Cretaceous fire-resistant angiosperms

Shuo Wang (✉ shuowang@qust.edu.cn)

 Qingdao University of Science and Technology   https://orcid.org/0000-0003-0412-3799

Chao Shi

 Qingdao University of Science and Technology

Hao-hong Cai

 Qingdao University of Science and Technology

Hong-rui Zhang

 Qingdao University of Science and Technology

Xiao-xuan Long

 Qingdao University of Science and Technology

Erik Tihelka

 University of Bristol

Wei-cai Song

 Qingdao University of Science and Technology

Qi Feng

 Qingdao University of Science and Technology

Ri-xin Jiang

 Qingdao University of Science and Technology

Chenyang Cai

 Nanjing Institute of Geology and Paleontology   https://orcid.org/0000-0002-9283-8323

Natasha Lombard

 National Herbarium, South African National Biodiversity Institute

Xiong Li

 Kunming Institute of Botany   https://orcid.org/0000-0002-1754-8721

Ji Yuan

 Shanghai World Expo Museum

Jian-ping Zhu

 Shandong Normal University

Hui-yu Yang

 Qingdao University of Science and Technology

Xiao-fan Liu

 Qingdao University of Science and Technology

Qiao-Ping Xiang

 Institute of Botany, Chinese Academy of Sciences

Zun-tian Zhao
  Shandong Normal University
Chunlin Long
  Minzu University of China
Xianchun Zhang
  The Herbarium, Institute of Botany   https://orcid.org/0000-0003-3425-1011
Hua Peng
  Kunming Institute of Botany, CAS   https://orcid.org/0000-0001-5583-537X
De-Zhu Li
  Kunming Institute of Botany   https://orcid.org/0000-0002-4990-724X
Harald Schneider
  Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences   https://orcid.org/0000-0002-4548-7268
Michael Engel
  University of Kansas   https://orcid.org/0000-0003-3067-077X
Yongdong Wang
  Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences   https://orcid.org/0000-0002-2873-9427
Robert Spicer
  The Open University   https://orcid.org/0000-0003-1076-2693

Article

Abstract

Background: Flowering plants (angiosperms) dominate most global ecosystems today, but their rapid Cretaceous diversification has remained poorly understood ever since Darwin referred to it as an 'abominable mystery'. Although numerous Cretaceous fossil flowers have been discovered in recent years, most are represented by incomplete charcoalified fragments that do not preserve delicate structures such as complete petals and surface textures, which means that their similarity to living forms is often difficult to discern. The scarcity of information about the ecology of early angiosperms makes it difficult to test hypotheses about the drivers of their diversification. Among other factors, frequent fires in the Cretaceous have been postulated as having possibly facilitated the rise of angiosperms. However, to date no early fossil angiosperms displaying fire-adapted traits have been known, making the role of fire in shaping Cretaceous floras uncertain.

Results: We report the discovery of two exquisitely preserved fossil flower species, one identical to the inflorescences of the extant crown eudicot genus *Phylica* and the other recovered as a sister group to *Phylica*, both preserved as inclusions in Cretaceous amber from northern Myanmar (~99 Ma). These specialized flower structures, named *Phylica piloburmensis* sp. nov. and *Eophylica priscastellata* gen. et sp. nov., were adapted to surviving frequent wildfires, providing the earliest evidence of fire-resistance in angiosperms. The fossils suggest that fire was a significant selective force in Cretaceous angiosperm floras and that adaptations to fire resistance in some eudicot clades have been conserved for at least 99 Ma. This morphological stasis encompasses a range of floral characters, including the production of 'pseudo-flowers', and characteristic fruit and pollen architecture. Given its morphological distinctiveness, the *Eophylica-Phylica* clade represents one of the first well-documented angiosperm 'living fossil' genera from the Cretaceous.

Conclusion: Our study suggests that core eudicots with specialised flower morphology displaying hallmarks of fire resistance and identical to those of the extant south African genus *Phylica*, had originated by the mid-Cretaceous (~99 Ma). Palaeoenvironmental reconstructions indicate that these plants lived in conditions similar to those of present-day southern Africa where 70% of taxa survive frequent burning, and that fire resistance was probably widespread in the fire-prone Cretaceous. The results also provide new insights into the biogeographic origin of at least one element of the highly endemic Greater Cape Region biodiversity hotspot flora biota.

Significance Statement

Fire is a pervasive force across terrestrial biomes, shaping ecosystem composition and distribution. While fire was more prevalent in some periods of the Earth's past and is thought to have played a pivotal role in the Cretaceous diversification of flowering plants, little is known about the responses of ancient vegetation to fire. Here we describe new flowers from Cretaceous amber (~99 Ma) that display hallmarks of fire resistance, highlighting the role of fire in shaping the diversity of the earliest angiosperms. Eophylica and fossil Phylica demonstrate that despite the seemingly ephemeral and disturbance-

dominated nature of periodically burnt habitats, fire-prone angiosperm clades can persist over long geological timescales.

Main Text

The diversification of flowering plants was one of the major episodes in the history of life that transformed global ecosystems, bringing about the diversification of insects, amphibians, mammals, early birds[1−5], and other clades, ultimately marking the first time in geological history when life on land became more diverse than life in the sea[6]. The rapid radiation of angiosperms, between ~135 Ma and ~65 Ma, that led flowering plants to dominate many land environments by the end of the Cretaceous and replace the incumbent gymnosperms, has fascinated evolutionary biologists starting with Darwin who famously referred to the angiosperm radiation as an "abominable mystery". However, our knowledge of the early angiosperm's most distinctive feature, the flower, is scarce owing to its delicate construction and thus low fossilization potential. Much of what is known about early angiosperm floral diversity comes from flowers that were rendered biologically inert through burning and conversion to charcoal[9], but this mode of preservation is only partial, reducing the flower core with petals and surface features to mere stubs. In the absence of fine morphological detail, there has been a tendency to reconstruct such remains with the presumption that such flowers must have been simpler than extant forms. As a result, the ecology of early angiosperms remains poorly known, hampering attempts at disentangling the potential drivers of their diversification. Diverse ecological explanations have been proposed to account for the rapid radiation of angiosperms in the Cretaceous, including co-diversification with insect pollinators, high growth rates, adaptation to new fire regimes, and evolution of novel dispersal modes[10], but many of these remain hardly testable without a better appreciation of the ecological diversity of early flowering plants.

Amber, fossilized resin of ancient plants that often preserves flowers with life-like fidelity alongside their pollen and fruits, offers an alternative but little-explored window into early angiosperm diversity. Here we document two types of fossil flowers, one identical to those of extant *Phylica* (Rhamnaceae) and another sister to the genus, preserved in Cretaceous amber from the Hkamti and Tanaing mines (Supplementary Figs. 1−3) in northern Myanmar dated to at least 99 Ma (Supplementary notes)[11−14]. These fossil flowers were previously misidentified as conifers[15] or green algae[16], and are quite common in the Tanaing mines, where the flora is dominated by gymnosperms including the extinct Bennettitales (Supplementary Fig. 4) and accompanied by diverse angiosperms[17−19]. The exceptionally preserved flowers possess linear pubescent xeromorphic leaves (seemingly needle-like and tightly clustered with densely stellate or linear hairs) typical of fire-prone vegetation adapted to dry conditions (Fig. 1). Our results provide the first direct evidence of fire-resistant angiosperms from the Cretaceous, supporting the hypothesis that fire represented a biologically significant selective pressure in some Cretaceous ecosystems. The fossils demonstrate that specialized floral adaptations associated with resistance to frequent burning arose early in angiosperm evolution and remained more or less unchanged for over 99 Ma in Rhamnaceae. Extant *Phylica* is restricted to the South African Cape biodiversity hotspot and represents one of the most characteristic members of the endemic Fynbos flora[20,21]. The finding of inflorescences related to and

even identical with *Phylica* in a mid-Cretaceous Gondwanan deposit backdates the origin of a key component of the Fynbos by ~70 Ma[22] and suggests that at least this distinctive element of the Fynbos flora may represent an ancient type similar to the floras of the fire-prone Cretaceous[23].

Results

Ecomorphological conservatism in fire-resistant Rhamnaceae

Our fossils preserve the primary reproductive features characteristic of extant *Phylica*, a diverse genus within the Rhamnaceae, in which all ~150 extant species are endemic to southern Africa[24,25]. Specifically, leaves clustered at the twig tip surrounding either a flower, or a 'pseudo-flower head', is a feature unique to *Phylica* (Fig. 1 and Supplementary Figs. 7–20 and Supplementary Video 1)[26]. Based on the presence or absence of petals, the number of sepals, and the form of hairs of the indumentum, we assign our fossils to two new species: *Eophylica priscastellata* gen. et sp. nov. (Figs. 2–3) and *Phylica piloburmensis* sp. nov. (Fig. 4 and Supplementary Fig. 6), the first character reflecting morphologies seen in extant *Phylica*[26]. A close relationship between *Eophylica* and *Phylica* is supported by comparative morphological and phylogenetic reconstruction based on flowers, fruits, and pollen grains (Figs. 2–4 and Supplementary Figs. 21–31 and Supplementary Videos 2–3). *Eophylica* can be distinguished from *Phylica* on the basis of the number of sepals and the absence of petals. The second species is morphologically indistinguishable from extant *Phylica*, and our phylogenetic analyses recovered the species as robustly nested within the *Phylica* clade. Given the completeness of our observed character suite, with the exceptional fidelity of amber preservation, that flower morphology is the greatest source of data for ascribing species to supraspecific taxa, and the robustness of our phylogenetic results, we have placed this species in the extant genus *Phylica*. This greatly extends the age of this clade and represents the first extant angiosperm genus documented from the Mesozoic. While this seems controversial, we believe the extraordinary nature of these fossils and the data compel such a conclusion. Extant species in Myanmar amber are exceptionally rare, but are known to occur, and believe future data shall corroborate our conclusions regarding the identity of *P. piloburmensis*. We provide formal descriptions of the new fossil taxa in the Supplementary Material.

