Earliest Cretaceous cocoons or plant seed structures from the Wealden Group, Hastings, UK.

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Abstract

Complete metamorphosis evolved in insects towards the end of the Palaeozoic Era. A wide range of pupation strategies existed, and numerous biosedimentary structures associated with these have been described. The fossil record of endogenous materials associated with pupation, e.g. cocoons, however is more limited. Here we report six amber-coloured specimens from the earliest Cretaceous of southern England tentatively identified on collection as insect cocoons. These were analysed by FTIR, stereomicroscopy and X-ray microtomography to elucidate their origin. Interpretation of FTIR data was inconclusive as the spectra showed some differences from those of amber. A seed pod origin seems likely for at least two of the objects, based on their size, shape and lineations on their surfaces. Three specimens are more cocoon-like, based on overall morphology and a fibrous surface texture. Whilst plant megaspore membranes have features analogous with these specimens, and cannot be ruled out, the similarity to and variability found within insect cocoons, coupled with the range of potential insect architects present at the time of origin, make an insectan

origin more likely. We review a number of hymenopteran clades whose extant members construct comparable cocoons. It is possible the possible cocoons were resin-coated to protect the larva inside from predation, or passively came into contact with resin prior to burial.

Introduction

Entombment of arthropods and other small invertebrates in amber is common, particularly over the last 100 Ma. Examples older than this are rare (Brasier *et al*., 2009). Such preservation occurs when organisms become trapped in tree resins that harden around them. These then become buried and lithified, preserving the animals over millions of years. Insects are adept at modifying the natural world to their advantage and, as such, also leave trace fossils in the geological record. Modern examples of this modification include, among others, beehives, wasp nests, termite mounds, Trichoptera (caddisfly) and chironomid (midge) larval cases, and cocoons in the orders Lepidoptera and Hymenoptera. The preservation potential of these structures depends, in part, on the materials from which they are constructed, and also on the environment in which they are built. Numerous examples of fossilised insect structures exist. Larval tubes constructed from calcite by chironomids and Trichoptera are commonly found fossilised in tufa-precipitating alkaline streams (Janssen *et al*., 1999; Leggit & Cushman, 2001; Brasier *et al*., 2011). Nests and pupation chambers have been studied as ichnofabrics (Genise *et al*. 2004), and reported within continental carbonates (Genise *et al*., 2010), calcrete-precipitating vertisols (Genise *et al*., 2013), lacustrine/palustrine deposits (Edwards *et al*. 1998), volcanic soils (Genise *et al*. 2007), palaeosols interbbedded with pyroclastics (Sacchi and Petti 2008) and semi-arid palaeosols (Martin and Varricchio 2011), as well as within other materials such as dinosaur bone (Pirrone *et al*. 2014) and wood (Tapanila and Roberts 2012). The occurrence of fossilised cocoons in the geological record is therefore not unexpected. This said, cocoons, and other endogenous structures, are not commonly preserved in the rock record. A cocoon has been reported as preserved within Oligocene-Miocene amber (Poinar 1998), and lithified and sediment-infilled cocoons, probably from a wasp, have been described from inside Cretaceous dinosaur eggs of Patagonia (Genise and Sarzetti, 2011). Sedimentary structures

associated with pupation have been placed within an ethological classification (Vallon *et al*. 2016), and a comprehensive overview can be found in Genise (2017). Due to the variety of structures and materials used, fragmented literature, and the fact that the insect building them is likely to be extinct, identifying pupation structures in the fossil record can provide challenges.

The earliest Cretaceous sedimentary rocks of the Wealden group of Sussex, southern England (Fig. 1), have long been known to be fossiliferous. They have yielded amber, some of the oldest spider silk (Brasier *et al*. 2009) and a number of dinosaurian fossils. Here we report a number of specimens that were tentatively identified on discovery as cocoons, and investigate their origins. These objects were found within the Fairlight Clay, associated with fossil charcoalified wood. The specimens consist of paper-thin and orange to red-brown semi-translucent pods or envelopes that outwardly resemble either insect cocoons or seed cases. The aim of the present study is therefore to determine their origin, and to understand their preservation mechanisms: are they of insect or botanic origin, or a combination of both?

Geological setting

The specimens were found in-situ within the ~140 Ma Fairlight Clays of the Ashdown Formation (Fig. 1; Lake & Shephard-Thorn 1987; Allen & Wimbledon 1991; Radley 2006 *a*,b), which crops out on the beach close to the town of Bexhill in the south of England (Fig. 1). The formation consists of a series of fluvial and floodplain sandstone and clay deposits and is known to be fossiliferous, yielding vertebrate, invertebrate and plant material. This includes the cranial endocast of an iguanodontid dinosaur with some cellular material preserved (Brasier, M.D. *et al*. 2016) and trackways attributed to *Iguanodon* (Beckles 1854). Some of the oldest amber containing spiders' silk (Brasier *et al.* 2005) has also been found within the same beds as those yielding the proposed cocoon specimens, indicating that terrestrial arthropods were present in the environment. The presence of charcoalified coniferous plant remains suggests that the environment of deposition was a coniferous forest with frequent forest fires (Brasier *et al.* 2009). Several of the specimens described herein were found in sandstones with abundant plant material.

Methods

All specimens are housed within the Oxford University Museum of Natural History (OUMNH), as part of the M.D. Brasier collection (registration numbers OUMNH K.65750 – K.65756). For consistency, specimens are here referred to by their collection numbers with mention of their OUMNH accession number (hereafter Cocoon 1 – OUMNH K.65750; Cocoon 2 – OUMNH K.65751; Cocoon 3 – OUMNH K.65752; Fragment used for FTIR – OUMNH K.65755; Amber Cocoon in situ – OUMNH K.65754; MDB1 – OUMNH K.65756). Names as given in the collection mostly included the word 'cocoon' because they were all suspected to be insect cocoons when first discovered, although their origins had not been substantiated by detailed study.

The specimens were examined using a Nikon SMZ25 Zoom stereomicroscope and imaged using a Nikon DS-FI2 camera and Nikon NIS Elements D software in the School of Geosciences at the University of Aberdeen. Z-stacking of multiple focal depths was used within the Elements D software to maintain focus of three dimensional aspects of the cocoon specimens. Where images shown are Z-stacked, this is indicated in the figure caption.

Fourier Transform Infrared Spectroscopy (FTIR) analysis was used to determine whether amber was present in the structures. Analysis was undertaken at OUMNH using a Mattson Galaxy 5000 spectrometer. A small piece (approximately 1 mm^2) of specimen OUMNH K.65755 was removed using a mounted needle. The fragment was crushed using an agate pestle and mortar, and mixed with potassium iodide powder. This was then compressed to make a disk, inserted into the specimen holder in the machine, and analysed.

