# TRIASSIC MICRO-CHARCOAL AS A PROMISING PUZZLE PIECE IN PALAEOCLIMATE RECONSTRUCTION: AN EXAMPLE FROM THE GERMANIC BASIN

Annette E. GÖTZ<sup>1\*</sup> & Dieter UHL<sup>2</sup>

<sup>1</sup> State Authority for Mining, Energy and Geology, Stilleweg 2, 30655 Hannover, Germany; e-mail: annette.goetz@lbeg.niedersachsen.de
<sup>2</sup> Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; e-mail: dieter.uhl@senckenberg.de
\* Corresponding author

Götz, A. E. & Uhl, D., 202X. Triassic micro-charcoal as a promising puzzle piece in palaeoclimate reconstruction: An example from the Germanic Basin. *Annales Societatis Geologorum Poloniae*, 92: 219–231.

Abstract: Fossil charcoal is the primary source of evidence for palaeo-wildfires and has gained increasing interest as a proxy in the reconstruction of past climates and environments. Today, increasing temperatures and decreasing precipitation/humidity appear to correlate with increases in the frequency and intensity of wildfires in many regions worldwide. Apart from appropriate climatic conditions, sufficient atmospheric oxygen (>15%) is a necessary precondition to sustain combustion in wildfires. The Triassic has long been regarded as a period without evidence of wildfires; however, recent studies on macro-charcoal have provided data indicating their occurrence throughout almost the entire Triassic. Still, the macro-palaeobotanical record is scarce and the study of micro-charcoal from palynological residue is seen as very promising to fill the gap in our current knowledge on Triassic wildfires. Here, the authors present the first, verified records of micro-charcoal from the Triassic of the Germanic Basin, complementing the scarce macro-charcoal evidence of wildfires during Buntsandstein, Muschelkalk and Keuper (Anisian-Rhaetian). The particles analysed by means of scanning electron microscopy (SEM) show anatomical features typical of gymnosperms, a major element of the early Mesozoic vegetation following the initial recovery phase after the PT-boundary event. From the continuously increasing dataset of Triassic charcoal, it becomes apparent that the identification of wildfires has a huge potential to play a crucial role in future studies, deciphering Triassic climate dynamics. The first SEM study of micro-charcoal from palynological residue spanning the entire Triassic period, presented here, is a key technique to further unravel the charcoal record as a puzzle piece in palaeoclimate reconstruction.

Key words: Wildfire, palaeoclimate, Triassic, Peri-Tethys, Germany.

Manuscript received 8 January 2022, accepted 15 June 2022.

# **INTRODUCTION**

Wildfires are an integral part of modern, terrestrial ecosystems and at the same time, increasing temperatures and changing precipitation patterns, related to ongoing global change, strongly affect global fire regimes (e.g., Jolly *et al.*, 2015; Veraverbeke *et al.*, 2017; Turco *et al.*, 2018; Halofsky *et al.*, 2020). Increases in the frequency, extent, and severity of wildfires appear to correlate with a warming climate, highlighting the fire-climate relationship. From this background, the study of fossil charcoal, the primary source of evidence for wildfires in the geological record, is seen as a powerful tool in the reconstruction of past climates (e.g., Whitlock and Larsen, 2001; Hu *et al.*, 2006; Vannière *et al.*, 2008; Cardoso *et al.*, 2018; Xu *et al.*, 2020; Lu *et al.*, 2021). Although the oldest records known so far date from the mid- to late Silurian (Glasspool *et al.*, 2004; Glasspool and Gastaldo, 2022), it is not until the Late Devonian when extensive charcoal deposits document globally widespread wildfires (Lu *et al.*, 2021). At that time, certainly sufficient fuel was available in the form of the first lignophytic forests (e.g., Decombeix *et al.*, 2005; Gerrienne *et al.*, 2010) and the atmospheric oxygen reached a level to sustain combustion in wildfires (Scott and Glasspool, 2006; Scott, 2010). The Permian and Triassic have long been regarded as periods without considerable evidence of wildfires (cf. Scott, 2000); however, over the past two decades the increasing number of reports of Permian and Triassic charcoal (e.g., Uhl and

Kerp, 2003; Uhl et al., 2004, 2007, 2012; Abu Hamad et al., 2012; Mahesh et al., 2015; Yan et al., 2016; Arzadún et al., 2017; Shivanna et al., 2017; Pole et al., 2018; Kubik et al., 2020; Murthy et al., 2020; Jasper et al., 2021; Wan et al., 2021; Murthy et al., 2022) has changed this view of a late Palaeozoic-early Mesozoic fire gap. Likewise, as more robust datasets have been published integrating geochemical, palaeontological, and sedimentological proxies, our understanding of the climate of the Triassic period changed from a stable hot-house world (e.g., Frakes, 1979) to a dynamic system, punctuated by numerous oscillations to and from humid conditions (e.g., Trotter et al., 2015; Sun et al., 2020; Forte et al., 2022). In contrast, the patchy published record of charcoal still hampers the use of this terrestrial proxy to further refine the Triassic climate history. In this regard, the study of micro-charcoal from palynological residue is seen as very promising to complement the still scarce macro-palaeobotanical record of Triassic wildfires. Although a number of palynological studies have reported the occurrence of putative Triassic micro-charcoal (cf. Abu Hamad et al., 2012), none of these studies has verified the charcoal nature of such material based on techniques such as SEM analyses of homogenized cell walls, which are widely accepted as standard in the analysis of macro-charcoal (e.g., Scott, 2000, 2010; Jasper et al., 2021). In fact, such an approach has only very rarely been used for the analysis of micro-charcoal from palynological samples (e.g., Martill et al., 2012; Pole et al., 2018), whereas most studies tried to identify micro-charcoal by means of transmitted light microscopy (e.g., Mangerud and Rømuld, 1991).

This paper presents the first SEM study on micro-charcoal from the Germanic Basin to fill the gap in our current knowledge on the fossil record of Triassic wildfires, both on a regional and global scale. The Germanic Basin is proposed as an excellent field lab for the study of the taphonomic processes of micro-charcoal in a well-established sedimentological and stratigraphical context (Fig. 1; Bachmann *et al.*, 2021; Franz and Barnasch, 2021; Franz *et al.*, 2021; Paul, 2021a). Moreover, this study aims to highlight the potential of pre-Quaternary micro-charcoal as a palaeoclimate proxy and to motivate further integrated palynological-palaeobotanical studies of charcoal in research on early Mesozoic palaeoclimates.

