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Production and preservation of resins – past and present

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ABSTRACT

Amber is fossilised plant resin. It can be used to provide insights into the terrestrial conditions at the time the original resin was exuded. Amber research thus can inform many aspects of palaeontology, from the recovery and description of enclosed fossil organisms (biological inclusions) to attempts at reconstruction of past climates and environments. Here we focus on the resin itself, the conditions under which it may have been exuded, and its potential path to fossilisation, rather than on enclosed fossils. It is noteworthy that not all plants produce resin, and that not all resins can (nor do) become amber. Given the recent upsurge in the number of amber deposits described, it is time to re-examine ambers from a botanical perspective. Here we summarise the state of knowledge about resin production in modern ecosystems, and review the biological and ecological aspects of resin production in plants. We also present new observations on conifer-derived resin exudation, with a particular focus on araucarian conifer trees. We suggest that besides disease, insect attacks and traumatic wounding from fires and storms, other factors such as tree architecture and local soil conditions are significant in creating and preserving resin outpourings. We also examine the transformation of resin into amber (maturation), focusing on geological aspects of amber deposit formation and preservation. We present new evidence that expands previous understanding of amber deposit formation. Specific geological conditions such as anoxic burial are essential in the creation of amber from resin deposits. We show that in the past, the production of large amounts of resin could have been linked to global climate changes and environmental disruption. We then highlight where the gaps in our knowledge still remain and potential future research directions.

Key words: amber, burial, deposit, exudation, maturation, resin, transport.

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I. INTRODUCTION

Amber is a remarkable substance in both biological and geological terms. It is fossilised plant resin often famous for the biological inclusions that it contains. The originally liquid resin solidifies through polymerisation, and on deposition undergoes maturation to become amber – so, despite being chemically altered, ambers also retain chemical traces of the environment in which the resin was originally secreted. The last 20 years have seen rapid development in amber research, as many new amber-bearing localities have been discovered, broadening amber research and deepening the value of amber to palaeobiologists.

During the 20th century, amber research was known for the numerous, often delicate species described from entombed organisms (inclusions). These usually three-dimensional fossils can have surface and structural details preserved, with most preserved at least roughly in life aspect and before much decay has set in. Many of these are arthropod inclusions, although other very rare organisms have occasionally been found which only have a fossil record in amber (see Penney, 2010*a*).

During the 1990s, there was the excitement surrounding the potential of preserved DNA in amber (the premise for the *Jurassic Park* film franchise: dinosaur DNA inside a blood-sucking insect preserved in amber), but previously published DNA sequences are now known to result from contamination (see for example: Austin, 1997; Hebsgaard, Phillips & Willerslev, 2005; Reiss, 2006; Rosselló, 2014). Penney *et al.* (2013) showed that DNA from insect inclusions does not even survive in copal, which is immature amber, so that DNA preserved on geological timescales (millions of years) is extremely unlikely. Organelles and cell membranes have been reported from amber (Koller, Schmitt & Tischendorf, 2005), but even resistant macromolecules like lignin are significantly degraded (Stankiewicz *et al.,* 1998).

Heading into the 21st century, a plethora of new discoveries, including Triassic ambers [*ca.* 230 million years ago (Mya); Gianolla, Roghi & Ragazzi, 1998], and even Carboniferous amber (*ca.* 320 Mya; Bray & Anderson, 2009), significantly pushed back the oldest known amber occurrences. There were notable discoveries of various Southern Hemisphere amber-bearing localities, such as those in Australia (Hand *et al.,* 2010), Brazil (in minute amounts; Martill *et al.,* 2005), Peru (Antoine *et al.,* 2006), South Africa (Gomez *et al.,* 2002), Ethiopia (Schmidt *et al.,* 2010), Congo (Perrichot *et al.,* 2016), and New Zealand (Schmidt *et al.,* 2018). Many of the new localities discovered are accurately dated, and sometimes, their botanical origin is also known; for example, Indian ambers were produced by members of the Dipterocarpaceae (Mallick *et al.,* 2009; Rust *et al.,* 2010; Dutta *et al.,* 2011*b*).

This recent explosion in amber-bearing localities (significant amber deposits are listed in Table 1) has led to a key observation: amber was once thought to be generally rare across the fossil record and in most cases only in very small amounts (Krumbiegel & Krumbiegel, 1994), such as in the tiny amount of English and German Eocene amber found inside resin canals of Mastixiaceae (Cornaceae) fruit (van Aarssen *et al.,* 1994); however, amber occurrences are in fact a worldwide phenomenon, rather than a local one. The previous view was based on far fewer localities representing fewer time points and geographical locations. In fact, based on the plethora of new data, we can distinguish for the first time potential ‘amber bursts’: time windows

Table 1. Significant amber deposits

Age (Mya)	Geological age	Deposit name	Location	Geological formation	Geological setting	Fossils present?	Inferred resin source (from resin chemistry analyses)	Inferred resin source (from associated plant remains)	References
5–23	Miocene	Cape York amber	Cape York, Australia	Beach deposits, potential diverse sources?	Not known	Yes	*Agathis* (Araucariaceae), Dipterocarpaceae	–	Hand *et al.* (2010); Sonibare *et al.* (2014)
10–18	Miocene, Tortonian-Burdigalian	Amazonian amber	Tamshiyacu, Peru	Pebas Fm.	Para.–alloch. bay or lagoon	Yes	*Hymenaea* (Fabaceae) class Ic	Undetermined angiosperm	Gingras *et al.* (2002); Antoine *et al.* (2006); V. Perrichot (unpublished spectroscopic data)
ca. 14	middle Miocene, Langhian	Zhangpu amber	Zhangpu county, Fujian Province, China	Fotan Group	Para.–alloch. in sandy mudstone or in lignite	Yes	Dipterocarpaceae (Class II)	–	Shi *et al.* (2014); Wang (2016)
13–19	Miocene, Serravallian-Burdigalian	Mexican amber	Chiapas, Mexico	La Quinta Fm., Mazantic Shale, Balumtun Sst.	Alloch. in limestone and shale	Yes	*Hymenaea* (Fabaceae)	*Hymenaea mexicana*† (Fabaceae)	Cunningham *et al.* (1983); Poinar & Brown (2002); Solórzano Kraemer (2010)
16–18	early Miocene, Burdigalian	Dominican amber	Cordillera Septentrional/ Cordillera Oriental, Dominican Republic	La Toca Fm.	Autoch.–para. in lignites	Yes	*Hymenaea protera*† (Fabaceae)	*Hymenaea protera*† (Fabaceae)	Poinar (1991); Langenheim (1995); Penney (2010*b*)
15–23	Miocene	Ethiopian amber	Semien Shewa, Ethiopia	Not known	Para.–alloch. in siltstones	Yes	Fabaceae (*Hymenaea*$^{?}$) (Class Ic)	–	Schmidt *et al.* (2010); Perrichot *et al.* (2016); V. Perrichot (unpublished data)
15–25	late Oligocene-early Miocene, (Burdigalian)	New Zealand amber	various	various	Autoch.– alloch. in lignites	Yes, few	*Agathis* (Araucariaceae)	*Agathis* (Araucariaceae)	Schmidt *et al.* (2018)
23.5–25.5	late Oligocene, Chattian (minimum age)	Bitterfeld amber	Bitterfeld, Saxony-Anhalt, Germany	Cottbus Fm. 'Glimmersand'	Alloch. washed into lagoon	Yes	*Picea*, *Pinus* (Pinaceae)	*Cupressospermum saxonicum*† (Cupressaceae) *Geinitzia formosa*† (Geintiziaceae)	Yamamoto *et al.* (2006); Dunlop (2010)
34–48	mid-late Eocene, predominantly Priabonian	Baltic amber	Eastern Baltic Sea, especially Kaliningrad, Russia	Prussian Fm.	Alloch. reworked & redeposited during glaciations	Yes	*Sciadopitys*$^{?}$ (Sciadopityaceae) *Cedrus*$^{?}$ (Pinaceae) *Agathis*$^{?}$ (Araucariaceae)	*Pinus succinifera*† *Pinus* sp. (Pinaceae) Cupressaceae *Sciadopitys* (Sciadopityaceae)	Langenheim (1969); Katinas (1987); Weitschat & Wichard (2002); Koller *et al.* (2005); Wolfe *et al.* (2009); Sadowski *et al.* (2016); Sadowski *et al.* (2017*a*)
37.8–41.2	late Eocene, Bartonian	Rovno amber	Rovno and Zhitomir regions, Ukraine	Mezhygorje Fm.	Alloch. redeposited in sandy clays	Yes	$^{?}$same source as Baltic succinite amber	–	Perkovsky, Zosimovich & Vlaskin (2010)
41.2–47.8	mid Eocene, Lutetian	Fushun amber	Wanghua District, Fushun Prefecture, China	Guchengzi Fm.	Autoch.–para. in coal	Yes	*Metasequoia*$^{?}$ (Cupressaceae)	*Metasequoia*$^{?}$ (Cupressaceae)	Wang *et al.* (2014)
41.2–47.8	mid Eocene, Lutetian	Sakhalin amber	Sakhalin Island, E Russia	Naibuchi Fm.	Autoch.–para. in coal	Yes	–	–	Baranov, Andersen & Perkovsky (2015)
41.2–47.8	mid Eocene, Lutetian	Tiger Mt amber	Tiger Mt, Washington, USA	Tiger Mt Fm.	Autoch.–para. in lignite		Araucariaceae Cupressaceae	*Metasequoia*$^{?}$ (Cupressaceae)	Mustoe (1985)

Table 1. Continued

Age (Mya)	Geological age	Deposit name	Location	Geological formation	Geological setting	Fossils present?	Inferred resin source (from resin chemistry analyses)	Inferred resin source (from associated plant remains)	References
52	early Eocene, Ypresian	Cambay amber	Anand District, Gujurat State, India	Cambay shale Fm.	Alloch. in 'amber conglomerate'	Yes	Dipterocarpaceae (Class II)	Dipterocarpaceae	Rust *et al.* (2010)
53	early Eocene, Ypresian	Oise amber	Oise, France	Argiles à lignites du Soissonnais	Para.–alloch. in clayey-sand with lignite	Yes	Fabaceae (class Ic)	*Aulacoxylon sparnacense*† (Combretaceae)	Nel & Brasero (2010); Nohra *et al.* (2015)
66–67	Late Cretaceous, Maastrichtian	Hell Creek amber	Harding Co., South Dakota, USA	Hell Creek Fm.	Alloch. in siltstone (oxbow lake deposit)	Very few	–	–	DePalma, Cichocki & Dierick (2010)
78–79	Late Cretaceous, Campanian	Canadian amber	Grassy Lake, Cedar Lake, Canada	Foremost Fm.	Grassy Lake Autoch. in coals, washed out into Cedar Lake	Yes	Cupressaceae Araucariaceae°	*Parataxodium* sp.† (Cupressaceae)	McKellar & Wolfe (2010)
83.6–86.3	Late Cretaceous, Santonian	Eutaw amber	E. Alabama, USA	Eutaw Fm.	Para.–alloch. mud in sandstones	Yes	–	–	Bingham *et al.* (2008)
83.6–86.3	Late Cretaceous, Santonian	Taimyr amber	Various, Taimyr Peninsula, Siberia	Kheta Fm.	Para.–alloch. in coal-bearing sands	Yes	Class I	–	Anderson (1994); Perkovsky & Makarkin (2015)
85– 86.3	Late Cretaceous, early Santonian	Provence amber	Piolenc, Vaucluse, France	unnamed	Alloch. in coal-bearing sands	Yes, few	Cupressaceae (class Ib)	–	Nohra *et al.* (2015)
89.9–93.9	Late Cretaceous, Turonian	Raritan/ New Jersey amber	Middlesex Co., New Jersey, USA	Raritan and Magothy Fms.	Autoch.–para. in lignite	Yes	Cupressaceae Araucariaceae°	*Juniperus hypnoides*†? other *Juniperus* sp. (Cupressaceae)	Grimaldi & Nascimbene (2010)
89.8–93.9	Late Cretaceous, Turonian	Vendean amber	La Garnache, Vendée, France	unnamed	Alloch. in lignitic clay	Yes	Cupressaceae (class Ib)	Pinaceae, *Taxodioxylon*† (Cupressaceae)	Nohra *et al.* (2015); Néraudeau *et al.* (2017)
~98	Late Cretaceous, Cenomanian	Burmese amber	Hukawng Valley Kachin state, Myanmar	unnamed	Para.–alloch. coastal setting	Yes	*cf*. *Agathis* sp. (Araucariaceae)?	–	Cruickshank & Ko (2003); Ross *et al.* (2010)
~100	Cretaceous, Albian	Charentese amber	various, Charentes region, France	unnamed	Autoch.–para. in lignite and clay, coastal setting	Yes	Araucariaceae Cheirolepidiaceae† (class Ib)	*Agathoxylon gardoniense*† (Araucariaceae) Cheirolepidiaceae†	Perrichot, Néraudeau & Tafforeau (2010); Nohra *et al.* (2015)
101–113	Early Cretaceous, Albian	Spanish amber	Various across Spain	Various	Autoch.–para. in coals	Yes	*Agathis* sp. (Araucariaceae) (and undetermined sp.) Cupressaceae, Cheirolepidiaceae†	*Frenelopsis* sp.† Cheirolepidiaceae† Araucariaceae	Delclòs *et al.* (2007); Najarro *et al.* (2010); Peñalver & Delclòs (2010); Menor-Salván *et al.* (2016)
125–129	Early Cretaceous, Barremian	Lebanese amber	Various across Lebanon	Chouf Sst. & Abeih Fm.	Alloch. in clay-sandstones	Yes	? *Agathis levantensis*† (Araucariaceae)	*Araucarioxylon* sp.† (Araucariaceae) *Protocarpoxylon* sp.† (Cheirolepidiaceae†)	Poinar & Milki (2001); Azar, Gèze & Acra (2010); Maksoud *et al.* (2017)
132.9–~135	Early Cretaceous, Valanginian	South Africa	Algoa Basin, South Africa	Kirkwood Fm.	Alloch. in coaly clay-sandstones	No	–	–	Gomez *et al.* (2002)
113–~139	Early Cretaceous, Valanginian–Aptian	Isle of Wight amber	Isle of Wight, UK	Wessex Fm.	Alloch. flood plain pool deposit	Yes	Araucariaceae	Araucariaceae	Jarzembowski, Azar & Nel (2008)
~129–~139	Early Cretaceous, Valanginian–Hauterivian	Israeli amber	Various, Israel	Heletz Fm.	Alloch. in silts and sandstones	Yes	Araucariaceae	–	Nissenbaum (1975)
~150	Late Jurassic, Tithonian	Lebanese amber	Various, North Lebanon	Various	Autoch.–para.–alloch. in lignites to clay-sandstones	V. few	? Araucariaceae	*Araucarioxylon* sp.† (Araucariaceae) *Protocarpoxylon* sp.† (Cheirolepidiaceae†)	Azar *et al.* (2010); Nohra *et al.* (2013)

in which amber production or preservation appears to be heightened (Fig. 1). These in part reflect Labandeira's (2014) four evolutionary phases of amber deposits (1: Carboniferous; 2: Triassic to Jurassic; 3: Cretaceous and 4: Eocene onwards). We exclude the trace amounts from Carboniferous deposits (van Bergen *et al.,* 1995; Bray & Anderson, 2009), since they are very uncommon, and mostly preserved inside the original plant tissues, rather than as an exudate. We also discount the Jurassic deposits, as to date there are only two very small deposits known. Rasnitsyn & Quicke (2002) list 34 amber deposits containing insects, Langenheim (2003) also lists smaller deposits, and Martínez-Delclòs, Briggs & Peñalver (2004) listed 167 localities, many of which have very small amounts of amber present as small pieces and very localised – however, some of these individual localities are actually part of larger, significant named deposits (e.g. Canadian and Dominican: see Table 1).