Micro-computed tomography (Micro-CT) scanning of specimen OUMNH K.65751 was carried out at Naturalis Biodiversity Center in Leiden, the Netherlands using a Bruker SkyScan 1172 micro-CT scanner. 1281 projections of 575ms exposure were collected with a 2000x1336 detector, using a source voltage of 59kV, and current of 167μA. No filtration was employed, and the scan provided a reconstructed dataset with 13.2μm voxels.

Digital visualisation was achieved following the methods of Hickman-Lewis *et al.* (2016). In brief: Drishti was used for volume rendering (sf.anu.edu.au/Vizlab/drishti; Limaye 2012), and SPIERS for surfacing (spiers-software.org; Sutton *et al.* 2012). Surfaces were rendered using Blender (blender.org; cf. Garwood & Dunlop 2014 for overview).

Studied Material and Results

OUMNH K.65750 ('Cocoon 1')

OUMNH K.65750 is a three-dimensional but rather flattened paper-thin folded sheet, with red-brown colouration and leathery texture when examined under reflected light, and translucent amber under transmitted light (Fig. 2A). The specimen is approximately 5.5 mm long and 2.8 mm wide. The thickness of the specimen was more difficult to accurately measure, due to the flattened - and fragile - nature of the specimen, but was approximately 1 mm. The morphology of OUMNH K.65750 is distinctive with a roughly "bean shaped" outline. One of two long edges forms a smooth and convex curve. The other is more ornate, marked by a series of concave cusps that seem to reflect original biotic morphology. The specimen is closed at one of the narrow ends (top of Fig. 2 A, B) and along the convexly curved edge (left of Fig. 2A), while the remaining sides are open. Five distinctive concave depressions were observed in transmitted light at the narrow open end of the specimen. These depressions each measured approximately 45 µm in diameter, and were visibly sand-filled in reflected light (Fig. 2D). Further similar sized sand-filled pits were observed on the outer surface of the specimen (Fig. 2C).

OUMNH K.65751 ('Cocoon 2')

OUMNH K.65751 is a red-brown to amber coloured specimen that is less flattened than OUMNH K.65750 and therefore has a more three-dimensional shape preserved (Fig. 3). Its general morphology bears some resemblance to that of OUMNH K.65750; it is roughly bean-shaped in outline, with a smooth convex-curved back and an open front that is cuspate and ornate, the front edge being somewhat dentate on a micron-scale (Figs 3 & 4). A mesh-like layer of threads, approximately 20-30 µm thick covers the outer surface, creating a pattern of irregular, 50 – 100 µm wide, polygons (Fig. 5A). The entire inner surface is smooth (Fig. 4) apart from more than 50 pits - similar to those seen on OUMNH K.65750 - at the open end of the specimen (Fig. 3). The images from the micro-CT analysis show that the pits are actually perforations with many going through the specimen (Fig. 4; Supplementary Movie). Each perforation is approximately 150 to 300 µm in diameter, and filled with fine sand, which is clearly visible in CT-data (Fig. 4; below). Close examination reveals the pits to have been coated in places by an amber-coloured substance, probably amber (Fig. 5B). Grains of sediment and charcoalified plant material (fusain) adhere to the outer surface of OUMNH

K.65751. Inside this specimen was lithified sandstone that, when removed, moulded the internal morphology the specimen.

The three dimensional preservation of OUMNH K.65751 allowed for additional morphological details to be obtained through CT scanning (Fig. 4A-F; Supplementary Movie). This demonstrates that the material filling the pits is of a higher attenuation than the surrounding materials (and thus is either more dense, or compositionally different; Sutton *et al.* 2014). Digital visualisations demonstrate that the pits are larger and most regular at the open end of the specimen (Fig. 4; Supplementary Movie). Towards the closed end, denser objects are present, but are less uniform in spacing and size (Fig. 4D, G). The CT scan also reveals the interior surfaces within the closed end of the specimen (Fig. 4C, F), which appear to be relatively smooth throughout. Furthermore, the scans demonstrate that the specimen is relatively thick (0.5 mm; Fig. 4B) towards the open end, and that the pits are actually perforations through the entirety of the structure (Fig. 4E; Supplementary Movie) that narrow in the centre, giving them an hourglass shape.

OUMNH K.65752 ('Cocoon 3')

OUMNH K.65752 is a triangular paper-thin fragment, with red colouration in reflected light, and is translucent and amber coloured in transmitted light. The specimen measures a maximum of 6.4 mm in length and a maxiumum of 3.3 mm in width (Fig. 6A, B). One surface of this fragment is crossed by a mesh of amber-coloured threads, each measuring less than a few microns in width, but several can be traced for several millimetres in length (Fig. 6A, C). Sandstone is adhered to the surface of the specimen and underlies the threads (Fig. 6C). In some areas the threads part from the surface and are not attached, although there are signs they were originally bound to the specimen. The reverse side of the specimen is notably lacking these threads, and has a leathery textured surface, with areas of fusain and matrix sediment still adhered to the specimen. These fusain and sediment patches are particularly visible in transmitted light. (Fig. 6D).

OUMNH K.65755 ('Fragment used for FTIR')

OUMNH K.65755 is an irregularly shaped fragment with red colouration under reflected light (Fig. 7) and is dark orange in colour when viewed in transmitted light. The specimen

measures approximately 5.8 mm long and 2.6 mm wide (Fig. 7A, B). Small amounts of buff to white coloured matrix sandstone are attached to the surface (Fig. 7C). The specimen has a leathery appearance on one side (Fig. 7A), and orange-coloured threads crossing its other surface (Fig. 7B), similar to those on specimens OUMNH K.65751 and K.65752. These threads are not broken by bends in the three-dimensional specimen (Fig. 7C), indicating their original pliability. Pits in the specimen are filled with white sandstone that post-dates the underlying fibres (Fig. 7C).

Destructive FT-IR analysis was undertaken at the OUMNH on specimen OUMNH K.65755. This fragment (Fig. 7) has a rather crystalline texture, which ground down to a yellowish powder. Results for this sample were inconclusive, as when compared with known amber FT-IR spectra there were some differences in peak positions. This may suggest that the specimen was not composed of amber, but reaching a firm conclusion on this requires further analysis, and probably testing of additional samples to establish how homogeneous the material is.

OUMNH K.65754 (*Cocoon in matrix*)

OUMNH K.65754 is preserved within a small block of coarse-grained lithic sandstone with abundant fusain fragments (Fig. 8A). The specimen is dark red under reflected light with a leathery texture. It is roughly bean-shaped, and is approximately 6.6 mm in length and approximately 2.5 mm in width (Fig. 8B). There is a prominent ridge running diagonally across the width, which may be a fold in the structure (Fig. 8B, C). Beneath this part of the specimen is a second fragment of similar looking composition (Fig. 8B, C). This second red, resinous fragment had an embayed edge, and may have connected with the 'cocoon-shaped' section, having been folded underneath. A third piece of similar material is also present in the matrix and may have also once been part of the same specimen (Fig. 8D). The surfaces of all fragments are covered in unidirectional striae at a tangent to the long axis (Fig. 8C), however no thread-like structures were visible.

