

# ENDOBEUTHOS PALEOSUM IN 99-MILLION-YEAR-OLD AMBER DOES NOT BELONG TO THE PROTEACEAE

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## ABSTRACT

Species in the family Proteaceae are almost invariably tetramerous with the stamen adnate to a tepal. Andromonoecious inflorescences bearing many male flowers composed of a single (spathuloid) stamen and a female flower with a pubescent stigma, as described in *Endobeauchos paleosum*, are unknown. We suggest that the specimen is a bisexual flower with scores of stamens surrounding a single stigma-style. Further, the specimen is too old to fit with current understanding of the migratory history of the Proteaceae.

## RESUMEN

Las especies de la familia Proteaceae son casi invariablemente tetrámeras con el estambre adosado a un tépalo. No se conocen inflorescencias andromonoicas con muchas flores masculinas compuestas de un solo estambre (espatuloide) y una flor femenina con un estigma pubescente, como en *Endobeauchos paleosum*. Sugerimos que el espécimen es una flor bisexual con decenas de estambres que rodean un único estigma. Además, el espécimen es demasiado antiguo para encajar con los conocimientos actuales de la historia migratoria de las Proteaceae.

## INTRODUCTION

Chambers and Poinar (2023) have recently re-assigned their specimen of *Endobeauchos paleosum* in 99-million-year-old Burmese amber from the family Dilleniaceae to the Proteaceae. Here, we question this new assignment as not meeting the morphological requirements for inclusion in this family. We also relate the fossil age to current understanding of the migratory history of the Proteaceae.

## RESULTS AND DISCUSSION

Flowers (florets if in inflorescences) of the family Proteaceae possess a perianth composed of four tepals each with an adnate stamen (Fig. 1). Flowers in most species are bisexual. However two genera (*Xylomelum*, *Stirlingia* in SW Australia) are andromonoecious but do not have flowers in a head, and three genera are dioecious. The Madagascan *Dilobeia*, with two species, has a branching inflorescence rather than a bract-enclosed capitulum. Female flowers have a bulbous stigma sessile on the ovary while, in male flowers, the anthers face a short columnar, vestigial gynoeceum. *Dilobeia* separated from its sisters, *Cenarrhenes* (Tasmania) and *Beaupreopsis* (New Caledonia), < 60 million years ago (Ma), although the clade can be traced to 97 Ma (Lamont et al. 2024a).

The small South African genus, *Aulax*, possesses a complex inflorescence comprising bracts, bracteoles, reduced peduncles and unisexual florets in the axils (Rourke 1998). The parent clade can be traced to 95 Ma with current molecular methods (Lamont et al. 2024a). The large, dioecious, South African genus, *Leucadendron*, possesses cones with tightly imbricate, spiralling bracteoles each subtending a floret whose stamens or stigmas protrude from each bracteole (Rebello 2001). This genus can be traced to 37 Ma, although the basally bisexual, parent clade (subtribe Leucadendrineae) may have originated 96 Ma. Male flowers in these three genera retain a vestigial gynoeceum.

Typically in Proteaceae, pollen is released from the anthers onto the swollen apex of the pistil while the flower is still in bud (Lamont 1982). The pollen presenter is usually smooth but may sometimes possess eight

lines of short, rigid, horizontally aligned hairs to which the released pollen may adhere (*Petrophile*, Ladd and Bowen 2020). Some Grevilleoideae, such as *Gevuina* and *Kermadecia*, have dense hairs on the pollen presenter (not stigma) but they are unlike those shown in *Endobeauchos*. Among bisexual taxa, the true stigma emerges, or becomes exposed in a terminal or lateral slit, a day or so after anthesis (protandry) when the pollen has usually been removed by pollinators (Lamont 1982). A limited number of clades with bisexual flowers does not 'present' its pollen to pollinators. These include the subfamily Persoonioideae, with no history in Africa (Lamont et al. 2024b), and a few genera of the Proteoideae in Australia [Fig. 1, *Cenarrhenes* (Tasmania), *Franklandia*, *Conospermum*, *Stirlingia*, and *Synaphea* (southwestern Australia, Ladd & Bowen 2020)], *Symphionema* (NSW) and *Beaupreopsis* (New Caledonia).

