pacific, only *R. praetor* and *R. exulans* are found east of the Remote Oceania Line, but Micronesia appears to have perhaps two species of *Rattus*—*R. exulans* and what has been identified *as R. rattus mansorius* (Davidson, 1971) or *R. tanezumi*.

Previously, it was thought that the distribution of *R. praetor* extended only as far east as Tikopia (Flannery *et al.*, 1988), leading Roberts (1994) to identify an '*exulans* only' line, running between Tikopia and the rest of Remote Oceania. However, it appears that there may be a second species of rat beyond Tikopia, extending

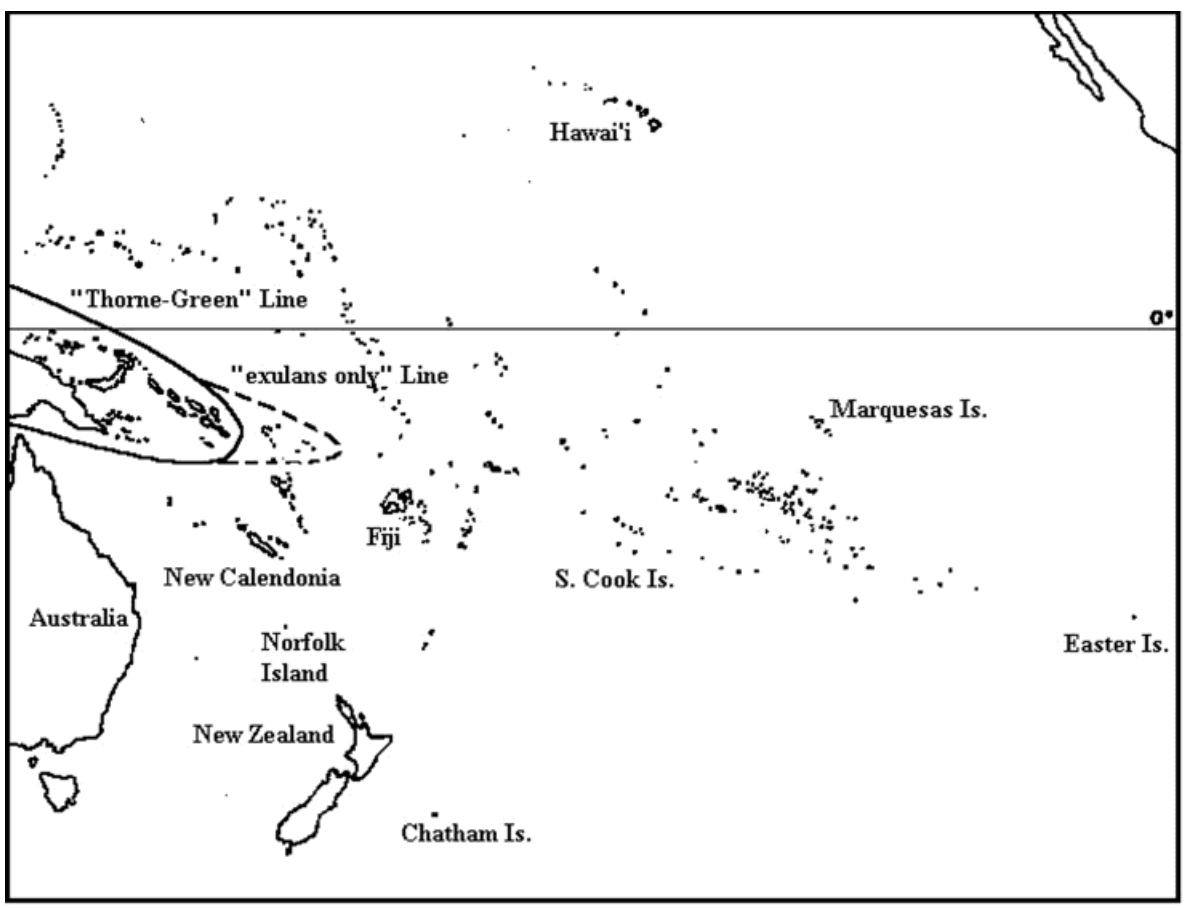

Figure 1. Map of the Pacific, showing the 'Thorne-Green Line' delineating Near and Remote Oceania (solid line), and the 'exulans only Line' (dotted line) identified by Roberts (1994).