OUMNH K.65756 (MDB1)

OUMNH K.65756 differs from the other specimens in being ovoid in shape (Fig. 9), although the three dimensional morphology is difficult to ascertain since the specimen is within a

fusain containing, fine-grained litharenitic matrix, but is approximately 4.8 mm long, 1.9 mm wide (Fig. 9A), and approximately 2mm thick (Fig. 9B). The specimen is amber coloured under transmitted light and has a resinous texture. The surface of the specimen appears polished and is covered by with linear grooves running the length of the fossil (Fig. 9A).

Specimen	Length (mm)	Width (mm)
OUMNH K.65750	5.5	2.8
OUMNH K.65751	9.0	4.1
OUMNH K.65752	6.4	3.3
OUMNH K.65755	5.8	2.6
OUMNH K.65754	6.6	2.5
OUMNH K.65756	4.8	1.9

Table 2: Dimensions of possible cocoon specimens studied here

Discussion

The specimens described in this study are not readily comparable to other known fossil materials, making it challenging to ascertain their exact origin. Hence, below we use what gross morphology can be identified, as well as their finer structures and geological context, to suggest which are consistent with origins as either seed cases or insect cocoons.

Possible insect origins

Extant holometabolous insects have trimorphic development, meaning that their life cycle includes a transitional resting stage between the larval and adult forms known as a pupa. The pupae of holometabolous insects are usually quiescent, and have a chitinous exterior (Heming

2003). Numerous endopterygote groups create additional structures for protection through camouflage during pupation, such as cocoons, tubes and pupation chambers. These are often constructed from their own silk, but can also incorporate other natural substances and minerals. Others use polymeric substances to bind sediment particles, and some groups – such as tortricid moths – use rolled plant leaves. Some species also show a combination of constructional materials and methods. Different pupation structures have significant variability in preservation potential. This, combined with the broad range of resulting structures, preclude the establishment of definitive criteria for attributing fossil cocoons to a particular taxon. The specimens reported here are challenging to compare with *Pupichnia* and associated taxa, as the latter represent bio-sedimentary structures (i.e. were pupation chambers, for example see Genise *et al.* 2007). Fossils representing endogenous materials are less prevalent in the fossil record. As such, the numerous criteria that exist for identifying *Pupichnia* – such as layering on the burrow margins, emergence holes, and shape – are difficult to apply to isolated, fragmentary and deformed fossils. Rather we rely on other criteria, largely microstructure – including surface texture, pores, and threads – that can be observed. Of these, the thread like morphologies and, to an extent, the nature of the pores seen on several of the specimens, show similarity with modern insect cocoons.

Various insect groups fashion pupal structures similar to some of the specimens reported herein. For example, several hymenopteran clades create pupation structures broadly comparable in size and shape to these fossils, which in some species are red or orange in colour, and have translucent, sometimes thin, paper or cellophane-like walls. A number of hymenopteran pupation structures show a fibrous surface, and sometimes they also exhibit pores similar to those of the Wealden fossils described here. For example, potential architects are the ancestors of sawflies (Family Diprionidae, Order Hymenoptera), since modern sawfly cocoons (Fig. 10) are constructed of bundles of fibres that are similar in microscopic appearance to the textures in OUMNH K.65751, K.65752, and K.65755. Furthermore, modern larvae within this early branching hymenopteran group are known to use plant resins to defend against predators (Eisner *et al.* 1974; Heitland & Pschorn-Walcher, 1993), which may account for the amber-like appearance of these fossils. Alternatively, these could have been in passive contact with resin if they were cocoons attached to plants as is common in extant hymenoptera, for example. Specimens of sawfly cocoons in the Life Collections at OUMNH measured 13 mm long by 6 mm wide (*Diprion pini*) and 10 mm long by 5 mm wide (*Neodiprion sertifer*), which is broadly similar to the dimensions of OUMNH K.65751. We

also note that the fossil record of the sawflies is not at odds with this hypothesis: members of the stem group family Xyelotomidae have been found in the Late Jurassic and Early Cretaceous, and putative crown group members of the most diverse sawfly family, the Tenthredinidae, were probably present in the Early Cretaceous (Grimaldi & Engel, 2005). Modern sawfly cocoons are, however, rather more pellet-shaped than the fossil specimens of the Wealdon Group (Fig. 10A), and tend to lack the pits seen in OUMNH K.65751.

Possible seed/spore interpretations

Some of these specimens are also similar to fossilised conifer seeds and plant megaspores. Modern pine seeds are around 12 mm long by 5 mm wide, and are therefore broadly similar in dimensions to the largest of the fossils studied here (Table 2). Under the microscope, the wings of pine seeds exhibit a surface lineation parallel to their length (Fig. 11B, C) similar to that on OUMNH K.65754 (Fig. 8). Other plant types, such as ginkgo from the Wealden beds (Batten 1974) have lineations on their seed pods that could match those of OUMNH K.65754, but if these are indeed seed pods, then the type of plant is undetermined. Such seed pod-like lineations are absent or less clear on the other fossil specimens.

The mesh of fine threads characteristic of OUMNH K.65751, K.65752 and K.65755 is not analogous to any part of either pine seed wings or gingko seed cases. There is however some similarities between the internal pitting at the wide end of OUMNH K.65751 and textures of the robust seed megaspore membranes (cf. *Spermatites pylophorus* megaspores of Batten & Zavattieri 1996, Fig. 7). The megaspore membranes reported by Batten and Zavattieri (1996) range from 0.28 to 2.5mm in size, but these structures vary considerably in both size and morphology between plant groups. The megaspore membranes of conifers possess resin canals, which could explain the amber-like appearance of these fossils.

Because insects are known to construct cocoons from pre-existing materials it is possible that these Cretaceous specimens are of both plant and insect origin. The pits in OUMNH K.65751, for example could have been inherited from the construction material, and the micro-dentate edge of that specimen (Fig. 3) could represent a torn margin of a seed pod.

Combined interpretations

If the specimens with mesh-like networks of 'fibres' (OUMNH K.65751, OUMNH K.65752 and OUMNH K.65755; Figs 3-7) were produced by an insect they would represent the woven silk used by, for example, hymenopteran taxa. Coating of these in a toxic plant resin material, explaining the amber material associated with the specimens, could be interpreted as an attempt to avoid predation. Such behaviour was recently noted in modern lepidopteran caterpillars of Borneo (Symondson *et al.* 2015). Some small solitary wasps of the genus *Passaloecus*, and possibly *Pemphredon*, collect pine resin to separate breeding cells in their nest, and as a final plug to the entrance (Ivan Wright, Shotover Wildlife, personal communication), partly to avoid predation, primarily from other insects. It seems logical that their ancestors, the earliest Cretaceous insect larvae, would have been subject to similar predatory pressures, but establishing diagnostic criteria for distinguishing plant fossils from hybrid plant-insect fossils remains as a challenge.

