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Distinct origins for Rovno and Baltic ambers: Evidence from carbon and hydrogen stable isotopes

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ABSTRACT

Ambers—fossilized plant resins—are a rich and unique source of paleoecological data due to their ability to preserve soft body fossils. However, interpretations concerning their environmental context are often hampered by uncertainties in the relationship between assemblages of inclusions and geological context, particularly in the case of secondarily redeposited ambers such as those from the Paleogene of Central Europe. Here we use stable carbon and hydrogen isotope analyses, as well as FTIR spectroscopy, from the northwestern Ukrainian Rovno amber deposit, to provide independent constraints on the geographic and temporal origins of Rovno amber. These analyses address the relationship between the Rovno and Baltic amber deposits as well as German Bitterfeld amber—a subject of considerable debate regarding their provenance. Rovno amber has a $\delta^{13}C$ signature of -23.3 ± 0.9‰, similar to both Baltic and Bitterfeld ambers. Since there is a secular decreasing $\delta^{13}C$ trend among amber deposits since the Early Eocene, a roughly contemporaneous origin of these deposits in the Eocene can be deduced. However, Rovno amber displays a δ^2H signature of -258 ± 9‰, 19‰ more positive than Baltic amber, and directly comparable to Bitterfeld amber. This difference relates to precipitation sources and mean annual temperatures of the amber source regions, and suggests a much more southerly origin of Rovno amber relative to Baltic amber. FTIR spectra of each of these ambers are nearly identical and suggest that resin-producing trees were from similar families, despite contrasting source regions. Thus, we provide the first clear geochemical evidence for the distinct origin of Rovno and Baltic amber deposits, with implications for paleoecological studies involving inclusions from these deposits, and for determining the provenance of archaeological amber finds.

1. Introduction

Ambers are a well-recognized paleontological archive due to their ability to encapsulate and preserve soft-bodied fossils in pristine condition (e.g., Sendel, 1742; Martínez-Delclòs et al., 2004; Penney, 2010). Ambers are also well-suited for stable isotopic analyses, due to the stability of their highly cross-linked hydrocarbon structures (Nissenbaum and Yakir, 1995; Tappert et al., 2013; Dal Corso et al., 2017). However, the utility of amber records and inclusions as proxies for changes in paleoecology and paleoclimate depends on our understanding of the provenance of the studied amber material.

Due to the richness of paleoentomological material preserved as inclusions in European amber, comparisons between fossil assemblages have been the most popular way to differentiate between the provenance times and source areas of different amber deposits. Yet, the complexity of factors affecting such paleoecological reconstructions, and the extent to which amber deposits have been reworked and secondarily redeposited can leave much room for differing interpretations of amber source environments and entomological ranges. Problems can stem from uncertainties in the climatic preference of some arthropod families (Archibald and Farrell, 2003; Perkovsky, 2016), from sampling artifacts (Perkovsky et al., 2007), and from amber deposits being reworked and deposited in sediments that are millions of years younger than the original time of production (Weitschat and Wichard, 2002).

Studies of the chemical-physical characteristics of amber, such as the infrared (IR) spectra or isotopic composition of deposits, are

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valuable additions to paleontology in assessing amber provenance (e.g., Tappert et al., 2011, 2013; Wolfe et al., 2016). In a recent example, Wolfe et al. (2016) used micro-Fourier transform infrared spectroscopy (micro-FTIR) and time of flight-secondary ion mass spectrometry (ToF-SIMS), together with carbon ($\delta^{13}C$) and hydrogen ($\delta^{2}H$) isotopic measurements, to resolve a long-standing debate about the relationship between the Baltic (southeast coast of the Baltic Sea) and Bitterfeld (NE-Germany) amber deposits (Dunlop, 2010; Szwedo and Sontag, 2013). Contrary to several comparative paleoentomological overviews that supported the equivalence of these deposits, consistent differences in $\delta^{2}H$ and the relative abundances of compositional acids were found, definitively establishing the deposits as having distinct source areas (Wolfe et al., 2016). Uncertainties related to comparisons of fossil assemblages have led many authors to rely on this independent geochemical check on the amber source tree (Heinrichs et al., 2016b; Feldberg et al., 2017; Lee et al., 2017), as well as the chronological (Poinar, 2016a, 2016b; Gillung and Winterton, 2018) and geographical (Barden, 2017; Lyubarsky and Perkovsky, 2017; Stebner et al., 2017) origin of Baltic and Bitterfeld amber.

Another European amber that has received much research interest is the northwestern Ukrainian Rovno deposit, which is generally thought to have formed in the Late Eocene (Perkovsky et al., 2010). A long-standing question regarding this deposit is its relation to the better-known Baltic amber—whether these represent different reworked deposits of essentially the same material, or whether Rovno amber was formed autochtonously, but in a different source area than the Baltic deposit (Perkovsky et al., 2007; Szwedo and Sontag, 2013). Numerous systematic analyses have recently been conducted on the rich fossil assemblage of Rovno amber inclusions (see Perkovsky et al., 2010 for review). While many studies have reported notable differences between the arthropod assemblages of Baltic and Rovno ambers (Perkovsky et al., 2007; Dlussky and Rasnitsyn, 2009; Perkovsky, 2013, 2016), there is still discussion on whether these are substantial (Szwedo and Sontag, 2013). By contrast, previous work on the comparative mineralogical and chemical composition of the ambers found few differences between Rovno and Baltic ambers in either color, texture, mechanical properties or major chemical components (Bogdasarov, 2007). Thus, no consensus currently exists pertaining to the relationship between these two ambers (Heinrichs et al., 2016a; Engel, 2016; Harms and Dunlop, 2017; Alekseev, 2017; Stebner et al., 2017).

