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Fossil legume woods of the *Prioria*-clade (subfamily Detarioideae) from the lower Miocene (early to mid-Burdigalian) part of the Cucaracha Formation of Panama (Central America) and their systematic and palaeoecological implications

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ABSTRACT

Three fossil wood specimens are described from the Miocene (early to mid-Burdigalian) part of the Cucaracha Formation of Panama, Central America. The calcareously-permineralised fossils, which contain *Teredolites* borings, occur in erosive-based pebbly conglomerate lenses, interpreted as tidally-influenced fluvial channel deposits. Detailed investigation of fossil wood anatomy reveals features characteristic of the *Prioria*-clade, a supergenus of the legume subfamily, Detarioideae. Based on quantitative comparison with extant material in the micromorphology slide collection at the Royal Botanic Gardens, Kew, the fossil material is referred to two new species, *Prioria hodgesii* sp. nov. and *Prioria canalensis* sp. nov. Facies data imply that these new taxa may have occupied a similar ecological niche to the extant *Prioria copaifera*, a saline-tolerant tropical genus that forms wetland gallery forests along tidal estuaries in Panama today. Findings contribute to the understanding of the palaeoecology of this early-diverging subfamily within the basal Leguminosae. They, also, further extend knowledge of the coastal forests along the leading edge of North America during its Miocene convergence with South America.

1. Introduction

Leguminosae (colloquially referred to as legumes; also validly known as Fabaceae) is the third most speciose family of flowering plants after the orchids (Orchidaceae) and daisies (Asteraceae/Compositae) with ~765 genera and ~19,328 species (Sprent, 2001; Lewis et al., 2005; LPWG, 2017). Molecular evidence points to an early Paleogene (~60 Ma) (Sprent, 2007) origin, with the oldest well-accepted fossils of Eocene age (~52 Ma; Herendeen et al., 1992); the family now constitutes a major ecological component of the Earth's vegetation, including many taxa of economic importance (LPWG, 2017).

Based on comprehensive analyses of plastid *matK* gene sequences, a new phylogeny has revealed six subfamilies in two clades (LPWG, 2017): a basal clade comprises Cercidoideae (12 genera) and Detarioideae (84 genera) and a more derived and diverse clade comprises Duparquetioideae (1 genus), Dialioideae (17 genera), Caesalpinioideae (148 genera) and Papilionoideae (503 genera). This interpretation differs from the traditional view of a basal paraphyletic caesalpinioid-grade from which arise the derived 'Mimosoideae' and 'Papilionoideae' clades (Lewis et al., 2005).

In this paper, we describe new fossil woods from lower Miocene strata of Panama, Central America that may be confidently referred to the Leguminosae. While some legume genera show very distinctive wood anatomy (e.g., *Robinia* and *Dalbergia* in the Papilionoideae; Wheeler and Baas, 1992), others show a very generalised structure with many intergrading features (e.g., *Lonchocarpus* and *Millettia*, also in the Papilionoideae; Baretta-Kuipers, 1981; Gasson et al., 2004). As a result, the attribution of isolated fossil wood types to the Leguminosae family can be very challenging indeed (Wheeler and Manchester, 2002). Nonetheless, the following constellation of features seen in our material is generally characteristic of legumes: simple perforation plates, alternate intervessel pitting, vessel–ray pits similar to intervessel pits in size and shape, fibres with simple

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pits, vestured pits present (with some exceptions) and paratracheal axial parenchyma with mostly 2–4 cells per strand (Baretta-Kuipers, 1981; Herendeen, 2000; Gasson et al., 2003).

The fossils reported here are of especial interest, however, because not only do they bear close comparison with legumes in general, but also they may be confidently referred to the early-diverging Detarioideae clade, which is sister to almost all other Leguminosae (LPWG, 2017) and mostly comprises large pan-tropical rainforest trees, distributed through Africa, Asia and South America (Herendeen et al., 2003). This group underwent initial diversification in Eocene times (De Franceschi and De Ploëg, 2003), with a secondary diversification event commencing in early Miocene times (De la Estrella et al., 2017). The earliest fossil records of the Detarioideae are probably *Sindora*-like pollen grains from the Eocene of North America (Muller, 1981, 1984); however, the oldest known fossils in Central America occur near the Oligocene–Miocene boundary (Hueber and Langenheim, 1986; Poinar and Poinar, 1999; Poinar and Chambers, 2015). The Detarioideae subfamily is particularly important because it is the subject of intense anatomical and molecular investigation, for the information it might provide about the evolution and systematics of the Leguminosae family (Redden et al., 2010; LPWG, 2017). Our new fossils therefore contribute to the understanding of the evolution of the subfamily, and findings also add to the wealth of new systematic and biogeographical knowledge about the Miocene forests of Central America, prior to the formation and uplift of the Isthmus of Panama.