We have identified four amber 'bursts' in the geological record, the first is in the early Late Triassic (Carnian, 237–228.4 Mya), within a span of probably less than 1 million years (Zhang *et al.,* 2015) and coincident with the 'Carnian Pluvial Episode', a global and abrupt climate change (Roghi *et al.,* 2006). The younger three 'burst' events are potentially quite different from the Carnian burst since they cover far larger time spans and their production may be linked to different triggers (Fig. 1). The second 'burst' occurs during the Early to mid-Cretaceous (145–96 Mya), covering a significant portion of the Cretaceous Terrestrial Revolution (Lloyd *et al.,* 2008), and is exemplified by the Albian–Cenomanian deposits from France, Spain, Myanmar, and the Early Cretaceous of Lebanon. The third occurs during the Eocene (56–33.94 Mya, Fig. 1), with the final occurring from the late Oligocene to the Miocene (28–5.8 Mya, Fig. 1). Some younger resin deposits are also found in various locations, but we do not include them here as these deposits are not fully mature fossil resins.

There are also additional significant local occurrences such as the Late Cretaceous Raritan (Grimaldi & Nascimbene, 2010), Canadian (McKellar & Wolfe, 2010), Taimyr (Rasnitsyn *et al.,* 2016) and Hell Creek (DePalma *et al.,* 2010) deposits, all giving repeated access to terrestrial ecosystems (Fig. 1, Table 1). The causes of both local occurrences and amber bursts are unknown, but are suspected to have both a geological and biological/ecological component, and it is not yet clear whether our observed synchronicity is just coincidence or whether there are underlying linking, potentially global factors.

What do significant amber deposits represent in terms of a palaeoecosystem? This is vital to understand the vast numbers of inclusions and for reconstructing their habitats. Does amber derive from representative normal ecosystems, or were these resin outpourings, subsequently fossilised as amber, the results of stressed ecosystems? The debate is heated and ongoing (e.g. Conwentz, 1890; Gianolla *et al.,* 1998; Weitschat & Wichard, 2002, 2010; Najarro *et al.,* 2010; McKellar *et al.,* 2011; Dal Corso *et al.,* 2012, 2013, 2015), and it has a large impact on how we view amber

Table 1. Significant amber deposits

Age (Mya)	Geological age	Deposit name	Location	Geological formation	Geological setting	Fossils present?	Inferred resin source (from resin chemistry analyses)	Inferred resin source (from associated plant remains)	References
145–174	Mid-Late Jurassic, Aalenian–Tithonian	Khlong Min amber	Khlong Thom Province, Krabi, Thailand	Khlong Min Fm.	Para. in silty clay, oxbow$^?$ lake	No	–	*Agathoxylon* sp.† (Araucariaceae)	Philippe *et al.* (2005)
~230	Late Triassic, Carnian	Chinle amber	Petrified Forest National Park, Arizona USA	Chinle Fm.	Alloch. in slack water deposits	No	–	Needs revision [*Agathoxylon arizonicum*]° (Araucariaceae)	Savidge (2007); Litwin & Ash (1991)
230	Late Triassic, Carnian	Dolomites amber	Cortina, Dolomite Alps, Italy	Heiligkreuz Fm.	Autoch. in palaeosols	Yes	Class II (& some Class I)	Cheirolepidiaceae†	Roghi, Ragazzi & Gianolla (2006); Schmidt *et al.* (2006, 2012)

Mya, million years ago; Fm., Formation; Mt., Mountain; Sst., Sandstone.
$^?$indicates uncertainty about assignment;
†indicates extinct species or family;
°indicates original interpretation;
alloch., allochthonous – amber transported and buried some distance away from the original area/habitat; autoch., autochthonous – amber buried *in situ*, where no transport occurred so the amber is preserved in the original area/habitat; para., parautochthonous – ambers transported a short distance from their original deposition site, but still within their original habitat.

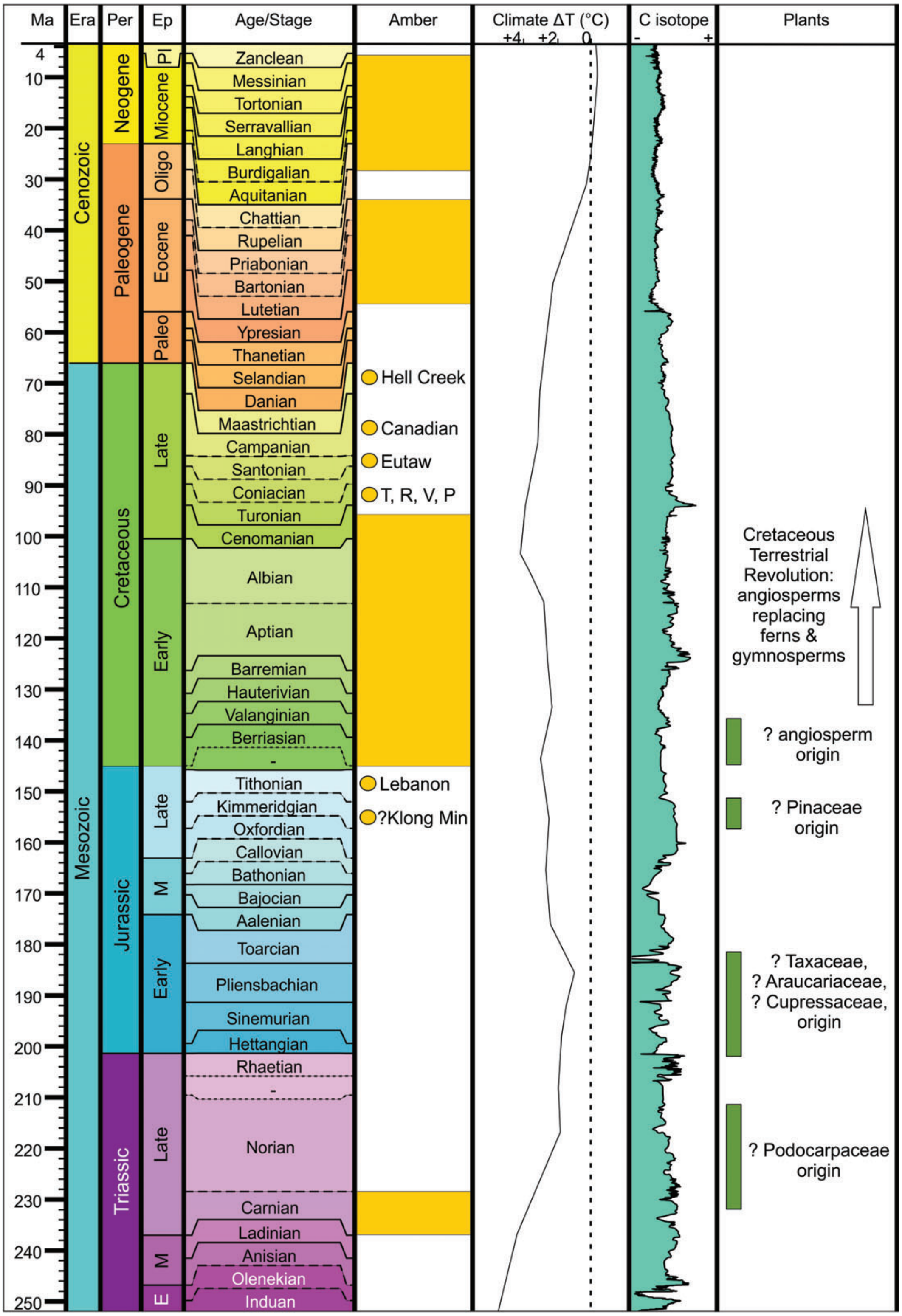

Fig. 1. Amber occurrences in the Mesozoic and Cenozoic. Apparent amber bursts are shown as orange blocks correlated against time, circles indicate significant local deposits (T, Taimyr; R, Raritan; V, Vendean; P, Provence), shown against the inferred difference in temperature from today's mean temperature (where 0°C is no inferred temperature difference) (Adapted from Royer *et al.*, 2004), the carbon isotope record (composite per-mil relative to the Pee Dee Belemnite, PDB) and key phases in plant evolution (E, Early; Ep, Epoch; M, Middle; Oligo, Oligocene; Paleo, Paleocene; Per, Period; Pl, Pleistocene).

deposits, how they relate to modern resin production, and how well the entombed fossil record represents conditions in ancient forests (whether the fossil record is more accurately viewed along the lines of catastrophism or more 'normal' conditions).

Not all amber deposits contain fossils, but the largest known fossiliferous amber deposit is the Baltic, where several hundred tons are extracted annually (Weitschat & Wichard, 2010). For significant, usually fossiliferous deposits see Table 1, and for more depth see Langenheim (2003), Martínez-Delclòs *et al.* (2004), Penney (2010*a*), Rust *et al.* (2010), Schmidt *et al.* (2018). Clearly amber is not as rare in the fossil record as previously thought.

Ambers are fossilised plant resins, so the biological/ecological aspects of resin production and secretion in plants are key to understanding amber; enough resin must be produced in the biosphere before it can enter the geosphere and become amber. What are the causes of resin production and secretion in plants today, and are there underlying reasons for particularly large resin secretions which could then form the basis for a large amber accumulation? The second key is the geological aspect, where the resin becomes amber through maturation following burial. Explaining amber in the fossil record must cover both these biotic and geological aspects, which we shall examine herein.

II. MATERIALS AND METHODS

To be able to answer the major questions about amber deposits posed above, a new integrated approach is needed. We therefore examined biological, ecological and environmental reasons for massive resin production, alongside the preservation of resin, and the fossilisation process of amber at the geological timescale. We reviewed previous literature and provide new observations using mainly araucarian resinous ecosystems as analogues, as well as summarising our perspectives and directions for future research. All absolute ages in the text follow Gradstein *et al.* (2012).

III. RESIN AND HOW IT RELATES TO AMBER

Since amber is a fossilised resin, and resin is a toxic plant product, what are the reasons for resin production, particularly on a massive or prolonged scale? Resin has numerous functions, but which were key to significant amber accumulations? Answers to these questions could help, in part at least, to answer questions about the state of a resinous ecosystem, and whether the observed synchronicity of amber bursts is merely a coincidence or whether there were underlying factors responsible.

Resins can be defined as a complex mixture of primarily terpenoid and/or phenolic compounds (Langenheim, 1994, 1995, 2003), with the majority being terpenoid resins. Resins are chemically distinct from other plant exudates such as polysaccharide gums and mucilages, oils, waxes and latex, which have little preservation potential (Langenheim, 2003). Resins are produced inside specialised secretory structures or ducts, and contain two fractions: a volatile fraction composed of mono- and sesquiterpenoids that add to resin fluidity and act as plasticisers; and a non-volatile fraction which is either diterpenoid (mainly indicating a coniferous origin) or triterpenoid (indicating angiospermous origin; Otto & Wilde, 2001). These chemical differences are the basis for amber classification (see Section III.2).

(1) **Defining amber**

Amber can be defined as a fossilised, cross-polymerised resin from higher plants (Anderson & Crelling, 1995; Langenheim, 2003). Resin polymerisation is rapid on exposure to air and sunlight (Cunningham *et al.,* 1987). Resins become ambers through maturation (a process sometimes refered to as amberisation); hardening and burial in sediment, effectively fossilisation, where the temperature, pressure and permeating fluids affect the rate of chemical transformation (Anderson & Crelling, 1995; Ragazzi & Schmidt, 2011). Maturation is thought to take millions of years, as it involves loss of volatiles and the polymerisation and cross-linking of terpenes (Chaler & Grimalt, 2005), and their cyclisation and isomerisation (Clifford & Hatcher, 1995). Resin maturation is age-related, but it also depends on its thermal history (Anderson, Winans & Botto, 1992) and its original structure and composition (Langenheim, 2003). Maturity can sometimes indicate age (e.g. in the thermal analysis of Ragazzi *et al.,* 2003), but correlation can be difficult as the chemical transformation of resin increases at higher temperatures. Therefore, amber age must be deduced from the surrounding sediments (e.g. Grimaldi, 1995), if it has not been redeposited (which is a concern for many deposits). However, diagenetic chemical and isotopic changes in amber chemistry are minor (Nissenbaum & Yakir, 1995; Stout, 1995; Aquilina *et al.,* 2013; Dal Corso *et al.,* 2013, 2017).

