

# First flower inclusion and fossil evidence of *Cryptocarya* (Laurales, Lauraceae) from Miocene amber of Zhangpu (China)

Simon Beurel<sup>1</sup>, Julien B. Bachelier<sup>2</sup>, Jérôme Munzinger<sup>3</sup>, Fuchen Shao<sup>2</sup>, Jörg U. Hammel<sup>4</sup>, Gongle Shi<sup>5</sup>, Eva-Maria Sadowski<sup>1</sup>

<sup>1</sup> Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany

<sup>2</sup> Freie Universität Berlin, Institute of Biology/Dahlem Centre of Plant Sciences, Altensteinstraße 6, 14195 Berlin, Germany

<sup>3</sup> AMAP, Université Montpellier, IRD, CIRAD, CNRS, INRAE, 34000 Montpellier, France

<sup>4</sup> Institute of Materials Physics, Helmholtz-Zentrum Hereon, Max-Planck-Straße 1, 21502 Geesthacht, Germany

<sup>5</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China

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Corresponding author: Simon Beurel ([Simon.Beurel@mfn.berlin](mailto:Simon.Beurel@mfn.berlin))

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## Abstract

Lauraceae have one of the oldest fossil records of angiosperms with the earliest known evidence from the mid-Cretaceous. However, most of these records are based on leaves, especially from the Cenozoic of Asia, which are often challenging to assign to extinct or extant genera or species. In contrast, fossils of reproductive organs are more informative, but remain scarce. We here described the first Cenozoic Lauraceae flower of Asia and confirmed the presence of *Cryptocarya* in the Miocene Zhangpu flora (Fujian Province, south-eastern China) based on an amber inclusion. We scanned the specimen using synchrotron radiation-based micro-computed tomography (SR $\mu$ CT) and then compared the fossil with extant flowers of the genus. The present fossil flower is small, bisexual, and polysymmetric, with a whorled and trimerous perianth and androecium along with a hypanthium around the gynoecium. The perianth comprises six undifferentiated tepals, the androecium consists of nine stamens and three innermost staminodes, and the gynoecium of a single carpel with a superior, unilocular (and uniovulate) ovary. Our study also shows that the fossil shares an unusual position of the typical staminal glands and a short androecial tube on the rim of the hypanthium with at least one extant Australian species of *Cryptocarya*, which have not been reported before. Nowadays, Lauraceae are still present in tropical to subtropical regions, mostly in American and Asian rainforests. The discovery of many Lauraceae leaf fossils in Zhangpu, as well as the amber flower of this study, is consistent with the current reconstruction of the amber source environment as a megathermal seasonal rainforest during the Mid-Miocene.

## Key Words

Angiosperm, Cenozoic, palaeobotany, synchrotron X-ray tomography, 3D reconstruction

## Introduction

The Lauraceae are one of the most species rich families of Magnoliidae, with worldwide ecological and economic importance. Some taxa are key ecosystem components, especially in Asian and American tropical lowland and montane forests. Lauraceae also

comprise crops and spices, such as avocado, cloves and cinnamon (Rohwer 1993). This family has a vast meso- to megafossil record, mostly consisting of leaves from all over the world (Friis et al. 2011). Lauraceous leaves are notoriously difficult to assign to species but also to generic level, as key features are widespread across extinct and extant taxa and geographical areas

(Hill 1986; Christophel et al. 1996). In contrast, fossil fruits and flowers show more diagnostic features than leaves and are particularly valuable for generic or even species level identification (Rohwer 1993). Such reproductive structures are nevertheless rare, as they are not often preserved in the sedimentary fossil record (Friis et al. 2011).

The oldest currently known lauraceous fossil flower stems are from the Early Cretaceous Puddledock locality (von Balthazar et al. 2007). Additionally, fossils of lauraceous origin from North America (Drinnan et al. 1990; Friis et al. 2011), Europe (Kvaček 1992; Eklund and Kvaček 1998; Kvaček and Eklund 2003; Viehofen et al. 2008; Coiffard et al. 2009; Moreau et al. 2016) and South Asia (Poinar 2017) show that early members of the family were already widely distributed and diverse by the mid-Cretaceous. In Asia, the earliest Lauraceae fossil records date back to the Cenomanian with a flower inclusion of *Cascolaurus burmitis* Poinar in Burmese amber (Poinar 2017) and inflorescences and flowers of *Mauldinia hirsuta* Frumin, Eklund and Friis from Kazakhstan (Frumin et al. 2004). Additional Cretaceous fossils include flowers from the Coniacian of Japan (Takahashi et al. 1999, 2001, 2014). However, molecular clock study infers that diversification of modern Lauraceae in Asia is more recent, and probably took place during the early Cenozoic (Chanderbali et al. 2001). This is supported by the large fossil leaves record, mostly from China (e.g. Hu et al. 2007; Jacques et al. 2011; Sun et al. 2011; Shi et al. 2014c; Huang et al. 2016; Wang et al. 2019; Wang et al. 2021), but fossil flowers from this time period remain scarce. Therefore, the discovery of additional Cenozoic lauraceous reproductive organs is particularly interesting to gain more insight into the evolution and diversification of Lauraceae.

In this paper, we aim to describe a new fossil flower of Lauraceae from Chinese Miocene Zhangpu amber by using non-destructive X-ray imaging techniques. We noticed similarities, such as an the unusual position of the staminal glands and an androecial tube, with an extant member of *Cryptocarya* R. Br. from Australia, and discuss the significance of the oldest unambiguous fossil of the genus in the Miocene Zhangpu flora.

## Material and methods

The amber specimen derives from the Zhangpu amber deposit of the Fotan Group, in Zhangpu County (Fujian province, SE China; see detailed map in Wang et al. 2021: fig. 1). The group is formed by sedimentary layers of conglomerates, sandstone and mudstone alternating with layers of basaltic rocks (Zheng and Wang 1994; Wang et al. 2021). Plant macro-remains are commonly found co-occurring with the amber in the same layers of blue-grey mudstone with lignite and diatomite (Wang et al.

2021). Based on the  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of the basaltic units associated the fossil layers, the age of the amber has been well constrained at  $14.8 \pm 0.6$  Ma to  $14.7 \pm 0.4$  Ma, corresponding to the Langhian stage of the Middle Miocene (Ho et al. 2003; Zheng et al. 2019; Wang et al. 2021). This is consistent with the previous palynological studies of the Fotan Group (Zheng and Wang 1994). The terpenoid composition of Zhangpu amber indicates that it derived from the tropical Dipterocarpaceae. Additionally, fossilized winged fruits with affinities to this angiosperm family were found in the same deposit (Shi and Li 2010; Shi et al. 2014a, b). The amber piece was deposited in the palaeobotanical collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences in China (NIGPAS) under the collection number PB21525.

Separation of the fossil flower from other syninclusions in the same amber piece was achieved by using the sawing machine ALGE. Then, the piece containing the fossil was ground and polished with a LaboPol-25 machine (Struers, Sarasota, Florida, USA) using wet silicon polishing papers with successively finer grit sizes (250 to 4000 nm, Struers) to create even surfaces parallel to the inclusion (see Sadowski et al. 2021 for details).

The amber specimen was studied under a Carl Zeiss AxioScope A1 compound microscope (Carl Zeiss, Oberkochen, Germany), using incident and transmitted light simultaneously. Images were taken with a Canon EOS 80D digital camera (Canon, Tokyo, Japan) that was mounted on the microscope. To accommodate the three-dimensionality of the inclusion, 65 single photographs were taken and then digitally stacked to a composite image, by applying the HeliconFocus 7.7 software.