The clustered, needle-like dry leaves are typical of fire-prone angiosperms (Fig. 1)[16,23]. Taxonomically, needle-like leaves clustered around the stems of a small shrub (Fig. 1 and Supplementary Figs. 7–20) are typical of *Phylica* and quite distinct from other genera of Rhamnaceae[26]. Non-*Phylica* species in Rhamnaceae have broader leaves, except for some species in the genera *Trymalium*, *Siegfriedia,* and *Colletia*. Specialised narrow leaves have been considered an adaptation to the relatively dry Cape climate[27], and frequent wildfires[28]. Many Fynbos angiosperms (e.g., *Erica* (Ericaceae), *Aspalathus* (Fabaceae), *Ruschia* (Mesembryanthemaceae), and *Agathosma* (Rutaceae)[20]) and some non-Fynbos clades (e.g., *Brunia* and *Berzelia* (Bruniaceae)) also have narrow, clustered leaves. However, species of *Phylica* differ in having one or more of the following[26]: leaves at the tip of the stem form 'pseudo-flower heads' unique to the genus (Fig. 1); leaves and flowers are covered by dense hairs; unarmed but villous-

pubescent, branched twigs; the absence of stipules, and leaves with only one main vein (Supplementary Figs. 7−20).

Importantly, the typical pseudo-flower head in these fossils is distinctive within angiosperms[26]. It is exclusive to some extant species of *Phylica* (e.g., *P. pubescens* and *P. plumosa*; Supplementary Fig. 10e−j)[26,29], where it represents an intermediate developmental stage from vegetative growth to the flowering phase (Fig. 1 and Supplementary Figs. 7−20 and Supplementary Video 1). The head comprises many tightly clustered scale-like leafy bracts, with mature leaves or bracts (below the true flower) developing later. Despite having a similar 'head' shape, the pseudo-flower bracts are morphologically distinct from those of the true flower (Fig. 2m).

True flowers of *Phylica* are small (~1.0 mm), capitated, 5(4)-merous, have an inferior ovary, and are densely pubescent. They combine the following diagnostic characters (Figs. 2−4 and Supplementary Figs. 21−26 and Supplementary Video 2)[26,29,30]: flowers are terminal/solitary and include leafy or scale-like bracts; the flowers are semi-opened; sepals are enlarged and triangular; sepals have a prominent median vein; receptacles are turbinate in shape; the petals are either small and alternate with the sepals or are completely absent; stamens are opposite the petals; the disc is intrastaminal, thin to more or less fleshy; the ovary is below the disc and completely fused to the receptacle; the style is columnar, simple, shorter than the calyx tube; and the stigma is slightly lobed. In extant *Phylica*, such tubular flowers are pollinated by long-proboscid flies[26,30]. Both fossils presented herein have a lengthened calyx tube (Figs. 2 a, c−h, 4e−g and Supplementary Figs. 21−24, 26), corresponding with coeval long-proboscid flies and scorpionflies known from Myanmar amber[31,32].

The fruits of the two new fossil species are typical capsules (Supplementary Figs. 3f, 4k, 27−28 and Supplementary Video 3). Although capsule-like fruits are common in Rhamnaceae, *Phylica* fruit morphologies are shaped by their specific flower characters (such as the lengthened calyx tube and dense hairs). Differing from other capsules that lack sepal elements and usually have an exposed mature pistil, fruits of *Phylica* and *Eophylica* are crowned by the persistent calyx (or sepal) that includes a hidden pistil (Figs. 3f−h, 4k−l). The pericarp develops from the base of the persistent calyx, and in the fossil fruit appears hard, ribbed (Fig. 3f and Supplementary Fig. 27), or covered with thick hairs originating from the flower (Fig. 4k and Supplementary Fig. 28). As in extant species[26], fossil fruits of *Eophylica* and *P. piloburmensis* are significantly larger than the flower (≥5 mm wide) (Supplementary Figs. 27, 28). Similar fruits occur in the genus *Rosa* in Rosaceae, but those fruits have the achenes inside, rather than having septal polycarpels as in our fossils and extant *Phylica* (Fig. 4m and Supplementary Fig. 27 m, n). As in extant *Phylica*[26], petals are either present or absent in our fossil flowers, with *E. priscastellata* lacking petals (Fig. 3a,b) and *P. piloburmensis* possessing petals (Fig. 4a).

Several pollen grains of similar morphology exist within our flower specimens (Figs. 2n, 4b and Supplementary Fig. 29). Although we failed to resolve a clear exine pattern, these grains exhibit characters similar to those of extant *Phylica* (Fig. 2t−v and Supplementary Fig. 29), namely single grains with an isopolar, 3-colporate, oblate-spheroidal, and triangular in polar view. An affinity with the

Rhamnaceae is further supported by the following features[33]: (i) medium-sized with polar axes of 21−24 μm and equatorial diameters of 18−21 μm (P/E ratio: 1.2); (ii) colpi long, narrow and with blunt ends; and (iii) the middle of the aperture lalongate, with two ends connected with a thinned part of the exine to form an H-shape (Fig. 2q−v and Supplementary Fig. 29).

Our fossils also preserve several other features whose combination is diagnostic of the family Rhamnaceae[34]. As in our fossils, extant *Phylica* is a morphologically divergent clade of the Rhamnaceae that exhibits only some plesiomorphic characters seen in the family[26]. Although a lengthened cyathiform calyx tube and enfolding sepals and petals are important flower characteristics of living *Phylica*, they obscure important internal Rhamnaceae characters (i.e., four- or five-parted with a single whorl of stamens opposite the petals). We used micro-XCT scanning to show that our fossils preserve simple leaves, small flowers with 5(4)-merous sepals (five in *P. piloburmensis* and eight (2 × 4-merous) in *E. priscastellata*), which are valvate in the bud (Figs. 2b,l and 4e−g); five or eight (2 × 4-merous; *E. priscastellata*) stamens, that alternate with the sepals and opposite the petals and anthers, which are tightly enfolded by the hooded petal apices (if petals are present; *P. piloburmensis*) (Fig. 4a and Supplementary Figs. 21n, 22l,m and 23k); and the presence of an intrastaminal disc (Fig. 2b)[33]. These features, combined with crowding leaves (Fig. 1), are characteristic of Rhamnaceae[35].

Our new fossil species exhibit other features common to extant *Phylica*. In *E. priscastellata*, the leaves and twigs are like those of extant *P. pubescens* or *P. ambigua* (Supplementary Fig. 10), but the presence of stellate hairs and absence of petals distinguish it. Its fruits lack a covered indumentum as in extant *P. parviflora* (Supplementary Fig. 27 m, n). Moreover, the leaves, flower and fruit characteristics of *P. piloburmensis* are also present in many other extant species of *Phylica* (represented by *P. axillaris*; Fig. 4 c, h−j, m, n)[26]. Overall, the unique combination of characters in our fossil flowers and fruits suggest that they represent an early form of *Phylica*, rather than other angiosperm clades[36].

Phylogenetic analysis integrating morphological and molecular partitions (Supplementary notes) confirmed crown-group membership of both fossil species (Supplementary Fig. 30). One major character (the presence of stellate hairs) makes the fossil *E. priscastellata* different from all extant species of *Phylica* (Supplementary Table 1). Ancestral-state reconstruction based on the phylogenetic tree shows stellate hairs were present in the common ancestor of the tribes Phyliceae and Pomaderreae (Supplementary Fig. 31). Since extant species of Pomaderreae are only distributed in Australia and New Zealand (i.e., Gondwana)[29], this demonstrates a common origin of stellate hairs in these two Gondwanan clades. All in all, our fossils provide evidence of a remarkable case of morphological, and probably also ecological, conservatism within a crown-eudicot clade since the mid-Cretaceous.

