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ORIGINAL ARTICLE

The diversification of thecae horns and their putative significance—a case study of Schismatoglottideae (Araceae)

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Abstract

Thecae horns are specialized anther extensions present in two tribes of Araceae: Cryptocoryneae and Schismatoglottideae. This structure is important in defining the generic boundaries and segregations within Schismatoglottideae. Eleven convergent lineages of thecae horns have evolved within Schismatoglottideae, contributing to the diverse stamen structures and thecae orientations. Here, we investigated the stamens of 22 taxa belonging to eight genera (*Aridarum*, *Burttianthus*, *Hera*, *Heteroaridarum*, *Pursegloveia*, *Naiadia*, *Tawaia*, and *Toga*) of Schismatoglottideae. We assessed the floral biology by focusing on the angle and movement of the thecae horns during the pistillate and staminate phases of anthesis. The angle of the thecae horns changed at the start of anthesis and, in several species, elevated further during staminate anthesis. Papillae cells, smooth or verrugated surface, are present on the thecae horns with the excavated connective often found to be smooth vs. non excavated connective, with verrugated surface. The presence of calcium oxalate packages decreases from pistillate phase to staminate phase of anthesis and is postulated to be a defense mechanism against predators.

Keywords Borneo · Calcium oxalate crystals · Flowering mechanism · Rheophytes · Stamen

Introduction

The flower is the main reproductive structure in angiosperms and is composed of diverse parts such as sepals, petals, stamens, carpels, perianths, staminodes (Ronse De Craene et al., 2003). Transitional changes in traits of various components of flowers facilitate interactions between plant host and pollinators (Paudel et al., 2016). For instance, various colours of sepals and scents released offer visual and olfactory signals to attract pollinators (Dobson, 2006; Valenta et al., 2017; Wright & Schiestl, 2009). Further, the diverse reproductive traits have effectively complemented pollinator-mediated selection for successful co-evolutionary processes. The pistil and stamen mediate selection of pollinator types as evidenced by numerous studies (Alexandersson & Johnson, 2002; De Jager & Peakall, 2019; Nattero et al., 2010; Solís-Montero & Vallejo-Marín, 2017).

Fitness between reproductive traits and pollinators can be determined through the pistillate (when stigma is receptive) and staminate (when stamen matures and is ready for pollen dispersal) phases of anthesis. These phases usually occurred over a different time span, to avoid autogamy, and thus narrow the probability of intra-population genetic flow (Darwin, 1876). During the staminate anthesis, pollen grains are deposited onto pollinators to be carried to the next receptive stigma. To ensure a maximum lodge of pollen carriage by the pollinator, floral traits of host plants evolve to match the traits of pollinators. Convergent evolution is observable from the interacting traits with the pollinators; for example, a study of reciprocal coevolution between the corolla tube length of *Roscoea purpurea* and proboscis length of *Philoliche longirostris* showed a strong linear selection imposed by the pollinators on the corolla tube length and vice versa (Paudel et al., 2016).

In Araceae, thecae horns are the specialized anther extensions belonging to the tribes Cryptocoryneae and

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