Imaging of the flower inclusion was performed using synchrotron-radiation based X-ray microtomography (SR $\mu$ CT) at beamline P05 of the storage ring PETRA III (Deutsches Elektronen-Synchrotron, DESY, Hamburg, Germany) that is operated by Helmholtz-Zentrum Hereon (Haibel et al. 2010; Greving et al. 2014; Wilde et al. 2016). The amber piece was mounted on a sample-stub with beeswax and imaged using an attenuation contrast setup (Greving et al. 2014). The specimen was scanned using a commercial CMOS camera system with an effective pixel size of  $0.45 \mu\text{m}$ , a sample to detector distance of 75 mm and a photon energy of 18 keV. A total of 3501 projections were recorded for the tomographic scan, at equal intervals between 0 and  $\pi$ . A transport of intensity phase retrieval approach and a filtered back projection was used to perform the tomographic reconstruction implemented with the Astra Toolbox (Palenstijn et al. 2011; van Aarle et al. 2015, 2016) and Matlab (MathWorks), integrated in a bespoke reconstruction pipeline (Moosmann et al. 2014). Raw projections were binned twice during processing, resulting in an effective voxel size of  $0.91 \mu\text{m}$  for the reconstructed volume.

The size of the resulting tomographic images was decreased from 32-bit floating point data to 16-bit, by applying ImageJ 1.52 (Wayne Rasband, National Institutes of Health, Bethesda, Maryland, USA). The software Volume Graphics Studio Max, version 3.4 (Volume Graphics, Heidelberg, Germany) was used to complete the segmentation, 3D reconstructions, and length measurements.

We additionally examined flowers of some extant species of *Cryptocarya* from the Oceanic region, including one from Australia (originally *C. hypotephra* F. Muell., now *C. vulgaris* B. Hyland; MB.Pb.HB.00569 [Schrader Herbarium (BHUPM), Museum für Naturkunde Berlin (MfN)]), and four from New Caledonia (*C. adpressa* Munzinger & McPherson [Munzinger *et al.* 5832, P, Type specimen], *C. aristata* Kosterm. [Munzinger *et al.* 5866, P], *C. cf. odorata* Guillaumin [Munzinger (*leg. Waikedre*) 6716, MPU], and Vanuatu (*C. wilsonii* Guillaumin [Munzinger & Bruy 8232], NOU). Each flower sample was mounted on a specimen holder to facilitate microCT scanning with a Phoenix X-ray Nanotom at the MfN. The scans comprised 1440 to 2000 projections and were conducted using the following settings: voltage = 80 to 100 kV, current = 75 to 100  $\mu$ A, exposure time = 0.75 to 1 s, average = 3 to 6, skip = 1 and isotropic resolution = 1.64 to 3.6  $\mu$ m.

## Data resources

Supplementary data including SR $\mu$ CT videos, 3D models of the *Cryptocarya* flower inclusion and of extant flowers of the genus are available here: <https://doi.org/10.7479/pzxcg-2x16>.

## Results

### Systematic palaeontology

**Order Laurales Juss. ex Bercht. & J. Presl, 1820**

**Family Lauraceae Juss. 1789**

**Genus *Cryptocarya* R. Br., 1810**

***Cryptocarya* sp.**

Figs 1, 2

**Specimen studied.** PB21525. Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences in China (NIGPAS).

**Locality.** Zhangpu County, Fujian Province, China.

**Horizon and age.** Middle part of the Fotan Group, Langhian (ca. 14.7–14.8 Ma), Middle Miocene.

**Description.** The flower is 3.11 mm long and 1.66 mm wide (without the pedicel, not preserved) (Fig. 1A, B). It is perfect, polysymmetric, and comprises six tepals, nine stamens, and three staminodes, which are arranged in six

trimerous and alternate whorls around the gynoecium (Fig. 1C–G). It is also perigynous with a hypanthium (1.71 mm long and 0.60 mm wide) that encloses the superior ovary and lowest third of the style entirely (Fig. 1D). The position of perianth organs forming a narrow opening and of the apical flaps still covering the pollen sacs suggest a late pre-anthetic stage or early (female) anthetic phase.

The tepal lobes (1.72–2.04 mm long and 0.66–1.05 mm wide) are free and arranged in an outer and inner whorl, and share a similar narrowly ovate to elliptical shape and an acute tip (Fig. 1A, B).

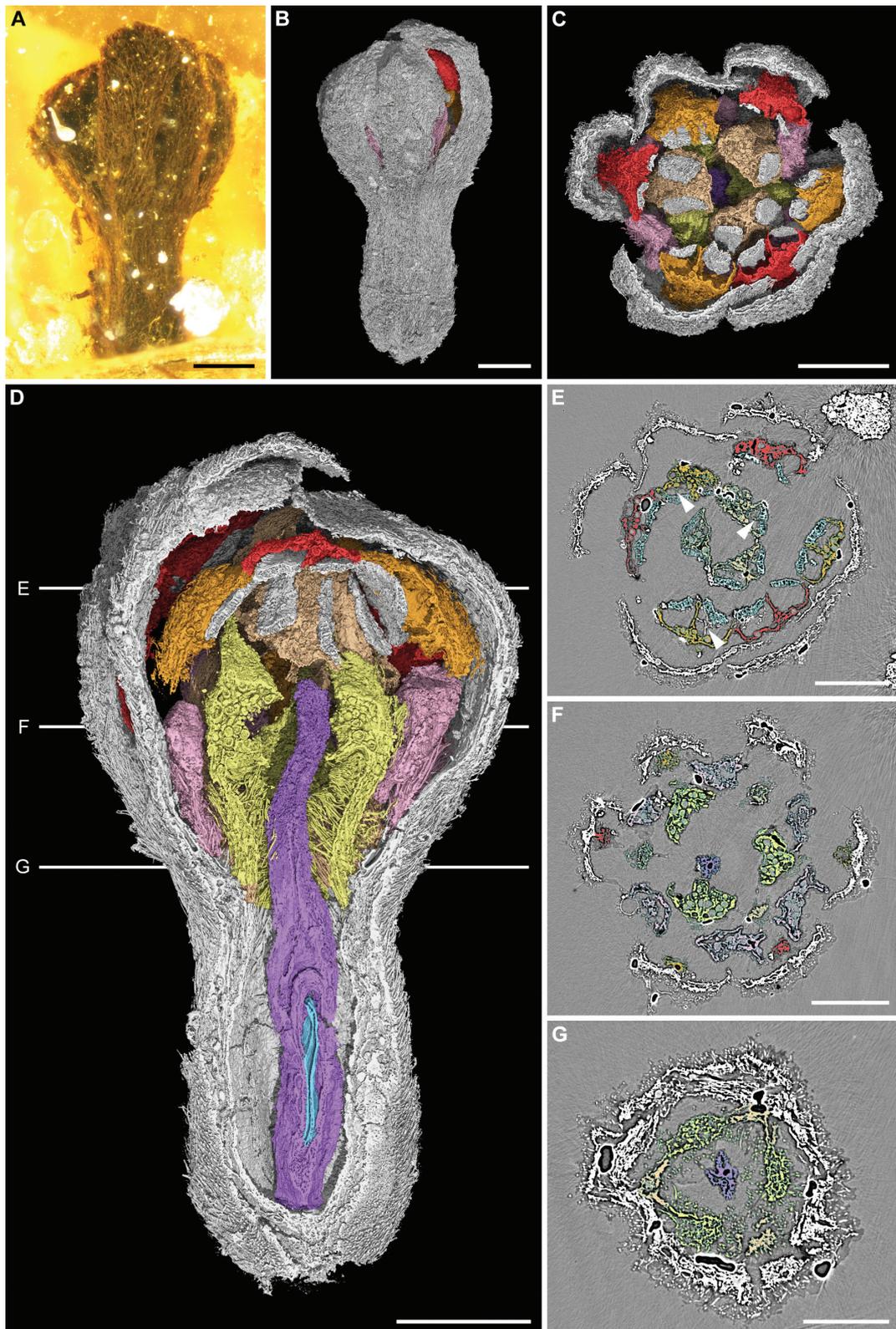
All stamens are shorter than the tepals in length and have basifixed anthers with unilocular thecae opening by two slightly lobed to flattened apically attached or hinged flaps (Figs 1C–E, 2A, C). Stamens of the first and second whorls have introrse, ovate and incurved anthers (ca. 0.57–0.68 mm long and 0.40–0.50 mm wide). Their filaments are adnate to a tepal lobe (Fig. 1F) and distinctly shorter than their anthers (ca. 0.25–0.48 mm long and 0.08–0.11 mm wide). Three pairs of large glands are inserted on the hypanthium rim, between the united bases of the tepals and filaments (Fig. 1D). These glands are formed by a subglobose distal part (ca. 0.34–0.56 mm long and 0.29–0.38 mm wide) and a long stalk (ca. 0.31–0.40 mm long and 0.09–0.12 mm wide; Figs 1D, F, 2B). Stamens of the third whorl have latero-extrorse, erect and narrow anthers (ca. 0.68–0.75 mm long and 0.37–0.39 mm wide). The filaments are just about as long as their anthers (ca. 0.64–0.74 mm long and 0.09–0.14 mm wide) and their bases form, together with those of the staminodes, a short staminal tube projecting beyond the rim of the hypanthium (ca. 0.13 mm long and 0.45 mm wide; Figs 1D, G, 2C). The staminodes have a sagittate (triangular-ovate and acuminate) sterile anther and a short and stout filament (ca. 0.60–0.65 mm long and 0.38–0.40 mm wide and 0.31–0.41 mm long and 0.15 mm wide respectively; Figs 1D, F–G, 2C).

