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Fire-prone Rhamnaceae with South African affinities in Cretaceous Myanmar amber

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The rapid Cretaceous diversification of flowering plants remains Darwin's 'abominable mystery' despite numerous fossil flowers discovered in recent years. Wildfires were frequent in the Cretaceous and many such early flower fossils are represented by charcoalified fragments, lacking complete delicate structures and surface textures, making their similarity to living forms difficult to discern. Furthermore, scarcity of information about the ecology of early angiosperms makes it difficult to test hypotheses about the drivers of their diversification, including the role of fire in shaping flowering plant evolution. 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 together with burned plant remains in Cretaceous amber from northern Myanmar (~99 million years ago). These specialized flower species, named *Phylica piloburmensis* sp. nov. and *Eophylica priscastellata* gen. et sp. nov., exhibit traits identical to those of modern taxa in fire-prone ecosystems such as the fynbos of South Africa, and provide evidence of fire adaptation in angiosperms.

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 million years ago (Ma) and ~65 Ma, that led flowering plants to dominate many land environments by the end of the Cretaceous and replace the incumbent gymnosperms[7], has fascinated evolutionary biologists starting with Darwin who famously referred to the angiosperm radiation as an 'abominable mystery[8]'. However, our knowledge of the early evolution of 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[9–11], but this mode of preservation is only partial, reducing 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 fire regimes and evolution of novel dispersal modes[12–16]; however, to be properly evaluated, all require 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 the other a sister to the genus, both preserved in Cretaceous amber from the Hkamti and Tanaing mines (Supplementary Figs. 1–3), northern Myanmar, dated to at least 99 Ma (110–99 Ma for *Eophylica priscastellata* and 99 Ma for *Phylica piloburmensis*; Supplementary Note 1)[17–20]. These fossil flowers were previously misidentified as conifers[21] or green algae[22], and are quite common in amber assemblages, where the flora

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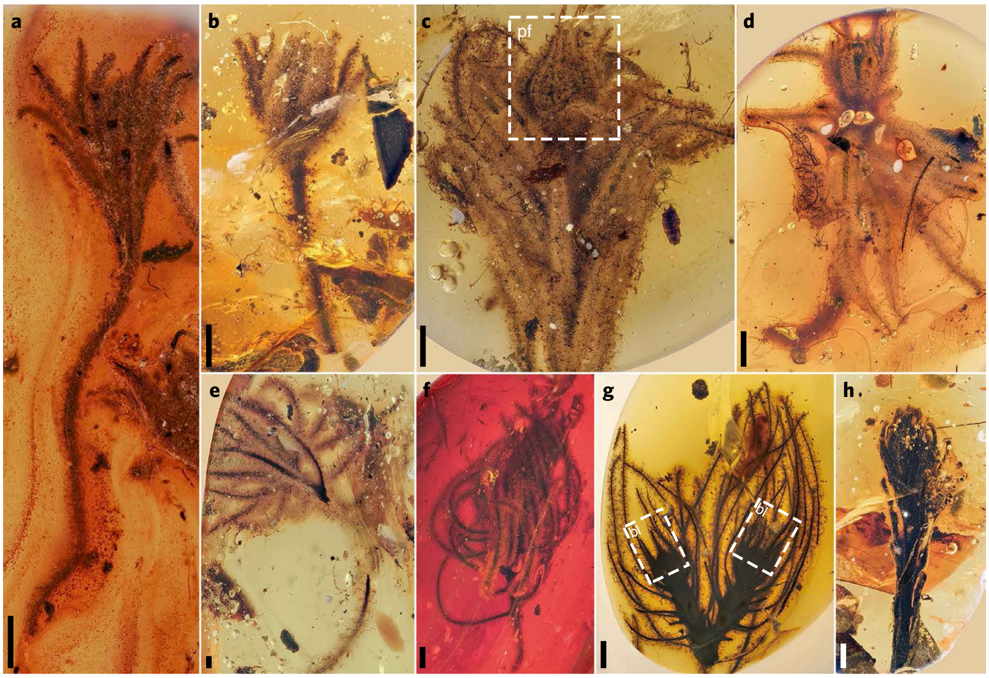

Fig. 1 | Morphological diversity of *E. priscastellata* and *P. piloburmensis* 'pseudanthium head' in amber. a–g, *E. priscastellata*. QUST-AM20502 (**a**), QUST-AM20501 (**b**), QUST-AM20505 (**c**), QUST-AM20506 (**d**), QUST-AM20504 (**e**), QUST-AM20510 (**f**), QUST-AM20509 (**g**). **h**, *P. piloburmensis*, QUST-AM20513. These 'feather heads' comprise clustered leaves (or leafy bracts), forming different developmental stages of 'pseudanthium head', similar to that seen in extant species of *Phylica*[26]. pf, 'pseudanthium head' (dashed rectangle in **c**); bl, bract-like leaves (dashed rectangle in **g**). Scale bars, 0.5 mm.

is dominated by gymnosperms, including the extinct Bennettitales (Supplementary Fig. 4), accompanied by diverse angiosperms[23–25]. The exceptionally preserved flowers possess linear pubescent xeromorphic leaves (seemingly needle-like and tightly clustered with densely stellate or linear hairs) typical of vegetation adapted to seasonally dry and fire-prone conditions (Fig. 1), and burned plant remains also occur within the amber assemblages. Our results provide evidence of fire-adapted angiosperms from the Cretaceous, supporting the hypothesis that fire represented a biologically important selective pressure in some Cretaceous ecosystems. The fossils demonstrate that specialized floral adaptations to frequent burning arose early in angiosperm evolution and have 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 and fire-prone fynbos flora[26,27]. 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 ~35 Ma[28,29] and suggests that the fynbos flora may contain other elements typical of an ancient vegetation type that evolved in the fire-prone Cretaceous[30].