## **GEOLOGICAL SETTING**

During Triassic times, the western Tethys Ocean was bordered northwards by the peripheral Germanic Basin, the socalled northern Peri-Tethys (Szulc, 2000; Feist-Burkhardt *et al.*, 2008). This type region of the Triassic reflects the tripartition of the system, including the Lower Triassic continental, fluvial-aeolian deposits of the Buntsandstein, the Middle Triassic shallow-marine carbonates and evaporites of the Muschelkalk, and the fluvial, playa and deltaic to shallow-marine deposits of the Upper Triassic Keuper (Fig. 1). The well-established bio- and lithostratigraphic framework enables the genetic interpretation of depositional sequences across the basin (Aigner and Bachmann, 1992; Geluk and Röhling, 1997; Szulc, 2000; Pöppelreiter and Aigner, 2008; Götz and Lenhardt, 2011; Franz *et al.*, 2014, 2015) that is the basis for regional and global correlation. A generally arid to semi-arid climate predominated during the entire Triassic, though fluctuations in response to warming, induced by volcanic events, as well as recurrent marine flooding, have been recognized (Sellwood and Valdes, 2007; Preto *et al.*, 2010; Trotter *et al.*, 2015; Paul, 2021b). Isotopic data indicate extremely hot conditions in the Early Triassic, dropping slightly in the remainder of the Triassic (e.g., Scotese *et al.*, 2021). However, the timing of climate trends is still in flux and continuously improving with new geochronological data becoming available, as reflected in the recently updated Triassic timescale (Ogg and Chen, 2020) and the most recent version, 2022/02, of the International Chronostratigraphic Chart (Cohen *et al.*, 2013; updated 2022).

## **MATERIALS AND METHODS**

The palynofacies of Triassic deposits of the Germanic Basin is characterized by high amounts of opaque phytoclasts (e.g., Hauschke and Heunisch, 1990; Fijałkowska, 1994; Götz, 1996; Götz et al., 2001), which represent oxidized plant debris and in parts micro-charcoal (Fig. 2; particles smaller than 180 µm, as defined by Scott, 2010). However, so far none of the palynofacies studies carried out in the Germanic Triassic has addressed the identification of phytoclasts as charred particles, providing evidence of wildfire activity. Therefore, palynological residue of 62 samples from outcrops and wells, previously studied in detail with regard to stratigraphy (including palynology) and depositional environment (Tab. 1), and yielding phytoclasts of various sizes and shapes, was reanalysed by means of scanning electron microscopy to identify pyrogenic particles. These samples, housed at the Geozentrum Hannover, were processed using standard palynological preparation techniques (Wood et al., 1996; Traverse, 2007). For each sample, palynological residue was mounted on a glass disc, which was then fixed on a standard stub with an adhesive tab. After drying, the residue was platinum/palladium-coated for analysis under a FEI Sirion 200 scanning electron microscope at the Geozentrum Hannover. The identification of micro-charcoal is based on the presence of homogenized cell walls of phytoclasts, which are anatomically interpretable as originating from (woody) plant tissues (e.g., Jones and Chaloner, 1991; Scott, 2000, 2010). Anatomical details can be seen on a "sub-cellular" level, e.g., on tracheid fragments exhibiting pits. Already early studies in the 1970s and 1980s point to the need for SEM analysis to identify charcoal (Komarek et al., 1973; Patterson et al., 1987) and since then numerous SEM studies on fossil and modern charcoal have demonstrated that homogenized cell walls are a reliable feature to identify fossil charcoal fragments (e.g., Scott and Jones, 1991; Heinz and Barbaza, 1998; Rowe and Jones, 2000; Thevenon and Anselmetti, 2007; Tanner et al., 2012; El Atfy et al., 2019; Huang et al., 2021; Cai et al., 2021; Li et al., 2022).

# RESULTS

The palynological residue of 62 samples, reanalysed for the present study, reveals equidimensional and lath-shaped



**Fig. 1.** Locality map (left) and stratigraphic framework of charcoal discoveries in the Germanic Basin (right). Chronostratigraphy after Cohen *et al.* (2013, updated 2022), lithostratigraphy and facies from German Stratigraphic Commission (2016). Charcoal discoveries (right column): micro-charcoal occurrence (this study) with numbers of the sample localities provided on the locality map (stars indicate discoveries of solely oxidised phytoclasts; see results); macro-charcoal

discoveries (literature review): a – Uhl *et al.* (2010); b – Kelber (2021); c – Kelber (2007); d – Havlik *et al.* (2013), Kubik *et al.* (2015); e – Kelber (2007, 2021), Uhl and Montenari (2011). Abbreviations used: E. – Early; L. – Lower; M. – Middle; U. – Upper; Fm. – Formation; D1-D8 – Late Triassic unconformities.



Fig. 2. Palynofacies of the Germanic Basin, characterized by phytoclasts of different sizes, shapes, and preservation (Muschelkalk, Steudnitz). A. Opaque tracheid fragment (top) and equidimensional, angular-subrounded phytoclasts (below). B. Opaque, lath-shaped phytoclast (? charcoal). C. opaque phytoclast with bordered pits (? charcoal). D. Translucent wood remain. E. Translucent plant tissue.
F. Opaque, subangular phytoclasts. G. Opaque, angular phytoclast (? charcoal). H. Translucent tracheid fragment. I. Opaque tracheid fragment.

(elongate), charred particles in the range of 30–120 µm length, exhibiting homogenized cell walls and well-preserved anatomical details, such as bordered pits (Fig. 3). The particles mainly represent fragments of tracheids displaying anatomical features typical of gymnosperms, a major element of the early Mesozoic vegetation, following the initial recovery phase of the PT-boundary event (e.g., Grauvogel-Stamm and Ash, 2005). However, the taxonomic affinity remains unknown owing to the small size of phytoclasts.

The micro-charcoal studied occurs in terrestrial and shallow-marine deposits (Fig. 1), stratigraphically covering the early Anisian claystones of the Röt Formation (4 samples), the Anisian mud- and wackestones of the Lower Muschelkalk (7 samples), the late Anisian–early Ladinian mudstones of the Upper Muschelkalk (6 samples), the Ladinian clay- and siltstones of the Lettenkeuper (5 samples), the Carnian siltstones of the Schilfsandstein (6 samples) and Gipskeuper (7 samples), the Norian claystones of the Steinmergelkeuper (6 samples), and the Rhaetian clay- and siltstones of the Rhätkeuper (15 samples). All opaque phytoclasts of the Lower and Middle Buntsandstein siltstones (6 samples), analysed so far by means of SEM, lack diagnostic features of charcoal and are thus classified as oxidised particles.

Fluvial deposits (Buntsandstein, Lettenkeuper, Schilfsandstein) show abundant equidimensional particles, whereas shallow-marine and sabkha deposits (Röt, Muschelkalk, Gipskeuper, Steinmergelkeuper) reveal a wider spectrum of sizes and shapes (elongate to equidimensional).

Stratigraphy	Locality	No. of samples	Reference
Lower Buntsandstein (Induan)	Wulften-1 (Lower Saxony)	3	Backhaus et al. (2013)
Middle Buntsandstein (Olenekian)	Bockenem A100 (Lower Saxony)	3	Backhaus et al. (2013)
Röt (early Anisian)	Steudnitz (Thuringia)	4	Rameil et al. (2000)
Lower Muschelkalk (Anisian)	Steudnitz (Thuringia)	7	Rameil et al. (2000)
Upper Muschelkalk (Ladinian)	Sehnde (Lower Saxony)	6	Beutler et al. (1996)
Lettenkeuper (Ladinian)	Sehnde (Lower Saxony)	5	Beutler et al. (1996)
Schilfsandstein (Carnian)	Eisenach (Thuringia)	6	Franz et al. (2014)
Gipskeuper (Carnian)	Kümmelbach (Baden-Wurttemberg)	7	Heunisch and Nitsch (2011)
Steinmergelkeuper (Norian)	Wachsenburg (Thuringia)	6	Schulz (1996)
Rhätkeuper (Rhaetian)	Sehnde (Lower Saxony), Seeberg (Thuringia)	7 8	Beutler <i>et al.</i> (1996) Schulz (1962, 1967)

Selected samples for SEM analysis from outcrop and well sections located in the central part of the Germanic Basin, Germany.