This study aims to provide constraints on the source region and formation time of Rovno amber by using carbon and hydrogen stable isotope analyses together with micro-FTIR spectroscopy. Recent advances in the classification of resin using FTIR-spectra (Tappert et al., 2011; Wolfe et al., 2016) and in the understanding of secular trends in the carbon isotope composition of fossil resin (Tappert et al., 2013) provide a context that helps elucidate the relationship between Rovno and Baltic ambers.

2. Materials and methods

The samples used in this study are from the Rovno amber deposit in northwestern Ukraine, and the geological setting of this deposit has recently been reviewed by Perkovsky et al. (2010). This amber is mainly found in the Lower Oligocene Mezhygorje Formation in the Rovno region, whereas more recent reworking has carried some of the same amber into Quaternary deposits in southern Belarus. Previous reports of amber in the Upper Eocene Obukhov Formation were not confirmed by later studies (Perkovsky et al., 2010). Rovno amber usually appears as variously shaped lumps, surrounded with a dark opaque oxidation crust (Fig. 1). Underneath the crust, its colors range from clear and transparent to a deeply oxidized, opaque, dark red. While Rovno amber has been used for jewelry-making purposes since antiquity, large-scale commercial mining of the deposit near the village of Klesov began only in 1991, leading to a relatively small number of studied samples in comparison with Baltic amber (Perkovsky et al., 2010).

Due to the semi-precious nature of amber and a comparative scarcity of samples from this deposit in museum collections worldwide (Rovno amber has only come under intensive study since the beginning of the 21st century; Perkovsky et al., 2010), the analyses rely on refined and unprocessed batches of Rovno amber purchased from commercial vendors in Ukraine. While the relatively low cost of Rovno amber in Ukraine leaves no financial incentive for vendors to mislead on the origin of such amber, it was decided to reduce the risk of an origin misunderstanding by analyzing three different batches of Rovno amber pieces, all purchased at different times from different vendors in Ukraine. Two batches of polished, jewelry-grade Rovno amber pieces were acquired for this study—batch Comm1 was purchased in 2017 from vendor “SanaGem”, based in Khmelnytskyi, Ukraine and Comm2 in 2006 from a jewelry store in Rovno, Ukraine. Both sample sets are housed at the University of Alberta, Edmonton, Canada. One collection of raw, unprocessed amber pieces—batch RSKM—was analyzed from the collection of the Royal Saskatchewan Museum, Regina, Canada (specimen number RSKM P3300.136; bulk amber collection, originally purchased in 2016 from Boris Tatarnjuk, an amber vendor in Ternopil, Ukraine).

Thirty pieces representing a variety of colors and transparency levels were chosen for analysis, ranging from transparent and clear to dark reddish and opaque. For further analyses, small chips were cut either with pliers or a scalpel, to select amber subsamples near the core of each piece, far removed from oxidation rinds.

Stable isotope analyses of 30 amber pieces were carried out at the University of Alberta on a Finnegan MAT 252 dual-inlet mass spectrometer. Chips of amber ~3–5 mg in weight were combusted at 800 °C for 12 h in evacuated quartz tubes, together with ~1–2 g of CuO as an oxygen source. After this, the H_2O and CO_2 gases were extracted and separated. Before isotope analyses, H_2O was converted to H_2 using a heated reaction with zinc. Results for stable carbon isotope analyses are presented in $\delta^{13}C$ notation as ‰ relative to the Vienna Pee Dee Belemnite (VPDB; Coplen et al., 1983), calibrated internally against NBS-18 and NBS-19 carbonate standards (7.16 ± 0.19‰ and 28.65‰ $\delta^{13}C$, respectively; Reed, 1992), and hydrogen isotopes in $\delta^{2}H$ notation relative to Vienna Standard Mean Ocean Water (VSMOW; Gonfiantini, 1978), calibrated internally against GISP, SLAP and VSMOW waters (−189.5 ± 1.2‰, −428.0‰ and 0‰ $\delta^{2}H$ respectively; Gonfiantini, 1978; Göring, 2007). Instrumental precision on the former analysis was ± 0.1‰ and the latter ± 3‰. It should be noted that our new data were obtained in the same laboratory and using the same standards as the Tappert et al. (2013) and Wolfe et al. (2016) studies.

FTIR micro-spectroscopy was carried out on 10 RSKM samples (specimens within the Royal Saskatchewan Museum P3300.136 bulk amber set). Untreated flakes of amber < 50 × 50 μm in size were chipped onto an infrared-transparent silicon wafer (orientation 100, 450 μm thick, type N/Phosphorus, resistivity > 10 Ω-cm). The analyses were carried out at University of Alberta on a Thermo Nicolet Continuum FTIR microscope attached to an 8700 FTIR main bench. Absorption spectra were obtained for the 650 to 4000 cm^{-1} (wavenumber) interval with a spectral resolution of 4 cm^{-1} using transmission mode, with the resulting spectra presented in absorbance units versus wavenumber. The number of scans for the sample and background was 128. A square beam size of 100 × 100 μm was used. The software utilized to collect the spectra and manipulate the data was OMNIC version 8.3. The CO_2 peak was automatically removed by software and only manual baseline correction was performed. No zero-filling or smoothing functions were applied to the spectra.