The gynoecium consists of a single carpel (ca. 2.03 mm long). The slender superior ovary (1.22 mm long and 0.18 mm wide) is entirely enclosed in the hypanthium. The style (ca. 0.81 mm long and 0.14 mm wide) ends in an inconspicuous stigma (Fig. 1D). The ovary has a single locule and an apical pendulous ovule (ca. 0.71 mm long and 0.16 mm wide).

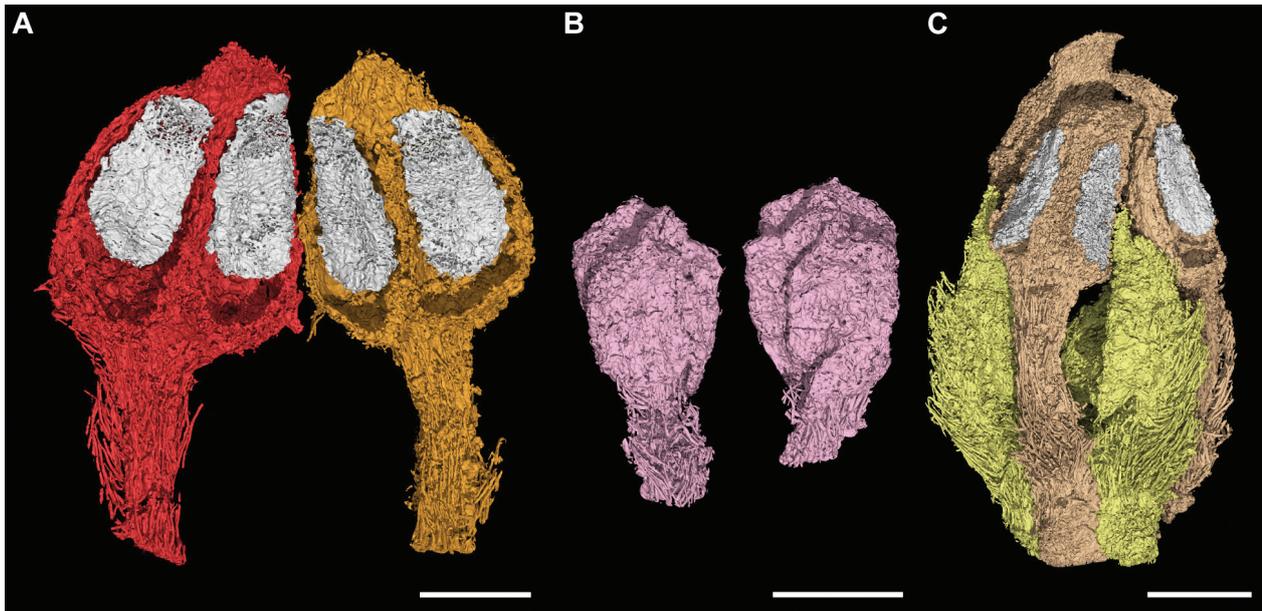
The flower is densely pubescent with appressed simple acute trichomes covering all organs, except for the inner surface of the distal part of the hypanthium, the fertile and sterile anthers and the gynoecium (Fig. 1).

### Syninclusions

The specimen contains inclusions of two *Tetramorium* and five *Carebara* ants (Formicidae), one Collembola, two Chironomidae, and wood fragments.



**Figure 1.** *Cryptocarya* fossil flower from Miocene Zhangpu amber, PB21525. **A.** Overview of the flower inclusion, taken under the light microscope; **B–D.** Virtual 3D reconstruction from segmented SR $\mu$ CT data; **B.** Overall flower; **C.** Cross section; **D.** Longitudinal section; **E–G** SR $\mu$ CT cross-sections, indicated in **D** and arranged from top to bottom; **E.** Bilocular anthers with two valves and laterally fused pollen sacs (septa indicated by white arrowheads); **F.** Style, staminodes, glands, and the filaments of the fertile stamens adnate to a tepal lobe; **G.** Short staminal tube resulting from the fusion of the third whorl of stamens with the whorl of staminodes. Perianth – grey; Stamens of the first whorl – red; Stamens of the second whorl – orange; Stamens of the third whorl – beige; Anther valves – white; Staminal glands – pink; Staminodes – yellow; Gynoeceium – purple; Ovule – blue. Scale bars: 0.5 mm (**A–D**); 0.4 mm (**E–F**); 0.3 mm (**G**).



**Figure 2.** Androecium of the *Cryptocarya* flower from Miocene Zhangpu amber, PB21525. **A.** Stamens of the first and second whorl; **B.** Staminal glands; **C.** Stamens of the third whorl fused with the staminodes at the base of the filaments, forming a short staminal tube. Stamen of the first whorl – red; Stamen of the second whorl – orange; Stamens of the third whorl – beige; Anther valves – white; Staminal glands – pink; Staminodes – yellow. Scale bars: 0.2 mm (**A**); 0.3 mm (**B–C**).

