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Short communication

Phylogeography of Kauri Snails and their allies from Northland, New Zealand (Mollusca: Gastropoda: Rhytididae: Paryphantinae)

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1. Introduction

The carnivorous snails of the family Rhytididae occur in parts of the continental remnants of Gondwana—southern Africa, Madagascar, Seychelle Islands, Australia, Indonesia, New Guinea, New Caledonia, and New Zealand—and on many islands in the tropical western Pacific, including Caroline Is, Bismarck Is, Solomon Is, Vanuatu, Fiji, Tonga, and Samoa (Emberton, 1990; Solem, 1959). New Zealand has a particularly rich and diverse rhytidid fauna, with 10 genera, 32 species, and 9 further subspecies listed in Spencer et al. (2004). Some of the New Zealand species are large (the shell of *Powelliphanta hochstetteri superba* reaches 90 mm), with spectacularly colored shells, and many are now of conservation concern, mostly because of habitat degradation, but also from introduced predators such as pigs, rats, and brush-tailed possums (Brook, 2002a; Efford, 1998; Walker, 2003).

The status of many of the nominal species of New Zealand rhytidids and the relationships among the various genera are currently unclear. The most recent attempt at resolving the higher classification was by Climo (1977), who grouped the New Zealand genera in two subfamilies, Rhytidinae and Paryphantinae, on the basis of differences in reproductive anatomy. The latter subfamily comprised the endemic genera *Paryphanta*, *Rhytidarex*, *Amborhytida* (which Climo treated as a subgenus of *Rhytidarex*), and *Schizoglossa*. Only the last of these genera occurs naturally south of the Hunua Ranges, near Auckland, and most species are restricted to Northland and its various offshore islands (Fig. 1). In this note we use genetic tools to investigate the relationships among the species Climo included in the Paryphantinae. In doing so we also examine Climo's (1977) subfamilial classification. Finally, we interpret our genetic findings in light of the geologic history of Northland.

The taxa we examined are listed using their currently recognized nomenclature (Spencer et al., 2004) in Table 1. The genus *Paryphanta* Albers, 1850; contains just two named species, popularly known as Kauri Snails, which have disjunct distributions in Northland. *Rhytidarex* Powell, 1948; comprises two species restricted to the Three Kings Islands, which lie ~50 km northwest of Cape Reinga at the northern tip of the North Island (see Fig. 1). Five species are listed in *Amborhytida* Climo, 1974; which has most recently been treated as being of generic status (Brook, 1999a,b,c), all but two of which (*A. dunniae* and *A. forsythi*) are mutually allopatric. Finally, there are four recognized extant species and subspecies in *Schizoglossa* Hedley, 1892, but only two are included in this study.

We show that neighbour-joining, parsimony, and Bayesian analyses give very similar trees, in which the subfamily is monophyletic and all currently recognized genera (*Paryphanta*, *Rhytidarex*, *Amborhytida*, and *Schizoglossa*) are well supported. Relationships within genera, however, often fail to correspond to current taxonomy. We argue that sea level changes during the Late Miocene and Pliocene were important in the isolation of *Rhytidarex* on the Three Kings and in cladogenesis within a subgroup of *Amborhytida*. Nevertheless, within Northland proper, *Amborhytida* and *Paryphanta* were found to have biogeographically discordant distributions. This study illustrates the importance of examining several groups of related taxa before trying to reconcile their evolutionary history with past geological events, an approach that has previously proved productive in elucidating the phylogeography of pulmonate landsnails

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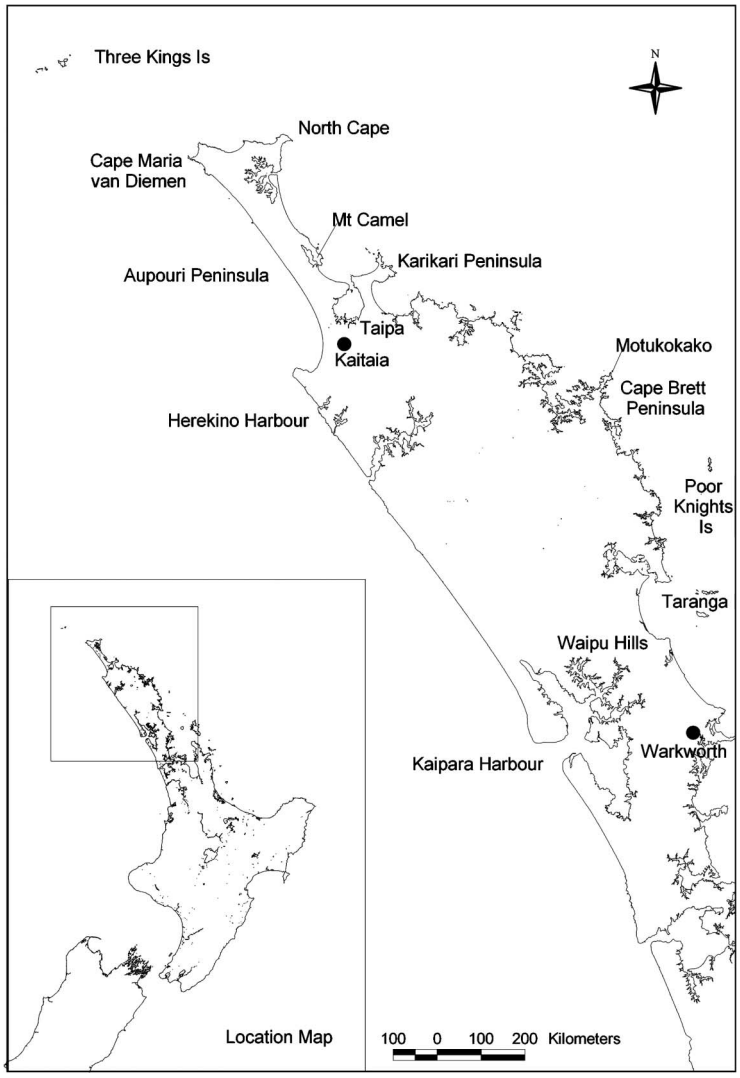