3. Results and discussion

3.1. Carbon stable isotopes

The mean $\delta^{13}C$ value of the Rovno ambers sampled in this study is

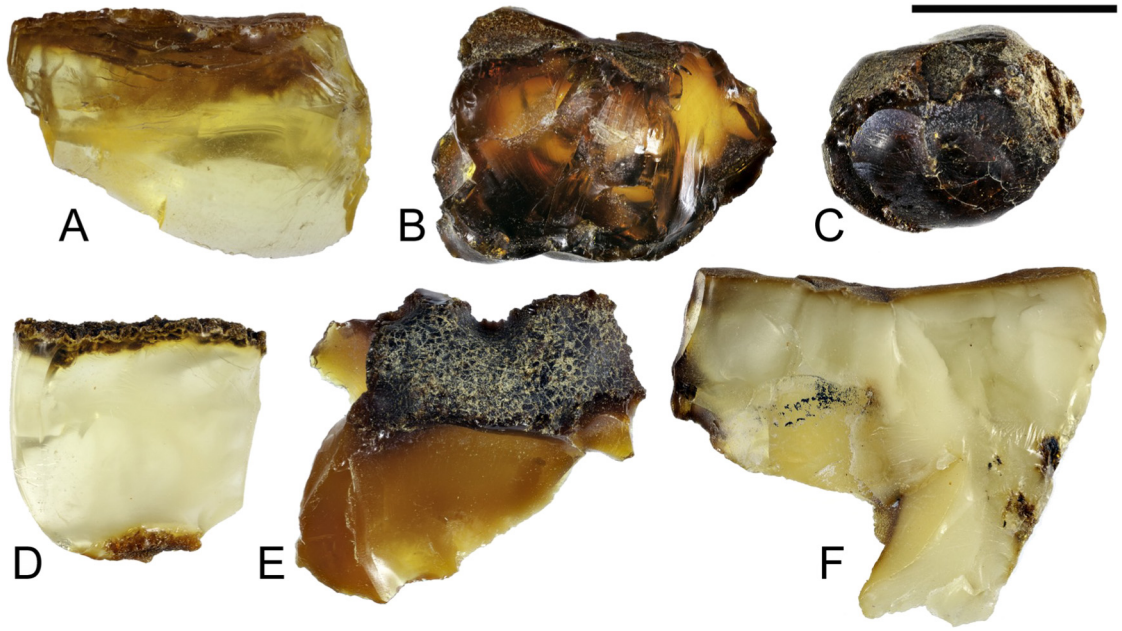

Fig. 1. Variation and weathering in Rovno amber fragments (RSKM P3300.136). Colors in translucent pieces range from pale yellow, to deep orange, and dark red (A–C). Clarities range from nearly transparent with stringers of milky amber, to turbid orange 'butterscotch', and opaque 'bone-grade' amber (D–F). Oxidized weathering surfaces are near the top of each image, and can be quite thick (B–E). Scale bar = 1 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

−23.3 ± 0.9‰, $n = 30$ (Fig. 2), which is very similar to the values reported for both Baltic (−23.6 ± 1.0‰, $n = 77$) and Bitterfeld ambers (−23.9 ± 1.7‰, $n = 34$; Fig. 3; Supplementary Table 1; Wolfe et al., 2016). The $\delta^{13}C$ value of amber is a reasonably faithful proxy for the carbon isotope composition of the plant that produced the resin. The mean value of resins has been demonstrated to broadly track the value for leaf biomass in modern resin-producing plants, though some fractionation within plant tissue and a loss of volatiles after resin exudation can result in an up to 6‰ offset between resins and other plant material (Diefendorf et al., 2012; Tappert et al., 2013; Dal Corso et al., 2011, 2017). Furthermore, little carbon isotopic exchange has been shown to occur between polymerized resins and their environment after burial (Nissenbaum and Yakir, 1995; Dal Corso et al., 2017).

Physiological characteristics and local environmental conditions both have a major effect on ^{13}C discrimination during photosynthesis and thus, the $\delta^{13}C$ of plant matter (Cernusak et al., 2013). C_3, C_4 and CAM plants all fractionate carbon to characteristically different degrees—so much so that leaf $\delta^{13}C$ has been used for distinguishing the photosynthetic pathway for species where none was previously known (Bender, 1968, 1971; Farquhar et al., 1989). In the case of amber-producing plants, which employ the C_3 photosynthetic pathway, local environmental conditions affect carbon fractionation mostly through the modulation of intercellular to ambient CO_2 concentrations (Farquhar et al., 1982). Water availability has recently been shown to account for about 50% of the variation in plant biomass $\delta^{13}C$ globally—low mean annual precipitation means that plants have to limit their gas exchange in order not to lose too much water vapor, which leads to lower intercellular CO_2 concentrations and less ^{13}C discrimination during photosynthesis (Diefendorf et al., 2010; Kohn, 2010). Higher nutrient availability—at least in the case of nitrogen—has been shown to increase intercellular CO_2 demand and lead to a smaller $\delta^{13}C$ fractionation (Duursma and Marshall, 2006; Cernusak et al., 2007). A similar effect has been shown for increasing irradiance (Ehleringer et al., 1986), altitude (Körner et al., 1988; Hultine and Marshall, 2000) and other parameters (reviewed in Farquhar et al., 1989; Cernusak et al., 2013), while a +1.1‰ offset was found in the $\delta^{13}C$ of resins produced by trees affected by the ongoing mountain pine beetle outbreak in Western Canada (McKellar et al., 2011).

