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A time-calibrated phylogeny of southern hemisphere stoneflies: Testing for Gondwanan origins ☆

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ABSTRACT

For more than two centuries biogeographers have attempted to explain why terrestrial or freshwater lineages have geographic distributions broken by oceans, with these disjunct distributions either attributed to vicariance associated with Gondwanan fragmentation or trans-oceanic dispersal. Stoneflies (order: Plecoptera) are a widespread order of freshwater insects whose poor dispersal ability and intolerance for salt water make them ideal candidates for Gondwanan relicts – taxa whose distribution can be explained by vicariant isolation driven by the breakup of Gondwana. Here we reconstruct the phylogenetic relationships among southern hemisphere stoneflies (5 families; 86 genera) using 2864 bp of mitochondrial (COI) and nuclear (18S, H3) DNA, with a calibrated relaxed molecular clock used to estimate the chronology of diversification. Our analysis suggests that largely antitropical stonefly sub-orders, Arctoperlaria (northern hemisphere) and Antarctoperlaria (southern hemisphere), were formed approximately 121 Ma (95% prior probability distribution 107–143 Ma), which may reflect the vicariant rifting of the supercontinent Pangaea. Subsequently, we infer that a single Arctoperlaria lineage has dispersed into southern hemisphere 76 Ma (95% range 65–98 Ma). The majority of divergences between South American and Australian stonefly lineages appear to coincide with the opening of Drake Passage around 40 Ma, suggesting vicariant isolation of these landmasses may be responsible for these biogeographic disjunctions. In contrast, divergences between New Zealand lineages and their sister taxa appear to postdate vicariant timeframes, implying more recent dispersal events.

1. Introduction

The widespread but disjunct distributions of many southern hemisphere taxa have fascinated biogeographers for more than two centuries (Treviranus, 1803; De Candolle, 1820; Hooker, 1853, 1860; Darwin, 1859). Prior to the current understanding of continental movement, these biogeographic links were explained in terms of trans-oceanic dispersal (Darwin, 1859), which remained the predominant explanation for over a century (Nelson, 1978). After the widespread acceptance of plate tectonic theory in the late 1960s, however, these southern hemisphere links were typically explained in terms of vicariance: isolation of previously connected ancestral lineages as a result of the sequential fragmentation of the Gondwanan landmass (Croizat, 1958; Brundin, 1966; Raven and Axelrod, 1972; Croizat et al., 1974; Rosen, 1978; Humphries, 2000; Nelson and Ladiges, 2001; Ebach et al., 2003). Subsequently, the biogeographic importance of trans-oceanic dispersal was largely dismissed, until a recent upsurge in molecular studies suggested that vicariance alone could not explain many southern hemisphere radiations (Cooper et al., 1992; Haddrath and Baker, 2001; McDowall, 2002; Briggs, 2003; Givnish and Renner, 2004; Sanmartin and Ronquist, 2004; Knapp et al., 2005; McGlone, 2005; Queiroz, 2005; Phillips et al., 2010; Krosch et al., 2011).

New Zealand (NZ) in particular provides a fascinating system for biogeographers given its isolation and particularly dynamic geological history, including major reduction of land area during the Oligocene (ca. 25–22 Ma) (Cooper, 1989; Cooper and Millener, 1993; Cooper and Cooper, 1995; Campbell and Hutching, 2007; Graham, 2008). The extent of NZ's submergence remains controversial (Wallis and Trewick, 2009): many geological studies have suggested that NZ was reduced to a few low-lying islands (Cooper, 1989; Cooper and Millener, 1993; Cooper and Cooper, 1995), although more recent analyses have suggested that NZ may have been submerged almost completely (Landis et al., 2008), with dramatic biological implications (Pole, 1994, 2001; Campbell and Landis, 2001; Waters and Craw, 2006; Campbell

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and Hutching, 2007; Trewick et al., 2007; Goldberg et al., 2008; Landis et al., 2008). Although there is evidence that some NZ lineages may have survived the Oligocene transgression (Knapp et al., 2007; Allwood et al., 2010), post-Oligocene arrival has been inferred for a large number of NZ lineages (Stöckler et al., 2002; Ericson and Johansson, 2003; Zhang and Renner, 2003; Donald et al., 2005; Knapp et al., 2005; Waters and Craw, 2006; Wallis and Trewick, 2009). Gibbs (2006) suggested that freshwater limited taxa, due to their intolerance for marine conditions, may provide the strongest evidence for a continuous presence of land in NZ.

