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Evolutionary diversification of alpine ginger reflects the early uplift of the Himalayan–Tibetan Plateau and rapid extrusion of Indochina

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ABSTRACT

The evolutionary diversifications of many taxonomic groups, especially those with limited dispersal ability, are often driven by key geological events, such as tectonic drift, continental collisions, and uplifts of mountains. Here, we use full range geographic sampling to create a dated molecular phylogeny for two genera of alpine gingers (*Cautleya* and *Roscoea*) in the Pan-Himalaya, and test the correlations between evolutionary diversification of this group and major geological events in the studied region. Our results revealed that the origination of their common ancestor and evolutionary split between the two genera occurred during the middle Eocene and the late Eocene to the early Oligocene, corresponding well to the proposed two early uplifts of the Himalayan–Tibetan Plateau. *Roscoea* species, the highest elevation gingers known, were then divided into distinct Himalayan and Indochinese clades, simultaneous with the rapid extrusion of Indochina and accompanied by the third Himalayan uplift around the Oligocene/Miocene boundary. This study highlights the importance of evolutionary diversification of plants as an independent line of evidence to reflect tectonic events in the Himalayan–Indochinese region.

1. Introduction

The collision of India with Eurasia, beginning in the early Cenozoic time is the most important geological event in Asia (Yin and Harrison, 2000; Jain, 2014). This long-lasting and still ongoing tectonic process has triggered obvious geological events in the Pan-Himalaya, including the early uplifts of the Himalayan–Tibetan Plateau during the middle Eocene (~40–50 Ma), the Oligocene (~30–40 Ma) (Harrison et al., 1992; Raymo and Ruddiman, 1992; Chung et al., 1998; Tapponnier et al., 2001; Replumaz and Tapponnier, 2003; Aikman et al., 2008), and the Oligocene/Miocene boundary (~22–25 Ma) (Tapponnier et al., 1990; Leloup et al., 2001; Guo et al., 2002; Cao et al., 2011; Liu et al., 2012a) possibly with the further extrusion of Indochina (Yang and Liu, 2009; Che et al., 2010) and the later uplifts from the Miocene to the Pliocene (~15 Ma, ~9–7 Ma and ~5–3 Ma) (Harrison et al., 1992; Shi et al., 1998; An et al., 2001; Spicer et al., 2003). The later large-scale uplifts were believed to have driven evolutionary diversifications of numerous plant and animal groups on/around the Himalayan–Tibetan Plateau (e.g., Rüber et al., 2004; Liu et al., 2006; Zhang et al., 2006; Wang et al., 2009; see also Favre et al., 2014; Liu et al., 2014). However, up to now, no evidence indicated that the early uplifts and rapid extrusion had driven the continuous diversification of a single plant group (but see Che et al., 2010 for animals), which in turn reflects the successive occurrence of these geological events.

The Ginger Family (Zingiberaceae), a Gondwanan monocot lineage, originated around 105 Ma in the middle Cretaceous, and experienced a major radiation in the late Cretaceous (Kress and Specht, 2005). More than 95% of the species in this family are confined to the lowland tropics (Kress et al., 2002), but two genera (Fig. 1), *Cautleya* (~2 species) and *Roscoea* (~21 species), are found at high elevations in the Pan-Himalaya (Cowley, 2007; Auvray and Newman, 2010). Their sister lineage, the genus *Hedychium* (Kress et al., 2002), is distributed at lower elevations in tropical and subtropical Asia, including the Himalayas (HIM) and the Northern Indochina (NIC). Distribution pattern among these three genera was proposed to be caused by the Himalayan–Tibetan orogeny (Wu, 1994).

The two high-elevation genera are of different species richness and geographic distribution. *Cautleya*, comprising only two species, is continuously distributed across HIM and NIC (Auvray and Newman, 2010); whereas the species-rich *Roscoea* forms two disjunct groups in HIM and NIC, respectively, and they were separated by a ~500-kilometer gap (Fig. 1) (Ngamriabsakul et al., 2000;

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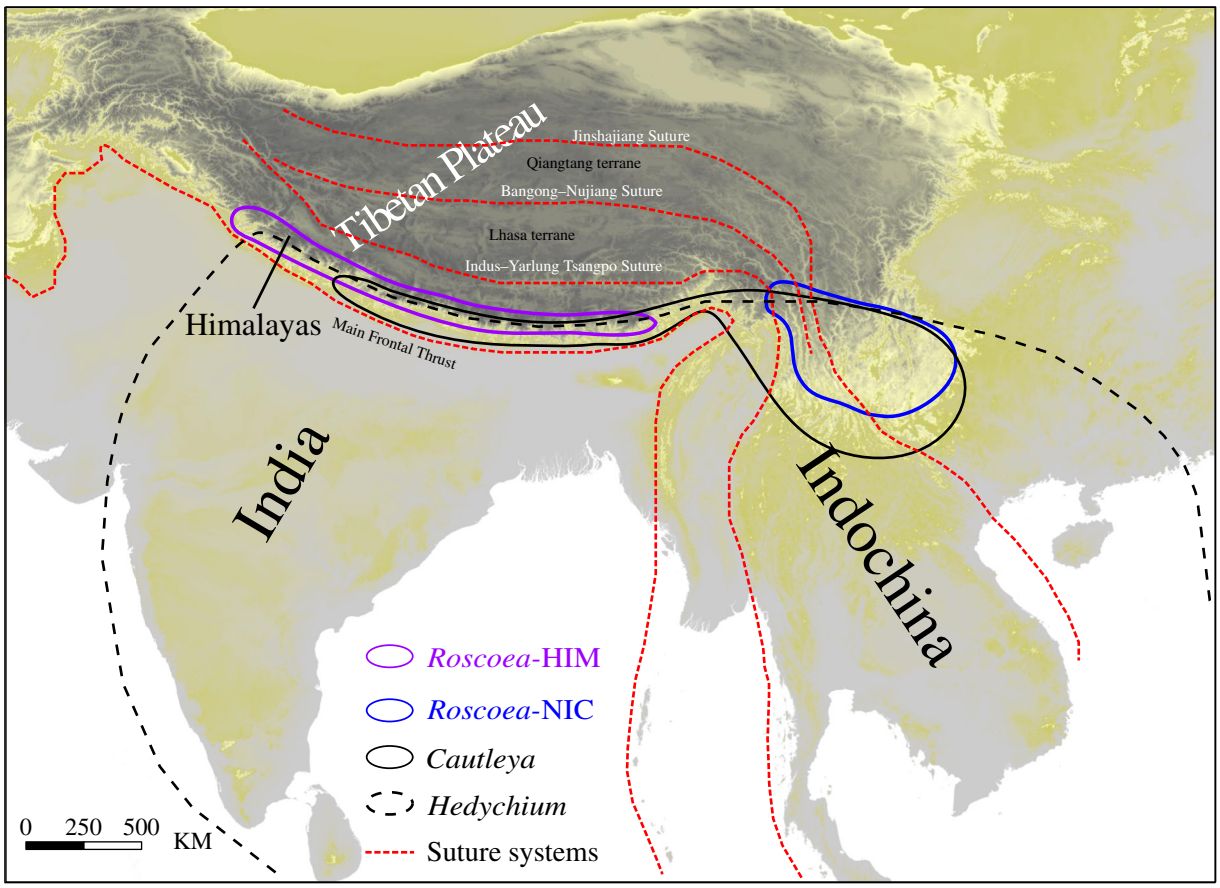