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Table 1. Maxillary alveolar length for New Guinea rodents (from Taylor *et al.*, 1985)

Species	*n*	Alveolar M^{1-3} (mm)	S.D.	Range (mm)
New Guinea				
R. exulans	763	5.2 ± 0.01	0.28	43–6.2
R. rattus	78	6.5 ± 0.04	0.32	5.8–7.2
R. mordax mordax	101	7.4 ± 0.04	0.40	63–8.3
R. mordax fergussoniensis	15	8.4 ± 0.22	0.70	7.6–9.7
R. praetor praetor	20	7.4 ± 0.07	0.32	6.6–8.0
R. praetor coenorum	69	7.4 ± 0.07	0.57	6.1–9.3

Alveolar M^{1-3} measurements shown are for maxillary M^{1-3}, and are, therefore, not comparable with mandibular measurements in Table 4.

at least as far as Fiji. Remains of a currently unidentified species of large rat have been recorded from prehistoric levels in the Lakeba site (S. Best, personal communication). Given the limited number of rat species present in prehistoric Remote Oceania, it is most likely that if these do not represent intrusive European rats, and are indeed representative of a second species in Fiji, they belong to *R. praetor*, or perhaps *R. tanezumi*.

This difficulty in defining the distribution of Pacific rat species is a result of a number of factors. Archaeological investigations have yet to be conducted on all Pacific islands. Even on islands/archipelagos where excavations have been conducted, collection and identification of rodent and other microfaunal remains has not always been a high priority. As a result, large sieves are often used for screening, and small rat skeletal remains, if present, are not collected (e.g. see discussion in Flannery *et al.*, 1988). Even when microfaunal remains are collected, species identification of Pacific rodents is not straightforward. Unfortunately, there appears to be no standard method of measurement for Pacific rodent remains, and no clear understanding of the range of variation in size within and between species across the Pacific. Few of the standard measurements designed for complete crania (e.g. those used by Johnson, 1962, or Taylor *et al.*, 1985) can be applied to archaeological remains, which are almost always fragmentary, and often postcranial.

Table 1 shows the range in maxillary alveolar length for New Guinea populations of the rat species found in the island Pacific. The study from which these data originate, 'A revision of the genus *Rattus* (Rodentia, Muridae) in the New Guinea region' (Taylor *et al.*, 1985), is, undoubtedly, the most comprehensive study of Pacific rodents conducted to date. While maxillary and other cranial measurements are not generally applicable for archaeological material, which, as mentioned earlier, rarely consist of cranial material other than mandibular remains, these measurements do suggest relative sizes for New Guinea populations of these species. It is clear from these data that *R. exulans* does appear to be significantly smaller than the other species. However, there is also some overlap in range, particularly between *R. exulans* and *R. rattus*. What is not apparent from these data, however, is how other Pacific populations of *R. exulans* compare in size with those found in New Guinea.

There is a wide range of variation in size of extant populations of *R. exulans* across the Pacific, with the maximum weights in New Zealand reaching 187 g in males and 150 g in females, compared with 62 g for males and 60 g for females in New Guinea populations (Atkinson & Moller, 1989). Though we do not know how this relates specifically to skeletal measurements, it clearly suggests a high degree of size variation within at least one Pacific rat species. Therefore, comparative collections from specific locations may not be appropriate when used to identify rodents from other archipelagos.