Fig. 1. A map of northern New Zealand, showing the place names mentioned in the text.

in Hawaii (Rundell et al., 2004) and the eastern Mediterranean (Parmakelis et al., 2005).

2. Methods

2.1. Sample collection

Whole specimens of all but three of the taxa currently assigned to the Paryphantinae (Spencer et al., 2004) were sampled from at least two locations where possible and collected into ethanol (see Table 1). The taxa not sampled were *Rhytidarex buddlei* (Powell, 1948), which is critically endangered, having an estimated total population of less than 100 individuals in a 0.03 ha area on one of the Three Kings Islands (Brook, 2002b), and two members of *Schizoglossa*, *S. gigantea* Powell, 1930; and *S. novoseelandica barrierensis* Powell, 1949; neither of which occur in Northland. We also included representatives of several other New Zealand rhytidid genera (*Rhytida*, *Powelliphanta*, and *Wainuia*), as well as *Victaphanta* from Australia to check the monophyly of the subfamily.

2.2. Sequence data

Foot tissue was dissected from each snail and placed in a 5% Chelex 100 solution. After being incubated overnight at 65 °C each sample was briefly vortexed, the solution was then boiled for 10 min, and then centrifuged at 15,000*g* for 10 min. The DNA in the supernatant was used in the subsequent amplifications. Negative controls were included with each set of extractions.

Following extraction, DNA was amplified by the polymerase chain reaction (PCR) for the mitochondrial gene cytochrome oxidase subunit I (COI) using the universal invertebrate COI primer LCO1490 (Folmer et al., 1994) and the primer H7005 (Hafner et al., 1994). For those taxa that H7005 would not amplify, an alternative reverse primer, H7005-modl (Donald et al., 2005) was used. For the few taxa that neither H7005 nor H7005-modl would amplify, the reverse primer HCO2198 (Folmer et al., 1994) was used to produce a shorter fragment of COI. The PCR conditions were an initial denaturation step of 94 °C (3 min), followed by 40 cycles of 94 °C (30 s), 45 °C