Results

Systematic paleontology. 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. (Figs. 2 and 3).

Etymology. The generic name is a combination of the Greek words, Ēṓs (*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 8 sepals (2 × 4-merous) (versus 5 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*). 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 Supplementary Note 2.

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').

Eophylica priscastellata Shi, Wang et Engel sp. nov.

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 epigynous and covering inside of calyx tube. Sepals 8 (2 × 4-merous). Petals absent. A complete description is provided in Supplementary Note 2.

Genus *Phylica* L., 1753

Phylica piloburmensis Shi, Wang et Engel sp. nov. (Fig. 4)

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

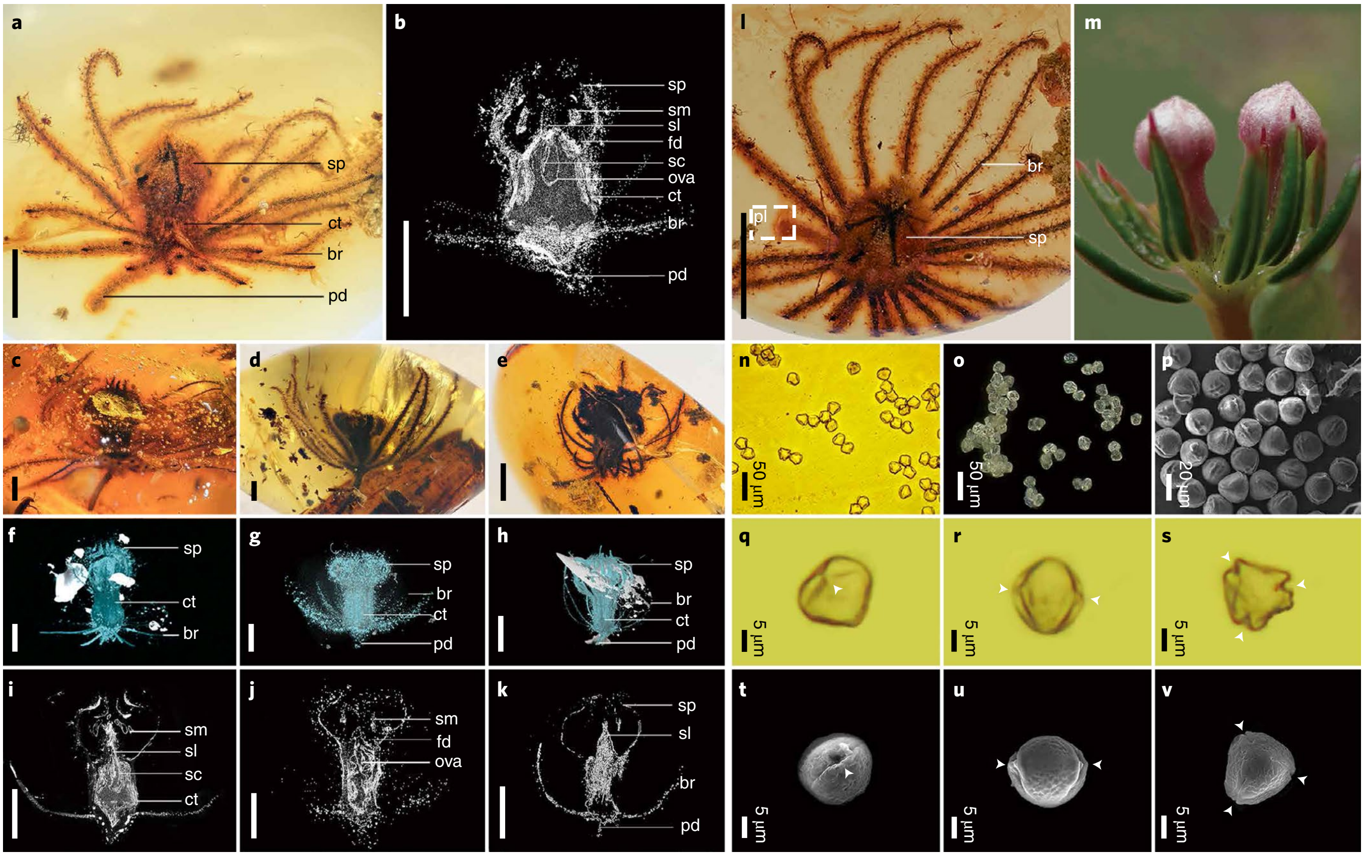

Fig. 2 | Flowers and pollen of *E. priscastellata* gen. et sp. nov. a,**b**, Holotype of *E. priscastellata*, QUST-AM32413. Lateral view (**a**) and micro-XCT scan, longitudinal section (**b**). **c**–**e**, Lateral view of QUST-AM32414 (**c**), QUST-AM32415 (**d**) and QUST-AM32416 (**e**). **f**–**h**, Micro-XCT reconstruction, lateral view of QUST-AM32414 (**f**), QUST-AM32415 (**g**) and QUST-AM32416 (**h**). **i**–**k**, Micro-XCT scans, longitudinal section of QUST-AM32414 (**i**), QUST-AM32415 (**j**) and QUST-AM32416 (**k**). **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 pollen grains from QUST-AM32413 (position indicated by white border in **l**) were photographed with the light microscope. **o**,**p**,**t**–**v**, Images of extant pollen grains extracted from **m**, taken with light microscope (**o**) and with scanning electron microscope (**p**,**t**–**v**). **t**–**v** Single pollen grain of different side view. White arrowheads on the pollen indicate the colporate ('H') form. 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).

