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Palaeozoic and Mesozoic palaeo–wildfires: An overview on advances in the 21st Century

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ABSTRACT

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Fire is a major driver for the evolution of biodiversity throughout the Phanerozoic and occurs in continental palaeoenvironments since the advent of the first land plants in the Silurian. The detection of palaeo–wildfire events can be based on different proxies, and charcoal is widely accepted as the most reliable evidence for such events in sedimentary layers. Although the identification of sedimentary charcoal as the product of incomplete combustion was the subject of controversial scientific discussions, palaeobotanical data can be used to confirm the pyrogenic origin of such material. In an overview on Palaeozoic and Mesozoic charcoal remains, differences in the number of published records can be detected for individual periods; including phases with both, lower (Silurian, Triassic, Jurassic) and higher (Devonian, Carboniferous, Permian, Cretaceous) numbers of published evidences for palaeo–wildfires. With the aim to discuss selected advances in palaeo–wildfire studies since the beginning of the 21st Century, we present an overview on the published occurrences of charcoal for an interval from the Silurian up to the Cretaceous. It was possible to confirm that a lack of detailed palaeobotanical data on the subject is detected in some intervals and regions, despite the high potential of occurrences detected in form of pyrogenic inertinites by coal petrographic studies. Although such temporal and regional gaps can be explained by taphonomic and palaeoenvironmental biases, it also indicates the scientific potential of future studies in diverse palaeogeographical and temporal settings.

Key–words—Palaeo–wildfire, Charcoal, Pyrogenic Inertinites, Silurian, Devonian, Carboniferous, Permian, Triassic, Jurassic, Cretaceous.

INTRODUCTION

DURING the last years wildfires have become a focus of public interest, as in many regions worldwide the intensity and frequencies of such wildfires increases, with often devastating effects on human settlements and economies, but also on certain ecosystems (e.g. Cochrane, 2019; McLauchlan *et al.*, 2020; dos Reis *et al.*, 2021). However, in the public and political perception of wildfires it is often neglected that wildfires are an integral part of many ecosystems, with more or less frequent wildfires being essential for the reproduction and survival of many plants and animals (e.g. Scott *et al.*, 2014). The complex interdependencies between fires on the one side and many ecosystems and organisms on the other side, evolved over millions of years, ever since the first wildfires occurred in the Late Silurian (Glasspool *et al.*, 2004).

For a long time, most geoscientists ignored the widespread and sometimes abundant evidence for such palaeo–wildfires, although the first studies interpreting fossil charcoal (aka fusain or pyrogenic inertinites when occurring in coals and lignites) as direct evidence for wildfires were already published in the middle of the 19th Century. Probably the first to propose a pyrogenic origin for the coal maceral fusinite was the French miner Daubrée (1844). Based on the chemical analysis of such material from the Carboniferous of the Saar–Coalfield in Germany (Daubrée, 1844, 1846) and the Triassic/Jurassic of Skane in Sweden (Daubrée, 1846), he found that there is no difference between charcoal produced by fire and these macerals. From this he concluded that these macerals were produced by wildfires, a view that was immediately questioned and even ridiculed (e.g. Göppert, 1850).

For more than a century the discussion whether fossil charcoal was the product of palaeo–wildfires or not went back and forth amongst palaeobotanists and coal–petrographers. A summary of this historical discussions was provided by Scott (1989, 2000), and although the discussion is still not fully settled for some scientists (e.g. Valentim *et al.*, 2016; Wang *et al.*, 2020) there seems to be a broad agreement, at least amongst palaeobotanists, that fossil charcoal (including most of the inertinite group of coal macerals) can be regarded as the product of palaeo–wildfires (e.g. Scott, 2000, 2010; Scott *et al.*, 2014; Moroeng *et al.*, 2018a, b; Wang *et al.*, 2019).

In 2000, Scott published a seminal review on the pre–Quaternary history of fire, in which he summarized the knowledge about palaeo–wildfires that had accumulated at this time (Scott, 2000). This review sparked a broader international interest in pre–Quaternary wildfires, which is evidenced by the ever–growing number of studies published on this topic during the last two decades in international journals.