## Discussion

### Systematic affinity

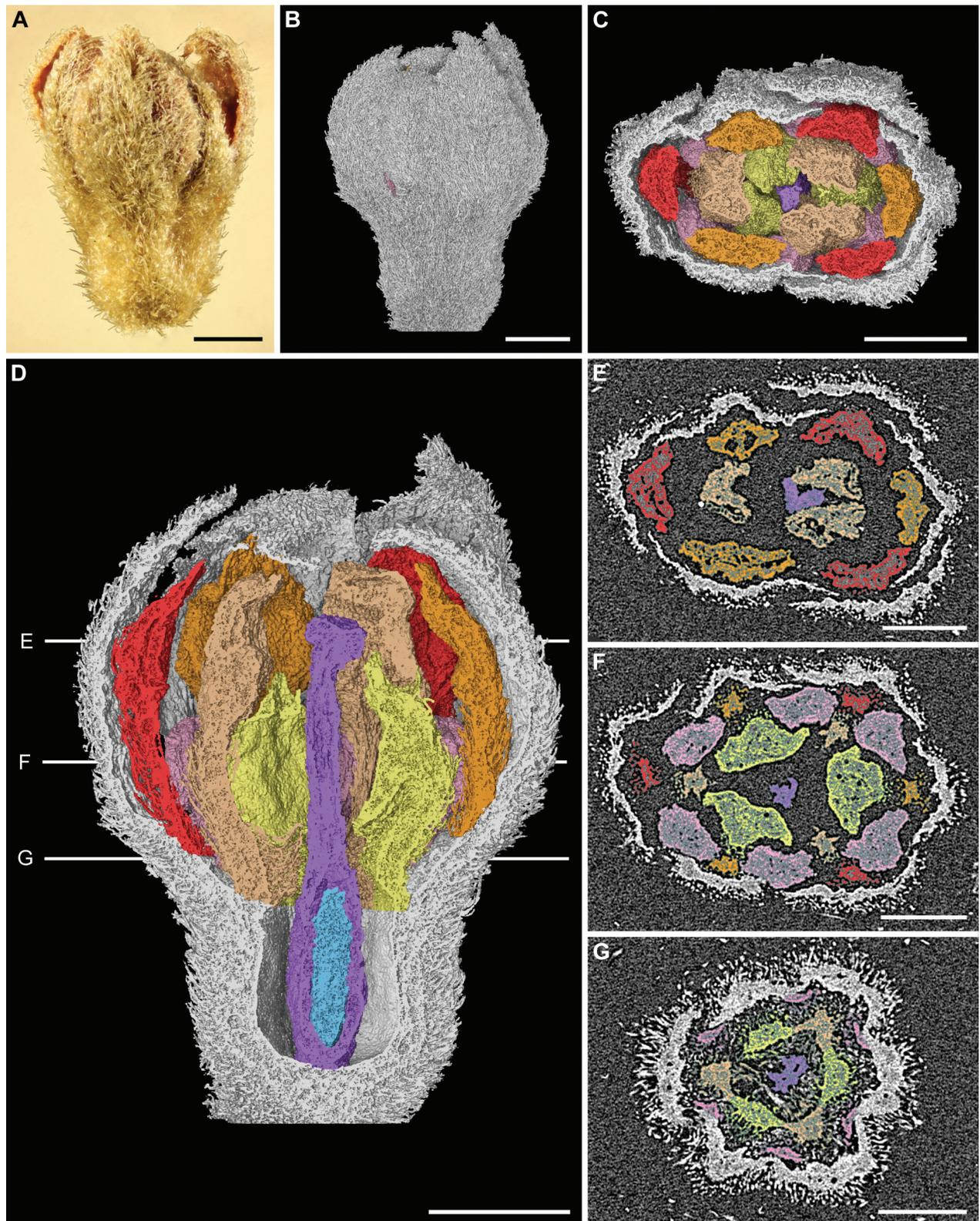
Our non-invasive and non-destructive approach shows that our fossil flower exhibits essentially the same Bauplan as most extant Lauraceae, with two trimerous whorls of tepals, followed by three trimerous whorls of fertile stamens and an innermost trimerous whorl of staminodes, and a unicarpellate gynoecium. In addition, like in all Lauraceae, the anthers are unmistakably valvate with apical flaps, and the single ovary is superior and unilocular with one apical ovule (Rohwer 1993; van der Werff 2001; Li et al. 2008a; Simpson 2010). The bithecal anthers also exhibit a bilocular structure with septal remains in some thecae. However, whether lateral fusion of the two pollen sacs happened before anthesis or earlier is unclear, but such anthers may have evolved multiple times in Lauraceae, with intermediate forms observed in several genera (Rohwer 1994). According to Rohwer (1993), bilocular anthers most likely originated in Lauraceae from the reduction of the upper or lower pollen sac(s) but may also have been formed by the lateral fusion of the pair of pollen sacs, which is a synapomorphy of the “larger part of the *Cryptocarya* group” that contains at least the genera *Cryptocarya*, *Beilschmiedia* Nees, *Endiandra* R. Br., *Aspidostemon* Rohwer & H.G. Richt., *Potameia* Thouars, *Eusideroxylon* Teijsm. & Binn., *Potoxylon* Kosterm., *Dahlgrenodendron* J.J.M. van der Merwe & A. E. van Wyk, *Sinopora* J. Li, N.H. Xia & H.W. Li, *Triadodaphne* Kosterm. and *Yasunia* van der Werff (Rohwer et al. 2014).

Within this group, the fossil flower exhibits a combination of distinctive features with members of the extant genus *Cryptocarya*, including six tepals, nine stamens that are all fertile and a deep hypanthium entirely encompassing the ovary (Fig. 3; van der Werff 1991, 2001; Rohwer 1993; Moraes 2007; Li et al. 2008b).

Extant *Cryptocarya* flowers are small (about 3–5 mm, Fig. 3), actinomorphic, bisexual and perigynous. The perianth also consists of six tepals arranged in an outer and inner whorl usually of similar size and shape. The androecium comprises three whorls with three fertile stamens and an innermost whorl of staminodes. The first and second whorl of stamens have introrse anthers, while the ones of the third whorl can be extrorse, lateral or rarely introrse (Kostermans 1937; Moraes 2007). The stamen filaments are inserted on the rim of the hypanthium, each close or connected to the base of a tepal. In addition, stamens of the first/second or third whorl bear a pair of glands, distant or adnate to the base of their filament (Fig. 3G; Hyland 1989; Moraes 2007). A fourth whorl of conspicuous, sagittate staminodes also occurs in the flowers. The style is long and the stigma is small or inconspicuous (Kostermans 1937; Moraes 2007).

### Position of glands and staminal tube in *Cryptocarya*

Androecial characters are highly variable among extant Lauraceae and may also vary within genera. In most cases, the pairs of staminal glands are connected to or born on the filament bases of the third whorl of stamens (Rohwer 1993). However, they can also occur on the outermost



**Figure 3.** Extant *Cryptocarya vulgaris* flower from Australia, MB.Pb.HB.00569. **A.** Overview of a flower, taken under the light microscope; **B–D.** Virtual 3D reconstruction from segmented microCT data; **B.** Overall flower; **C.** Cross section; **D.** Longitudinal section; **E–G.** microCT cross-sections, indicated in **D** and arranged from top to bottom; **E.** Immature bilocular anthers of the androecium and the bilobed stigma; **F.** Style, staminodes, glands, and filaments of the fertile stamens; **G.** Staminal tube resulting from the fusion of the third whorl of stamens with the whorl of staminodes; note the glands inserted at the division point of the tepal lobes. Perianth – grey; Stamens of the first whorl – red; Stamens of the second whorl – orange; Stamens of the third whorl – beige; Staminal glands – pink; Staminodes – yellow; Gynoecium – purple; Ovule – blue. Scale bars: 0.4 mm (**A–D**); 0.3 mm (**E–G**).

androecial whorl such as in *Rhodostemonodaphne* Rohwer and Kubitzki, *Urbanodendron* Mez, *Chlorocardium* Rohwer, Richter and van der Werff, and *Brassiiodendron* C.K. Allen (Rohwer 1993). Also, in some extant representatives of *Cryptocarya* from Australia and South America, the paired staminal glands are associated with the two outer whorls of stamens or rather distant from the filaments (in *C. brassii* C.K. Allen, *C. grandis* B. Hyland, *C. pleurosperma* C.T. White and W.D. Francis, *C. putida* B. Hyland, *C. vulgaris* in Hyland 1989; *C. moschata* Nees and Martius, *C. guianensis* Meisner, *C. riedeliana* P.L.R. Moraes in Moraes 2007). As in some of these extant species, the staminal glands of our *Cryptocarya* fossil flower are free from the filament and inserted towards the distal end of the floral cup (Fig. 1D). However, it is often unclear in the literature and in our material which whorl the glands are associated with. For instance, we observed in the herbarium specimen *C. vulgaris* (MB.Pb.HB.00569) that they are inserted at the division point of the tepal lobes (Fig. 3G) whereas Hyland (1989) associates the glands with the first whorl of stamens (fig. 37G).