Table 1
Specimen collection data

Locality	Taxon	Locality description	Lat.	Long.
1	*Rhytidarex johnsoni*	West Island, Three Kings Is	34°11′S	172°02′E
2	*Rhytidarex johnsoni*	South West Island, Three Kings Is	34°11′S	172°04′E
3	*Rhytidarex johnsoni*	North East Island, Three Kings Is	34°08′S	172°10′E
4	*Amborhytida duplicata*	Tapotupotu Bay, Reinga	34°26′S	172°43′E
5	*Amborhytida duplicata*; *Paryphanta watti*	Te Paki trig	34°28′S	172°46′E
6	*Paryphanta watti*	Kohuronaki, Te Paki	34°29′S	172°50′E
7	*Amborhytida duplicata*	Maungapika Hill, Kapowairua	34°25′S	172°52′E
8	*Amborhytida duplicata*	Whareana Stream	34°28′S	172°60′E
9	*Amborhytida duplicata*	Ngaroku Stream, North Cape	34°25′S	173°02′E
10	*Amborhytida* sp. "Aupouri"	Mt Camel, Houhora	34°49′S	173°10′E
11	*Amborhytida* sp. "Aupouri"	Whangatupere Bay, Karikari Peninsula	34°50′S	173°27′E
12	*Amborhytida* sp. "Aupouri"; *Paryphanta busbyi*	Waiatua Stream, Herekino	35°16′S	173°10′E
13	*Amborhytida* sp. "Aupouri"; *Paryphanta busbyi*	Kaitaia Walkway, Diggers Valley	35°12′S	173°17′E
14	*Amborhytida dunniae*; *Paryphanta busbyi*	Taumata Rd, Parapara	35°03′S	173°24′E
15	*Amborhytida forsythi*	Taipa River, Doubtless Bay	35°01′S	173°28′E
16	*Amborhytida dunniae*; *Paryphanta busbyi*	Kukupae Reserve, Kaeo	35°06′S	173°50′E
17	*Amborhytida forsythi*	Whangape Harbour entrance	35°22′S	173°13′E
18	*Amborhytida dunniae*; *A. forsythi*	Moetangi Stream, Mitimiti	35°26′S	173°17′E
19	*Amborhytida dunniae*; *A. forsythi*; *Paryphanta busbyi*	Mangataipa Reserve, Mangamuka River	35°15′S	173°32′E
20	*Amborhytida forsythi*; *Paryphanta busbyi*	Omapere, Hokianga Harbour	35°33′S	173°23′E
21	*Amborhytida dunniae*	Mataraua Rd, Kaikohe	35°31′S	173°46′S
22	*Paryphanta busbyi*	Kaikohe Scenic Reserve	35°23′S	173°48′E
23	*Amborhytida forsythi*	Waitata Bay, Russell	35°15′S	174°08′E
24	*Amborhytida* sp. "Motukokako"	Deepwater Cove, Bay of Islands	35°12′S	174°18′E
25	*Amborhytida* sp. "Motukokako"	Motukokako (Piercy) Island	35°10′S	174°20′E
26	*Amborhytida dunniae*	Ruapekapeka Rd, Towai	35°26′S	174°07′E
27	*Paryphanta busbyi*	Helena Bay	35°27′S	174°20′E
28	*Amborhytida pycrofti*	Tawhiti Rahi, Poor Knights Is	35°28′S	174°44′E
29	*Amborhytida pycrofti*	Aorangi, Poor Knights Is	35°29′S	174°44′E
30	*Amborhytida dunniae*	Kauri Mountain, Ocean Beach	35°47′S	174°33′E
31	*Amborhytida forsythi*	Otaika Valley Rd, Whangarei	35°47′S	174°17′E
32	*Amborhytida forsythi*; *Paryphanta busbyi*	Drinnon Rd, Mangakahia Range	35°41′S	173°59′E
33	*Paryphanta busbyi*	Trounson Kauri Park, Kaihu	35°44′S	173°39′E
34	*Paryphanta busbyi*	Tangihua Range	35°54′S	174°08′E
35	*Amborhytida forsythi*	Tokatoka, north Kaipara	36°04′S	173°58′E
36	*Amborhytida dunniae*; *Paryphanta busbyi*	Whenuanui Reserve, Ruawai	36°05′S	174°02′E
37	*Paryphanta busbyi*	Arcadia Rd, Paparoa	36°04′S	174°14′E
38	*Paryphanta busbyi*	Mareretu Forest, Waipu Hills	36°01′S	174°22′E
39	*Amborhytida dunniae*	Bream Tail, Mangawhai	36°04′S	174°35′E
40	*Amborhytida tarangaensis*; *Paryphanta busbyi*	Taranga (Hen) Island	35°58′S	174°43′E
41	*Amborhytida dunniae*; *Paryphanta busbyi*	Woodcocks, Warkworth	36°27′S	174°35′E
42	*Amborhytida dunniae*	Taylor Rd, Waimauku	36°45′S	174°30′E
43	*Amborhytida dunniae*; *Rhytida greenwoodi*	Huia, Waitakere Ranges	36°60′S	174°34′E
44	*Amborhytida dunniae*	Red Hill, Papakura	37°04′S	174°59′E
45	*Schizoglossa worthyae*	Puhipuhi	35°28′S	174°16′E
46	*Schizoglossa worthyae*	Bream Head	35°51′S	174°34′E
47	*Schizoglossa novoseelandica*	Old Mountain Rd, Whatawhata	37°51′S	175°05′E
48	*Schizoglossa novoseelandica*	New Plymouth	39°04′S	174°06′E
49	*Wainuia urnula*	Orongorongo Valley		
50	*Powelliphanta hochstetteri*	Canaan, Takaka Hill	40°57′S	172°52′E
51	*Rhytida stephenensis*	Irongate Stream, Malborough	42°17′S	173°46′E
52	*Victaphanta compacta*	Otway Ranges, Victoria		
53	*Victaphanta lampra*	Scotsdale, Tasmania		

(1 min), and 72 °C (1 min) and a final extension phase at 72 °C for 4 min. Negative controls were included with each PCR. The PCR products were purified using High Pure PCR Purification Columns (Roche) and then sequenced in both directions on an automated sequencer using the PCR primers.

2.3. Sequence analysis and phylogenetic inference

The COI sequences were aligned by eye. The sequences have been submitted to GenBank (Accession Nos. DQ298451–DQ298517) and the aligned data matrices and phylogenetic trees to TreeBASE (www.treebase.org).

Phylogenetic analyses were performed with PAUP* version 4b10 (Swofford, 2002) for neighbor-joining (NJ) searches and bootstrapping [NJ and maximum parsimony (MP)], whereas MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was used for Markov-chain Monte-Carlo (MCMC) Bayesian analysis. The number of within-species samples precluded searching for the "best" tree using maximum parsimony or maximum likelihood. For visualization purposes the *Victaphanta* species were defined as outgroup taxa. The model of sequence evolution was selected using the hierarchical likelihood ratio test of Modeltest (Posada and Crandall, 1998). The NJ tree was constructed using GTR-corrected distances. The NJ and the MP bootstrap analyses consisted of 10,000 replicates (with the fast heuristic search for MP). In the MP bootstrapping, transversions were weighted 5 times transitions, a value estimated by maximum likelihood. Bayesian analysis was performed using MrBayes v3.0 with the following settings: the maximum likelihood model employed 6 substitution types ("nst = 6") and rate variation across sites was modelled using a gamma distribution, with a proportion of the sites being invariant ("rates = invgamma"). The Markov-chain Monte-Carlo search was run with four chains for 5,000,000 generations, with trees being sampled every 100 generations (the first 10,000 trees, i.e., 1,000,000 generations, were discarded as "burnin").