2. Geological context

The fossil wood specimens, reported here, were collected from Hodges Hill on the Gaillard Cut of the Panama Canal (Fig. 1), c. 25 km west of Panama City (Latitude 09°02′51.75″N; Longitude 79°39′14.02″ W). Fossil woods are abundant at this important fossil locality, and comprise calcareously-permineralised trunks, 0.31–3.0 m long and typically 0.25–0.80 m in diameter, commonly with *Teredolites* borings. The allochthonous assemblage is preserved within a pebbly sandstone bed, interpreted as the deposits of a tidally-influenced fluvial channel (Rodríguez-Reyes et al., 2014). The bed containing the fossil wood assemblage is positioned ~20 m above the base of the Cucaracha Formation, that has been dated as early Miocene (early to mid-Burdigalian) age (MacFadden et al., 2014). A welded silicic tuff (known as the "Cucaracha Tuff"), positioned stratigraphically ~50 m above the fossil wood layer, has a U–Pb age of 18.81 ± 0.30 Ma and Ar/Ar age of 18.96

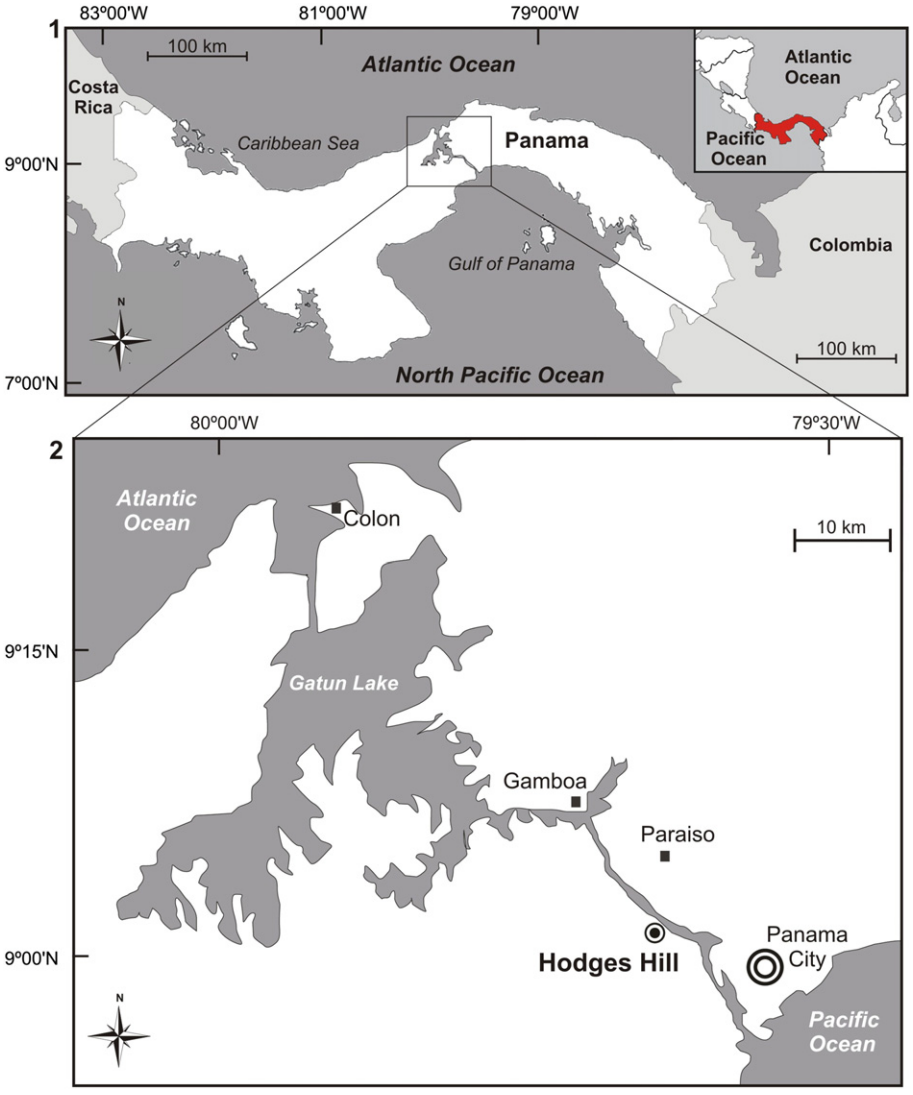

Fig. 1. Location details for the fossil site. 1., Panama in Central America. 2., The Panama Canal Zone showing the location of the Hodges Hill locality. Taken from Rodríguez-Reyes et al. (2014).