

AMBER DROPLETS IN THE SOUTHERN ALPS (NE ITALY): A LINK BETWEEN THEIR OCCURRENCES AND MAIN HUMID EPISODES IN THE TRIASSIC

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Associate Editor: Giovanni Muttoni.

To cite this article: Forte G., Kustatscher E., Ragazzi E. & Roghi G. (2022) - Amber droplets in the Southern Alps (NE Italy): a link between their occurrences and main humid episodes in the Triassic. *Riv. It. Paleontol. Strat.*, 128(1): 105-127.

Keywords: Anisian; Pelsonian; fossil resin; conifers; *Voltzia recubariensis*; Norian amber.

Abstract. The Anisian amber from the “*Voltzia* beds” of the Recoaro area, produced by *Voltzia recubariensis*, represents the most ancient Triassic amber known so far. The discovery of amber in the Anisian localities of Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres, in the Dolomites area, fills a gap in the amber fossil record and contributes to the knowledge of Triassic amber. The finding of amber droplets, both dispersed in the sediment and anatomically connected to shoot fragments of *V. recubariensis*, demonstrates that during the Anisian this species was a resin-producer and that the favorable conditions for the preservation of resin and plant remains were present at regional scale. The contribution of *Voltzia* to Middle Triassic resin production in Northern Italy is also testified by the Ladinian amber from the “Wengener Schichten” of Wengen Formation, produced by *Voltzia ladinica*, whereas the Upper Triassic amber from Heiligkreuz Formation was mainly produced by cheirolepidiaceae conifers. The finding of an unidentified inclusion in the amber of Kühwiesenkopf/Monte Prà dalla Vacca is noteworthy, although difficult to interpret, and shows once again its capability to entrap and preserve witnesses of past life. Moreover, the correspondence between the Triassic amber occurrences and regional/global scale humid shifts, suggests a cause-and-effect relationship, in which the rise of amber production/preservation potential is related to climate/environmental changes, particularly in marginal marine/coastal environments.

INTRODUCTION

Triassic climate

The Triassic period was characterized by major climate oscillations. The greenhouse conditions were interrupted by significant humid episodes (e.g., Hallam 1985; Simms & Ruffell 1989, 1990; Parrish 1993; Mutti & Weissert 1995; Simms et al. 1995; Ahlberg et al. 2002, 2003; Galfetti et al. 2007;

Berra et al. 2010; Hochuli & Vigran 2010; Kustatscher et al. 2010a; Preto et al. 2010; Stefani et al. 2010; Dal Corso et al. 2012, 2015, 2018; Fig. 1). At the onset of the Triassic the exposed lands were assembled into the Pangea supercontinent (e.g., Ziegler et al. 1983, 2003; Miller & Baranyi 2021). This continental configuration played a critical role in determining terrestrial climatic conditions in the Triassic. The concentration of the exposed landmasses at mid- and low-latitudes combined with presence of a warm seaway as source of moisture,

Received: April 01, 2021; accepted: September 07, 2021

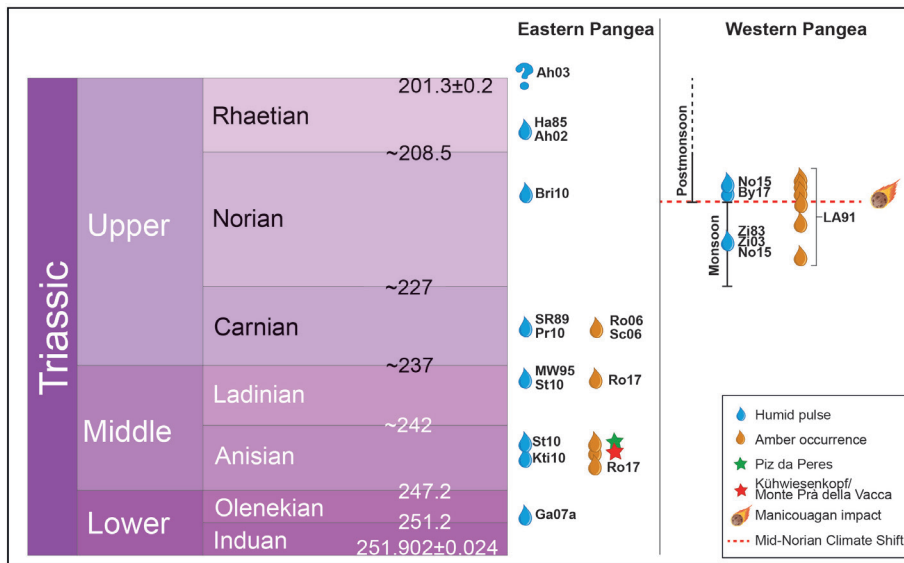


Fig. 1 - Synthesis of the most relevant humid episodes during the Triassic (modified from Preto et al. 2010). The stars in different colors indicate the new amber localities described in this paper, respectively Kühwiesenkopf/Monte Prà della Vacca in red and Piz da Peres in green. Legend of referring literature in figure: Ah02: Ahlberg et al. 2002; Ah03: Ahlberg et al. 2003; Bri10: Berra et al. 2010; By17: Baranyi et al. 2017; Ga07: Galfetti et al. 2007a; Ha85: Hallam 1985; Kti10: Kustatscher et al. 2010; LA: Litwin & Ash 1991; MW95: Mutti & Weissert 1995; No15: Nordt et al. 2015; Pri10: Preto et al. 2010; Ro06: Roghi et al. 2006; Ro17: Roghi et al. 17; Sc06: Schmidt et al. 2006; SR89: Simms & Ruffell 1989; St10: Stefani et al. 2010; Zi83: Ziegler et al. 1983; Zi03: Ziegler et al. 2003.

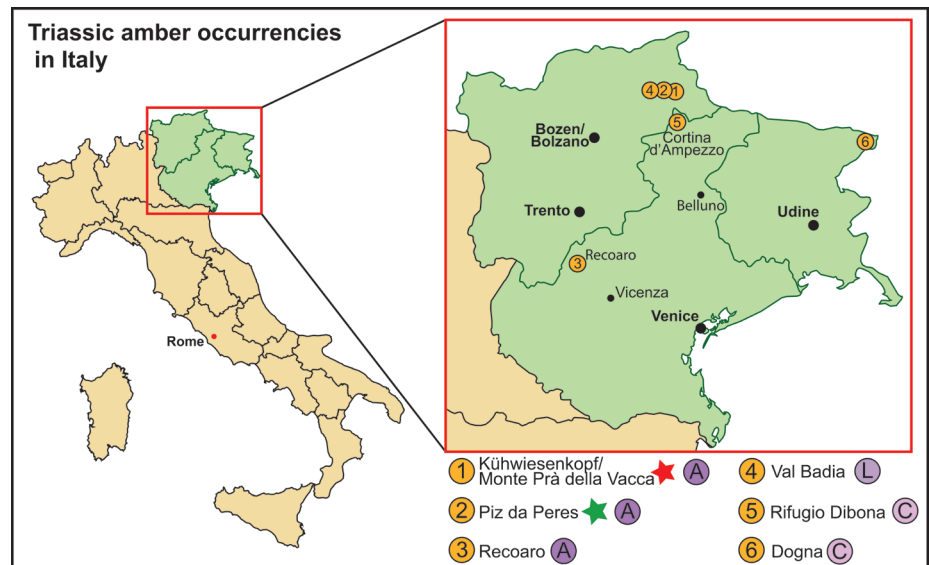
resulted in a megamonsoonal regime (e.g., Ziegler et al. 1983, 2003; Parrish 1993; Preto et al. 2010; Miller & Baranyi 2021). Several humid episodes were indeed recorded during the Triassic (e.g., Preto et al. 2010) starting from the Smithian (Campil) Event (Olenekian, Early Triassic; e.g., Galfetti et al. 2007; Stefani et al. 2010; Zhang et al. 2019; Fig. 1). In the Middle Triassic, the Bithynian–Pelsonian (Anisian) humid pulse (e.g., Brugman 1986; Breda et al. 2009; Kustatscher et al. 2010a; Stefani et al. 2010) and the late Ladinian humid pulses (Mutti & Weissert 1995; Fig. 1) were recorded from several areas (e.g., Köppen & Wegener 1924; Grodzicka-Szymanko & Orłowska-Kwolińska 1972; Szulc 1999; Kustatscher & Van Konijnenburg-van Cittert 2005; Hounslow & Ruffell 2006). In the Late Triassic, the best-known humid episode is the Carnian Pluvial Episode (CPE, 234–232 Ma; e.g., Simms & Ruffell 1989; Gianolla et al. 1998b; Roghi et al. 2006b; 2010; Preto et al. 2010; Dal Corso et al. 2012, 2015, 2018; Fig. 1), which triggered an important biological crisis and the resulting radiation of several modern groups of plants and animals (Dal Corso et al. 2020), although further humid episodes were recorded during the late Norian and early Rhaetian (e.g., Hallam 1985; Ahlberg et al. 2002; Berra et al. 2010; Nordt et al. 2015; Trotter et al. 2015; Fig. 1). This general picture shows how the Triassic climate was more complex

than previously known. New data about the Triassic climate are essential for a better understanding of the palaeoecosystems and provide accurate palaeo-reconstructions.

Triassic amber of Italy

So far, the amber fossil record dates back to the Paleozoic (ca. 320 Mya; Van Bergen et al. 1995; Bray & Anderson 2009) and was traditionally considered poor and very patchy. However, in the last decades, the renewing and increasing interest in amber and the discovery of new amber-bearing localities, gave us new insight, filling little by little the amber fossil record (Seyfullah et al. 2018a). The renewed interest is not just about the amber as a time capsule able to envelope and trap pieces of past life, but also about palaeoenvironmental, palaeoecological and palaeoclimate information that amber encompasses (Dal Corso et al. 2017). We know from the extant plants that many causes induce the production of resin (e.g., diseases, infestations, ecological disasters and environmental changes) and climate change can be one of these (e.g., Conwentz 1980; Gianolla et al. 1998b; Langenheim 2003; Wolfe et al. 2009; Seyfullah et al. 2018a). Most of the Italian Triassic amber comes from Carnian sediments of the Heiligkreuz (e.g., Rifugio Dibona, Rumerlo, Dolomites; Figs. 2, 3) and the Tor formations (Dogna,

Fig. 2 - Geographic location of the Triassic amber localities in northeastern Italy. The stars indicate the new Anisian amber localities. Encircled letters indicate Anisian (A), Ladinian (L) and Carnian (C) localities.