The inflorescence of *Endobeauchos paleosum* illustrated in Chambers and Poinar (2023) is characterized by an involucre of bracts (florets absent in the axils) or bracteoles (if florets were present in the axils). These are compared favourably with the genus *Protea* whose bracts also increase in size apically and are arranged spirally. However, the uppermost bracts in *Protea* become petaloid and embrace the open florets to produce a pseudanthium that is not the case here. (In passing, we note that the illustrated species is *P. subvestita*, not *P. mundii*, Tony Rebelo, pers. comm.). This is not necessarily a problem as *Protea* is one of the few proteaceous genera whose bracts function as the visually attractive part of the inflorescence (section *Dryandra* in *Banksia*, and *Telopea*, are other examples). As with *Endobeauchos*, the bracts/bracteoles remain scale-like in most Proteaceae with extrafloral involucres. However, the styles with their pollen presenters in the *Protea* illustrated are also misinterpreted as tepals with "long apical bristles" with neither interpretation consistent with *Endobeauchos*.

Figure 4 in Chambers and Poinar (2023) purports to show longitudinal, (sub)sessile anthers attached to subapical concavities in the tepals. This would certainly be consistent with proteaceous flowers (Fig. 1). But we do not share this interpretation. There is no spatial distinction between tissues that would indicate an anther attached to a tepal (Fig. 2A). The apex is slightly swollen and involute but individual anthers may show a similar feature in other taxa (e.g., Fig. 2B). The anther is spatuloid (like the spathe of Araceae) and merges imperceptibly with the filament. There is no indication of any arrangement of floral parts in fours that is near universal in Proteaceae.

Further, we detect only one stigma—the bulbous apex covered in soft, radiating (receptive?) hairs. The other two structures previously arrowed as stigmas have a minutely rounded apex that expands immediately underneath, in contrast to the other structure—these are simply anthers (Fig. 2B). The anthers surround the pistil, essentially opening in its direction (introrse). No other floral or extrafloral structures are apparent within the confines of the androecium. We conclude that this is a single bisexual flower with scores of stamens and a single style and stigma, along the lines of many flowers, as say, in the Myrtaceae (Fig. 2C). This arrangement implies an epigynous flower with its receptacle covered by an involucre of bracteoles (phyllomes) that appears unique for an individual flower. There are no ribs on the style to indicate if there are multiple carpels (syncarpous).

The single pollen grain shown is tricolpate, which implies it is a Eudicot, with a smooth, or possibly finely reticulate, exine, spheroidal shape and diameter ~30  $\mu\text{m}$ . In contrast, the oldest palynomorphs with Proteaceae affinities are strongly triangular and triporate with variable surfaces (Lamont et al. 2024a, b). Proteaceae grains are rarely 'bloated' like this grain; an important exception is *Franklandia* that can be traced to 100 Ma in Antarctica and Australia (He et al. 2016) but its diameter is much greater (80  $\mu\text{m}$ ). It is beyond our competence to suggest an alternative clade, but the important point, from a biogeographic point of view, is our conclusion that *Endobeauchos paleosum* is not a member of the Proteaceae.