## DISCUSSION

#### Refining the Triassic charcoal record

After two decades of collection of charcoal data, the previously assumed "Triassic tranquillity" with regard to wildfires (Scott, 2000) is no longer valid. To date, the record of Triassic charcoal is based on macro-charcoal findings from Central Europe (Kelber, 1999, 2007; Uhl et al., 2008, 2010; Uhl and Montenari, 2011; Havlik et al., 2013; Kubik et al., 2015; Philippe et al., 2015), the Southern Alps (Uhl et al., 2014), the Middle East (Abu Hamad et al., 2013, 2014), Russia, China, Greenland, USA, Argentina, Brazil, Australia and Antarctica (review in Abu Hamad et al., 2012; Kumar et al., 2013; Cardoso et al., 2018), indicating stratigraphic occurrence throughout almost the entire Triassic (Jasper et al., 2021). The so far oldest known, verified Triassic record was only recently reported from the uppermost Lower Triassic of China (Wan et al., 2021). Regionally, the scarce charcoal record of the Early Triassic, with findings mainly from localities at higher latitudes, might be explained by the central Pangaean "dead zone" (Sun et al., 2012), lacking sufficient vegetation as fuels. However, a marked increase in drought-tolerant plant taxa took place in central Pangaea during the early Permian (Marchetti et al., 2022), documenting the potential of certain plant groups for adaptation to increased temperature and aridity.

Macro-charcoal discoveries in the Germanic Basin are so far known from southern Germany and Poland (Kelber, 1999, 2007; Uhl *et al.*, 2008, 2010; Uhl and Montenari, 2011; Havlik *et al.*, 2013; Kubik *et al.*, 2015; Philippe *et al.*, 2015). Stratigraphically, these findings include the Anisian Voltzia Sandstone, the Ladinian Lettenkeuper, the Carnian Coburg Sandstone, the Norian Patoka Member and the Rhaetian Rhät-Sandstein.

The micro-charcoal discoveries presented in this study complement the macro-charcoal record of the Germanic Basin, highlighting certain times of extensive wildfire activity. In addition, the new data in the present study even provide a more nearly complete record (Fig. 1), especially in depositional settings, where macro-charcoal has not been reported so far, e.g., in shallow-marine Muschelkalk (Anisian–early Ladinian) deposits. On the other hand, the Germanic Basin is stratigraphically limited by the presence of Carnian/Norian unconformities. Thus, a global dataset is required to fill this missing stratigraphic record.

The single mention of late Olenekian–Anisian micro-charcoal in palynological slides from samples of the Barents Sea (Mangerud and Rømuld, 1991), studied by means of transmitted light microscopy, is questionable as the present authors showed that SEM analysis is imperative for distinguishing between oxidised phytoclasts and pyrogenic particles. So far, the data of the authors from the Germanic Basin reveal the oldest micro-charcoal within the early Anisian (Röt), confirming the previously recognized Early Triassic charcoal gap (cf. Abu Hamad *et al.*, 2012). The question remains, whether the Early Triassic charcoal gap reflects an Early Triassic wildfire gap or has to be seen as an artefact due to various taphonomic biases, as discussed in Abu Hamad *et al.* (2012).

#### Deciphering regional vs. local signals

Iversen (1941) was the first to realize that micro-charcoal in palynological slides could be used as a fire proxy. However, this method holds limitations with regard to size and source, as larger charcoal particles can break during transport, creating a high abundance of small particles (smaller than 100  $\mu$ m). Quantification of micro-charcoal is also extremely difficult, especially in deposits, which also contain macro-charcoal. Owing to the compaction of sediments, larger specimens of macro-charcoal are often shattered *in situ* to smaller pieces (e.g., Uhl *et al.*, 2010: see fig. 5 therein; Kubik *et al.*, 2015: see fig. 7 therein). Although macro-charcoal can be transported by water over large distances (e.g., Scott *et al.*, 2014), it is usually interpreted as a signal for local fires. In contrast, micro-charcoal documents



**Fig. 3.** Examples of micro-charcoal of the Germanic Basin. **A.** Tracheid fragment with a bordered pit (Röt, Steudnitz). **B.** Tracheid fragment with homogenized cell walls (Muschelkalk, Steudnitz). **C.** Tracheid fragment with homogenized cell walls (Lettenkeuper, Sehnde). **D.** Tracheid fragment with homogenized cell walls (Schilfsandstein, Eisenach). **E.** Tracheid fragment with homogenized cell walls (Steinmergelkeuper, Wachsenburg). **F.** Tracheid fragment with bordered pits (Rhätkeuper, Seeberg).

ongoing distribution during widespread fires and is thus considered as a regional signal. The knowledge of the exact source area remains generally vague, owing to possible transport (see discussion in Whitlock and Larsen, 2001).

For the Triassic period, the above-mentioned limitations with regard to distinguishing between regional and local signals can be overcome by an integrated palynological-palaeobotanical-sedimentological study within a distinct sedimentary basin. Here, the Germanic Basin, representing an intra-cratonic basin, is well suited to analysis of the transport and taphonomic processes of charred particles. Different fluvial styles (meandering, straight, braided, anastomosing), well documented in the Early Triassic Buntsandstein and Late Triassic Keuper deposits (Feist-Burkhardt *et al.*, 2008; Paul, 2021a; Franz and Barnasch, 2021), enable the study of the effect of different hydrodynamic regimes on fragmentation of charred particles during transport. Different bed load is another aspect to consider, when interpreting size and shape of these particles. Moreover, sorting and fragmentation of organic particles within a shallow-marine setting is well documented in Middle Triassic Muschelkalk carbonates (Rameil *et al.*, 2000) and needs to be assessed with regard to potential source areas. Furthermore, taphonomic biases, as previously discussed in detail by Abu Hamad *et al.* (2012), have to be considered, especially the low preservation potential of charcoal in typical red beds, which predominate in the Early Triassic Buntsandstein of the Germanic Basin.

#### Implications for palaeoclimate reconstruction

An important factor, influencing the occurrence of palaeo-wildfires, is atmospheric oxygen concentration (e.g., Scott, 2000). Some studies related the absence of wildfires during the Early Triassic to extremely low oxygen concentrations and the subsequent increase of evidence for wildfires during the Middle and Late Triassic with increasing oxygen concentrations (e.g., Tanner et al., 2006). However, different geochemical models differ considerably regarding the development of atmospheric oxygen during the Triassic (e.g., Berner and Canfield, 1989; Bergman et al., 2004; Berner, 2005, 2006, 2009; Glasspool and Scott, 2010). Notably, more recent models reconstructed oxygen levels above 15% O<sub>2</sub> for the Early Triassic, which is in accordance with palaeontological evidence other than charcoal, such as the occurrence of large-bodied amphibians (e.g., Schroeder, 1913; Schoch, 1999; Damiani, 2001), which definitely require relatively high oxygen levels to breathe through both their lungs and through their skin (see discussion in Abu Hamad et al., 2012). At such a concentration (>15%), oxygen would not necessarily be the limiting factor for the ignition and spread of wildfires (e.g., Belcher and McElwain, 2008; Abu Hamad et al., 2012).

