



DETECTION OF IN SITU RESINOUS TRACES IN JURASSIC CONIFERS FROM FLORAS LACKING AMBER

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Abstract: Amber deposits are rare in Jurassic successions, occurring in small quantities, whereas Lower Cretaceous strata host many substantial and commonly fossiliferous amber deposits worldwide. Minor amounts of Early Jurassic amber have been reported from Italy, and small amounts of Late Jurassic amber are known from Lebanon, Jordan and Thailand. Other Jurassic amber deposits that require reinvestigation of their age and provenance have also been reported from Denmark and France. Few of these amber deposits contain fossils, the others lack inclusions, suggesting a ‘Jurassic amber gap’ in the fossil record. Here, we surveyed fossil plant collections held at the Swedish Museum of Natural History, Stockholm, for amber and amber-producing plants from Jurassic floras. We focused on the collection of plants from Shaanxi, China and the Middle Jurassic floras of Iran and Afghanistan from the H.-J. Schweitzer collection. Using a hand-held UV light microscope, we scanned the collections for resinous remains as ambers can show autofluorescence with UV light, but found no dispersed amber fragments or droplets. Some researchers refer to fossilized resin within plant tissues under that name to differentiate it from exuded resins preserved as amber, and we follow this convention. We identified a conifer fragment of *Elatocladus* sp. from China with in situ rods of resin preserved in the leaves and a unique conifer twig (*Elatides* sp.) from Afghanistan with tiny linear resin traces in leaves that were only visible via autofluorescence with UV light. These resinous traces likely define the former position of resin canals in the leaves, but the resin is not preserved as in situ rods. Instead, it has impregnated the coalified mesophyll, likely during fossilization, to form thin lines (chemical ‘ghosts’ of preserved resin) within the conifer leaf remains.

Key words: Afghanistan, autofluorescence, Cheirolepidiaceae, China, Cupressaceae, *Elatides*, *Elatocladus*, fluorescence, Jurassic amber gap, resin, UV light

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Introduction

Amber (fossilised exuded plant resin) is known from the rock record as finely disseminated droplets to massive aggregates tens of kilograms in mass that sporadically contain excellently preserved fossils. However, amber is not uniformly distributed through the geological record. Instead, four time intervals are particularly rich in amber deposits: the Carnian (Late Triassic), the Cretaceous, the Eocene to Oligocene, and the Miocene (Seyfullah et al. 2018a). In sharp contrast to the amber-rich Carnian (e.g., Roghi et al. 2006a, b, 2022, Seyfullah et al. 2018b) and Cretaceous (as summarised by Delclòs et al. 2023 and references therein), the intervening Jurassic is conspicuously depauperate in significant amber deposits, a phenomenon here termed the ‘Jurassic amber gap’.

To date, only four confirmed very small amber occurrences are known from Jurassic strata. Trace amounts of amber have been recovered from Lower Jurassic strata at Verona, Italy (Neri et al. 2017); minute amounts are known from the Middle-Upper Jurassic of Thailand, some of which are found within fossilised wood (Philippe et al. 2005); and sparse amber clasts have been documented from the Upper Jurassic of Lebanon (Azar et al. 2010, Nohra et al. 2013) and Jordan (Abu Hamad and Uhl 2015). The sole mention of an amber from Denmark (Langenheim 1969) is not confirmed as Jurassic in age, and the brief reference to mid-Jurassic ambers from France (Lacroix 1910, Nel et al. 2004) requires age and locality confirmation. These few records represent the entirety of known Jurassic ambers. Nevertheless, resinite

(a maceral inferred to derive from plant resins) is sparse to moderately common in Jurassic coals across the world (Suwarna 1999, Petersen et al. 2013, Zhao et al. 2014, Zamani et al. 2023), suggesting that the apparent scarcity of amber of this age might be a taphonomic artefact.