When then does resin become amber? This is debatable and still unclear, with many different criteria used; see discussions in Anderson (1996) and Vávra (2009) (Table 2). Here we examine significant, usually fossiliferous fossil resin (fully polymerised amber) deposits from the Triassic to the Miocene (Table 1). In terms of fossiliferous subfossil resins (not fully polymerised resins) there are several deposits, likely Pleistocene–Recent in age, known from New Zealand, Colombia, and East Africa (Tanzania and Madagascar) (Penney & Preziosi, 2010). The term copal is ambiguous, applied to both modern and subfossil resins.

(2) **Amber classification**

Amber is now classified according to its chemical and physical properties and most is well characterised. There are various techniques for analysing the chemistry of resins such as various gas chromatography mass spectroscopy (GC–MS) methods, infrared spectroscopic (e.g. Fourier Transform, FTIR) methods, and nuclear magnetic resonance (NMR)

Table 2. Definitions used to define amber *versus* resin

Method to define amber	Proponent
Resin over 1 million years old	Schlee & Glöckner (1978)
Resin that is over 3–4 million years old, and meets mineralogical criteria (e.g. solubility, hardness, melting point, specific gravity)	Poinar (1992)
Based on carbon-14 dating of resin: I Ambers – resins over 40000 years old II Subfossil resin (copal) – between 40000 and 5000 years old III Ancient resin – 5000 to 250 years old IV Modern or recent resin – less than 250 years old	Anderson (1996)
Use physical characteristics of the fossil resin, e.g. solubility, hardness, melting point (no age given) to allow for variability in the maturation process.	Vávra (2009)

spectroscopy. Ambers are usually placed into one of five classes (Table 3) on the basis of their chemical structural character [as summarised by Anderson & Crelling, 1995 using pyrolysis GC–MS], with the majority of ambers in the rock record being Class I. Classes I–III comprise the major fossil resin deposits, as they are based on various polymeric skeletons. Classes IV and V are based on non-polymeric skeletons, which are thus unable to polymerise to form true ambers, making them rare in the fossil record (Table 3). There is also extensive work using chemotaxonomy of resins (e.g. Otto & Wilde, 2001) in order to identify the source plant of amber deposits (e.g. Otto *et al.,* 2002; Dutta *et al.,* 2011*a*; Dutta, Saxena & Singh, 2014). Amber is a chemofossil (a fossil composed of chemicals) itself, sometimes containing body fossils of other organisms.

(3) Plant sources for amber deposits

The sources of some amber deposits have been clearly identified (Table 1). In these cases the source plants are preserved either in the amber, or as plant remains containing amber, and chemical analyses of the fossil resins often reinforce the relationships.

Many other deposits have currently unknown or uncertain sources like Lebanese amber, in fact, this is the case for the majority of ambers in Table 1. This is because either the deposit has only recently been discovered, or the source plants are either not preserved along with the deposits, or many different taxa are preserved, and the chemical analyses have not been able to clarify the affinities. Extinct taxa may be responsible for a deposit and have no extant analogue to enable comparisons. Some affinities have been speculatively inferred from the amber being associated with determinable plant remains, such as the sole 'Podocarp-derived' amber in the fossil record from New Zealand, which was collected from a coal with Podocarpaceae pollen present (Grimalt, Simoneit & Hatcher, 1989). However, Lyons, Masterlerz & Orem (2009) chemically inferred an *Agathis* source for this amber, demonstrating the level of care needed in determining botanical sources. Other deposits are more complicated as they are actually a mixture of fossil resins from various sources; the best known examples are the Baltic and Bitterfeld ambers, both of which are predominated by the succinite (Class Ia) amber type. The Bitterfeld deposit actually encompasses nine different amber varieties, so potentially nine different source plants (Yamamoto *et al.,* 2006). The sources of most ambers throughout the fossil record are gymnosperms. Angiosperms, which appear during the Cretaceous, only contribute from the Cenozoic onwards (Labandeira, 2014; Table 1).

IV. RESIN PRODUCTION IN THE MODERN WORLD

Despite having no clear physiological role (Langenheim, 1995), resins are produced across many plant taxa, but only some are found in the fossil record. In gymnosperms, three conifer families are resinous: Araucariaceae, Cupressaceae *s.l.*, and Pinaceae, although only the Araucariaceae and Pinaceae are highly resinous today. Cupressaceae are less resinous today but are thought to be the source plants for some Cretaceous and younger amber deposits (Table 1). However, Pinaceae resin (Class V, Table 3) does not preserve well, and so is rare in the fossil record. Sciadopityaceae has been proposed as the source of Baltic amber (Wolfe *et al.,* 2009; see also Sadowski *et al.,* 2016, 2017*a*), but this is contentious and the extant member of this group is not highly resinous today. Among the angiosperms there are many resinous lineages, mostly in tropical to warm-temperate areas: Burseraceae, Combretaceae, Dipterocarpaceae, Fabaceae, and Hamamelidaceae (Langenheim, 2003; Nel *et al.,* 2004). The reasons for resin production today are not completely clear (Henwood, 1993), with several suggestions having been made: (*i*) as a physical sealant in response to wounding or physical damage (Farrell, Dussourd & Mitter, 1991; Henwood, 1993); (*ii*) to prevent opportunistic pathogen or insect attack (Langenheim *et al.,* 1986; Henwood, 1993; Grimaldi & Engel, 2005) – resin even actively squirts out of insect-attacked *Bursera* leaves (Becerra *et al.,* 2001); (*iii*) storage of cellular waste products (Henwood, 1993); (*iv*) a role in chemical defence of plants – particularly oleoresin, the viscous secretion mobilised at wound and infection sites (Phillips & Croteau, 1999; Trapp & Croteau, 2001) – as well as influencing interactions among plants and between plants and other organisms (Langenheim, 1994, 1995, 2003), resins also coat or are constituents in plant organs to stop herbivory/parasitism (Litvak & Monson, 1998; Farrell *et al.,* 1991); (*v*) to be attractive to particular pollinators (Armbruster, 1993), including some stingless bees which add

Table 3. Amber classification based on chemistry, adapted from Anderson & Crelling (1995), Anderson & Botto (1993), Bray & Anderson (2009), Wolfe *et al.* (2009), Rust *et al.* (2010) and Poulin & Helwig (2012).

Class	Characteristics	Examples	Inferred botanical affinity
Class I	Polymeric skeleton of labdanoid diterpenes, including especially labdatriene carboxylic acids, alcohols and hydrocarbons		
Class Ia	Based on polymers and copolymers of labdanoid diterpenes (regular configuration), including communic acid and communol; incorporation of significant amounts of succinic acid	Succinite: Baltic shore area, Samland	Pinaceae? Araucariaceae? Sciadopityaceae?
		Glessite	Burseraceae, *Betula* (Betulaceae)
Class Ib	Based on polymers and copolymers of labdanoid diterpenes (regular configuration), including/not limited to communic acid, communol and biformene; devoid of succinic acid	Raritan amber	Cupressaceae
		Burmese amber	*Agathis* (Araucariaceae)
		New Zealand amber	*Agathis* (Araucariaceae)
Class Ic	Based on polymers and copolymers of labdanoid diterpenes (enantio configuration), including/not limited to ozic acid, ozol and enantio bioformenes; devoid of succinic acid	Mexican amber	*Hymenaea mexicana* (Fabaceae)
		Dominican amber	*Hymenaea protera* (Fabaceae)
		African amber (Zanzibar, Kenya)	
		Carboniferous amber from Illinois	Pre-conifer gymnosperm
Class Id	Based on polymers and copolymers of labdanoid diterpenes with *enantio* configuration; incorporating significant amounts of succinic acid	Canadian Arctic (Nunavut) and British Columbia	unknown
Class II	Polymeric skeleton of bicyclic sesquiterpenoid hydrocarbons, especially cadinene; triterpenoid including di-sesquiterpenoid component as occluded material	Indian amber	Dipterocarpaceae (*Shorea*)
Class III	Polymeric skeleton; basic structural feature is polystyrene	Siegburgite: Siegburg and Bitterfeld (in part)	Hamamelidaceae (*Liquidambar*)
		some New Jersey ambers	
Class IV	Non-polymeric, basic structural feature is sesquiterpenoid, based on cedrane (IX) skeleton	Ionite: Pliocene of California	unknown
Class V	Non-polymeric diterpenoid carboxylic acid, especially based on abietane, pimarane and iso-pimarane carbon skeletons	Highgate Copalite: Eocene of Highgate Hill area, London	Pinaceae
		Settlingite: Northumberland, UK	

terpenes from resin to their cuticular profiles (Leonhardt, Wallace & Schmitt, 2011); (*vi*) as a protective barrier to reduce temperature and water loss (Dell & McComb, 1978; Langenheim, 1994). These reasons are usually tissue-specific and account for very small resin amounts. Resin can also vary in composition among tissues of the same plant (Thomas, 1969, 1970; Langenheim, 1994, 2003), perhaps with different functions depending on the organ of production.

Resin amounts are partly controlled by resin viscosity, which depends on environmental temperature and the internal sap pressure, which are both higher during spring and summer, and during the day rather than at night (Langenheim, 2003), resulting in a less-viscous secretion. Low soil nitrogen also decreases resin production. Resin production is greater in *Hymenaea* trees when water is more available (Langenheim, 1967), and also higher in *Pinus taeda* L. trees towards the mid-late summer when water availability is low, but growth is reduced (Lorio & Sommers, 1986). Seasonal fluctuation of resin production is thought to be recorded in Baltic amber by the overwhelming presence of oak flower stellate hairs, which now appear predominantly during spring and early summer (Weitschat & Wichard, 2002).

(1) Physical damage

This is the primary reason suggested for resin production: acting to seal the resultant wounds to prevent later damage by opportunistic infections/infestations (Henwood, 1993). The amounts of resin secreted appear to be related to the size of the injury. Defining injury to the plant can become complicated. Obvious trauma from an herbivore attack,

Fig. 2. External mechanical damage: damage to bark exposing underlying tissues, resulting in resin flows. (A, B) Bear damage to a *Picea* tree, British Columbia, Canada: (A) trunk with bark stripped off; (B) close-up of resin on damaged surface with several attached dipterans. (C) Woodpecker holes with resin on a trunk of *Pinus ponderosa*, Sierra Nevada, California. (D) Severe (vehicle) damage to roadside tree of *Agathis moorei*, Parc Provincial de la Rivière Bleue, New Caledonia. (E) Wind-rock damage to *Araucaria columnaris*, Bourail, New Caledonia. (F) Slash to *Agathis ovata* with outpouring resin, Yaté, New Caledonia.

removing some leaves or tree limbs, is different in scale, and potential for opportunistic pathogen attack, to widespread ecosystem trauma after a hurricane or tsunami event, where entire trees could have their trunks snapped. Likewise, insect attacks primarily cause physical damage that takes different forms from leaf feeding to wood-boring, but insects can also be vectors for pathogens.

The damaged areas in the plant need to be quickly sealed, but the scale of the sealing and subsequent wound healing differs (Fig. 2). Given these variables, we can divide physical damage into three more clearly defined categories: (*i*) insect infestation: small actual holes/canals, but may be numerous, sometimes with larger, linked galleries inside plant tissues; (*ii*) ecological disaster: large-scale ecological damage, major damage/destruction of plants (e.g. from hurricane, flood, tsunami, wild fires, explosive volcanism events), may actually kill trees that cannot regenerate from stumps; (*iii*) physical damage: smaller scale traumatic injuries other than those associated with ecological disaster (e.g. herbivory, parasitism by mistletoes, or localised wind-damage), where injuries can be compartmentalised and the plant usually survives. The resultant resin amounts can be fairly small, as confirmed by our observations of small amounts of damage (cut branches) to both *Agathis ovata* (Moore ex Vieill.) Warb. and *Araucaria columnaris* (G. Forst.) Hook. in New Caledonia, and to *Agathis australis* (D. Don) Loudon in New Zealand.

(2) Other causes

Two further categories are defined here from our field observations. (*i*) Fire also causes physical damage to plants, but on a smaller scale heat and smoke may have different effects on the resin secretion (rather than just drying and cracking), so we consider this separately from a large-scale 'disastrous' wild fire (see Section V.4). (*ii*) Disease is also considered separately from physical damage. We define disease as plant pathogens that do not require a novel entry point into a plant but attack the plant through naturally occurring pores (e.g. lenticels, stomata) that cannot all be sealed without killing the plant (see Section V.1). Some opportunistic diseases [e.g. Dutch elm disease *Ophiostoma* spp. Syd. & P.Syd. spread by the elm bark beetles (Curculionidae: Scolytinae)], or apparent symbioses [e.g. Mountain pine beetle *Dendroctonus ponderosae* Hopkins and the blue stain fungus *Grosmannia clavigera* (Robinson-Jeffrey & Davidson) Zipfel, de Beer & Wingfield] start with an insect attack and would be placed under that category.

(3) Relationship to tree habit

Tree crown forms appear to be key to some types of 'normal' resin production, particularly among the conifer family Araucariaceae. This is based on both the architectural model (the genetically determined growth plan; for more information see Hallé, Oldeman & Tomlinson, 1978) and the reiteration of the plant (the partial or total repetition of this model as the plant develops; Tomlinson, 2009). Thus the physical structure of the plant and its ecology predispose it to produce large amounts of resin naturally at certain places, like where the branch originates from the trunk.

(*a*) *Araucariaceae*

Among the conifers, Pinaceae are often highly resinous, but very little Pinaceae-derived amber is thought to have been preserved (see Table 3), whereas araucarian resins can form amber (Class 1b). Other conifers are not highly resinous today, despite being potential source plants of some amber deposits (see Table 1), so we focus here on Araucariaceae, with three genera: *Agathis* Salisb., *Araucaria* Juss. and *Wollemia* W.G. Jones, K.D. Hill & J.M. Allen.

Young Araucariaceae are typically cone-shaped (Veillon, 1978), but the adult trees (except *Wollemia*) fall into one of two (columnar or round) habits, based on their canopy development. Tomlinson (2009) suggests that the columnar shape (particularly of New Caledonian araucarians) is an adaptation to cyclone-prone habitats, where the tall trees withstand high winds with small canopies that can be quickly replaced after damage (often only on one side of the tree). Obviously this wind damage to the canopy would result in resin exudation. Our observations of highly resinous ecosystems in New Caledonia have given a slightly different insight, as the tall columnar trees exposed at the coast (*Araucaria columnaris*) can also exhibit severe wind-rock, even longitudinal cracking down the trunk, sometimes causing substantial resin flows along cracks in the trunk (Figs 2E and 3).