Discussion

Early origin of fire resistance in the Cretaceous

The mid-Cretaceous (Albian–Turonian; 112–90 Ma) was anomalously warm, with some of the highest temperatures in Phanerozoic geological history[37] and a relatively shallow temperature gradient between the poles and the tropics. Elevated atmospheric oxygen levels in the Cretaceous (23–29% compared with 21% at present) and abundance of charred plant fossil remains in the rock record suggest that fires were frequent during this period. Some hypotheses of angiosperms diversification highlight that Cretaceous fire regimes may have opened land up for the first flowering plants, whose rapid colonization of regeneration gaps may have provided an advantage over the then-dominant gymnosperms that are intrinsically slower growing[40,41]. By providing a new source of fuel, angiosperms may have also substantially altered the existing fire regimes, to the disadvantage of gymnosperm trees. However, the role of fire in fuelling the diversification of angiosperms has proven difficult to test. In fact, the earliest angiosperms have been reconstructed as weedy understory herbs, shrubs and small trees growing in humid and aquatic habitats[44], making it unclear how these plants may have benefited from Cretaceous fire regimes.

Previous molecular clock studies have inferred a Cretaceous origin of fire-proneness in some gymnosperm (Pinaceae) and angiosperm (Proteaceae, Myrtaceae, Haemodoraceae, and Restionaceae⁻) lineages. However, direct palaeontological evidence of fire-adapted traits (i.e., those that that promote survival or reproductive success in the presence of wildfire[51]), are scarce, primarily because such traits evidently have low preservation potential. Cones that open to release seeds in the presence of fire (serotiny), have been reported from mid-Cretaceous gymnosperms, namely *Widdringtonia* (Callitroideae; Cenomanian), *Protodammara*, *Sphenolepis*, and *Dammara* (Cupressaceae; Cenomanian–Turonian[51]). To our knowledge, no Cretaceous angiosperms possessing fire-adapted traits have been known to date. While charcoal (fusain) and fire scars[54] on fossil trees indicate the antiquity of fire-proneness, these lines of evidence do not show if ancient fire regimes were sufficient to have an evolutionary impact on early flowering plants and whether these plants possessed fire-adapted traits[55].

Fossil *Eophylica* and *Phylica* inflorescences preserve unambiguous morphological hallmarks of fire resistance. Fire causes direct, or indirect, fatal damage to plant hydraulic systems, and the burned plants ultimately die of drought[56]. Many fire tolerance plants are 'drought-resisters and *Eophylica-Phylica* belong to this group. Numerous Cape species (such as species in families Ericaceae and Proteaceae) that are drought-resisters are able to produce new growth after fires, from buds on buried lignotubers at the base of killed stems[56]. In contrast, some broad-leaved plants (such as banana) are typically adapted to a moist environment but are quite sensitive to heating, and quickly die after suffering significant water stress immediately post-fire[56]. *Phylica* are small shrubs whose clustered, needle-like dry leaves are typical of fire-prone vegetation; these characters in turn ensure relatively rapid renewal after fire and confer resistance to severe drought. *Phylica* flowers are surrounded by several leaves, which may provide protection from direct heat during fire. While some extant members of the genus *Phylica* typically do not survive wildfires, which may in itself have an adaptive value in environments that burn frequently[57], their seeds accumulate in the soil and germinate after fire[58]. Their relatively small and rounded seeds are

easily incorporated into the soil and reach greater depths, which is linked to their ability to form long-term persistent seed banks. The discovery of unambiguous morphological adaptations to fire tolerance make *Eophylica* and *P. piloburmensis* the earliest fire-adapted angiosperms in the fossil record. This pushes the origin fire resistance in crown angiosperms back to 99 Ma, into the mid-Cretaceous.

While the exquisitely preserved *Eophylica* and *Phylica* flowers support the hypothesis that Cretaceous fire regimes did exert a significant selective pressure on early angiosperms, the extent to which Cretaceous fire regimes may have promoted the spread of early angiosperms remains open to testing. Palaeofire models suggest that intense Cretaceous fires supported by novel fuels from weedy flowering plants may have enabled fast-growing angiosperms to outcompete tall gymnosperm trees[42]. However, since the drivers of angiosperm diversification appear to be largely clade-specific, it is likely that the changing fire regimes were just one of many factors associated with angiosperm radiation. Future discoveries of exquisitely preserved plants in Cretaceous amber deposits may shed further light on the how widespread fire-related traits were in early angiosperms.

An early Gondwanan origin for the Fynbos

Fossil *Eophylica* and *P. piloburmensis* flowers are distinct from those of any angiosperms that grow in the subtropics of northern Myanmar today. *Phylica* is endemic to the fire-prone Fynbos flora of the South African Cape. The Fynbos represents one of the most remarkable global floral biodiversity 'hotspots', characterized by unique species richness and endemism, with over 9,000 recorded plant species restricted to a small geographic area ($\pm$90,000 km^2), of which almost 70% are endemic[61]. Much of this diversity is due to a handful of speciose clades, the 'Cape floral clades'[25,62,63], mostly consisting of plants with short, needle-like leaves such as *Phylica*[20,21], that have traditionally been regarded as having originated and radiated within the Cape[25,62,63]. Our discovery of a fossils identical to *Phylica* from the Cretaceous of southeast Asia challenges the traditional interpretation that the fire-adapted Fynbos flora is of a relatively recent origin[20,21,64–66] and arose in the aftermath of climatic drying near the Miocene-Pliocene boundary[65,67]. Paleomagnetic studies[68] and fossil evidence[69–73] indicate that the West Burma Block is of a Gondwanan origin; it rifted from north-western Australia between the late Triassic and late Jurassic and was an isolated landmass in the Tethys Ocean in the mid-Cretaceous[68,74]. As such, our results demonstrate that a key element of the xeromorphic Fynbos vegetation existed as long as 99 Ma ago, supporting the great antiquity of open fire-prone vegetation in Gondwana. Given that southern Gondwana during the middle Cetaceous (Albian–Turonian; 112–90 Ma) was arid to semi-arid[75,76], possessing a similar climate as the South African Cape today, the Fynbos could provide a recent proxy for understanding fire-prone plant communities in the Cretaceous[23] (Fig. 5). Whether the Fynbos biome itself dates to the Cretaceous remains to be tested with the aid of further plant fossils. Coetzee and Muller[77] noted that the Miocene pollen assemblages from southwestern Cape are comparable with Australian floras, although some of these Gondwanan elements were lost after the climatic changes at the end of the Miocene. Taken together, these lines of evidence point towards a much more ancient and complex history of the Fynbos biome than previously thought.

The Myanmar amber tropical forest palaeoenvironment

The presence of abundant fire-prone vegetation in amber from northern Myanmar has important implications for interpreting the palaeoenvironment of this key Mesozoic Konservat-Lagerstätten. Myanmar amber harbours perhaps the most diverse Cretaceous amber biota known to date[78], famous for its well-preserved vertebrate remains and abundant insect fossils. The Myanmar amber palaeoenvironment is most often reconstructed as a hot tropical forest[78], with a near-equatorial climate[68] located in the vicinity of brackish water and the seashore[13], perhaps akin to modern swamp forests[81]. *Eophylica* and *Phylica* fossils suggest that the Myanmar amber forest may have been prone to seasonal fires, similar to some tropical peat swamp forests in more recent geological history[82]. Major fires and subsequent draught may have been associated with some amber deposits, such as Cretaceous New Jersey amber that contains abundant charred remains of plants and insects[83]. It is possible that seasonal fires may have also played a role in the production of Myanmr amber, one of the largest amber deposits in the world, since resin secretion can be triggered by wounding[84], as well as any stresses that impact water uptake (e.g., insect infestation, drought, etc [85].). Notably, burned plant remains are abundant in our ambers (Supplementary Fig. 5) although it is not clear if these remains were charred prior to entrapment in resin or are the consequence of post-burial taphonomic processes. Abundant seasonal fire may also partly explain the abundance of amber in the Cretaceous rock record, as fossiliferous ambers of older age are exceedingly rare and largely occur only as traces[86].

Amber provides a complementary window of early angiosperm diversity

The unique floral architecture preserved in *Eophylica* and *Phylica* fossils is identical to that seen in extant members of the genus *Phylica*, predating molecular clock estimates for the genus by at least 70 Ma[22]. This makes *Eophylica-Phylica* one of the best documented 'living fossil' genera in the angiosperm fossil record. It is not generally possible to assign Mesozoic flower compression fossils and charcoalified fragments to extant genera with high confidence[10]. Our study demonstrates that amber provides a complementary window into the early evolution of flowering plants, by overcoming some biases inherent to compression and carbonified fossils that make up the majority of the early angiosperm fossil record. Firstly, most compression fossils are preserved primarily in wetlands, while amber paleoenvironments range from warm forests to seashores[83], capturing a different set of palaeoenvironments. Secondly, amber inclusions are often preserved with extreme fidelity, comparable to the inflorescences of modern plants. The discovery of further well-preserved angiosperm fossils in Cretaceous amber deposits may eventually backdate other crown angiosperm clades, helping to provide more calibration points for understanding the tempo of Cretaceous angiosperm radiation and ultimately contributing to reconciling the often-perceived incongruence between the angiosperm fossil record and molecular clock estimates[87,88].