Some amber contains animal, plant or fungal inclusions. However, few inclusions have been reported from the sparse occurrences of Jurassic ambers. Early Jurassic amber from Italy encloses fragments of wood (Neri et al. 2017). Two specimens of amber with inclusions have been reported from the Late Jurassic. These include a scale insect (coccid) from Lebanese amber, the amber is interpreted to derive from a cheirolepidiacean botanical source (Vršanský et al. in press). The other specimen represents micro-inclusions from Klong Min amber, Thailand, hosting a diatom, fungal remains and plant spores, dated by the authors to the Late Jurassic (Girard et al. 2020). Although the study of fossil inclusions has been the main driver of amber research, identifying the source plants for these exuded resins is vital for understanding the floristic constituents of ancient resin-producing ecosystems and their ecological interactions. However, identifying the botanical source of amber can be challenging. Most deposits contain allochthonous amber, and the vegetative and reproductive remains of the original source plants may not be present in the same sediments (Grimaldi 1996, Martínez-Delclòs et al. 2004, Seyfullah et al. 2018a, Delclòs et al. 2023). Chemical fingerprinting of fossil plants and amber may provide clues for their taxonomical placement (e.g., Anderson et al. 1992, Anderson and Crelling 1995, Pereira et al. 2009, Menor-Salván et al. 2016, Vajda et al. 2017, 2021, Seyfullah et al. 2024). However, the chemical fingerprints of Mesozoic ambers from different (gymnosperm) botanical sources and from widely separate localities can be very similar and so cannot be solely relied on to differentiate specific botanical sources (Gomez et al. 2002, Seyfullah et al. 2020, Delclòs et al. 2023).

One of the most compelling pieces of evidence for identifying the botanical source of Mesozoic amber is the presence of resin preserved within plant tissues. Such resin was not exuded and, consequently, it is devoid of inclusions. The only reported occurrence of preserved resin inside Jurassic plant remains is that found within *Agathoxylon* HARTIG, 1848 trunks from Thailand co-preserved with the amber deposit (Philippe et al. 2005). In situ traces of preserved resin have been reported from various plant groups and tissues of other ages including the Cretaceous (e.g., Perrichot 2003: fig. 60, Kunzmann 2010, Mays et al. 2017, Seyfullah et al. 2020). Microscopic traces of amber associated with Triassic fossil plants (e.g., Roghi et al. 2006a, b, Fischer et al. 2017, Forte et al. 2022) have been detected with UV light via autofluorescence with various emission wavelengths.

The use of UV light to detect amber or internally preserved resin is beneficial where it can be otherwise difficult to observe small quantities of such material with ambient light (e.g., Forte et al. 2022). Plant cuticles may also have the ability to autofluoresce when exposed to UV light. This is also the case for marine algae, spores and pollen where, for example, details of spore-wall ornamentation used for taxonomical assessments can be resolved through autofluorescence (Peng et al. 2021). However, the extent of autofluorescence varies among plant groups, and the process

of diagenesis can either increase, reduce or even prevent fluorescence in cuticles (Kerp 1990, Fischer et al. 2017, Vajda et al. 2023). Further, chemical processing of fossil plant remains may alter their chemistry via formation of new compounds in the cuticle (Cavalcante et al. 2023).

Here we report the results of our investigation of amber and resin-producing Jurassic plants from Iran and Afghanistan in the Schweitzer Collection, and from the Shaanxi collection from China, with an objective to close the 'Jurassic amber gap'. We used ambient light and a portable, hand-held UV-light microscope to scan the collection for the presence of amber.

Material and methods

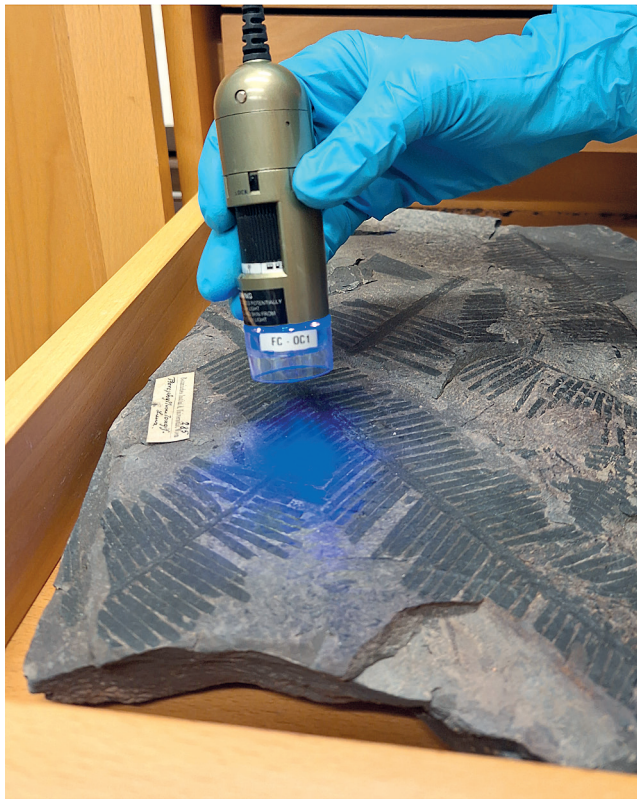
Collections

As part of an investigation of Jurassic and Cretaceous plants and amber we scanned two collections held in the Department of Palaeobiology, Swedish Museum of Natural History, Stockholm (NRM).

