

Endogenous and Exogenous Koala Retrovirus Patterns in Wild Koalas across Australia

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ABSTRACT. Our understanding of koala retrovirus (KoRV) has advanced dramatically in recent years. Cross-sectional studies examining hundreds of wild koalas (*Phascolarctos cinereus*) from populations across their natural Australian range (Queensland–New South Wales–Victoria) have shed new light on KoRV abundance and diversity in the wild. A single strain of KoRV (the originally characterized Hanger strain from 2000) appears to be the dominant KoRV strain within koalas, endogenous in northern populations and the predominant exogenous strain in southern populations. Alongside this strain are potentially exogenous variants representing both intact and defective versions of some of the many recognized KoRV subtypes (KoRV-A to KoRV-M). The patterns of these may suggest a transition from endogenous KoRV in the north to exogenous KoRV in the south, occurring in southern New South Wales. They also highlight how actively the hypervariable region of the envelope gene of KoRV is diversifying, with fragmented koala populations across the country containing unique and distinctive KoRV proviral profiles. As more koala populations are examined with increasingly sensitive and specific genetic tools, our understanding of KoRV is poised to continue to evolve as quickly as the virus itself.

Introduction

Koala retrovirus (KoRV) is known to exist both endogenously and potentially exogenously in koalas (*Phascolarctos cinereus*) (Hanger *et al.*, 2000; Quigley & Timms, 2020). At some point in the last 49,900 years, KoRV began endogenizing or permanently incorporating its provirus into koala germline genomes in the northern Australian koala population (Tarlinton *et al.*, 2006; Ishida *et al.*, 2015). In parallel, within almost all koala populations across Australia, potentially exogenous strains of KoRV have continued to diversify into 13 recognized subtypes (KoRV-A to -M, based on differences in the receptor binding domain region of the envelope gene (Shojima *et al.*, 2013; Xu *et al.*, 2013; Xu *et al.*, 2015; Chappell *et al.*, 2017; Blyton *et al.*, 2021). Targeted studies of both endogenous and exogenous KoRV strains in recent years have led to impressive advances in our understanding of this virus across the natural koala range in Australia (Table 1).

Endogenous KoRV-A

KoRV-A is the original and most prevalent subtype of KoRV detected across Australia (Hanger *et al.*, 2000; Chappell *et al.*, 2017; Quigley & Timms, 2020). Genetic analysis identified KoRV-A provirus to be present in northern Australian koalas in a pattern consistent with it being endogenously incorporated into their genomes (Tarlinton *et al.*, 2006). Additional studies have supported this endogenous status with quantified KoRV provirus within Queensland and northern New South Wales koala cells at levels at or above one copy per cell, with the majority of provirus being KoRV-A (Simmons *et al.*, 2012; Hobbs *et al.*, 2017; Sarker *et al.*, 2020; Quigley, Wedrowicz, *et al.*, 2021).

Recent examination of KoRV proviral strains across Australia has revealed that every KoRV positive koala examined, from anywhere in Australia, contained a single dominant KoRV proviral sequence, identical to the originally published Hanger *et al.* (2000) KoRV sequence (accession

Keywords: koala retrovirus, KoRV

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Submitted: 9 January 2022 **Accepted:** 5 May 2023 **Published:** 21 June 2023 (online only)

Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

Citation: Quigley, Bonnie L., and Peter Timms. 2023. Endogenous and exogenous koala retrovirus patterns in wild koalas across Australia. In *Proceedings of the Second Koala Retrovirus Workshop*, ed. D. E. Alquezar-Planas, D. P. Higgins, C. L. Singleton, and A. D. Greenwood. *Technical Reports of the Australian Museum Online* 38: 7–9. <https://doi.org/10.3853/j.1835-4211.38.2023.1832>

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