Other shorter, 'rounder' New Caledonian araucarians with a more open canopy growing in upland areas do not appear to suffer from wind damage [e.g. *Araucaria humboldtensis* and *Agathis ovata* (L.J. Seyfullah, J. Rikkinen & A.R. Schmidt, personal observations)] as Tomlinson (2009) suggests, and we do not see resin exudation from wind damage here, but from other causes (Fig. 3).

Agathis australis is the most resinous southern conifer today under normal conditions (i.e. no obvious infection/infestation/environmental stress). In a forest, *Agathis australis* displays a 'top heavy' growth form with a tall clear trunk, which results from its emergence through the canopy and growth to dominate the area (Tomlinson, 2009). In Malesian dipterocarp forests *Agathis dammara* (Lamb.) Rich., another highly resinous conifer, has the same form (Edelin, 1986). Other *Agathis* species, which produce highly prized resins, also follow this habit including the highly resinous *Agathis borneensis* Warb., and *Agathis labillardierei* Warb. (Tomlinson, 2009).

Significant resin accumulations can occur where heavy branches originate from the trunk, and these were exploited alongside the 'bleeding' of these trees in New Zealand as a source of kauri (*Agathis australis*) resin, a major export in the early 20th century. The weight of the branches, particularly when laden with high numbers of epiphytes, stresses the branch junction, leading to fissures in the wood tissue and subsequent resin exudation. We currently have no measurement of the effects of epiphyte loading on resin exudation, but typical amounts of resin at the forking of branches is 1–2 kg, however lumps of 23–90 kg have be obtained from a single tree (McNeill, 1991; Fig. 4).

The roots of the Araucariaceae may also exude copious resin, usually as a result of damage or disturbance. The shallow araucarian rooting system, where 1–2 pseudowhorls of 4–5 major roots extend from a tap root collar, is anchored by subsequent 'peg' or 'sinker' roots that develop later (Veillon, 1978). This configuration may mean that these trees are more susceptible to root disturbance where the soil is thinner and the environment is perhaps less stable. In New Zealand, extensive *Agathis australis* resin deposits are found in the soil, but it is not clear from where on the tree they are derived, nor precisely how old some deposits are, as they appear to persist for tens to thousands of years (Thomas, 1969). We observed large root resin masses in *Araucaria columnaris* on a New Caledonia beach, as the substrate had eroded away exposing the roots. Other araucarian soil resins have also been described and exploited on a massive scale for commercial use (*Agathis borneensis*, western Malesia, Borneo;

Fig. 3. Extremes of Araucariaceae tree architecture in New Caledonia. (A, B) *Araucaria columnaris*, Bourail, an exposed coastal site. (A) Distinctive narrow habit. The trees reach *ca.* 60 m height. (B) Extreme resin secretion caused by wind-rock and subsequent opportunistic infection. (C, D) *Agathis ovata*, Yaté, emerging in dry maquis minier vegetation. (C) Characteristic widely extending branches are prone to mechanical stress. (D) Massive resin exudation.

Agathis dammara, eastern Malesia; and *Agathis labillardierei*, New Guinea; Langenheim, 2003), but again the location of resin exudation on the parent plant is not clear.

The family Araucariaceae is thought to have diversified in the Early Jurassic (Escapa & Catalano, 2013) and araucarians are considered to be the source plant of some deposits (Table 1).

(*b*) *Angiosperms*

The earliest angiosperms date to the Early Cretaceous (Friis, Pedersen & Crane, 2010), and angiosperm-derived amber accumulations become significant during the Cenozoic (Table 1). Resinous angiosperms show a high diversity of habits and growth forms even in one family. Here we summarise only those resinous angiosperms that are thought to be the source plants of some amber deposits. Within the Dipterocarpaceae, the resinous *Shorea* Roxb. ex C.F. Gaertn. is a genus consisting mainly of tall, emergent, or canopy rainforest trees, whereas trees in the resinous genus *Hopea* Roxb. are understorey trees, or in the canopy of lowland rainforests. Today's *Hymenaea* L. (Fabaceae) species are mostly large evergreen, usually emergent, trees and this genus is thought to be the source plant for the Mexican, Dominican, Ethiopian and Peruvian (Amazonian) amber deposits (Table 1).

Root-derived resins are well documented for some angiosperms. In *Hymenaea*, root resins build up in the soil

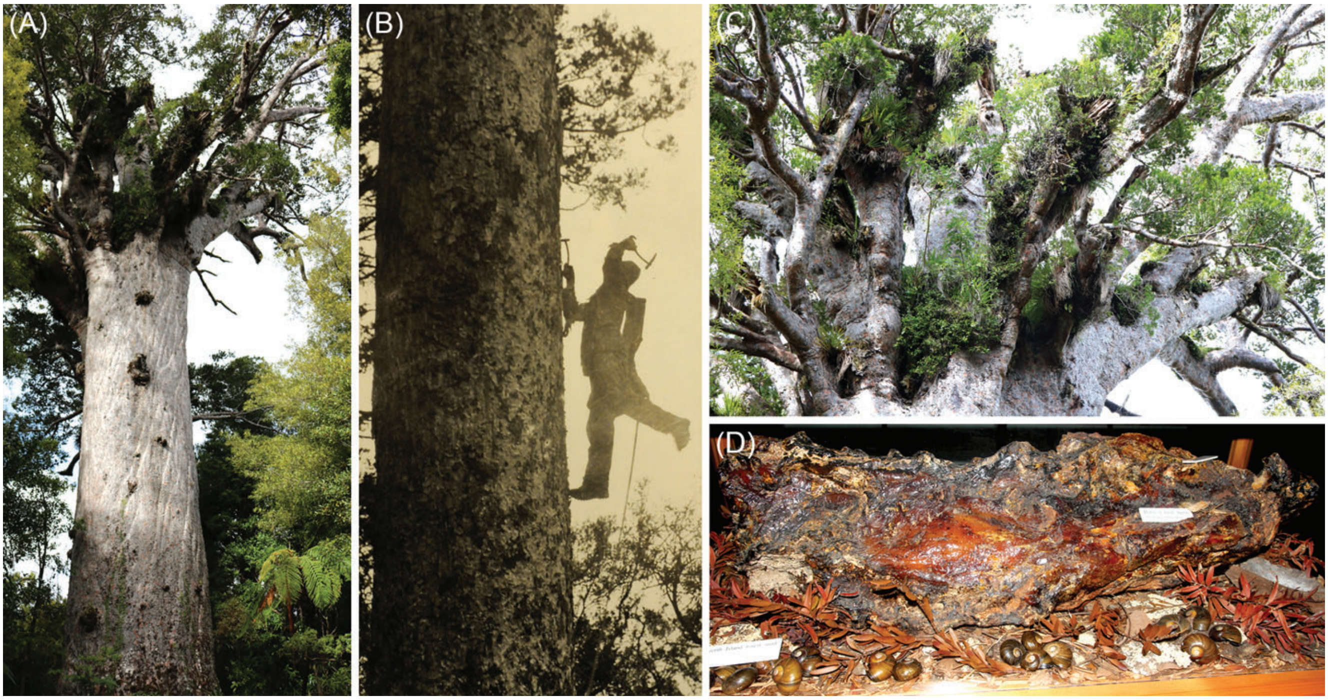

Fig. 4. Tree architecture of *Agathis australis* from New Zealand. (A) Typical mature tree (Tane Mahuta, Waipoua Forest) with a long, clear bole and spreading crown. (B) Historic photograph of a resin collector climbing to the canopy to collect resin (image credit: Kauri Museum, Matakohe, New Zealand). (C) Dense epiphyte loading (Tane Mahuta, Waipoua Forest) may break these heavy branches ('widow makers'). (D) Massive resin piece weighing 65.5 kg from the canopy (now in the Kauri Museum, Matakohe, New Zealand).

along with resins from other parts of the trees (Langenheim, 1967, 2003). African *Shorea* and *Copaifera* L. resins are also found in soil but it is not clear from where on the trees these resin deposits are derived (Henwood, 1993).

V. REASONS FOR RESIN PRODUCTION SUPPORTED BY THE FOSSIL RECORD AND MODERN ANALOGUES

Using modern resin-production observations, several reasons for larger amber deposits have been postulated: ecological disasters like typhoons, volcanic activity or climate change (e.g. Gianolla *et al.,* 1998), leading to catastrophic forest damage or emergent disease of the plants [e.g. Conwentz's, (1890) 'succinosis']; the evolution of new wood-dwelling insect groups, leading to tree damage and subsequent resin outpouring which can perhaps be detected through chemical analysis (McKellar *et al.*, 2011), and heightened fire incidence as evidenced by charcoal occurring with and even within some ambers (Najarro *et al.*, 2010).

To aid us in understanding the reason(s) for massive resin production in the past, it is crucial to know the precise age of amber deposits (see Dal Corso *et al.,* 2017). This allows linking of the amber to the climate and environment under which it was produced. Unfortunately, many amber deposits are often only approximately dated, sometimes with an age uncertainty of several millions of years (Table 1). The only large occurrence of amber in the geological record that is accurately dated is the Carnian (Late Triassic) amber, which is found in stratigraphic sections that are well constrained by biostratigraphy (Table 1).

We here examine both modern resinous ecosystems and the fossil record for evidence to understand amber deposits.

(1) In response to disease

One of the oldest suggestions for large amber accumulations is that they are a product of the plants' response to infections, causing extreme resin production – hyper-resinosis. Disease was one of the potential explanations for the Baltic amber deposit, where infected trees in a large forest 'wept' vast amounts of resin. Conwentz (1890) termed this anomalous production of resin 'succinosis', and suggested it might be linked with a larger 'disaster' allowing the disease (or infestations) to take hold.

Agathis australis trees from northern New Zealand are highly resinous, but in trees infected with recently identified Kauri Dieback *Phythophthora* 'taxon *agathis*' (PTA; Beever *et al.,* 2009), now *Phytophthora agathidicida* (Weir *et al.,* 2015), we observed hyper-resinosis (Fig. 5).

Phytophthora agathidicida is a water- and soil-borne oomycete that enters *Agathis australis* trees through their surface-feeding roots. It is highly pathogenic to *Agathis australis*, and it infects and kills trees of all ages. Symptoms include yellowing of

Fig. 5. Microbial infection: *Phytophthora agathidicida* disease-induced hyper-resinosis in *Agathis australis*, New Zealand. (A) Upright dead tree with a thick resin mantle (hyper-resinosis) surrounding the entire trunk base, Waitakere Ranges. (B) White patches of resin (front and side of trunk base) of tree succumbing to infection (Trounson Forest). (C) Initial symptoms of infection, resin exudation from lenticels in lower part of trunk, Waitakere Ranges. (D) Fresh exudation continues over older resin flows, Waitakere Ranges.

the leaves, thinning of the canopy, and lesions on the lower stem which often encircle the base and produce copious amounts of resin [Beauchamp, Dick & Bellgard, 2011; B. Burns (Auckland), personal communication; L.J. Seyfullah, personal observations]. Infection leads to the death of the tree, typically over a few years, and is confirmed from a number of locations across New Zealand. Thus pathogenic attack could be a reasonable cause of some deposits. Dwarf mistletoe infections induce host deformities and increase resin production at these sites, and they are known to increase the risk of *Phytophthora* infections in their host trees, complicating the resin response (Fig. 6). Interestingly, dwarf mistletoes were found to be diverse in the 'Baltic amber forest', with six species described from Baltic amber (Sadowski *et al.,* 2017*b*).

By contrast, Henwood (1993) suggested that pathology might not underlie periods of extensive resin production, as the quantity of resin produced by healthy modern trees (such as *Agathis australis* and *Hymenaea* spp.) is sufficient to explain the amount of amber in the fossil record (see Sections IV.3 & V.3). However, if the quantity of resin produced by 'healthy' modern trees is enough to explain the amount of amber in the past, why amber is not found continuously in the geological record? This will be explored in Section VI.2*a*.

(2) In response to insect infestation

Bark beetles (Coleoptera: Curculionidae: Scolytinae) can be a particular problem for many coniferous forests, reducing tree vigour, but often they are held in check [see Krokene, 2015 for an overview of conifer defence mechanisms]. In some cases, such as the mountain pine beetle, coordinated mass attacks occur, causing vast tree dieback with tell-tale multiple insect holes and often with large amounts of exuded resin (Fig. 7A, B). Drought and other stresses (e.g. root infection, defoliation, and fire injury) of the trees leads to reduced resinosis at the site of attack and a lower chance of tree survival in many cases (see Raffa, Grégoire & Lindgren, 2015).

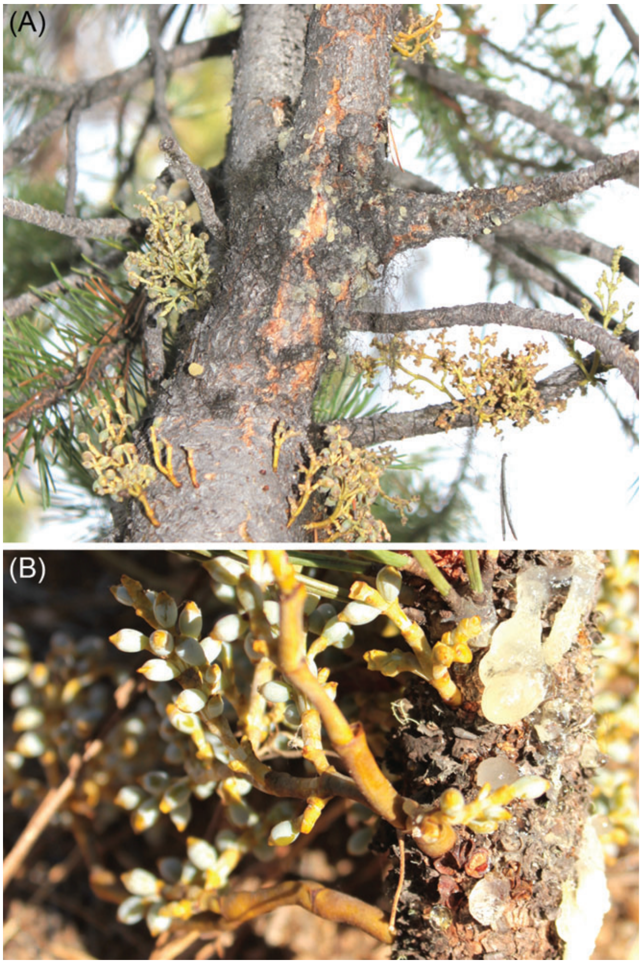

Fig. 6. Dwarf mistletoe-induced resin exudation increases the hosts' risk of *Phytophthora* infection, and increases fire risk due to deformities (witches brooms) in the hosts (Oregon, USA; images courtesy of Eva-Maria Sadowski, Göttingen). (A) *Pinus contorta ssp. latifolia* host with swelling, deformities, and resin at bark fracture sites following infection and growth with *Arceuthobium americanum*. Black elongate lichens are also present. (B) *Pinus ponderosa* resin exudation (right) due to *Arceuthobium campylopodum* infection (extensive growth on left side of slender twig).