Julian Alps; e.g., Koken 1913; Zardini 1973; Wendt & Fürsich 1980; Gianolla et al. 1998a; 1998b; Roghi et al. 2002a, 2002b, 2006a, 2013; Preto & Hinnov 2003; Preto et al. 2005; Schmidt et al. 2006; Caggiati et al. 2018, 2019; Dalla Vecchia 2020; Figs. 2, 3). The Carnian amber from the Dolomites is the oldest major amber occurrence (latest Julian, late Carnian, ca. 233 Mya; Dal Corso et al. 2020) known so far in the world and is considered unique for its abundance and the presence of inclusions (e.g., Gianolla et al. 1998b; Csillag & Földvári 2005; Roghi et al. 2006b, 2010; Schmidt et al. 2006; Sidorchuk et al. 2015; Fischer et al. 2017; Baranyi et al. 2019). Its production is attributed to the family Cheirolepidiaceae and other stressed conifers (e.g., Roghi et al. 2006b, 2017; Dal Corso et al. 2011; Schmidt et al. 2012; Seyfullah et al. 2018b). Amber drops, found in association with voltzialean conifers, come also from the Anisian (lower Middle Triassic) and upper Ladinian (upper Middle Triassic) of northern Italy (Roghi et al. 2017; Kustatscher et al. 2019; Fig. 2).

A case of serendipity led to the discovery of two new Italian amber localities (Fig. 3). During the detailed study of conifer shoots from Pelsonian Kühwiesenkopf/Monte Prà della Vacca flora (northern Dolomites; Forte et al. 2021; Figs. 2, 3), several tiny amber droplets and fragments were detected, both dispersed in the sediment and associated with conifer shoots of *Voltzia recubariensis*. This led us to the reappraisal of other specimens from the almost coeval (lower Illyrian, Anisian) and geographically close fossiliferous locality of Piz da Peres (Figs. 2, 3), and to the discovery of addition-

al amber droplets dispersed in the sediment and in anatomical connection with shoot fragments of *Voltzia recubariensis*. The aim of this paper is to provide new amber records and to correlate the various amber findings of the Southern Alps with the climate shifts described so far for the Triassic. This is particularly interesting since the climate change can be one of the causes that induce the production of resin and its accumulation, favoring its preservation in the fossil record (e.g., Conwentz 1980; Grimaldi 1996; Gianolla et al. 1998b; Langenheim 2003; Seyfullah et al. 2018a, 2018b).

GEOLOGICAL SETTING

Kühwiesenkopf/Monte Prà della Vacca

The Anisian Kühwiesenkopf/Monte Prà della Vacca (Northern Dolomites, Bozen/Bolzano Province, NE Italy; Fig. 2) is considered a *Fossilagerstätte* (e.g., Tintori et al. 2001, 2016; Broglio Loriga et al. 2002; Posenato et al. 2004; Kustatscher et al. 2006, 2010a, 2010b; Van Konijnenburg-van Cittert et al. 2006). Plant fossils from this area have been known since 1970, when Bechstädt & Brandner reported the presence of a rich fossiliferous bed (Bechstädt & Brandner 1970). Plant debris occur along the section of Kühwiesenkopf/Monte Prà della Vacca; however, the main plant bed crops out about 75 m above the base of the Dont Formation (Fig. 4), which consists of a hemipelagic carbonate-terrigenous interval deposited in a marginal marine environment (e.g., Delfrati et al. 2000; Tin-

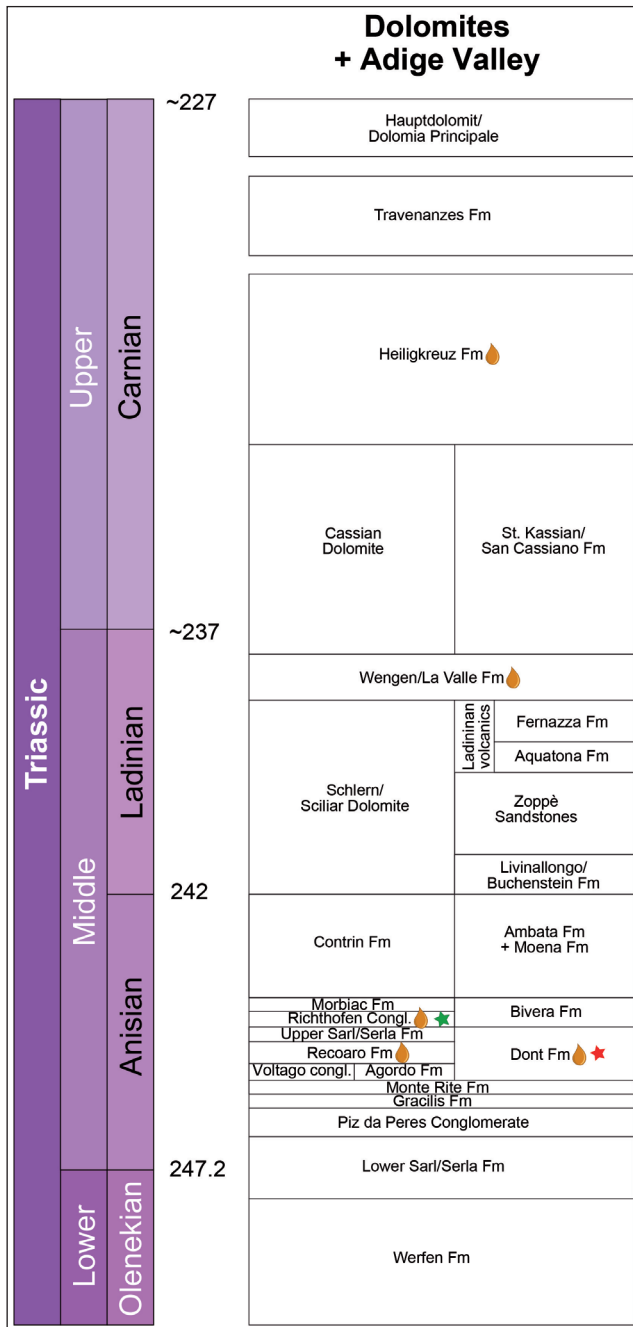


Fig. 3 - Chronostratigraphic record of Triassic amber from northern Italy (orange drops). The red and green stars indicate the new Anisian amber localities, respectively Kühwiesenkopf/Monte Prà della Vacca (Dont Formation) and Piz da Peres (Richthofen Conglomerate).

tori et al. 2001; Broglio Loriga et al. 2002; Fig. 4) during the Pelsonian (e.g., Fugagnoli & Posenato 2004; Kustatscher & Roghi 2006; Kustatscher et al. 2006). The plant fossiliferous level is ca. 1 m thick (Fig. 4) and represents a rapid burial event caused by submarine flows within a marine basin, triggered by heavy storm events in the terrestrial domain (e.g., Tintori et al. 2001; Broglio Loriga et al. 2002; Van

Konijnenburg-van Cittert et al. 2006). The fossil assemblage is very rich in marine biota, including brachiopods, bivalves, fishes, and ammonoids (e.g., Tintori et al. 2001, 2016; Broglio Loriga et al. 2002; Posenato et al. 2004; Renesto & Kustatscher 2019; Fig. 4). Moreover, it is famous for its very rich and diverse plant fossil assemblage (e.g., Van Konijnenburg-van Cittert et al. 2006; Kustatscher et al. 2006, 2007, 2010a, 2010b, 2019) and for the small reptile *Megachirella wachtleri* Renesto et Posenato, 2003 (Fig. 4), which is considered the oldest known squamate (Renesto & Posenato 2003; Renesto & Bernardi 2014; Simões et al. 2018a, 2018b).

Piz da Peres

The stratigraphic succession of Piz da Peres (Northern Dolomites, Bozen/Bolzano Province, NE Italy; Fig. 4) is well-known since the 20th century for its expanded Anisian stratigraphic succession and its rich fossiliferous content (e.g., Abel 1926; Pia 1937; Bechstädt & Brandner 1970; Brandner 1973; De Zanche et al. 1992; Senowbari-Daryan et al. 1993; Zaninetti et al. 1994). Plant fossils come from the Richthofen Conglomerate (Fig. 4), Illyrian in age (e.g., De Zanche et al. 1992; Delfrati & Farabegoli 2000; Avanzini et al. 2007; Gianolla et al. 2018). The Richthofen Conglomerate mainly consists of red sandstones and siltstones and subordinatedly of conglomerate beds, which reflect fluvial to transitional marine depositional environment in the lower part (e.g., De Zanche et al. 1992, 1993; Avanzini et al. 2007; Todesco et al. 2008; Stefani et al. 2010; Gianolla et al. 2018; Fig. 4). The first descriptions of tetrapod footprints from the area were carried out by Abel (1926). The re-study of the succession revealed a nearshore palaeoecosystem with marine biota (e.g., jellyfish and bivalves), numerous tetrapod tracks, and a rich plant assemblage from the Richthofen Conglomerate (De Zanche et al. 1992, 1993; Todesco et al. 2008; Avanzini & Wachtler 2012; Fig. 4), and a reptile skeleton, putatively assigned to *Eusauropsphargis dalsassoii* Nosotti et Rieppel, 2003, were found from the lower part of the overlying Livinallongo/Buchenstein Fm. (Wotzlanw et al. 2018; Mietto et al. 2020; Renesto et al. 2020; Fig. 4). Plant debris are common in some centimeters-thick lenses of grey/yellow siltstone and marly carbonate siltstone, a few centimeters above the boundary between the Upper Serla Fm. and Richthofen Conglomerate (e.g., Todesco et al. 2008; Figs. 3, 4).