Here we provide a short overview of the progress that has been achieved in the last 20 years on selected aspects of our knowledge about Palaeozoic and Mesozoic wildfires. This overview is definitely not intended as a full–scale review of this topic, we just want to draw the attention of potential readers to some of the most interesting and important (at least in our opinion) aspects of the many progresses that palaeo–wildfire research has done during the last 20 years. Additionally, we point out some open questions that remain unanswered so far, hopefully stimulating further scientific interest in this topic.

PALAEOZOIC AND MESOZOIC FIRES

Since the seminal review by Scott (2000) a large number of studies reported the occurrence of charcoal/fusain (including pyrogenic inertinites) and/or pyrogenic polyaromatic hydrocarbons (PAHs) and interpreted such findings as evidence for palaeo–wildfires (see below for more details). A number of studies has already compiled and analysed data for individual periods (e.g. Devonian: Lu *et al.*, 2021; Triassic: Abu Hamad *et al.*, 2012; Cretaceous: Brown *et al.*, 2012) or for the entire Palaeozoic (e.g. Scott & Glasspool, 2006; Glasspool & Scott, 2010) and Mesozoic (e.g. Belcher & McElwain, 2008).

One aspect that has repeatedly been the focus of such studies, is the connection between atmospheric oxygen concentrations and palaeo–wildfires. Scott &Glasspool (2006) compared charcoal abundance from the Silurian up to the end of the Permian with large scale changes in Palaeozoic vegetation and climate. They found that the abundance of charcoal, interpreted as a proxy for fire occurrence and the diversification of fire systems, was indeed related to changes in atmospheric oxygen concentration during this period, as reconstructed by geochemical modelling, as well as with the increasingly complex vegetation types that developed during this period. Using this relationship between fire and oxygen through time, Glasspool & Scott (2010) compiled a dataset of pyrogenic inertinites in Phanerozoic coals to reconstruct atmospheric oxygen concentrations from the Silurian up to the Cenozoic.

Belcher and McElwain (2008) compiled a dataset of Mesozoic wildfire occurrences, using published records of charcoal, inertinites and PAHs, which they used in connection with experimental burns of modern plant material under different oxygen concentrations, to find the lower limits of atmospheric oxygen for sustaining wildfires and thus test the results of geochemical modelling. These authors found that the lower limit of atmospheric oxygen to sustain fires is approximately 15% (and not 12% as assumed earlier) and that the fossil record of wildfire is incompatible with low oxygen phases (10 to 12%; i.e. during the Early Triassic and the Jurassic), as reconstructed by different geochemical models. Besides these studies on atmospheric oxygen and its long–term connection with palaeo–wildfires, also a large number of other experimental studies on modern plants and charcoal, which are not the subject of this overview, has significantly increased our ability to interpret the existing evidence for palaeo–wildfires (e.g. McParland *et al.*, 2007; Gerards *et al.*, 2007; Belcher *et al.*, 2010; Osterkamp *et al.*, 2018). During the last decades also a number technical advances have been made that enabled new insights into palaeo–wildfires and their interactions with climate and environment. An example are studies using a combination of different proxies (i.e. charcoal, inertinites and/or pyrogenic PAHs) to reconstruct information about Palaeozoic and Mesozoic wildfires (e.g. Marynowski *et al.*, 2011, 2014; Kubik *et al.*, 2020; Murthy *et al.*, 2021). Such a combined approach is very promising to provide comprehensive and profound information about palaeo–wildfire, but rather complex and still mostly expensive.

Another example, relatively new to palaeo–wildfire research, is the usage of pre–charring decay to reconstruct various aspects of palaeo–wildfires (e.g. El–Atfy *et al.*, 2019b). The massive occurrence of charcoal with traces of pre–charring decay has, for example, been used by Uhl *et al.* (2019) to reconstruct a surface fire from material occurring at the Early Cretaceous locality Rüthen–Kallenhardt in Germany. Based on the extreme scarcity or even absence of such evidence the same authors reconstructed a crown fire for the nearby and more or less contemporary locality Brilon–Nehden (Fig. 1). However, taphonomical studies on modern charcoal derived from decaying litter are largely missing so far, rendering such interpretations somewhat speculative (e.g. Uhl *et al.*, 2019, 2020).