3. Results

PCR amplification of COI yielded a product of approximately 1100 bp, which when sequenced in both directions gave 948 bp of sequence (the data set were trimmed at each end to include only those sites for which more than half the taxa had sequenced). Modeltest selected the GTR + I + G model of nucleotide substitution for the data set.

The trees produced by NJ (Fig. 2) and Bayesian (Figs. 2 and 3) analysis of the data set are generally concordant with one another as are the levels of support inferred by the bootstrap and Bayesian analyses. Those relationships that do differ between the two forms of analysis are only in areas where none of the methods provide strong support for any particular relationship (see Figs. 2 and 3). The close match between the trees produced by different phylogenetic methods gives an informal measure of the robustness of these estimates (Kim, 1993).

The levels of genetic divergence within and between our groups may be found in the supplementary information available online. A likelihood ratio test (Felsenstein, 1981; Page and Holmes, 1998) was performed to determine whether the molecular data were clock-like. Although the phylogenies (Figs. 2 and 3) visually appear relatively clock-like, the molecular clock was rejected by a likelihood ratio test (twice the log-likelihood difference = 112.2231, df = 65, $P = 0.0003$). When the four most basal species on the Bayesian tree were excluded the data still narrowly fail the test for a molecular clock (twice the log-likelihood difference = 88.70668, df = 61, $P = 0.0118$). Although the data fail the test for a molecular clock, the lack of fossil calibration points (there are no known paryphantine fossils older than Late Pleistocene in age; Beu and Maxwell, 1990; Brook, 1999c) precludes the use of most relaxed-clock methods of dating (reviewed in Welch and Bromham, 2005). Moreover, Ho et al. (2005) have recently argued that even when a data set fails to be ultrametric, it is not clear whether relaxed-clock methods should be applied. Thus, given that we are only interested in whether the level of genetic divergence is consistent with known geological events, we used a range of calibrated rates of change for molluscan COI (from 0.7 to 2.4%/my; Hellberg and Vacquier, 1999; Marko, 2002) to calculate a coarse level estimate of the approximate timing of divergence events from our simple distance measures.

4. Discussion

Our genetic data confirm Climo's (1977) conclusion that the four paryphantine genera are each other's closest relatives: the branch giving monophyly of the subfamily has 98% NJ and 80% MP bootstrap support and Bayesian posterior probability of 1.0. The genera are all well supported, with NJ bootstraps $\geqslant 91\%$, MP $\geqslant 65\%$, and Bayesian posterior probabilities of $\geqslant 0.99$.

Nevertheless, the relationships among these genera are not as Climo's taxonomy (1977) suggests. In particular, *Rhytidarex* and *Amborhytida* are not sister groups, even though the relationships among the genera are not well resolved and there are differences among the trees constructed with different methods. At this point, all we can unequivocally deduce is that the four genera are well separated and probably diverged from each other over a relatively short albeit geological time. Nevertheless, our Bayesian and MP bootstrap analyses suggest that *Rhytidarex* is probably the most basal genus. Within each genus, however, there are some clear patterns, although these patterns do not occur across genera. We discuss each group of species in turn. Because we did not sample all species of *Schizoglossa*, we do not discuss its relationships here.

4.1. Amborhytida dunniae Group

The most widespread of the species we examined in detail, *A. dunniae*, showed no obvious pattern of mitochondrial variation across its geographical range (Fig. 3A). Moreover, the morphologically divergent forms restricted to some of the islands off the eastern coast of Northland—*A. tarangaensis* from Taranga (Hen) Island, *A. pycrofti* from the Poor Knights Islands and *Amborhytida* sp. "Motukokako" from Motukokako (Piercy Island) and nearby Cape Brett peninsula—fitted clearly within the genetic variation ascribed to *A. dunniae*. Nevertheless, in the latter two cases, where we had samples from two populations of each, the forms grouped together with strong bootstrap and Bayesian support. Indeed, they were the only groups to obtain significant support within *A. dunniae*. This result

