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# Ichnotaxonomy of new boring taxa: linking insect activity and fossil resins formation

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## Abstract

The fossil record reveals palaeoecological interactions between plants and insects. This study describes a singular conifer xylite specimen from the Baltic amber-bearing deposits, with preserved resin ducts and cylindrical insect borings designated as *Bivium* **ichnogen. nov.** with *Bivium diluviandi* **ichnosp. nov.** The borings, characterized by longitudinal tunnels connected by cross tunnels and chambers, were likely created by xylophagous beetles belonging to the family Curculionidae (subfamily Scolytinae). The associated resin production reflects an adaptive plant response to insect and fungal activity, evidenced by fungal hyphae preserved within the specimen. This work contributes to the knowledge of Baltic amber stratigraphy, and the formation of resin-bearing deposits, and shows, that the wood-boring insects may have been a cause, among others, of resin exudation.

**Keywords:** Baltic amber, fossil resins, succinite, Talpinidae, taphonomy, xylite

## Introduction

Resins are secondary metabolites of plants, complex mixtures, which include volatile and non-volatile terpenoid and/or phenolic compounds, which could be preserved in form of fossilized resin, so-called ambers and/or copals, or resinites—macerals in lignite (brown coal) that predominantly originate from resinous and waxy components of the original plant material (Langenheim, 2003; Florjan & Worobiec, 2016; Murthy, 2022). These plant exudates play a significant role in enabling plants to adapt to their environments, particularly by mediating bio-interactions and protecting plants from herbivores, insects, and pathogens. They are synthesized by epithelial cells surrounding intercellular spaces, called ducts, where they are stored under pressure. Despite the structural and distributional differences between resin ducts in gymnosperms and angiosperms, as well as the mechanisms of resin loading, there are similarities in the importance of the role of resin in plant defense in both groups of plants (Langenheim, 2003; Cabrita, 2021; Câmara *et al*., 2024).

The resins serve a number of functions in plant defense against fungi, viruses, bacteria and feeding herbivores. Additionally, they provide an optimal medium for the preservation of past biota in the form of inclusions following fossilization. Among the most extensively studied fossil resins known in the world, commonly referred to as ambers (Penney, 2010; Kosmowska-Ceranowicz, 2017), a significant group are those derived from conifer resins and their inclusions, particularly in the Eocene of Europe. These fossil resins frequently contain inclusions of organisms associated with the resin-producing tree (Penney, 2010; Solórzano Kraemer *et al*., 2018). However, in the majority of cases, the tree remains are not preserved in any other manner than as resin inclusions and tissue fragments (Fergusson, 2005; Florjan & Worobiec, 2016). Consequently, amber studies are incomplete, as the fossil record of conifers provides insights into palaeoecosystems, plant-insect interactions, and plant defense mechanisms.

Conifer resin is produced, stored and translocated within specialized secretory structures, which range from single cells or blisters to interconnected resin ducts (Franceschi *et al*., 2005; Vázquez-González *et al*., 2020; Nagy *et al*., 2022). It is thought that these structures rarely contain biological inclusions other than fragments of

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plant tissue, given that the resin was not secreted outside the plant stem and was not in contact with the external environment. Therefore, such ambers are not a primary focus of paleontological studies.

The fossilized wood of conifer trees with preserved resin is known as far back as the Triassic period (Seyfullah *et al*., 2018). However, studies conducted on fossil wood remains (xylites, lignites, or peat deposits) rarely refer to any resinous components other than resinites. This paper presents a distinctive specimen of a coniferous tree branch-like stem—xylite, defined as a type of fossilized plant remains, comprising stems, roots, trunks and other such elements, which are considered to represent an early stage of the process of lignification (Suárez-Ruiz & Crelling, 2008; Florjan & Worobiec, 2016) with well-preserved resin canals and insect traces from the amber deposits of the Baltic region. The wood specimen also exhibits traces of activity, which have been designated a new ichnogenus and ichnospecies of cylindrical borings. These traces may have been correlated with intense resin production in the specimen. Additionally, we discuss the potential significance of this finding in the context of the broader Baltic amber deposits and their formation.

*Age and relations to Baltic amber deposits formations*

The work presents a case study of a unique fossilized wood specimen, which has been preserved with fossil resin in an intact state. This is a rare occurrence within the Baltic amber material. The specimen was derived from raw Baltic amber material extracted from marine Quaternary sand deposits, which constituted the majority of the material utilized in our studies. In this instance, the detailed sedimentology and the age of the material are not ascertainable. The resin is classified as succinite (fossil resin characterized by its high content of succinic acid, typically ranging between 3% and 8% by weight; see Vávra, 2009; Wagner-Wysiecka, 2023), and is referred to as 'Baltic amber' based on the presence of 'Baltic amber shoulder' in FT-IR spectra (Stout *et al*., 1995; Kosmowska-Ceranowicz, 2015).

The age of the succinite, which is typically referred to as exclusively Eocene, remains a topic of ongoing geological inquiry (Aleksandrova & Zaporozhets, 2008; Perkovsky & Makarkin, 2020; Kuzmina *et al*., 2023; Kuzmina & Iakovleva, 2023; Drohojowska *et al*., 2024). The sedimentology of Baltic amber deposits is primarily based on studies of the strata in Königsberg/Kaliningrad, where amber is most abundant in a geological stratum known as the 'Blaue Erde', 'Blue earth' or 'Blue ground'. The term 'Blue earth' is used historically to refer to the middle bed of the Prussian Formation. However, it should be noted that Baltic amber is not solely sourced from this area. The fossil resins are present both above and below the strata (Kharin & Eroshenko, 2017). The Polish section of the amber-bearing deposits (Pomeranian Formation) has been investigated through the analysis of drill samples, which have revealed similarities to the Prussian Formation (Piwocki *et al*., 1996; Piwocki & Olszewska, 1996). This has led to the conclusion that there is a correlation between the Polish deposits and those in Kaliningrad (Piwocki *et al*., 1985; Kosmowska-Ceranowicz, 2008).