Materials And Methods

Fossil Provenance and Ethical Statement

The material described herein originates from two amber mines, Tanaing and Hkamti, located in the Hukawng Valley, Kachin State in northern Myanmar[11]. The mines are introduced in Supplementary Text 1.1. The amber has been radiometrically dated to the earliest Cenomanian, ~99 Ma, and was not produced earlier than the late Albian[12,13]. Our study was initiated in 2015 and all amber specimens were acquired from local sellers before December 2016, prior to the escalation of the humanitarian crisis in the region (https://doi.org/10.6084/m9.figshare.13317890.v1). The present fossils were briefly introduced in a lecture and poster presentation at the XIX International Botanical Congress (IBC) in ShenZhen, China, July 2017 (lecture title 'Mid-Cretaceous Seed Plant Diversity in Burmese Amber', presented by Shuo Wang).

Authenticity of the 21 amber pieces studied herein was verified by the National Gemstone Testing Center (NGTC) of China with Certificate Numbers XCXNo20200903 to XCXNo20200923. These tests included examination of physical and chemical properties of the specimen such as colour, density, optical character, refractive index, amber flow characteristics, and absorption spectrum.

All 21 pieces of amber pieces, preserving 22 fossils, are curated at the Qingdao University of Science and Technology under the collection numbers QUST-AM20501−12, QUST-AM32413−17 and QUST-AM33310 for *E. priscastellata* sp. nov., and QUST-AM32127, QUST-AM33311, QUST-AM20513−14 for *P. piloburmensis* sp. nov. (Supplementary Fig. 6). Of the 21 pieces of amber in this study, 19 originate from the 'Tanaing' amber mine in Hukawng Valley, except for QUST-AM20511 and QUST-AM32414 which originate from the nearby 'Hkamti' mine, which is further shown in (Supplementary Figs. 1−3 and 6).

Photography

Fossils were photographed with a digital camera (Fujifilm GFX 50 R with Laowa C11625 2.6 X, Cambo Actar 105 hr or Mitutoyo 5-10 X lens) fitted to a macro rail (Cognisys). For every photograph, 30 to 200 images were stacked with Combine ZP and Photoshop CS4. Some specimens were also photographed using Leica DVM6 and M205FA microscopes (Leica AG, Heerbrugg, Switzerland).

To examine internal structures of the flowers, fossils were scanned with Xradia Versa Micro-XCT 620 (Carl Zeiss X-ray Microscopy Inc., Pleasanton, USA) housed in the Advanced Materials Research Institute of Yangtze Delta. All specimens were scanned with the same beam energy of 40 kV, 3 W, and the LE1 filter, but with different exposure times and pixel sizes that depended on the sample size and condition. Of the 22 fossil specimens, clear scanned images were obtained for 20, but the other 2 samples lack sufficient contrast for scanning. The obtained image stacks were reconstructed with Dragonfly (Ors, Montreal, Canada). Final figures were prepared with Photoshop CS5 and Illustrator CS5 (Adobe, San Jose, USA).

Morphological description

Family Rhamnaceae Jussieu 1789

Tribe Phyliceae Reissek ex Endl. 1840

Genus *Eophylica* Shi, Wang, et Engel gen. nov.

Type species: *Eophylica priscastellata* Shi, Wang, et Engel sp. nov.

Etymology: The generic name is a combination of the Greek words, *Ēŏs* (ἠώς, meaning "dawn") and the extant genus *Phylica* L. (itself derived from Greek: *phyllikos*, meaning, "leafy"). The gender of the name is feminine.

Generic diagnosis: Identical to *Phylica* except with eight sepals (2 × 4-merious) (versus five in *Phylica*), lacking petals (present in most *Phylica*, although secondarily reversed independently in several crown species), and indumentum composed of stellate Rhamnaceous hairs (simple in *Phylica*). Additionally: Ovary inferior, fused to receptacle. Style columnar, simple. Fruit a typical capsule, obovoid, about 5.0 mm long, crowned with persistent base of calyx with a convex calyx-area. A complete description is provided in the Supplementary Material.

Species *Eophylica priscastellata* Shi, Wang, et Engel sp. nov.

Holotype (*hic designatus*): No. QUST-AM32413 (Fig. 2a–b, l, n–v and Supplementary Fig. 21, deposited in the collection of the Qingdao University of Science and Technology, Qingdao, China.

Paratypes (17 specimens): No. QUST-AM20501–QUST-AM20512, QUST-AM32414–QUST-AM32417 and QUST-AM33310, same repository as holotype.

Type locality and age: No. QUST-AM20501–QUST-AM20510, QUST-AM20512, QUST-AM32413, QUST-AM32415–QUST-AM32417 and QUST-AM33310 are from Tanaing mines, earliest Cenomanian, 98.79 Ma ± 0.62 (ca. 99) Ma. QUST-AM20511 and QUST-AM32414 are from 'Hkamti' mines, early Albian, 109.7 ± 0.4 (ca. 110) Ma.

Etymology: The specific epithet is a combination of the Latin terms *priscus* (meaning, "ancient") and *stellatus* (meaning, "starry").

Species diagnosis: Plants covered in stellate and linear hairs. Leaves long linear, spirally arranged. Head of flower terminal surrounded by interior spreading, sub-incurved, linear leafy bracts. Bracts about twice as long as flower. Flower single on twig tip. Disc epignynous and covering inside of calyx tube. Sepals 8 (2 × 4-merious). Petals absent. A complete description is provided in the Supplementary Material.

Genus *Phylica* L. 1753

Species *Phylica piloburmensis* Shi, Wang, et Engel sp. nov.

Etymology: The specific epithet is a combination of the Greek term *pîlos* (πῖλος, meaning, "hair") and *burmensis* (itself a combination of Burma and the Latin suffix *–ensis*, denoting place).

Holotype (*hic designatus*): No. QUST-AM32127 (Fig. 4a–g and Supplementary Fig. 26, deposited in the collection of the Qingdao University of Science and Technology, Qingdao, China.

Paratypes (3 specimens): No. QUST-AM33311, QUST-AM20513–QUST-AM20514, same repository as holotype.

Type locality and age: Tanaing mines, earliest Cenomanian, 98.79 Ma ± 0.62 (ca. 99) Ma.

Species diagnosis: Leaves slightly wider (1.5–2.0 mm wide, 4.5–8.0 mm long) and both ad- and abaxial sides covered with simple linear hairs. Flowers not single but forming a corymb. Petals present. Fruit covered with dense indumentum. A complete description is provided in the Supplementary Material.

Character scoring and phylogenetic analysis

Morphological characters scored from leaf, habit, flower, fruit, and pollen were compiled from previous studies[29,30,89] and are described in the Supplementary notes. The combined phylogenetic tree was reconstruction based on morphological characters and molecular data following the method of Wilf et al.[90]; the procedure is further described in the Supplementary notes.

Declarations

Acknowledgements

Author Contributions

S.W. and C.S. conceived the study and wrote the paper. R.A.S., M. S. E., H. S., E.T., S.W., C. C., and C. S. revised the paper. C.S., S.W., H.P, N.L., X.L., Q.P.X., Z.T.Z., C.L.L., Y.D.W, D.Z.L., Z.K.Z., X.C.Z., and H. S. performed specimen identification and morphological analyses. H.H.C., X.X.L., H.R.Z., J.Y., R.X.J., Q.F.,

W.C.S., H.Y.H., X.F.L., and J.P.Z. performed fossil photograph and Micro-XCT data analyses. All authors discussed the results and commented on the manuscript.

Competing interests

The authors declare no competing interests.

Data availability

The Micro-XCT scanning data are available from Zenodo (doi: 10.5281/zenodo.3997200). Videos of the 3D reconstruction of internal and external structures of the fossil specimens are available from Figshare database (doi: 10.6084/m9.figshare.12865859). High resolution images of all the figures are available from Figshare database (doi: 10.6084/m9.figshare.12845144).

References

1. Lloyd, G. T. et al. Dinosaurs and the Cretaceous terrestrial revolution. *P. R. Soc. B* **275**, 2483–2490 (2008).
2. Bininda-Emonds, O. R. P. et al. The delayed rise of present-day mammals. *Nature* **446**, 507–512 (2007).
3. Herrera-Flores, J. A., Stubbs, T. L. & Benton, M. J. Ecomorphological diversification of squamates in the Cretaceous. *R. Soc. Open Sci.* **8**, 201961 (2021).
4. Benton, M. J. The origins of modern biodiversity on land. *Philos. Trans. R. Soc. B* **365**, 3667–3679 (2010).
5. Roelants, K. et al. Global patterns of diversifcation in the history of modern amphibians. *Proc. Natl Acad. Sci. USA* **104**, 887–892 (2007).
6. Grosberg, R. K., Vermeij, G. J. & Wainwright, P. C. Biodiversity in water and on land. *Curr. Biol.* **22**, 900–903 (2012).
7. Condamine, F. L., Silvestro, D., Koppelhus, E. B. & Antonelli, A. The rise of angiosperms pushed conifers to decline during global cooling. *Proc. Natl Acad. Sci. USA* **117**, 28867–28875 (2020).
8. Buggs, R. J. The deepening of Darwin's abominable mystery. *Nat. Ecol. Evol.* **1**, 1–2 (2017).
9. Friis E. M., Crane, P. R., Pedersen, K. R., Stampanoni, M. & Marone, F. Exceptional preservation of tiny embryos documents seed dormancy in early angiosperms. *Nature* **528**, 551–554 (2015).
10. Soltis, P. S., Folk, R. A. & Soltis, D. E. Darwin review: angiosperm phylogeny and evolutionary radiations. *Proc. R. Soc. B* **286**, 20190099 (2019).
11. Cruickshank, R. D. & Ko, K. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *J. Asian Earth Sci.* **21**, 441–455 (2003).
12. Shi, G. H. et al. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretac. Res.* **37**, 155–163 (2012).