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 and 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 capitulum. Petals present. Fruit covered with dense indumentum. A complete description is provided in Supplementary Note 2.

Ecomorphological conservatism in 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[31]. Specifically, leaves clustered at the twig tip surrounding either a flower, or a 'pseudanthium head', is a feature unique to *Phylica* (Fig. 1, Supplementary Figs. 7–20 and Video 1)[32]. On the basis of presence or absence of petals, the number of sepals and the form of hairs of the indumentum, we assigned 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 presence or absence of petals reflecting morphologies seen in extant *Phylica*[32]. A close relationship between *Eophylica* and *Phylica* is supported by comparative morphological and phylogenetic reconstructions based on flowers, fruits and pollen grains (Figs. 2–4, Supplementary Figs. 21–30 and Videos 2–3). *E. priscastellata* can be distinguished from *P. piloburmensis* 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, afforded by 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 are exceptionally rare in Myanmar amber, but are known to occur, and we believe future data will corroborate our conclusions regarding the identity of *P. piloburmensis*. We provide formal descriptions of the new fossil taxa in Supplementary Note 2.

The clustered, needle-like dry leaves are typical of fire-adapted angiosperms (Fig. 1)[26,30]. Taxonomically, needle-like leaves clustered around the stems of a small shrub (Fig. 1 and Supplementary

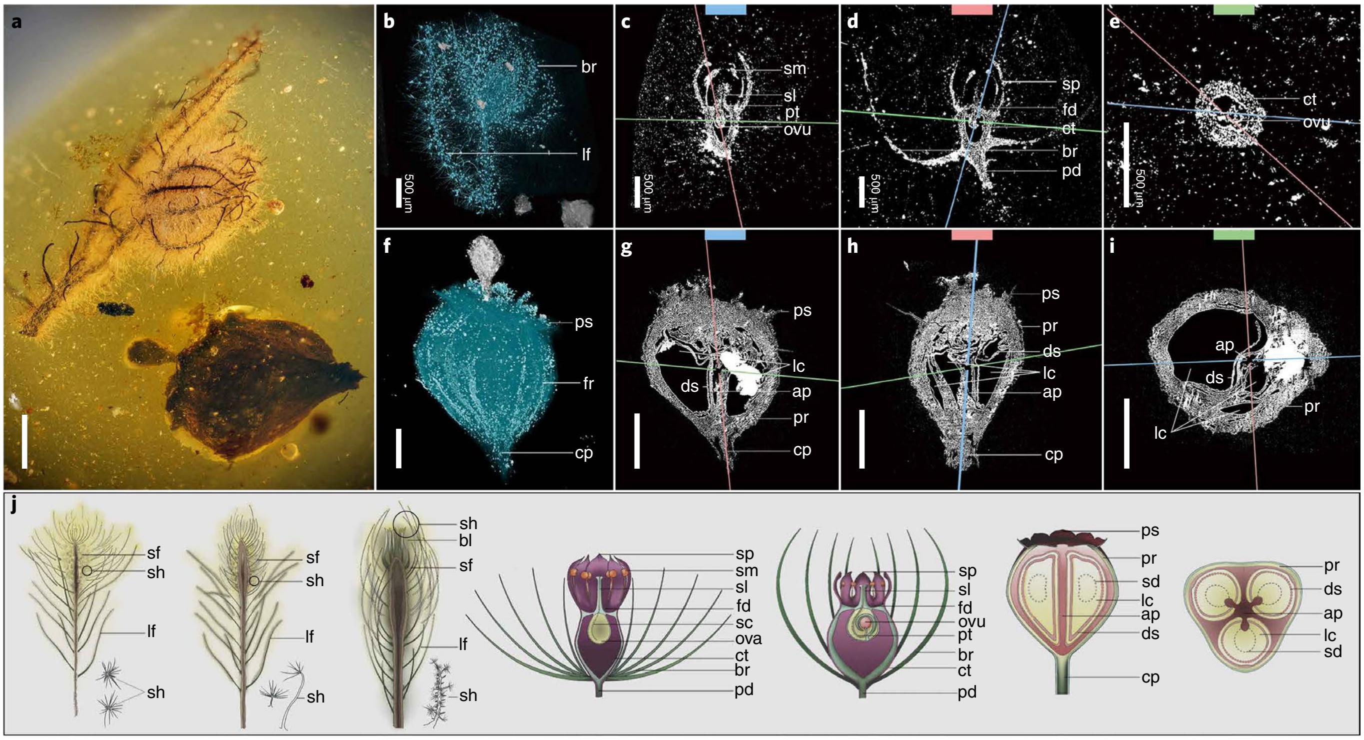

Fig. 3 | Fruit of *E. priscastellata* gen. et sp. nov. a, Overall picture showing QUST-AM32417 and QUST-AM33310. **b**, Micro-XCT reconstruction of QUST-AM32417, lateral view. **c**,**d**, Two different angles of micro-XCT scan of QUST-AM32417, both longitudinal section. **e**, Micro-XCT scan of QUST-AM32417, 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. **i**, 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 'pseudanthium head', followed by the immature flower, mature flower, and fruit (viewed in longitudinal and transverse sections). ap, placental axis; bl, bract-like leaf; cp, peduncle carpopodium; ds, dissepiment; fr, fruit; lc, locule; lf, leaf; ovu, ovule; pr, pericarp; ps, persistent sepal; pt, pollen tube; sd, seeds; sf, pseudanthium; sh, stellate hairs. Scale bars, 0.5 mm (unless otherwise indicated).