Conclusions

The size, shape and surface lineations on OUMNH K.65754 and OUMNH K.65756 make a seed pod origin likely for these specimens, and the same could be true of specimen OUMNH K.65750. In contrast, the resin-coated silk-like fibres, size and shape of specimens OUMNH K.65751, K.65752, and K.65755 are all in keeping with an insect origin. On the basis of the number of potential trace-makers, coupled with the variability of cocoon structure and microstructure across the Endopterygota, we consider a cocoon origin the most plausible explanation for these three specimens. We note that plant megaspore membranes have a comparable structure, and arrangements of pits, so these cannot be definitively ruled out on current evidence. If our assumptions are correct, then these resin-coated cocoons are plausible evidence for insect use of plant resins to deter predators (perhaps other insects, or even the ancestors of birds) in the earliest Cretaceous.

Supplementary Information

Supplementary information for this paper is available through the Zenodo data archive (DOI: XXXXXXXXXX). The datasets archived comprise:

i) A zipped archive with all tiff CT slices from the scan, and the CT log file.

ii) A surfaced model of the specimen, with the denser perforations separated and rendered separately, and the specimen split into separate sides down the middle. This is in the form of a VAXML file (more information on this format is available in Sutton *et al*. 2012), which can be viewed with the freely available SPIERS software suite.

iii) A HDMI supplementary movie showing digital visualisations of both the whole specimen, rendered in Drishti, and the perforations, rendered in Blender.

PLEASE NOTE: For review purposes, this SI is currently available from the following location:

https://drive.google.com/file/d/0B2KhlzGhKIfTLTMzQjRlM2FOenM/view?usp=sharing

and will be uploaded to Zotero on acceptance of the paper.

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Figure captions
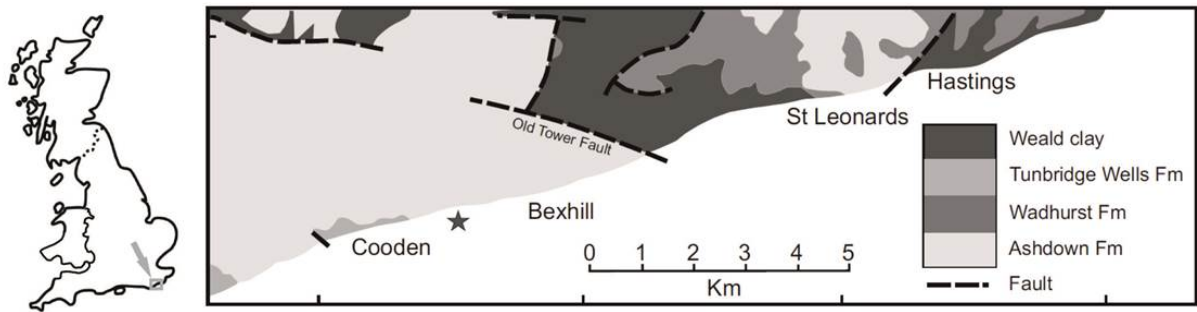
Fig. 1: Map showing location near Bexhill, southern England where specimens were found in the Ashdown Formation. Map on the left shows Great Britain, with location of the main map given by the grey box (arrowed) on south coast of England.

Fig. 2: OUMNH K.65750 under the stereomicroscope. A) Z-stacked focussed image produced under a combination of transmitted and reflected light, showing the morphology and amber colour of the specimen in transmitted light. B) part of the specimen in reflected light only, showing the leathery surface texture and red colour, with sand-filled pits visible (near the top). C) close-up of sand-filled pit, with sand grains arrowed (Z-stacked image). D) Concave depressions (black, arrowed) as seen in transmitted light (visible to the right of the crack at the base of the specimen in A). In reflected light these are seen as sand-filled depressions like those of (C).

Fig. 3: OUMNH K.65751 in reflected light (montage of two images). Note sand-filled pits inside the specimen at the bottom of the image, and resin-coated fibres on the external

surfaces. Fusain fragments and sandstone grains are also adhered to the outside. The long edges are micro-dentate.
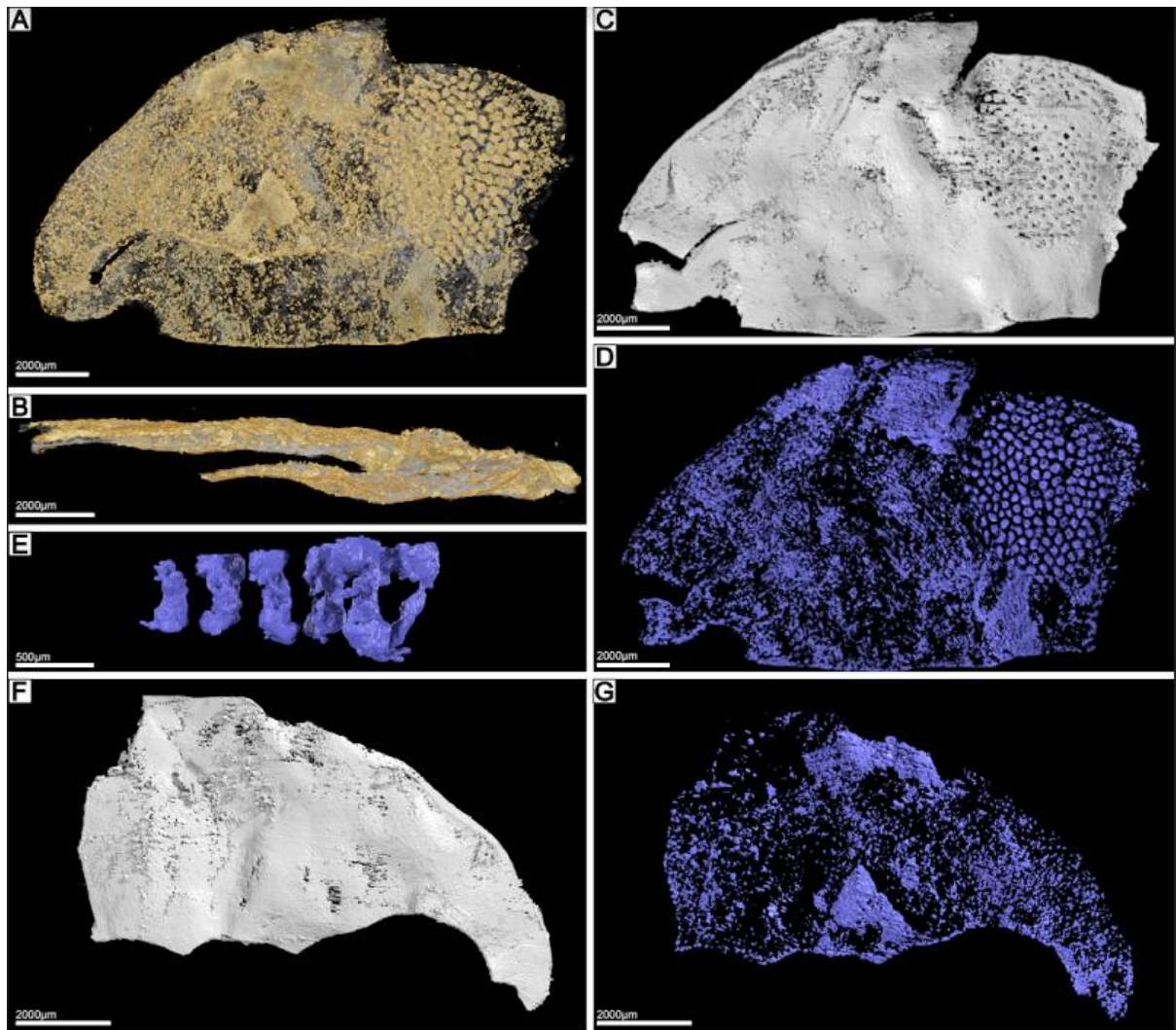