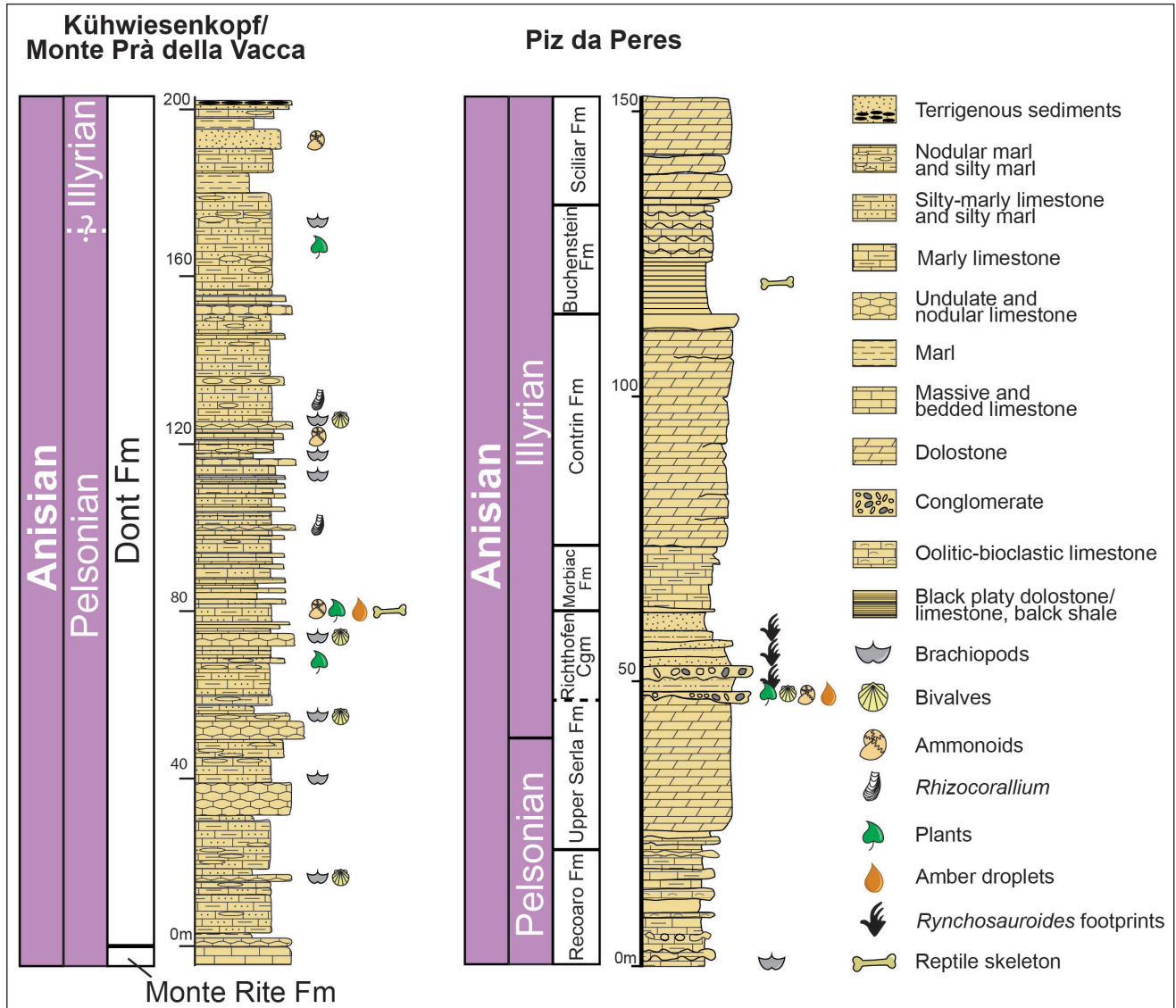


Fig. 4 - Stratigraphic sections of the new amber-bearing localities of Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres (modified from Forte et al. 2021 and Renesto et al. 2020).

MATERIAL AND METHODS

Kühwiesenkopf/Monte Prà della Vacca

The flora of Kühwiesenkopf/Monte Prà della Vacca is rich and very diversified including 37 taxa that belong to lycophytes, sphenophytes, pteridophytes, pteridosperms, cycadophytes, and conifers (e.g., Kustatscher & Roghi 2006; Kustatscher et al. 2006, 2007, 2010a, 2010b, 2019; Van Konijnenburg-van Cittert et al. 2006; Tab. 1). The conifers are the dominant group in the flora and, among them, *Voltzia recubariensis* (De Zigno, 1862) Schenk, 1868, is the commonest species, but also other species of *Voltzia* are identified, such as *Voltzia heterophylla* (Brongniart) Schimper et Mougeot, 1844, *Voltzia walchiaeformis* Fliche, 1910 and *Voltzia edithae* Forte, Kustatscher et Van Konijnenburg-van Cittert, 2021 (Forte et al. 2021). The plant fossils consist of compressions/impressions mainly with organic material preserved. The amber droplets were found both dispersed in the sediment, associated with conifer shoot fragments and, at least in one case, attached to a shoot fragment of *Voltzia recubariensis*. The plant fossils are stored at the Museum of Nature South Tyrol in Bozen/Bolzano, labelled with the prefix “NMS PAL” followed by progressive numbers.

Piz da Peres

The plant fossils from Piz da Peres consist of 20 slabs with plant remains preserved as compressions/impressions. The small amber droplets were found dispersed in the sediments and amber was also found anatomically connected to shoot fragments of *Voltzia recubariensis*. The flora of Piz da Peres includes 14 taxa that belong to sphenophytes, pteridophytes, pteridosperms, cycadophytes, conifers (*Voltzia recubariensis*) and some *incertae sedis* leaves (e.g., Todesco et al. 2008; Kustatscher et al. 2019; Tab. 1). The plant assemblage is dominated by *Voltzia recubariensis*, although *V. edithae* is also present (e.g., Todesco et al. 2008; Kustatscher et al. 2019). Almost all taxa described so far from Piz da Peres are also known from the Kühwiesenkopf/Monte Prà della Vacca flora (e.g., Kustatscher et al. 2019; Tab. 1). Amber was found associated with shoot fragments of *Voltzia recubariensis*, and further amber droplets were found dispersed in the sediment. The specimens were collected during paleontological fieldworks in 2007–2008 (Todesco et al. 2008) and are stored at the Museum of Nature South Tyrol in Bozen/Bolzano, labelled with the prefix “NMS PAL” followed by progressive numbers. Further samples have been collected along the section for palynological

Anisian floras	Kühwiesenkopf/ Monte Prà della Vacca	Piz da Peres	Recoaro	Agordo	Val di Non
Lycophytes					
<i>Isoetes brandneri</i>	x				
<i>Lepacyclotes bechstaedtii</i>	x				
<i>Lycopodium dezanchei</i>	x				
<i>Selaginellites leonardii</i>	x				
Sphenophytes					
<i>Echinostachys</i> sp.	x		x		
<i>Equisetites arenaceus</i>			x		
<i>Equisetites conicus</i>					x
<i>Equisetites mougeotii</i>	x	?			
<i>Equisetites</i> sp.			x	?	
<i>Neocalamites</i> sp.	x				x
Pteridophytes					
<i>Anomopteris mougeotii</i>	x	x		x	
<i>Cladophlebis leuthardii</i>		x			
<i>Cladophlebis remota</i>	x			x	
<i>Cladophlebis</i> sp.	x				
<i>Danaeopsis angustifolia</i>	?	?			
<i>Gordonopteris lorigae</i>	x	x			x
<i>Marattiopsis</i> sp.	?				
<i>Neuropteridium elegans</i>	x	x			x
<i>Neuropteridium grandifolium</i>	x				
<i>Neuropteridium voltzii</i>	x	x		x	
Pteridophyta incertae sedis	x				
<i>Scolopendrites grauvogelii</i>	x				
<i>Scolopendrites scolopendroides</i>	x				
<i>Scolopendrites</i> sp.		x		x	
<i>Sphenopteris schoenleiniana</i>	x				
Pteridopspermophytes					
<i>Peltaspermum bornemannii</i>	x	x			
<i>Peltaspermum</i> sp.				x	
<i>Ptilozamites</i> sp.	?				
<i>Sagenopteris</i> sp.	x				
<i>Scytophyllum bergeri</i>	x	x			
Cycadophytes					
<i>Bjuvia dolomitica</i>	x	x			
<i>Dioonitocarpidium</i> sp.	x	x			x
<i>Nilssonia</i> sp.	x				
Coniferophytes					
<i>*Aethophyllum foetterlianum</i>			x		
<i>Albertia latifolia</i>	x				
<i>Albertia</i> sp.			x	x	
<i>*Araucarites agordicus</i>			x		
<i>*Araucarites albuctenoides</i>			x		
<i>*Araucarites massalongii</i>			x		
<i>*Araucarites pachyphyllus</i>			x		
<i>Pagiophyllum</i> sp.			x		
<i>Pelourdea vogesiaca</i>	x				
<i>*Taxites massalongii</i>			x		
<i>*Taxites vicentinus</i>			x		
<i>*Taxodites saxolimbiae</i>			x		
<i>Voltzia edithae</i>	x				
<i>Voltzia heterophylla</i>	x		x		
<i>Voltzia recubariensis</i>	x	x	x	x	x
<i>Voltzia walchiaeformis</i>	x				?
<i>Voltzia</i> sp.	x		x	x	
Incertae sedis					
<i>Carpolithes</i> sp.	x				
<i>Lugardonia paradoxa</i>	x				
<i>Taeniopteris</i> sp.	x	x		x	

Tab. 1 - Taxa occurrences in three Italian Anisian floras were *Voltzia recubariensis* is present. Taxa marked with * need revision. Updated after Forte et al. 2021.

analyses. The analysis of these samples revealed the occurrence of amber droplets. The small amount of amber found in the Piz da Peres specimens is unfortunately insufficient for any physico-chemical analyses able to produce a characterization of this amber. Moreover, the reduced size of droplets did not allow any investigation about possible amber inclusions.