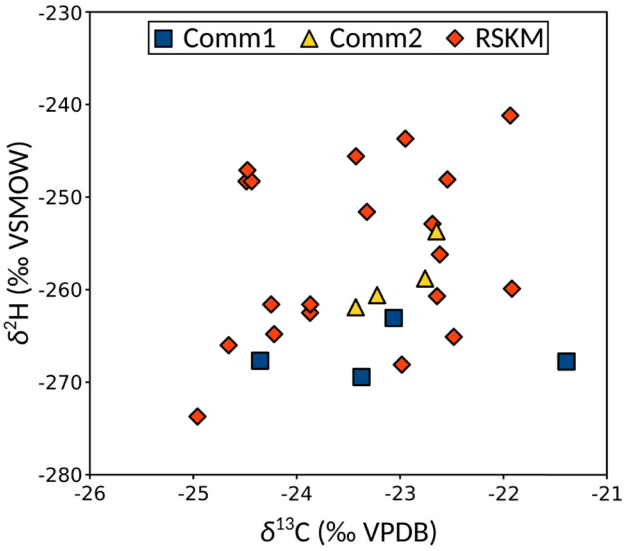

Fig. 2. Results for carbon and hydrogen stable isotope measurements of Rovno ambers. Squares and triangles represent independently sourced commercial amber samples, diamonds represent raw museum samples.

Within similar plant groups, and on longer time scales, the isotopic composition of plant matter can also be affected by global conditions (Tappert et al., 2013; Dal Corso et al., 2017). For instance, Tappert et al. (2013) revealed a secular trend among the mean $\delta^{13}C$ of 26 different amber deposits from the Mesozoic onward, which they attributed to changing atmospheric composition. In the last 50 million years (since the early Eocene), this trend is expressed as a monotonous decrease of 6‰, allowing for the use of amber $\delta^{13}C$ values as an indirect dating tool (Tappert et al., 2013). Taken at face value, this observation leads to a simple inference that the −23.3 ± 0.9‰ average $\delta^{13}C$ of Rovno amber can be related to its formation age, the latter being either 65–54 Ma or 42–26 Ma (Fig. 4). However, while long-term trends in amber $\delta^{13}C$ are

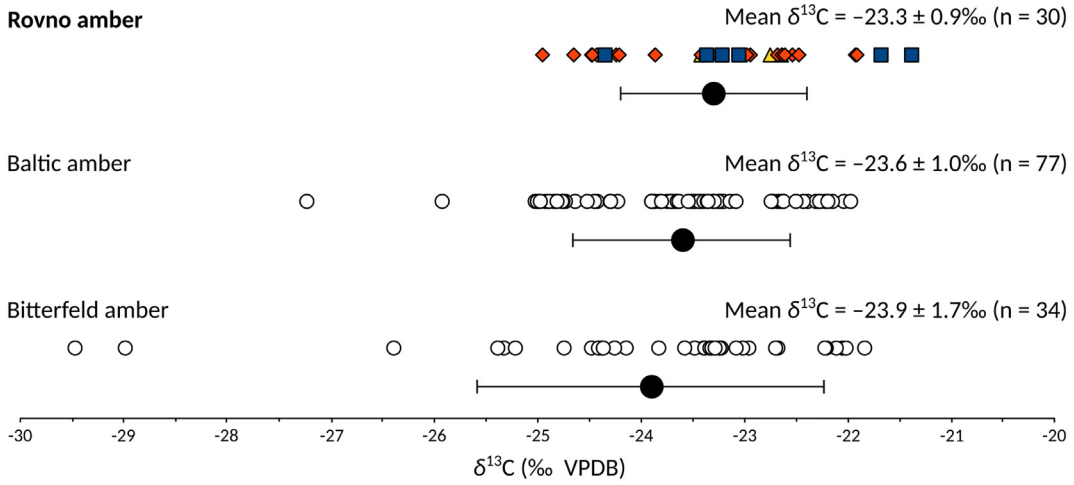

Fig. 3. Carbon stable isotopic ratios ($\delta^{13}C$) in Rovno amber, compared to Baltic and Bitterfeld amber. Baltic and Bitterfeld data from Wolfe et al. (2016); Rovno sample symbols identical to Fig. 1.

undeniable, a substantial problem with using $\delta^{13}C$ for absolute dating is the large uncertainty in the ages of the ambers from which this trend is compiled. Amber cannot be dated directly—its age can only be estimated through its surrounding sediments and the paleofauna contained in inclusions, which can lead to large uncertainties when sedimentary redeposition or uncertain age relationships of fossil fauna are taken into consideration (e.g., Dunlop et al., 2018). Therefore, a conservative approach is to use $\delta^{13}C$ only for the relative dating of amber deposits. In this regard, Rovno amber is a close match in $\delta^{13}C$ both to Baltic and Bitterfeld ambers (23.3 ± 0.9‰, −23.6 ± 1.0‰ and −23.9 ± 1.7‰ respectively). The similarity is borne out by unpaired *t*-tests that yielded no statistically significant difference between either Rovno and Baltic, or Rovno and Bitterfeld carbon isotope compositions ($P = 0.097$, $t = 1.67$, d.f. = 105; and $P = 0.075$, $t = 1.81$, d.f. = 62, respectively). However, Rovno amber $\delta^{13}C$ is also comparable to that of the Paleocene Genesee, Evansburg and Alaskan ambers; and the Middle Eocene Giraffe kimberlite (Fig. 4; Tappert et al., 2013). Thus, in order to arrive at a more precise age estimate, $\delta^{13}C$ data needs to be used in concert with other age constraints.