(1) The few compression and impression fossil plants collected by Chang in 1921 from poorly age-constrained Jurassic successions in Shaanxi, China, were investigated for cuticles and amber/preserved resin. No exuded amber has been recorded for this locality (Sze 1933). The single previously unidentified conifer shoot (S125897) with in situ fossil resin preserved in its tissue occurs on a slab with the impression of other smaller plant fragments (*Cladophlebis* sp.) and other undetermined remains. Little work has been carried out on this flora or the geology of the host rocks, except that the plant assemblage contains *Sphenopteris diamensis* (SEWARD) SZE, 1933, *Coniopteris hymenophylloides* (BRONGN.) SEWARD, 1900, *Coniopteris* sp., *Pecopteris lobifolia* LIND. et HUTTON, 1836, *Coniopteris* cf. *arguta* (LIND. et HUTTON) SEWARD, 1900, *Phoenicopsis* aff. *angustifolia* HEER, 1876, *Podozamites lanceolatus* (WILL.) BRAUN in Münster (1843), *Elatocladus manchuricus* (M.YOKOY) H.YABE, 1922, *Ctenis* sp., and *Nilssonia* sp. (Sze 1933).

(2) We investigated all the Jurassic slabs from Iran and Afghanistan, collected by Schweitzer on expeditions in 1971, 1972 and 1975 to assess whether conifer cuticle or amber/preserved resin were present. The fossils represent a mix of impressions and compressions preserved predominantly in carbonaceous siltstones that derive from a series of locations mostly in northern Iran, details of which are available at: <https://samlingar.nrm.se/faces/pages/results.xhtml>. The single resin-bearing fossil detailed here co-occurs on a rock specimen with *Ginkgo cordilobata* H.-J.SCHWEITZ. et M.KIRCHN., 1995 (JE-Sch1574). This specimen derives from the Ishpushta Coal Formation, part of the Saighan Series, in Bamian, Afghanistan. The material is from the lower Middle Jurassic of Afghanistan based on the palynology presented by Ashraf (1977) and interpreted originally to be from the Dogger (= Middle Jurassic) by Schweitzer and Kirchner (1995), and, later, more specifically as mid-Bajocian to mid-Bathonian by Schweitzer et al. (2009).

Other plants recorded from the Ishpushta Coal Formation include *Hepaticites arcuatus* (LINDL. et HUTTON) T.M.HARRIS, 1961, *Klukia exilis* (J.PHILLIPS) RACIB., 1890, *Nilssonia* sp., *Nilssonia herriesii* (T.M.HARRIS) SCHWEITZ.



Text-fig. 1. Using the hand-held Dino-Lite Edge Digital Microscope (Dino-Lite Europe) to examine a specimen, here showing UV light use on a non-autofluorescent specimen. Safety precautions for skin and eyes must be followed when using UV light.

et al., 2009, *Nilssonia macrophylla* K.JACOB et B.N.SHUKLA, 1955, *Pterophyllum* sp., *Todites* sp., and *Xenoxylon barberi*

(SEWARD) KRÄUSEL, 1949. Other Middle Jurassic plants from Afghanistan include *Ginkgo dissecta* SCHWEITZ. et M.KIRCHNER, 1995, *Nilssonia kaiseri* SCHWEITZ. et al., 2009, *Nilssonia orientalis* HEER, 1878, *Nilssonia* sp., *Otozamites ptilophylloides* P.D.W.BARNARD et J.C.MILLER, 1976, and *Pachypteris lanceolata* BRONGN., 1929 (Schweitzer and Kirchner, 1995, 1996, Schweitzer et al. 2009).