13. Yu, T. et al. An ammonite trapped in Burmese amber. *Proc. Natl. Acad. Sci. USA* **166**, 11345–11350 (2019).

14. Xing, L. D. & Qiu, L. Zircon U–Pb age constraints on the Hkamti amber biota in northern Myanmar. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **558**, 109960 (2020).

15. Xia, F. Y., Yang, G., Zhang, Q. & Shi, G. L. Amber: life through time and space. (Beijing: Science Press, 2015).

16. Poinar, G. O. & Brown, A. E. A green algae (Chaetophorales: Chaetophoraceae) in Burmese amber. *Hist. Biol.* **33**, 323–327 (2019).

17. Liu, Z. J., Huang, D., Cai, C. Y. & Wang, X. The core eudicot boom registered in Myanmar amber. *Sci. Rep.* **8**, 16765 (2018).

18. Poinar, G. O. & Chambers, K. L. *Tropidogyne pentaptera*, sp. nov., a new mid-Cretaceous fossil angiosperm flower in Burmese amber. *Palaeodiversity* **10**, 135–14 (2017).

19. Poinar, G. O. & Chambers, K. L. *Palaeoanthella huangii* gen. and sp. nov., an Early Cretaceous flower (Angiospermae) in Burmese amber. *SIDA* **21**, 2087–2092 (2005).

20. Goldblatt, P. An analysis of the flora of Southern Africa: Its characteristics, relationships, and orgins. *Ann. Missouri Bot. Gard.* **65**, 369–436 (1978).

21. Verboom, G. A. et al. Cenozoic assembly of the Greater Cape flora. in Fynbos: ecology, evolution and conservation of a megadiverse region. (Oxford Univ. Press, 2014).

22. Hauenschild, F., Favre, A., Michalak, I. & Muellner-Riehl, A. N. The influence of the Gondwanan breakup on the biogeographic history of the ziziphoids (Rhamnaceae). *J. Biogeogr.* **45**, 2669–2677 (2018).

23. Brown, S., Scott, A. C., Glasspool, I. J. & Collinson, M. E. Cretaceous wildfires and their impact on the Earth system. *Cretac. Res.* **36**, 162–190 (2012).

24. Xing, L. D. et al. A feathered dinosaur tail with primitive plumage trapped in mid-Cretaceous amber. *Curr. Biol.* **26**, 3352–3360 (2016).

25. Richardson, J. E. et al. Rapid and recent origin of species richness in the Cape flora of South Africa. *Nature* **412**, 181–183 (2001).

26. Pillans, N. S. The genus *Phylica*. *J. S. Afr. Bot.* **8**, 1–164 (1942).

27. Rebelo, T. et al. Fynbos Biome. In: Mucina, L. & Rutherford, M. C. (eds.), *The vegetation of South Africa, Lesotho and Swaziland*. **19**, 52–219 (2006).

28. Gimingham, C. H. & Cowling, R. The ecology of fynbos: nutrients, fire and diversity. *J. Ecol.* **81**, 195–196 (1993).

29. Richardson, J. E., Fay, M. F., Cronk, Q. C. B. & Cronk, M. W. Species delimitation and the origin of populations in island representatives of *Phylica* (Rhamnaceae). *Evolution* **57**, 816–827 (2003).

30. Richardson, J. E. Molecular systematics of the genus *phylica* L. with an emphasis on the island species. *PhD dissertation of The University of Edinburgh February* (1999).

31. Lin, X., Labandeira, C. C., Shih, C., Hotton, C. L. & Ren, D. Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber. *Nat. Commun.* **10**, 1–14 (2019).

32. Zhao, X. et al. Mouthpart homologies and life habits of Mesozoic long-proboscid scorpionflies. *Sci. Adv.* **6**, 1259 (2020).

33. Schirarend, C. & Köhler, E. World Pollen and Spore Flora: Rhamnaceae Juss. (Scandinavian Univ. Press, 1993).

34. Medan, D. & Schirarend, C. Rhamnaceae. in Flowering Plants · Dicotyledons. (Springer Berlin Heidelberg, 2004).

35. Gotelli, M. M., Galati, B. G. & Medan, D. Morphological and ultrastructural studies of floral nectaries in Rhamnaceae. *J. Torrey Bot. Soc.* **144**, 63–73 (2017).

36. Endress, P. K. Evolutionary diversification of the flowers in angiosperms. *Am. J. Bot.* **98**, 370–396 (2011).

37. Friedrich, O., Norris, R. D. & Erbacher, J. Evolution of middle to Late Cretaceous oceans–a 55 my record of Earth's temperature and carbon cycle. *Geology* **40**, 107–110 (2012).

38. Huber, B. T., Hodell, D. A. & Hamilton, C. P. Middle-Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradients. *Geol. Soc. Am. Bull.* **107**, 1164–1191 (1995).

39. Belcher, C. M., Yearsley, J. M., Hadden, R. M., Mcelwain, J. C. & Rein, G. Baseline intrinsic flammability of Earth's ecosystems estimated from paleoatmospheric oxygen over the past 350 million years. *Proc. Natl. Acad. Sci. USA* **107**, 22448–22453 (2010).

40. Bond, W. J. & Scott, A. C. Fire and the spread of flowering plants in the Cretaceous. *New Phytol.* **188**, 1137–1150 (2010).

41. Bond, W. J. & Midgley, J. J. Fire and the angiosperm revolutions. *Int. J. Plant Sci.* **173**, 569–583 (2012).

42. Belcher, C. M. & Hudspith, V. A. Changes to Cretaceous surface fire behaviour influenced the spread of the early angiosperms. *New Phytol.* **213**, 1521–1532 (2017).

43. Bradshaw, S. D., Dixon, K. W., Hopper, S. D., Lambers, H. & Turner, S. R. Little evidence for fire-adapted plant traits in Mediterranean climate regions. *Trends Plant Sci.* **16**, 69–76 (2011)

44. Feild, T. S. & Arens, N. C. The ecophysiology of early angiosperms. *Plant Cell Environ.* **30**, 291–309 (2007).

45. He, T., Pausas, J. G., Belcher, C. M., Schwilk, D. W. & Lamont, B. B. Fire-adapted traits of Pinus arose in the fiery Cretaceous. *New Phytol.* **194**, 751–759 (2012).

46. Cornwell, W. K. et al. Flammability across the gymnosperm phylogeny: the importance of litter particle size. *New Phytol.* **206**, 672–681 (2015).

47. Lamont, B. B. & He, T. Fire-adapted Gondwanan angiosperm floras evolved in the Cretaceous. *BMC Evol. Biol.* **12**, 1–11 (2012).

48. He, T., Lamont, B. B. & Manning, J. A. Cretaceous origin for fire adaptations in the Cape flora. *Sci. Rep.* **6**, 1–6 (2016).

49. Crisp, M. D., Burrows, G. E., Cook, L. G., Thornhill, A. H. & Bowman, D. M. J. S. Flammable biomes dominated by eucalypts originated at the Cretaceous–Paleogene boundary. *Nat. Commun.* **2**, 1–8 (2011).

50. He, T., Lamont, B. B. & Downes, K. S. Banksia born to burn. *New Phytol.* **191**, 184–196 (2011).

51. Mays, C., Cantrill, D. J. & Bevitt, J. J. Polar wildfires and conifer serotiny during the Cretaceous global hothouse. *Geology* **45**, 1119–1122 (2017).

52. Midgley, J. & Bond, W. Pushing back in time, the role of fire in plant evolution. *New Phytol.* **191**, 5–7 (2011).

53. Mciver, E. E. Cretaceous Widdringtonia Endl. (Cupressaceae) from North America. *Int. J. Plant Sci.* **162**, 937–961 (2001).

54. Byers, B. A., Ash, S. R., Chaney, D. & DeSoto, L. First known fire scar on a fossil tree trunk provides evidence of Late Triassic wildfire. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **411**, 180–187 (2014).

55. Lamont, B. B. & He, T. Fire-proneness as a prerequisite for the evolution of fire-adapted traits. *Trends Plant Sci.* **22**, 278–288 (2017).

56. Midgley, J. J., Kruger, L. M. & Skelton, R. How do fires kill plants? the hydraulic death hypothesis and cape proteaceae "fire-resisters". *S. Afr. J. Bot.* **77**, 381–386 (2011).

57. Schwilk, D. W. & Kerr, B. Genetic niche-hiking: an alternative explanation for the evolution of flammability. *Oikos* **99**, 431–442 (2002).

58. Kilian, D. & Cowling, R. M. Comparative seed biology and co-existence of two fynbos shrub species. *J. Veg. Sci.* **3**, 637–646 (1992).

59. Ruprecht, E., Fenesi, A., Fodor, E. I., Kuhn, T. & Tklyi, J. Shape determines fire tolerance of seeds in temperate grasslands that are not prone to fire. *Perspect. Plant Ecol.* **17**, 397–404 (2015).