An independent constraint is the occurrence of Rovno amber predominantly in the Lower Oligocene Mezhygorje Formation (Perkovsky et al., 2003, 2010). While an Oligocene age does not conflict with $\delta^{13}C$ data (Fig. 4; Tappert et al., 2013), possible reworking means that the depositional context can serve only as a minimum age constraint. By contrast, paleontological studies of amber inclusions provide strong evidence for the sourcing of Rovno amber in the Eocene, contemporaneously with Baltic and Bitterfeld ambers, and practically exclude its Paleocene origin. This mainly refers to a large overlap of Rovno and Baltic amber fossil arthropod assemblages—many species of ants, spiders, flies, harvestmen, termites and other orders are found in

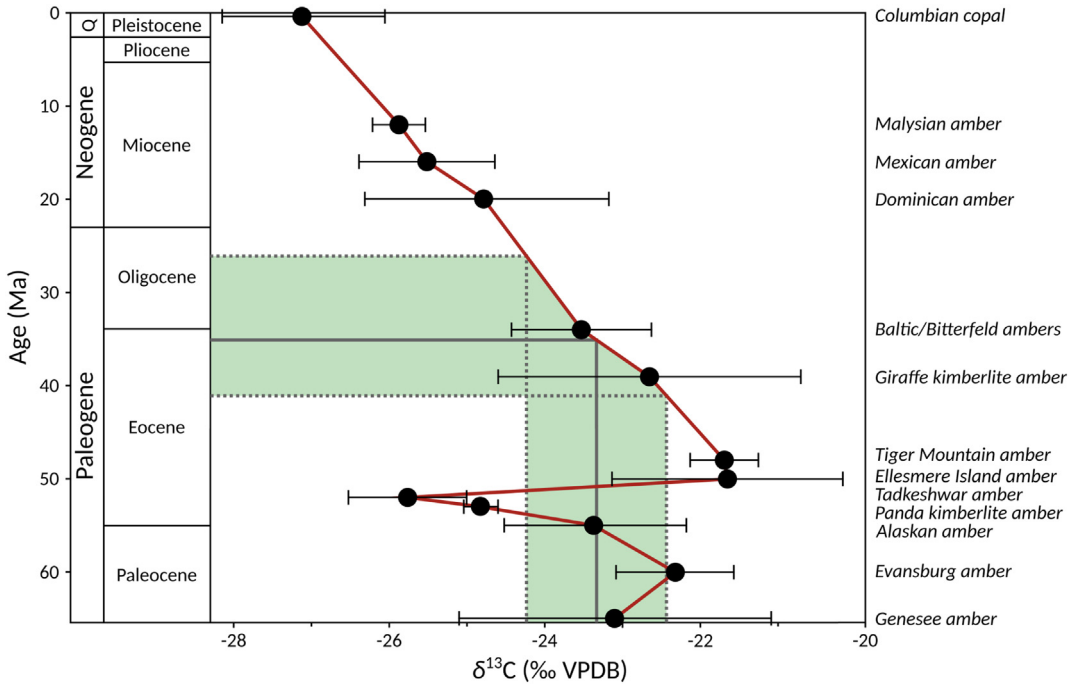

Fig. 4. Rovno amber $\delta^{13}C$ values in the context of the secular trend in amber carbon isotope ratios over the course of the Cenozoic. Shaded green area represents the mean plus standard deviation of Rovno samples and the corresponding range in formation age, not taking into account the age uncertainties associated with the constituent amber deposits of the trend line. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) Modified after Tappert et al. (2013).

both of these deposits (Dlussky and Rasnitsyn, 2009; Perkovsky et al., 2010; Sontag and Szadziewski, 2011; Szwedo and Sontag, 2013; Perkovsky and Rasnitsyn, 2013; Perkovsky, 2016). Such a high degree of overlap is most parsimoniously explained by a similar formation age (Perkovsky et al., 2010). Despite the long history of Baltic amber research, there is still much uncertainty in precise dates, largely owing to its repeated redeposition (Grigelis et al., 1971; Perkovsky et al., 2007) and production over potentially millions of years in a vast and heterogeneous northern European forested region (Weitschat and Wichard, 2010; Szwedo and Sontag, 2013; Alekseev and Alekseev, 2016; Bogri et al., 2018). Age estimates thus range from the Early to Middle Eocene (e.g., Ritzkowski, 1997; Alekseev and Alekseev, 2016), to the Late Eocene (e.g., Kaplan et al., 1977; Perkovsky et al., 2007), and even Early Oligocene (Vitali and Daamgard, 2016). Nonetheless, most researchers broadly agree on an Eocene age for Baltic amber (see reviews in Perkovsky et al., 2007; Weitschat and Wichard, 2010; Bogri et al., 2018). Judging by the close paleontological affinity and the matching carbon isotope composition, this age estimate can be extended to Rovno amber.

3.2. Hydrogen stable isotopes

The mean δ^2H of Rovno amber analyzed in this study is $-258 \pm 9‰$, $n = 28$ (Fig. 2), compared with $-277 \pm 22‰$, $n = 68$ for Baltic amber and $-256 \pm 9‰$, $n = 33$ for Bitterfeld amber (Fig. 5; Supplementary Table 1; Wolfe et al., 2016). The δ^2H signature in amber is ultimately derived from that of water accessed by the amber producing plant, but oxidation can have a significant effect—a 19‰ difference was found between fresh amber and its oxidized rinds (Nissenbaum and Yakir, 1995). However, all of our geochemical analyses used material from the unoxidized cores of amber pieces and are thus unlikely to be affected by post-depositional alteration. The 19‰ difference between Baltic and Rovno amber δ^2H values is statistically highly significant ($P \leq 0.0001$, $t = 4.47$, d.f. = 94) and can be most easily explained by contrasts in the isotopic composition of waters accessed by the resin-producing conifers. Hence, Rovno amber plant waters originated from a significantly different area than those that produced Baltic amber—the Rovno source area appears to be much further south, at a similar latitude to that of Bitterfeld amber, which is not significantly different from Rovno amber in its δ^2H ($P = 0.439$, $t = 0.78$, d.f. = 59). As a comparison, a 20‰ difference in leaf water δ^2H corresponds to a 7° latitudinal difference in the isoscape of modern Central Europe (West et al., 2008). Such a degree of geographic separation between the Baltic and Rovno amber source areas would be consistent with paleoentomological evidence from amber inclusions and fossil plants from the area. These have generally supported a temperate to subtropical interpretation of the paleohabitat, although one that is warmer and more xeric than that assigned to Baltic amber (Pimenova, 1937; Popov et al., 2001; Perkovsky et al., 2007, 2010; Lyubarsky and Perkovsky, 2012; E. E. Perkovsky, personal communication). In addition to different averages, Baltic amber δ^2H is much more variable than Rovno amber and many data points overlap with Rovno amber. This large variance in Baltic amber is mirrored in its paleoentomological record which contains a mixture of taxa with tropical and boreal affinities (Weitschat and Wichard, 2010). A possible explanation for this finding is a significantly larger catchment area or a longer period of formation for Baltic amber, so that the deposit records a more varied climatic regime than Rovno amber (Wolfe et al., 2016).