In the fossil flower from Zhangpu, as well as in the herbarium flowers of *Cryptocarya vulgaris* (MB.Pb.HB.00569), the filaments of the third stamen whorl are similarly fused with those of the staminodes whorl (Figs 1G, 2C, 3G), forming a short staminal tube extending beyond the rim of the hypanthium. Judging from flowering stage, the staminal tube in the fossil is less prominent than in the extant specimen. In addition, the tube observed in extant *Cryptocarya* flowers is more defined when the flower is less mature, suggesting that, depending on the developmental stage of the specimen, a staminal tube is only temporarily present in the early development of some *Cryptocarya* flowers. They can thus be superficially different in older stages and prevent a detailed comparison with classic descriptions of fully developed flowers in the literature. These morphological variations should be considered in future morphological studies of the genus.

The glands and the staminal tube are distinctive in the herbarium flower (MB.Pb.HB.00569) and in the fossil. However, such a staminal tube elaborated only by the third and fourth androecium whorls has, to our knowledge, never been pictured or mentioned before in Lauraceae. Similarly, pairs of staminal glands on different whorls were also only occasionally depicted (Hyland 1989, figs 13G, 21G, 31I, 32G, 37G; Moraes 2007, figs 33D, 52D). Therefore, future morphological and anatomical studies are needed to gain more insight into the variation of the gland position and staminal tube development in *Cryptocarya*. Additionally, our results show that X-ray based methods, like micro-CT scanning, is a valuable tool for analysing extant plant specimens, as they allow detailed observations of reproductive plant organs non-invasively, compared to standard methods like microtome sections, which are usually applied in botany.

Due to the morphological variations in *Cryptocarya* flowers and the lack of distinctive characters in the fossil, it does not seem reasonable to assign the flower inclusion to any extant species of *Cryptocarya*. Furthermore, additional plants organs, such as leaves or fruits would be necessary to clarify the affiliation of the fossil to the species level. For all these reasons, we refrain from describing the amber inclusion as a new fossil species.

## Fossil records and challenges in assigning *Cryptocarya* and Lauraceae fossils

According to molecular data, *Cryptocarya* diverged around about  $90 \pm 20$  million years ago and is probably of Gondwanan origin (Chanderbali 2001). Nevertheless, fossils with affinities to the *Cryptocarya* group, and more specifically to *Cryptocarya*, are only known since the Cenozoic. The oldest representatives are possibly fossil leaves from the Eocene of Australia (Hill 1986, 1988; Conran and Christophel 1998; Carpenter et al. 2004) and North America (MacGinitie 1941). In addition, numerous putative leaves and fruit fossils were discovered in the Miocene and Pleistocene of New Zealand (Holden 1982; Pole 1993, 2007, 2019; Bannister et al. 2012), the Miocene of New Caledonia (Garrouste et al. 2021), as well as in the Oligocene, Miocene and Pleistocene of China (Liu 1993; Shi et al. 2014c; Wang et al. 2019), while fewer were discovered in the New World (i.e. in the Paleogene of Patagonia; Carpenter et al. 2018). It is only recently that a fossil has been reliably assigned to the genus in Asia, based on Pleistocene wood (Huang et al. 2023).

However, most of those fossils are leaf impressions and compressions or cuticle fragments. Moreover, the fossil pollen record of Lauraceae is scarce, as their pollen has a low fossilisation potential (Herendeen et al. 1994; Friis et al. 2011) and thus the pollen record for *Cryptocarya* is inexistent. Although placement of fossil leaves in Lauraceae is unequivocal, the assignment to genera or even species is more complex with vegetative organs alone, as leaf morphology varies greatly. This is also the case in extant and fossil *Cryptocarya* (Hill 1986; Christophel et al. 1996; van der Werff 1991, 2001; Bannister et al. 2012). For instance, Christophel et al. (1996) observed that the presumed diagnostic cuticular “butterfly-shaped” ledges of Australian *Cryptocarya* also occur in other extant Lauraceae genera of South America.

Additionally, van der Werff (1991, 2001) noted that the majority of extant genera are defined by floral characters; however, extant flower and fruit samples are difficult to obtain or even unavailable for study (Rohwer 1993; Li et al. 2008a). This makes the identification of fossil Lauraceae even more challenging. Moreover, small delicate reproductive organs are often not preserved as fossils. It should be noted that the presence of *Cryptocarya* in the Miocene of China was previously suggested by fossil fruits found in Zhangpu county which showed similarities

to extant *Cryptocarya bhutanica* Long (Wang et al. 2019), but could not be unambiguously assigned to the genus. Therefore, the fossil flower of this study confirms the occurrence of *Cryptocarya* in the Miocene of Zhangpu and gives new insight into its flower morphology in the geological past.

## Extant biodiversity and palaeoecological implications

Lauraceae are pantropical with about 50 genera and probably 2500 to 3500 species that are mostly evergreen trees and shrubs (Rohwer 1993). While they are mainly distributed in tropical to subtropical regions of Central and South America as well as Southeast Asia, the family is particularly diverse and sometimes dominant in rainforests (Rohwer 1993; Li et al. 2008a; Simpson 2010). About 25 genera and 445 species occur in China and mainly inhabit the southern provinces (Li et al. 2008a, Tan et al. 2023). In the family, *Cryptocarya* is one of the most widespread genera throughout the tropics, with between 200 and 350 species growing in South America, South Africa, Madagascar, Asia, Australia and Oceania, and a centre of diversity in Malaysia (Hyland 1989; van der Werff 1992, 2001; Rohwer 1993; Moraes 2007; Li et al. 2008b; Rohwer et al. 2014). It has been noted that the disjunct distribution of some *Cryptocarya* species was probably caused by fruits dispersion of birds from Gondwana across the Pacific, but that the genus was nonetheless, explicitly monophyletic (Rohwer et al. 2014). Although *Cryptocarya* as a whole still requires a global extensive revision (Rohwer 1993; Rohwer et al. 2014), some studies have recently improved our knowledge of the taxonomy of this genus in South Asia (de Kok 2015, 2016; Nishida et al. 2016).

The Zhangpu amber deposit, where the fossil flower was collected, is a highly diverse megathermal rainforest biome. Amber inclusions of arthropods include more than 250 families, with at least 200 being insects. Bryophytes are represented by about seven liverworts genera, as well as five extant moss taxa (Wang et al. 2021). In contrast, seed plant inclusions from Zhangpu amber are rare and up to date; only three species were described (*Canarium wangboi* Beurel et al. and *Canarium leenhoutsii* Beurel et al. (Burseraceae); Beurel et al. 2023; *Parrotia zhiyanii* Wu et al. (Hamamelidaceae); Wu et al. 2023). Nevertheless, plant megafossils from the amber-bearing sedimentary rocks are extremely rich, including about 24 families. Most of them are megathermal pantropical plant families, such as Annonaceae, Melastomataceae and Moraceae. Among these taxa, Dipterocarpaceae, Leguminosae, Lauraceae and Clusiaceae are the most abundant and diverse ones, with only slight morphological variations compared to their modern members, indicating a possible morphological stasis in the plant community (Wang et al. 2019, 2022; Wang et al. 2021). Within Lauraceae, fossils leaves with probable affinities to *Aseodaphne* Nees, *Cinnamomum* Schaeff. and *Lindera* Thunb. were recently discovered

(Wang et al. 2021, supplementary material, table S1). The palaeoclimate of Zhangpu, as well as the fossil plant taxa are similar to tropical rainforests of Southeast Asia today, suggesting that the Zhangpu amber forest was a megathermal seasonal rainforest during the Mid-Miocene Climatic Optimum (Jacques et al. 2015; Zheng et al. 2019; Wang et al. 2021). Nowadays, *Cryptocarya* is still an important element of evergreen broad-leaved forests in South China, where it is part of the canopy and subcanopy (Wang et al. 2003; Li et al. 2008b). For instance, *C. chinensis* Hemsl. can be found in lower subtropical monsoon evergreen broad-leaved forests (Wang et al. 2003). Thus, the presence of *Cryptocarya* in the Zhangpu amber forest is consistent with the current palaeoclimatic and palaeoenvironmental interpretations (Jacques et al. 2015; Wang et al. 2021).