## Material and methods

A single piece of fossilized conifer stem (xylite) with fossil resin preserved in resin ducts from the Collection of the Museum of Amber Inclusions, University of Gdańsk, stored under the catalogue number MAIG 6826. The specimen measures 5.8 cm in length and 2.8 cm in width at its greatest diameter and was obtained from an amber mining company operating in the Gulf of Gdańsk, in the area close to the Port of Gdańsk. The specimen was cut from one side at approximately 5 mm in length, slightly ground, and polished in order to reveal the intricate details of wood anatomy and resin flows.

Observations were conducted in the Laboratory of Evolutionary Entomology and Museum of Amber Inclusions University of Gdańsk using a Leica M205A stereoscopic microscope, equipped with a Leica DFC 495 digital camera, operated under the control of the Leica Application Suite 3.7 application for microphotography. Macro and micro photographic documentation was generated using the same Leica microscope and a Canon EOS 90D DSLR (Digital Single Lens Reflex) camera. For UV photography, 350 nm light was employed. Fourier Transform Infrared (FT-IR) spectra were obtained in the Amber Experts company laboratory, Gdańsk with Thermo Scientific Nicolet 380 FT-IR Spectrometer, with ATR and baseline correction, for the reasons and according to the procedure proposed by Szwedo & Stroiński (2017). The received spectrum was compared with data provided in Kosmowska-Ceranowicz (2015).

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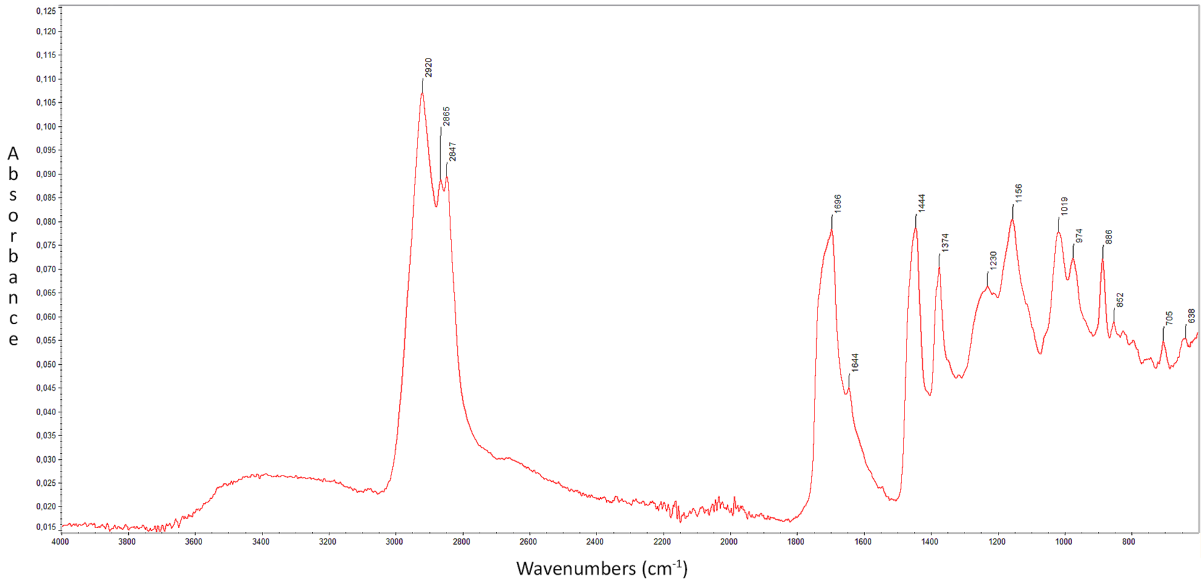


**FIGURE 1.** FT-IR spectrum of the resin from resin canals of the specimen.

## Results

*Xylite specimen as a substrate*

The conifer stem specimen displays a preserved structure of wood tissues, with tracheids, parenchyma cells, and resin ducts. Additionally, it exhibits structures that have been damaged by the activity of fungi and insects, as well as open spaces (sockets) that have been filled with resin. FT-IR spectrum (Fig. 1) of the fossil resin exhibits a 'Baltic amber shoulder', which is an indicator of succinite (Kosmowska-Ceranowicz, 2015). On the edges of the specimen, longitudinal original resin flows are observed, with one reaching almost the full length of the preserved section of stem. In the cross-section, the flows are connected by the space between the tissues originally filled with resin, both at the top of the specimen and the bottom, which is not cut. This system of canals is recognized as an insect-originated trace fossil, assigned to the new ichnogenus and ichnospecies.

## Ichnotaxonomy

### Ichnofamily Talpinidae Wisshak, Knaust & Bertling, 2019

**Type ichnogenus.** *Talpina* Hagenow, 1840; by original designation.

**Diagnostic characters.** Branched cylindrical borings that may anastomose (Wisshak *et al*., 2019).

### Ichnogenus *Bivium* ichnogen. nov.

LSID: urn:lsid:zoobank.org:act:FCDA1D5A-A9D3-4B80-8F6E-37F43FFB2E30

**Type ichnospecies.** *Bivium diluviandi* **ichnosp. nov.**; by present designation (Fig. 2A–E).

**Ethological category.** Domichnia (dwelling traces) or agrichnia (farming traces).

**Etymology.** Name derived from Latin noun 'bivium'—'a place with two ways', 'fork in the road', 'crossroad' and refers to the shape of the tunnels. Gender: neuter.

**Diagnosis.** The tunnels are longitudinal, parallel to the xylic substrate, round and straight, without lining. They have a single, short entrance perpendicular to the main tunnel axis. The branching is slightly curved and parallel to the main tunnel. The main tunnels are interconnected by curved cross tunnels, which may take the form of chambers. In those tunnels single, elongated coprolites are present (Fig. 2F).