Scanning and imaging procedure

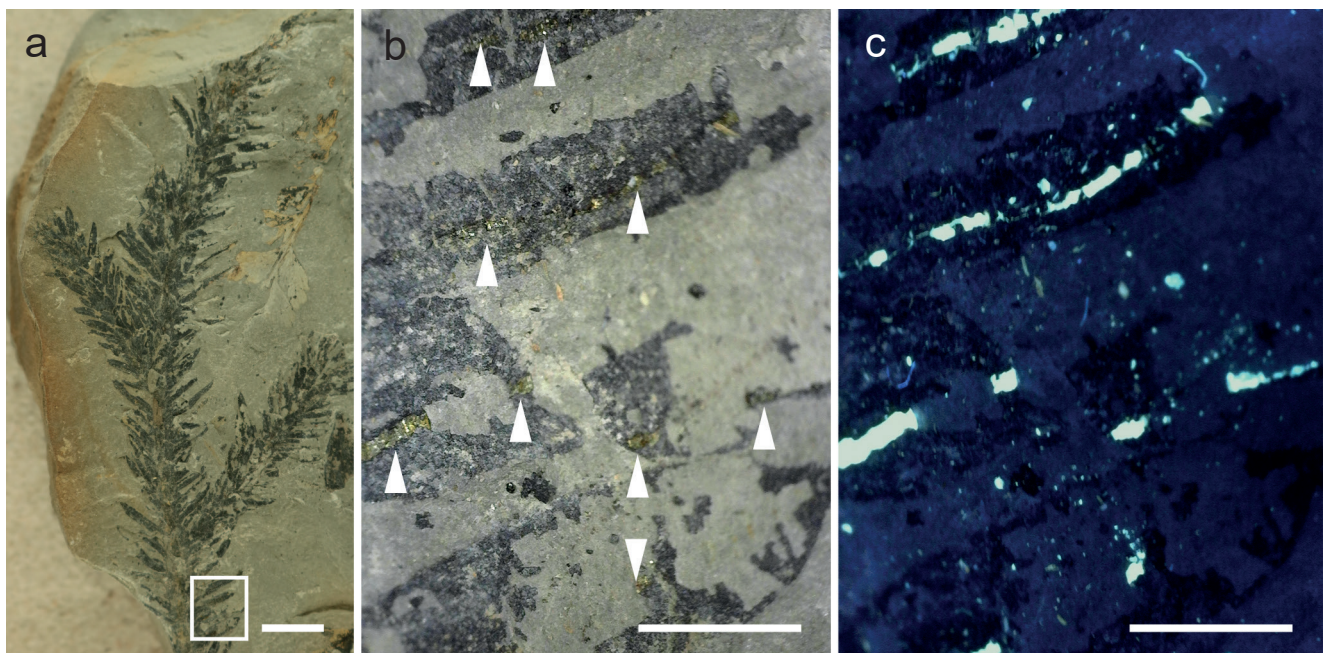
As the first step, we studied all specimens using ambient light to search for traces of amber visible to the naked eye. Since our initial attempt to detect amber was unsuccessful, we employed a Dino-Lite Edge Digital Microscope (Dino-Lite Europe) to examine the specimens using both ambient and UV light (Text-fig. 1). This USB-powered device has the capacity to switch between these two types of illumination and capture digital images, allowing for direct comparison.

Once the minute traces of preserved resin were detected in the specimen from Afghanistan with the UV light setting of the Dino-Lite Edge Digital Microscope, the specimen was further photographed and imaged using an Olympus BX-51 light microscope fitted with an epifluorescence UV light source and photographed with an Olympus DP-71 digital camera to ensure the best images of such small autofluorescent structures.

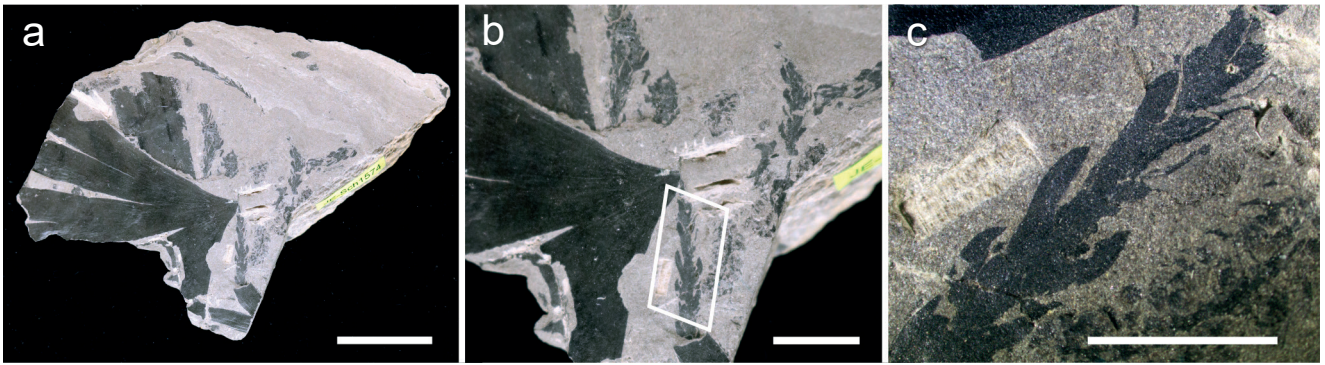
Results

Conifer shoot with in situ fossil resin rods from Shaanxi, China

We investigated the Jurassic fossil plants from Shaanxi, China. No cuticle or exuded amber pieces were observed.