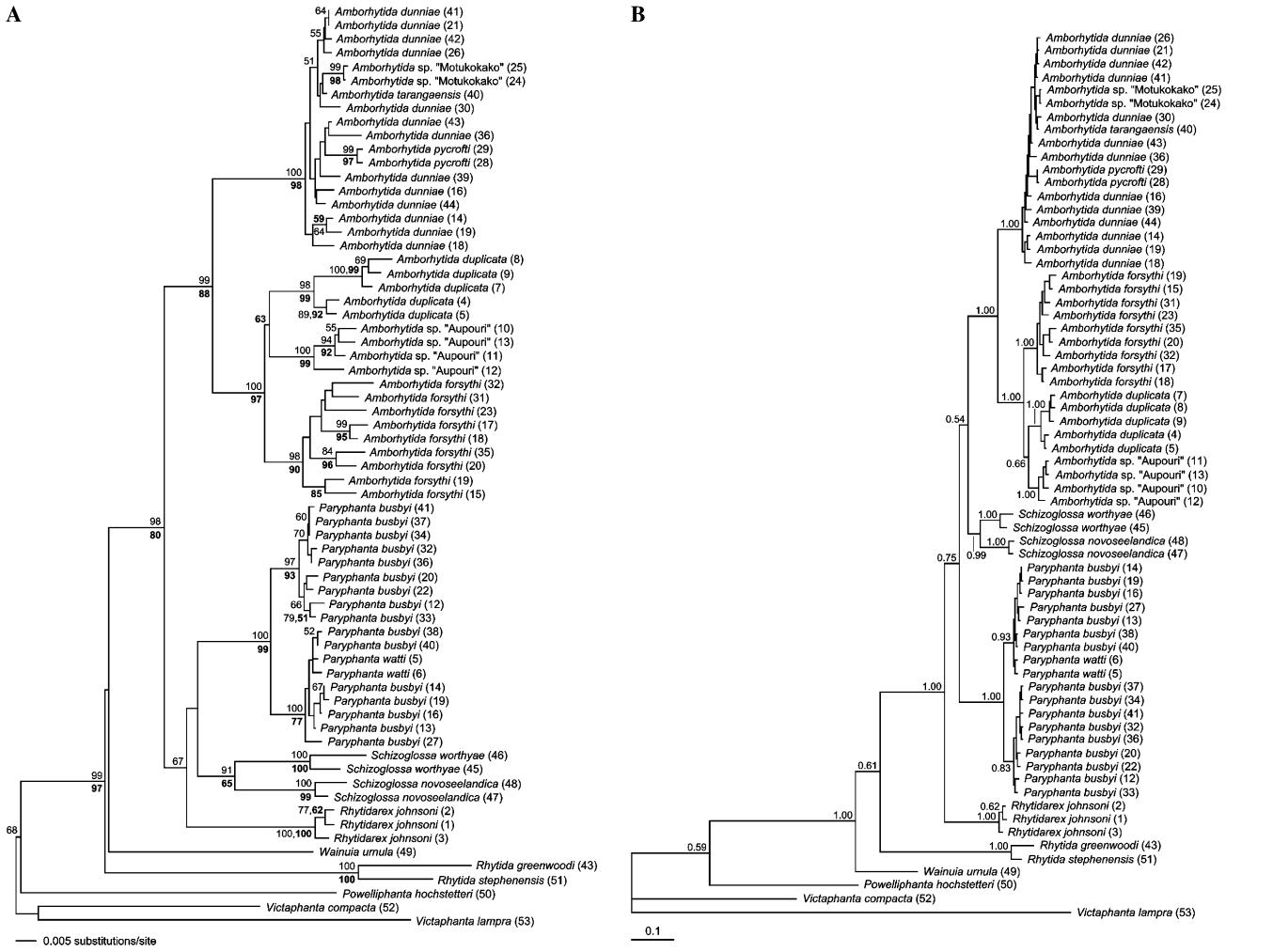

Fig. 2. (A) The neighbor-joining phylogram. The numbers associated with the branches represent support values ⩾50% from 10,000 NJ bootstraps and from 10,000 MP bootstraps (the MP values in bold were generated using a fast heuristic search with transversions weighted 5 times transitions, a weight estimated by maximum likelihood). In some positions on the figure the NJ and MP bootstrap values disagree with NJ phylogram, or there is not enough room to insert the bootstrap values. For MP there is 52% support for *Rhytidarex* being basal to a *Schizoglossa*, *Paryphanta*, and *Amborhytida* group. For MP there is 56% support for grouping *Amborhytida pycrofti* (28, 29) and *Amborhytida dunniae* (21, 26, 41, and 42) together. There is 74% (NJ) and 62% (MP) support for grouping *Pa. busbyi* (14), *Pa. busbyi* (16), and *Pa. busbyi* (19). For NJ there is 52% support for grouping all the *Amborhytida* sp. "Aupouri" and all the *A. forsythi*. For MP there is 54% support for grouping *A. duplicata* (7) and A *duplicata* (8). (B) The Bayesian phylogram. The numbers associated with the branches represent posterior probabilities ⩾0.5 from Bayesian MCMC searches. The Bayesian support values not shown on this figure are shown on the magnified versions, Fig. 3.

suggests that populations of each of these island (or near-island) endemics are very closely related, possibly as a consequence of evolutionarily recent founder events. We can estimate the date of divergence of these forms by converting from genetic distances. Assuming a rate of neutral molecular change of between 0.7 and 2.4%/my, implies that the various island taxa within the *A. dunniae* group all separated during Pleistocene time, within the last 0.5–1.8 mya (although there are numerous sources of errors in such calculations, which should be treated with caution).

4.2. *Amborhytida forsythi* Group

The remaining populations of *Amborhytida*, originally attributed to *A. forsythi* and *A. duplicata*, formed a group with very strong support (100%, 97%, 1.0) and were considerably divergent from *A. dunniae* (see Fig. 2). Thus, Powell's (1979) view of *A. forsythi* as only subspecifically distinct from *A. dunniae* is not tenable, and in fact the two taxa are locally microsympatric (e.g., at locations 18 and 19; see Table 1). Moreover, the samples originally identified from shell morphology as *A. forsythi* grouped in a most unexpected way, falling into two well-supported non-sister clades, although the non-sisterhood itself was not well supported. Populations from Mt Camel, Karikari Peninsula, and hill country north of Herekino Harbour, subsequently referred to in this study as *Amborhytida* sp. "Aupouri," were weakly grouped (<50%, 63%, 0.66) with *A. duplicata*, which is endemic to the area between Cape Maria van Diemen and North Cape at the northern tip of Aupouri Peninsula. Populations of morphologically similar *A. forsythi* from elsewhere in Northland between Taipa (the type