Fig. 4: CT-based digital visualisations of OUMNH K.65751. A, B) Renders created with Drishti showing the denser phase (gold) and their spacing in context of the exterior of the specimen (translucent white). C, D) Blender renders showing the inside surface of one side of the specimen (white), and the distribution of the denser phase (purple) in this portion of the specimen. E) A render showing just the denser phase, from the side (exterior surface top, interior bottom). F, G) Blender renders showing the inside surface of the opposing side of the to C and D (white), and the distribution of the denser phase (purple) within this side.
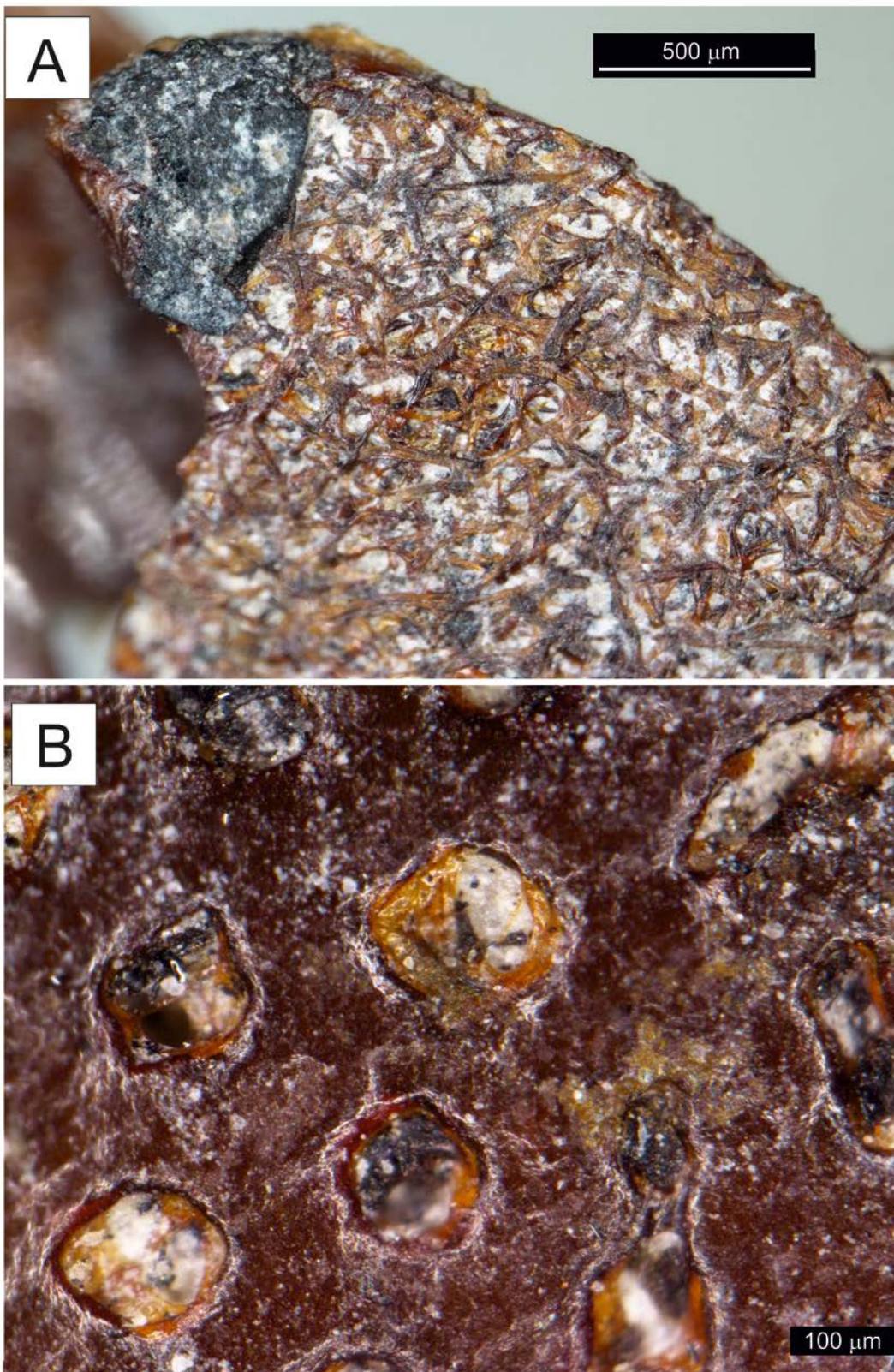
Fig. 5: OUMNH K.65751 close up. A) sand-filled pits as seen near bottom of image in Fig. 3) with amber-coloured resinous substance coating the sand grains (Z-stacked focussed image). B) external surface of the specimen is coated in web of amber-coloured and