Stoneflies (Plecoptera) are an ancient lineage of freshwater insects with fossils dating back to the early Permian (Sinitshenkova, 1987; Sinichenkova, 1997; Zwick, 2000). They are a widely distributed group, with almost 4000 species described worldwide (Fochetti and Figueroa, 2008). Plecoptera is divided into two geographically separated sub-orders: Antarctoperlaria in the southern hemisphere (Fig. 1), and Arctoperlaria in the northern hemisphere. These two sub-orders are believed to have been formed by breakup of the super-continent Pangaea at the end of the Triassic (Illies, 1965; Banarescu, 1990; Zwick, 1990, 2000). The subsequent breakup of Gondwana has been invoked to explain the southern hemisphere distribution of the four Antarctoperlaria families throughout Australia, NZ, southern South America, and several subantarctic islands (Fig. 2) (Illies, 1965; Zwick, 2000; Fochetti and Figueroa, 2008), with their absence in southern Africa ascribed to climatic change (Banarescu, 1990; Zwick, 2003). The level of endemicity of stoneflies in the southern hemisphere is high, with only one genus shared between distinct land masses (*Notonemoura*, NZ and Australia) (McLellan, 2000a, 2006). This high endemicity is perhaps unsurprising given that stoneflies are generally considered to be very poor dispersers due to their limited flight ability (Brundin, 1967, 1972; Zwick, 2000; Schultheis et al., 2002; Fochetti and Figueroa, 2008; McCulloch et al., 2009).

In addition to Antarctoperlaria, two families (Perlidae and Notonemouridae) of the otherwise northern hemisphere Arctoperlaria are found in southern temperate regions (Fig. 2). These southern hemisphere Arctoperlaria representatives are thought to reflect recent independent invasions from the north (Illies, 1965; Stark and Gaufin, 1976; Zwick, 2000; Fochetti and Figueroa, 2008). Perlidae is the only stonefly family found in both hemispheres, with genera in central South America, southern Africa, and throughout the northern hemisphere (Fochetti and Figueroa, 2008). Unlike Perlidae, the family Notonemouridae is restricted to the southern hemisphere, and has a classical 'Gondwanan' distribution, resembling that of the Antarctoperlaria families. It has been suggested that Antarctica may have been an important dispersal route among the southern continents for this family (Illies, 1965; Zwick, 1981, 1990). The monophyly of Notonemouridae is, however, in question, with suggestions that it may be a polyphyletic assemblage, representing multiple southern invasions of northern lineages (Zwick, 1981, 1990, 2000; McLellan, 2000a; Fochetti and Figueroa, 2008).

In this paper we use DNA sequences (mitochondrial COI, nuclear 18S and H3) to reconstruct phylogenetic relationships among southern hemisphere stoneflies, and use a relaxed molecular clock to estimate the chronology of diversification. Evolutionary timescales are constrained using a variety of internal calibration

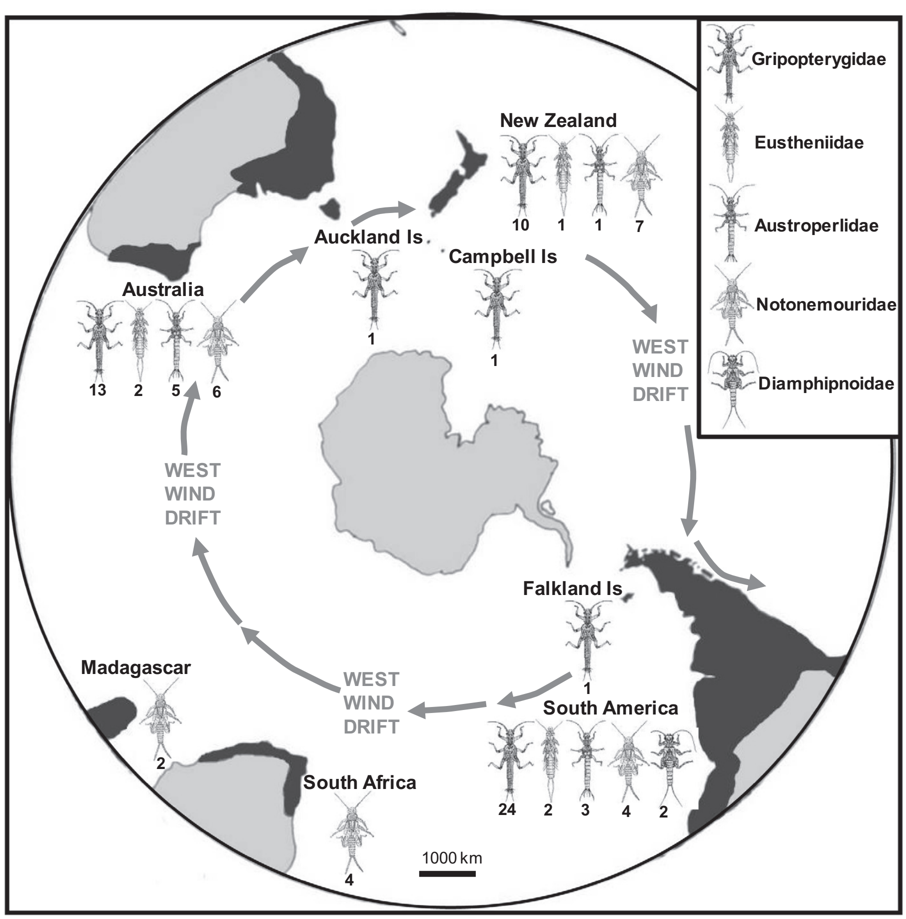

Fig. 1. Contemporary distribution of Plecoptera (black shading) in the southern hemisphere, with the number of genera in each family found in each region inset.