**Remarks.** The known morphotypes of the Talpinidae ichnofamily can be distinguished from the described new ichnotaxon by the following characters. In the case of the boring substrate being calcareous, the following ichnogenera were described: *Cunctichnus* Fürsich, Palmer & Goodyear, 1994; *Talpina* von Hagenow, 1840; and *Lapispecus* Voigt, 1970. In the case of xylic substrates, the new ichnogenus *Bivium* **ichnogen. nov.** differs in terms of both shape and content from the following ichnogenera: *Cycalichnus* Genise, 1995, is characterized by a constant width of the tunnel length (3 mm), short tangential (cross) tunnels that do not intersect with the main tunnels, and the occurrence of hexagonal fecal pellets in *Cycalichnus* in contrast to oval coprolites in the proposed ichnogenus. *Ipites* Wisshak, Knaust & Bertling, 2019, lacks cross tunnels or chambers (Karpiński, 1962). Furthermore, it is defined by the occurrence of short radiating tunnels. In comparison, *Paleoscolytus* Walker, 1938 differs in terms of tunnel orientation and width (10 mm), which is at least twice as wide as the new genus. Additionally, *Xylonichnus* Genise, 1995 differs in terms of tunnel shape (flattened) and the absence of fungal activity (Walker, 1938; Philippe *et al*., 2005, 2022; Donovan *et al*., 2015; Buatois *et al*., 2017; Wisshak *et al*., 2019).

***Bivium diluviandi* ichnosp. nov.**
LSID: urn:lsid:zoobank.org:act:0ECCF9B3-AD78-45BE-8B58-3A08454A281E
(Fig. 2A–E)

**Holotype.** Specimen MAIG 6826, deposited in the Museum of Amber Inclusions, University of Gdańsk, Gdańsk, Poland.

**Etymology.** Ichnospecific epithet is derived from Latin verb 'dīluviō' meaning 'to inundate', 'deluge' which reflects the borings filled up with fossil resin.

**Diagnosis.** Macroboring, 2.1–5.0 mm wide. The main tunnel is 5.0–5.5 cm long, slightly wider than the parallel branching tunnel. Main and branching tunnels posteriorly conjoining to form forking ending points. Opening tunnels 4.5–7.0 mm long. Interconnected tunnels form chambers with cylindrical areas (pouches) located in the wall of the chamber. Additional tunnels in various forms branching from wider, conjuring tunnels or chambers.

**Remarks.** The tunnels are filled up with fossilized resin (succinite) and preserved on the edges of the conifer wood specimen, resembling modern galleries of Scolytinae formed under the bark of a stems and young trees (Ranger *et al*., 2016; Greppi *et al*., 2021). Opening of boring marked with a round drop of fossilized resin (Fig. 2E) formed when the tree produced resin that was pushed out of the tunnel. The chamber filled up with resin shows fungal hyphae covering chamber walls (Fig. 2G), which the authors do not interpret as an outer layer. Wooden areas tangent to borings are damaged by fungal activity (Fig. 2G, H).

## Discussion

*Tracemaker and the boring*

The newly proposed ichnogenus, *Bivium* **ichnogen. nov.**, exhibits similarities to the *Paleoscolytus* morphotypes. It is characterized by the formation of tunnels beneath conifer bark, which bears resemblance to the activity of modern members of the Curculionidae beetles of the subfamily Scolytinae (Walker, 1938; Labandeira, 2001; Dominik & Starzyk, 2004, 2010). Scolytine weevils (bark and ambrosia beetles) have a unique ecological significance in forest ecosystems, and intrinsically interesting biology (Cognato & Grimaldi, 2009; Hulcr *et al*., 2015; Kirkendall *et al*., 2015) Fossilized galleries of scolytines have been reported in Late Mesozoic wood (Cognato & Grimaldi, 2009; Legalov, 2024). The morphology of both *Bivium* **ichnogen. nov.** and *Paleoscolytus* galleries is similar, yet differs in detailed morphology, which leads to the conclusion that the borings were left by different representatives of the Curculionidae beetles subfamilies. The presence of fungal activity is indicated by the preservation of mycelium on the edges of resin sockets (Fig. 2G) and the occurrence of fungal damage tissue in the form of structures that resemble a modern brown rot pocket (Fig. 2H). This differs from the occurrence of coprolites, fecal pellets, or other feeding traces (Eriksson *et al*., 1990; Tanner & Lucas, 2013; Feng *et al*., 2019, 2021; Biswas *et al*., 2020; Nagy *et al*., 2022). Isolated coprolites found in tunnels represent an ichnotaxon, designated as *Coprulus* Mayer, 1952. Further investigations of the cellular structure and damage to the tissue have yet to be conducted. Conversely, if these structures are regarded as feeding traces, this would indicate the coexistence of another borer. The presence of single coprolites in the tunnels is unlikely to occur in such a small plant stem, although this cannot be fully ruled out. The presence of a gallery in the stem with high fungal activity indicates the potential involvement of an ambrosia beetle borer, a common inclusion observed in fossil resins (Nagy *et al*., 2000; Labandeira, 2014; Peris *et al*., 2021).

*Specimen preservation and taphonomy*

The growth rings in the specimen are indistinct and irregular, likely resulting from the influence of environmental factors and the angle at which the specimen grew out from the trunk. The occurrence and arrangement of the resin canal (high abundance in the observed tissues and within annual rings) resembles those often referred to as traumatic resin canals (Fig. 2H). These canals are interpreted as a plant response to damage caused by insects or fungal activity, among others (Franceschi *et al*., 2005; Nagy *et al*., 2000; Werker & Fahn, 1969; Xu *et al*., 2018), which corroborate the presented interpretation of the described traces as an insect gallery.