Figs. 7–20) are typical of *Phylica* and quite distinct from other genera of Rhamnaceae[32]. Non-*Phylica* species in Rhamnaceae have broader leaves, except for some species in the genera *Trymalium*, *Siegfriedia* and *Colletia*. Specialized narrow leaves have been considered an adaptation to the relatively dry Cape climate[33] and frequent wildfires[34]. Many fynbos angiosperms (for example, *Erica* (Ericaceae), *Aspalathus* (Fabaceae), *Ruschia* (Mesembryanthemaceae), and *Agathosma* (Rutaceae)[26]) and some non-fynbos clades (for example, *Brunia* and *Berzelia* (Bruniaceae)) also have narrow, clustered leaves. However, species of *Phylica* differ in having one or more of the following[32]: leaves at the tip of the stem form 'pseudanthium head' 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 pseudanthium head in these fossils is distinctive within angiosperms[32]. It is exclusive to some extant species of *Phylica* (for example, *P. pubescens* and *P. plumosa*; Supplementary Fig. 10e–j)[32,35], where it represents an intermediate developmental stage from vegetative growth to the flowering phase (Fig. 1, Supplementary Figs. 7–20 and Video 1)[32]. The head comprises many tightly clustered scale-like bracts, with mature leaves or bracts (below the true flower) developing later. Despite having a similar 'head' shape, the pseudanthium bracts are morphologically distinct from those of the true flower (Fig. 2m)[32].

True flowers of *Phylica* are small (~1.0 mm), 5(4)-merous, have an inferior ovary and are densely pubescent. They combine the following diagnostic characters (Figs. 2–4, Supplementary Figs. 21–26 and Video 2)[32,35,36]: 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; hypanthia 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. Specially, as in extant *Phylica*[32,36], both fossils presented herein have a lengthened perianth tube (Figs. 2a,c–h, 4e–g and Supplementary Figs. 21–24, 26).

The fruits of the two new fossil species are typical capsules (Figs. 3f, 4k, Supplementary Figs. 27–28 and 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 and 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[32], fossil fruits of *Eophylica* and *P. piloburmensis* are notably larger than the flower (≥5 mm wide) (Supplementary Figs. 27 and 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. 27m,n). As in extant *Phylica*[32], 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).