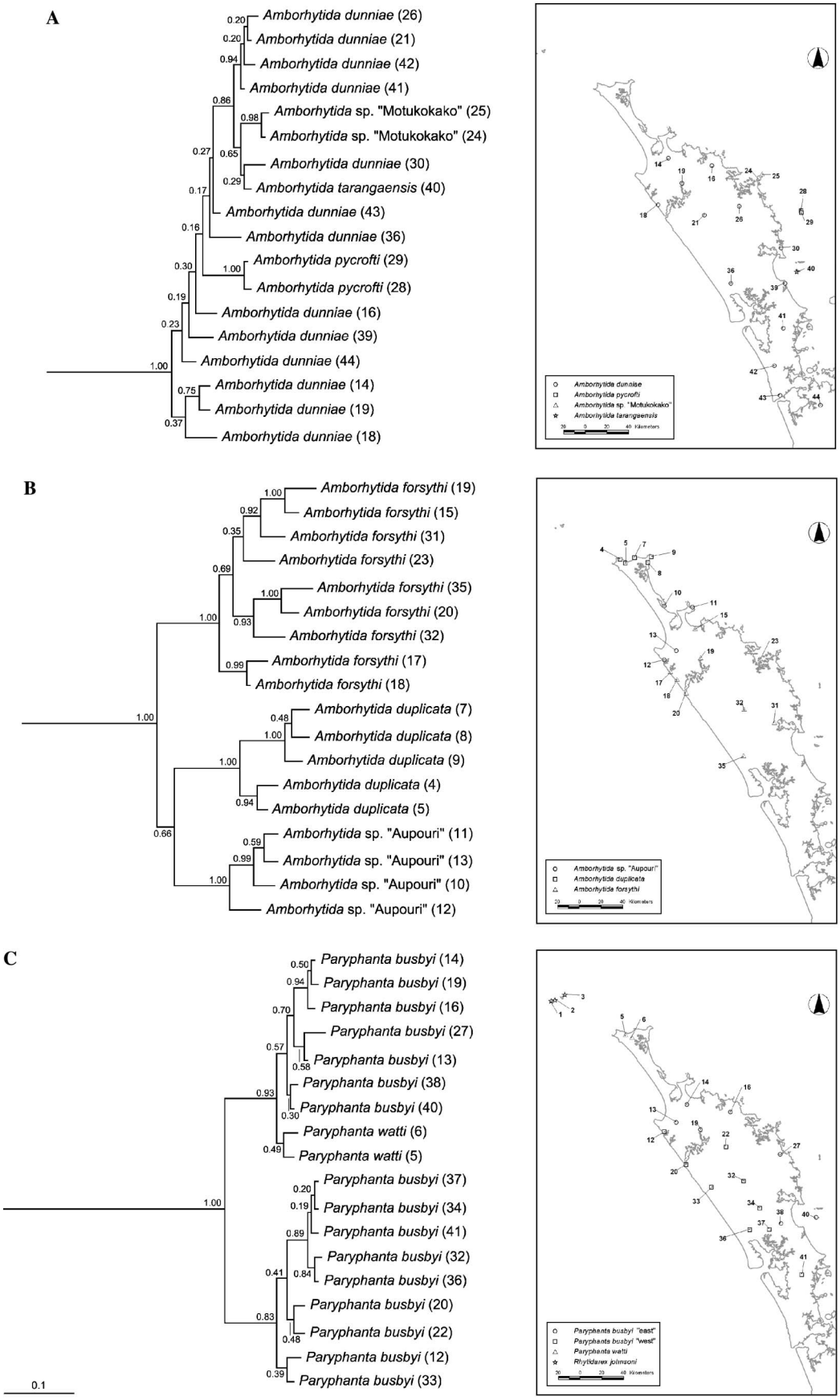

Fig. 3. Magnified sections of the Bayesian phylogram with corresponding distribution maps. The numbers associated with the branches represent posterior probabilities from Bayesian MCMC searches. (A) The *A. dunniae* clade. (B) The *A. forsythi* clade. (C) The *Paryphanta* clade.

locality) and north Kaipara, formed a separate, well-supported (98%, 90%, 1.0) clade. The level of genetic divergence between these taxa implies that *A. forsythi* and the *A. duplicata* + *Amborhytida* sp. "Aupouri" group separated between 1.9 and 6.6 mya, and that *A. duplicata* and *Amborhytida* sp. "Aupouri" separated more-or-less simultaneously between 1.8 and 6.2 mya. Within *A. duplicata*, there was significant phylogenetic structure that correlated with geography. Samples from western localities 4 and 5 grouped together (89%, 92%, 0.94) as did those from eastern localities 7–9 (100%, 99%, 1.00). The mean genetic distance between them was 2.25%, compared to a mean of 0.79% within the two clades, implying a separation date of 0.9–3.2 mya.