Another factor, which may influence the amount of charcoal that is initially produced and, after transport, preserved in sedimentary deposits, is the source vegetation. Besides the amount of biomass produced in different ecosystems (e.g., Early Triassic Pleuromeia and fern-dominated vegetation versus Middle/Late Triassic conifer-dominated vegetation) that can be consumed by fires as fuel, also the morphology and anatomy of different plant taxa of the source vegetation greatly influence wildfires and the amount of charcoal that can be produced during a fire (e.g., Abu Hamad et al., 2012; Scott et al., 2014; Belcher, 2016; Crawford et al., 2018; Hudspith et al., 2018). However, this problem can probably be overcome by combining charcoal analysis with traditional palynological and macro-palaeobotanical data. In the case of the Germanic Basin, palynofloras were dominated by bisaccate pollen-producing conifers (cf. Grauvogel-Stamm and Kustatscher, 2021; Heunisch and Wierer, 2021; Kelber, 2021).

Ultimately, for Triassic climate reconstruction, micro-charcoal can be added as a vital terrestrial proxy for wildfires (Fig. 4). From the continuously increasing dataset of Triassic charcoal, it becomes apparent that the identification of wildfires will play a crucial role in future studies, deciphering Triassic climate dynamics, as it seems at first sight that the occurrence of wildfires correlates with warming phases. This observation is supported by the conclusions drawn from a recent review of the published records of combustion products and inferred wildfire activity across major episodes of greenhouse-gas-induced global warming (Baker, 2022), demonstrating the striking link between periods of increased wildfire activity and phases of major climatic change in Earth's past. For the Triassic, multiple warming phases were first highlighted by Trotter et al. (2015). At the same time, Whiteside et al. (2015) argued that variations in  $\delta^{13}C_{org}$ , pointing to rapidly fluctuating extreme climatic conditions during the Late Triassic, seem to correlate with elevated and increasing  $pCO_2$  and pervasive wildfires. The link of wildfire occurrence to warming phases and palaeoenvironmental perturbation as well as the potential role of fire-climate-vegetation interactions and feedbacks as discussed by Baker (2022) is the next research goal to detect a possible Triassic fire-climate relationship. As recent models indicate that climate change affects fire activity differently in different biomes (Harris et al., 2016) and ecosystems with positive fire-vegetation feedbacks are vulnerable to climate-change-driven increases in fire activity (Tepley et al., 2018), the understanding of vegetational patterns of the past becomes even more vital in palaeoclimate research. Here, palynology and palaeobotany are key disciplines. Additionally, the Germanic Basin is well suited to study the potential role of additional nutrients from wildfires on marine phytoplankton production during the Middle Triassic, as recently documented from modern fire-prone coastal regions (Liu et al., 2022). Finally, our understanding of deep time data will benefit from studies of the Quaternary (cf. Seddon et al., 2014), especially the Holocene, as processes and ecological patterns in a warming world should be comparable to those of the Triassic period.

### **CONCLUSIONS**

Various Triassic deposits of the Germanic Basin yield micro-charcoal in terrestrial and shallow-marine environments. Their stratigraphic distribution provides additional information on wildfire occurrence and complements the scarce macro-palaeobotanical record. The nature of opaque phytoclasts - whether oxidised particles or micro-charcoal – as prominent organic components in palynological slides, needs to be verified by scanning electron microscopy. The unambiguous identification of pyrogenic particles is best based on the presence of homogenized cell walls, one of the diagnostic features of charcoal. Comparison with the global record indicates that charcoal occurrence corresponds to warming phases and thus is vital in Triassic climate reconstruction. Ultimately, quantitative studies are needed to capture frequency and intensity of wildfires and to detect whether these events correlate with warming phases or periods of environmental instability.



**Fig. 4.** First-order warming cycles (W1-3) based on Tethyan surface open-marine temperatures inferred from the conodont  $\delta^{18}O_{phos}$  record of stratigraphic sections of the central and western Tethyan realm (modified from Trotter *et al.*, 2015). Major biotic events of the Triassic period (right column; compiled by Trotter *et al.*, 2015) and occurrence of micro- and macro-charcoal in the Germanic Basin (this study and literature review, highlighted by red stars) as source of evidence for wildfires. The question mark indicates the recognized Early Triassic wildfire gap. Abbreviations used: PTB – Permian-Triassic boundary, Ind. – Induan, Olen. – Olenekian, G. – Griesbachian, D. – Dienerian, Sm. – Smithian, Sp. – Spathian, An. – Aegean, B. – Bithynian, P. – Pelsonian, I. – Illyrian, F. – Fassanian, Lo. – Longobardian, J. – Julian, T. – Tuvalian, La. – Lacian, Al. – Alaunian, S. – Sevatian.

#### Acknowledgements

We thank G. Grützner for palynological slide preparation and S. Stäger for assistance during SEM analyses at the Geozentrum Hannover. Discussions with P. Stojakowits on charcoal in Quaternary terrestrial ecosystems provided a modern view on the fossil record. The comments of Michał Matysik, an anonymous reviewer, and technical editor Paweł Filipiak improved the manuscript and are gratefully acknowledged. This research was first presented at the online Annual Meeting of the Palynological Society (AASP) in August 2021, when firefighters in the western part of North America and southern Europe battled to bring under control devastating wildfires.