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Table 2. Rat Morphology and Identification Criteria for Polynesia (after McCormack, no date, and Cunningham & Moors, 1983)

Common name	House mouse	Pacific rat	Ship rat	Norway rat
Scientific name	*Mus musculus*	*R. exulans*	*R. rattus*	*R. norvegicus*
Weight	Up to 25 g	Up to 100 g (187 g in New Zealand)	Up to 220 g	Up to 400 g
Body length	Up to 90 mm	Up to 150 mm (160 mm in New Zealand)	Up to 200 mm	Up to 275 mm
Tail length compared with body length	Slightly shorter or longer than body length	Usually 1.25 × body length (1.0–1.5 ×). Thin and dark	Usually 1.5 × body length (1.2–1.5 ×)	Less than 1.0 × body length. Thick with pale underside
Right ear length	12–18 mm	12–19 mm (15.5–20.5 mm in New Zealand)	17–26 mm	14–22 mm
Hindfoot length	16–20 mm	18–30 mm (24.5–31 mm in New Zealand)	28–38 mm	30–42 mm
Hindfoot colour—topside and along outside edge	Uniformly grey	Topside pale, grey, darkened bar along outside edge only	Topside pale or dark grey	Uniformly pale
Nipple number, F(ront) and B(ack)	F6 + B4 = 10	F4 + B4 = 8	F4 + B6 = 10. Rarely F6 + B6 = 12	F6 + B6 = 12
Fur on back is usually	Grey–brown, agouti	Grey–brown, agouti	Brown agouti–black	Brown
Fur on belly is usually	Uniformly grey	Pale grey agouti	Uniformly grey, white or cream	Grey agouti
Habits	Capable climber, but lives mainly on the ground. Nests in holes	Agile climber, feeds on ground and trees. Usually nests on ground	Very agile climber, nests mainly in shrubs and trees	Burrowing ground-dweller, nesting underground. Strong swimmer

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Morphological and molecular identification of extant rodent species

Initial studies of genetic variation in *R. exulans* were based on collections from extant populations from throughout Polynesia. *R. exulans* was the only rat species present in central and east Polynesia prior to European contact. However, the arrival of Europeans also resulted in the arrival of three other rodents—*R. rattus*, *R. norvegicus* and the house mouse, *Mus domesticus*. Consequently, on most Polynesian islands, *R. exulans* is joined by at least one of the European introduced rodents, if not all three. Collection of tissue for DNA analyses involved setting snap-type rat traps in locations where *R. exulans* were likely to occur. Inevitably, other rodents were caught in the traps, and some form of species identification in the field was required.

The features identified in Table 2 were developed by Gerald McCormack of the Cook Islands Natural Heritage Trust, based on Cunningham & Moors (1983), for field identification of extant rodents in Polynesia. These features are fairly reliable for identification of species in tropical Polynesia; however, as noted in Table 2, New Zealand *R. exulans* are significantly larger than tropical populations. As Johnson (1962, p. 26) points out in his discussion of Micronesian rodents, 'The four species are quite distinct . . . Within the respective species, however, there is variation that makes identification of individual specimens difficult'. Errors made in basic field identifications of species were common, and a simple, inexpensive molecular test for species identification was developed (Matisoo-Smith, 1996, pp. 57–59).

Figure 2 shows the results of species specific restriction fragment length polymorphism (RFLP) patterns for rodent species currently found in Polynesia. The species identifications at the top of the figure were those made in the field, based on the morphological features described in Table 2. It is clear that the individual represented in lane 2, tentatively identified in the field as a *R. rattus*, was, in fact, a *R. exulans*. This result makes clear the point that identification of rat species is not simple. Even when all features including fur colour, full body measurements, nipple number etc., are available, errors in species identification are possible—even by the most experienced field biologists. This problem of species identification is even more difficult when additional species are present, as is potentially the case in the rest of the Pacific. Yet, perhaps the most complicated and unreliable situation is encountered when species identification has to be made based on limited archaeological skeletal remains

