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Perspective

Biogeographic barriers in north-western Australia: an overview and standardisation of nomenclature

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Within Australia, the biodiverse monsoon tropics are of considerable biogeographical interest. However, this vast and relatively undisturbed area with its high endemicity has only recently become the focus of phylogeographic research (Bowman *et al*. 2010; Fujita *et al*. 2010; Melville *et al*. 2011; Toon *et al*. 2010). A major challenge to understand the biogeographical processes that have shaped the distribution and diversity of taxa in this region is the lack of detailed fossil and palaeoecological data (Bowman *et al*. 2010). Although molecular data are able to contribute to our understanding of the biogeographic history of the region (e.g. Lee and Edwards 2008; Toon *et al*. 2010), relatively few studies have focussed on the geologically old and topographically complex north-west region of Australia (Jennings and Edwards 2005; Fujita *et al*. 2010; Melville *et al*. 2011). It is becoming increasingly clear that the biogeographic patterns of this region and the accompanying terminology are complex (Potter *et al*. 2012). Here we seek to provide an historical overview of the biogeographic nomenclature used for this region in order to bring greater clarity and concordance. We also propose a standard nomenclature that could be used in future biogeographic/phylogeographic studies of north-western Australia.

The tropical monsoon region of north-western Australia represents a unique biome comprising a range of habitats. Proterozoic sandstone dominates the landscape and forms ranges and dissected escarpments set within widespread savannah woodlands. Smaller areas of monsoon rainforest, gallery forest and seasonally wet grasslands also occur. The monsoonal climate is characterised by dry winters and wet summers, which drives the vegetation type and associated distribution of taxa (Bowman *et al*. 2010). Tropical habitats contracted north during aridification in the Miocene and late Pliocene and the monsoonal conditions commenced following the rise of the Tibetan Plateau (3.4–7.2 million years ago) and the closing of the Isthmus of Panama (see Bowman *et al*. 2010; Fujita *et al*. 2010). However, it was not until the Pleistocene that the monsoonal tropics experienced fluctuating environmental changes associated with global glacial cycles that developed the more contemporary arid-adapted vegetation (reviewed in Bowman *et al*. 2010; Fujita *et al*. 2010). The less topographically complex lowlands between the disjunct sandstone outcrops have been identified as potential biogeographic barriers for a wide variety of fauna (e.g. Bowman *et al*. 2010).

Keast (1961) regarded north-west Australia (including both the Kimberley region and Top End of the Northern Territory, Fig. 1) as a single major mesic refuge area (North-West refuge) for Australian fauna. Earlier, Keast (1958) noted that the region of the Joseph Bonaparte Gulf formed a distributional barrier for some mangrove-dependent birds, due to a lack of habitat.

After an examination of the North-West refuge bird fauna, Ford (1978) identified the presence of three 'minor biogeographic barriers' in the region between the Kimberley and northern Northern Territory (i.e. the Top End). These were identified as 'arid country round the Joseph Bonaparte Gulf and the Victoria River valley, a discontinuity in sandstone ranges in the region of the Daly River drainage and a stretch of coastline poor in mangroves on western side of the Joseph Bonaparte Gulf'. More specifically, the lowlands of the Daly River drainage were identified as a significant barrier for many sandstone-range-adapted taxa (Ford 1978). The arid country around the head of the Joseph Bonaparte Gulf (in the region of the Ord and Victoria Rivers) was considered a significant barrier for monsoon and gallery forest species, as well as for moist grassland taxa, while the break in mangrove habitat in the western Joseph Bonaparte Gulf had significantly influenced mangrove specialists (Ford 1978). This later gap in the distribution of mangroves was subsequently examined in greater detail by Ford (1982), who identified it as a significant biogeographical barrier for mangrove birds, which he termed the 'Bonaparte Gap'. Subsequently, 'Bonaparte Gap' has entered the literature as a more general term

for the break in distribution between many Kimberley and Top End taxa (e.g. Ford 1987; Braby 2008; Toon *et al*. 2010).

The other two biogeographic barriers identified, but not named, by Ford (1978) have also subsequently become more widely adopted: the strip of arid country at the head of the Joseph Bonaparte Gulf became known as the 'Ord Arid Intrusion' (e.g. Woinarski 1992; Ford and Blair 2005; Bowman *et al*. 2010; Melville *et al*. 2011), and the lowlands of the Daly River region as the 'Victoria River Drainage Barrier' (Schodde and Mason 1999; Joseph and Omland 2009). Along with the previously mentioned 'Bonaparte Gap', these two terms have tended to lose their original narrow meaning (i.e. Ford 1978) in recent usage, with each being used largely interchangeably to refer more generally to a single biogeographic barrier separating many Kimberley and Top End taxa. In addition, Cracraft (1986, 1991) (referencing Ford 1978) defined this barrier as the lowlands of the Victoria and Daly Rivers, while Jennings and Edwards (2005) used the term 'Kimberley Plateau–Arnhem Land Barrier' to describe the barrier comprising the Ord, Victoria and Daly River valleys, again referencing Ford (1978). The variety of terms and definitions currently in use has resulted in a rather confused literature.

