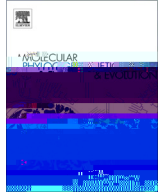
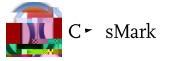


Molecular Phylogenetics and Evolution

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A phylogeny of Southern Hemisphere whelks (Gastropoda: Buccinulidae) and concordance with the fossil record



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to other regions (Powell, 1929; Dell, 1956; Willan, 1978; Powell, 1979; Spencer et al., 2009), and they exhibit significant morphological variation (Powell, 1927; Powell, 1947; Dell, 1956; Ponder, 1973; Powell, 1979).

preceded by “M.” Specimens were collected either via trawling (20–500 m depth for most sampling) or by hand from the intertidal zone. Some specimens were caught as trawling fishery bycatch. Captured individuals were swiftly frozen to prevent tissue and DNA degradation. Snails were subsequently thawed and bodies were removed from shells for preservation in 95% ethanol. All sampled specimens were identified by experienced molluscan taxonomists: Bruce A. Marshall (Collection Manager Sciences, Museum of New Zealand Te Papa Tongarewa) and Alan G. Beu (Palaeontologist, GNS). We used a public database (GenBank) to retrieve sequence data from other Northern Hemisphere taxa (from [Claremont et al., 2008](#); [Vendetti, 2009](#); [Barco et al., 2010](#); [Oliverio and Modica, 2010](#); [Zou et al., 2011a,b](#); [Kim et al., 2012](#); see [Tables 1 and 2](#)). We were unable to sample the putative buccinulid genera *Aacdelia* Dell, 1972 and *Erebia* Powell, 1929 from southern New Zealand and the subantarctic.

We sampled all species of the buccinulid genera *Aacelia* Dell, 1972 and *Keelia*, and selected representatives of *Aeolia* Finlay, 1926, *A. f.* Kobelt, 1879, *Buccina* Deshayes, 1830, *Celesia*, *Paesia*, and *Pelesia* ([Tables 1 and 2](#)). These genera are dominate

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we sampled whole mitochondrial genome sequences for *T. albica* (Say, 1822) and *T. ecata* (Linnaeus, 1758) generated by previous studies ([Simison et al., 2006](#); [Cunha et al., 2009](#)). Both of these species are restricted to the Northern Hemisphere.

mitochondrial genes cytochrome oxidase I (*cox 1*) and 16S rRNA, as

combined mtDNA and rDNA calibrated phylogeny using 27 sequences, two partitions were used based on jModelTest results: (1) mtDNA protein-encoding and rRNA genes and nuclear rDNA genes (15,891 bp), and (2) tRNA genes (1065 bp) using the GTR + I + G and HKY + I + G substitution models respectively. The calibrated phylogeny of 25 mtDNA sequences also used two partitions: (1) protein-encoding and rRNA genes (10,635 bp), and (2) tRNA genes (1065 bp) using the GTR + I + G and HKY + I + G substitution models respectively.

The key implication of this phylogenetic analysis is therefore that assumptions of geographic isolation and separate evolutionary radiation in the Southern Hemisphere are not valid for all lineages of buccinulid whelks. The occurrence of multiple, separate lineages in New Zealand implies that whelks have transversed long distances over evolutionary time. As in other marine molluscs, these findings indicate that dispersal can be common on an evolutionary timescale, even in lineages that undergo direct development (e.g. Donald et al., 2005; Huelsken et al., 2013; Cumming et al., 2014; Donald et al., 2015). New Zealand may be sufficiently remote to allow an increased frequency of endemism in benthic marine snail species, but over millions of years the islands are clearly not so biologically isolated. This finding corresponds with many studies of terrestrial fauna (e.g. Battley, 1997; Trewick, 2000; Goldberg et al., 2008). Studies of other marine molluscs have demonstrated that a high rate of endemism, as observed in *Aeolaea*, *Cerata* and *Pepono*, is not mutually exclusive with dispersal ability (e.g. Huelsken et al., 2013).

4.2. *Cerata* and *Fasciolaridae* and *Buccidae*

The sampled Fascioliariidae in our phylogenies (*Gastropoda* - *da*, *Pa* - *ca*, *Ta* - *b*), are monophyletic and sister to all other taxa included (Figs. 2 and 3; Supplementary Figs. 1–3). Recent taxonomic summaries of Buccinidae (e.g. Bouchet et al., 2005), have suggested that *Buccina* and *Volutopsini* reside within tribes Buccinini and Volutopsini respectively. However, the relatively small genetic distance (0.44% and 2.30% pair wise variability for rDNA and mtDNA respectively) estimated by our phylogenetic analysis suggests a close relationship between these taxa (Figs. 2 and 3; Supplementary Figs. 1–3). A previous assessment of soft-body and radula morphology hypothesised that *Pepono* represent an early split among Buccinidae (Harasewych,

1990), but this might instead be an example of morphological convergence.

4.3. *Pepono* and *Acaelaea*

Our molecular phylogenies indicate that *Pepono* and *Keelaea* are closely related (Figs. 2 and 3; Supplementary Figs. 1–6). This result agrees with the previous analysis of mitochondrial 16S rRNA gene data (Hayashi, 2005), and hypotheses based on shell morphology and soft-body anatomy (Powell, 1929; Wenz, 1941; Ponder, 1973; Stilwell and Zinsmeister, 1992), and it justifies previous taxonomic confusion of the genera (Palmer and Bran, 1965). In addition, our phylogenetic evidence also indicates that *P. beccarii* is not closely related to other *Pepono*, forming instead a clade with *Acaelaea* (Supplementary Fig. 4). Since its discovery, the evolution and classification of *A. acaelaea* (puzzF31ri28.3(aalla-)-

between *K. c. e.* and *K. e. e.* (median 33.0 Ma; [Fig. 3](#)). In addition, later fossil species of *Ke. e. a.* are also known from Ecuador, dated to approximately 5.33–7.00 Ma (stratigraphy uncertain; [Fig. 5](#) label 7; [Olsson, 1964](#)). Previously these fossils were hypothesised to represent a southward dispersal of *Ke. e. a.* from California ([Lindberg, 1991](#)).

and Bran, 1965; Anderson, 1973; Gilbert, 1973; Kollmann and Peel, 1983; CoBabe and Allmon, 1994; Moths and Albrecht, 2010), is not as incongruous as it first appeared.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2017.06.018>.

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