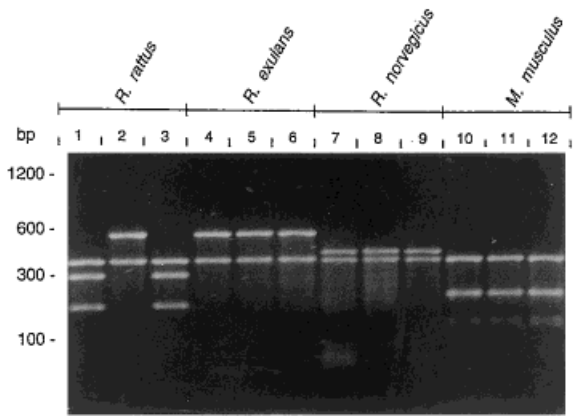

Figure 2. Species specific restriction fragment polymorphism (RFLP) patterns for four rodent species present in Polynesia.

Morphological and molecular identification of archaeological rodent remains

As a follow on from the initial studies of extant populations of *R. exulans*, analyses of mitochondrial DNA (mtDNA) variation in archaeological samples is now underway in the Pacific Palaeo-Ecological Research Laboratories (PPERL), at the University of Auckland (Allen *et al.*, 1996). Over 400 *R. exulans* bones (primarily femora and mandibles) have been collected from museum and archaeological collections, representing populations throughout the Pacific and island southeast Asia. Unfortunately, recovery of ancient DNA from skeletal remains requires destruction of the entire bone. However, samples are weighed and measured before being processed. Measurements taken are as shown in Figure 3. As a result of our studies, we have assembled data for morphological variation in *R.*

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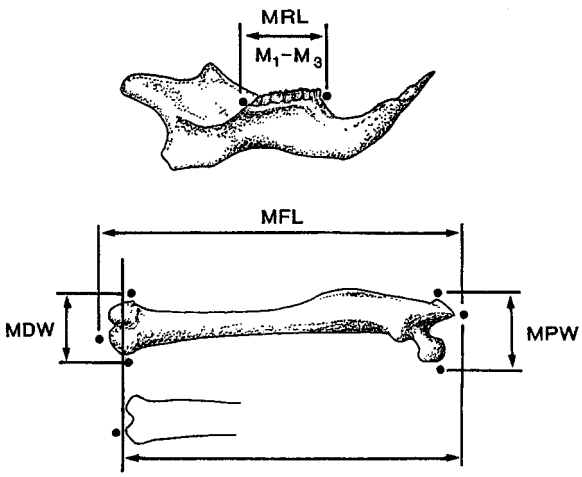

Figure 3. Measurements taken for *R. exulans* mandibles and femora.

exulans from throughout the Pacific in terms of maximum femoral length (MFL), maximum proximal and distal width (MPW and MDW) and mandibular alveolar row length, M_1–M_3 (MRL).

Morphological variation in *R. exulans*

MFL data for 75 individuals, all from archaeological contexts of less than 3000 years BP, were determined (Table 3). Often epiphyses, particularly distal epiphyses, are missing from the samples, and, therefore, maximum length cannot be calculated for all femora collected. In addition, many archipelagos are represented only by single specimens. The range for maximum length covers nearly 10 mm. The largest sample (30.3 mm) comes from Mangaia, in the southern Cook Islands, while the smallest (20.5 mm) comes from the Chatham Islands. In general, the larger samples are derived from East Polynesia; however, there are a number of non-East Polynesian samples that are well over the mean of 25.19 mm, including Norfolk Island (29.15 mm) and New Caledonia (26.35 mm).