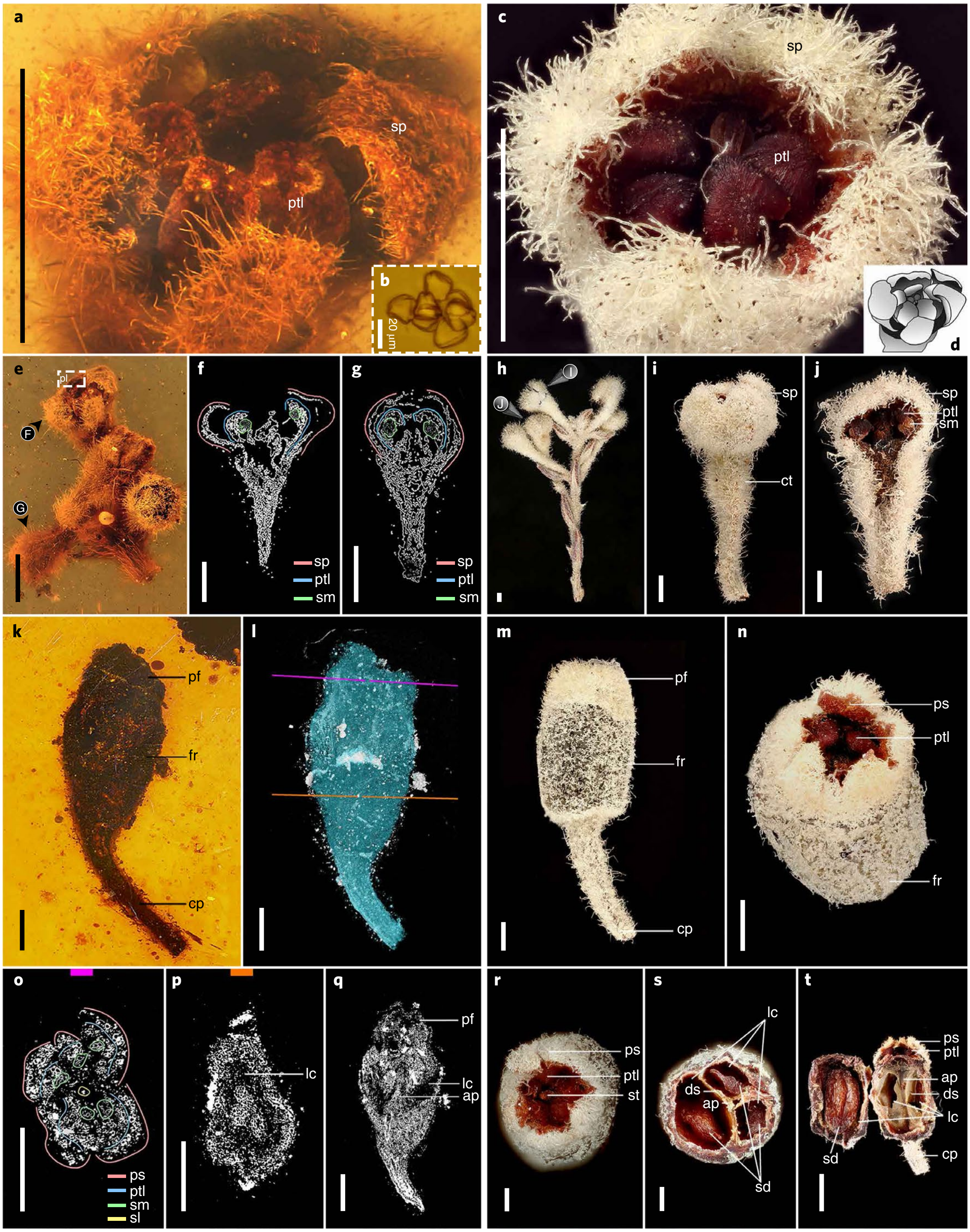

Fig. 4 | Reproductive organs of *P. piloburmensis* sp. nov. a–d, Flowers of QUST-AM32417 holotype (**a**,**b**) and extant *P. axillaris* (**c**,**d**). QUST-AM32417: top view of a semi-opened fossil flower (**a**) and pollen grains (**b**), with location indicated in **e** (pl, pollen). *P. axillaris*: top view of a semi-opened extant flower (**c**) and structural representation of the flower (**d**). **e**–**j**, Whole inflorescence of QUST-AM32417 (**e**) and extant *P. axillaris* (**h**). **e** shows four semi-opened and unopened flowers of QUST-AM32417, with micro-XCT scans of semi-opened and unopened flowers (both longitudinal section) shown in **f** and **g**, respectively. Colours (**f**,**g**) distinguish the sepal (sp), petal (ptl) and stamen (sm). **i** and **j** show longitudinal views of the closed and semi-opened flowers of extant *P. axillaris*, respectively (cf. **f** and **g**). **k**–**n**, Fruit of QUST-AM33311 (**k**, side view; **l**, side view, micro-XCT scan) and extant *Phylica* fruit (**m**,**n**) of similar morphology. In **n**, the top view of the extant fruit shows the persistent flower on the fruit. **o**–**t**, Fruit internal structure of QUST-AM33311 (**o**–**q**) and extant *P. axillaris* (**r**–**t**). In **o**–**q**, micro-XCT scans of fossil fruit internal structure are shown, compared with internal structure of a dissected fruit of extant *P. axillaris* (**r**–**t**). **o**, **p** and **s** are transverse sections; **r** is top view; **q** and **t** are longitudinal views. pf, persistent flower; ptl, petal. Scale bars, 0.5 mm (unless indicated otherwise).

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 polar view. An affinity with the Rhamnaceae is further supported by the following features[37]: (1) medium-sized with polar axes of 21–24 μm and equatorial diameters of 18–21 μm (P/E ratio: 1.2); (2) colpi long, narrow and with blunt ends; and (3) the middle of the aperture lalongate, with two ends connected to 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[38]. As in our fossils, extant *Phylica* is a morphologically divergent clade of the Rhamnaceae that exhibits only some plesiomorphic characters seen in the family[32]. Although a lengthened cyathiform calyx tube and enfolding sepals and petals are important flower characteristics of living *Phylica*, they obscure important internal Rhamnaceae characters (that is, 4- or 5-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 (5 in *P. piloburmensis* and 8 (2 × 4-merous) in *E. priscastellata*), which are valvate in the bud (Figs. 2b,l and 4e–g); 5 or 8 (2 × 4-merous; *E. priscastellata*) stamens that alternate with the sepals and are 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)[39]. These features, combined with crowding leaves (Fig. 1), are characteristic of Rhamnaceae[39].

Phylogenetic analysis integrating morphological and molecular partitions (Supplementary Notes 6 and 7) confirmed crown-group membership of both fossil species (Fig. 5a and Supplementary Fig. 30). Although one major character (the presence of stellate hairs) makes the fossil *E. priscastellata* different from all extant species of *Phylica* (Supplementary Table 1), our new fossil species exhibit other features common to extant *Phylica*. In *E. priscastellata*, the leaves and twigs are similar to 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. 27m,n). Moreover, the leaves, flower and fruit characteristics of *P. piloburmensis* are also present in many other extant species of *Phylica* (represented by extant *P. axillaris*; Fig. 4c,h–j,m,n)[32]. 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-adapted angiosperms in the Cretaceous. The mid-Cretaceous (Albian–Turonian; 112–90 Ma) was exceptionally warm, with some of the highest temperatures in Phanerozoic geological history[40,41] and a relatively shallow temperature gradient between the poles and the tropics[42]. Elevated atmospheric oxygen levels in the Cretaceous (23–29% compared with 21% at present[43–46]) and abundance of charred plant fossil remains in the rock record[47–51] suggest that fires were frequent during this period[14,52–58]. Some hypotheses of angiosperm 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[13,14,59]. By providing a new source of fuel, angiosperms may have also substantially altered the existing fire regimes, to the disadvantage of gymnosperms[13,15,60]. There is abundant evidence that fires burnt vegetation containing angiosperms in the Cretaceous[13], the most remarkable examples being three-dimensionally preserved charcoalified flowers, fruits, seeds and other organs of angiosperms co-occurring with burned remains of gymnosperms and free-sporing plants[10,11,61]. Moreover, previous molecular clock studies have inferred a Cretaceous origin of fire-proneness in some gymnosperm (Pinaceae[62,63]) and angiosperm (Proteaceae, Myrtaceae, Haemodoraceae and Restionaceae[54,64–66]) lineages. However, direct palaeontological evidence of fire-prone traits are scarce, primarily because such traits evidently have low preservation potential[67,68].

Fossil *Eophylica* and *Phylica* inflorescences preserve unambiguous morphological hallmarks of fire-adapted angiosperms. Many fire-prone plants are 'drought resisters'[34,69] and *Eophylica*–*Phylica* belong to this group. Numerous Cape species (such as species in the 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 burned stems[69]. *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[70,71]. 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[72], their seeds accumulate in the soil and germinate after fire[73,74]. Their relatively small and rounded seeds are easily incorporated into the soil and reach greater depths than larger seeds, and is linked to their ability to form long-term persistent seed banks[75,76]. Our discoveries of burned plant remains in associated amber pieces further provide direct evidence for a community living in a fire-prone environment (Supplementary Fig. 5).