Were this 99 My old fossil to belong to the Proteaceae, it would require a re-appraisal of recent conclusions about the family's evolutionary history. The approach involved construction of a DNA-based chronogram accompanied by collation of location and age of ~500 Proteaceae-related palynomorphs for Africa, South America, Antarctica and Australia (Lamont et al. 2024a, b). This showed an origin for the family in NW Africa 132 Ma followed by migration of descendants east and west. The east then south, then southwest pathway led

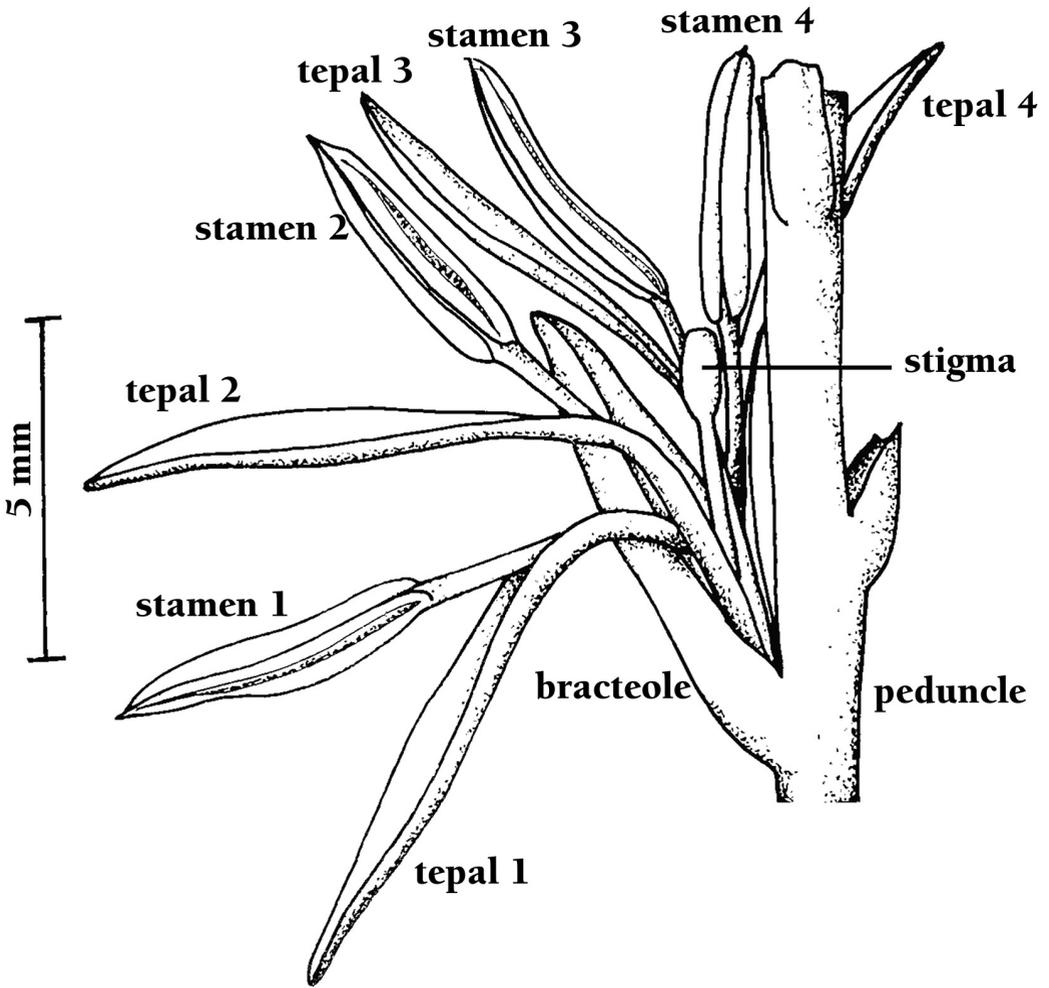


FIG. 1. Floret of *Agastachys odorata* showing some standard features of the subfamily Proteoideae in the family Proteaceae. Exceptionally in the family, as in this species, pollen is not secondarily presented on the apex of the pistil but the stigma remains immersed within the perianth. Adapted from a drawing by D. Boyer in Telford (1995).

to its arrival in the Cape of South Africa 70–80 Ma. *Endobeuthos paleosum* would need to have existed in Madagascar-India 100 Ma, i.e., before Greater India began its northern journey ~88 Ma (Lamont et al. 2022; Shi et al. 2022). Madagascar separated from SE Africa ~125 Ma. These estimates indicate that the Proteaceae would have arrived in SE Africa at least 45 My too late to reach Madagascar overland. Even if transoceanic dispersal was possible (there is no support for this prospect from the studies of Lamont et al. 2022, 2024a, b), it would have arrived in Madagascar or India at least 8 My after India had begun its northward journey. Essentially, *Endobeuthos paleosum* is too old and geographically isolated to have been a potential ancestor of the Proteaceae, according to detailed recent research on its migratory history.