Table 3. MFL in archaeological pacific populations of *R. exulans*

Location	*n*	Mean (mm)	S.D.	Range (mm)
Mariana Island	2	24.57	0.10	24.50–24.65
Kapingamarangi	2	24.66	0.26	24.48–24.85
New Caledonia	17	24.46	1.60	21.33–26.35
Norfolk Island	3	27.69	1.26	26.99–29.15
Fiji	4	24.34	1.05	22.70–25.07
Rotuma	1	–	–	25.51
Cook Islands	2	28.33	1.97	26.36–30.30
Hawaii	1	–	–	26.35
Mangareva	2	26.39	0.82	25.81–26.97
New Zealand	30	25.64	1.56	22.80–28.30
Chatham Islands	10	24.43	1.46	20.50–25.75
Easter Island	1	–	–	23.27
Total	75	25.19	1.76	20.50–30.30

The alveolar length for 142 mandibles from populations across the Pacific was measured (Table 4). Again, there is a wide range of variation, yet while the New Zealand and Marquesan samples are, on average, larger than those elsewhere, there does not appear to be a regional trend. The Marianas samples are large, and though the smallest samples are from island southeast Asia (Indonesia and Philippines), there are also samples from those populations that are relatively large.

Molecular variation in Pacific rodents

The recently developed tools of molecular archaeology have proven useful in addressing issues previously contentious in archaeozoology. Perhaps one of the most useful applications of these techniques has been in species identification of previously unidentifiable skeletal remains (Loreille *et al.*, 1997). Similarly, this approach will be valuable in clarifying rodent species identification problems in the Pacific. By obtaining DNA sequences from unknown or questionable rat bones, we can compare them with known rodent sequences, and positively identify the species.

All of the samples included in our analysis of size variation within *R. exulans* have been confirmed, through DNA sequencing, as belonging to *R. exulans*. DNA is extracted using a modified silica extraction protocol and a hypervariable region of the mitochondrial d-loop is amplified, as described previously (Matisoo-Smith *et al.*, 1997). In addition to extracting and sequencing mtDNA from *R. exulans* skeletal remains, we

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Table 4. Mandibular alveolar length in Pacific populations of *R. exulans*

Location	Source	*n*	Mean (mm)	S.D.	Range
Philippines	AMNH	6	5.87	0.74	4.79–6.98
Indonesia	AMNH	11	5.66	0.60	4.74–6.64
Sulawesi	AMNH	5	5.63	0.10	5.50–5.77
Borneo	AMNH	9	5.60	0.39	5.11–6.45
Island Papua New Guinea	AMNH	11	5.68	0.45	5.03–6.46
Vanuatu	Arch	2	5.68	0.30	5.47–5.90
New Caledonia	Arch	20	5.61	0.45	5.10–6.44
Rota, Mariana Island	Arch	3	6.50	0.70	5.88–7.27
New Zealand	Arch	44	6.20	0.46	5.35–7.30
Chatham Islands	Arch	12	5.94	0.35	5.51–6.65
Tubuai	AMNH	3	5.91	0.30	5.64–6.05
Marquesas	AMNH	6	6.30	0.37	5.95–6.70
Henderson	AMNH	4	6.62	0.50	5.88–7.00
Tuamotu	AMNH	2	5.79	0.71	5.29–6.30
Rapa	AMNH	2	5.87	0.32	5.64–6.10
Easter Island	Arch	2	6.02	0.65	5.56–6.48
Total		142	6.01	0.54	4.74–7.30

AMNH = American Museum of Natural History samples collected from extant populations this century; Arch = archaeological samples.

have obtained cranial samples of *R. praetor* and *R. mordax*, which we have now sequenced and added to our previous comparative mtDNA sequences of *R. norvegicus* and *R. rattus*. The aligned mtDNA sequences for the five *Rattus* species present in the island Pacific are shown in Figure 4. Not only is it possible to identify the species, but there are clear regional markers within Pacific populations of *R. exulans*.