New Caledonian *Araucaria humboldtensis* exudes resin from beetle-infested branches, with particular drop-like morphologies (Fig. 7C, D; Beimforde *et al.,* 2017), reminiscent of the Dolomites amber drops with arthropods entrapped (Schmidt *et al.,* 2012) and those in French amber (Saint Martin *et al.,* 2013; Néraudeau *et al.,* 2017). The actual quantities observed are relatively small in terms of 'geologically significant' resin volumes, and are due to the low density of the *Araucaria humboldtensis* trees on Mont Humboldt. However, given the stature of the *Araucaria humboldtensis* trees, the resin amounts exuded appear fairly significant in terms of plant resources. Interestingly, Beimforde *et al.* (2017) showed complex animal and fungal interactions with the resinous *Araucaria humboldtensis* in New Caledonia, where the fungi depend on long-term resin flows, under natural conditions in a stable ecosystem that lacks fire. Overall, the amount of resin that could collect over time is not thought to be very extensive, but given larger resinous trees growing at a much higher density, such as with the pines attacked by bark beetles (see below), 'geologically significant' resin volumes are possible.

Wood-boring insect evolution was suggested to be linked to the origin of Early Cretaceous ambers (Chaloner, Scott & Stephenson, 1991; Grimaldi & Engel, 2005). Insect attack is potentially the underlying reason for resin secretion in two particular amber deposits: the Raritan amber (Grimaldi, Shedrinsky & Wampler, 2000) and the Dominican amber (Iturralde-Vinent & MacPhee, 1996), although the evidence remains equivocal.

The Dominican amber was produced by the angiosperm *Hymenaea*, and the modern taxa secrete large amounts of resin after injury (Langenheim, 1969, 2003). The deposit was thought to have arisen from natural catastrophic events such as hurricane damage leading to significant resin production (Grimaldi, 1995), although a large number of bark beetles are preserved within the amber (Penney, 2010*b*). The Raritan amber has very few wood-boring beetle inclusions (Grimaldi *et al.,* 2000), but has some evidence of fire damage (see Section V.4) in the form of bubbled amber with fusainised wood inclusions (Grimaldi *et al.,* 2000).

McKellar *et al.* (2011) argued for insect attack being responsible for both amber deposits using ^{13}C-enriched carbon isotope signatures. However, they noted that the isotopic enrichment seen in the resins and ambers can mimic those brought on by drought responses, since water transport in trees is abruptly affected during and after insect attack. These complications mean that support for this argument is also not clear cut. Dal Corso *et al.* (2017) showed that carbon isotope signatures in resins of the same species are actually variable and dependent on several factors (e.g. location on tree, height above sea level), complicating the McKellar *et al.* (2011) scenario.

Regarding older Cretaceous amber deposits, there is no support for resin production in response to insect attacks. A study of coleopteran diversity recorded in Early/middle Cretaceous ambers from France and Spain shows a majority of saproxylic and detritivorous, rather than wood-boring beetles (Peris *et al.,* 2016).

Hypotheses about deposit formation that hinge upon insect infestations may remain difficult to test in the amber record. An insect-associated pathogenic microorganism may not be preserved in the amber, and even if it was, definitive identification as the disease-causing agent is not possible.

(3) In response to an ecological change or disaster

Hurricane damage leading to significant resin production has been suggested for the Dominican amber deposit (Grimaldi, 1996), although insect attack (see Section V.2) has also been suggested as the potential primary cause.

Today it is difficult to sample areas where modern highly resinous trees have suffered a natural catastrophe. The closest example is the subfossil resin deposits of *Agathis australis* in northern New Zealand where there are numerous sites of 'swamp kauri gumlands'. At these sites *Agathis australis* trees

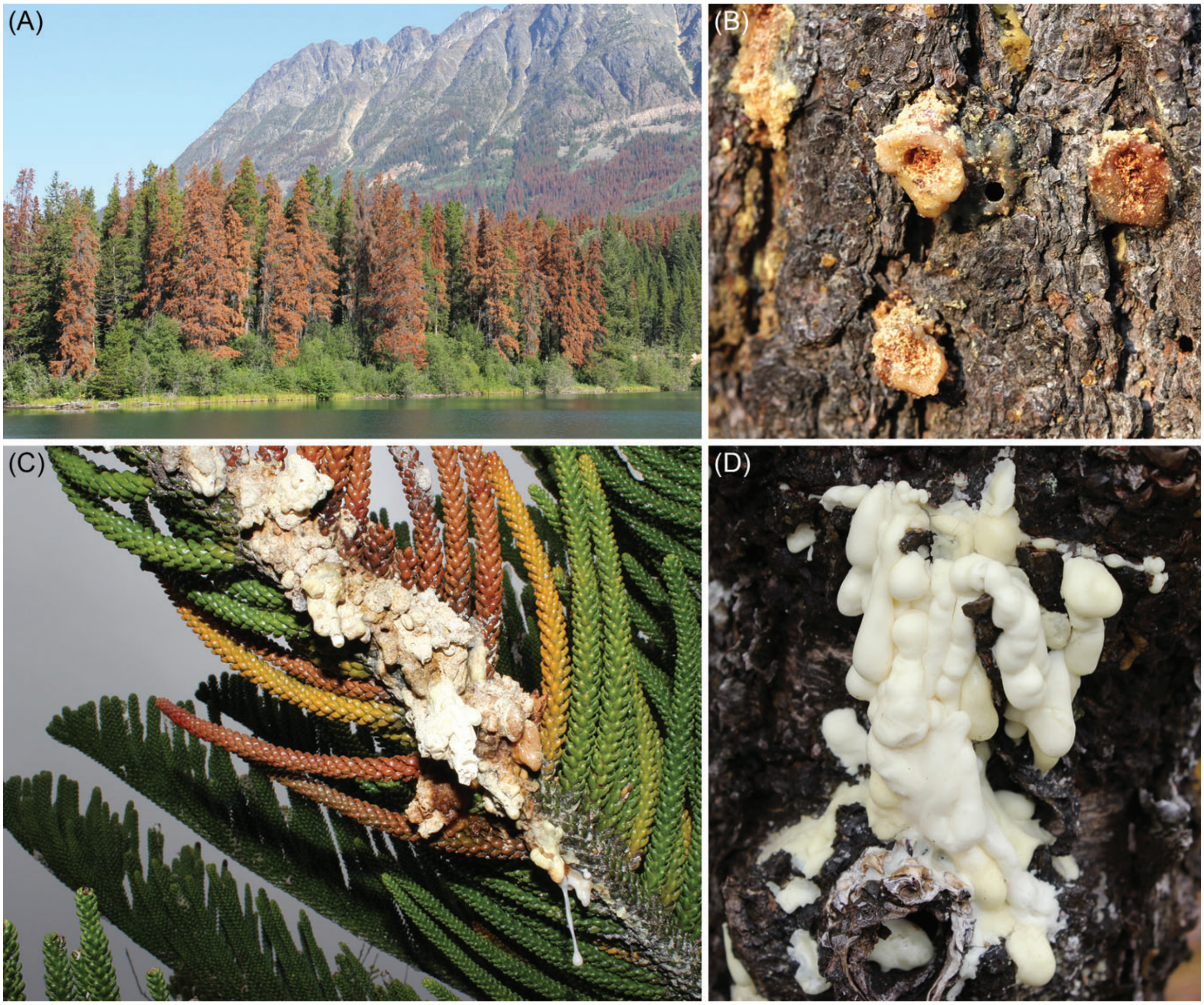

Fig. 7. Insect attacks and resin secretion. (A, B) Dying *Pinus contorta* forest after bark beetle outbreak in British Columbia, Canada. Resin outpourings at the borings are shown in B. (C, D) *Araucaria humboldtensis* with internal weevil infestation, Mont Humboldt, New Caledonia. (C) Infested branch with resin. (D) Resin outpouring on tree trunk.

and resin are preserved in peats (Fig. 8A–C) and were commercially exploited. The trees did not actually grow in the swamps, these wetlands developed later. Swamps were then buried by sediments, indicating changing environmental and/or depositional conditions (D'Costa, Boswijk & Ogden, 2009; Turney *et al.*, 2010; Fig. 8E, F). The preserved swamps vary in age from approximately 20000 to 100,000 years old (based on carbon-dating; Boswijk, 2005).

Agathis australis is naturally highly resinous (see Section IV.3*a*) and large deposits accumulated over a relatively short time span of only thousands of years, potentially contradicting ideas proposed by Poinar (1992) and Weitschat & Wichard (2010) that the exudations required to form the Baltic amber deposit occurred over millions of years.

Much of these New Zealand resin deposits have been lost due to collection (Fig. 8D) in the early 20th century (around 8000 tons per annum were removed for sale between 1907 and 1914 (Anon, 1921). Over 450,000 tons of resin in total have been removed (Haywood, 1989) with some nuggets weighing more than 270 kg each (McNeill, 1991). Most of this massive amount of resin is reported to have come from within 3 m of the surface, although it could also be found up to 9 m deep and sometimes occurring in a couple of bands (Matich, Matich & Mataga, 2011).

The exact cause(s) that led to the huge resin outpourings in New Zealand is not certain. The leading suggestion for the cause behind the buried swamps is Holocene global climate change (during the latter part of the last Glacial period: 60000 to 11700 years ago) combined with associated eustatic (sea level) change, as well potential rainfall and drainage-pattern changes (e.g. D'Costa *et al.*, 2009; Turney *et al.*, 2010). Clearly then these large resin deposits were produced in much less

Fig. 8. Subfossil *Agathis australis* resin, New Zealand. (A) Lake Ohia, a lake that formed over an *Agathis australis* forest 30000 years ago. (B) Subfossil resin fragments in the peat of Lake Ohia. (C) Exposed *in situ* subfossil *Agathis australis* trunk, carbon dated to 100,000 years old, and surrounding swamp, Gumdiggers Park, Awanui. (D) Historic photograph of gumdiggers with recovered subfossil resin (image credit: Kauri Museum, Matakohe, New Zealand). (E) Section exposing buried swamp at the base of the image, with layers of sediments indicating several episodes of covering, and preserving the swamp, Gumdiggers Park, Awanui. (F) *In situ* subfossil resin (yellow masses) from the swamp shown in E, Gumdiggers Park, Awanui.

than one million years. Additionally, there were volcanic eruptions during this time, often with significant damaging events or deposits (e.g. Marra, Alloway & Newnham, 2006), which may have had associated tsunamis. Hurricane damage has not been ruled out either. Ultimately it is likely that a period of ecological upheaval is recorded here, and further study is recommended.

Martínez-Delclòs *et al.* (2004) and Philippe *et al.* (2005) suggested that the lack of inclusions in some ambers resulted from resin exuded directly into water as a response to flooding. Swamp-type conditions were noted by Langenheim (2003) as important for the accumulations of large masses of leguminous resin in the Congo basin of East Africa, and in Amazonia, and so might also be relevant for the New Zealand subfossil resins.

(4) In response to fire

The Raritan amber shows fire damage in the form of bubbled amber with fusainised wood inclusions (Grimaldi *et al.*, 2000).

The fire hypothesis for the New Jersey amber is hard to test, given that fire may have not been the primary cause of resin secretion, and that a fire subsequent to the secretion bubbled and melted the resin (Najarro *et al.,* 2010; Brasier, Cotton & Yenney, 2009).

Heightened fire incidence related to atmospheric oxygen levels has been suggested (e.g. Scott, 2000; Brasier *et al.,* 2009; Najarro *et al.,* 2010) as a cause of amber deposits. Fires (Fig. 9) can cause bark to split in the heat (Hillis, 1987). Resin from *Araucaria columnaris* in New Caledonia, which is produced in response to physical damage or on the surface of delicate organs is clear-white to pale yellow, but is darkened to red-brown when a product of fire-damage (Fig. 9; L.J. Seyfullah, C. Beimforde, V. Perrichot & A.R. Schmidt, personal observations). When the darkened resin is produced (at the time of the fire or afterwards) is not clear, nor how intense the fire needs to be. It has also been shown that *Pinus resinosa* trees injured by simulated ground fires doubled resin production within a few days because of increased fungal and insect (e.g. bark beetle) attack on the wounded plants (Lombardero, Ayres & Ayres, 2006).