# REFERENCES

- Abu Hamad, A. M. B., Jasper, A. & Uhl, D., 2012. The record of Triassic charcoal and other evidence for palaeo-wildfires: Signal for atmospheric oxygen levels, taphonomic biases or lack of fuel? *International Journal of Coal Geology*, 96–97: 60–71.
- Abu Hamad, A. M. B., Jasper, A. & Uhl, D., 2013. Charcoal remains from the Mukheiris Formation of Jordan – the first evidence of palaeowildfire from the Anisian (Middle Triassic) of Gondwana. *Jordan Journal of Earth and Environmental Sciences*, 5: 17–22.
- Abu Hamad, A. M. B., Jasper, A. & Uhl, D., 2014. Wood remains from the Late Triassic (Carnian) of Jordan and their paleoenvironmental implications. *Journal of African Earth Sciences*, 95: 168–174.
- Aigner, T. & Bachmann, G. H., 1992. Sequence-stratigraphic framework of the German Triassic. *Sedimentary Geology*, 80: 115–135.
- Arzadún, G., Cisternas, M. E., Cesaretti, N. N. & Tomezzoli, R. N., 2017. Presence of charcoal as evidence of paleofires in the Claromecó Basin, Permian of Gondwana, Argentina: Diagenetic and paleoenvironment analysis based on coal petrography studies. *GeoResJ*, 14: 121–134.
- Bachmann, G. H., Beutler, G., Franz, M., Hagdorn, H., Hauschke, N., Kozur, H. W. & Röhling, H.-G., 2021. Stratigraphie der Germanischen Trias in Deutschland und Nachbarländern. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias Aufbruch in das Erdmittelalter*. Pfeil, Munich, pp. 22–39.
- Backhaus, E., Hagdorn, H., Heunisch, C. & Schulz, E., 2013. Biostratigraphische Gliederungsmöglichkeiten des Buntsandstein. In: Deutsche Stratigraphische Kommission (ed.), Stratigraphie von Deutschland XI. Buntsandstein. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, 69: 151–164.
- Baker, S. J., 2022. Fossil evidence that increased wildfire activity occurs in tandem with periods of global warming in Earth's past. *Earth-Science Reviews*, 224: 103871.
- Belcher, C. M., 2016. The influence of leaf morphology on litter flammability and its utility for interpreting palaeofire. *Philosophical Transactions of the Royal Society of London: Biological Sciences*, 371: 20150163.
- Belcher, C. M. & McElwain, J. C., 2008. Limits for combustion in low O<sub>2</sub> redefine paleoatmospheric predictions for the Mesozoic. *Science*, 321: 1197–1200.
- Bergman, N. M., Lenton, T. M. & Watson, A. J., 2004. COPSE: a new model of biogeochemical cycling over Phanerozoic time. *American Journal of Science*, 304: 397–437.
- Berner, R. A., 2005. The carbon and sulfur cycles and atmospheric oxygen from middle Permian to middle Triassic. *Geochimica et Cosmochimica Acta*, 69: 3211–3217.
- Berner, R. A., 2006. GEOCARBSULF: a combined model for Phanerozoic atmospheric O<sub>2</sub> and CO<sub>2</sub>. *Geochimica et Cosmochimica Acta*, 70: 5653–5664.
- Berner, R. A., 2009. Phanerozoic atmospheric oxygen: new results using the GEOCARBSULF model. *American Journal of Science*, 309: 603–606.
- Berner, R. A. & Canfield, D. E., 1989. A new model for atmospheric oxygen over Phanerozoic time. *American Journal of Science*, 289: 333–361.

- Beutler, G., Heunisch, C., Luppold, F. W., Rettig, B. & Röhling, H.-G., 1996. Muschelkalk, Keuper und Lias am Mittellandkanal bei Sehnde (Niedersachsen) und die regionale Stellung des Keupers. *Geologisches Jahrbuch*, A145: 67–197.
- Cai, Y.-F., Zhang, H., Feng, Z. & Shen, S.-Z., 2021. Intensive wildfire associated with volcanism promoted the vegetation changeover in Southwest China during the Permian–Triassic transition. *Frontiers in Earth Science*, 9: 615–841.
- Cardoso, D., Mizusaki, A. M. P., Guerra-Sommer, M., Menegat, R., Jasper, A. & Uhl, D., 2018. Wildfires in the Triassic of Gondwana Paraná Basin. *Journal of South American Earth Sciences*, 82: 193–206.
- Cohen, K. M., Finney, S. C., Gibbard, P. L. & Fan, J.-X., 2013 [updated 2022]. The ICS International Chronostratigraphic Chart. *Episodes*, 36: 199–204.
- Crawford, A. J., Baker, S. J. & Belcher, C. M., 2018. Fossil charcoals from the Lower Jurassic challenge assumptions about charcoal morphology and identification. *Palaeontology*, 61: 49–56.
- Damiani, R. J., 2001. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). Zoological Journal of the Linnean Society, 133: 379–482.
- Decombeix, A.-L., Meyer-Berthaud, B., Rowe, N. & Galtier, J., 2005. Diversity of large woody lignophytes preceding the extinction of *Archaeopteris*: New data from the middle Tournaisian of Thuringia (Germany). *Review of Palaeobotany* and Palynology, 137: 69–82.
- El Atfy, H., Anan, T., Jasper, A. & Uhl, D., 2019. Repeated occurrence of palaeo-wildfires during deposition of the Bahariya Formation (early Cenomanian) of Egypt. *Journal of Palaeogeography*, 8: 28.
- Feist-Burkhardt, S., Götz, A. E., Szulc, J. (coord.), Borkhataria, R., Geluk, M., Haas, J., Hornung, J., Jordan, P., Kempf, O., Michalík, J., Nawrocki, J., Reinhardt, L., Ricken, W., Röhling, G.-H., Rüffer, T., Török, Á. & Zühlke, R., 2008. Triassic. In: McCann, T. (ed.), *The Geology of Central Europe. Vol. 2.* Geological Society, London, pp. 749–821.
- Fijałkowska, A., 1994. Palynostratigraphy of the Lower and Middle Buntsandstein in north-western part of the Holy Cross Mts. *Geological Quarterly*, 38: 59–96.
- 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. *Rivista Italiana di Paleontologia e Stratigrafia*, 128: 105–127.
- Frakes, L. A., 1979. Climates throughout Geologic Time. Elsevier, Amsterdam, 310 pp.
- Franz, M. & Barnasch, J., 2021. Der Keuper im zentralen Germanischen Becken. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias – Aufbruch in das Erdmittelalter*. Pfeil, Munich, pp. 83–108.
- Franz, M., Kaiser, S. I., Fischer, J., Heunisch, C., Kustatscher, E., Luppold, F. W., Berner, U. & Röhling, H.-G., 2015. Eustatic and climatic control on the Upper Muschelkalk Sea (late Anisian/Ladinian) in the Central European Basin. *Global and Planetary Change*, 135: 1–27.
- Franz, M., Nowak, K., Berner, U., Heunisch, C., Bandel, K., Röhling, H.-G. & Wolfgramm, M., 2014. Eustatic control on epicontinental basins: the example of the Stuttgart Formation

in the Central European Basin (Middle Keuper, Late Triassic). *Global and Planetary Change*, 122: 305–329.