A recent phylogeographic study (Potter *et al*. 2012) of the *brachyotis* species group of rock-wallabies (*Petrogale*), endemic to north-west Australia, has provided the first molecular evidence that this region consists of a series of biogeographic barriers spread over ~500 km. Since several of the barriers identified in this study are coincident with previously named biogeographic barriers, there is now a need for the standardisation of definitions and greater consistency in usage, so that both broad and narrow definitions can be unambiguously communicated and tested in future studies.

We propose that the term 'Kimberley Plateau–Arnhem Land Barrier' be applied to the whole region and its broad biogeographic impact. Each of the more localised and specific barriers should then be defined as follows:

- 'Bonaparte Gap': the break in mangrove habitat on the western side of the Joseph Bonaparte Gap (Fig. 1),
- 'Ord Arid Intrusion': arid country and lowlands surrounding the Ord River basin (Fig. 1),
- 'Victoria River Drainage' Barrier: low arid country and break in sandstone structure surrounding the Victoria River valley (Fig. 1),
- 'Daly River Drainage' Barrier: lowlands and major discontinuity in sandstone ranges surrounding the Daly River drainage (Fig. 1).

Potter *et al*. (2012) have also detected the molecular signal of an additional potentially novel barrier in the central Kimberley, which they term the 'East–West Kimberley Divide' (Fig. 1). Currently, the precise location and nature of this barrier is unclear. It is also uncertain whether a similar phylogeographic break occurs in other Kimberley taxa. As suggested by Potter *et al*. (2012), this putative barrier may be related to the presence of a band of basalt country that runs from north to south through the central Kimberley, or it could represent a boundary between populations that expanded from past mesic refugia within the Kimberley. Intriguingly, the biogeographically significant break

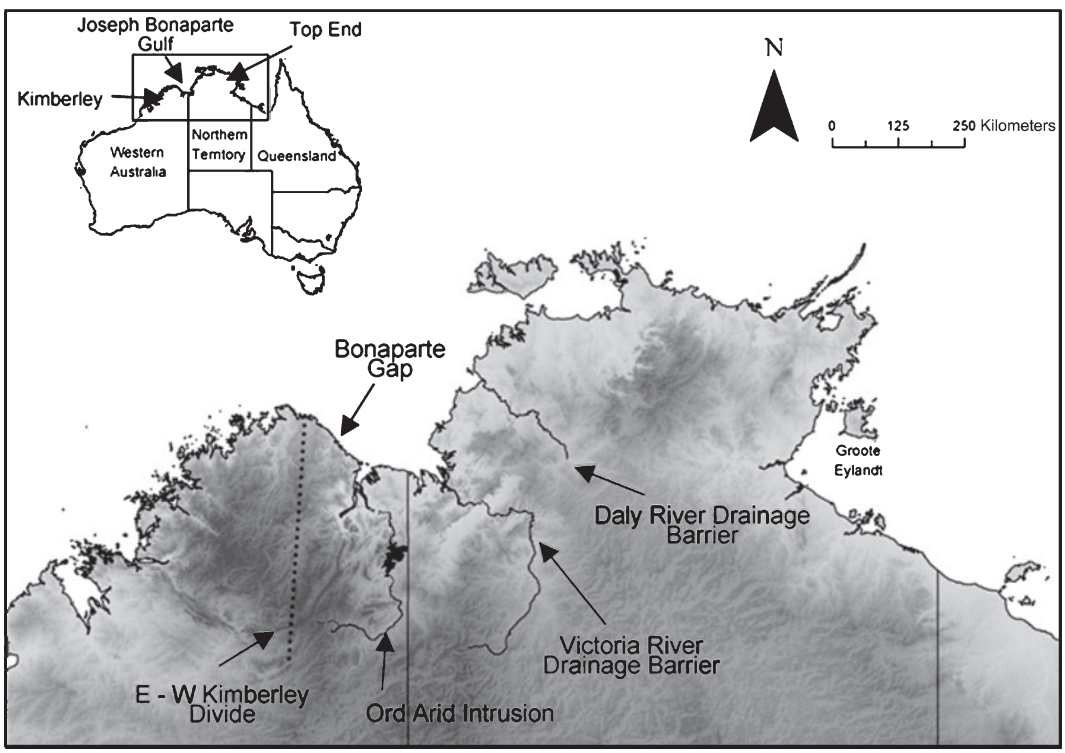

Fig. 1. North-west Australia, showing the location of the identified biogeographic barriers. Increasing elevation is indicated by darker shading (up to ~1000 m).

in coastal mangrove habitat (i.e. the Bonaparte Gap) also occurs in this general area, as does the boundary between two major freshwater fish biogeographic Provinces (Unmack 2001), further hinting that some significant landscape feature or combination of geoclimatic attributes has significantly impacted gene flow in a variety of taxa in this region.

Additional phylogeographic studies of a variety of codistributed taxa are now urgently needed in order to better understand and characterise the East–West Kimberley Divide and the other barriers identified within north-west Australia. It will be important that both habitat specialist and generalist species are examined, since the impact of the identified barriers is likely to vary considerably in intensity through both time and space, depending on species biology and the habitat occupied. Potter *et al*. (2012) found different levels of divergence across different barriers, indicating that vicariance was not a one-off event, but likely to be a recurrent process. These additional studies will enable a much clearer picture of the evolutionary history of this region to emerge and enable the impact of landscape features and climatic changes in shaping the distribution of biodiversity to be assessed.

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