The specimens from Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres were studied under visible and UV light (365 nm). The latter allowed to detect the occurrence of thin amber layers on plant remains, and small droplets dispersed in the sediment. All specimens were also photographed with a digital reflex camera (Canon EOS D550). Specimens bearing amber were also photographed un-

der UV light with a digital camera (Sony A7r III) at the Department of Geosciences of the University of Padova. Amber droplets were studied under a dissecting stereomicroscope (Olympus SZ40). The droplet fragment from NMS PAL508b and its micro-inclusions were studied under a LEICA DM2500 LED microscope and photographed with a LEICA DMC4500 camera. The photographs were adjusted with LAS4.8[®] software, and all the specimens were measured digitally by using ImageJ64[®] software (National Institute of Health, Bethesda, MD).

RESULTS

Amber from Kühwiesenkopf/Monte Prà della Vacca

Dispersed amber droplets. Thirty-six amber droplets and fragments were identified in the Kühwiesenkopf/Monte Prà della Vacca collection. Amber mainly occurs dispersed in the sediment forming droplets, and sometimes occurs spread on the sediment surface (e.g., NMS PAL508a; Fig. 5H, 5I) or on plant remains (e.g., NMS PAL544, 1325, 2105, 2167; Figs. 5A–C, 6A–C, 6D, 6E, 6F, 6G). Amber droplets that do not exceed 1 mm in diameter are very common, often reaching the same grain size as the sediment, therefore, they are difficult to detect with the naked eye, and their study needs the use of a dissecting microscope and/or the UV light. Amber droplets that exceed 1 mm in diameter are less common. The amber droplets are roundish, elongate to irregular (e.g., NMS PAL508a, 508b, 544, 1318, 1325; Figs. 5E–G, 6A–C, 6H, 6I, 7A, 7B), 0.45–9 mm long and 0.16–4 mm wide (Tab. 2a, b). The color ranges from light yellow–yellow (e.g., NMS PAL508b, 1318; Figs. 6H, 7B; Tab. 2a, b), to orange (e.g., NMS PAL508a, 1318; Figs. 6A, 7A) and brown (e.g., NMS PAL381, 1325; Figs. 5E, 5G; 6A, 6B; Tab. 2a, b). The droplets are often translucent, with resiniferous brilliance (e.g., NMS PAL381, 1318, 1325; Figs. 5E, 5G, 6A, 6B, 6H; Tab. 2a, b), sometimes they also look opaque (e.g., NMS PAL508a, Figs. 5H, 7A; Tab. 2a, b).

An elongate amber droplet was found associated with a fertile frond of *Scolopendrites grauwogelii* (NMS PAL381, 382 part and counterpart; Fig. 5E–G). The droplet is 2.8 mm long and 0.92 mm wide, translucent, brownish in color, with conchoidal fracture, and occurs in the central part of the *S. grauwogelii* specimen (e.g., NMS PAL381; Fig. 5E; Tab. 2a, b), and apparently on the surface of the plant remain. Due to the separation of part and counterpart, amber is preserved in two halves and this allowed us to look at the inner structure of the

droplet (NMS PAL381; Fig. 5G; Tab. 2a, b). The droplet has indeed an external cortex about 60–80 μm thick, indicating a differential drying and hardening of the external than the inner part (NMS PAL381; Fig. 5G; Tab. 2a, b). Well defined and thick external cortex (120–150 μm) is also visible on other dispersed droplets (e.g., NMS PAL1318; Fig. 6H; Tab. 2a, b). The roundish edges of the amber droplets reflect the shape that resin assumes once it is exuded out by the plant and starts to harden (NMS PAL381, 382, 1318; Figs. 5E–G, 6H).

Since UV fluorescence is present in all amber droplets (e.g., NMS PAL381, 508a, 544, 1318, 1325, 2105; Figs. 5C, 5F, 5I, 6C, 6E, 6G, 6I; Tab. 2a, b), the use of the UV light was crucial especially for the identification of droplets that do not exceed 1 mm in diameter, which are very abundant. The main difference observed is the different photoluminescence color of the amber under UV light, which can range from light yellow, to orange, dark orange (Tab. 2a, b), reflecting different composition, probably as a consequence of diagenetic alterations, but also possibly due to different palaeobotanical source.

Amber in association with plant remains. Amber was found in anatomical connection with a conifer shoot fragment of *Voltzia recubariensis* (NMS PAL544; Fig. 5A–C). The shoot fragment is 40 mm long and 10 mm wide, covered by helically arranged leaves that arise with an upper angle of 42–62° and a lower one at 35–60°. The amber, translucent and orange–brownish in color, is spread on the surface of one leaf, covering almost all the proximal leaf surface and partly the leaf base, close to the attachment area to the axis (NMS PAL544; Fig. 5A–C; Tab. 2a, b).

Two small amber droplets were found associated with a branch fragment of *Voltzia recubariensis*, although not connected to the plant remain (NMS PAL2144; Fig. 5D; Tab. 2a, b). The branch fragment, 26 mm long and 9.5 mm wide, is stout, with ultimate shoots arising at 30–40° from the axis (NMS PAL2144; Fig. 5D). The leaves, 5–9 mm long, are preserved in lateral view and are typically coriaceous, helically arranged, and arise from the axis with an upper angle of ca. 90° and a lower one of ca. 45° (NMS PAL2144; Fig. 5D). The amber droplets are respectively 1.5 x 0.3 mm and 0.46 x 0.16 mm, occurring close to the basal part of the main axis (NMS PAL2144; Fig. 5D, white arrows; Tab. 2a, b).

Amber inclusions. An amber fragment was found detached from the rock slab (NMS PAL508a, 508b Figs. 5H, 5I, 7A–D). The amber droplet fragment, 2.30 mm long and 1.7 mm wide (NMS PAL508b; Fig. 7B; Tab. 2a, b), is transparent, light yellow in color and characterized by conchoid fractures well visible along the margins (Fig. 7B). The observation under the microscope revealed the presence of air bubbles trapped in the droplet, with a diameter of 30–35 μm (Fig. 7B), and inclusion of likely organic origin (NMS PAL508b; Fig. 7D). This inclusion (indicated by the black arrow in Fig. 7C) is 20 μm long and 16 μm wide, brownish and appears formed by three roundish segments, roughly resembling a bisaccate pollen grain where the putative body is slightly darker than sacci (Fig. 7D). Further putative organic inclusions were observed (Fig. 7C), however, the presence of many conchoidal fractures and the absence of sharp margins, which characterize the amber inclusions, do not allow us to obtain a clear identification.

Amber from Piz da Peres

Twenty dispersed amber droplets and amber associated to conifer remains come from Piz da Peres (e.g., NMS PAL3337, 3338; Fig. 7E, 7F). On two specimens, amber was found anatomically connected to shoot fragments of *Voltzia recubariensis* (NMS PAL3337; Fig. 7E, 7F; Tab. 2a, b). The first shoot fragment is 23 mm long and 10 mm wide with helically arranged falcate and coriaceous leaves that arise with an upper angle of ca. 60° and a lower one of 35–50° (NMS PAL3337; Fig. 7E). Amber is reddish to brownish in color, translucent, with conchoidal fracture and partly covers the upper side of the leaf lamina and the axis surface (NMS PAL3337; Fig. 7E; Tab. 2a, b). On a second specimen, amber was found associated with a badly preserved conifer shoot fragment, 14 mm long and 9.5 mm wide, also attributable to *Voltzia recubariensis* (NMS PAL3338; Fig. 7F; Tab. 2a, b). Amber is solid, reddish to brownish in color, occurring along the outline of the conifer shoot fragment (NMS PAL3338; Fig. 7F) and being mainly concentrated both between the axis and the leaf base attachment points and over the axis. The dispersed amber droplets are 1–2 mm long and 1 mm wide, roundish to irregular in shape, orange to reddish-brown in color and translucent, with resinous brilliance. Because of their small sizes, the use of a UV lamp was essential

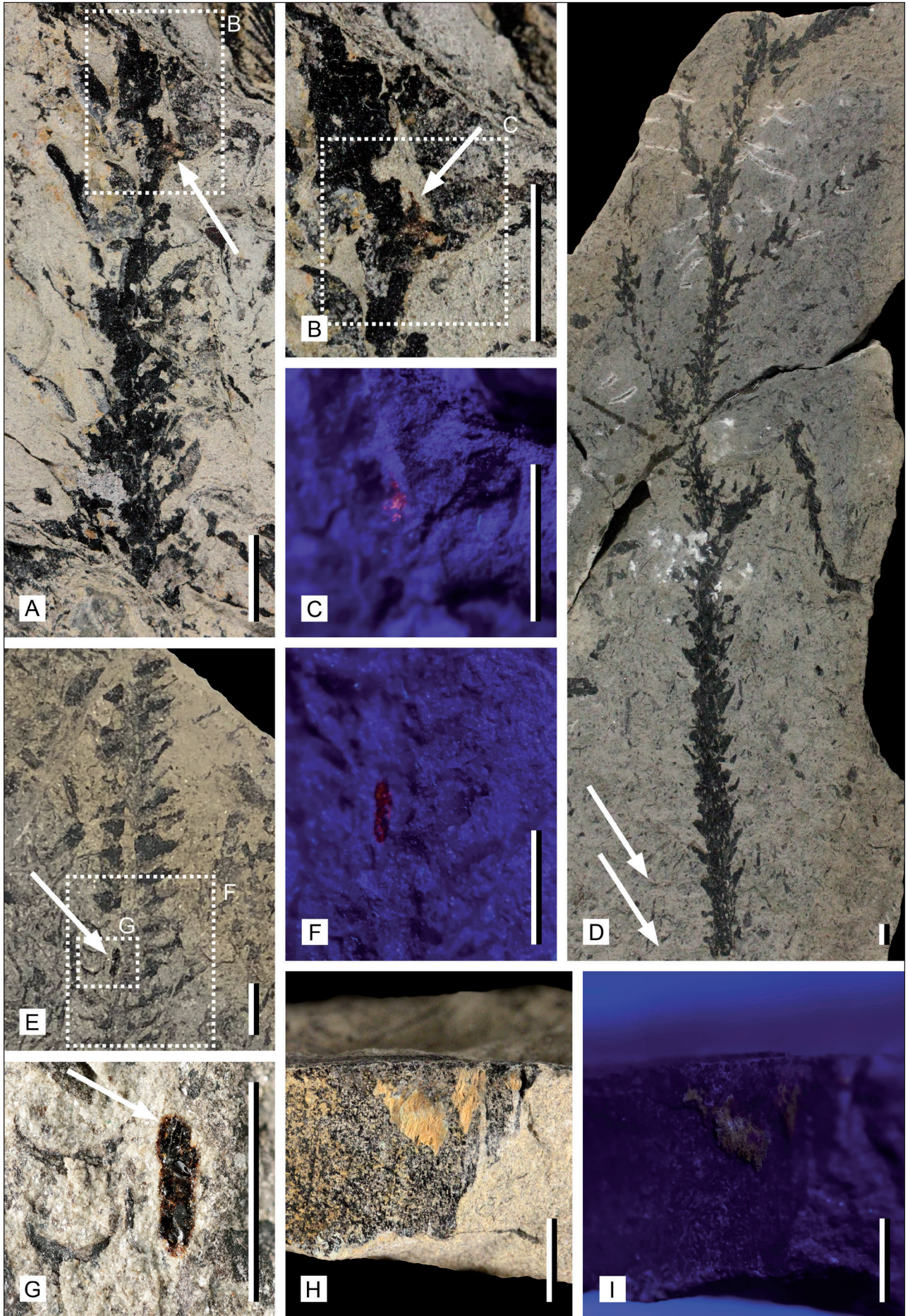
to detect their occurrence. In fact, similarly to the amber from Kühwiesenkopf/Monte Prà della Vacca, the amber from Piz da Peres is characterized by UV fluorescence and samples appear from yellow to orange in color under UV light (Tab. 2a, b).