An early Gondwanan origin. Fossil *Eophylica* 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 (±90,000 km^2), of which almost 70% are endemic[77]. Much of this diversity is due to a handful of speciose clades (the 'Cape floral clades') that, including *Phylica*[31,78,79], have traditionally been regarded as having radiated within the Cape[31,78,79]. Geological studies and fossil evidence[80–84] indicate a Gondwanan origin for the diverse biota in Myanmar ambers, but two alternative pathways for its transport to Myanmar, either via the West Burma Block or the Indian Plate, were possible[80]. Although palaeomagnetic studies indicate that the West Burma Block 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[85,86], our result indicates that the biota may equally well have drifted northward on the Indian Plate after it separated from Madagascar and southern Africa at approximately 88–90 Ma[64,80,87], just after the formation of the Myanmar amber (110–99 Ma; Fig. 5). Thus, when the Myanmar ambers were forming, the ancestor of *Phylica* had an ancient distribution within the united Gondwana and was possibly widespread at middle southern latitudes, including parts of Africa. Its survival today at a similar latitudinal band, but under a cooler global climate, suggests that it may be close to the edge of its natural climatic tolerance envelope (Fig. 5).

Our results demonstrate that a key element of the xeromorphic fynbos vegetation existed as long as 99 Ma ago, as well as the great antiquity of open fire-prone vegetation in Gondwana[64]. Given that southern Gondwana during the middle Cretaceous (Albian–Turonian; 112–90 Ma) was arid to semi-arid[88,89], possibly 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[30] (Fig. 6). However, whether or not the fynbos biome itself dates back to the Cretaceous remains to be tested with the aid of further plant fossils. Miocene pollen assemblages from the southwestern Cape are noted to be comparable with those of Australian floras[90], although some of these Gondwanan elements were lost after climatic changes at the end of the Miocene. There are no Cretaceous fossil records in the Cape, but offshore records from the West Coast exhibit abundant conifer pollen[91–93]. This could be