60. Davies, T. J. et al. Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proc. Natl Acad. Sci. USA* **101**, 1904–1909 (2004).

61. Forest, F. et al. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **445**, 757–760 (2007).

62. Linder, H. P. Evolution of diversity: The Cape flora. *Trends Plant Sci.* **10**, 536–541 (2005).

63. Linder, H. P. The radiation of the Cape flora, southern Africa. *Biol. Rev.* **78**, 597–638 (2003).

64. Latimer, A. M., Silander, J. A. & Cowling, R. M. Ecology: Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hotspot. *Science* **309**, 1722–1725 (2005).

65. Linder, H. P. &Verboom, G. A. The evolution of regional species richness: The history of the southern African flora. *Annu. Rev. Ecol. Evol. Syst.* **46**, 393–412 (2015).

66. Schnitzler, J. et al. Causes of plant diversification in the cape biodiversity hotspot of South Africa. *Syst. Biol.* **60**, 343–357 (2011).

67. Barraclough, T. G. What can phylogenetics tell us about speciation in the Cape flora? *Divers. Distrib.* **12**, 21–26 (2006).

68. Westerweel, J. et al. Burma Terrane part of the Trans-Tethyan Arc during collision with India according to palaeomagnetic data. *Nat. Geosci.* **12**, 5–6 (2019).

69. Poinar, G. O. Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. *Hist. Biol.* **31**, 1304–1309 (2019).

70. Oliveira, I. D. S. et al. Earliest onychophoran in amber reveals Gondwanan migration patterns. *Curr. Biol.* **26**, 2594–2601 (2016).

71. Poinar, G. O., Lambert, J. B. & Wu, Y. Araucarian source of fossiliferous Burmese amber: Spectroscopic and anatomical evidence. *J. Bot. Res. Inst. Texas.* **1**, 449–455 (2007).

72. Cai, C. Y. et al. Basal polyphagan beetles in mid-Cretaceous amber from Myanmar: Biogeographic implications and long-term morphological stasis. *Proc. R. Soc. B* **286**, 2175 (2019).

73. Zhang, W., Li, H., Shih, C., Zhang, A. & Ren, D. Phylogenetic analyses with four new Cretaceous bristletails reveal inter-relationships of Archaeognatha and Gondwana origin of Meinertellidae. *Cladistics* **34**, 384–406 (2018).

74. Metcalfe, I. Palaeozoic and Mesozoic geological evolution of the SE Asia region: multidisciplinary constraints and implications for biogeography. *Biogeography and geology of SE Asia* p. 25–41 (1998).

75. Enay, R. Atlas of mesozoic and cenozoic coastlines. *Geobios* **27**, 572 (1994).

76. Klages, J. P. et al. Temperate rainforests near the South Pole during peak Cretaceous warmth. *Nature* **580**, 81–86 (2020).

77. Coetzee, J. A. & Muller, J. The phytogeographic significance of some extinct Gondwana pollen types from the Tertiary of the southwestern Cape (South Africa). *Ann. Mo. Bot. Gard.* **71**, 1088–1099 (1984).

78. Grimaldi, D., Engel, M. S. & Nascimbene, P. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *Am. Museum Novit.* **3361**, 1–72 (2002).

79. Mao, Y., Liang, K., Yitong, S. U., Jianguo, L. I. & Huang, D. Various amberground marine animals on Burmese amber with discussions on its age. *Palaeoentomology* **1**, 91 (2018).

80. Smith, R. D. & Ross, A. J. Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish waters, and the age of the amber. *Earth Env. Sci. T. R. So.* **107**, 239–247 (2018).

81. Schmidt, A. R. & Dilcher, D. L. Aquatic organisms as amber inclusions and examples from a modern swamp forest. *Proc. Natl. Acad. Sci. USA* **104**, 16581–16585 (2007).

82. Cole, L. E., Bhagwat, S. A. & Willis, K. J. Fire in the swamp forest: palaeoecological insights into natural and human-induced burning in intact tropical peatlands. *Front. For. Glob. Change* **2**, 48 (2019).

83. Labandeira, C. C. Amber. In: Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization. (Paleontological Society, 2014).

84. Seyfullah, L. J. et al. Production and preservation of resins-past and present. *Biol. Rev.* **93**, 1684–1714 (2018).

85. McKellar, R. C. et al. Insect outbreaks produce distinctive carbon isotope signatures in defensive resins and fossiliferous ambers. *Proc. R. Soc. B* **278**, 3219–3224 (2011).

86. Schmidt, A. R. et al. Arthropods in amber from the Triassic Period. *Proc. Natl Acad. Sci. USA* **109**, 14796–14801 (2012).

87. Silvestro, D. et al. Fossil data support a pre-Cretaceous origin of flowering plants. *Nat. Ecol. Evol.* 1–9 (2021).

88. Donoghue, P. Evolution: the flowering of land plant evolution. *Curr. Biol.* **29**, 753–756 (2019).

89. Thulin, M. et al. Family relationships of the enigmatic rosid genera *Barbeya* and *Dirachma* from the Horn of Africa region. *Plant Syst. Evol.* **213**, 103–119 (1998).

90. Wilf, P, Carvalho, M. R., Gandolfo, M. A. & Cúneo, N. R. Eocene lantern fruits from Gondwanan Patagonia and the early origins of Solanaceae. *Science* **355**, 71–75 (2017).
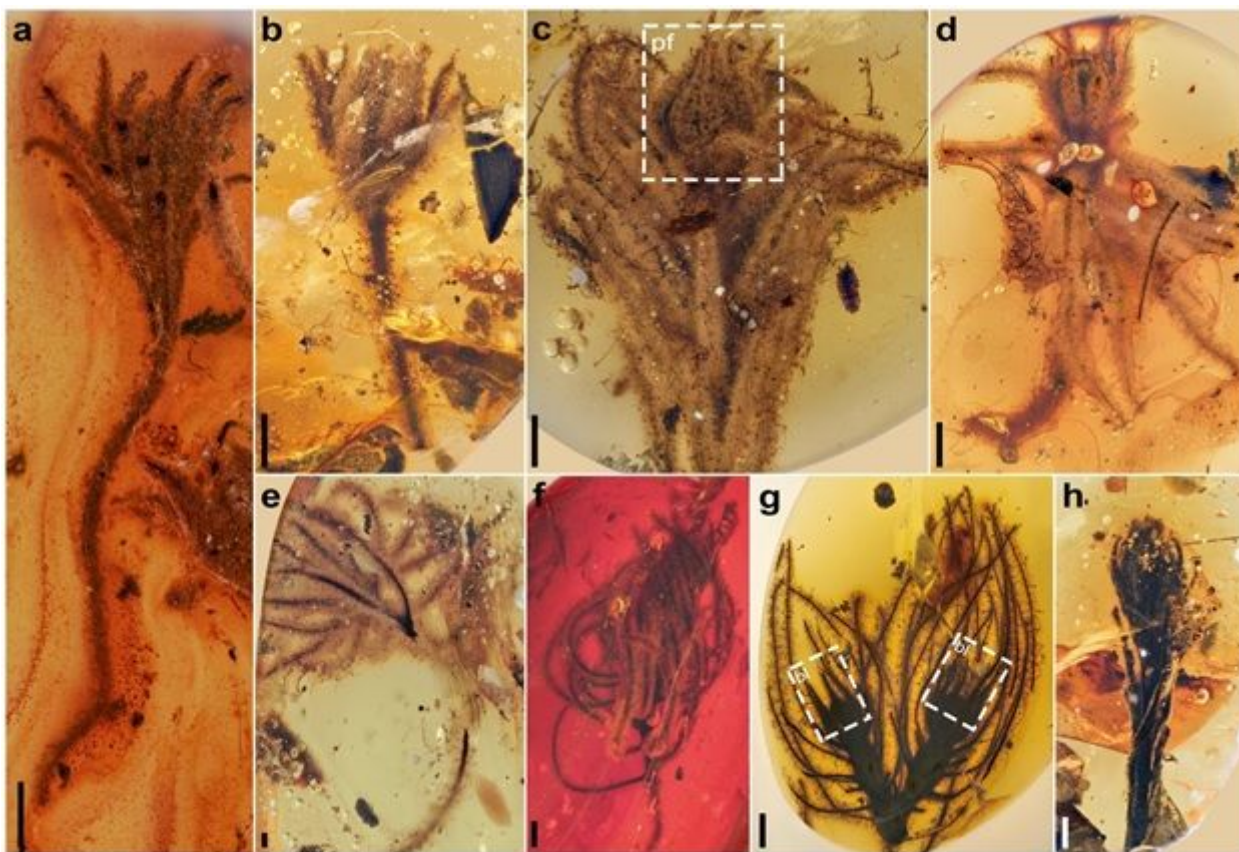
Figures

