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Phylogenetic analysis of New Zealand earthworms (Oligochaeta: Megascolecidae) reveals ancient clades and cryptic taxonomic diversity

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ABSTRACT

We have constructed the first ever phylogeny for the New Zealand earthworm fauna (Megascolecinae and Acanthodrilinae) including representatives from other major continental regions. Bayesian and maximum likelihood phylogenetic trees were constructed from 427 base pairs from the mitochondrial large subunit (16S) rRNA gene and 661 base pairs from the nuclear large subunit (28S) rRNA gene. Within the Acanthodrilinae we were able to identify a number of well-supported clades that were restricted to continental landmasses. Estimates of nodal support for these major clades were generally high, but relationships among clades were poorly resolved. The phylogenetic analyses revealed several independent lineages in New Zealand, some of which had a comparable phylogenetic depth to monophyletic groups sampled from Madagascar, Africa, North America and Australia. These results are consistent with at least some of these clades having inhabited New Zealand since rifting from Gondwana in the Late Cretaceous. Within the New Zealand Acanthodrilinae, major clades tended to be restricted to specific regions of New Zealand, with the central North Island and Cook Strait representing major biogeographic boundaries. Our field surveys of New Zealand and subsequent identification has also revealed extensive cryptic taxonomic diversity with approximately 48 new species sampled in addition to the 199 species recognized by previous authors. Our results indicate that further survey and taxonomic work is required to establish a foundation for future biogeographic and ecological research on this vitally important component of the New Zealand biota.

1. Introduction

The New Zealand native oligochaete fauna includes 199 recognized species (Lee, 1959a,b; Lee et al., 2000; Blakemore, 2006). All New Zealand native species are placed in the Megascolecidae, and within this family both subfamilies of Megascolecinae and Acanthodrilinae are represented. The Acanthodrilinae contains the greatest diversity with 17 genera and 125 species; the Megascolecinae is less diverse with 9 genera and 50 species (Table 1). Initial taxonomic work was performed by Baird (1871), Beddard (1889), Benham (1901, 1904, 1905) and Michaelsen (1920). However, the seminal revision by Lee (1959b) contained descriptions of 193 species, including 54 new species and 4 new genera. This publication and the key of Lee (1959a) remain the most recent revision and only taxonomic tool available that covers the entire known fauna. Lee's revision (1959b) has since been updated by the reviews of Lee et al. (2000) and Blakemore (2006), which listed nomenclatural changes by other authors, but did not provide any novel taxonomic descriptions.

Although the key from Lee (1959b) is an excellent tool, it has been widely acknowledged that undescribed species are likely to exist. Based on the relative land area of New Zealand and Tasmania, Blakemore (2006) estimated that the size of the New Zealand earthworm fauna could be as high as 900 species, but was probably lower due to large areas of relatively inhospitable soils. Since the revision of Lee (1959b), there has been a small amount of ecological work, mainly focussed on the endemic species *Octochaetus multiporus* within modified pastures (Springett and Gray, 1998a; Springett et al., 1998b) but there have been no detailed studies of earthworm ecology in native ecosystems. Earthworms are a key component of many ecosystems (Lee, 1985), are the highest animal biomass component of the New Zealand forest (Brockie and Moeed, 1986), and provide a food source for several critically endangered New Zealand species such as kiwi (Buller, 1888; Roach, 1954; Reid et al., 1982) and giant land snails (Efford, 2000; Barker and Efford, 2004; Stringer et al., 2005). Given the propensity for

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Table 1
Current classification of the New Zealand native Megascolecidae (following Lee et al., 2000), with new species detected in the current study and sampled described species.

Taxon	Number of recognized species	Number of recognized species sampled	Number of novel species sampled
Acanthodrilinae			
Acanthodrilacea			
Acanthodrilus Perrier	1		
Decachaetus Lee	2		
Deinodrilus Beddard	8	1	3
Dinodriloides Benham	1	1	
Diplotrema Spencer	9		
Eudinodriloides Lee	1	0	1
Hoplochaetina Michaelsen	8	2	5
Leucodrilus Lee	4		1
Microscolex Rosa	6	1	0
Octochaetus Beddard	13	0	2
Perieodrilus Michaelsen	4	0	1
Rhododrilus Beddard	29	5	7
Sylvodrilus Lee	1	0	0
Neodrilacea			
Maoridrilus Michaelsen	28	11	≈9
Neochaeta Lee	2		
Neodrilus Beddard	5		
Plagiochaeta Benham	3	1	1
Megascolescinae			
Anisochaeta Beddard	3	1	0
Celeriella Gates	4		
Diporochaeta Beddard	11	2	1
Graliophilus Jamieson	3		
Megascolides McCoy	12	7	13
Notoscolex Fletcher	11		
Perionychella Michaelsen	4	1	0
Pontodrilus Perrier	2	0	1
nov. gen. 1			1
nov. gen. 2			1
nov. gen. 3			1
Total	175	33	48