## Conclusion

In our study, we present the first Cenozoic Lauraceae flower of Asia, based on an amber inclusion from Zhangpu. The application of non-invasive X-ray computed tomography techniques facilitated a detailed morphological examination of the amber inclusion and an in-depth comparison of the fossil flower with extant *Cryptocarya* flowers, revealing their remarkable resemblances. The fossil and extant flowers both have a perianth with six tepals, an androecium comprising nine fertile stamens with bilocular anthers and three staminodes, and a gynoecium with a unicarpellate carpel forming a superior ovary with one apical ovule surrounded by a hypanthium. The distinct presence of a similar staminal tube and position of staminal gland pairs are reported for the first time in *Cryptocarya*, in both the examined extant *C. vulgaris* from Australia and our fossil. This highlights the need to re-evaluate the occurrence (and potential significance) of those characters in other species.

In addition, the amber fossil supports the morphological stasis of Zhangpu plant communities alongside insects in tropical rainforests of Asia since at least the Middle Miocene (Wang et al. 2019, 2022; Wang et al. 2021; Beurel et al. 2023). However, it should be noted that previous affinities of Lauraceae fossil leaves to *Cryptocarya* are still debatable, as the family exhibits a wide range of leaf characters and morphological convergence between genera (Christophel et al. 1996). Nevertheless, the inclusion of this study represents the first fossil record of a flower of *Cryptocarya* and confirms the presence of this genus in the Miocene Zhangpu flora, which was only previously assumed from putative fossil fruits (Wang et al. 2019).

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## References

- Bannister JM, Conran JG, Lee DE (2012) Lauraceae from rainforest surrounding an early Miocene maar lake, Otago, southern New Zealand. *Review of Palaeobotany and Palynology* 178: 13–34. <https://doi.org/10.1016/j.revpalbo.2012.03.015>
- Beurel S, Bachelier JB, Hammel JU, Shi GL, Wu XT, Rühr PT, Sadowski EM (2023) Flower inclusions of *Canarium* (Burseraceae) from Miocene Zhangpu amber (China). *Palaeoworld* 32(4): 592–606. <https://doi.org/10.1016/j.palwor.2023.02.006>
- Carpenter RJ, Iglesias A, Wilf P (2018) Early Cenozoic vegetation in Patagonia: new insights from organically preserved plant fossils (Ligorio Márquez Formation, Argentina). *International Journal of Plant Sciences* 179(2): 115–135. <https://doi.org/10.1086/695488>
- Carpenter RJ, Hill RS, Greenwood DR, Partridge AD, Banks MA (2004) No snow in the mountains: Early Eocene plant fossils from Hotham Heights, Victoria, Australia. *Australian Journal of Botany* 52(6): 685–718. <https://doi.org/10.1071/BT04032>
- Chanderbali AS, van der Werff H, Renner SS (2001) Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104–134. <https://doi.org/10.2307/2666133>
- Christophel DC, Kerrigan R, Rowett AI (1996) The use of cuticular features in the taxonomy of the Lauraceae. *Annals of the Missouri Botanical Garden* 83: 419–432. <https://doi.org/10.2307/2399871>
- Coiffard C, Gomez B, Thiébaud M, Kvaček J, Thévenard F, Néraudeau D (2009) Intramarginal veined Lauraceae leaves from the Albian-Cenomanian of Charente-Maritime (Western France). *Palaeontology* 52(2): 323–336. <https://doi.org/10.1111/j.1475-4983.2009.00845.x>
- Conran JG, Christophel DC (1998) A new species of triplinerved *Laurophyllum* from the Eocene of Nerriga, New South Wales. *Alcheringa* 22(4): 343–348. <https://doi.org/10.1080/03115519808619332>
- De Kok RPJ (2015) A revision of *Cryptocarya* (Lauraceae) from Thailand and Indochina. *Gardens' Bulletin Singapore* 67(2): 309–350. <https://doi.org/10.3850/S2382581215000277>
- De Kok RPJ (2016) A revision of *Cryptocarya* R. Br. (Lauraceae) of peninsular Malaysia. *Kew Bulletin* 71(1): 1–26. <https://doi.org/10.1007/s12225-016-9613-1>
- Drinnan AN, Crane PR, Friis EM, Pedersen KR (1990) Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. *Botanical Gazette* 151(3): 370–384. <https://doi.org/10.1086/337838>
- Eklund H, Kvaček J (1998) Lauraceous inflorescences and flowers from the Cenomanian of Bohemia (Czech Republic, central Europe). *International Journal of Plant Sciences* 159(4): 668–686. <https://doi.org/10.1086/297585>
- Friis EM, Crane PR, Pedersen KR (2011) Early flowers and angiosperm evolution. Cambridge University Press, 585 pp. <https://doi.org/10.1017/CBO9780511980206>
- Frumin S, Eklund H, Friis EM (2004) *Mauldinia hirsuta* sp. nov., a new member of the extinct genus *Mauldinia* (Lauraceae) from the Late Cretaceous (Cenomanian-Turonian) of Kazakhstan. *International Journal of Plant Sciences* 165(5): 883–895. <https://doi.org/10.1086/421479>
- Garrouste R, Munzinger J, Leslie A, Fisher J, Folcher N, Locatelli E, Foy W, Chaillon T, Cantrill DJ, Maurizot P, Cluzel D, Lowry II PP, Crane P, Bahain JJ, Voinchet P, Jourdan H, Grandcolas P, Nel A (2021) New fossil discoveries illustrate the diversity of past terrestrial ecosystems in New Caledonia. *Scientific reports* 11(1): 1–10. <https://doi.org/10.1038/s41598-021-97938-5>
- Greving I, Wilde F, Ogurreck M, Herzen J, Hammel JU, Hipp A, Friedrich F, Lottermoser L, Dose T, Burmester H, Müller M, Beckmann F (2014) P05 imaging beamline at PETRA III: first results. In: Stock SR (Eds) *Developments in X-ray Tomography IX, Proceedings of SPIE 9212*, 166–173. <https://doi.org/10.1117/12.2061768>
- Haibel A, Beckmann F, Dose T, Herzen J, Ogurreck M, Müller M, Schreyer A (2010) Latest developments in microtomography and nanotomography at PETRA III. *Powder Diffraction* 25(2): 161–164. <https://doi.org/10.1154/1.3428364>
- Herendeen PS, Crepet WL, Nixon KC (1994) Fossil flowers and pollen of Lauraceae from the Upper Cretaceous of New Jersey. *Plant Systematics and Evolution* 189(1): 29–40. <https://doi.org/10.1007/BF00937576>
- Hill RS (1986) Lauraceous leaves from the Eocene of Nerriga, New South Wales. *Alcheringa* 10(4): 327–351. <https://doi.org/10.1080/03115518608619144>
- Hill RS (1988) Australian Tertiary angiosperm and gymnosperm leaf remains – an updated catalogue. *Alcheringa* 12(3): 207–219. <https://doi.org/10.1080/03115518808619133>
- Ho KS, Chen JC, Lo CH, Zhao HL (2003) <sup>40</sup>Ar–<sup>39</sup>Ar dating and geochemical characteristics of late Cenozoic basaltic rocks from the Zhejiang-Fujian region, SE China: eruption ages, magma evolution and petrogenesis. *Chemical Geology* 197(1–4): 287–318. [https://doi.org/10.1016/S0009-2541\(02\)00399-6](https://doi.org/10.1016/S0009-2541(02)00399-6)
- Holden AM (1982) Fossil Lauraceae and Proteaceae from the Longford Formation, Murchison, New Zealand. *Journal of the Royal Society of New Zealand* 12(1): 79–90. <https://doi.org/10.1080/03036758.1982.10427169>