presumed resin-coated fibres. Spaces between fibres are sand-filled, with some adherent fusain fragments (top left).
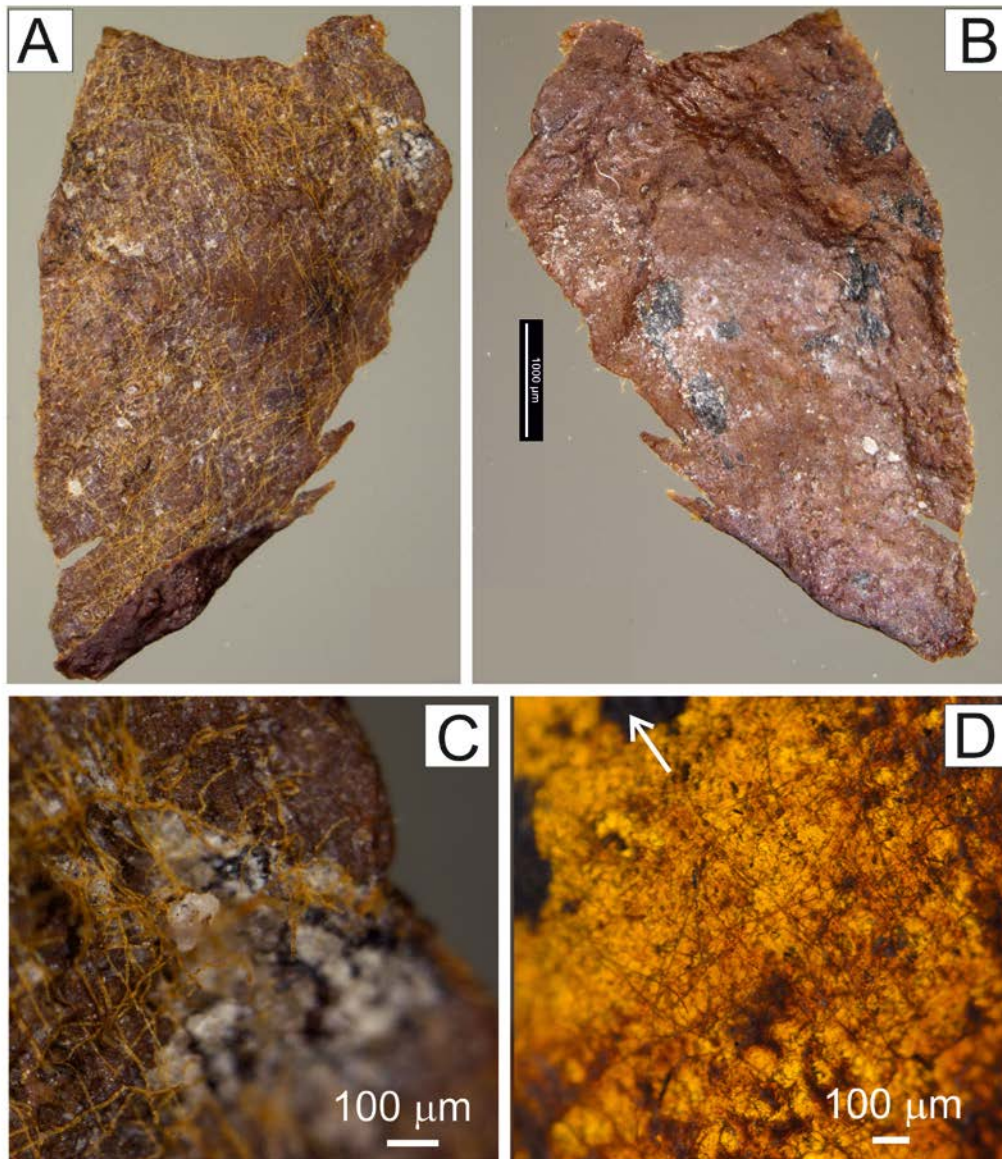

Fig. 6: OUMNH K.65752 in reflected light (A, B and C) and transmitted light (D). This is a triangular-shaped fragment, with one side coated in an amber-coloured web of fibres (A) and the other red and leathery (B). Sand grains underlie the amber web in places (C). In

transmitted light the fragment glows amber (D), with the network of amber threads visible and a fragment of fusain arrowed.
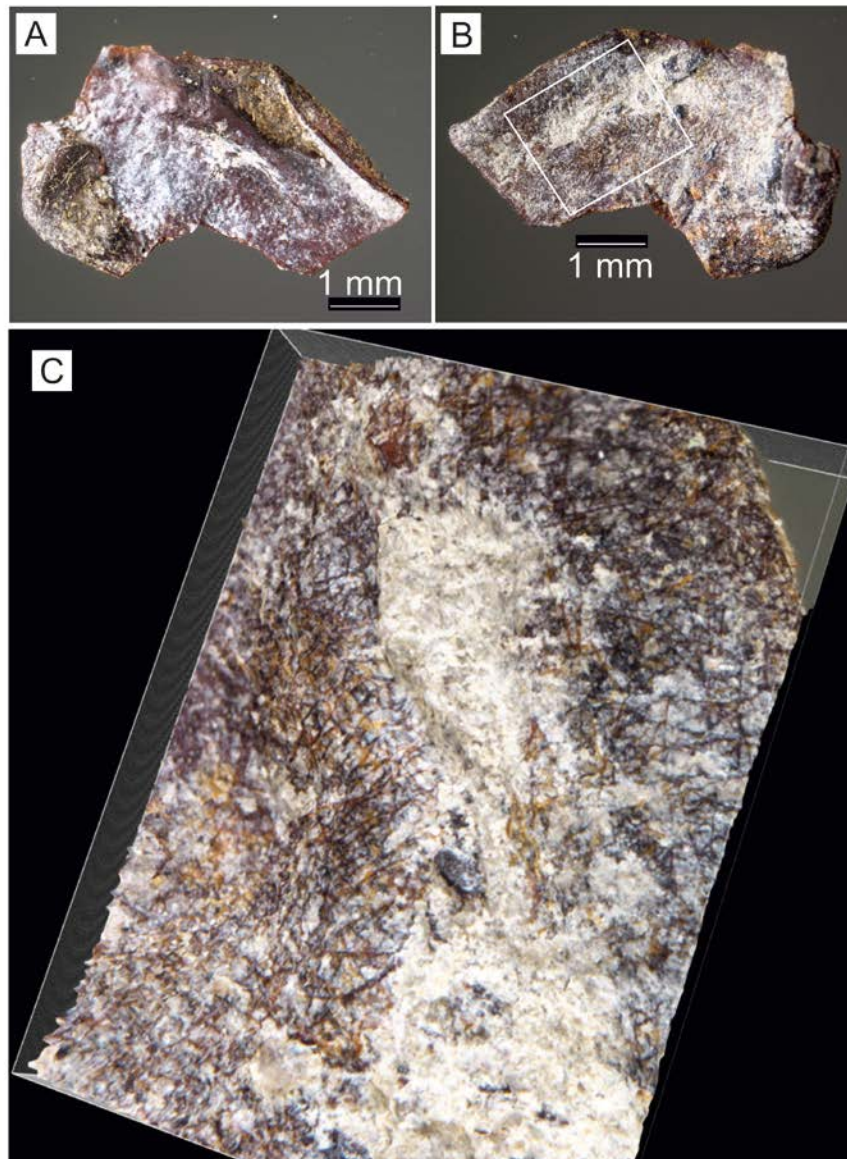