Besides such methodological advances, a major advance to increase our knowledge about palaeo–wildfires and their interactions with climate and environments through time, were numerous studies dealing with fossil charcoal from various periods and localities that enlarged our data base about such fires considerably. For this overview we compiled a list of

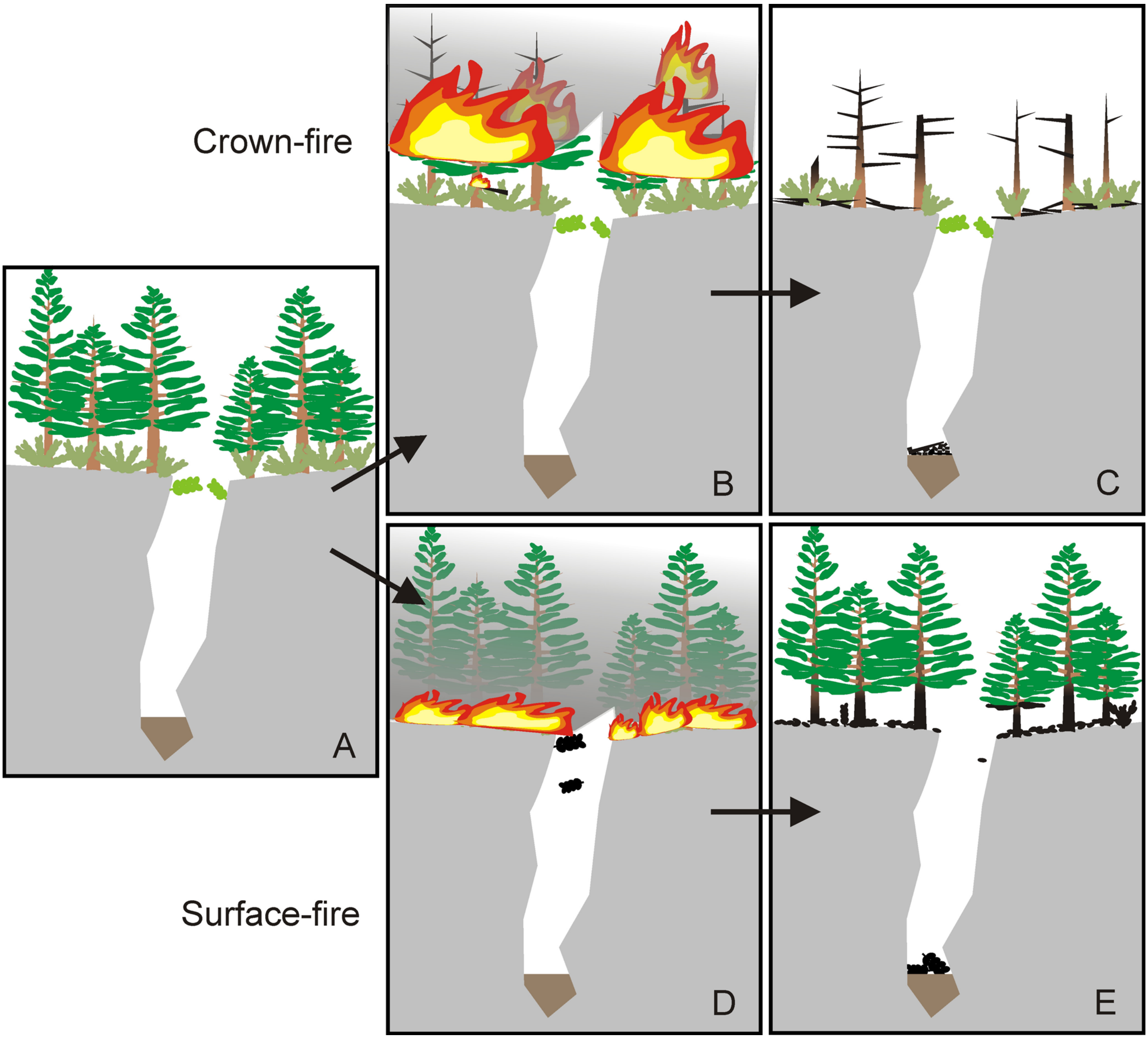

Fig. 1—Schematic reconstruction of two wildfire scenarios that might explain the differences regarding pre–charring decay between the charcoal accumulations within the fissure fills of Brilon–Nehden (crown fire) and Rüthen–Kallenhardt (surface fire), Early Cretaceous, W–Germany (from Uhl *et al.*, 2019, Fig. 14).

published evidence for palaeo–wildfire in form of charcoal from clastic sediments, as well as inertinites (assuming that this equals pyrogenic inertinites; cf. Scott, 2000, 2010; Scott & Glasspool, 2007, Glasspool & Scott, 2010), from the Silurian up to the Cretaceous (Fig. 2). This compilation is based on previous studies that summarized charcoal records from diverse intervals (e.g. Glasspool *et al.*, 2004; Diessel, 2010; Abu Hamad *et al.*, 2012; Brown *et al.*, 2012; Benício *et al.*, 2019a; El–Atfy *et al.*, 2019a; Yun Xu *et al.*, 2020; Lu *et al.*, 2021) and on the authors database for this paper. A selection of SEM images of Palaeozoic and Mesozoic charcoals is presented in Pl. 1.

In the following sections we summarize some selected advances in palaeo–wildfire research for the individual periods of the Palaeozoic and Mesozoic:

Silurian

The Silurian is known as the period of the advent of the first terrestrial plants (Taylor *et al.*, 2009 and citations therein) but vegetation was very scarce and restricted to very marginal wet settings. Scott (2000) stated that due to this scarcity of vegetation it was unlikely that there was enough fuel to sustain larger fires that would produce enough charcoal to be preserved in the fossil record.