- Hu YQ, Ferguson DK, Li CS, Xiao YP, Wang YF (2007) *Alseodaphne* (Lauraceae) from the Pliocene of China and its paleoclimatic significance. *Review of Palaeobotany and Palynology* 146(1–4): 277–285. <https://doi.org/10.1016/j.revpalbo.2007.06.002>
- Huang LL, Li SF, Huang WY, Jin JH, Oskolski AA (2023) *Cryptocarya chinensis* from the Upper Pleistocene of South China and its biogeographic and paleoecological implications. *Iscience* 26(8): 107313. <https://doi.org/10.1016/j.isci.2023.107313>
- Huang Y, Jia L, Wang Q, Mosbrugger V, Utescher T, Su T, Zhou Z (2016) Cenozoic plant diversity of Yunnan: a review. *Plant Diversity* 38(6): 271–282. <https://doi.org/10.1016/j.pld.2016.11.004>
- Hyland BPM (1989) A revision of Lauraceae in Australia (excluding *Cassytha*). *Australian Systematic Botany* 2(2): 135–367. <https://doi.org/10.1071/SB9890135>
- Jacques FM, Guo SX, Su T, Xing YW, Huang YJ, Liu YSC, Ferguson DK, Zhou ZK (2011) Quantitative reconstruction of the Late Miocene monsoon climates of southwest China: a case study of the Lincang flora from Yunnan Province. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304(3–4): 318–327. <https://doi.org/10.1016/j.palaeo.2010.04.014>
- Jacques FM, Shi G, Su T, Zhou Z (2015) A tropical forest of the middle Miocene of Fujian (SE China) reveals Sino-Indian biogeographic affinities. *Review of Palaeobotany and Palynology* 216: 76–91. <https://doi.org/10.1016/j.revpalbo.2015.02.001>
- Kostermans AJGH (1937) Revision of the Lauraceae II. The genera *Endlicheria*, *Cryptocarya* (American species) and *Licaria*. *Recueil des Travaux Botaniques Néerlandais* 34(2): 500–609. <https://naturtijdschriften.nl/pub/552261>
- Kvaček Z (1992) Lauralean angiosperms in the Cretaceous. *Courier Forschungsinstitut Senckenberg* 147: 345–367.
- Kvaček J, Eklund H (2003) A report on newly recovered reproductive structures from the Cenomanian of Bohemia (Central Europe). *International Journal of Plant Sciences* 164(6): 1021–1039. <https://doi.org/10.1086/378824>
- Li XW, Li J, Huang PH, Wei FN, Cui HB, van der Werff H (2008a) Lauraceae. In: Wu ZY, Raven PH, Hong DY (Eds) *Flora of China*, Vol. 7. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis, 102–254. [http://www.efloras.org/florataxon.aspx?flora\\_id=2&taxon\\_id=10479](http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=10479)
- Li XW, Li J, van der Werff H (2008b) *Cryptocarya*. In: Wu ZY, Raven PH, Hong DY (Eds) *Flora of China*, Vol. 7. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis, 247–254. [http://www.efloras.org/florataxon.aspx?flora\\_id=2&taxon\\_id=108511](http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=108511)
- Liu YS (1993) A palaeoclimatic analysis on early Pleistocene flora of Changsheling Formation, Baise Basin, Guangxi. *Acta Palaeontologica Sinica* 32(2): 151–169. [in Chinese, with English abstract]
- MacGinitie HD (1941) A Middle Eocene flora from the central Sierra Nevada. *Carnegie Institute Washington Publication* 534: 1–169. <http://sierrageology.org/documents/references/a-middle-eocene-flora-from-the-central-sierra-nevada/>
- Moosmann J, Ershov A, Weinhardt V, Baumbach T, Prasad MS, LaBonne C, Xiao X, Kashef J, Hofmann R (2014) Time-lapse X-ray phase-contrast microtomography for in vivo imaging and analysis of morphogenesis. *Nature Protocols* 9(2): 294–304. <https://doi.org/10.1038/nprot.2014.033>
- Moraes PLR de (2007) Taxonomy of *Cryptocarya* species of Brazil. *ABC Taxa* 3: 1–191.
- Moreau JD, Gomez B, Daviero-Gomez V, Néraudeau D, Tafforeau P (2016) Inflorescences of *Mauldinia* sp. (Lauraceae) and associated fruits from the Cenomanian of Languedoc Roussillon, France. *Cretaceous Research* 59: 18–29. <https://doi.org/10.1016/j.cretres.2015.10.018>
- Nishida S, De Kok R, Yang Y (2016) Cuticular features of *Cryptocarya* (Lauraceae) from Peninsular Malaysia, Thailand and Indo-China and its taxonomic implications. *Phytotaxa* 244(1): 26–44. <https://doi.org/10.11646/phytotaxa.244.1.2>
- Palenstijn WJ, Batenburg KJ, Sijbers J (2011) Performance improvements for iterative electron tomography reconstruction using graphics processing units (GPUs). *Journal of Structural Biology* 176(2): 250–253. <https://doi.org/10.1016/j.jsb.2011.07.017>
- Poinar Jr G (2017) A mid-Cretaceous Lauraceae flower, *Cascolaurus burmitis* gen. et sp. nov., in Myanmar amber. *Cretaceous Research* 71: 96–101. <https://doi.org/10.1016/j.cretres.2016.11.015>
- Pole M (1993) Early Miocene flora of the Manuhierikia Group, New Zealand. 6. Lauraceae. *Journal of the Royal Society of New Zealand* 23(4): 303–312. <https://doi.org/10.1080/03036758.1993.10721228>
- Pole M (2007) Lauraceae macrofossils and dispersed cuticle from the Miocene of southern New Zealand. *Palaeontologia Electronica* 10(1): 1–38.
- Pole M (2019) A Survey of Pliocene to Mid Quaternary leaf cuticle from the North Island, New Zealand. *Palaeontologia Electronica* 22(1): 1–32. <https://doi.org/10.26879/862>
- Rohwer JG (1993) Lauraceae. In: Kubitzki K, Rohwer JG, Bittrich V (Eds) *The families and genera of vascular plants*, vol 2. Springer, Berlin, 366–391. [https://doi.org/10.1007/978-3-662-02899-5\\_46](https://doi.org/10.1007/978-3-662-02899-5_46)
- Rohwer JG (1994) A note on the evolution of the stamens in the Laurales, with emphasis on the Lauraceae. *Botanica Acta* 107: 103–110. <https://doi.org/10.1111/j.1438-8677.1994.tb00415.x>
- Rohwer JG, Moraes PLR de, Rudolph B, Van der Werff H (2014) A phylogenetic analysis of the *Cryptocarya* group (Lauraceae), and relationships of *Dahlgrenodendron*, *Sinopora*, *Triadodaphne*, and *Yasunia*. *Phytotaxa* 158(2): 111–132. <https://doi.org/10.11646/phytotaxa.158.2.1>
- Sadowski EM, Schmidt AR, Seyfullah LJ, Solórzano-Kraemer MM, Neumann C, Perrichot V, Hamann C, Milke R, Nascimbene PC (2021) Conservation, preparation and imaging of diverse ambers and their inclusions. *Earth-Science Reviews* 220: 103653. <https://doi.org/10.1016/j.earscirev.2021.103653>
- Shi G, Li H (2010) A fossil fruit wing of *Dipterocarpus* from the middle Miocene of Fujian, China and its palaeoclimatic significance. *Review of Palaeobotany and Palynology* 162(4): 599–606. <https://doi.org/10.1016/j.revpalbo.2010.08.001>
- Shi G, Jacques FM, Li H (2014a) Winged fruits of *Shorea* (Dipterocarpaceae) from the Miocene of Southeast China: Evidence for the northward extension of dipterocarps during the Mid-Miocene Climatic Optimum. *Review of Palaeobotany and Palynology* 200: 97–107. <https://doi.org/10.1016/j.revpalbo.2013.09.003>
- Shi G, Dutta S, Paul S, Wang B, Jacques FM (2014b) Terpenoid compositions and botanical origins of Late Cretaceous and Miocene amber from China. *PLoS ONE* 9(10): e111303. <https://doi.org/10.1371/journal.pone.0111303>
- Shi GL, Xie ZM, Li HM (2014c) High diversity of Lauraceae from the Oligocene of Ningming, South China. *Palaeoworld* 23(3–4): 336–356. <https://doi.org/10.1016/j.palwor.2014.08.001>