Figure 1

Morphological diversity of Eophylica priscastellata and Phylica piloburmensis 'pseudo-flower heads' in amber. a-g, E. priscastellata. a, QUST-AM20502. b, QUST-AM20501. c, QUST-AM20505. d, QUST-AM20506. e, QUST-AM20504. f, QUST-AM20510. g, QUST-AM20509. h, P. piloburmensis, QUST-AM20513. These 'feather heads' comprise clustered leaves (or leafy bracts), forming different developmental stages of 'pseudo-flower heads', same as seen in extant species of Phylica26. Abbreviations: pf, 'pseudo-flower heads'; bl, bract-like leaves. Scale bars = 0.5 mm.
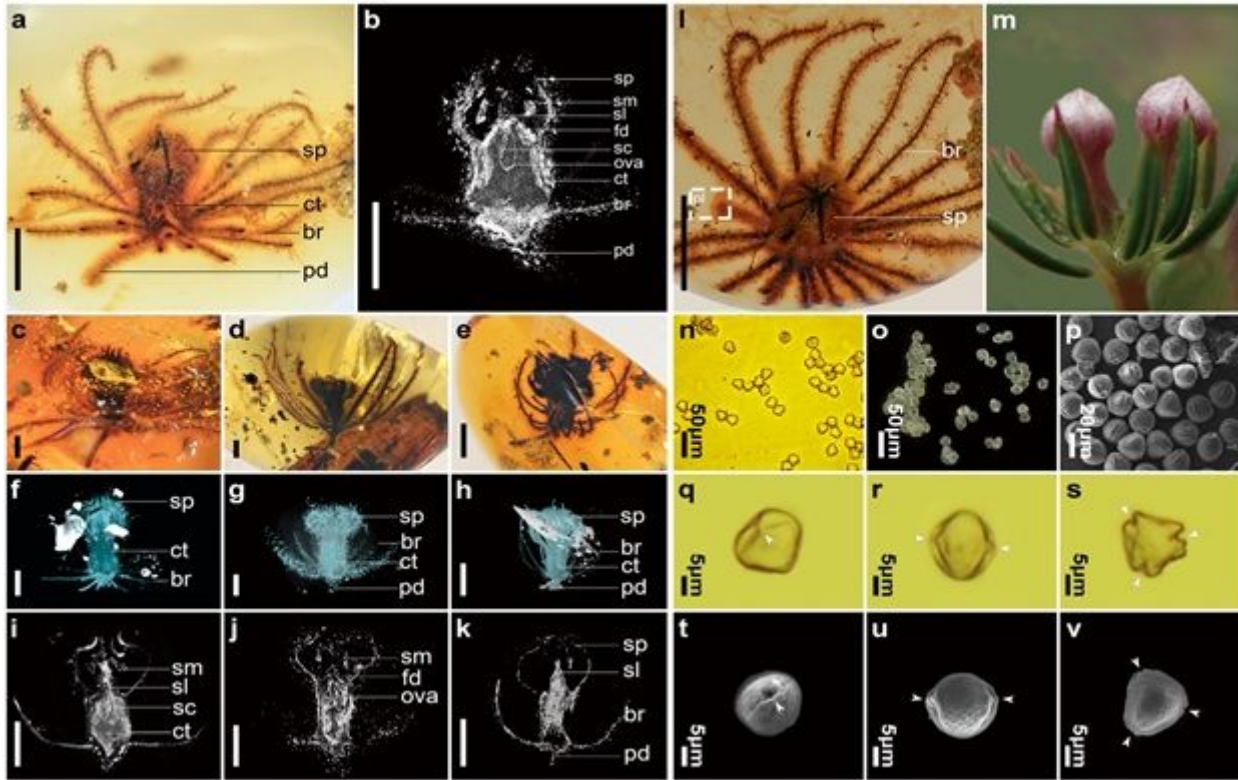

Figure 2

Flowers and pollen of Eophylica priscastellata gen. et sp. nov. a, Lateral view of the holotype of E. priscastellata, QUST-AM32413. b, Micro-XCT scanning of QUST-AM32413, longitudinal section. c, Lateral view of QUST-AM32414. d, Lateral view of QUST-AM32415. e, Lateral view of QUST-AM32416. f, Micro-XCT reconstruction of QUST-AM32414, lateral view. g, Micro-XCT reconstruction of QUST-AM32415, lateral view. h, Micro-XCT reconstruction of QUST-AM32416, lateral view. i, Micro-XCT scanning of QUST-AM32414, longitudinal section. j, Micro-XCT scanning of QUST-AM32415, longitudinal section. k, Micro-XCT scanning of QUST-AM32416, longitudinal section. l, Top view of the holotype of E. priscastellata, QUST-AM32413, clearly showing eight sepals. m, An extant Phylica flower with similar morphology to E. priscastellata. n, q−s, Fossil pollens from QUST-AM32413, position indicated with white border in l. o, Extant pollens extracted from m, image taken with light microscope. p, t−v, Extant pollens extracted from m, image taken with SEM. White arrows on the pollen indicates the colporate ('H') form. Abbreviations: br, bract; ct, calyx tube; fd, flower disc; ova, ovary; pd, peduncle; sc, stylar canal; sl, style; sm, stamen; sp, sepal; pl, pollen. Scale bars = 0.5 mm (unless otherwise indicated).
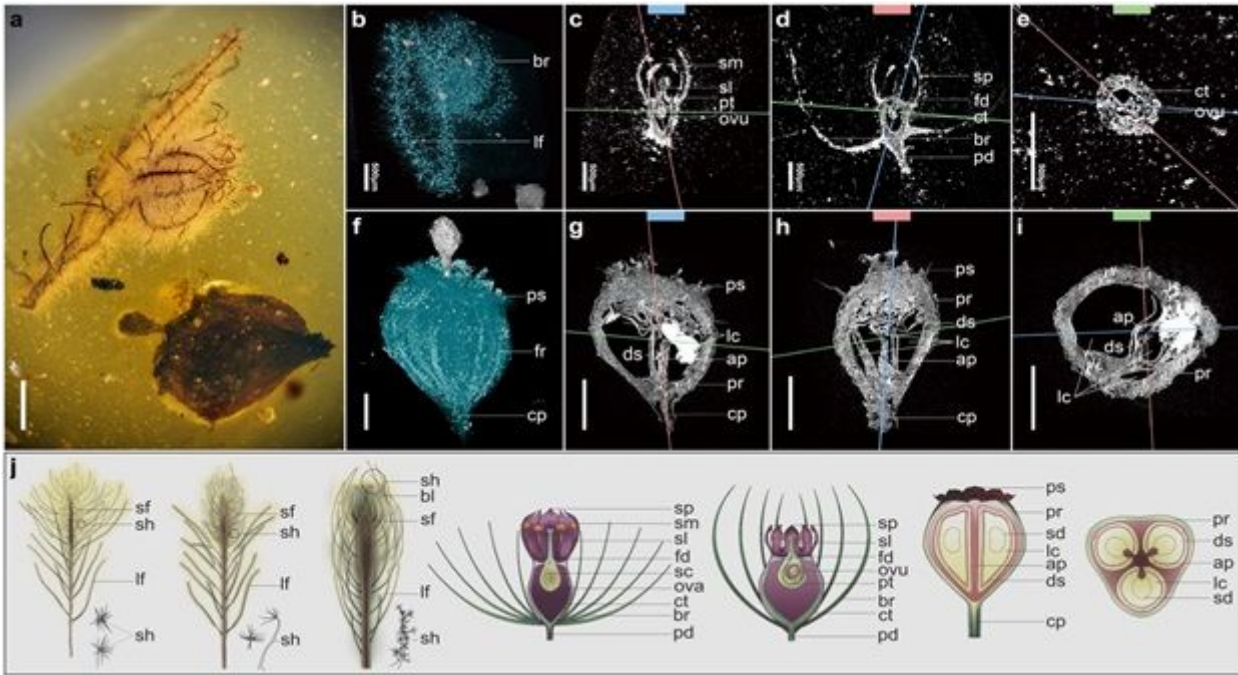
Figure 3