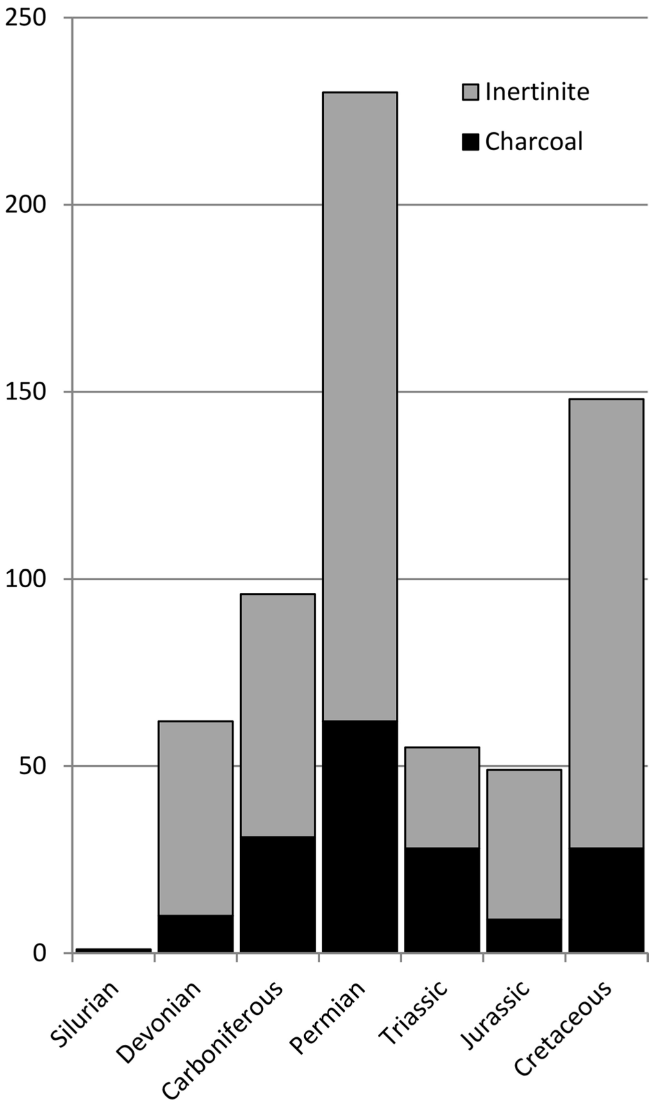

Fig. 2—The numbers of published records of sedimentary charcoal and pyrogenic inertinites throughout the Palaeozoic and Mesozoic. Based on previous summaries by Glasspool *et al.* (2004)–Silurian; Lu *et al.* (2021)–Devonian; Benício *et al.* (2019a)–lower Permian; Abu Hamad *et al.* (2012) Permo–Triassic; Yun Xu *et al.* (2020)–Jurassic; Brown *et al.* (2012)–Cretaceous; El–Atfy *et al.* (2019a)–Cretaceous; and the authors database.

Only a few studies have so far dealt with charcoal as evidence for wildfires in the Silurian (Scott & Glasspool, 2006). The oldest record of charcoal, morphologically resembling the rhyniophytoid *Hollandophyton colliculum*, was described by Glasspool *et al.* (2004) from the *Platyschima* Shale Member of the Downton Castle Formation, England. These findings provide evidence that wildfires, although probably not very widespread, affected ecosystems, as soon as fuel (= combustible biomass) was available on the continents.

Devonian

Dominating continent marginal ecosystems, diverse vascular plants emerged during the early Devonian (Taylor *et al.*, 2009 and citations therein). The oldest forest consisting of lignophytes, meaning a diversified vascular flora providing abundant fuel within an individual habitat, has recently been described from the middle Devonian (Stein *et al.*, 2020). Once fuel was present in larger quantities, the occurrence of wildfires became more common (e.g. Lu *et al.*, 2021) (Fig. 2).

Scott (2000) speculated that during the mid–late Devonian the vegetation would have been dense and complex enough to sustain fires, and the oldest known charcoal reported by this author came from the Late Devonian. In the following years a number of different studies has reported the occurrence of Devonian charcoal (e.g. Cressler, 2001; Scott & Glasspool, 2006; Glasspool *et al.*, 2015; Rimmer *et al.*, 2015; Lenton *et al.*, 2016).