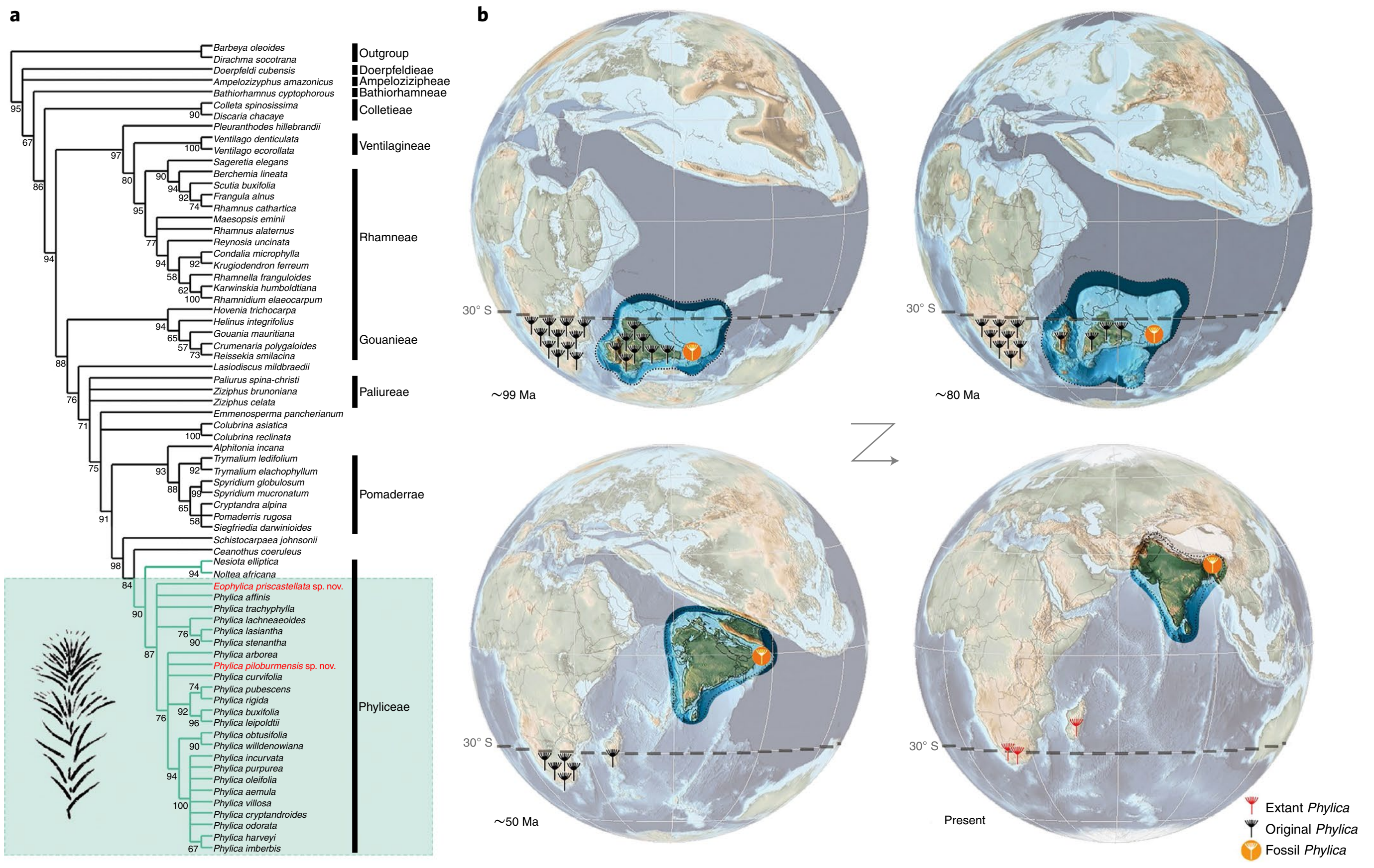

Fig. 5 | Early origin in Gondwana. a, Strict consensus phylogenetic tree (consistency index = 0.418968, retention index = 0.834995) showing the phylogenetic position of two fossil species (*E. priscastellata* gen. et sp. nov. and *P. piloburmensis* sp. nov.) on a total evidence analysis using morphology and seven gene partitions. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) is shown next to the branches. **b**, Transportation of amber fossils from Gondwana after 99 Ma to present-day Myanmar via northward drift of the Indian Plate. At ~99 Ma, the Indian Plate (including Madagascar) split from southern Gondwana (Southern Africa, Australia, Antarctica) and began to move north. At ~80 Ma, India and Madagascar separated, and Madagascar became isolated as the Indian Plate moved northward, colliding with Asia (at ~60–50 Ma), after which the fossils reached their current location in Myanmar. The proposed distributions of extant and fossil *Phylica* are also indicated on the map. Most of the extant *Phylica* species are distributed near 30° S, while the ancient distribution of this genus was at slightly higher latitudes (Supplementary Note 8).

a taphonomic effect due to the high productivity and wind dispersal of conifer pollen compared with the lower pollen productivity and more targeted dispersal of the insect-pollinated shrub and herb components typical of fynbos-type vegetation[94]. Notably, herb pollen declines in abundance moving offshore[94]. Inland records from kimberlite pipes show a mixed flora with some fynbos elements (Proteaceae, Ericaceae and Restionaceae) in the Palaeogene in a tropical to warm temperate environment[95]. From the southwestern Cape coast (where fynbos occurs today), fynbos elements were present (restios, ericas, proteas) during the Oligo-Miocene, mixed with palm and miombo floras, and interpreted as tropical to subtropical forest with lianas, vines, evergreen trees, palms and ferns[96–98]. Taken together, these lines of evidence point towards a much more 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[99], famous for its well-preserved vertebrate remains and abundant insect fossils. The Myanmar amber palaeoenvironment is most often reconstructed as a hot tropical forest[99], with a near-equatorial climate[85] located in the vicinity of brackish water and the seashore[19,100,101], perhaps akin to modern swamp forests[102]. *Eophylica* and *Phylica* fossils and associated burned plant remains 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[103]. Major fires and subsequent drought may have been associated with some amber deposits, such as the Cretaceous New Jersey amber that contains abundant charred remains of plants and insects[104], and fire is a common cause of resin production in fire-prone vegetation today[105]. It is probable that seasonal fires may have also played a role in the production of Myanmar amber, one of the largest amber deposits in the world, since resin secretion can be triggered by wounding, including fire wounds[105,106], as well as any stresses that impact water uptake (for example, insect infestation, drought, etc[107,108].). Notably, burned plant remains are abundant in our ambers (Supplementary Fig. 5) and it is clear that these remains were charred prior to resin entrapment. 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[109].