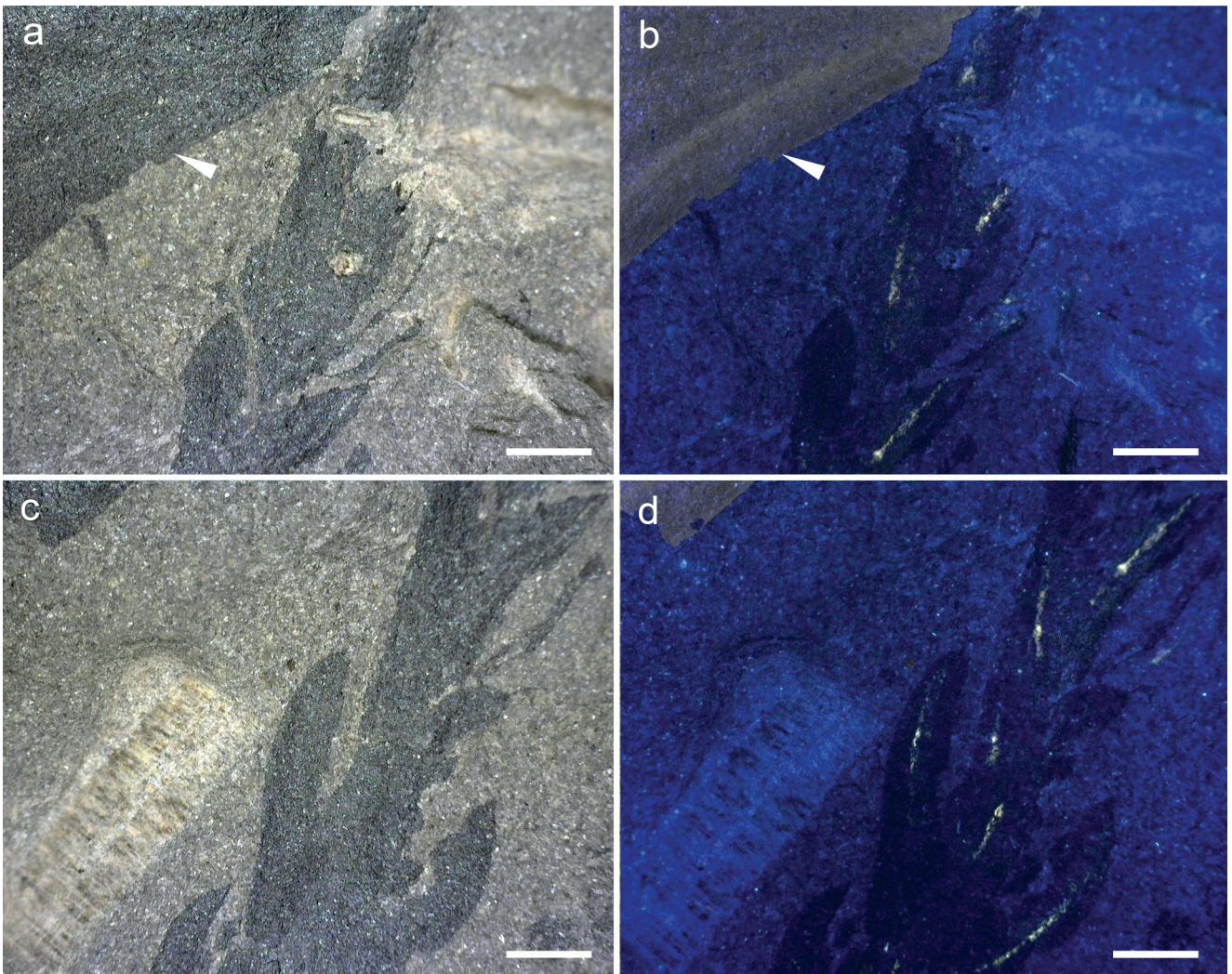
Text-fig. 2. In situ traces of preserved resin rods in a Jurassic *Elatocladus* sp. conifer shoot from Shaanxi, China (S125897). a: Overview of the conifer shoot; b, c: Detail of the shoot as shown in the boxed area in part (a), b – in ambient incident light of boxed area of part (a), c – detail imaged with UV (fluorescent) light of boxed area of part (a). The preserved resin is not clearly visible to the naked eye, and is just visible under hand-held light microscopy as small light yellow tubular traces in the leaves (arrowheads). With UV light microscopy the tubular preserved resin fragments fluoresce a bright light green throughout the lamina, and the leaf cuticles are very dark grey to black and the matrix is dark blue, both showing no fluorescence. Scale bars = 10 mm (a), 2 mm (b, c).