Recently discovered evidence in the geological record indicates that anomalous resin production is associated with increasing wildfire activity at the Triassic/Jurassic boundary (*ca.* 201 Mya; Williford *et al.,* 2014). Although no major amber deposits have been found so far for this time interval, there is a sharp peak of molecules derived from burnt resin and polycyclic aromatic hydrocarbons from charcoals coincident with end-Triassic mass extinction and carbon cycle perturbation in East Greenland (Williford *et al.,* 2014). Other evidence of increased wildfire activity at the Triassic/Jurassic boundary has been found in other stratigraphic sections (e.g. Belcher *et al.,* 2010; Petersen & Lindström, 2012). The disappearance of Triassic fauna and flora is associated with a major global carbon cycle perturbation caused by injection of CO_2 into the atmosphere, as testified by coeval doubling of CO_2 partial pressure (PCO_2) levels and a negative carbon isotope shift recorded in carbonates and organic matter (e.g. Pálfy *et al.,* 2001; Ward *et al.,* 2001; Hesselbo *et al.,* 2002; Whiteside *et al.,* 2010; Ruhl *et al.,* 2011; Steinthorsdottir, Jeram & McElwain, 2011; Dal Corso *et al.,* 2014). This carbon cycle disruption and mass extinction has been closely linked to the eruption of the Central Atlantic Magmatic Province (CAMP; Marzoli *et al.,* 1999) and the associated volcanic release of CO_2 and SO_2 (e.g. Hesselbo *et al.,* 2002; Callegaro *et al.,* 2014). According to the scenario proposed by Belcher *et al.* (2010), increasing CO_2 levels and associated global warming at the end of the Triassic would have increased the likelihood of storms and lightning strikes, causing an increase in wildfire activity.

(5) In response to climate change

Moisture availability and temperature influence exudation pressure (Lorio & Hodges, 1968), thus more resin is produced in wetter conditions than in drier ones (Langenheim, 2003). During the Carnian, for example, amber is found in several deposits around the world that are accurately dated to the late Julian–early Tuvalian, an interval of known global climate change and biotic turnover called the 'Carnian Pluvial Episode' (CPE; Simms & Ruffell, 1989; Preto, Kustatscher & Wignall, 2010; Roghi *et al.,* 2010; Dal Corso *et al.,* 2015; Dal Corso *et al.,* 2018, Fig. 10). This allows the linking of the Carnian amber to climate change, and understanding this cause and effect relationship.

The CPE marks a change to humid climate conditions in the terrestrial realm from mostly arid conditions (Fig. 10) which predominated in the Middle Triassic (Preto *et al.,* 2010). It is linked to an increased siliciclastic (sediment) input into the basins, probably indicating a more vigorous hydrological and weathering cycle (Rigo *et al.,* 2007; Dal Corso *et al.,* 2015).

As for the Triassic/Jurassic boundary, the onset of the CPE occurs in correspondence with a major carbon cycle perturbation as evidenced by a sharp negative shift in the carbon isotope records across the Carnian, probably caused by a large injection of isotopically ^{13}C-depleted CO_2 into the atmosphere–ocean system (Dal Corso *et al.,* 2012, 2015; Mueller, Krystyn & Kürschner, 2016). This perturbation would have likely led to global warming (Hornung *et al.,* 2007; Rigo & Joachimski, 2010) and enhancement of the hydrological cycle, thereby increasing the magnitude of rainfall and continental weathering (Dal Corso *et al.,* 2015). Given its common correlation in the geological record, the most likely cause for depleted CO_2 is the eruption of the extensive Wrangellia Large Igneous Province volcanism (Furin *et al.,* 2006; Greene *et al.,* 2010; Dal Corso *et al.,* 2012). During the CPE, extinction among marine taxa is well documented and dated to the Julian–Tuvalian boundary, when early Carnian ammonoids like the Trachyceratinae, and 70% of conodont genera disappeared (Simms & Ruffell, 1989; Rigo *et al.,* 2007; Balini *et al.,* 2010). A major turnover in terrestrial fauna and flora is also documented. Important groups of herbivorous tetrapods became extinct and were replaced by dinosaurs (e.g. Benton, 1986; Brusatte *et al.,* 2008; Lucas & Tanner, 2015). In the late Carnian, pollen and spore diversity declined by approximately 50%, which is the second most severe microfloristic reduction after the mass extinction at the Permian–Triassic boundary (Kürschner & Herngreen, 2010). It is notable that the evolution and radiation of modern conifers, some of which are major resin producers, may also have occurred during the Late Triassic (Willis & McElwain, 2013).

In the geological sections of the Southern Alps (Italy), the Northern Calcareous Alps (Austria) and in the Transdanubian range (Hungary), Carnian amber occurs just after the negative carbon isotope perturbation, during the wet climate conditions that mark the CPE (Fig. 10).

Some Eocene amber deposits also have been linked to global climate changes. Cambay amber has been found in lignitic deposits in India that have been dated to the early to middle Ypresian (early Eocene), and has been linked to the peak of the Early Eocene Climatic Optimum

Fig. 9. Resin exudation after fire damage. (A, B) Freshly burned *Picea engelmannii* forest, Jasper National Park, British Columbia, Canada; trees subjected to the most intense fire died, those at the fire's periphery survived but were damaged and secreted resin. (C–E) *Araucaria columnaris*, Maré, New Caledonia. (C) Extensively damaged tree. (D) Much darkened resin from fire-damaged tissue from the tree shown in C. (E) Darkened resin from a tree exposed to a less-intense fire than C.

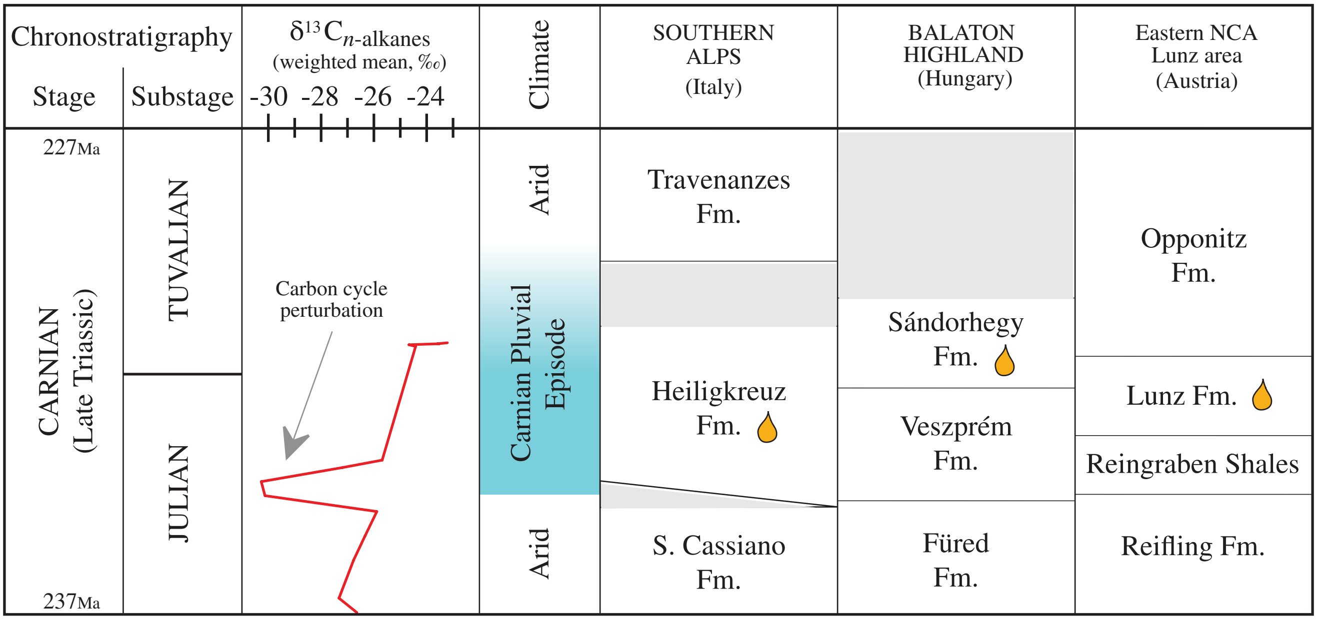

Fig. 10. Triassic amber occurrences and the Carnian Pluvial Episode (CPE). Carnian amber is found in several localities in Europe, North America, and South Africa, within the same chronostratigraphic interval (Schmidt *et al.*, 2012), and appears to be coincident with the CPE, a major climate change. The figure shows amber occurrences (drip shapes) in the geological sections where the stable carbon-isotope perturbation (negative δ^{13}C excursion) has been defined, and the Carnian Pluvial Episode is biostratigraphically well constrained. Weighted mean δ^{13}C of odd n-C_{25}–n-C_{31} alkanes is from Dal Corso *et al.* (2012, 2015). NCA, Northern Calcareous Alps, Fm., Formation.

(EECO; Rust *et al.*, 2010). Similarly, Fushun amber is found in early–middle Ypresian coal beds in China (Wang *et al.*, 2014), and Oise amber is also dated to the earliest Ypresian (‘Sparnacian’; Nel *et al.*, 1999). Other Eocene amber, i.e. Baltic and Rovno amber, seem to have been produced much later in the late Eocene (Standke, 2008; Dunlop, 2010; Perkovsky *et al.*, 2010). The EECO was a long-term climate shift marked by high CO_2 levels and global temperature, and an increase in precipitation probably triggered by high volcanic emissions (e.g. Zachos, Dickens & Zeebe, 2008; Hyland, Sheldon & Cotton, 2017). During early Eocene short-term abrupt climate changes also took place, i.e., the Palaeocene–Eocene thermal maximum (PETM) and the Eocene thermal maximum 2 (ETM2; e.g. Zachos *et al.*, 2008). Such events, known as hyperthermals, are associated with massive injections of CO_2 into the atmosphere–ocean system, a brief increase in global temperature, and increased seasonal precipitation or intense storms (McInerney & Wing, 2011). A link between the PETM and the emplacement of the North Atlantic Igneous Province has been proposed (Storey, Duncan & Swisher, 2007; Saunders, 2016). In fact, French Oise amber (Ypresian, 53 Mya) is reported to occur during ETM2 (Aria, Perrichot & Nel, 2011).

The temporal coincidence thus suggests a cause-and-effect relationship between climate change and resin exudation. However, to identify its primary trigger is not straightforward. Increasing moisture is indeed one of the effects of increasing PCO_2 levels in the atmosphere and could alone explain the anomalous resin production (Langenheim, 2003). The associated increase in storminess, however, likely would have damaged plants mechanically in addition to the effects of lightning and the accompanying wildfire, as for the end-Triassic (see Section V.4). On the other hand, volcanism itself could also be invoked, as it has been for Carnian and Eocene amber, as well as for the end-Triassic peak of resin molecules (see Section V.4), which appear to have been produced at the time of the emplacement of large igneous provinces. The release of a huge amount of volcanic SO_2, for example, could have caused extensive acid rainfall (Wignall, 2001), strongly damaging the forests (although we would classify this as an ecological disaster here). However, other large igneous provinces, like the Deccan Traps at the end of the Cretaceous, do not seem to be temporally linked with large amber deposits. So climate change can be a plethora of potential causes acting in concert to induce resin exudation, but differs from a large-scale ecological disaster like a tsunami/hurricane. Future studies should focus on precisely defining the temporal relationships between past climate changes and amber deposits to constrain possible climatically driven causes of large-scale resin production more accurately.

VI. FORMATION OF AMBER DEPOSITS

Resin has to survive and pass from the biosphere of the resinous tree that exuded it into the geosphere in order to become fossilised as amber (Fig. 11).

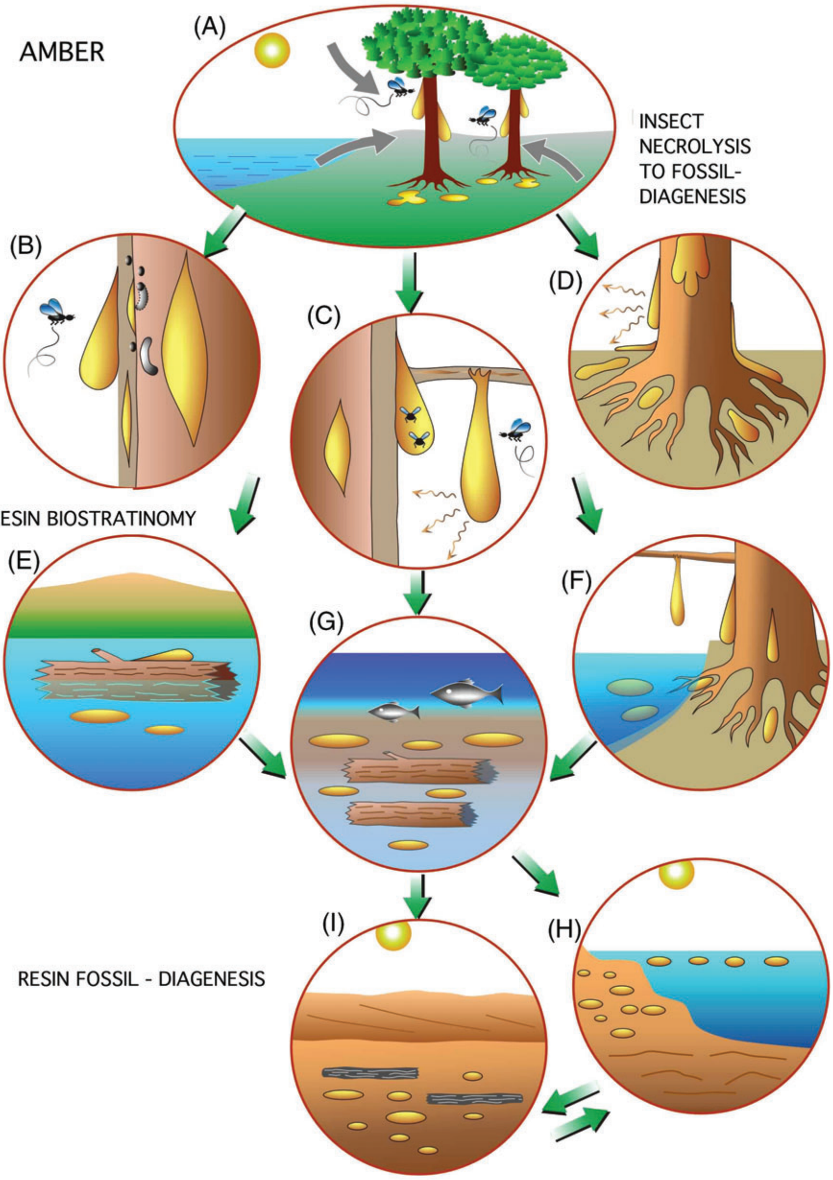

Fig. 11. Amber taphonomy. (A) Terrestrial, aquatic and underground insects are trapped by resin. (B) Resin may accumulate in the internal cracks and pockets within the wood, and under and between the bark. (C) When resin is unconstrained it may form stalactites, drops and flows, and may trap insects and other organisms. Under subaerial conditions resins lose volatiles. (D) Subterranean deposits of resins also form, produced by roots and by the aerial parts of the tree, and accumulate as large masses around the tree base. (E) In the majority of cases it is not known whether resin is transported to the deposit in which it becomes fossilised with the tree or separately. (F) Resins are introduced into water directly from the tree or following erosion of the soil. (G) Initial deposition of the resin, usually associated with organic-rich sediments. (H) Diagenesis of the resin begins with burial. Nevertheless, some prediagenetic processes that affect insects in resins are difficult to distinguish from the effects of diagenesis. (I) Amber is usually reworked and deposits are time-averaged. Image courtesy of Xavier Martínez-Delclòs (Barcelona).