- Simpson MG (2010) Laurales. In: Simpson MG (Ed.) Plant Systematics. Academic Press, Amsterdam, 190–192. <https://doi.org/10.1016/B978-0-12-374380-0.50001-4>
- Sun BN, Wu JY, Liu YSC, Ding ST, Li XC, Xie SP, Yan DF, Lin ZC (2011) Reconstructing Neogene vegetation and climates to infer tectonic uplift in western Yunnan, China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304(3–4): 328–336. <https://doi.org/10.1016/j.palaeo.2010.09.023>
- Takahashi M, Crane PR, Ando H (1999) Fossil flowers and associated plant fossils from the Kamikitaba locality (Ashizawa Formation, Futaba Group, lower Coniacian, upper Cretaceous) of Northeast Japan. *Journal of Plant Research* 112(2): 187–206. <https://doi.org/10.1007/PL00013872>
- Takahashi M, Herendeen PS, Crane PR (2001) Lauraceous fossil flower from the Kamikitaba locality (Lower Coniacian; Upper Cretaceous) in northeastern Japan. *Journal of Plant Research* 114(4): 429–434. <https://doi.org/10.1007/PL00014008>
- Takahashi M, Herendeen PS, Xiao X, Crane PR (2014) Lauraceous fossil flowers from the Kamikitaba assemblage (Coniacian, Late Cretaceous) of northeastern Japan (Lauraceae). *Systematic Botany* 39(3): 715–724. <https://doi.org/10.1600/036364414X681464>
- Tan C, Ferguson DK, Tang ZY, Yang Y (2023) Distribution and conservation of Lauraceae in China. *Global Ecology and Conservation* 46: e02566. <https://doi.org/10.1016/j.gecco.2023.e02566>
- van Aarle W, Palenstijn WJ, De Beenhouwer J, Altantzis T, Bals S, Batenburg KJ, Sijbers J (2015) The ASTRA Toolbox: A platform for advanced algorithm development in electron tomography. *Ultramicroscopy* 157: 35–47. <https://doi.org/10.1016/j.ultramicro.2015.05.002>
- van Aarle W, Palenstijn WJ, Cant J, Janssens E, Bleichrodt F, Dabrovolski A, De Beenhouwer J, Batenburg KJ, Sijbers J (2016) Fast and flexible X-ray tomography using the ASTRA toolbox. *Optics Express* 24(22): 25129–25147. <https://doi.org/10.1364/OE.24.025129>
- van der Werff H (1991) A key to the genera of Lauraceae in the New World. *Annals of the Missouri Botanical Garden* 78(2): 377–387. <https://doi.org/10.2307/2399567>
- van der Werff H (1992) Proposal to conserve 2813 *Cryptocarya* against *Ravensara* (Lauraceae). *Taxon* 41: 129. <https://doi.org/10.2307/1222506>
- van der Werff H (2001) An annotated key to the genera of Lauraceae in the Flora Malesiana region. *Blumea* 46(1): 125–140. <https://repository.naturalis.nl/pub/525118>
- Viehofen A, Hartkopf-Fröder C, Friis EM (2008) Inflorescences and flowers of *Mauldinia angustiloba* sp. nov. (Lauraceae) from middle Cretaceous karst infillings in the Rhenish Massif, Germany. *International Journal of Plant Sciences* 169(7): 871–889. <https://doi.org/10.1086/589975>
- von Balthazar M, Pedersen KR, Crane PR, Stapanoni M, Friis EM (2007) *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of Eastern North America. *American Journal of Botany* 94(12): 2041–2053. <https://doi.org/10.3732/ajb.94.12.2041>
- Wang B, Shi G, Xu C, Spicer RA, Perrichot V, Schmidt AR, Feldberg K, Heinrichs J, Chény C, Pang H, Liu X, Gao T, Wang Z, Ślipiński A, Solórzano-Kraemer MM, Heads SW, Thomas MJ, Sadowski E-M, Szwedo J, Azar D, Nel A, Liu Y, Chen J, Zhang Q, Zhang Q, Luo C, Yu T, Zheng D, Zhang H, Engel MS (2021) The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in East Asia. *Science Advances* 7(18): eabg0625. <https://doi.org/10.1126/sciadv.abg0625>
- Wang Z, Shi G, Sun B, Jia H, Dong C, Yin S, Wu X (2022) A new *Cercis* (Leguminosae) from the middle Miocene of Fujian, China. *Historical Biology* 34(1): 94–101. <https://doi.org/10.1080/08912963.2021.1900170>
- Wang Z, Sun F, Wang J, Yan D, Dong J, Sun M, Sun B (2019) New fossil leaves and fruits of Lauraceae from the Middle Miocene of Fujian, southeastern China differentiated using a cluster analysis. *Historical Biology* 31(5): 581–599. <https://doi.org/10.1080/08912963.2017.1379517>
- Wu XT, Shu JW, Yin SX, Sadowski EM, Shi GL (2023) *Parrotia* flower blooming in Miocene rainforest. *Journal of Systematics and Evolution*. <https://doi.org/10.1111/jse.13001>
- Wang ZF, Peng SL, Liu SZ, Li Z (2003) Spatial pattern of *Cryptocarya chinensis* life stages in lower subtropical forest, China. *Botanical Bulletin of Academia Sinica* 44: 159–166.
- Wilde F, Ogurreck M, Greving I, Hammel JU, Beckmann F, Hipp A, Lottermoser L, Khokhriakov I, Lytaev P, Dose T, Burmester H, Müller M, Schreyer A (2016) Micro-CT at the imaging beamline P05 at PETRA III. In: Shen Q, Nelson C (Eds) Proceedings of the 12<sup>th</sup> International Conference on Synchrotron Radiation Instrumentation, New York (USA), 2015. American Institute of Physics Conference Proceedings 1741(1): 030035. <https://doi.org/10.1063/1.4952858>
- Zheng D, Shi G, Hemming SR, Zhang H, Wang W, Wang B, Chang SC (2019) Age constraints on a Neogene tropical rainforest in China and its relation to the Middle Miocene Climatic Optimum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 518: 82–88. <https://doi.org/10.1016/j.palaeo.2019.01.019>
- Zheng Y, Wang W (1994) Sequence of Miocene Fotan Group in SE Fujian and its palyno-assemblages. *Acta Palaeontologica Sinica* 33(2): 200–216. [in Chinese, with English abstract]