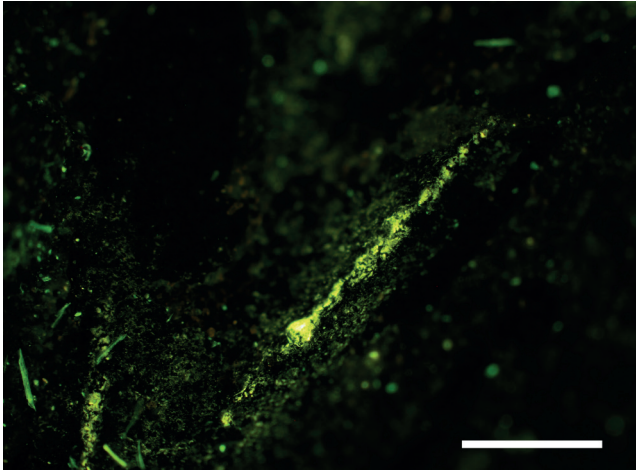
Text-fig. 3. Slab from Afghanistan with *Ginkgo cordilobata* H.-J.SCHWEITZ. et M.KIRCHN. (JE-Sch1574) and with fragments of *Elatides* sp. conifer remains. a: Overview of specimen; b: Position of the *Elatides* sp. conifer fragment on the specimen (inside diamond shape); c: Detail of *Elatides* sp. fragment (from (b)) with no preserved resin traces visible in ambient light. Scale bars = 20 mm (a), 10 mm (b), 5 mm (c).

We did discover one previously unidentified branched coalified conifer shoot (S125897) approximately 90 mm long containing rods of fossil resin (approximately 100 to

150 μm wide) inside some of the leaf tissues (Text-fig. 2). The plant is preserved as a dark grey compression on a light grey mudstone as seen under ambient light. The leaves do



Text-fig. 4. Fine traces of preserved resin within the *Elatides* sp. coalified plant tissue (detail from diamond area in Text-fig. 2b) preserved on specimen JE-Sch1574 from Afghanistan. a, c: Detail of *Elatides* sp. conifer twig with hand-held ambient light microscopy; a – distal part of conifer twig, arrowhead indicates *Ginkgo* cuticle; c – proximal part of conifer twig. b, d: Same conifer fragment with hand-held UV light microscopy, b – same as (a), with fluorescent *Ginkgo* cuticle (arrowhead) and the light yellow-green lines of in situ preserved resin present inside the non-fluorescent (black) coalified conifer remains, d – same as (c) with the light yellow-green lines of in situ preserved resin inside the non-fluorescent (black) coalified conifer remains. Scale bars = 1 mm.



Text-fig. 5. Detail of bright *in situ* preserved resin trace inside a leaf of *Elatides* sp. preserved on specimen JE-Sch1574 from Afghanistan, imaged with epifluorescence. Scale bar = 1 mm.

not fluoresce with UV light, so no cuticle could be observed, and they appear black on a sediment that reflects the light with a blue hue (Text-fig. 2). The fossil resin rods were barely discernible to the naked eye with ambient light, given their small size, but were immediately obvious through autofluorescence with exposure to UV light (Text-fig. 2). The lack of cuticular details prevents definitive taxonomic determination. However, we tentatively identify the conifer shoot as *Elatocladus* sp., based on the broad description of *Elatocladus* HALLE, 1913 (Cupressaceae s.l.) as having elongate linear uni-veined, dorsiventrally flattened leaves that diverge from the stem and are pseudodistichous.

Conifer shoot with in situ fossil resin traces from Afghanistan

Although we carried out an extensive and thorough investigation of the Jurassic plant remains in the Schweitzer Collection, we detected only one slab with minute traces of in situ resin preserved within plant remains, and no isolated fragments or droplets of amber. Fossil resin was not visible to the naked eye (Text-fig. 3). However, using the hand-held UV light microscope we found a small fragment of conifer twig <20 mm long (JE-Sch1574: referable to *Elatides*, HEER) with bright autofluorescent lines (all <0.1 mm wide) within the leaves (Text-fig. 3).