(1) Traditional view

The majority of fossiliferous amber deposits are considered allochthonous (Martínez-Delclòs *et al.,* 2004; Table 1), i.e. transported to their current location, usually by rivers to a coastal/deltaic/lagoonal setting (Fig. 12). This interpretation contrasts with an autochthonous origin, where deposits are formed *in situ* (Grimaldi, 1996; Iturralde-Vinent, 2001; Gomez *et al.,* 2002). The transport and deposition of resins is poorly understood, but water plays a key role; many ambers come close to floating in saltwater and sink in fresh and brackish water (Iturralde-Vinent, 2001), so this transport means ambers are not often found associated with their fossilised source plants (Martínez-Delclòs *et al.*, 2004; see also Fig. 4.3 in Langenheim, 2003; Figs 11 and 12, Table 1). Indeed, the Spanish, Oise and Charentes ambers occur in sandy channels of the delta plain (Alonso *et al.,* 2000; Nel & Brasero, 2010; Perrichot *et al.,* 2010), having been washed into these settings (Fig. 12). Burmese amber was deposited in a nearshore marine setting, with abundant bivalve borings suggesting sea transport (Cruickshank & Ko, 2003; Ross *et al.,* 2010). Bitterfeld amber is thought to have been washed into a lagoon and concentrated there (Dunlop, 2010). Lebanese amber (Azar *et al.,* 2010) is usually present in clays and shales deposited in fluvial (river) to coastal (intertidal) environments (Azar, 2007). Some Carnian amber from the Southern Alps of Italy is found in sandstones with plant and marine invertebrate remains, which indicates that the amber was transported and re-deposited (Gianolla *et al.,* 1998; Roghi *et al.,* 2006; Breda *et al.,* 2009).

Amber may also occur in association with coal seams (Table 1) formed by ancient swamps. Examples include Grassy Lake (Canada), Mexican, Cambay, and Wadi Zerka (Jordan, Lower Cretaceous; Poinar, 1992), and at least some of Cape York (Australia), most of the Dominican, Raritan, Spanish (Peñalver & Delclòs, 2010), and New Zealand amber (Seyfullah, Sadowski & Schmidt, 2015). However, whether the amber from these seams is preserved *in situ* as was thought by Pike (1993), or has been (minimally) transported, is not always clear. These deposits are better termed 'parautochthonous', as they appear somewhere between truly autochthonous and allochthonous.

Some Lower Cretaceous amber from Israel may be an autochthonous (*in situ*) occurrence (Nissenbaum & Horowitz, 1992). The prevalence of original resin exudation shapes (e.g. drops and stalagmites), or uneroded surfaces in a deposit show that little transport can have occurred since amber pieces are not damaged (Martínez-Delclòs *et al.,* 2004). Some ambers, however, are clearly reworked, where they are eroded from their original embedding sediment, transported for long distances and re-deposited. This includes deposits such as Baltic and Cedar Lake amber (Canada; McKellar & Wolfe, 2010; Table 1), complicating the identification of where, how and why these deposits originated.

As most ambers are found in sediments with fluvial to marine influences, Grimaldi (1996) suggested that the buoyant resin is washed downstream with logs, becoming concentrated on the ocean shore, or in a lagoon or river delta. Once concentrated there, the resin and logs are buried by sediments, and in time the resin becomes amber and the wood becomes lignite (an early stage of low-grade coal). Oxygen must be excluded (with clay or sand deposits) to prevent the oxidation of the amber and its degradation. Langenheim (2003) added that resin also falls to the soil around the source tree and is buried in the soil, then washed into rivers (Fig. 11). In fact there are soil litter organisms found in the Albian (Cretaceous) Archingeay amber (Perrichot, 2004), supporting this idea. So four factors are involved in amber accumulations (Grimaldi, 1996): (*i*) the right kind of resin must be exuded in order to be able to become amber, (*ii*) a near-shore forest must be present as the source of large resin quantities, (*iii*) resins have to become concentrated, and lastly, (*iv*) there has to be appropriate burial in sediments.

By contrast, as seen with subfossil resin deposits, it is possible to have large *in situ* deposits. However these deposits have not yet matured to amber, and it is not clear if they will survive in their current depositional setting, in order to be preserved on a geological timescale, and therefore transport may be an important step in the process.

The duration of the source forest providing the resin has been cited as another potential factor. Weitschat & Wichard (2002) suggested that the Baltic amber deposit represents at least 10 million years. Yet our observations based on the vast subfossil resin deposits from *Agathis australis* in New Zealand (Sections IV.3*a* and V.3), and those of Langenheim (2003) on leguminous resin from the Congo basin (East Africa) and Amazonia, indicate that very large time spans are not always necessary (see Section V.3).

(2) Field observations

(*a*) *Initial preservation* versus *degradation of resin in the forest*

Knowing how long resins could last in an ecosystem would indicate the window of burial opportunity (Fig. 13), which is important for understanding the potential preservation of resin as amber. There has been little research on this topic to date. We have examined the fates of exuded araucarian resins.

(*i*) *In New Caledonia.* *Agathis lanceolata* Warb. trees at the Parc Provincial de la Rivière Bleue had large resin bodies attached to their trunks (Fig. 13B) and roots in a humid environment (Fig. 13G). Many resin bodies on the forest floor had traces of resinicolous fungal mycelia on their outer surfaces, in time the holes left by the fungal hyphae will initiate further degradation, so that the resin will most likely not survive over decades. Large resin bodies of up to 30 cm size observed in 2005 (Fig. 13G) had degraded or disappeared within about five years. Searches of leaf litter-rich soils yielded a little resin (Fig. 13H).

At one locality in the hills of south-eastern New Caledonia, *Agathis ovata* resin balls varying from under 1 cm to 3 cm in diameter were discovered (provenance provided by FTIR analysis; L.J. Seyfullah, unpublished data), but the source tree was actually missing. The tree involved had already rotted away in this moderately humid environment, perhaps within a decade, but the polymerised resin was still present on the soil surface and apparently uncovered by leaf litter (Fig. 13D).

(*ii*) *In New Zealand.* The *Agathis australis* (kauri) swamps (Section V.3) show that subfossil resin can survive for a significant time period (up to *ca.* 100,000 years confirmed: Boswijk, 2005) when buried in the soil. However, at these sites changing water levels are important for their preservation, as resin is now found in waterlogged swamps that provide anoxic conditions capable of slowing down the weathering and break-down of the resin. The soil profile under *Agathis australis* trees may also have a strong bearing on resin preservation, as the acidic organic soil layer can be up to 2 m deep (Wyse & Burns, 2013). Tannins in these soils cause leaching and podosolisation, inhibiting microorganism

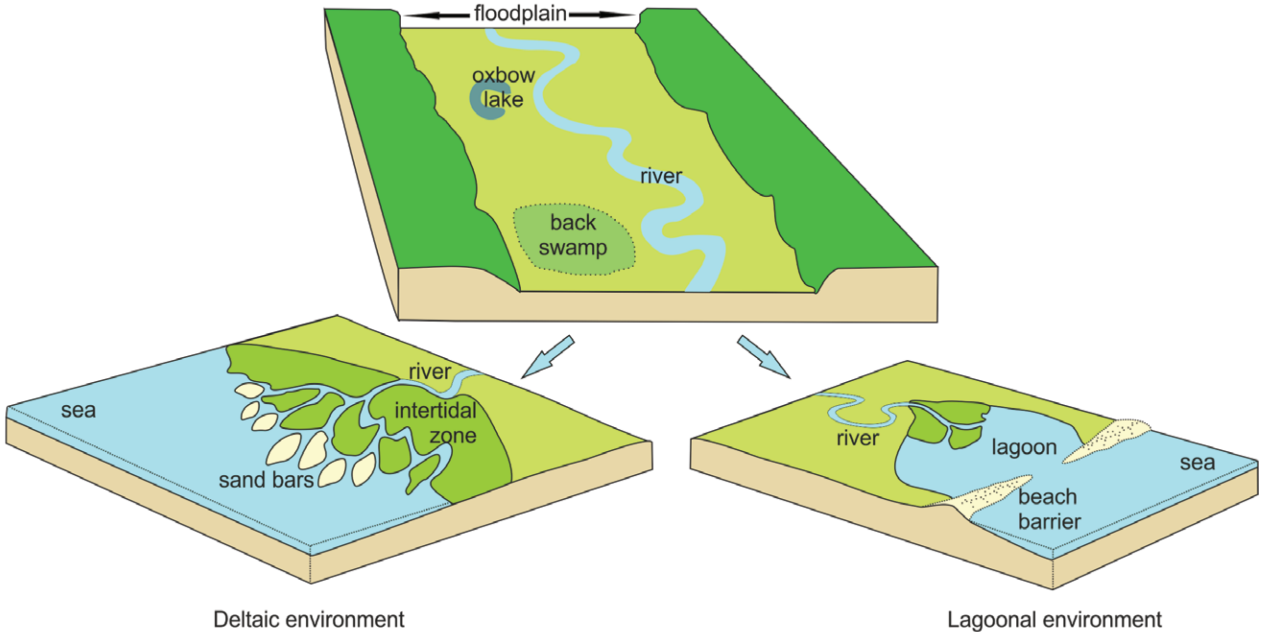

Fig. 12. Amber accumulations. Amber deposits are thought to be allochthonous and have a 'double' depositional history, first an initial resin deposition in forest soil, which is then eroded and transported by rivers along the floodplain. Some deposits are thought to be related to this floodplain (potentially parautochthonous), but the majority are thought to be transported further by rivers and become concentrated and deposited in either deltaic or lagoonal settings (see Table 1).

growth (Wyse, 2012), and potentially further slowing resin breakdown.

(*b*) *Deposit formation*

Information from the New Zealand 'swamp kauri' deposits (Section V.3) shows that the resinous forests were sometimes inundated by water allowing swamp development. Additional material would have been washed into the swamp, so some resin is preserved *in situ*, and some is transported short distances. If the swamps were buried and undisturbed for a geologically significant period, autochthonous and parautochthonous amber in a lignite deposit would be the end product.

Our observations at Baylys Beach (Fig. 14) show erosion of former swamp deposits. This resin is then transported by the sea along the coast (small isolated resin fragments have been found rarely on the beach). Subsequently the resin either eroded away or sinks in brackish estuaries. It may be accumulating locally, perhaps being sorted and mildly eroded, and then forming new reworked (allochthonous) coastal deposits in the future (Fig. 15).

Recent discoveries of ambers in southern New Zealand preserved *in situ* within lignites of varying ages (Eocene, Oligocene and Miocene; e.g. Thomas, 1969; Lambert *et al.*, 1993; Lyons *et al.*, 2009) suggest that these swamp environments (not unlike the swamp kauri deposits described in Section V.3) are key to resin preservation. Miocene ambers from southern New Zealand may also be *in situ* or parautochthonous (Schmidt *et al.*, 2018). Early Miocene amber from the Idaburn Coal Mine (Oturehua Seam lignite) matches this profile: the palaeoenvironmental reconstruction has the resinous trees situated within swampy forests, on a flood plain at the edge of a developing lake (Seyfullah *et al.*, 2015). Other New Zealand deposits may be allochthonous and need further investigation.

To date, a unique example of *in situ* (autochthonous) deposition is the Carnian amber from the Dolomites, which is found embedded in palaeosols (unlike the majority of Carnian amber). These amber-bearing palaeosols (*ca.* 2–5% of the palaeosol comprises amber droplets 3–6 mm in length: Schmidt *et al.*, 2012) are found within the Heiligkreuz Formation, a succession deposited in a deltaic to coastal environment, and are characterised by the presence of well-developed histic horizons (levels of water-saturated organic matter) and iron-illuviation (spodic) horizons or ironstones (Breda *et al.*, 2009). These features suggest that the palaeosols developed in a tropical humid climate (Köppen's A class) with a short or absent dry season (Breda *et al.*, 2009).

VII. THE FUTURE OF FOSSIL RESIN RESEARCH

(1) Resin exudation reasons today

Testing whether different resin exudation reasons today have separate chemical fingerprints that are observable (e.g. carbon stable isotopes) may allow us to examine the same traces in ambers. This work is currently underway (e.g. Dal Corso *et al.*, 2017). Linking of these signals to molecular signalling pathways in plants would be the next step. The exact internal signals that trigger resin production in plants

Fig. 13. Accumulations of resin in forests. (A) Resin outpourings on maturing cones of *Pinus lambertiana* in the Sierra Nevada, California. (B) Resin stalactite composed of successive layers, dropped from the canopy of *Agathis lanceolata* in the Parc Provincial de la Rivière Bleue, New Caledonia. (C) Small resin flows from a trunk of *Pseudotsuga menziesii* in British Columbia, Canada. (D) Resin 'balls' persisting on the soil surface of a dry maquis minier, deriving from an already decomposed tree of *Agathis ovata*. (E) *Araucaria columnaris* resin dropping directly on the leaf litter, Maré, New Caledonia. (F) *Agathis ovata* resin degrading at the leaf litter horizon, Yaté, New Caledonia. (G) *Agathis lanceolata* root resin protected from degradation by the root and soil around it, Parc Provincial de la Rivière Bleue, New Caledonia. (H) Freshly exposed *Agathis lanceolata* resin preserved in the soil of a humid primary forest, Parc Provincial de la Rivière Bleue, New Caledonia.