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

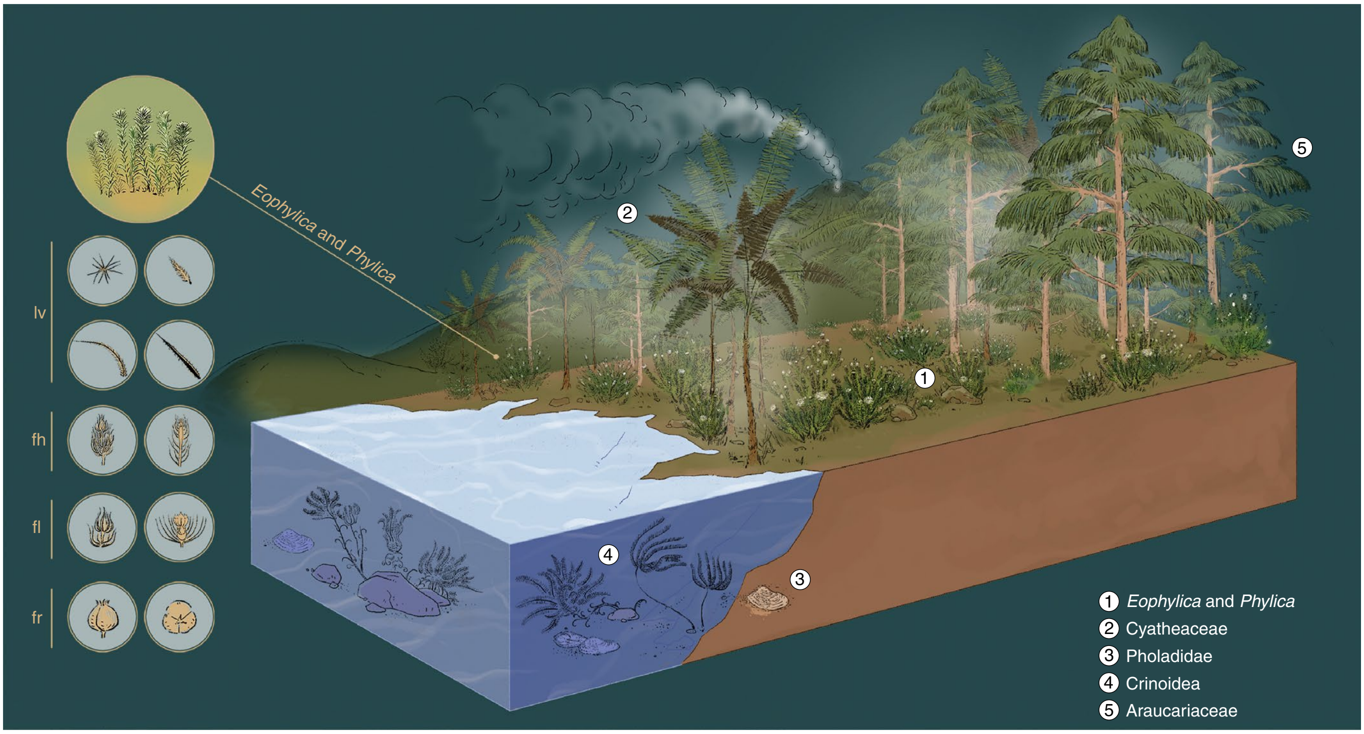

Fig. 6 | Reconstruction of the palaeoenvironment. The environment of 99 Ma, when *Eophylica* and *Phylica* lived alongside diverse other plants and animals. lv, leaves; fh, feather head; fl, flower.

at least 35 Myr[28,29]. This makes *Eophylica–Phylica* one of the best documented 'living fossil' clades in the angiosperm fossil record. Our study also 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[10,11]. First, most compression fossils are preserved primarily in wetlands, while amber palaeoenvironments range from warm forests to seashores[104], capturing a different set of palaeoenvironments. Second, 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[71,110,111].

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[17]. The mines are introduced in Supplementary Note 1. The amber has been radiometrically dated to the earliest Cenomanian, ~99 Ma, and was not produced earlier than the late Albian[18,19]. 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, in 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 specimens, such as colour, density, optical character, refractive index, amber flow characteristics and absorption spectrum.

All 21 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* gen. et sp. nov., and QUST-AM32127, QUST-AM33311, QUST-AM20513–14 for *P. piloburmensis* sp. nov. (Supplementary Fig. 6). Of the 21 pieces of amber, 19 originate from the 'Tanaing' amber mine in Hukawng Valley, except for QUST-AM20511 and QUST-AM32414, which originate from the nearby 'Hkamti' mine (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).

To examine internal structures of the flowers, fossils were scanned with Xradia Versa Micro-XCT 620 (Carl Zeiss X-ray Microscopy) 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. Clear scanned images were obtained for 20 of the 22 fossil specimens, but the other 2 samples lacked sufficient contrast for scanning. The obtained image stacks were reconstructed with Dragonfly (ORS). Final figures were prepared with Photoshop CS5 and Illustrator CS5 (Adobe).

Character scoring and phylogenetic analysis. Morphological characters scored from leaf, habit, flower, fruit and pollen were compiled from previous studies[35,36,112] and are described in Supplementary Note 6. The combined phylogenetic tree was reconstructed on the basis of morphological characters and molecular data following the method of Wilf et al.[113]; the procedure is further described in Supplementary Note 7.

Statistics and reproducibility. During the photographing, micrographs for each fossil were taken repeatedly (5 to 30 repeats) to ensure consistency, and the detailed micrographs for each fossil are exhibited in Supplementary Figs. 5–29.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The Micro-XCT scanning data are available at Zenodo (https://doi.org/10.5281/zenodo.3997200). Videos of the 3D reconstruction of internal and external structures of the fossil specimens are available at Figshare (https://doi.org/10.6084/m9.figshare.12865859.v4). High resolution images of all the figures are available at Figshare (https://doi.org/10.6084/m9.figshare.12845144).

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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.-y.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., Y.F., X.-c.Z. and H.S. performed specimen identification and morphological analyses. C.S., H.-h.C., X.-x.L., H.-r.Z., J.Y., R.-x.J., Q.F., W.-c.S., H.-y.Y.,

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.

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	CT data were reconstructed with Dragonfly Pro 4.1.
Data analysis	Phylogenetic analyses were performed using TNT 1.1 and RAxML 8.2.

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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).

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Description of two fossil species from 21 amber pieces from Myanmar.
Research sample	A total of 21 amber pieces related to two fossil species were found among all our amber collection.
Sampling strategy	The fossil species were quite rare in the amber collection. Since we used all of them in the study, so no statistical methods were used to determine sample size.
Data collection	These 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). Some specimens were also supplementarily photographed using a microscope Leica DVM6 and M205FA (Leica AG, Heerbrugg, Switzerland). Chao Shi recorded the data.
Timing and spatial scale	Our study was initiated in 2015 and all amber specimens were acquired from local sellers before December 2016.
Data exclusions	No data were excluded.
Reproducibility	Every micrographs were taken repeatedly (5 to 30 repeats) to ensure consistency.
Randomization	All fossil specimens were selected (not randomly selected) for our study.
Blinding	The fossils were used for morphological description but not for experimental test, thus blinding is not applicable to our study.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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Methods

n/a	Involved in the study
☒	☐ ChIP-seq
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Palaeontology and Archaeology

Specimen provenance	The material described herein originates from two amber mines located in the Hukawng Valley, Kachin State in northern Myanmar 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 source and preservation of fossils are in full compliance with the laws of Myanmar and China, including Myanmar's import and export regulations of jewelry and China's laws and regulations on museum. The present fossils have been 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).
Specimen deposition	All 21 pieces of ambers (including 22 fossils) are curated at the Amber Museum of National University Science Park, Qingdao University of Science and Technology under collection number 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.

Dating methods	No new dates are provided.

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Ethics oversight	No ethical approval or guidance was required

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