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                    5         15        25        35        45
R.e. NZ             GTACATAAAA TGACATA.GG ACATTAAAAC ATTTATGTAT ATCGTACATT
R.e. Easter         GTACATAAAA TGACATA.GG ACATTAAAAC ATTTATGTAT ATCGTACATT
R.e. Cooks          GGACATAAAA TGACATA.GG ACATTAAAAC ATTTATGTAT ATCGTACATT
R.e. Bougainville   GTACATAAAA TGATATA-GG ACATTAAAAC ATTTATGTAT ATCGTACATT
R.e. Borneo         GTACATAAAA TGACATA.GG ACATTAAAAC ATTTATGTAT ATCGTACATT
R. rattus           .......... ....ATATGG ACATTAAAAC ATTTATGTAT ATCGTACATT
R. mordax           GTACATAAAA TG.GTACAGG ACATTAGGAC ATTAATGTAT ATCGTACATT
R. praetor          GTACATAAAA TG..ATATAG GACATAAGAC ACTAATGTAT ATCGTACATT
R. norvegicus       GTACATAAAA TTATCTA.GT ACATTAAAAC ATTTATGTAT ATCGTACATT

                    55        65        75        85        95
R.e. NZ             AATTTATCTA CCCCAAGCAT ATAAGC.ATG TAATATA.AG TCAATGTATT
R.e. Easter         AATTTATCTA CCCCAAGCAT ATAAGC.ATG TAATATA.AG TCAATGTATT
R.e. Cooks          AATTTATCTA CCCCAAGCAT ATAAGC.ATG TAATATA.AG TCAATGTATT
R.e. Bougainville   AATTTATCTA CCCCAAGCAT ATAAGC-ATG TAATATA-AA TCAATGTATT
R.e. Borneo         AATTTATCTA CCCCAAGCAT ATAAGC.ATG TAATATA.AA TCAATGTATT
R. rattus           AAATTATTTT CCCCAAGCAT ATAAGC-ATG TAATATATAT CTAATGATTT
R. mordax           AACTTCTTTT CCCCATGCAT ATAAGCAGTG TAAATCTTAA TTAATGTACT
R. praetor          AATTTCCTTT CCCCATGCAT ATAAGCAATG TAAATCTTAA TTAATGTATT
R. norvegicus       AATTTATCTT CCCCAAGCAT ATAAGC.ATG TAATATATAA TTAATGTATT

                    105       115       125       135       145
R.e. NZ             AAGACATAAT ATTTAAACTC AACTAGAAA. .TCCACG.TA ACATG
R.e. Easter         AAGACATAAT ATTTAAACTC AACTAGAAA. .TCCACGATA ACATG
R.e. Cooks          AAGACATAAT ATTTAAACTC AACTAGAAA. .TCCACGATA ACATG
R.e. Bougainville   AAGACATAAT ATTTAAACTC AACTAAAAA- -TCCACAACA ACATG
R.e. Borneo         AAGACATAAC ATTTAAACTC AACTAAAAA. .TCCATAATA ACATG
R. rattus           AGGACATA-C ATTTAAACTC AACTATAAA- -TTCACAACA ACATG
R. mordax           AAGATATAAC A.TTTTAATC AACCCAAAA. .ACCTATACA GCATG
R. praetor          AAGACATAAT A.TCTAAATC GACCT.AAN. .ATATATACN ACATG
R. norvegicus       AAGACATAA. ATTTAAACTC AACTATAAAA TTTAATACCA ACATG
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Figure 4. Aligned mtDNA sequences for Pacific *Rattus* species—*R. exulans*, *R. rattus*, *R. mordax*, *R. praetor* and *R. norvegicus*. Five sequences for *R. exulans* from populations across the Pacific are shown to demonstrate regional variation within the species.

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Conclusion

The identification of Pacific rodent remains is critical in understanding the geographic distribution of commensal species, and by extension, the movements of the humans who carried them. The results presented here clearly show both the difficulty in identifying rodents and rodent remains found in the Pacific, and the potential for molecular studies in solving some of these identification problems. Despite the value of lab based analyses, archaeological fieldwork is where the first step needs to be taken. The significance of rodent remains must be recognized by field archaeologists and palaeontologists. Only when microfaunal remains are collected from archaeological sites, and standardized morphological data are recorded and reported, can we begin to understand the complexities of species variation and distribution.

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