4.3. Paryphanta

The phylogeny of *Paryphanta* does not correspond with current taxonomy. The two populations of the Far-North endemic, *P. watti*, that we sampled fell within a clade including several populations of *P. busbyi* extending along the east of Northland, from near Kaitaia south to Hen Island and the Waipu Hills. Indeed, the two *P. watti* samples barely even grouped together, with no statistical confidence. Nevertheless, there was significant structure within *Paryphanta*, with this strongly supported clade (100%, 77%, 0.93) well separated from a second clade, also strongly supported (97%, 93%, 0.83), found in the western and southern areas of Northland between Herekino and north Kaipara, with an outlying population further south near Warkworth (Fig. 3C). There are no obvious consistent conchological differences between these two clades, whereas shells of *P. watti* are easily distinguished from those of *P. busbyi*: they have ~1 cm (~15%) smaller diameter as adults, and have different coloration (Powell, 1946). The mean genetic distance between individuals in these two *Paryphanta* clades (2.38%) was more than four times the mean distances within each (0.50 and 0.58%, respectively), implying a separation date of 1.0–3.4 mya.

4.4. Rhytidarex johnsoni

There was little genetic variation among populations of *R. johnsoni* on islands in the Three Kings group. The mean genetic distance was just 0.70%, with the sample from North East Island at the eastern end of the island chain being most distant genetically (mean 0.81%). These figures suggest separation dates of less than 1 mya.

4.5. Phylogeographic interpretation

The basal position of *Rhytidarex* in the Bayesian tree fits reasonably well with the inferred geological history of northern New Zealand. The Three Kings Islands, to which *Rhytidarex* is endemic, lack *Amborhytida*, *Paryphanta*, and *Schizoglossa*, and are believed to have been separated from the rest of New Zealand since mid-late Miocene time, ~10–15 mya (Brook, 2002c; Brook and Thrasher, 1991). The mean genetic divergence between *Rhytidarex* and the remainder of the Paryphantinae, 8.15%, gives a separation date of 3.4–11.6 mya, which suggests that the slower rates are more appropriate in this group of snails, at least at the base of the tree. Indeed, doing the reverse calculation and assuming the mean value of 12.5 mya for the separation of the Three Kings results in a molecular evolution rate of just 0.65%/my. In conjunction with the 6.93% genetic difference between the *A. dunniae* and *A. forsythi* groups, which corresponds (using rates in the range 0.7–2.4%/my) to a split 2.9–9.9 mya, we can infer that *Amborhytida*, *Paryphanta*, and *Schizoglossa* arose in the range of 2.9–11.6 mya, with later dates probably more likely.

The low degree of genetic divergence between the three extant island populations of *R. johnsoni*, and their inferred separation date of less than 1 mya, is presumably related to a history of gene flow between populations during Pleistocene periods of lowered sea level, when land connections existed between all the present-day islands in the Three Kings group (Brook, 2002c; Brook and Laurenson, 1992).

The almost simultaneous evolution of *Amborhytida duplicata*, *A. forsythi*, and *Amborhytida* sp. "Aupouri" between c. 1.9 and 6.6 mya accords with the inferred former existence of islands in the Cape Reinga-North Cape, Mt Camel and Karikari areas during Pliocene time (1.8–5.3 mya, Isaac et al., 1994). Clearly, *A. duplicate* evolved in the Far North and remained there, with eastern and western populations subsequently becoming genetically (but not conchologically) differentiated over the last 0.9–3.2 my. Possibly, *Amborhytida* sp. "Aupouri" evolved on what is now Mount Camel or Karikari Peninsula, which were also separate islands in the Pliocene, before spreading south to Herekino. *A. forsythi* presumably evolved in mainland Northland.

The mean genetic divergence between the *A. forsythi* group and *A. dunniae* is 6.93%, which implies a separation of 2.9–9.9 mya. Curiously, *A. dunniae* shows no significant differentiation over its range, even though it is the most widespread paryphantine species in Northland. We might presume that it evolved somewhere on the New Zealand mainland and spread to islands off the east coast of Northland during Pleistocene periods of lowered sea level. The relatively continuous native forest and shrubland cover, which is inferred to have existed in mainland Northland up until the last millennium, may have allowed sufficient gene exchange to swamp any local differentiation.

There is no simple geological explanation for the phylogeography of *Paryphanta*. The lack of genetic difference between far northern and eastern Northland populations of *Paryphanta* might suggest that individuals are highly mobile, far more so than individuals of *Amborhytida*, which are very different in these two areas. But such mobility, of course, would preclude the deep east–west genetic divide we found in *Paryphanta*.

The discordance in the phylogeographic patterns in the four groups of snails examined here means that it is difficult

to make strong inferences about common geological influences on the evolutionary history of paryphantines in Northland. If our work had been restricted to two of the groups (e.g., *R. johnsoni*, *A. duplicata*, and *A. forsythi*), we would have had no reason to be so cautious. This study thus illustrates the importance of examining several groups of related taxa before trying to reconcile the evolutionary history of a group with events in the geological past (Croizat, 1962). Failure to do so can lead to the phylogeographic equivalent of adaptationist 'just-so' stories.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2005.10.015.

References

Beu, A.G., Maxwell, P.A., 1990. Cenozoic Mollusca of New Zealand. N.Z.G.S. Pal. Bull., 58.

Brook, F.J., 1999a. Changes in the landsnail fauna of Lady Alice Island, northeastern New Zealand. J. R. Soc. NZ 29, 135–157.

Brook, F.J., 1999b. Stratigraphy and landsnail faunas of Late Holocene coastal dunes, Tokerau Beach, northern New Zealand. J. R. Soc. NZ 29, 337–359.