The specimen's preparation revealed a cellular-level anatomy consistent with that of xylites, yet it was preserved in an unusual manner, namely by filling it with fossilized resin (succinite). The resinous body fossils found in fossil conifers were previously regarded as resinites (Widera, 2015; Bechtel *et al*., 2020; Simoneit *et*

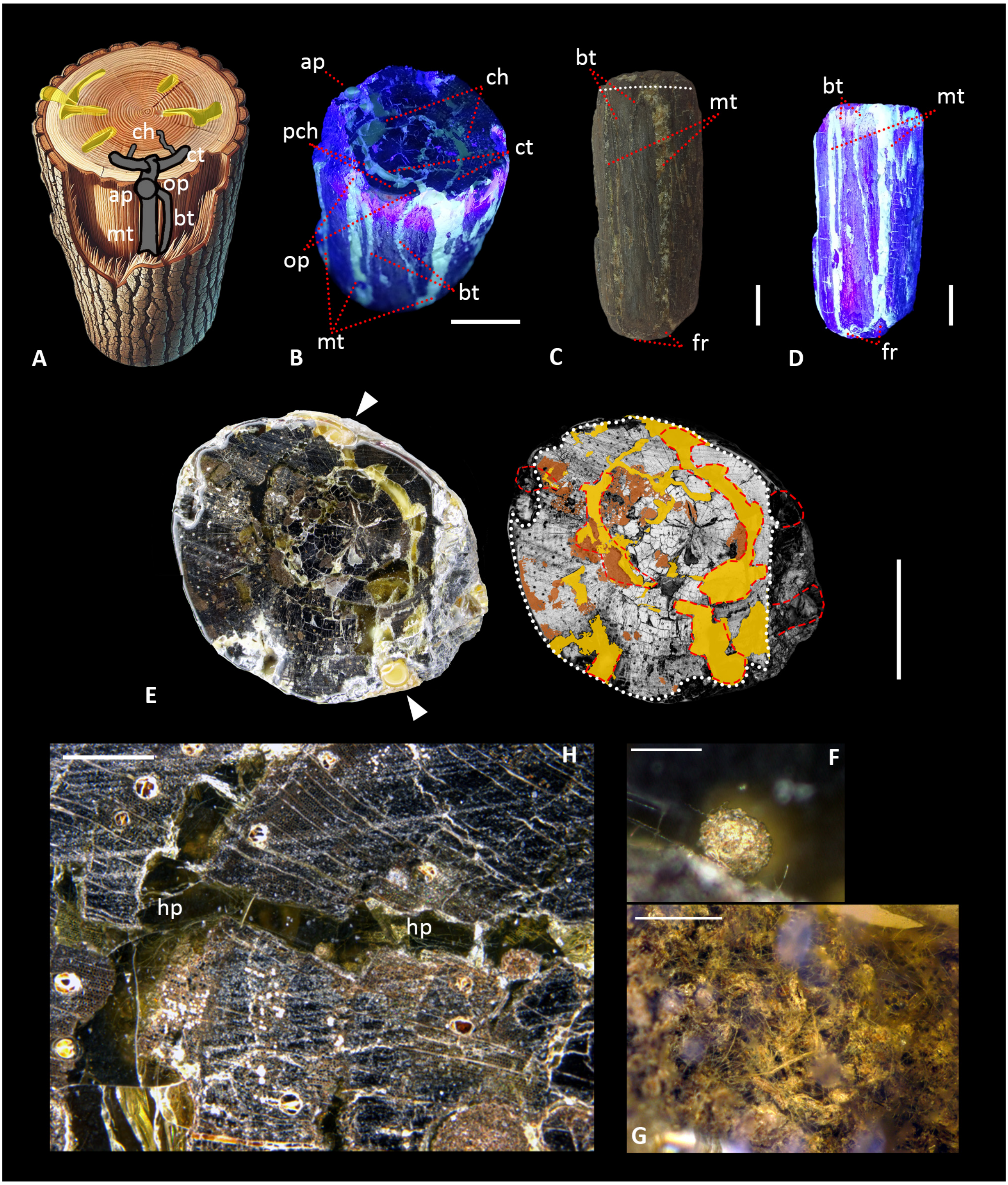


**FIGURE 2.** *Bivium diluviandi* **ichnogen. et ichnosp. nov.**, holotype MAIG 6826. **A**, Reconstruction of the boring. **B**, Morphology of borings in UV light. **C**, Lateral view of borings before exposing the top surface. **D**, Lateral view of the borings in UV after cutting the top, cut marked with a white dotted line. **E**, Exposed top of the specimen after preparation and a map of preserved structures: yellow zone—borings and wood blisters filled up with resin; brown zone—an area with damaged wood resembles wood-decaying fungal activity; red dashed line—openings and part of the tunnels of borings visible in the view; white dotted line—surface of the cut; arrows—opening marked by a round drop of fossilized resin. **F**, One of the coprolites preserved in tunnels. **G**, Wall of the chamber with damaged wood and hyphae. **H**, Resin ducts (round structures in wood tissue) close to one of the tunnels and fungal hyphae. ap: aperture; bt: branching tunnel; ch: chambers; ct: cross tunnel; fr: forking ending; hp: fungal hyphae; mt: main tunnel; op: opening tunnel; pch: pouch. Scale bars: **B**–**E** = 1cm, **F** = 500 µm, **G** = 200 µm, **H** = 1mm.

**FIGURE 3.** Proposed reconstruction of the specimen and wetlands it could originated from.

*al*., 2021; Philippe *et al*., 2022). This type of fossil resin permineralization or impregnation, in conjunction with the evidence of rapid burial in semi-aquatic or wet terrestrial environments, is indicated by the absence of any signs of long waterlogging and its lithology. Additionally, the presence of resin within pore spaces and surface cracking indicates a pathological state and extensive damage to the living tissue, rather than the typical permineralization that occurs following burial. In such cases, spaces should be filled with minerals (such as silica for example) from groundwater. The absence of sediment from the mining site precludes the possibility of determining whether the specimen was deposited *in situ* or not. However, the evidence suggests that it was not deposited *in situ* and therefore has to be considered as allochthonous rather than parautochthonous or semiautochthonous, even though it may have been reworked in the sediment rather than transported over a significant distance. In conclusion, the absence of phosphatised plant tissue and the absence of evidence of high-level abrasion or bioerosion (*e.g.*, molluscan borings) indicate that the piece of conifer was deposited in a terrestrial, humid environment forming lignite sediment, rather than being exposed to the marine environment before fossilization (Fig. 3) (Buurman, 1972; Fengel, 1991; Philippe *et al*., 2005, 2022; Björdal, 2012; Mustoe, 2017; McLoughlin, 2020).