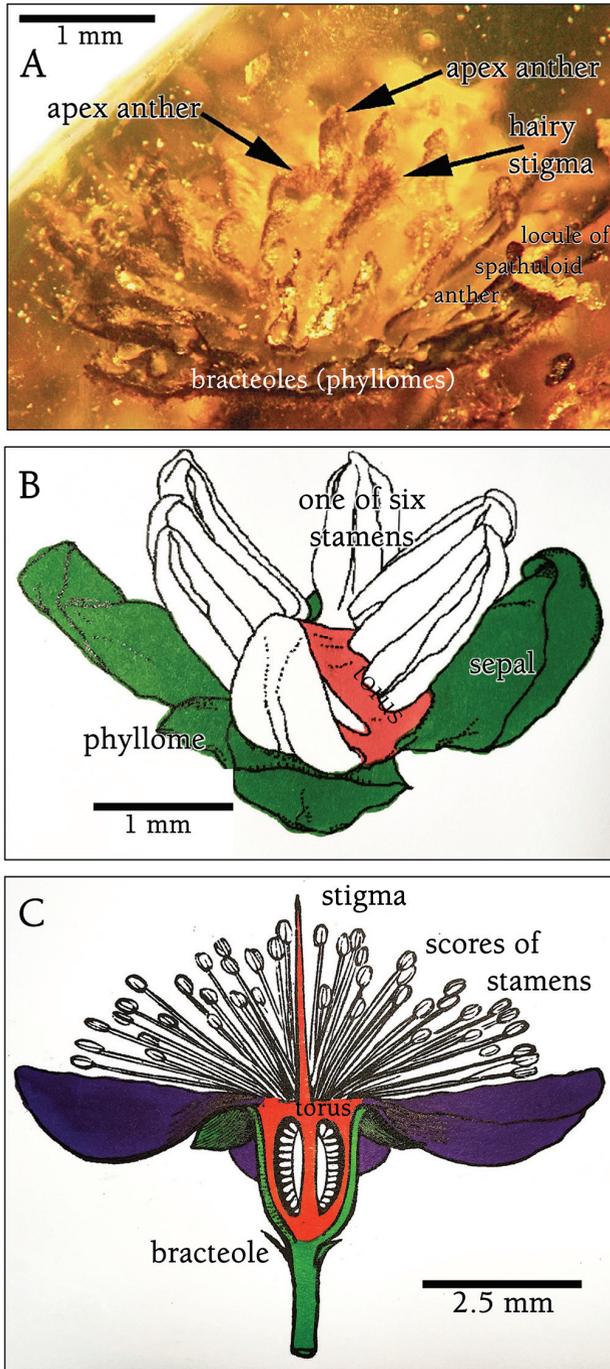


FIG. 2. **A.** Image of *Endobeaouthos paleosum* flower from semi-above showing bracteoles (phyllomes) around the receptacle, an involucre of stamens and central stigma-style. Note that the anthers tend to open towards the pistil (introrse). Adapted from Chambers and Poinar (2023). **B.** Male flower of *Notobuxus natalensis* (Buxaceae) showing subsessile anthers with a folded apex, not unlike those in A. Adapted from von Balthazar and Endress (2002). **C.** Half flower of *Feijoa sellowiana* (Myrtaeae) showing scores of stamens arising from the receptacle with anthers tending to face the central style, not unlike the arrangement in A. Adapted from Ilbusca, iStock, no.1207285155.

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