Fig. 7: Specimen OUMNH K.65755. A) and B) showing the specimen under reflected light. One side appears red and leathery (A), and the other is coated in resinous fibres, sandstone and fusain clasts. C) A three-dimensional image of the area within the white box in (B),

showing the resin fibres flexing around folds in the specimen, and underlying the lithified white sandstone and fusain fragments. This image was produced from a Z-stack of images using Nikon Elements D software. Scale bars in A and B are 1 mm. White box in B gives the scale for C.
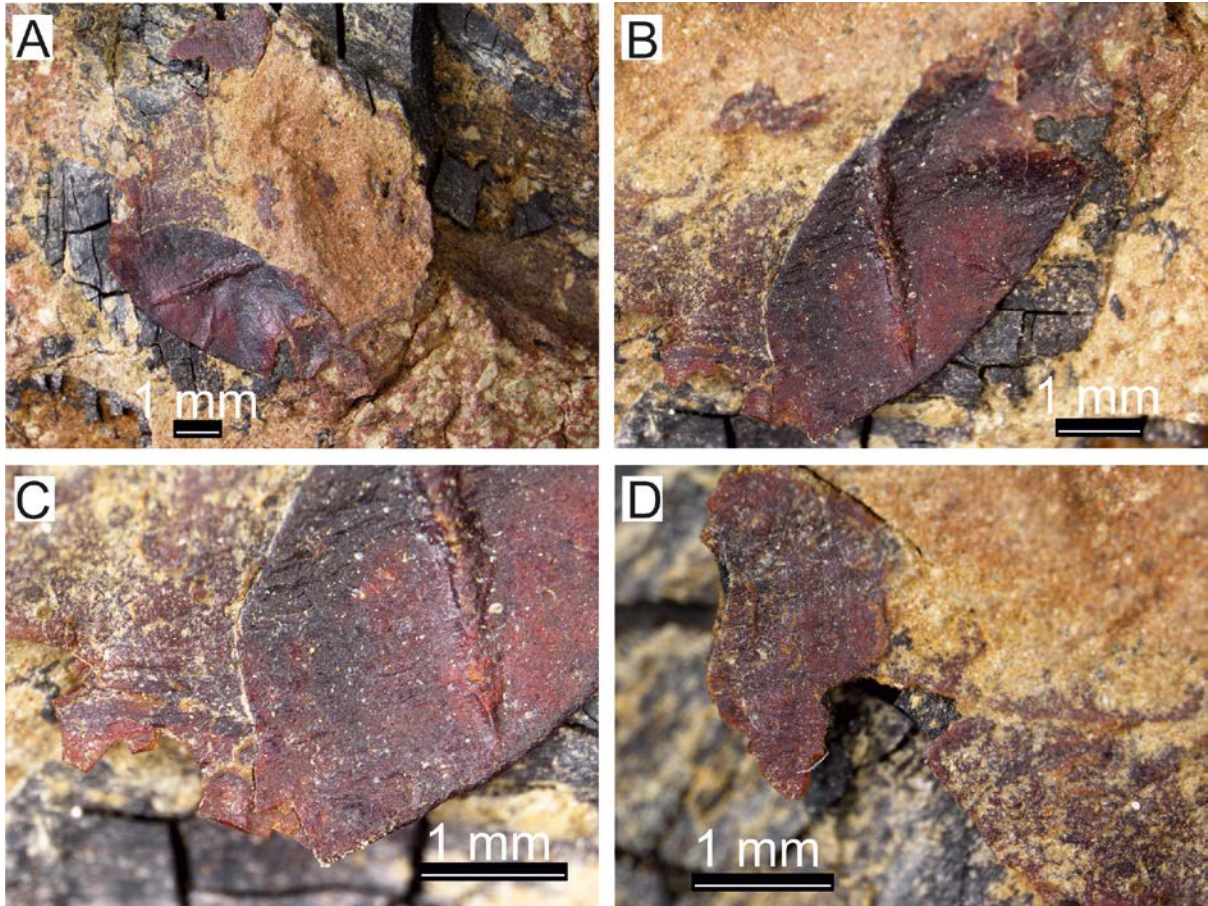