Conifer xylites can be present in the deposits, which are typically referred to as plant remains, brown coal, and lignite. These are related to the majority of the fossil resin assemblages from the region (Florjan & Worobiec, 2016). It can therefore be surmised that the specimen in question could be extracted from a lignite-bearing xenolith within the Quaternary deposits that are present in the sediments of the Baltic Sea coast. These deposits have been altered or moved by a number of factors, including the Pleistocene ice sheet, storm surges and tsunamis (Olszak *et al*., 2011; Widera, 2016; Piotrowski *et al*., 2017).

## Conclusions

The new ichnogenus and ichnospecies, *Bivium diluviandi* **ichnogen. et ichnosp. nov.**, a trace of the behavior of wood-boring insects within a conifer xylite specimen, offers new opportunities to study the so-called "amber forest". This work shows that the occurrence of such borings, and resin-filled structures, most likely represents an adaptive response of resin-producing trees to xylophagous insects in the Eocene. The presence of fungal hyphae within the resin-filled borings reveals a complex interaction between plants, insects, and fungi in those palaeoecosystems preserved by fossil resin.

This study not only contributes to the ichnotaxonomic studies of trace fossils within xylitic substrates but also provides data of intense resin production correlated with insect activity. This case study may suggest that the role of wood-boring insects in amber formation is significant to consider. It also emphasizes the lignite-bearing deposits, especially xylites as sources of fossil resins data.

Future research could benefit from the integration of taphonomical, palynological, and geochemical data. This approach could improve understanding of the stratigraphic correlations between amber-bearing deposits across the Baltic region, their formation, and the Eocene palaeoenvironments.

## References


Aleksandrova, G.N. & Zaporozhets, N.I. (2008) Palynological characteristics of Upper Cretaceous and Paleogene deposits on the west of the Sambian Peninsula (Kaliningrad region), Part 1. *Stratigraphy and Geological Correlation*, 16 (3), 295–316.
https://doi.org/10.1134/S0869593808030052

Bechtel, A., Widera, M., Lücke, A., Groß, D. & Woszczyk, M. (2020) Petrological and geochemical characteristics of xylites and associated lipids from the First Lusatian lignite seam (Konin Basin, Poland): Implications for floral sources, decomposition and environmental conditions. *Organic Geochemistry*, 147, 104052, 1–16.
https://doi.org/10.1016/j.orggeochem.2020.104052

Biswas, A., Bera, M., Khan, M.A., Spicer, R.A., Spicer, T.E.V., Acharya, K. & Bera, S. (2020) Evidence of fungal decay in petrified legume wood from the Neogene of the Bengal Basin, India. *Fungal Biology*, 124 (11), 958–968.
https://doi.org/10.1016/j.funbio.2020.08.003

Björdal, C.G. (2012) Microbial degradation of waterlogged archaeological wood. *Journal of Cultural Heritage*, 13 (3), S118–S122.
https://doi.org/10.1016/j.culher.2012.02.003

Buatois, L.A., Wisshak, M., Wilson, M.A. & Mángano, M.G. (2017) Categories of architectural designs in trace fossils: A measure of ichnodisparity. *Earth-Science Reviews*, 164, 102–181.
https://doi.org/10.1016/j.earscirev.2016.08.009

Buurman, P. (1972) Mineralization of fossil wood. *Scripta Geologica*, 12, 1–43.

Cabrita, P. (2021) A model for resin flow. *In*: Ramawat, K.G., Ekiet, H.M. & Goyal, S. (Eds), *Plant cell and tissue differentiation and secondary metabolites. Fundamentals and applications*. Reference series in phytochemistry. Springer Nature Switzerland AG, Cham, pp. 117–144.
https://doi.org/10.1007/978-3-030-30185-9_5

Câmara, J.S., Perestrelo, R., Ferreira, R., Berenguer, C.V., Pereira, J.A.M. & Castilho, P.C. (2024) Plant-derived terpenoids: a plethora of bioactive compounds with several health functions and industrial applications—a comprehensive overview. *Molecules*, 29 (16), 3861, 1–35.
https://doi.org/10.3390/molecules29163861

Cognato, A.I. & Grimaldi, D. (2009) 100 million years of morphological conservation in bark beetles (Coleoptera: Curculionidae: Scolytinae). *Systematic Entomology*, 34 (1), 93–100.
https://doi.org/10.1111/j.1365-3113.2008.00441.x

Dominik, J. & Starzyk, J.R. (2004) *Owady uszkadzające drewno,* [*Wood-damaging insects*]. Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa, 550 pp. [In Polish]

Dominik, J. & Starzyk, J.R. (2010) *Atlas owadów uszkadzających drewno* [*Atlas of wood-damaging insects*]. Vols. 1 & 2. Multico Oficyna Wydawnicza, Warszawa, 240+232 pp. [In Polish]

Donovan, S.K., Jagt, J.W.M. & Nieuwenhuis, E.A.P.M. (2015) The boring *Cunctichnus probans* Fürsich, Palmer and Goodyear, 1994, from the type Maastrichtian (Upper Cretaceous, Northeast Belgium). *Ichnos: An International Journal of Plant and Animal*, 22 (1), 19–21.
https://doi.org/10.1080/10420940.2014.988211

Drohojowska, J., Zmarzły, M. & Szwedo, J. (2024) The discovery of a fossil whitefly from Lower Lusatia (Germany) presents a challenge to current ideas about Baltic amber. *Scientific Reports*, 14, 23102, 1–9.
https://doi.org/10.1038/s41598-024-74197-8