3.3. FTIR spectroscopy

Infrared spectroscopy has long been used as a robust method to study and classify different ambers (Beck et al., 1964). A more modern development is micro-FTIR, which allows for easier measurements and smaller sample sizes (Tappert et al., 2011). Baltic amber is known for the consistency of its FTIR-spectra. Its diagnostic feature is the "Baltic shoulder", a wide shoulder of the 1170 cm^{-1} peak stretching to 1280 cm^{-1} (Beck et al., 1965; Beck, 1986), which corresponds to strong contributions from succinic acid and other succinates in Baltic amber (Wolfe et al., 2009, 2016). Wolfe et al. (2016) reported several bands which were consistently different when comparing Baltic and Bitterfeld ambers—Baltic amber had a stronger absorbance at the 1700–1800 cm^{-1} carbonyl band (C=O; corresponding to total carboxylic acids), the succinate "Baltic shoulder" band, and the out-of-plane aromatic C–H band at 870–900 cm^{-1}.

Examining the FTIR-spectra of Rovno amber in this framework (Fig. 6), it becomes clear that Rovno amber is very similar to both Baltic and Bitterfeld ambers in its chemical composition. A prominent "Baltic shoulder" can be seen in almost all samples (though some variability exists), which suggests considerable contributions from succinate compounds. In addition, the carbonyl bands and the out-of-plane aromatic C–H bands are prominent. These findings are not dissimilar to previous and more general overviews of Eurasian amber IR-spectra, which have reported succinite-like spectra for both Baltic and Ukrainian-Belarussian samples (Bogdasarov, 2007; Golubev and Martirosyan, 2012). It is, therefore, likely that Rovno and Baltic ambers were produced by a similar assemblage of amber-producing plants, perhaps related to Sciadopityaceae or Pinaceae (Wolfe et al., 2009; but see also Weitschat and Wichard, 2010).

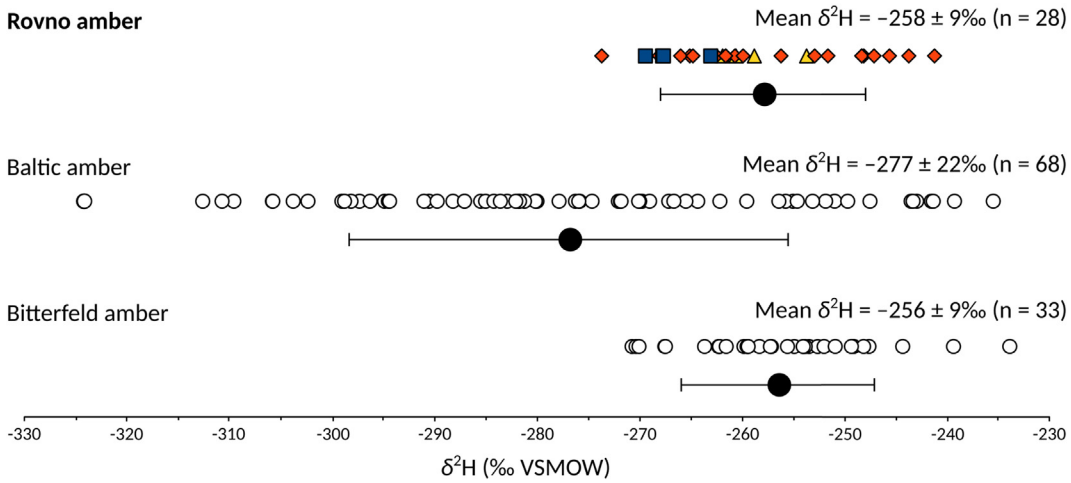

Fig. 5. Hydrogen stable isotopic ratios (δ^2H) in Rovno amber, compared to Baltic and Bitterfeld amber. Baltic and Bitterfeld data from Wolfe et al. (2016); Rovno sample symbols identical to Fig. 1.