Fig. 1. Ranges of alpine gingers (*Cautleya* and *Roscoea*) and related genus *Hedychium*. Species of *Cautleya* (black solid) are continuously distributed from the Himalayas (HIM) to the Northern Indochina (NIC), but two species groups of *Roscoea* are disjunct in distribution between HIM (purple solid) and NIC (blue border) by a ~500-kilometer gap. Range of *Hedychium* (black dash) covers Asian subtropics and tropics. Ranges are depicted according to field investigation and references (Wu, 1994; Cowley, 2007; Auvray and Newman, 2010). Sutures systems (red dash) referred to tectonic studies (Yin and Harrison, 2000; Tapponnier et al., 2001; Replumaz and Tapponnier, 2003; Yin, 2010; Chatterjee et al., 2013; Zheng et al., 2013).

Cowley, 2007). These distributional differences between the genera are due, in part, to their distinctive biologies. The species of *Cautleya* (Fig. 2) are terrestrial/epiphytic, insect-pollinated perennials that produce a brightly-colored red capsule with black seeds dispersed by birds (observed in field), and they do not form rhizomatous tubers. In contrast, species of *Roscoea* (Fig. 2) are completely terrestrial, mostly self-pollinated (Zhang and Li, 2008; Fan and Li, 2012) and possess ant-dispersed seeds, and rhizomatous tubers, which facilitated their frequently vegetative reproduction (Cowley, 2007). These characteristics suggest that long-distance seed dispersal by birds in *Cautleya* is common while seed dispersal capacity is limited in *Roscoea*. The latter genus was likely split into subdivisions by a sudden plate movement due to its poor dispersal ability. Thus, we propose that the contrasting distribution patterns in *Cautleya* and

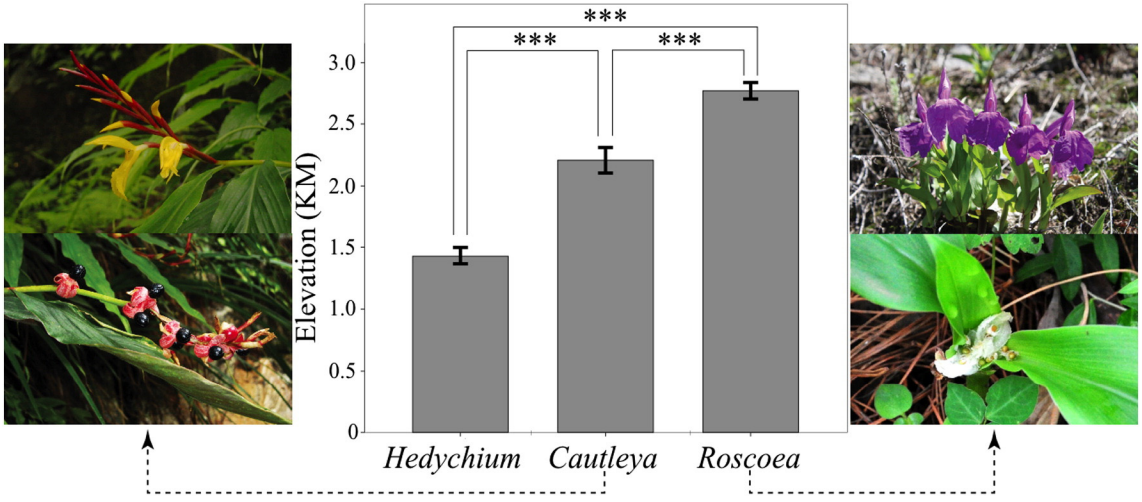

Fig. 2. Elevation differentiation among *Hedychium*, *Cautleya* and *Roscoea*. N is sample size. "***" indicates significant differences between genera ($P < 0.001$). Dashed-line arrows point to the flowers and fruits/seeds of *Cautleya* and *Roscoea*. Sampling sizes for elevation analysis are *Hedychium*: N = 493, *Cautleya*: N = 105 and *Roscoea*: N = 335. Elevation statistics are in Table S1.

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