some earthworm species to have limited geographic distributions and cryptic diversity (e.g., Chang et al., 2008; King et al., 2008; Briones et al., 2009; Novo et al., 2009) further survey, taxonomic and phylogenetic study is urgently required.

Earthworms are also ideal for investigating biogeographic processes and specifically, vicariance processes, because most species are poor dispersers due to an intolerance of sea water as indicated by their rarity and low diversity on oceanic islands (James, 2004). There have been a number of events in the geological history of New Zealand that have been demonstrated or hypothesized to have impacted on biodiversity (e.g., Cooper and Millener, 1993; Lee et al., 2001; Bunce et al., 2009). These include: (1) the rifting of New Zealand from the eastern margin of Australia that began approximately 85 million years ago (Gaina et al., 1998; Michaux, 2009); (2) the severing of direct land connections between New Zealand and New Caledonia in the late Cretaceous to early Tertiary (Ladiges and Cantrill, 2007); (3) the formation and movement of island arcs between New Zealand and New Caledonia in the mid- to late Tertiary, which possibly acted to transport biota between the two landmasses (Herzer et al., 1997; Ladiges and Cantrill, 2007; Schellart et al., 2009); (4) an extensive marine transgression in the New Zealand region during the late Oligocene (Fleming, 1979; Cooper and Cooper, 1995); (5) the persistence of large islands that formed in the Oligocene through to the late Tertiary (Fleming, 1979; Bunce et al., 2009); and (6) tectonic change and mountain uplift from the Late Miocene to recent times (Batt and Braun, 1999; King, 2000; Bunce et al., 2009). The impact of these events on the biota has been debated for years (e.g., Gaskin, 1970; Craw, 1978; Fleming, 1979; Lee et al., 2001; Pole, 1994, 2001; Waters and Craw, 2006; Buckley and Simon, 2007; Landis et al., 2008; Heads, 2009; Michaux, 2009; Wallis and Trewick, 2009; Allwood et al., 2010; Giribet and Boyer, 2010) and further understanding will require phylogenetic studies on clades that are ancient, highly diverse and widely distributed throughout the New Zealand region. The megascolecid earthworms clearly fit the last two of these categories and are usually assumed to fit the first (e.g., Lee, 1959b).

New Zealand earthworms have been discussed from a biogeographic perspective for well over 100 years. Early authors including Beddard (1895a,b), Michaelsen (1896), Benham (1902, 1909, 1922), and Stephenson, (1921, 1923, 1930) all argued for land connections between various southern continents to explain the distribution of the Megascolecidae. Michaelsen (1922) later also interpreted earthworm distribution in the context of continental drift and was possibly an influence on the development of Wegener's model of continental drift (James, 2004).

More recently, Lee (1959b) concluded that the New Zealand Acanthodrilinae taxa are related to those of South America, South Africa, Australia and the subantarctic islands. Lee (1959b) also invoked long-distance dispersal via the west-wind drift in euryhaline species such as *Microscolex*. Lee (1959b) hypothesized that the New Zealand Megascolecinae are closely related to species from Australia and Indo-Malaya. He thought that the more northern distribution of the New Zealand Megascolecinae is consistent with a northern origin and some sort of land bridge to the west of New Zealand in the Tertiary. The southern migration of the Megascolecinae was halted by the poor soils of the central North Island. Lee (1959b) thought that the wider distribution of the Acanthodrilinae is consistent with an earlier arrival in New Zealand from the south during the Cretaceous.

In a review of acanthodriles from Tasmania, Jamieson (1974) noted the affinities between the faunas of mainland Australia, Tasmania, New Zealand and New Caledonia. Omodeo (2000) hypothesized that the history of the Acanthodrilinae (excluding