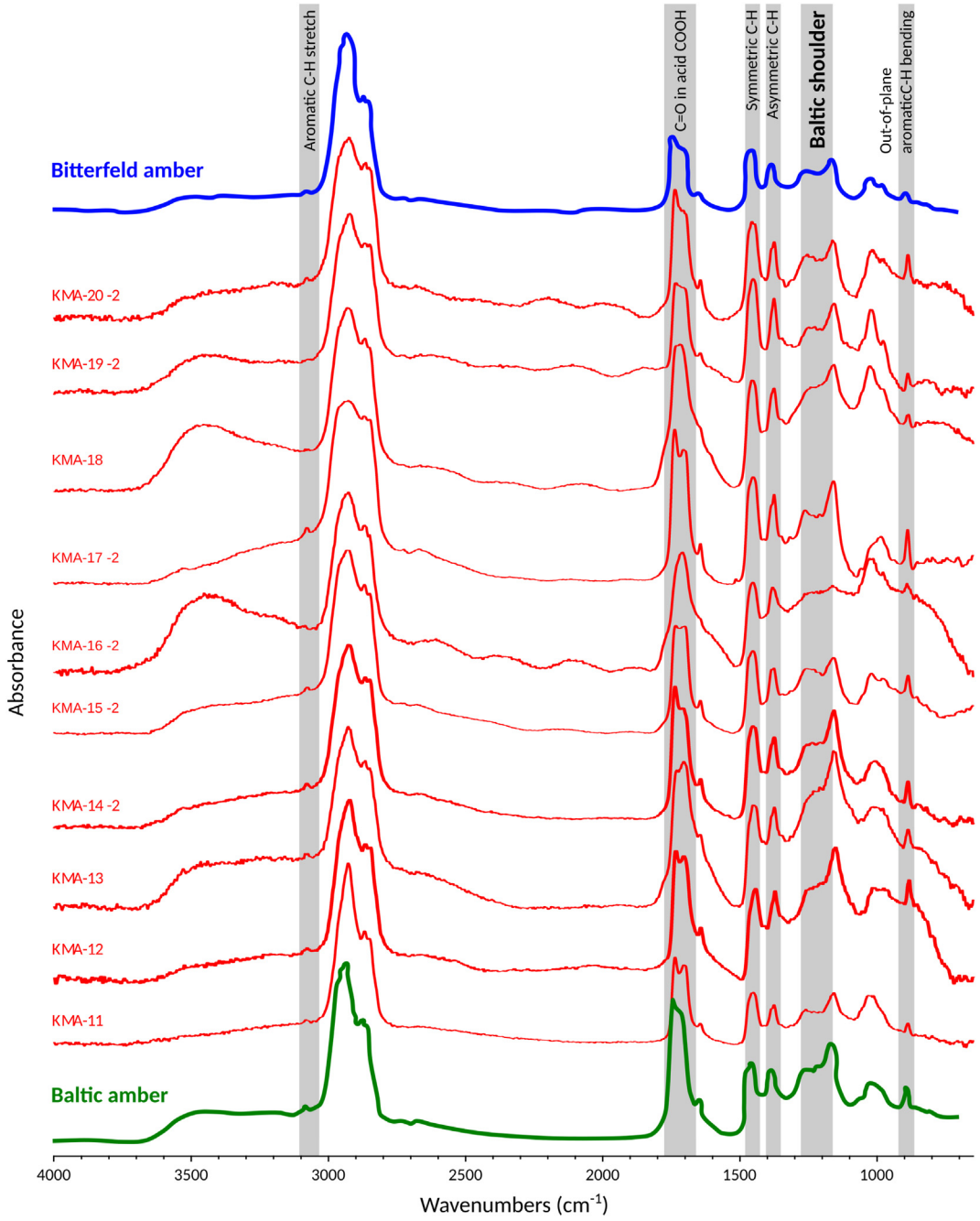

Fig. 6. Micro-FTIR spectra for individual Rovno ambers, compared to consensus Baltic and Bitterfeld amber spectra from Wolfe et al. (2016).

3.4. Source region

A potential limitation with the present study lies in our sampling of only three different collections of amber, which were all purchased from commercial vendors that did not retain detailed information about the stratigraphic and geographic context, other than their source being the Rovno region. Hence, there is a possibility that these analyses do not encompass the full range of $\delta^{13}C$ and $\delta^{2}H$ variation in Rovno amber. However, stable isotope values, at least in the case of carbon isotopes, have been found to be remarkably homogeneous within a single deposit (Nissenbaum and Yakir, 1995), yet differ to a large extent between different deposits (Nissenbaum and Yakir, 1995; Tappert et al., 2013; Wolfe et al., 2016; Dal Corso et al., 2017). The close overlap in hydrogen and carbon isotopic ratios between the three batches of amber samples analyzed here is further consistent with a relatively homogeneous isotopic composition of Rovno amber (Fig. 2). Although there is a paucity of sedimentological information on the potential redeposition of amber in the Mezhygorje Formation written in English, an Eocene age is well-supported by the co-occurrence of a large number of species in Rovno and Baltic ambers (Perkovsky et al., 2010). The age discrepancy between the Lower Oligocene Mezhygorje Formation host rocks, and the amber itself is most easily explained by reworking of the Rovno amber. This implies some mixing and homogenization within the deposit, similar to what has been reported for Baltic amber (Weitschat and Wichard, 2010). Thus, despite the limited sample size and sourcing information, our dataset is sufficient for a first approach to differentiating these Central European ambers based on their isotopic compositions. However, further work on the heterogeneity of Rovno amber isotopic composition based on a more comprehensive set of Rovno amber samples is warranted.

The stable isotope data presented in this study suggests a contemporaneous, but geographically distinct origin for Rovno and Baltic ambers. Rovno amber seems to have originated in a warmer climate, more similar to that which produced the Bitterfeld amber deposit. By inference, this point of origin was likely several degrees of latitude to the south of the Baltic amber source region. This interpretation is largely supported by the detailed comparative paleoentomological work carried out on European ambers. On the one hand, a large amount of overlap has been found between the fossil arthropod assemblages of Baltic and Rovno ambers. For instance, the ant assemblages of Baltic, Bitterfeld, Scandinavian and Rovno ambers share 17 species (80% of total inclusions; Dlussky and Rasnitsyn, 2009) and shared species are also found among members of many other arthropod orders, such as spiders (Araneae), flies (Diptera), harvestmen (Opiliones), termites (Isoptera), and several others (reviewed in Perkovsky et al., 2010; Sontag and Szadziewski, 2011; Perkovsky and Rasnitsyn, 2013; Perkovsky, 2016), suggesting a similar formation time for these deposits in the Eocene (Perkovsky et al., 2007, 2010). On the other hand, Rovno and Baltic paleofaunas have been found to differ in many aspects. For example, Rovno amber contains a greater proportion of low-abundance ant species (i.e., greater diversity; Dlussky and Rasnitsyn, 2009); a lower ratio of holarctic to tropical ant specimens and species (Perkovsky, 2016); a much higher percentage of non-biting midges (Chironomidae) with terrestrial larva (Zelentsov et al., 2012); a lower diversity of thrips (Thysanoptera); a scarcity of amphibiotic insects, etc. (Perkovsky et al., 2010). In addition, over 200 fossil species from Rovno have not been identified in Baltic ambers (Dlussky and Rasnitsyn, 2009; Perkovsky et al., 2010, 2015; Perkovsky, 2013, 2016).