DISCUSSION

Anisian amber from Southern Alps

The discovery of two new Anisian amber localities is noteworthy for several reasons. Together with the amber from the “*Voltzia* beds” of Recoaro (Roghi et al. 2017), the amber from Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres represent the oldest Triassic (Anisian) amber occurrences known so far. The flora of Kühwiesenkopf/Prà della Vacca (Todesco et al. 2008; Figs. 3, 4) and Recoaro (Roghi et al. 2017; Figs. 3, 4) are almost coeval (Pelsonian), whereas the one of Piz da Peres is slightly younger (Illyrian; e.g., De Zanche et al. 1992; Delfrati & Farabegoli 2000; Avanzini et al. 2007; Gianolla et al. 2018; Figs., 3, 4). The co-occurrence of these ambers in sediments associated with particular climate conditions like the humid pulse reported by some authors (e.g., Brugman 1986; Kustatscher et al. 2010a; Stefani et al. 2010; Fig. 1) might also enclose palaeoenvironment and palaeoclimate meanings.

Fig. 5 - Amber droplets from Kühwiesenkopf/Monte Prà della Vacca. A) Shoot fragment of *Voltzia recubariensis* with amber attached to the leaf (white arrow; NMS PAL544). B) Magnification of the dashed area in figure A showing the amber droplet (NMS PAL544). C) Magnification of the dashed area in figure B, showing the amber under UV light (NMS PAL544). D) Branch fragment of *Voltzia recubariensis* with two tiny dispersed amber droplets (white arrows; NMS PAL2144). E) Specimens of *Scolopendrites graunogelii* with an elongate amber droplet in the central part (white arrows; NMS PAL381). F) Detail of the amber droplet in figure E (dashed area) photographed under UV light (NMS PAL381). G) Magnification of the amber droplet in figure E (small dashed area), showing resiniferous brilliance, conchoidal fractures and an external cortex, indicating the faster drying and hardening of the resin outward than the inner one (NMS PAL381). H) Fossil resin with opaque and fibrous appearance spread on the edge surface of the slab (NMS PAL508a). I) Fluorescence of fossil resin of figure H under UV light (NMS PAL508a). Scale bars = 5 mm.



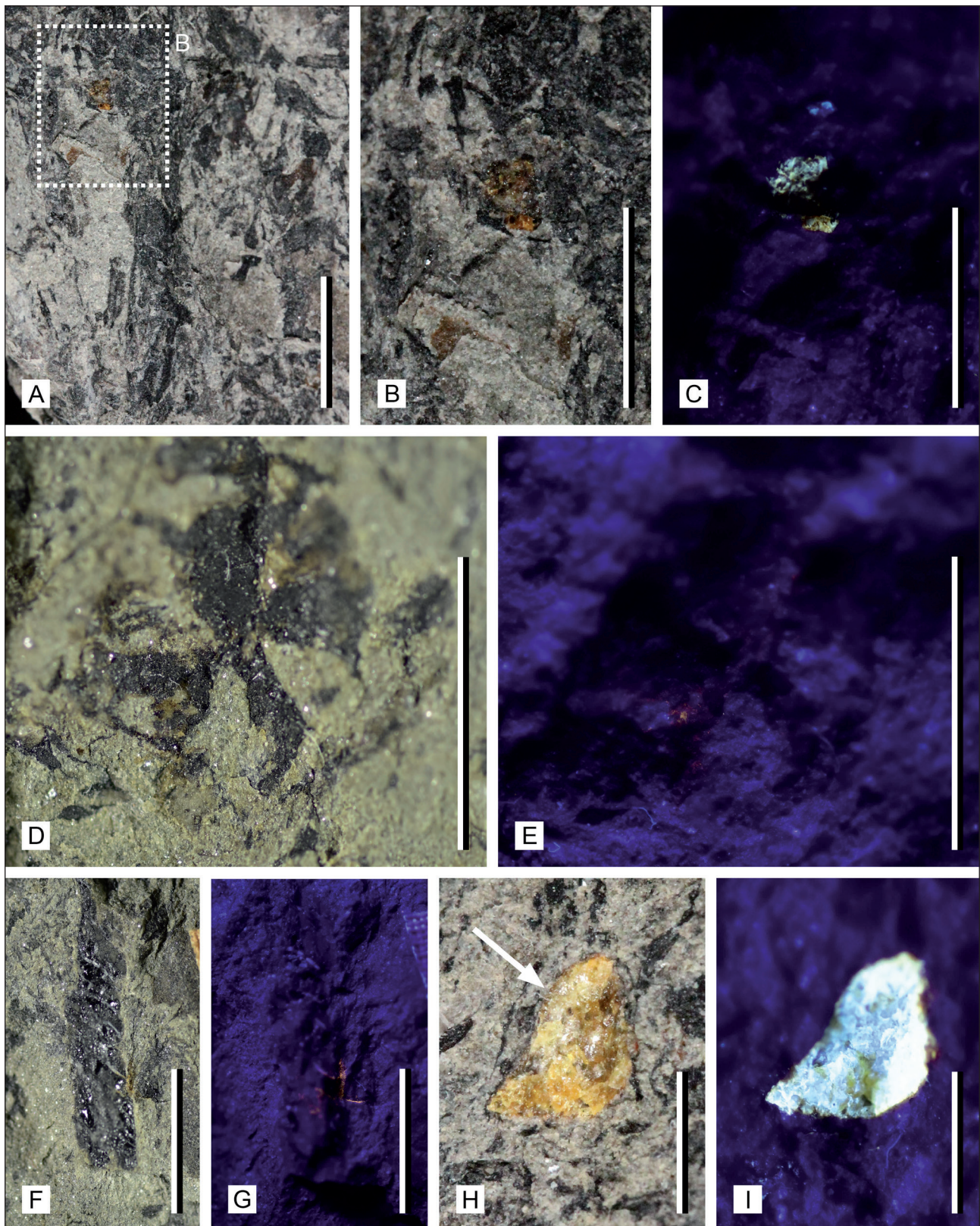


Fig. 6 - Amber droplets from Kühwiesenkopf/Monte Prà della Vacca. A) Dark orange amber droplet associated to a putative conifer shoot fragment (NMS PAL1325). B) Magnification of the dashed area in figure A, showing the translucent amber droplet in detail (NMS PAL1325). C) Detail of amber droplet in figure A and B with yellow to light orange UV fluorescence (NMS PAL1325). D) Amber in association with putative conifer cone in axial view (NMS PAL2105). E) Amber in figure D, showing orange UV fluorescence (NMS PAL2105). F) Light orange amber in association with a putative conifer shoot fragment, occurring partly within the axis and on its surface (NMS PAL2105). Amber in figure G showing dark orange UV fluorescence (NMS PAL2105). H) Yellowish-orange amber droplet with rounded angles, translucent appearance and well visible cortex (white arrow; NMS PAL1318). I) Amber droplet represented in figure H showing light yellow UV fluorescence (NMS PAL1318). Scale bars = 5 mm.