The resinous plant was preserved as a coalified compression. The leaf material is dark grey with ambient light on a lighter grey siltstone matrix (Text-fig. 4a, c). The leaves do not fluoresce with UV light, unlike certain other fossil plant cuticles, and appear black on a sediment that reflects the light with a blue hue (Text-fig. 4b, d). The co-preserved *Ginkgo* leaves are also dark grey in ambient light (Text-fig. 4a, arrowhead), but the cuticle slightly fluoresces a dull yellow-orange-brown with UV light exposure (Text-fig. 4b, arrowhead).

The minute autofluorescent traces follow the length of the leaves and are positioned inside the remaining coalified leaf mesophyll (Text-fig. 4). Based on the light yellow-green colour of the autofluorescence (Text-fig. 4), we interpret these bright lines as minute traces of in situ fossil resin (following, e.g., Fischer et al. 2017, Forte et al. 2022). The

fine traces of resin were further investigated with standard epifluorescence microscopy, which allowed visualization at higher magnification (Text-fig. 5), and verification of the images recovered from the hand-held UV light microscope. The traces of amber are very flat and minute with both UV light methods of visualization.

Discussion

Jurassic conifers with in situ fossil resin traces

Both compressed conifer shoots share a similar type of preservation in a fine-grained sedimentary rock where the original plant tissues are preserved as phytolite, a compressible carbonaceous film that remains after the geochemical alteration of the original leaf/twig material. The fossilised resin rods or traces are found inside these altered plant tissues, but only in certain parts of each specimen. Both conifer shoots derive from floras lacking reported amber pieces or droplets; nor were such isolated droplets discovered in our investigations. In both cases, UV light did not cause the cuticles of these conifer shoots to autofluoresce. This is likely owing to strong alteration and loss of volatile components during the coalification process (Natkaniec-Nowak et al. 2023), meaning that the cuticle morphology could not be observed for more secure taxonomic determinations of the fossils.

Despite the age of the plants collected from Shaanxi being not well-constrained within the Jurassic, the sole coalified *Elatocladus* sp. conifer shoot from China with in situ resin (where preserved; Text-fig. 2) is important. This specimen has rods of resin that were barely discernible without the aid of magnification but could be more clearly observed using UV light microscopy. The rods of resin in this specimen indicate the original position of the sole resin canal per leaf in the original material and that the resin could become preserved, thus representing the first Jurassic-aged specimen with resin traces from China.

The *Elatides* sp. conifer shoot with minute preserved resin traces is the first report of any preserved resin traces from Afghanistan, and is also the first evidence of such traces from the Middle Jurassic, globally. The single specimen bearing traces of in situ preserved resin were only visualized via autofluorescence and with higher magnification as the traces are so small. Numerous other Jurassic conifers in the collection yielded no evidence of resin. Moreover, no isolated amber pieces are present in the Schweitzer Collection of Jurassic fossil plants from Iran and Afghanistan based on our survey, and none has been reported previously. However, our discovery of a single example of a conifer twig from the Middle Jurassic of Afghanistan containing in situ preserved resin traces suggests the presence of at least one resinous plant. This specimen is evidence that resinous plants were present, albeit rare in Middle Jurassic strata of Afghanistan. Importantly, the specimen also indicates that Jurassic resin was preservable as not all resin chemistries are suitable for preservation and instead are lost from the fossil record (Seyfullah et al. 2018a).

In the Afghan *Elatides* sp. conifer specimen, the minute size, slender shape and distribution of the in situ resin traces suggest that they were originally located within resin canals embedded in the leaf mesophyll. As the leaf material

was coalified, the resin underwent maturation to the more chemically stable amber, which is detectable with UV light, using both a hand-held microscope and a desktop microscope fitted with epifluorescence (Text-figs 4, 5). This type of resin preservation is analogous to that we have previously observed inside coalified Jurassic conifer leaves from China (Text-fig. 2). However, in the Afghan fossil, the lack of discernible resin under ambient incident light might indicate a different type of preservation, where the coal itself was impregnated with diterpenes and other resin components, representing a chemical ‘ghost’ of preserved resin rather than rods of extractable amber. Given the minuscule amount present (Text-fig. 3), it is impossible to test the composition of the material or cause of fluorescence in the Afghan specimen.

The traces of amber within the Chinese conifer leaves reported here fluoresced in a very similar manner to the Afghan material (compare Text-figs 2 and 4). Ambers and preserved resins may yield a range of emission wavelengths observable as different autofluorescent colours with UV light. This is interpreted to derive from their different cyclic/aromatic chemistry and the local taphonomic conditions. Moreover, the colour intensity can increase with elevated maturity of the amber tested (Drzewicz et al. 2020, Natkaniec-Nowak et al. 2023). However, not all ambers fluoresce, and this may be affected by factors such as natural weathering through exposure to heat, light and oxygen (Natkaniec-Nowak et al. 2023).