Fruit of Eophylica priscastellata gen. et sp. nov. a, Overall picture showing QUST-AM32417 and QUST-AM33310. b, Micro-XCT reconstruction of QUST-AM32417, lateral view. c–d, Two different angles of micro-XCT scan of QUST-AM32417, both longitudinal section. e, Micro-XCT scan of QUST-AM32417, transverse section. f, Micro-XCT reconstruction of QUST-AM33310, lateral view. g–h, Two different angles of micro-XCT scan of QUST-AM33310, both longitudinal section. e, Micro-XCT scan of QUST-AM33310, transverse section. j, Reconstruction of different developmental stages of E. priscastellata. From left to right, the first three images are reconstructions representing three developmental stages of a 'pseudo-flower head', followed by the immature flower, mature flower, and fruit (viewed in longitudinal and transverse section). Abbreviations: ap, placental axis; bl, bract-like leaf; br, bract; cp, carpopodium; ct, calyx tube; ds, dissepiment; fd, flower disc; fr, fruit; lc, locule; lf, leaf; ova, ovary; ovu, ovule; pd, peduncle; pr, pericarp; ps, persistent sepal; pt, pollen tube; sc, stylar canal; sd, seeds; sf, pseudo-flower; sl, style; sm, stamen; sp, sepal. Scale bars = 0.5 mm (unless otherwise indicated).
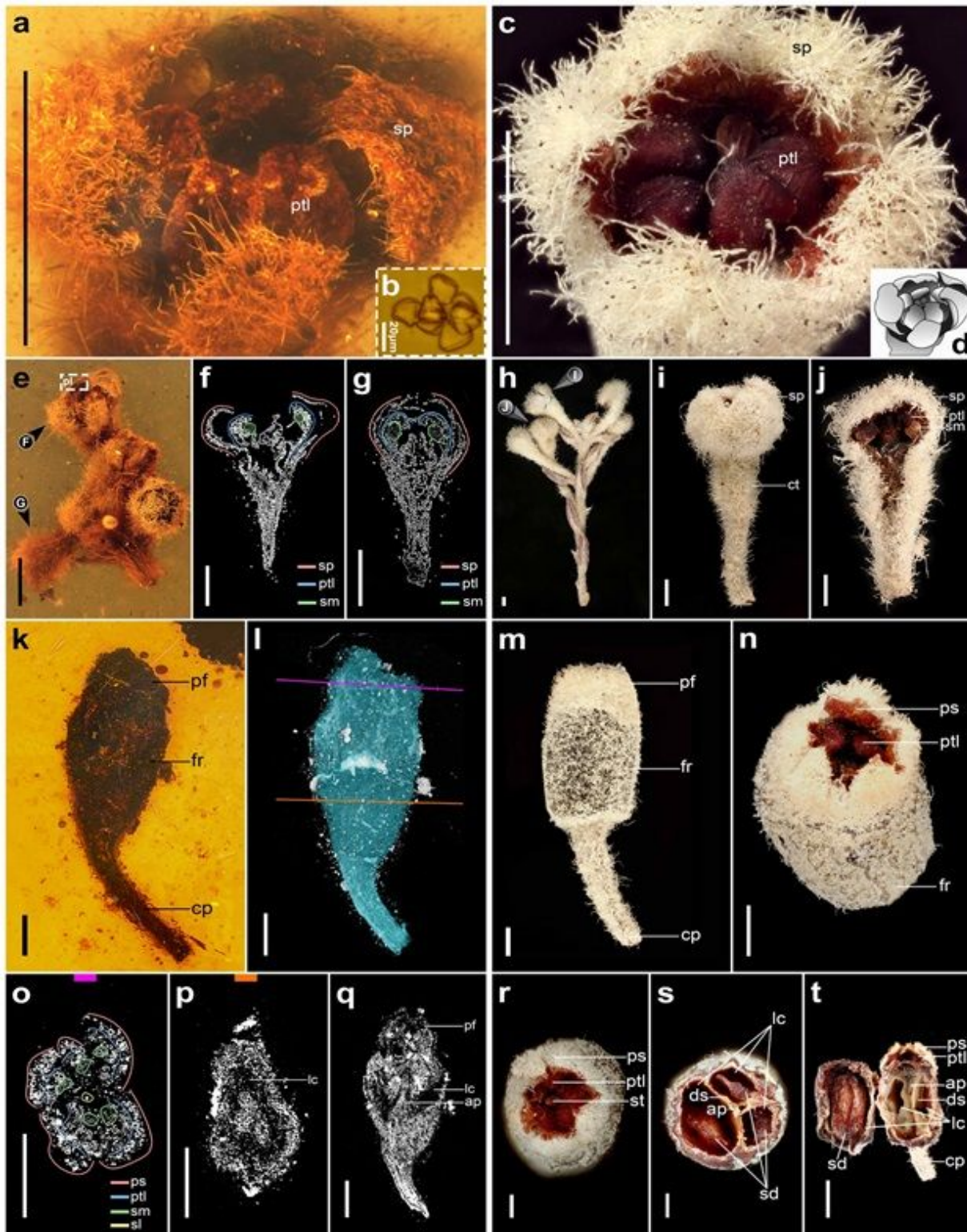
Figure 4

Reproductive organs of Phylica piloburmensis sp. nov. a, b, e−g, QUST-AM32417, holotype. k, l, o−q, QUST-AM33311. c, d, h−j, Flower of extant Phylica axillaries. m, n, r−t, Fruit of extant Phylica axillaries. a, Top view of a semi-opened fossil flower in QUST-AM32417. b, Pollen grains in QUST-AM32417, location indicated in e (pl, pollen). c, Top view of a semi-opened extant flower of P. axillaries. d, Structural representation of the flower of P. axillaries. e−g, The whole fossil inflorescence (e) showing four semi-

opened and unopened flowers. (f, g) Micro-XCT scans of semi-opened and unopened flowers, both longitudinal section. Colours (f, g) distinguish the sepal (sp), petal (ptl) and stamen (sm). h–j, A whole inflorescence of extant P. axillaries (h) longitudinal views of the closed and semi-opened flower (i, j), cf. f and g. k–n, Fruit fossil (k, l; side view) compared with extant Phylica fruit of similar morphology (m, n). (l) Micro-XCT scan of the fruit fossil (k). (n) Top view of the extant fruit showed the persistent flower on the fruit. o–t, Micro-XCT scans of fossil fruit internal structure (o–q) compared with internal structure of a dissected extant fruit (r, t). (o, p, s) transverse sections (colours as in i). (t) Top view. (q, t) Longitudinal view. Abbreviations: ap, axile placenta; cp, carpopodium; ds, dissepiment; fr, fruit; lc, locule; pf, persistent flower; pl, pollen; ps, persistent sepal; ptl, petal; sd, seeds; sh, stellate hairs; sl, style; sm, stamen; sp, sepal. Scale bars = 0.5 mm (unless indicated otherwise).
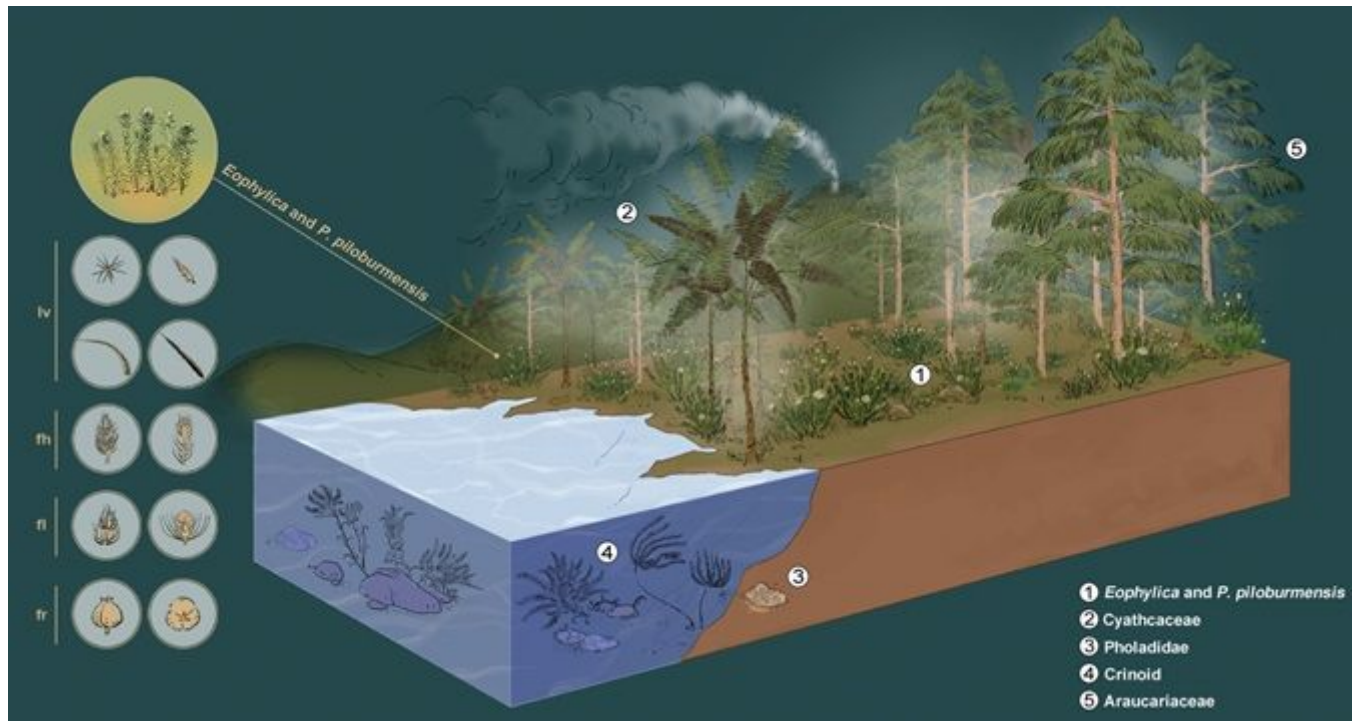

Figure 5

Reconstruction of the palaeoenvironment. This reconstructs the environment of 99 Ma, when Eophylica and P. piloburmensis lived alongside diverse other plants and animals. Abbreviations: lv, leaves; fh, feather head; fl, flower; fr, fruit.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ExtendedData1.docx
- ExtendedData1.docx
- MovieS1.mp4
- MovieS2.mp4

- ExtendedDataTable1.xlsx
- MovieS3.mp4