- Franz, M., Voigt, T. & Müller, A., 2021. Der Muschelkalk im zentralen Germanischen Becken. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias – Aufbruch in das Erdmittelalter*. Pfeil, Munich, pp. 57–82.
- Geluk, M. C. & Röhling, H.-G., 1997. High-resolution sequence stratigraphy of the Lower Triassic 'Buntsandstein' in the Netherlands and northwestern Germany. *Geologie en Mijnbouw*, 76: 227–246.
- German Stratigraphic Commission (ed.), 2016. *Stratigraphic Table* of Germany 2016. German Research Centre for Geosciences, Potsdam.
- Gerrienne, P., Meyer-Berthaud, B., Lardeux, H. & Régnault, S., 2010. First record of *Rellimia* Leclercq & Bonamo (Aneurophytales) from Gondwana, with comments on the earliest lignophytes. In: Vecoli, M., Clément, G. & Meyer-Berthaud, B. (eds), *The Terrestrialization Process: Modelling Complex Interactions at the Biosphere–Geosphere Interface. Geological Society, London, Special Publications*, 339: 81–92.
- Glasspool, I. J., Edwards, D. & Axe, L., 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology*, 32: 381–383.
- Glasspool, I. J. & Gastaldo, R. A., 2022. Silurian wildfire proxies and atmospheric oxygen. *Geology*, 50: 1048–1052.
- Glasspool, I. J. & Scott, A. C., 2010. Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. *Nature Geosciences*, 3: 627–630.
- Götz, A. E., 1996. Palynofazielle Untersuchungen zweier Geländeprofile im Unteren Muschelkalk Osthessens und Westthüringens. *Geologisches Jahrbuch Hessen*, 124: 87–96.
- Götz, A. E., Feist-Burkhardt, S. & Dittrich, D., 2001. Lithostratigraphie und Palynofazies des Unteren Muschelkalk (Mitteltrias, Anis) der Forschungsbohrung Onsdorf (Saargau). *Mainzer geowissenschaftliche Mitteilungen*, 30: 43–66.
- Götz, A. E. & Lenhardt, N., 2011. The Anisian carbonate ramp system of Central Europe (Peri-Tethys Basin): sequences and reservoir characteristics. *Acta Geologica Polonica*, 61: 59–70.
- Grauvogel-Stamm, L. & Ash, S. R., 2005. Recovery of the Triassic land flora from the end-Permian life crisis. *Comptes Rendus Palevol*, 4: 525–540.
- Grauvogel-Stamm, L. & Kustatscher, E., 2021. Makrofloren der Germanischen Trias: Buntsandstein und Muschelkalk. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias – Aufbruch in das Erdmittelalter*. Pfeil, Munich, pp. 218–227.
- Halofsky, J. E., Peterson, D. L. & Harvey, B. J., 2020. Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. *Fire Ecology*, 16: 1–26.
- Harris, R. M. B., Remenyi, T. A., Williamson, G. J., Bindoff, N. L.
  & Bowman, D. M. J. S., 2016. Climate-vegetation-fire interactions and feedbacks: trivial detail or major barrier to projecting the future of the Earth system? *WIREs Climate Change*, 7: 910–931.
- Hauschke, N. & Heunisch, C., 1990. Lithologie und Palynologie der Bohrung USB 3 (Horn – Bad Meinberg, Ostwestfalen): ein Beitrag zur Faziesentwicklung im Keuper. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 181: 79–105.

- Havlik, P., Aiglstorfer, M., El Atfy, H. & Uhl, D., 2013. A peculiar bonebed from the Norian Stubensandstein (Löwenstein Formation, Late Triassic) of southern Germany and its palaeoenvironmental interpretation. *Neues Jahrbuch für Geologie* und Paläontologie, Abhandlungen, 269: 321–337.
- Heinz, C. & Barbaza, M., 1998. Environmental changes during the Late Glacial and Post-Glacial in the central Pyrenees (France): new charcoal analysis and archaeological data. *Review of Palaeobotany and Palynology*, 104: 1–17.
- Heunisch, C. & Nitsch, E., 2011. Eine seltene Mikroflora aus der Mainhardt Formation (Keuper, Trias) von Baden-Württemberg (Süddeutschland). Jahresberichte und Mitteilungen des oberrheinischen geologischen Vereins, Neue Folge, 93: 55–76.
- Heunisch, C. & Wierer, J. F., 2021. Palynomorphe der Germanischen Trias. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias – Aufbruch in das Erdmittelalter*. Pfeil, Munich, pp. 205–217.
- Hu, F. S., Brubaker, L. B., Gavin, D. G., Higuera, P. E., Lynch, J. A., Rupp, T. S. & Tinner, W., 2006. How climate and vegetation influence the fire regime of the Alaskan boreal biome: the Holocene perspective. *Mitigation and Adaptation Strategies for Global Change*, 11: 829–846.
- Huang, Y.-J., Shen, H., Jia, L.-B., Li, S.-F., Su, T., Nam, G.-S., Zhu, H. & Zhou, Z.-K., 2021. Macroscopic fossil charcoals as proxy of a local fire linked to conifer-rich forest from the late Pliocene of northwestern Yunnan, Southwest China. *Palaeoworld*, 30: 551–561.
- Hudspith, V. A., Hadden, R. M., Bartlett, A. I. & Belcher, C. M., 2018. Does fuel type influence the amount of charcoal produced in wildfires? Implications for the fossil record. *Palaeontology*, 61: 159–171.
- Iversen, J., 1941. Land occupation in Denmark's Stone Age. Danmarks Geologiske Forenhandlungen II, 66: 1–126.
- Jasper, A., Pozzebon-Silva, Â., Siqueira Carniere, J. & Uhl, D., 2021. Palaeozoic and Mesozoic palaeo–wildfires: An overview on advances in the 21<sup>st</sup> Century. *Journal of Palaeosciences*, 70: 159–171.
- Jolly, W. M., Cochrane, M. A., Freeborn, P. H., Holden, Z. A., Brown, T. J., Williamson, G. J. & Bowman, D. M. J. S., 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, 6: 7537.
- Jones, T. P. & Chaloner, W., 1991. Charcoal, its recognition and palaeoatmospheric significance. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 97: 29–50.
- Kelber, K.-P., 1999. Der Nachweis von Paläo-Wildfeuer durch fossile Holzkohlen aus dem süddeutschen Keuper. *Terra Nostra*, 99/8: 41.
- Kelber, K.-P., 2007. Die Erhaltung und paläobiologische Bedeutung der fossilen Hölzer aus dem süddeutschen Keuper (Trias, Ladinium bis Rhätium). In: Schüssler, H. & Simon, T. (eds), Aus Holz wird Stein – Kieselhölzer aus dem Keuper Frankens. Offsetdruck Eppe GmbH, Bergatreute-Aulendorf, pp. 37–100.
- Kelber, K.-P., 2021. Makrofloren der Germanischen Trias: Keuper. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias* – Aufbruch in das Erdmittelalter. Pfeil, Munich, pp. 228–248.
- Komarek, E. V., Komarek, B. B. & Carlysle, T. C., 1973. The ecology of smoke particulates and charcoal residues from forest and grassland fires: a preliminary atlas. *Bulletin of Tall Timbers Research Station, Miscellaneous Publication*, 3: 1–75.