Brook, F.J., 1999c. Stratigraphy, landsnail faunas, and paleoenvironmental history of coastal dunefields at Te Werahi, northernmost New Zealand. J. R. Soc. NZ 29, 361–393.

Brook, F.J., 2002a. Uncommon and Rare Landsnails in the Northland Region of New Zealand, and An Assessment of Conservation Management Priorities. Department of Conservation, Whangarei, NZ.

Brook, F.J., 2002b. Conservation status of *Rhytidarex buddlei* (Mollusca: Pulmonata: Rhytididae) on the Three Kings Islands, northern New Zealand. J. R. Soc. NZ 32, 555–569.

Brook, F.J., 2002c. Changes in the landsnail fauna of Great Island, Three Kings Islands, northern New Zealand. J. R. Soc. NZ 32, 61–88.

Brook, F.J., Laurenson, CM., 1992. Ecology and morphological variation in *Placostylus bollonsi* (Gastropoda: Bulimulidae) at Three Kings Islands, New Zealand. Rec. Auckland Inst. Mus. 29, 135–166.

Brook, F.J., Thrasher, G.P., 1991. Cretaceous and Cenozoic Geology of Northernmost New Zealand. New Zealand Geological Survey Record 41.

Climo, F.M., 1977. A new higher classification of the New Zealand Rhytididae (Mollusca: Pulmonata). J. R. Soc. NZ 7, 59–65.

Croizat, L., 1962. Space, Time, Form: The Biological Synthesis. The Author, Caracas.

Donald, K.M., Kennedy, M., Spencer, H.G., 2005. Cladogenesis resulting from long-distance rafting events in South Pacific topshells (Gastropoda, Trochidae). Evolution 59, 1701–1711.

Efford, M.G., 1998. Distribution and Status of Native Carnivorous Landsnails in the Genera *Wainuia* and *Rhytida*. Department of Conservation, Wellington. pp. 48.

Emberton, K.C., 1990. Acavid land snails of Madagascar: subgeneric revision based on published data (Gastropoda: Pulmonata: Stylommatophora). Proc. Acad. Nat. Sci. Philadelphia 142, 101–117.

Felsenstein, J., 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. J. Mol. Evol. 17, 368–376.

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.

Hafner, M.S., Sudman, P.D., Villablance, F.X., Spradling, T.A., Demastes, J.W., Nadler, S.A., 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. Science 265, 1087–1090.

Hellberg, M.E., Vacquier, V.D., 1999. Rapid evolution of fertilization selectivity and lysine cDNA sequences in teguline gastropods. Mol. Biol. Evol. 16, 839–848.

Ho, S.Y.W., Phillips, M.J., Drummond, A.J., Cooper, A., 2005. Accuracy of rate estimation using relaxed-clock methods with a critical focus on the early metazoan radiation. Mol. Biol. Evol. 22, 1355–1363.

Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755.

Isaac, M.J., Herzer, R.H., Brook, F.J., Hayward, B.W., 1994. Cretaceous and Cenozoic Sedimentary Basins of Northland, New Zealand. Institute of Geological & Nuclear Sciences, 8.

Kim, J.H., 1993. Improving the accuracy of phylogenetic estimation by combining different methods. Syst. Biol. 42, 331–340.

Marko, P.B., 2002. Fossil calibration of molecular clocks and the divergence times of geminate species pairs separated by the Isthmus of Panama. Mol. Biol. Evol. 19, 2005–2021.

Page, R.D.M., Holmes, E.C., 1998. Molecular Evolution: A Phylogenetic Approach. Blackwell Science, Oxford.

Parmakelis, A., Pfenninger, M., Spanos, L., Papagiannakis, G., Louis, C., Mylonas, M., 2005. Inference of a radiation in Mastus (Gastropoda, Pulmonata, Enidae) on the island of Crete. Evolution 59, 991–1005.

Posada, D., Crandall, K.A., 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14, 817–818.

Powell, A.W.B., 1946. The Paryphantidae of New Zealand. No. 5. Further new species of Paryphanta, Wainuia and Rhytida. Rec. Auck. Inst. Mus. 3, 137–144.

Powell, A.W.B., 1979. New Zealand Mollusca: Marine, Land and Freshwater Shells. Collins, Auckland.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.

Rundell, R.J., Holland, B.S., Cowie, R.H., 2004. Molecular phylogeny and biogeography of the endemic Hawaiian Succineidae (Gastropoda: Pulmonata). Mol. Phylogenet. Evol. 31, 246–255.

Solem, A., 1959. Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. Fieldiana, Zool. 43, 359.

Spencer, H.G., Willan, R.C., Marshall, B.A., Murray, T.J., 2004. Checklist of the Recent Mollusca described from the New Zealand Exclusive Economic Zone. <http://www.molluscs.otago.ac.nz/>.

Swofford, D.L., 2002. PAUP* 4.0bl0. Sinauer Associates, Sunderland, MA.

Walker, K.J., 2003. Recovery Plans for *Powelliphanta* Land Snails. Threatened Species Recovery Plan 49. Department of Conservation, Wellington. p. 208.

Welch, J.J., Bromham, L., 2005. Molecular dating when rates vary. Trends Ecol. Evol. 20, 320–327.