Eriksson, K.-E.L., Blanchette, R.A. & Ander, P. (1990) Morphological aspects of wood degradation by fungi and bacteria. *In*: Eriksson, K.E.L., Blanchette, R.A. & Ander, P. (2012) *Microbial and enzymatic degradation of wood and wood components*. Springer Science & Business Media, Berlin/Heidelberg, pp. 1–87.
https://doi.org/10.1007/978-3-642-46687-8_1

Feng, Z., Bertling, M., Noll, R., Ślipiński, A. & Rößler, R. (2019) Beetle borings in wood with host response in early Permian

conifers from Germany. *Paläontologisches Zeitschrift*, 93 (3), 409–421.
https://doi.org/10.1007/S12542-019-00476-9

Feng, Z., Wang, J., Zhou, W.M., Wan, M.L. & Pšenička, J. (2021) Plant-insect interactions in the early Permian Wuda Tuff Flora, North China. *Review of Palaeobotany and Palynology*, 294, 104269, 1–12.
https://doi.org/10.1016/j.revpalbo.2020.104269

Fengel, D. (1991) Aging and fossilization of wood and its components. *Wood Science and Technology*, 25 (3), 153–177.
https://doi.org/10.1007/BF00223468

Fergusson, D.K. (2005) Plant taphonomy: ruminations on the past, the present, and the future. *Palaios*, 20 (5), 418–428.
https://doi.org/10.2110/palo.2005.P05-25p

Florjan, S. & Worobiec, G. (2016) *Skamieniałości roślinne: zarys tafonomii roślin* [*Plant fossils: an outline of plant taphonomy*]. Instytut Botaniki im. W. Szafera Polskiej Akademii Nauk, Kraków, 220 pp. [In Polish]

Franceschi, V.R., Krokene, P., Christiansen, E. & Krekling, T. (2005) Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist*, 167, 353–376.
https://doi.org/10.1111/j.1469-8137.2005.01436.x

Fürsich, F.T., Palmer, T.J. & Goodyear, K.L. (1994) Growth and disintegration of bivalve-dominated patch reefs in the Upper Jurassic of southern England. *Palaeontology*, 37, 131–171.
https://biostor.org/reference/166064

Genise, J.F. (1995) Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. *Ichnos: An International Journal of Plant & Animal Traces*, 3 (4), 287–299.
https://doi.org/10.1080/10420949509386399

Greppi, C.D., García Massini, J.L. & Pujana, R.R. (2021) Saproxylic arthropod borings in *Nothofagoxylon* woods from the Miocene of Patagonia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 571, 110369, 1–18.
https://doi.org/10.1016/j.palaeo.2021.110369

Hulcr, J., Atkinson, T.H., Cognato, A.I., Jordal, B.H. & McKenna, D.D. (2015) Morphology, taxonomy, and phylogenetics of bark beetles. *In*: Vega, F.E. & Hofstetter, R.W. (Eds), *Bark beetles. Biology and ecology of native and invasive species*. Elsevier/Academic Press, London, pp. 41–84.
https://doi.org/10.1016/B978-0-12-417156-5.00002-2

ICZN [International Commission on Zoological Nomenclature] (1999) International code of zoological nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, xxix + 306 pp. Available from: https://code.iczn.org/ (accessed 13.11.2024 ).

Karpiński, J.J. (1962) Odlew żerowisk kopalnego chrząszcza z rodziny Scolytidae z piaskowca oligomioceńskiego w Osieczowie (Dolny Śląsk) [Cast of the brood galleries of fossil beetle of the Scolytidae family from Oligocene/Miocene sandstone at Osieczów (Lower Silesia)]. *Prace Państwowego Instytu Geologicznego*, 30, 237–239. [In Polish]

Kharin, G.S. & Eroshenko, D.V. (2017) Amber in sediments of the Baltic Sea and the Curonian and Kaliningrad bays. *Lithology and Mineral Resources*, 52 (5), 392–400.
https://doi.org/10.1134/s0024490217050054

Kirkendall, L.R., Biedermann, P.H.W. & Jordal, B.H. (2015) Evolution and diversity of bark and ambrosia beetles. *In*: Vega, F.E. & Hofstetter, R.W. (Eds), *Bark beetles. Biology and ecology of native and invasive species*. Elsevier/Academic Press, London, pp. 85–156.
https://doi.org/10.1016/B978-0-12-417156-5.00003-4

Kosmowska-Ceranowicz, B. (2008) Glowing stone: Amber in Polish deposits and collections. *Przegląd Geologiczny*, 56 (8/1), 604–610+574.

Kosmowska-Ceranowicz, B. (2015) Infrared spectra of fossil, subfossil resins and selected imitations of amber. Atlas widm w podczerwieni żywic kopalnych, subfosylnych i niektórych imitacji bursztynu. *In*: Kosmowska-Ceranowicz, B. (Ed.), *Atlas. Infrared spectra the World's resins. Holotype characteristics / Widma IR żywic świata. Charakterystyka ich holotypów*. Polska Akademia Nauk, Muzeum Ziemi w Warszawie, Warsaw, pp. 5–213.

Kosmowska-Ceranowicz, B. (2017) *Bursztyn w Polsce i na świecie. Amber in Poland and in the World. Second edition*. Wydawnictwa Uniwersytetu Warszawskiego, Warsaw, 316 pp. [In Polish]
https://doi.org/10.31338/uw.9788323526117

Kuzmina, O.B. & Iakovleva, A.I. (2023) New spore and pollen data from the Upper Eocene deposits of the Sambian Peninsula, Kaliningrad Oblast. *Stratigraphy and Geological Correlation*, 31 (3), 200–214.
https://doi.org/10.1134/S086959382303005X

Kuzmina, O.B., Iakovleva, A.I. & Mychko, E.V. (2023) The age and depositional settings of the Upper Paleogene–Lower Neogene Kurshskaya Formation in its stratotype section (Kaliningrad Oblast) based on palynological data. *Stratigraphy and Geological Correlation*, 31 (6), 657–675.
https://doi.org/10.1134/S0869593823060072

Labandeira, C.C. (2014) Amber. *In*: Laflamme, M., Schiffbauer, J.D. & Darroch, S.A.F. (Eds), Reading and writing of the fossil record: Preservational pathways to exceptional fossilization Presented as a Paleontological Society Short Course at the Annual Meeting of the Geological Society of America, Vancouver, British Columbia, October 18, 2014. *Paleontological Society Papers*, 20, 163–216.
https://doi.org/10.1017/S108933260000276X

Labandeira, C.C., LePage, B.A. & Johnson, A.H. (2001) A *Dendroctonus* bark engraving (Coleoptera: Scolytidae) from a middle Eocene *Larix* (Coniferales: Pinaceae): early or delayed colonization? *American Journal of Botany*, 88 (11), 2026–2039.
https://doi.org/10.2307/3558429

Langenheim, J.H. (2003) *Plant resins: chemistry, evolution, ecology and ethnobotany*. Timber Press, Portland, 612 pp.