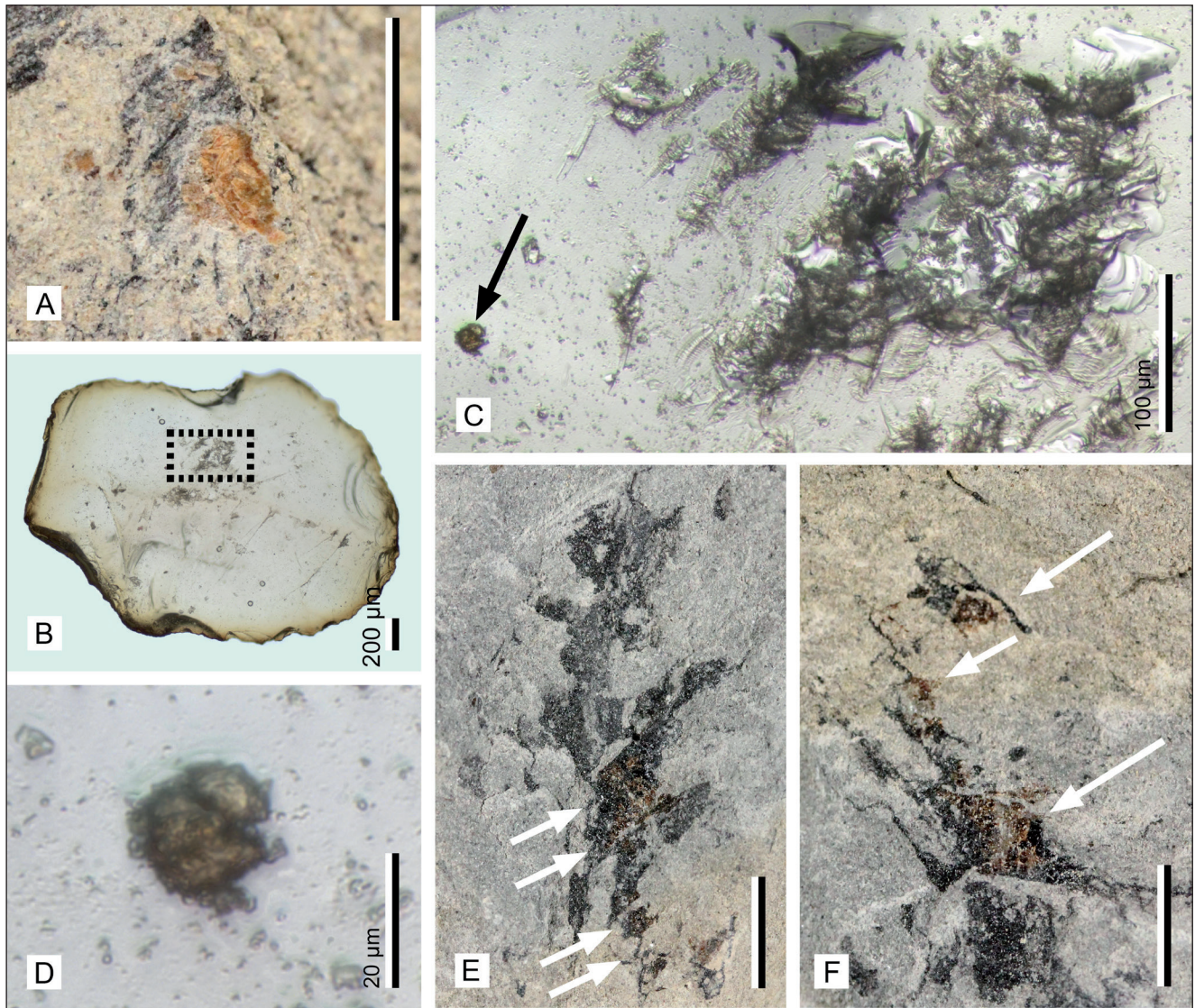


Fig. 7 - Amber droplets and organic inclusion in amber from Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres. A) Amber droplet with opaque appearance (NMS PAL508a). B) Fragment of amber droplet with inclusions, trapped air bubbles and several well-visible conchoid fractures on surface and margins (NMS PAL508b). C) Magnification of the dashed area in figure B showing organic inclusion (black arrow; NMS PAL508b). D) Magnification of the organic inclusion in figure C (NMS PAL508b). E) Solid amber pieces associated with a shoot fragment of *Voltzia recubariensis* from Piz da Peres covering at least two leaf fragments (NMS PAL3337). F) Shoot fragment of badly preserved ultimate shoot of *Voltzia recubariensis* from Piz da Peres with solid amber both concentrated between the leaf bases and the axis, and spread over the axis (NMS PAL3338). Scale bars = 5mm unless otherwise indicated.

The amber from Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres are similar in color, ranging from yellow-orange (e.g., NMS PAL508a, 508b, 544, 1318; Figs. 5A, 5B, 5H, 6H, 7A, 7B; Tab. 2a, b) to reddish-brown, with resiniferous brilliance (e.g., NMS PAL381, 1325, 3337, 3338; Figs. 5E, 5G, 6A, 6B, 7H, 7I; Tab. 2a, b) and comparable with the amber from Recoaro (Roghi et al. 2017). Nonetheless, some specimens from Kühwiesenkopf/Monte Prà della Vacca are sometimes lighter, yellowish and opaque (e.g., NMS PAL508a; Figs. 5H, 7A; Tab. 2a, b) and this can reflect a different diagenesis. Amber

droplets often occur dispersed in the sediments or concentrated between leaves and axis when they are in association with shoot fragments (e.g., NMS PAL544, 2167, 3337, 3338; Figs. 5A–C, 6F, 6G, 7E, 7F; Tab. 2a, b). No compelling evidence of amber within resiniferous channels was found either in the Kühwiesenkopf/Monte Prà della Vacca or in the Piz da Peres specimens, but amber was found spread over the axis (e.g., NMS PAL2167, 3337, 3338; Figs. 6F, 7E, 7F). Inside the amber fragment from Kühwiesenkopf/Monte Prà della Vacca tiny air bubbles and a small putative organic body, roughly resem-

Amber in association with plant remains	Description
NMS PAL544	Translucent amber, yellow to orange in color, found spread on the leaf surface, in a shoot fragment of <i>Voltzia recubariensis</i>
NMS PAL1325	Droplet, 1.5 x 1 mm, dark orange to reddish in color and yellowish UV fluorescence, with rounded edges in association with an indetermined conifer axes
NMS PAL2078	Droplet, 3.2 x 2.6 mm, with roundish shape, yellow to orange in color and with orange fluorescence under UV light. Amber, 1.43 x 0.56 mm, spread on a conifer leaf, appearing light orange and orange respectively under visible and UV lights
NMS PAL2105	Light orange amber, with resiniferous brilliance and orange to dark orange fluorescence under UV light, spread on the surface of a putative female conifer cone
NMS PAL2113	Amber, 2.56 x 2 mm, spread on unidentified plant remains, with dark orange to reddish UV fluorescence
NMS PAL2158	Elongated droplet, 3.2 x 0.9 mm, with evident external cortex, dark orange in color, with resiniferous brilliance and conchoidal fracture, orange to reddish UV fluorescence and found in association with an indetermined conifer shoot fragment
NMS PAL2163	Amber, 1.31 x 0.64 mm, spread on a conifer leaf, light yellow to orange in color respectively under visible and UV light
NMS PAL2167	Amber, 1.7 x 0.55 mm, orange with resiniferous brilliance, with orange UV fluorescence, and in association with a putative conifer axes, close to a leaf base attachment point, in axillary position, and within the axis
NMS PAL3337*	Massive amber, translucent, with resiniferous brilliance, dark orange to reddish in color, in association with a <i>Voltzia recubariensis</i> shoot fragment, mainly concentrated close to the leaf base and partly covering the axis
NMS PAL3338*	Massive amber, dark orange to reddish, translucent with resiniferous brilliance, found in association with a badly preserved <i>Voltzia recubariensis</i> shoot fragment and mainly occurring on the axis and in axillary position, corresponding to the leaf base attachment points

Tab. 2a - List and descriptions of the amber samples from the flora of Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres (*).

bling a pollen grain, were found trapped in the resin (e.g., NMS PAL508b Fig. 7B–D). However, none of the bisaccate pollen detected from Kühwiesenkopf/Monte Prà della Vacca (e.g., Kustatscher 2004; Kustatscher & Roghi 2006) have comparable dimensions with the putative grains in the amber droplet. Further putative organic inclusions were observed (Fig. 7C) but their observation is difficult. Therefore, the origin of the amber inclusions remains unknown.

Although the amber from Kühwiesenkopf/Monte Prà della Vacca is more abundant than the one from Recoaro (only one specimen) and from Piz da Peres (two macro-specimens and <1mm sized droplets; Fig. 7B, 7C), the small size of the droplets did not allow unfortunately any IR spectroscopy analyses to characterize the fossil resin (e.g., according to Beck et al. 1964; Langenheim & Beck 1965) or chemo-systematic assignment by the isolation of biomarkers to evaluate the botanical origin of the dispersed amber (e.g., Otto & Wilde 2001; Otto et al. 2002), nor any geochemical anal-

yses (e.g., Dal Corso et al. 2013, 2017; Tappert et al. 2013), in order to compare the physico-chemical characteristics of the amber from the different localities and to detect possible overlaps of the isotopic ranges between fossil resin and plant producer. Therefore, no comparison has been possible with the IR spectrum of the Carnian amber of the Dolomites and Julian Alps, which presents a peculiar pattern (Ragazzi et al. 2003; Roghi et al. 2006b).

The finding of Anisian amber in association with shoot fragments of *Voltzia recubariensis* both from the “*Voltzia* beds” of Recoaro, Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres, suggests that this species was a resin producer at that time. The findings of *Voltzia* known so far consist of compression/impression fossils and its wood anatomy is still unknown. Therefore, it is not possible to know if the *Voltzia* species had resin-bearing tissue or resin canals. The amber found in association with *Voltzia recubariensis* occurs on the upper

Tab. 2b - List and descriptions of the amber samples from the flora of Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres.

Dispersed amber droplets	
NMS PAL381	Elongated droplet, 2.81 x 0.92 mm, dark orange to reddish, light yellow UV fluorescence, with conchoidal fractures and evident cortex about 60–80 µm thick, occurring overlapping one specimen of <i>Scolopendrites grauvogelii</i>
NMS PAL488	Droplet, 2.4 x 1.12 mm, with resiniferous brilliance, orange to brown in color
NMS PAL505	Three droplets respectively: 1.22 x 0.28 mm, 0.44 x 0.24 mm, and 2.1 x 1.09 mm, with irregular margins, dark orange in color with resiniferous brilliance
NMS PAL508a, b	One droplet 2.26 x 0.93 mm (NMS PAL508a), with rounded edges, yellow in color, with conchoidal fracture and opaque appearance, and amber spread on the edge of rock slab, 8.9 x 3.9 mm (NMS PAL508a), yellow, with opaque and fibrous-like appearance, both samples show dark orange UV fluorescence; dispersed amber droplet fragment, 2.30 x 1.7 mm (NMS PAL508b), transparent, light yellow in color with well visible conchoid fractures along the margins
NMS PAL1318	Droplet, 2.8 x 2.6 mm, with rounded edges, yellow to orange, with resiniferous brilliance, conchoidal structure, well defined cortex about 120–150 µm thick, and with light yellow UV fluorescence
NMS PAL1709	Elongated droplet, 2.66 x 1.13 mm, dark orange to brown in color in visible light and with dark orange UV fluorescence
NMS PAL2078	Droplet 1.43 x 0.56 mm, light yellow, with irregular margins, and yellow to orange UV fluorescence
NMS PAL2093	Droplet with rounded edges, 1.4 x 0.81 mm, orange in color, with resiniferous brilliance and conchoidal fracture, dark orange under UV light
NMS PAL2094	Droplet 0.91 x 0.82 mm, dark orange with resiniferous brilliance and dark orange UV fluorescence
NMS PAL2106	Two droplets, respectively 3.3 x 1.02 mm and 1.5 x 0.9 mm, brownish to orange, with irregular edges, resiniferous brilliance, with orange UV fluorescence
NMS PAL2107	Two droplets respectively 3.07 x 1.82 mm and 0.88 x 0.43 mm, yellow to orange, with resiniferous brilliance and conchoidal fracture, dark orange to light yellow under UV light
NMS PAL2110	Three droplets: 2.15 x 1.8 mm, 1.27 x 0.51 mm, 2 x 0.97 mm with irregular margins, resiniferous brilliance, brownish in color, with orange fluorescence under UV light
NMS PAL2124	Droplet, 2.64 x 2 mm, with irregular margins, resiniferous brilliance, orange to brownish in color, with orange fluorescence under UV light
NMS PAL2144	Two droplets, respectively 1.5 x 0.3 mm and 0.46 x 0.16 mm, orange to brownish, with resiniferous brilliance
NMS PAL2150	Elongate droplet, 3.2 x 0.88 mm, orange to brownish in color with resiniferous brilliance
NMS PAL2163	Two droplets: 0.89 x 0.38 mm, brownish with resiniferous brilliance and irregular margins, with dark orange fluorescence under UV light