- Kubik, R., Uhl, D. & Marynowski, L., 2015. Evidence of wildfires during the deposition of the Upper Silesian Keuper succession, Southern Poland. *Annales Societatis Geologorum Poloniae*, 85: 685–696.
- Kubik, R., Marynowski, L., Uhl, D. & Jasper, A., 2020. Cooccurrence of charcoal, polycyclic aromatic hydrocarbons and terrestrial biomarkers in an early Permian swamp to lagoonal depositional system, Paraná Basin, Rio Grande do Sul, Brazil. *International Journal of Coal Geology*, 230: 103590.
- Kumar, K., Chatterjee, S., Tewari, R., Mehrotra, N. C. & Singh, G. K., 2013. Petrographic evidence as an indicator of volcanic forest fire from the Triassic of Allan Hills, South Victoria Land, Antarctica. *Current Science*, 104: 422–424.
- Li, G., Gao, L., Liu, F., Qiu, M. & Dong, G., 2022 (in press). Quantitative studies on charcoalification: Physical and chemical changes of charring wood. *Fundamental Research*, https:// doi.org/10.1016/j.fmre.2022.05.014
- Liu, D., Zhou, C., Keesing, J. K., Serrano, O., Werner, A., Fang, Y., Chen, Y., Masque, P., Kinloch, J., Sadekov, A. & Du, Y., 2022. Wildfires enhance phytoplankton production in tropical oceans. *Nature Communications*, 13: 1348.
- Lu, M., Ikejiri, T. & Lu, Y., 2021. A synthesis of the Devonian wildfire record: Implications for paleogeography, fossil flora, and paleoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 571: 110321.
- Mahesh, S., Murthy, S., Charaborty, B. & Roy, M. D., 2015. Fossil charcoal as palaeofire indicators: Taphonomy and morphology of charcoal remains in sub-surface Gondwana sediments of South Karanpura Coalfield. *Journal of the Geological Society* of India, 85: 567–576.
- Mangerud, G. & Rømuld, A., 1991. Spathian–Anisian (Triassic) palynology at the Svalis Dome, southwestern Barents Sea. *Review of Palaeobotany and Palynology*, 70: 199–216.
- Marchetti, L., Forte, G., Kustatscher, E., DiMichele, W., Spencer, L., Roghi, G., Juncal, M., Hartkopf-Fröder, C., Krainer, K., Morelli, C. & Ronchi, A., 2022. The Artinskian Warming Event: an Euramerican change in climate and the terrestrial biota during the early Permian. *Earth-Science Reviews*, 226: 103922.
- Martill, D. M., Loveridge, R. F., Mohr, B. A. R. & Simmonds, E., 2012. A wildfire origin for terrestrial organic debris in the Cretaceous Santana Formation Fossil Lagerstätte (Araripe Basin) of north-east Brazil. *Cretaceous Research*, 34: 135–141.
- Murthy, S., Mendhe, V. A., Kavali, P. S. & Singh, V. P., 2020. Evidence of recurrent wildfire from the Permian coal deposits of India: Petrographic, scanning electron microscopic and palynological analyses of fossil charcoal. *Palaeoworld*, 29: 715–728.
- Murthy, S., Uhl, D., Jasper, A., Sarate, O. S. & Mishra, D. P., 2022. New Evidence for Palaeo-wildfire in the Early Permian (Artinskian) of Gondwana from Wardha Valley Coalfield, India. *Journal of the Geological Society of India*, 98: 395–401.
- Ogg, J. G. & Chen, Z.-Q. with contributions of Orchard, M. J. & Jiang, H. S., 2020. The Triassic Period. In: Gradstein, F. M., Ogg, J. G., Schmitz, M. D. & Ogg, G. M. (eds), *Geological Time Scale 2020, Vol. 2.* Elsevier, Amsterdam, pp. 903–953.
- Patterson, W. A., Edwards, K. J. & Maguire, D. J., 1987. Microscopic charcoal as a fossil indicator of fire. *Quaternary Science Reviews*, 6: 3–23.

- Paul, J., 2021a. Der Buntsandstein im zentralen Germanischen Becken. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias – Aufbruch in das Erdmittelalter*. Pfeil, Munich, pp. 49–56.
- Paul, J., 2021b. Klima der Trias im Germanischen Becken. In: Hauschke, N., Franz, M. & Bachmann, G. H. (eds), *Trias – Aufbruch in das Erdmittelalter*. Pfeil, Munich, pp. 152–157.
- Philippe, M., Pacyna, G., Wawrzyniak, Z., Barbacka, M., Boka, K., Filipiak, P., Marynowski, L., Thevenard, F. & Uhl, D., 2015. News from an old wood *Agathoxylon keuperianum* (Unger) nov. comb. in the Keuper of Poland and France. *Review of Palaeobotany and Palynology*, 221: 83–91.
- Pole, M., Wang, Y. D., Dong, C., Xie, X. P., Tian, N., Li, L. Q., Zhou, N., Lu, N., Xie, A. W. & Zhang, X. Q., 2018. Fires and Storms – A Triassic-Jurassic transition section in the Sichuan Basin, China. *Palaeobiodiversity and Palaeoenvironments*, 98: 29–47.
- Pöppelreiter, M. & Aigner, T., 2008. High-resolution sequence stratigraphy, facies patterns and controls in a mixed epeiric shelf: Implications for reservoir prediction (Lower Keuper, Triassic, German Basin). *Geological Association of Canada, Special Paper*, 48: 283–301.
- Preto, N., Kustatscher, E. & Wignall, P. B., 2010. Triassic climates – State of the art and perspectives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290: 1–10.
- Rameil, N., Götz, A. E. & Feist-Burkhardt, S., 2000. Highresolution sequence interpretation of epeiric shelf carbonates by means of palynofacies analysis: an example from the Germanic Triassic (Lower Muschelkalk, Anisian) of East Thuringia, Germany. *Facies*, 43: 123–144.
- Rowe, N. P. & Jones, T. P., 2000. Devonian charcoal. Palaeogeography, Palaeoclimatology, Palaeoecology, 164: 331–338.
- Schoch, R. R., 1999. Comparative osteology of Mastodonsaurus giganteus (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). Stuttgarter Beiträge zur Naturkunde, Serie B, 278: 1–175.
- Schroeder, H. C., 1913. Ein Stegocephalen-Schädel von Helgoland. Jahrbuch der Preussischen Geologischen Landesanstalt und Bergakademie, 33: 232–264.
- Schulz, E., 1962. Sporenpaläontologische Untersuchungen zur Rhät-Lias-Grenze in Thüringen und der Altmark. *Geologie*, 11: 308–319.
- Schulz, E., 1967. Sporenpaläontologische Untersuchungen rätoliassischer Schichten im Zentralteil des Germanischen Beckens. Paläontologische Abhandlungen, Abteilung B 2: 541–633.
- Schulz, E., 1996. Eine Mikroflora aus dem Steinmergelkeuper vom SW-Hang der Wachsenburg bei Gotha (Thüringen). Neues Jahrbuch Geologie Paläontologie, Abhandlungen, 200: 75–86.
- Scotese, C. R., Song, H., Mills, B. J. W. & van der Meer, D. G., 2021. Phanerozoic paleotemperatures: The earth's changing climate during the last 540 million years. *Earth-Science Reviews*, 215: 103503.
- Scott, A. C., 2000. The pre-Quaternary history of fire. Palaeogeography, Palaeoclimatology, Palaeoecology, 164: 297–345.
- Scott, A. C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 291: 11–39.