Legalov, A.A. (2024) Fossil history of bark-beetles (Coleoptera: Scolytidae) with descriptions of two new species. *Historical Biology*, 36 (2), 378–388. https://doi.org/10.1080/08912963.2022.2157275

Mayer, G. (1952) Neue Lebensspuren aus dem Unteren Hauptmuschelkalk (Trochitenkalk) von Wiesloch: *Coprulus oblongus* n. sp. und *C. sphaeroideus* n. sp. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1952, 376–379.

McLoughlin, S. (2020) Marine and terrestrial invertebrate borings and fungal damage in Paleogene fossil woods from Seymour Island, Antarctica. *GFF*, 142 (3), 223–236. https://doi.org/10.1080/11035897.2020.1781245

Murthy, H.N. (Ed.) (2022) *Gums, resins and latexes of plant origin. Chemistry, biological activities and uses*. Springer Nature Switzerland AG, Cham, 912 pp. https://doi.org/10.1007/978-3-030-91378-6

Mustoe, G.E. (2017) Wood petrifaction: a new view of permineralization and replacement. *Geosciences*, 7 (4), 119, 1–17. https://doi.org/10.3390/geosciences7040119

Nagy, N.E., Franceschi, V.R., Solheim, H., Krekling, T. & Christiansen, E. (2000) Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): anatomy and cytochemical traits. *American Journal of Botany*, 87 (3), 302–313. https://doi.org/10.2307/2656626

Nagy, N.E., Norli, H.R., Fongen, M., Østby, R.B., Heldal, I.M., Davik, J. & Hietala, A.M. (2022) Patterns and roles of lignan and terpenoid accumulation in the reaction zone compartmentalizing pathogen-infected heartwood of Norway spruce. *Planta*, 255 (3), 1–16. https://doi.org/10.1007/s00425-022-03842-1

Olszak, I.J., Florek, W., Seul, C. & Majewski, M. (2011) Lithology of sediments and stratigraphy of glacial layers of some cliff sections on central and western Polish Coast. *Geologija*, 53 (1/73), 1–9. https://doi.org/10.6001/geologija.v53i1.1612

Penney, D. (Ed.) (2010) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, 304 pp.

Peris, D., Delclòs, X. & Jordal, B. (2021) Origin and evolution of fungus farming in wood-boring Coleoptera—a palaeontological perspective. *Biological Reviews*, 96 (6), 2476–2488. https://doi.org/10.1111/brv.12763

Perkovsky, E.E. & Makarkin, V.N. (2020) A new species of *Sympherobius* Banks (Neuroptera: Hemerobiidae) from the late Eocene Rovno amber. *Palaeoentomology*, 3 (2), 196–203. https://doi.org/10.11646/palaeoentomology.3.2.9

Philippe, M., Cuny, G., Suteethorn, V., Teerarungsigul, N., Barale, G., Thévenard, F., le Loeuff, J., Buffetaut, E., Gaona, T., Košir, A. & Tong, H. (2005) A Jurassic amber deposit in southern Thailand. *Historical Biology*, 17 (1-4), 1–6. https://doi.org/10.1080/08912960500284729

Philippe, M., McLoughlin, S., Strullu-Derrien, C., Bamford, M., Kiel, S., Nel, A. & Thévenard, F. (2022) Life in the woods: Taphonomic evolution of a diverse saproxylic community within fossil woods from Upper Cretaceous submarine mass flow deposits (Mzamba Formation, southeast Africa). *Gondwana Research*, 109, 113–133. https://doi.org/10.1016/j.gr.2022.04.008

Piotrowski, A., Szczuciński, W., Sydor, P., Kotrys, B., Rzodkiewicz, M. & Krzymińska, J. (2017) Sedimentary evidence of extreme storm surge or tsunami events in the southern Baltic Sea (Rogowo area, NW Poland). *Geological Quarterly*, 61 (4), 973–986. https://doi.org/10.7306/gq.1385

Piwocki, M. & Olszewska, B. (1996) Korelacja litostratygraficzna paleogenu Polski z krajami sąsiednimi. [Lithostratigraphic correlation of the Paleogene of Poland with other areas]. *In*: Malinowska L. & Piwocki M. (Eds), *Budowa geologiczna Polski, t. III. Atlas skamieniałości przewodnich i charakterystycznych, cz. 3a. Kenozoik, Trzeciorzęd, Paleogen* [*Geology of Poland, vol. III. Atlas of guide and characteristic fossils, part 3a Cainozoic, Tertiary, Paleogene*]. Państwowy Instytut Geologiczny, Warszawa, 37–44. [In Polish]

Piwocki, M., Olszewska, B. & Grabowska, I. (1996) Korelacja biostratygraficzna paleogenu Polski z innymi obszarami. [Biostratigraphic correlation of the Paleogene of Poland with other areas]. *In*: Malinowska L. & Piwocki M. (Eds), *Budowa geologiczna Polski, t. III. Atlas skamieniałości przewodnich i charakterystycznych, cz. 3a. Kenozoik, Trzeciorzęd, Paleogen* [*Geology of Poland, vol. III. Atlas of guide and characteristic fossils, part 3a Cainozoic, Tertiary, Paleogene*]. Państwowy Instytut Geologiczny, Warszawa, 25–37. [In Polish]