Fig. 8: Specimen OUMNH K.65754, as seen under reflected light. A) the area of the specimen in its entirety. B) close-up of the presumed 'cocoon', and C) end of the specimen as seen in B – note the brittle, resinous appearance of this specimen. D) close-up of the fragment seen in the top left of A. These fragments could all have been part of the same resin-coated folded leaf.
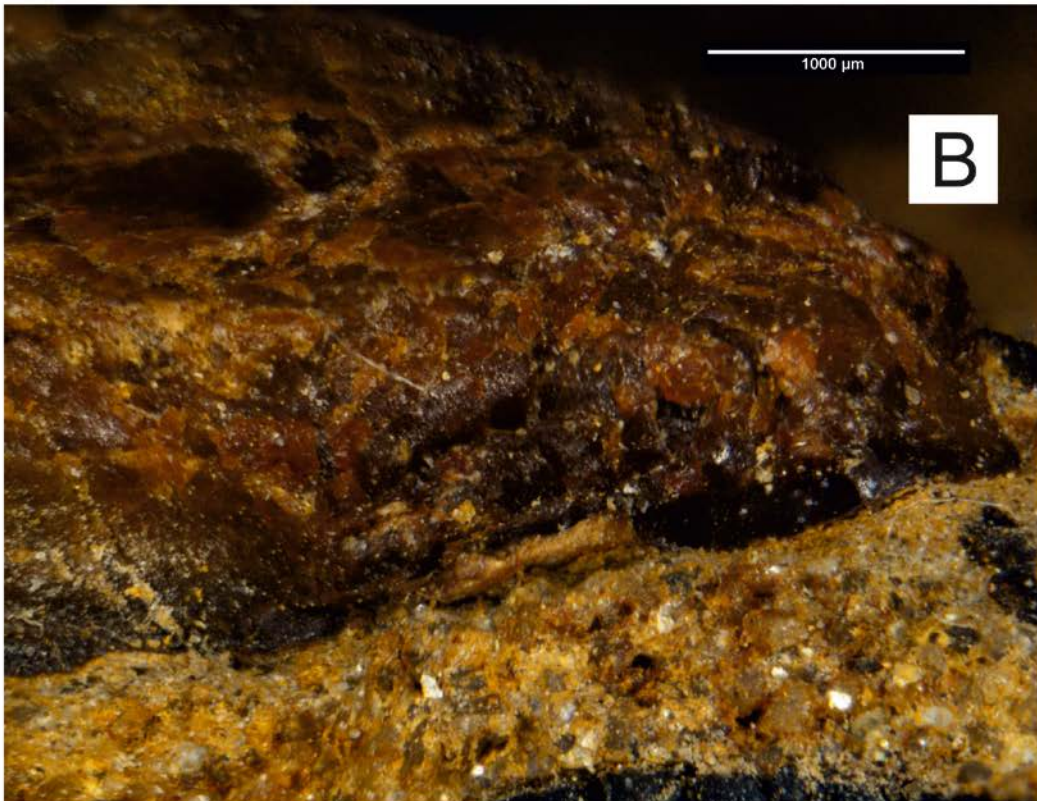
Fig. 9: OUMNH K.65756 in reflected light (Z-stacked focussed images). This is an ovoid specimen of an amber-like substance adhered to a substrate of fusain and lithified sandstone. A) shows the specimen in plan view, and B) in cross-section. Note polished appearance and lineations in (A).
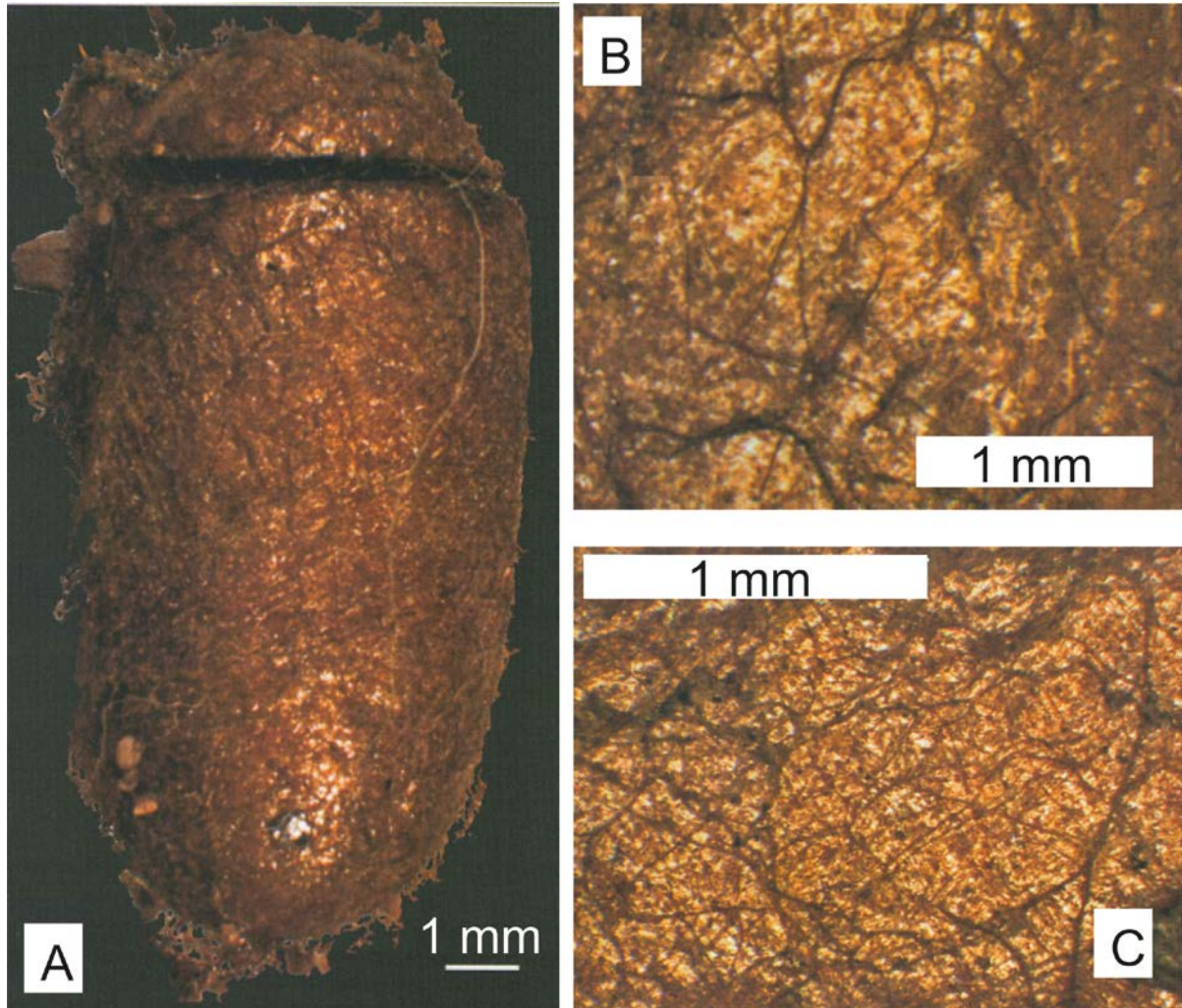
Fig. 10: Potential analogues: Sawfly cocoons. A) *Diprion pini* cocoon, showing its overall morphology. B) web of the *Diprion pini* cocoon at high magnification. C) Close-up of the inner surface of a *Neodiprion sertifer* cocoon.
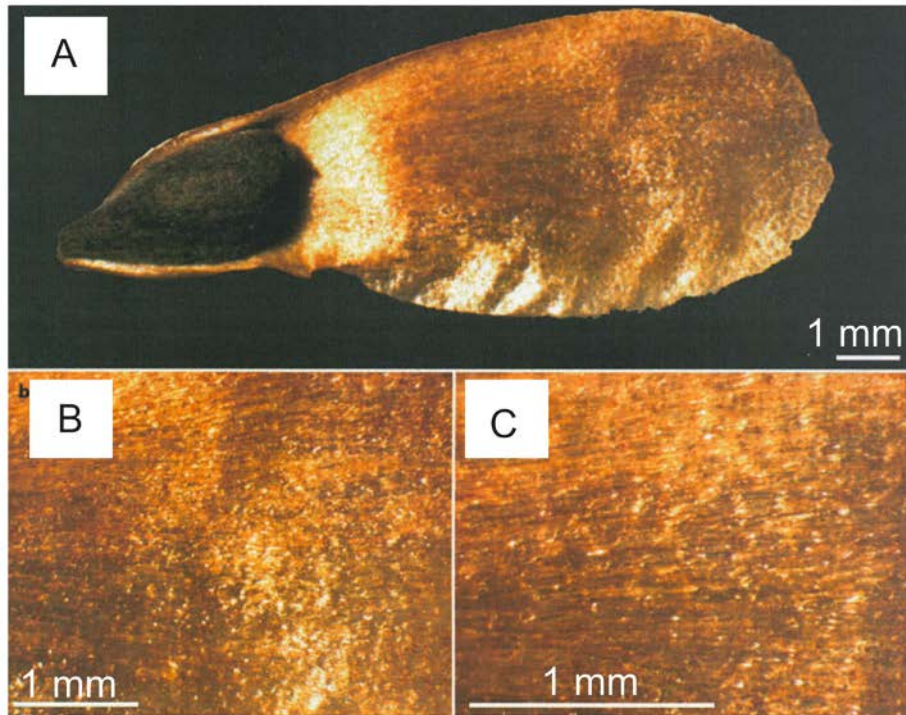
Fig. 11: Potential analogues: a pine seed as seen under the stereomicroscope. A) entire seed, including the dark brown seed pod on the left hand side, and orange-yellow 'wing' on the right hand side. B) and C) show details of the wing. Note the clear lineation along the length of the wing.