- Scott, A. C., Bowman, D. M. J. S., Bond, W. J., Pyne, S. J. & Alexander, M. E., 2014. *Fire on Earth: An Introduction*. Wiley Blackwell, Chichester, 413 pp.
- Scott, A. C. & Glasspool, I. J., 2006. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proceedings of the National Academy of Sciences of the United States of America*, 103: 10861–10865.
- Scott, A. C. & Jones, T. P., 1991. Microscopical observations of Recent and fossil charcoal. *Microscopy and Analysis*, 25: 13–15.
- Seddon, A. W. R., Mackay, A. W., Baker, A. G., Birks, H. J. B., Breman, E., Buck, C. E., Ellis, E. C., Froyd, C. A., Gill, J. L., Gillson, L., *et al.*, 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. *Journal of Ecology*, 102: 256–267.
- Sellwood, B. W. & Valdes, P. J., 2007. Mesozoic climate. In: Williams, M., Haywood, A. M., Gregory, F. J. & Schmidt, D. N. (eds), Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies. The Micropalaeontological Society, Special Publications. Geological Society, London, pp. 210–224.
- Shivanna, M., Murthy, S., Gautam, S., Souza, P. A., Kavali, P. S., Cerruti Bernardes-de-Oliveira, M. E., Ram-Awatar & Félix, M. C., 2017. Macroscopic charcoal remains as evidence of wildfire from late Permian Gondwana sediments of India: Further contribution to global fossil charcoal database. *Palaeoworld*, 26: 638–649.
- Sun, Y., Joachimski, M. M., Wignall, P. B., Yan, C., Chen, Y., Jiang, H., Wang, L., Lai, X., 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science*, 338: 366–370.
- Sun, Y. D., Orchard, M. J., Kocsis, Á. T. & Joachimski, M. M., 2020. Carnian–Norian (Late Triassic) climate change: Evidence from conodont oxygen isotope thermometry with implications for reef development and Wrangellian tectonics. *Earth and Planetary Science Letters*, 534: 116082.
- Szulc, J., 2000. Middle Triassic evolution of the northern Peri-Tethys area as influenced by early opening of the Tethys Ocean. Annales Societatis Geologorum Poloniae, 70: 1–48.
- Tanner, L., Spencer, G. L. & Zeigler, K. E., 2006. Rising oxygen levels in the Late Triassic: Geological and evolutionary evidence. In: Harris, J. D., Spencer, G. L. & Speilmann, J. A. (eds), *The Triassic–Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin*, 37: 5–11.
- Tanner, L. H., Wang, X. & Morabito, A. C., 2012. Fossil charcoal from the Middle Jurassic of the Ordos Basin, China and its paleoatmospheric implications. *Geoscience Frontiers*, 3: 493–502.
- Tepley, A. J., Thomann, E., Veblen, T. T., Perry, G. L. W., Holz, A., Paritsis, J., Kitzberger, T. & Anderson-Teixeira, K. J., 2018. Influences of fire-vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. *Journal of Ecology*, 106: 1925–1940.
- Thevenon, F. & Anselmetti, F. S., 2007. Charcoal and fly-ash particles from Lake Lucerne sediments (Central Switzerland) characterized by image analysis: anthropologic, stratigraphic and environmental implications. *Quaternary Science Reviews*, 26: 2631–2643.

Traverse, A., 2007. Paleopalynology. Springer, New York, 814 pp.

- Trotter, J. A., Williams, I. S., Nicora, A., Mazza, M. & Rigo, M., 2015. Long-term cycles of Triassic climate change: a new δ<sup>18</sup>O record from conodont apatite. *Earth and Planetary Science Letters*, 415: 165–174.
- Turco, M., Rosa-Cánovas, J. J., Bedia, J., Jerez, S., Montávez, J. P., Llasat, M. C. & Provenzale, A., 2018. Exacerbated fires in Mediterranean Europe due to anthropogenic warming projected with non-stationary climate-fire models. *Nature Communications*, 9: 3821.
- Uhl, D., Abu Hamad, A. M. B., Kerp, H. & Bandel, K., 2007. Evidence for palaeo-wildfire in the Late Permian palaeotropics – charcoalified wood from the Um Irna Formation of Jordan. *Review of Palaeobotany and Palynology*, 144: 221–230.
- Uhl, D., Butzmann, R., Fischer, T. C., Meller, B. & Kustatscher, E., 2012. Wildfires in the Late Palaeozoic and Mesozoic of the Southern Alps – The Late Permian of the Bletterbach-Butterloch area (northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 118: 223–234.
- Uhl, D., Hartkopf-Fröder, C., Littke, R. & Kustatscher, E., 2014. Wildfires in the late Palaeozoic and Mesozoic of the Southern Alps – The Anisian and Ladinian (Mid Triassic) of the Dolomites (Northern Italy). *Palaeobiodiversity and Palaeoenvironments*, 94: 271–278.
- Uhl, D., Jasper, A., Abu Hamad, A. M. B. & Montenari, M., 2008. Permian and Triassic wildfires and atmospheric oxygen levels. *Proceedings of the WSEAS Conferences – Special Issues*, 13: 179–187.
- Uhl, D., Jasper, A., Schindler, T. & Wuttke, M., 2010. First evidence of palaeo-wildfire in the early Middle Triassic (early Anisian) Voltzia Sandstone Fossil-Lagerstätte – the oldest post-Permian macroscopic evidence of wildfire discovered so far. *Palaios*, 25: 837–842.
- Uhl, D. & Kerp, H., 2003. Wildfires in the late Palaeozoic of Central Europe – the Zechstein (Upper Permian) of NW-Hesse (Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 199: 1–15.
- Uhl, D., Lausberg, S., Noll, R. & Stapf, K. R. G., 2004. Wildfires in the Late Palaeozoic of Central Europe – an overview of the Rotliegend (Upper Carboniferous–Lower Permian) of the Saar-Nahe Basin (SW-Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 207: 23–35.
- Uhl, D. & Montenari, M., 2011. Charcoal as evidence of palaeo-wildfires in the Late Triassic of SW Germany. *Geological Journal*, 46: 34–41.
- Vannière, B., Colombaroli, D., Chapron, E., Leroux, A., Tinner, W. & Magny, M., 2008. Climate versus human-driven fire regimes in Mediterranean landscapes: the Holocene record of Lago dell'Accesa (Tuscany, Italy). *Quaternary Science Reviews*, 27: 1181–1196.
- Veraverbeke, S., Rogers, B., Goulden, M., Jandt, R. R., Miller, C. E., Wiggins, E. B. & Randerson, J. T., 2017. Lightning as a major driver of recent large fire years in North American boreal forests. *Nature Climate Change*, 7: 529–534.
- Wan, M.-L., Yang, W., Wan, S. & Wang, J., 2021. Wildfires in the Early Triassic of northeastern Pangaea: Evidence from fossil charcoal in the Bogda Mountains, northwestern China. *Palaeoworld*, 30: 593–601.

- Whiteside, J. H., Lindström, S., Irmis, R. B., Glasspool, I. J., Schaller, M. F., Dunlavey, M., Nesbitt, S. J., Smith, N. D. & Turner, A. H., 2015. Extreme ecosystem instability suppressed tropical dinosaur dominance for 30 million years. *Proceedings of the National Academy of Sciences of the United States of America*, 112: 7909–7913.
- Whitlock, C. & Larsen, C., 2001. Charcoal as a fire proxy. In: Smol, J. P., Birks, J. B. & Last, W. M., (eds), *Tracking Environmental Change Using Lake Sediments. Vol. 3: Terrestrial, Algal, and Siliceous Indicators.* Kluwer Academic Publishers, Dordrecht, pp. 75–97.
- Wood, G. D., Gabriel, A. M. & Lawson, J. C., 1996. Palynological techniques – processing and microscopy. In: Jansonius, J.

& McGregor, D. C. (eds), *Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation*, 1: 29–50.

- Xu, Y., Uhl, D., Zhang, N., Zhao, C., Qin, S., Liang, H. & Sun, Y., 2020. Evidence of widespread wildfires in coal seams from the Middle Jurassic of Northwest China and its impact on paleoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 559: 109819.
- Yan, M., Wan, M., He, X., Hou, X. & Wang, J., 2016. First report of Cisuralian (early Permian) charcoal layers within a coal bed from Baode, North China with reference to global wildfire distribution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 459: 394–408.