Szwedo and Sontag (2013) suggested that many of the reported differences in Baltic and Rovno amber fossil assemblages might be the result of insufficient taxonomic knowledge of the studied faunal groups. For example, Sontag and Szadziewski (2011) compared the relatively well-studied assemblages of biting midges (Ceratopogonidae) and found that < 1% of the specimens in Rovno amber represent species not found in Baltic amber, though a later study by Perkovsky (2013) countered by showing that several genera of biting midges related to warmer climates are more abundant in Rovno amber.

Despite some tropical influences in the paleofauna of amber inclusions, the paleoflora of the Rovno region consists mostly of temperate to subtropical plants (Pimenova, 1937; Perkovsky et al., 2010; E. E. Perkovsky, personal communication) and there is little evidence for substantial differences in comparison to the paleoflora of Baltic amber (Perkovsky et al., 2010). Our FTIR-spectra also seems to suggest largely similar source plants for both Rovno and Baltic ambers. This is despite apparent large differences in precipitation patterns and the mean temperature during resin exudation, as suggested by our δ^2H data. Similar amber-producing plant communities seem to have spread over thousands of kilometers of Eocene forests, from Scandinavia to the southern shores of the Paratethys.

If our hypothesis is valid, then it becomes possible to make a paleogeographic reconstruction of the source region of Rovno amber (Fig. 7). Rovno amber is clearly separated by sea from the massive deposit of Baltic amber, with implications for how inclusions in both deposits are studied and compared to one another. While the Bitterfeld and Rovno amber deposits remain difficult to distinguish on the basis of FTIR or stable isotopic data, there is hope that future work may more clearly delineate these smaller deposits. Geological evidence from the sediments surrounding Rovno amber still suggests that their source regions were geographically distinct. The occurrence of andalusite and tourmaline minerals in the sediments containing the ambers can be taken as evidence for the sourcing of Rovno amber from the exposed area of the Ukrainian shield on the Volhynian high, to the southeast of the deposit (Perkovsky et al., 2003, 2010; Ivanov et al., 2016). Importantly, this means that there is a substantial geographic separation between the source areas of three of the major European amber deposits from the Eocene. Our hypothesis about the relative geographical position of these deposits suggests that collections from each area should be treated as distinct samples, opening the door for comparative paleontological studies to make more detailed inferences on the paleobiogeography of Eocene Europe.

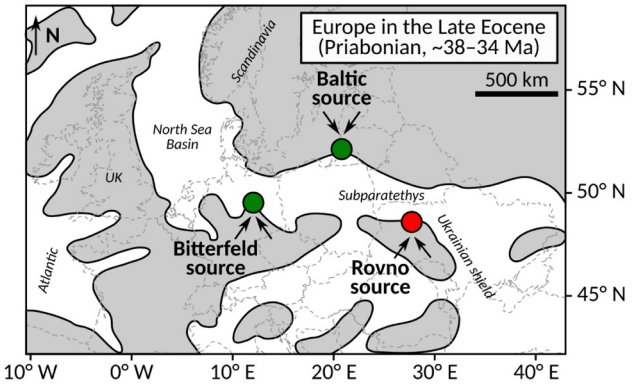

Fig. 7. A proposed paleogeographic reconstruction of the Rovno amber source area during the Late Eocene. Shaded areas represent Late Eocene landmass, contours are superimposed modern state borders.
Based on Wolfe et al. (2016) and Ivanov et al. (2016).

4. Conclusions

Stable carbon and hydrogen isotope analyses, as well as FTIR spectrometry, were carried out to study the relationship between Rovno, Baltic and Bitterfeld ambers, the three major variants of ambers grouped under the term "succinite". A close match in $\delta^{13}C$ and FTIR spectra supports a contemporaneous origin and similar source tree assemblages for Baltic, Bitterfeld and Rovno ambers. A 19‰ difference in δ^2H, however, suggests that Rovno amber originated much farther south than Baltic amber, perhaps at a similar latitude to Bitterfeld amber. We conclude that, despite similarities, inclusions from Central European ambers should not be lumped together into a broadly defined 'Baltic amber' assemblage. As such, these deposits offer an opportunity for detailed comparisons between roughly coeval assemblages created across a broad area and under a range of conditions.

Hydrogen isotopes are a compelling addition to the toolbox of amber studies, as they allow for a fine-scale paleolatitudinal differentiation between ambers. This would be more difficult to achieve using either resin type or fossil inclusions (e.g., bryophytes, arthropods), due to the reduced equator-pole thermal gradient during the Paleogene that blurred the latitudinal differences between plant and animal assemblages (Greenwood and Wing, 1995). A valuable future development would be an amber hydrogen isotope paleothermometer, if the substantial challenges inherent in the calibration of such a proxy can be successfully met.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.06.004.

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Competing interests

The authors have no competing interests to declare.

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