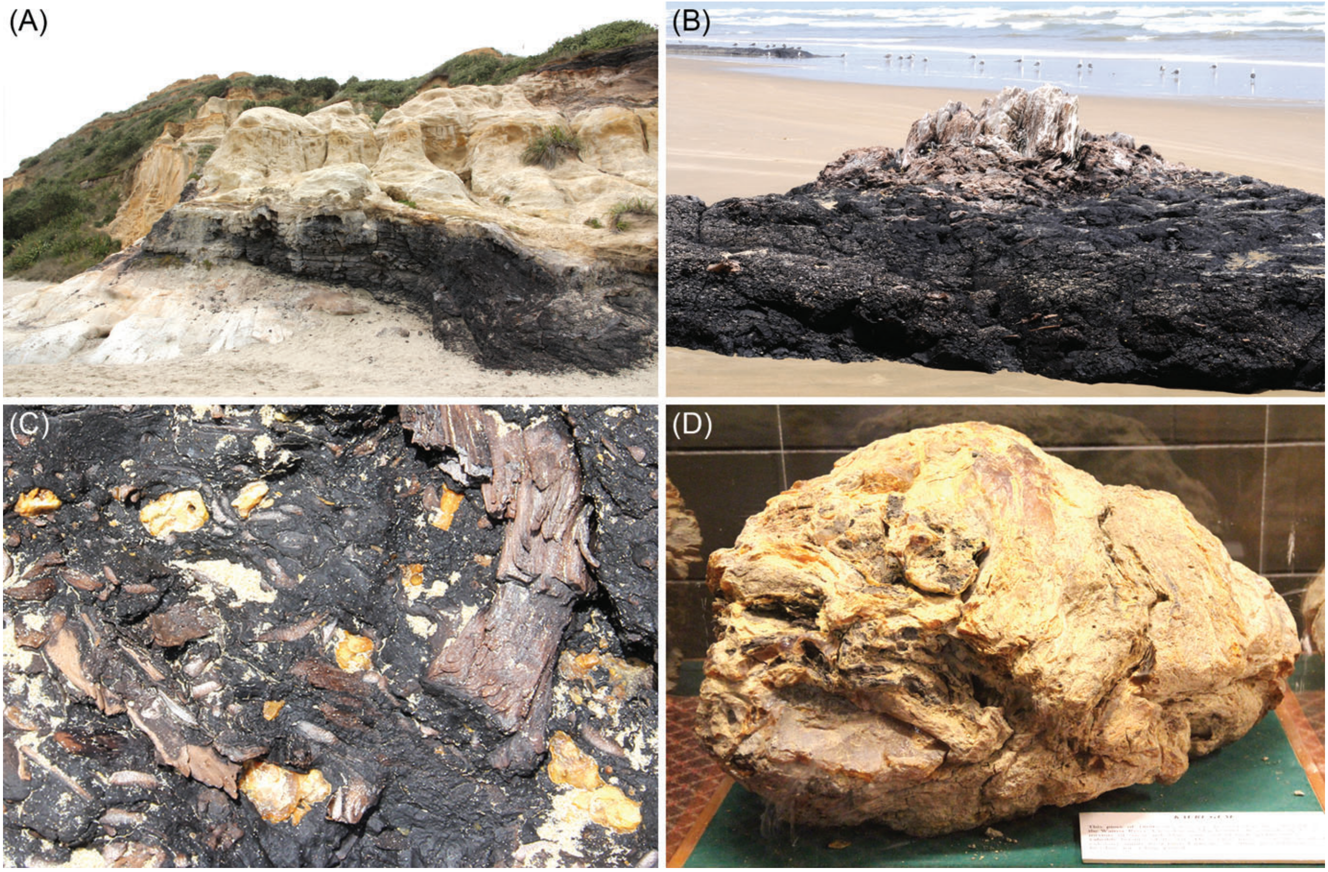

Fig. 14. Autochthonous subfossil resin and its transport to the sea (allochthonous deposition) in northern New Zealand. (A) *Agathis australis* swamp buried in sands, exposed as lignites by erosion at Baylys Beach near Dargaville. (B) Exposed large dark lumps of lignites eroding on beach with a lighter *Agathis australis* stump and roots protruding. (C) Close-up of B showing brown fragments of *Agathis australis*, and golden subfossil resin pieces. (D) An 83.3 kg piece of *Agathis australis* resin (impure) found in the salt mud of Wairoa River, Clevedon, now in the Kauri Museum, Matakohe, New Zealand.

(whether *de novo* production or lysis of resinous bodies) are also not yet clear.

(2) Resin survival in the ecosystem and early burial

Only a subset of conifer (e.g. araucarian; particularly *Agathis autralis*) and angiosperm (e.g. *Hymenaea, Copaifera,* dipterocarps) resins have been observed (see Langenheim, 2003). Little is known about their durability and the preservation potential of resins in their ecosystems.

(3) Further work on resin polymerisation and maturation

The exposure of resin to the atmosphere on exudation starts the polymerisation process, through the initial loss of volatiles (e.g. Lyons *et al.*, 2009; Ragazzi & Schmidt, 2011), but exactly which volatiles and when they are lost is not always clear. Occasionally volatiles are detected preserved in ambers (see Dutta *et al.*, 2017; McCoy *et al.*, 2017).

The process and controls of resin polymerisation and maturation across different amber chemistries is not well understood. Further experimental work (see Hautevelle *et al.*, 2006; Lu, Hautevelle & Michels, 2013) on maturation would help us understand chemical changes within the resin (and any fossils trapped within it), but also confirm what molecular compositions are unaffected by the maturation process and any weathering. This would aid us in understanding the original environment and perhaps why that resin was exuded.

(4) Identifying and filling 'amber gaps'

An obvious gap appears when looking at amber deposits through time (Table 1), is from the Triassic (post-Carnian) and during the Jurassic Period, with only the mid-late Jurassic Thailand amber (Philippe *et al.*, 2005), and the late Jurassic Lebanese amber (Nohra *et al.*, 2013) known. Philippe *et al.* (2005) suggest a geological or taphonomic (preservation) bias in the rock record, particularly for the early-mid Jurassic 'amber gap'. Fig. 1 highlights this gap as well as the Maastrichtian–Paleocene, and the early Oligocene 'amber gaps'.

Another noticeable gap is the 'collections gap': there are only a few small deposits recorded particularly from (*i*) the

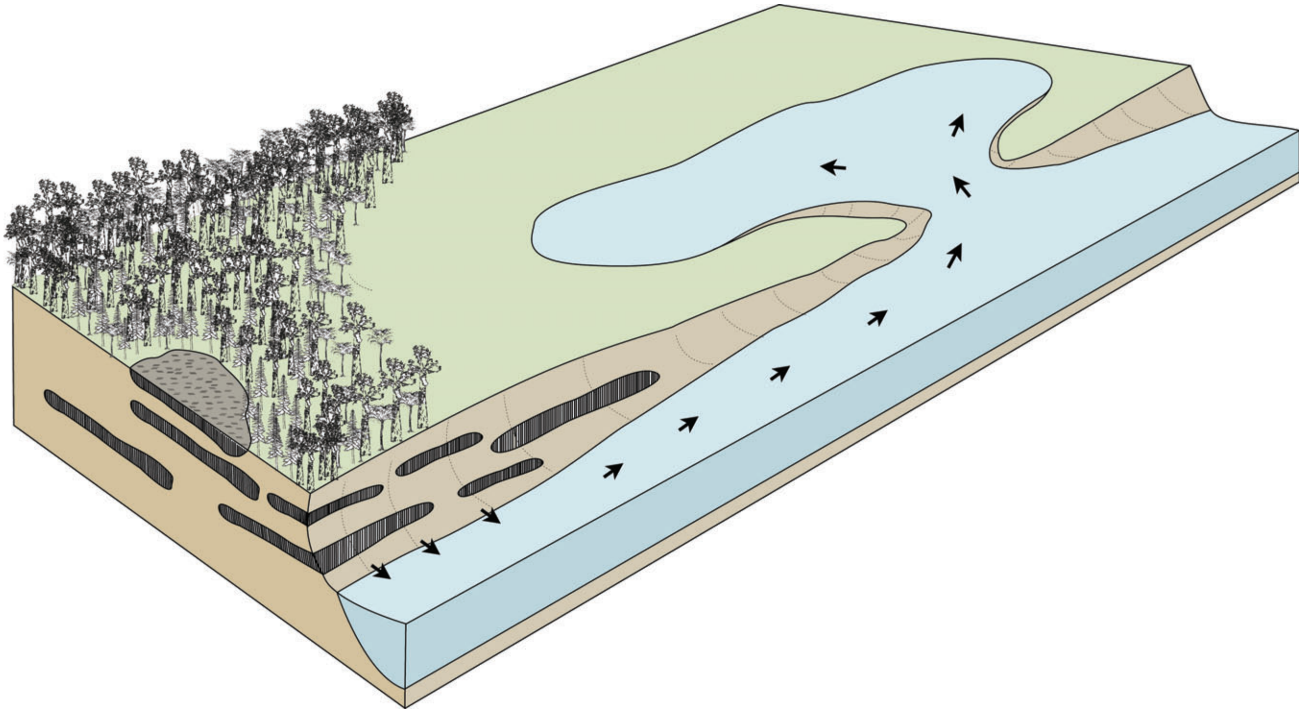

Fig. 15. Reconstruction of resin deposition scenarios in northern New Zealand leading to the mixture of autochthonous, parautochthonous and allochthonous subfossil resin deposits. Resin is deposited in forest soils and/or is washed into swamps (see Fig. 8). Buried swamps can become the source of amber-bearing lignites. These may be exposed at the coast (such as at Baylys Beach, see Fig. 14A–C) and become reworked, then redeposited in a deltaic or perhaps a lagoonal setting (see Fig. 14D). Arrows indicate the journey of the resin after erosion from the cliffs into the sea.

Gondwanan areas, and from (*ii*) China and other large parts of Asia, which is surprising given their size. The Gondwanan landmasses do have some, mostly small, deposits and more have been recently recognised (Table 4). In China there are the significant lower Eocene fossiliferous Fushun amber (Wang *et al.*, 2014), middle Miocene Zhangpu amber, and small Cretaceous and middle to upper Eocene deposits (Martínez-Delclòs *et al.*, 2004; Shi *et al.*, 2014; Wang, 2016).

(5) Clarifying amber depositional environments and ages

A major objective is to clarify the depositional environments for the recent discoveries, particularly those in the Southern Hemisphere. This will allow us to see whether the hypothesised swampy forest in a coastal-lagoonal setting is key for the preservation of amber in autochthonous or parautochthonous deposits, or if this is just where the amber is transported to and concentrated. Detailed sedimentological and palaeobotanical studies would help clarify this problem. This is also linked to one of the problems for some deposits – dating. Many deposits are poorly age-constrained and this means that we cannot be clear on how much time is represented by a deposit, nor where it fits chronologically. To overcome this, fuller understanding of the embedding sediments is really needed. Understanding entrapped fossils could also give an internal date for amber, which can be useful in understanding whether the amber has been reworked or not. Even for some of the most famous fossiliferous ambers, such as the Baltic and Burmese, work remains on identifying further entrapped organisms that may be helpful in dating the deposits.

(6) Ongoing research into the botanical affinities of ambers

An ongoing objective remains trying to understand the botanical affinities of ambers, using the available palaeobotanical evidence and chemical techniques [e.g. micro-FTIR (Tappert *et al.*, 2011); Time-of-Flight secondary ion mass spectrometry (ToF-SIMS) (Sodhi *et al.*, 2013)] to validate the proposed source plants. In cases where amber is not found *in situ*, this can be difficult, but with advances in understanding amber chemistry and the effects that maturation has, even these ambers might be determinable to perhaps the family level eventually.

VIII. CONCLUSIONS

(1) The study of amber is highly relevant today, not just for the fossils it can contain, but also for the potential wealth of palaeoenvironmental information that the amber chemistry may have encoded.

(2) The recent explosion in amber locality numbers worldwide highlights the fact that amber is neither as rare

Table 4. Recently discovered 'Gondwanan' amber deposits

Country	Age/Rock unit	Reference
Argentina	Eocene	Martínez-Delclòs *et al.* (2004)
	Eocene fossil *Agathis* with amber inside the tissues	Wilf *et al.* (2014)
Australia	Latrobe Valley Coal Mio-Pliocene	Lambert *et al.* (1993); Lyons *et al.* (2009)
	Cape York (post-Jurassic, pre-late Miocene)	Murray *et al.* (1994); Hand *et al.* (2010)
	Late Cretaceous Otway amber	Quinney *et al.* (2015)
Brazil	Miocene of Pará	Martínez-Delclòs *et al.* (2004)
	Early Cretaceous (Crato Formation of Araripe)	Martill *et al.* (2005)
Congo	Early Cretaceous (middle Aptian)	Perrichot *et al.* (2016)
Ethiopia	Early Miocene	Schmidt *et al.* (2010); Perrichot *et al.* (2016)
India	Eocene	Rust *et al.* (2010)
New Zealand	Eocene, Oligocene and Miocene ambers in coals	Thomas (1969); Lambert *et al.* (1993); Lyons *et al.* (2009); Seyfullah *et al.* (2015); Schmidt *et al.* (2018)
Peru	Middle Miocene	Antoine *et al.* (2006)
South Africa	Early Cretaceous	Gomez *et al.* (2002)

geographically, nor as temporally restricted as was once assumed. There are also potential 'bursts' of apparent synchronous amber deposition in the rock record, that may potentially imply linking causative factors across some of these deposits.

(3) Modern resin studies are vital in understanding why resins are exuded, with further work ongoing (particularly on chemical characterisation) to look for stress signals.

(4) Survival of resins in their ecosystem prior to burial, and early preservational factors are currently poorly known in most cases.

(5) The causes behind the formation of amber deposits are still debatable, particularly how transport and water influence them. The exact processes of maturation are not known for most amber chemistries.

(6) Gaps in the amber fossil record, in understanding the depositional environments and the source plants of ambers are being closed.

(7) Understanding the relationship between resin and amber and how they can survive though geological time helps us understand the (palaeo)ecosystem from which they derive.

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