Affinities of the conifer shoots

In both fossil conifer shoots the presence of a single resin canal that does not appear to continue into the stem from the leaf base suggests that these conifers had an extant *Torreya* ARN., 1838 type of resin canal distribution (Suzuki 1979a, b). This type is present in the majority of Cupressaceae, with the exception of *Cunninghamia* R.Br., 1826, and is also found in other conifers within Cupressales, i.e., *Torreya* ARN., 1838 and *Cephalotaxus* SIEBOLD et ZUCC. ex ENDL., 1842. This might indicate that this Afghan *Elatides* sp. and Chinese *Elatocladus* sp. shoots were members of the clade including Cupressaceae GRAY, 1821, Taxaceae GRAY, 1822, and Cephalotaxaceae NEGER, 1907, although a more precise assignment cannot be made given the lack of other sources of evidence, such as cuticle morphology or most importantly, attached reproductive structures (cones). Alternatively, the Afghan *Elatides* HEER fossil conifer might belong to the extinct family Cheirolepidiaceae TURUTANOVA-KETOVA, 1963, which is characterized by similar awl-shaped leaves (Tosolini et al. 2015), is known to contain resin canals, at least in the wood (dos Santos et al. 2022), and was abundant globally during the Jurassic (Alvin 1982). The morphology of the primary resin ducts (i.e., inside the leaves) of Cheirolepidiaceae is, however, unknown, meaning we cannot yet completely discount this possible affinity. The name of this family has been disputed and we continue to use Cheirolepidiaceae as it is the more commonly used name over Hirmeriaceae T.M.HARRIS, 1979, as the proposal to change the name has not yet been accepted by the Permanent Nomenclature Committee for Fossils.

The Late Triassic (Carnian) was an earlier interval rich in amber. In most cases, the botanical sources for the amber

deposits from this epoch have not been identified. However, Carnian ambers from Northern Italy have been suggested to have had cheirolepidiacean sources because amber is both associated with and within cheirolepidiacean plant fossils (see Roghi et al. 2006a, b, 2022). The Late Jurassic amber from Thailand also has an inferred cheirolepidiacean source, whereas various conifer families (Araucariaceae, Cheirolepidiaceae, Cupressaceae, Podocarpaceae and Pinaceae) and non-conifer gymnosperms have been proposed as sources for the Cretaceous ambers (as summarized by Delclòs et al. 2023 and references therein).

Why is there a lack of exuded amber pieces in these floras?

If the plants were resinous and the resin could become amber, why are there are no exuded resins preserved as amber pieces present at the same localities? The dearth of amber might suggest that these particular resinous plants produced little resin, despite having resin canals, or that there are other, perhaps taphonomic, factors involved in the preservation of exuded resins as isolated amber pieces.

The isolated Jurassic shoot fragments from China and Afghanistan with in situ resin preserved, together with the preserved resin-bearing wood from Thailand (Phillippe et al. 2005) suggest that resinous plants were present as rare elements in the Jurassic floras. It seems likely that collecting bias has played little part in fossil resin detection given the fragmentary nature of the studied material. These lines of evidence collectively suggest that there were Jurassic plants capable of producing resins that could become converted to amber, but they were sparse.

Conclusions

The ‘Jurassic amber gap’ results from a paucity of reports of amber from Jurassic strata globally. Reports of amber are particularly lacking from Middle Jurassic successions. Examining the Schweitzer Collection of Jurassic fossil plants from Iran and Afghanistan with a hand-held UV light microscope yielded no isolated amber pieces, but did reveal a unique conifer fragment with minute in situ preserved resin traces, and similar resin traces were detected in a Jurassic *Elatocladus* sp. conifer shoot from China, again from a flora with no amber reported. The Afghan *Elatides* sp. shoot has resin traces that are not visible to the naked eye nor preserved as rods. Instead, the resin has impregnated the surrounding coalified leaf material, allowing us to trace the location of the fine resin canals, but preventing extraction of the resin. The presence of single canals running through the leaves, but not originating from the stem, favours a cupressalean affinity for the conifer *Elatides*. This single specimen represents the first discovery of this type of resin preservation impregnating plant tissues.

Data availability

All data is provided in this manuscript as images in the figures and the specimens are available in the Palaeobotanical Collections of the Swedish Museum of Natural History, Stockholm.

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