side of the leaves, close to the leaf base, in axillary position, and partly on the axis (Roghi et al. 2017; this paper). The amber found in association with *Voltzia ladinica* occurs both on the upper side of the leaves and partly fills the spaces inside the main branches (Roghi et al. 2017). However, no evidence of resiniferous channels was observed.

During Triassic, the genus *Voltzia* was very diversified and particularly during the Anisian (e.g., Forte et al. 2021). *Voltzia recubariensis* is a typical Anisian conifer, restricted to the Southern Alps

area (e.g., Brack & Kustatscher 2013; Forte et al. 2021). This species was previously reported from Recoaro (Massalongo 1857; De Zigno 1862; Schenk 1868; Roghi et al. 2017) and Vallarsa Valley (Selli 1938). Later, it was also reported from Kühwiesenkopf/Monte Prà della Vacca (e.g., Broglio Loriga et al. 2002; Kustatscher 2004; Kustatscher & Roghi 2016; Kustatscher et al. 2010b, 2019), Piz da Peres (e.g., Todesco et al. 2008; Kustatscher et al. 2019), Agordo (San Lucano Valley; e.g., Kustatscher et al. 2011, 2019; Testa et al. 2013), Non Valley (e.g., Kus-

tatscher et al. 2012) and Bagolino (Brack & Kustatscher 2013; Kustatscher et al. 2019). Its occurrence in several floras (Tab. 1) of this area suggests a certain vegetational uniformity (Brack & Kustatscher 2013) in the very complex Anisian palaeogeography of the Southern Alps (Petti et al. 2013).

Anisian floras and depositional environments

The Anisian (Dolomites and Recoaro), Ladinian (Gadertal/Badia Valley) and part of the Carnian (Dolomites and Julian Alps) amber was deposited in marginal marine or coastal sediments (Roghi et al. 2006a, 2017; Figs. 2, 3). The Anisian paleogeographic scenario consisted of emergent land, wide carbonate platforms and deep basins (e.g., Assereto et al. 1977; Farabegoli et al. 1977; Neri et al. 2007; Petti et al. 2013). The presence of wide lands with marginal fluvial environments (Bechstädt & Schweitzer 1991), wide tidal flats and extensive floodplains sometimes interrupted by lagoons (De Zanche et al. 1993) and the onset of the humid Pelsonian climate phase (Brugman 1986; Kustatscher et al. 2010a) favored both the diversification of flora and fauna with the appearance of several endemic species (e.g., *Voltzia recubariensis*), and the higher preservation potential (e.g., Petti et al. 2013; Labandeira 2014). The three amber localities (Kühwiesenkopf/Monte Prà della Vacca, Piz da Peres and Recoaro) are approximately coeval (Pelsonian to early Illyrian) and their sediments were deposited under similar palaeoenvironment conditions. The plant-bearing “*Voltzia* beds” of Recoaro (Pelsonian) are very extended (e.g., Barbieri et al. 1980) including various lithologies (i.e. sandstones, siltstones, marls, marly limestones) that represent several depositional settings, ranging from alluvial plain to proximal marine (e.g., Mietto 1988, 2003; Gianolla et al. 1998a). The “*Voltzia* beds” were deposited during a transgressive phase, which could have created stressed conditions for the coastal and lowland vegetation, inducing amber production and creating favorable conditions for the preservation of fossil plants and resin at the same time (e.g., Labandeira 2014). The plant fossils from Kühwiesenkopf/Monte Prà della Vacca (Pelsonian) were found in the basinal, proximal marine sediments of the Dont Formation but linked to a stormy event (e.g., Delfrati et al. 2000; Tintori et al. 2001; Broglio Loriga et al. 2002), whereas the ones from Piz da Peres (Illyrian) come from the fluvial to marine sediments of

the Richthofen Conglomerate (e.g., De Zanche et al. 1992, 1993; Avanzini et al. 2007). Plant remains were so far reported from other outcrops of the Southern Alps, which were deposited under similar palaeoenvironmental and palaeoclimate conditions. These include the Anisian plant assemblage of Agordo in the San Lucano Valley (Kustatscher et al. 2011; Testa et al. 2013) that were deposited in a marine environment and come from the Agordo Formation (Bithynian–Pelsonian), the Richthofen Conglomerate and the Morbiac Limestone (Illyrian), and the plant assemblage of the Non Valley, deposited in a near-shore environment, and collected from the Voltago Conglomerate (Pelsonian; Kustatscher et al. 2012). These plant assemblages are also rich in conifers (e.g., *Voltzia recubariensis*, *Voltzia* sp.), dominated by *Voltzia recubariensis*, and also include rare fragments of sphenophytes, ferns, pteridosperms, and cycads (Tab. 1). Since also in these areas fossil resin may have been produced and could have been preserved in the beds containing plant fossils, the Agordo and Val di Non outcrops can both potentially yield amber. This encourages future investigations in coeval localities not only in the Southern Alps but worldwide, where amber could have been deposited under similar conditions. Moreover, although in the Anisian of the Southern Alps *Voltzia recubariensis* seems to be the main resin-producer plant, probably there were other resin-producers during this time that may have not been discovered as yet.

Triassic amber and humid pulses

Besides the rise of moisture, a global humid episode involves many other phenomena that can stress and physically damage plants (e.g., lightning strikes, hurricanes, propagation of parasites), inducing the production of a huge amount of resin and its accumulation (e.g., Grimaldi 1996; Langenheim 2003; Seyfullah et al. 2018a, 2018b). The coincidence of numerous amber deposits and major climate changes in the past indicates a clear link of cause and effect, which cannot be ignored in the study of amber. During the Triassic, the presence of all exposed lands concentrated at low to mid-latitudes and of a warm sea to the East, magnified heating during summer in the circum-Tethys area (e.g., Kutzbach & Gallimore 1989; Dubiel et al. 1991) and triggered a strong monsoonal circulation (e.g., Robinson 1973; Kutzbach & Gallimore 1989).

Extremely seasonal abundant rainfalls were concentrated in the Northern Hemisphere during the summer and a relatively dry equatorial region in the circum-Tethys area (Parrish 1993).

Several humid episodes have been recorded from Triassic sediments (e.g., Preto et al. 2010) starting from the Smithian (Campil) Event in the Olenekian (Early Triassic; e.g., Galfetti et al. 2007; Stefani et al. 2010; Li et al. 2018; Zhang et al. 2019; Fig. 1). This event represented a phase of efficient fluvial transport recorded from the western Southern Alps to Hungary (Broglia Loriga et al. 1990; Stefani et al. 2010), with similar conditions detected in the Central European Basin (Aigner & Bachmann 1992; Peron et al. 2005; Bourquin et al. 2006). The Bithynian–Pelsonian and the Illyrian (Anisian, Middle Triassic) humid pulses, according to several authors, have been considered two distinct events (Preto et al. 2010; Stefani et al. 2010; Li et al. 2018; Fig. 1), recorded in the western Tethys from the upper Anisian of the Southern Alps and Hungary (e.g., Brugman 1986; Kustatscher et al. 2010a; Haas et al. 2012). A correspondence between the Bithynian–Pelsonian and Illyrian humid shifts and the amber occurrence is observed (Fig. 1). The discovery of amber from three Pelsonian–Illyrian localities (Recoaro, Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres; Figs. 1–3) suggests indeed that the conditions for the large production (e.g., moisture increase, transgressive phase recorded from Recoaro that could have caused stress to the vegetation) and preservation of amber were diffused, at least at regional scale.

Humid phases are well documented during the late Ladinian of the Alps, where fluctuations in rainfall intensity indicates seasonal conditions, interpreted as monsoonal climate (Mutti & Weissert 1995; Preto et al. 2010; Stefani et al. 2010; Fig. 1) and supported by rich plant communities recovered from Southern Alps, England, Germany and Argentina (e.g., Köppen & Wegener 1924; Grodzicka-Szymanko & Orłowska-Kwolińska 1972; Szulc 1999; Kustatscher & Van Konijnenburg-van Cittert 2005; Hounslow & Ruffell 2006; Kustatscher et al. 2014). This humid phase might be the consequence of intense volcanism activity, which was recorded in the circum-Tethys area (e.g., Bechstädt et al. 1978; Brandner 1984; Baud et al. 1991; Szulc 1999; Trotter et al. 2015). The upper Ladinian amber consists so far of a single specimen part of an historical

collection of the Museum of Vienna. Based on the lithology, this specimen comes from the Wengen Fm. (e.g., Gianolla & Neri 2006; Neri et al. 2007), dated latest Longobardian (late Ladinian) based on ammonoids (Gianolla & Neri 2006; Gianolla et al. 1998a; Neri et al. 2007). The amber consists of a solid droplet, yellow to orange in color, found in anatomical connection with a large branch of *Voltzia ladinica* (e.g., Roghi et al. 2017). The amber is similar in color with the Anisian amber of Kühwiesenkopf/Monte Prà della Vacca and occurs on the upper side of the leaf lamina (Roghi et al. 2017). Although the Ladinian amber occurrence still remains a single find, it coincides with the worldwide scale humid event that occurred during the Longobardian (e.g., Mutti & Weissert 1995; Preto et al. 2010; Stefani et al. 2010; Trotter et al. 2015; Fig. 1). Once again, this would suggest the implications of particular climate conditions in the increase of the amber preservation potential.