Piwocki, M., Olkowicz-Paprocka, I., Kosmowska-Ceranowicz, B., Grabowska, I. & Odrzywolska-Bienkowa, E. (1985) Stratygrafia trzeciorzędowych osadów bursztynonośnych okolic Chłapowa koło Pucka [Stratigraphy of Tertiary amber-bearing sediments in the vicinity of Chłapowo near Puck]. *Prace Muzeum Ziemi*, 37, 61–77. [In Polish]

Ranger, C.M., Reding, M.E., Schultz, P.B., Oliver, J.B., Frank, S.D., Addesso, K.M., Chong, J.H., Sampson, B., Werle, C., Gill, S. & Krause, C. (2016) Biology, ecology, and management of nonnative ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in ornamental plant nurseries. *Journal of Integrated Pest Management*, 7 (1), 9. https://doi.org/10.1093/jipm/pmw005

Seyfullah, L.J., Roghi, G., Dal Corso, J. & Schmidt, A.R. (2018) The Carnian Pluvial Episode and the first global appearance of amber. *Journal of the Geological Society*, 175 (6), 1012–1018. https://doi.org/10.1144/jgs2017-143

Simoneit, B.R.T., Otto, A., Menor-Sálvan, C., Oros, D.R., Wilde, V. & Riegel, W. (2021) Composition of resinites from the Eocene Geiseltal brown coal basin, Saxony-Anhalt, Germany

and comparison to their possible botanical analogues. *Organic Geochemistry*, 152, 104138.
https://doi.org/10.1016/j.orggeochem.2020.104138

Solórzano Kraemer, M.M., Delclòs, X., Clapham, M.E., Arillo, A., Peris, D., Jäger, P., Stebner, F. & Peñalver, E. (2018) Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. *Proceedings of the National Academy of Sciences of the United States of America*, 115 (26), 6739–6744.
https://doi.org/10.1073/pnas.1802138115

Stout, E.C., Beck, C.W. & Kosmowska-Ceranowicz, B. (1995) Gedanite and gedano-succinite. *In*: Anderson, K.B. & Crelling, J.C. (Eds), Amber, resinite, and fossil resins. *American Chemical Society*, 617, 130–148.
https://doi.org/10.1021/bk-1995-0617.ch007

Suárez-Ruiz, I. & Crelling, J.C. (Eds) (2008) *Applied coal petrology. The role of petrology in coal utilization*. Elsevier/Academic Press, Amsterdam, 388 pp.

Szwedo, J. & Stroiński, A. (2017) Who's that girl? The singular Tropiduchidae planthopper from the Eocene Baltic amber (Hemiptera: Fulgoromorpha). *Palaeontologia Electronica*, 20.3.60A, 1–20.
https://doi.org/10.26879/784

Tanner, L.H. & Lucas, S.G. (2013) Degraded wood in the Upper Triassic Petrified Forest Formation (Chinle Group), northern Arizona: differentiating fungal rot from arthropod boring. *In*: Tanner, L.H., Spielmann J.A. & Lucas, S.G. (Eds), The Triassic System. *New Mexico Museum of Natural History and Science, Bulletin*, 61, 582–588.

Vávra, N. (2009) Amber, fossil resins, and copal—contributions to the terminology of fossil plant resins. *Denisia*, 26, 213–222.

Vázquez-González, C., Zas, R., Erbilgin, N., Ferrenberg, S., Rozas, V. & Sampedro, L. (2020) Resin ducts as resistance traits in conifers: linking dendrochronology and resin-based defences. *Tree physiology*, 40 (10), 1313–1326.
https://doi.org/10.1093/treephys/tpaa064

Voigt, E. (1970) Endolithische Wurm-Tunnelbauten (*Lapispecus cuniculus* n. g. n. sp. und *Dodecaceria*(?) sp.) in Brandungsgeröllen der oberen Kreide im nördlichen Harzvorlande. *Geologische Rundschau*, 60, 355–380.
https://doi.org/10.1007/BF01820950

von Hagenow, F. (1840) Monographie der Rügen'schen Kreide Versteinerungen, II. Abtheilung: Radiarien und Annulaten. Nebst Nachträgen zur ersten Abtheilung. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1839, 630–672.

Walker, M.V. (1938) Evidence of Triassic insects in the Petrified Forest National Monument, Arizona. *Proceedings of the United States National Museum*, 85 (3033), 137–141.
https://doi.org/10.5479/si.00963801.85-3033.137

Wagner-Wysiecka, E. (2023) Succinite, Baltic amber: a chemical masterpiece of nature. *Journal of Gems & Gemmology*, 25 (4), 69–87.
https://doi.org/10.15964/j.cnki.027jgg.2023.04.007

Werker, E. & Fahn, A. (1969) Resin ducts of *Pinus halepensis* Mill.—Their structure, development and pattern of arrangement. *Botanical Journal of the Linnean Society*, 62 (4), 379–411.
https://doi.org/10.1111/j.1095-8339.1969.tb01974.x

Widera, M. (2015) Compaction of lignite: a review of methods and results. *Acta Geologica Polonica*, 65 (3), 367–378.
https://doi.org/10.1515/AGP-2015-0016

Widera, M. (2016) Genetic classification of Polish lignite deposits: A review. *International Journal of Coal Geology*, 158, 107–118.
https://doi.org/10.1016/j.coal.2016.03.004

Wisshak, M., Knaust, D. & Bertling, M. (2019) Bioerosion ichnotaxa: review and annotated list. *Facies*, 65 (2), 1–39.
https://doi.org/10.1007/s10347-019-0561-8

Xu, B., Chao, J., Yang, Z.Y. & Li, W.D. (2018) The occurrence of resin canals in branches of *Cedrus deodara* with different inclination angles. *Wood Science and Technology*, 52 (2), 505–517.
https://doi.org/10.1007/s00226-017-0964-z