The CPE (Late Triassic; Fig. 1) is the most investigated and well-known Triassic humid episode (e.g., Simms & Ruffell 1989; Gianolla et al. 1998b; Roghi et al. 2006b; 2010; Preto et al. 2010; Dal Corso et al. 2012, 2015, 2018; 2020 Fig. 1), which triggered an important biological crisis and the resulting radiation of several modern groups of plants and animals (Dal Corso et al. 2020). A carbon isotope negative shift corresponds to the onset of CPE, which was probably caused by the huge injection of ^{13}C -depleted CO_2 in the atmosphere from the Wrangellia Large Igneous Province volcanism (e.g., Furin et al. 2006; Greene et al. 2010; Dal Corso et al. 2015, 2020; Tomimatsu et al. 2021). The consequent greenhouse effect and the enhancement of the hydrogeological cycle led to an increase of rainfall and, thus, of the continental weathering (e.g., Hornung et al. 2007; Rigo & Joachimski 2010; Dal Corso et al. 2012, 2015). The effects of the CPE are well-studied in the Dolomites and Julian Alps, where important amber-bearing localities were found (e.g., Rifugio Dibona, Dogna; Fig. 2). The palaeobotanical study of this fossil resin was crucial to understand the link between the Carnian amber and the CPE (Gianolla et al. 1998b; Preto & Hinnov 2003; Breda et al. 2009; Dal Corso et al. 2011, 2012, 2018, 2020; Roghi et al. 2006a, 2006b, 2017; Schmidt et al. 2006, 2012; Seyfullah et al. 2018a, 2018b; Bouju & Perrichot 2020; Fig. 1). The first report of Car-

nian amber is from Tyrol (Austria; Pichler 1868) but from the 21st century new amber-bearing localities were discovered, occurring globally (from Europe to New Zealand and Southern Africa) and belonging to a very restricted interval of time of the Carnian (e.g., Pichler 1868; Sigmund 1937; Soom 1984; Vávra 1984; Gianolla et al. 1998b; Budai et al. 1999; Csillag & Földári 2005; Roghi et al. 2006b; Schmidt et al. 2006, 2012; Ansoerge 2007; Peñalver & Delclòs 2010; Fischer et al. 2017; Seyfullah et al. 2018a, 2018b; Baranyi et al. 2019; Stilwell et al. 2020). Therefore, the Carnian amber is considered the first global appearance of amber so far (Seyfullah et al. 2018b). The origin of Carnian amber from the Dolomites is attributed to plants belonging to the family Cheirolepidiaceae, a conifer family considered typical of Jurassic and Cretaceous floras that mostly lived in coastal and deltaic areas (Sternberg et al. 1984; Nguyen Tu et al. 1999). Exceptionally well-preserved cuticles of *Brachyphyllum* type leaves were found abundantly dispersed in the paleosols of the Heiligkreuz Fm. (Rifugio Dibona; Figs. 2, 3) where amber droplets occur (e.g., Roghi et al. 2014). *Brachyphyllum* was also found in the Tor Fm. (Dogna; Figs. 2, 3), together with *Voltzia* (Roghi et al. 2006a). The CPE is thus the best documented example of a link between humid episodes and amber occurrence, in which the climate conditions favored the massive production and preservation of resin at global scale (e.g., Seyfullah et al. 2018a, 2018b; Dal Corso et al. 2020).

Further extreme humid episodes characterized the Late Triassic climate, and particularly the Norian and early Rhaetian with the intensification of the monsoonal regime (e.g., Robinson 1973; Hallam 1985; Ahlberg et al. 2002; Wang 2009; Berra et al. 2010; Nordt et al. 2015; Baranyi et al. 2017; Fig. 1). The occurrence of amber during the Norian was debated (Seyfullah et al. 2018a, 2018b; Dal Corso et al. 2020; Fig. 1) because the amber fragments that occur in the Chinle Fm. (Blue Mesa, Sonsela and Petrified Forest members) of the Petrified Forest National Park (PEFO; Arizona, USA) were originally considered Carnian in age (Litwin & Ash 1991; Litwin et al. 1991; Fig. 1). Preliminary infrared analysis suggested an araucarian origin for the amber droplets (Litwin and Ash 1991). The Norian climate is marked by the intensification of the megamonsoonal regime and its abrupt collapse

during the middle Norian (mid-Norian Climate Shift) about 214.7 Ma (e.g., Dubiel et al. 1991; Preto et al. 2010; Howell & Blakey 2013; Nordt et al. 2015; Baranyi et al. 2017). The monsoon is recorded in the Mesa Redondo, Blue Mesa, and lower part of the Sonsela members, which represent the lower part of the Chinle Fm., and range from ca. 228 to 214.7 Ma (Nordt et al. 2015). A faunal and floral turnover during the middle part of the Sonsela Member at the PEFO (Parker & Martz 2011) characterize the shift from monsoonal to post-monsoonal conditions (e.g., Parker & Martz 2011; Reichgelt et al. 2013; Lindström et al. 2016; Baranyi et al. 2017) but additional environmental perturbations (e.g., increase of atmospheric CO₂, volcanism, Manicouagan impact event) could have contributed to the ecosystem change (e.g., Hodych & Dunning 1992; Ramezani et al. 2005; Atchley et al. 2013; Nordt et al. 2015; Schaller et al. 2015; Whiteside et al. 2015). Short-term wet climatic shifts could have been present during the Norian gradual aridification trend (Fig. 1), and these humid spells persisted during the deposition of the Sonsela and Petrified Forest members, in agreement with paleosols data and palynological record (Nordt et al. 2015; Baranyi et al. 2017; Fig. 1). The Norian humid shifts could be correlated to the amber occurrences in the PEFO (Fig. 1), inducing the production and favoring the preservation of fossil resin during the megamonsoon (i.e. amber occurrences in the Sonsela and Blue Mesa members; Fig. 1) or the humid fluctuations recorded in the post-monsoon phase (i.e. amber occurrences in the Petrified Forest Member; Fig. 1). However, this correlation remains unclear, at least until new data and a more precise dating for the amber-bearing beds will be obtained.

CONCLUSIONS

The discovery of amber in the plant-yielding horizons of Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres increases the knowledge on Triassic amber as it fills gaps in the scattered fossil record of Lower Mesozoic amber. This discovery adds to those from Recoaro in the Southern Alps (*Voltzia* beds, Pelsonian) and increases the finding of fossil resin not only dispersed, but also in association with *Voltzia recubariensis*. It suggests that this species,

which was a dominant element of the Anisian flora of the Southern Alps, was a resin-producing plant. All Anisian amber drops found are similar in color (reddish to brownish), with resiniferous brilliance, although some specimens from Kühwiesenkopf/Monte Prà della Vacca are sometimes lighter, yellowish and opaque. This could, however, reflect a different diagenesis. Although of difficult interpretation, the discovery of a likely organic body trapped in the amber of Kühwiesenkopf/Monte Prà della Vacca is noteworthy and demonstrates once again how far the amber “time capsule” can go back and be able to trap and preserve fragments of the deep time life.

The occurrence of amber in several Anisian localities suggests how, during that time, the conditions that triggered the production of resin by plants and favored its preservation were present across different deposits, at least at regional scale. The evidence of several climate shifts during the Triassic overlaps in some cases with the shifts in the composition of the plant communities (e.g., Kustatscher et al. 2019; Dal Corso et al. 2020). In particular, the late Anisian, the late Ladinian and middle Carnian humid episodes (e.g., Brugman 1986; Mutti & Weissner 1995; Kustatscher et al. 2010a; Preto et al. 2010; Stefani et al. 2010; Dal Corso et al. 2020) coincide with regional and global shifts from xerophytic to hygrophytic floras and with amber findings in the eastern Southern Alps (Kustatscher et al. 2019; Fig. 1). This pattern suggests a cause-and-effect relationship between climate/environmental changes and the rise of amber production/preservation potential. This seems more evident in some kinds of environments. The Anisian, Ladinian and Carnian amber was all deposited in marginal marine or coastal sediments, both in the Dolomites and in the Julian Alps (Roghi et al. 2006a, 2017). The Middle Triassic amber of Northern Italy was produced by representatives of the Voltziales, respectively *Voltzia recubariensis* and *V. ladinica* (Roghi et al. 2017; this paper) whereas the Carnian amber of the Dolomites was mainly produced by cheirolepidiaceus conifers. Future investigations of further Anisian palaeobotanical deposits, but also at other Triassic humid pulses (Fig. 1) and searching in favorable depositional environments for fossil resin where key taxa occur (e.g., Voltziales and Cheirolepidiaceus conifers) will probably increase the number of Lower Mesozoic amber occurrences and improve understanding of resin production

in the Triassic. Although the different amber occurrence in the Chinle Fm. (Blue Mesa, Sonsela and Petrified Forest members) in the PEFO can be considered Norian in age, their origin and possible correlation to the megamonsoon and the following short-lived humid pulse is not clear and needs future investigations.

Acknowledgements: We thank Francesca Conci, Hendrik Nowak, Irene Tomelleri and Francesca Uzzo for their help during the analysis and the collection work. Our acknowledgements also go to Stefano Castelli (Department of Geosciences, University of Padova) for taking pictures under UV light of some specimens of the Kühwiesenkopf/Monte Prà della Vacca palaeobotanical collection. We also thank Patricia Mcgoldrick for the linguistic review and three anonymous reviewers that helped to improve the manuscript. This study was supported by the research project of the Museum of Nature South Tyrol: “PALDOTEC – The paleoflora of Kühwiesenkopf/Monte Prà della Vacca” funded by the Betrieb Landesmuseum/Azienda Provinciale dei Musei Altoatesini.

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