Recently a comprehensive summary of published evidence for Devonian wildfires, ranging from the Lochkovian up to the Upper Famennian, was presented by Lu *et al.* (2021). These authors demonstrated a strong statistical linkage between the diversification of land plants, i.e. lignophytes, and the increase of published evidence for wildfires in eastern Euroamerica. On the other hand, the authors demonstrated that the fluctuating patterns of pO_2 during the Devonian do not match with the published records of wildfires and argue that fire regimes were mainly driven by fuel availability and not by varying pO_2 during that interval (Lu *et al.*, 2021). Like other studies before (Scott & Glasspool, 2006; Algeo & Ingall 2007) these authors found a gap in the fossil record of charcoal during the "middle" Devonian (i.e. from the late Emsian up to the Givetian) with no or very few records during individual stages. However, the database on which this study is based, is

PLATE 1

SEM–images of Palaeozoic and Mesozoic macro–charcoals. →

A. Gymnospermous charcoal, Late Pennsylvanian, Germany (from Uhl & Jasper, 2021).
B. Gymnospermous charcoal, Early Permian, Quitéria, RS, Brazil.
C. Needle of the conifer *Ullmannia* sp., Late Permian, Frankenberg, Germany (from Uhl & Kerp, 2003).
D. Gymnospermous charcoal, Middle Triassic, Pirmasens, S–Germany (from Uhl *et al.*, 2010).
E. Gymnospermous charcoal, Late Triassic, S–Germany.
F. *Agathoxylon* sp., Late Jurassic, Nusplingen, S–Germany (from Uhl *et al.*, 2012).
G. Fern (?) crozier, Early Cretaceous, Kallenhardt, Germany (from Uhl *et al.*, 2019).
H. Pinnules of a fern, Early Cretaceous, Kallenhardt, Germany (from Uhl *et al.*, 2019).

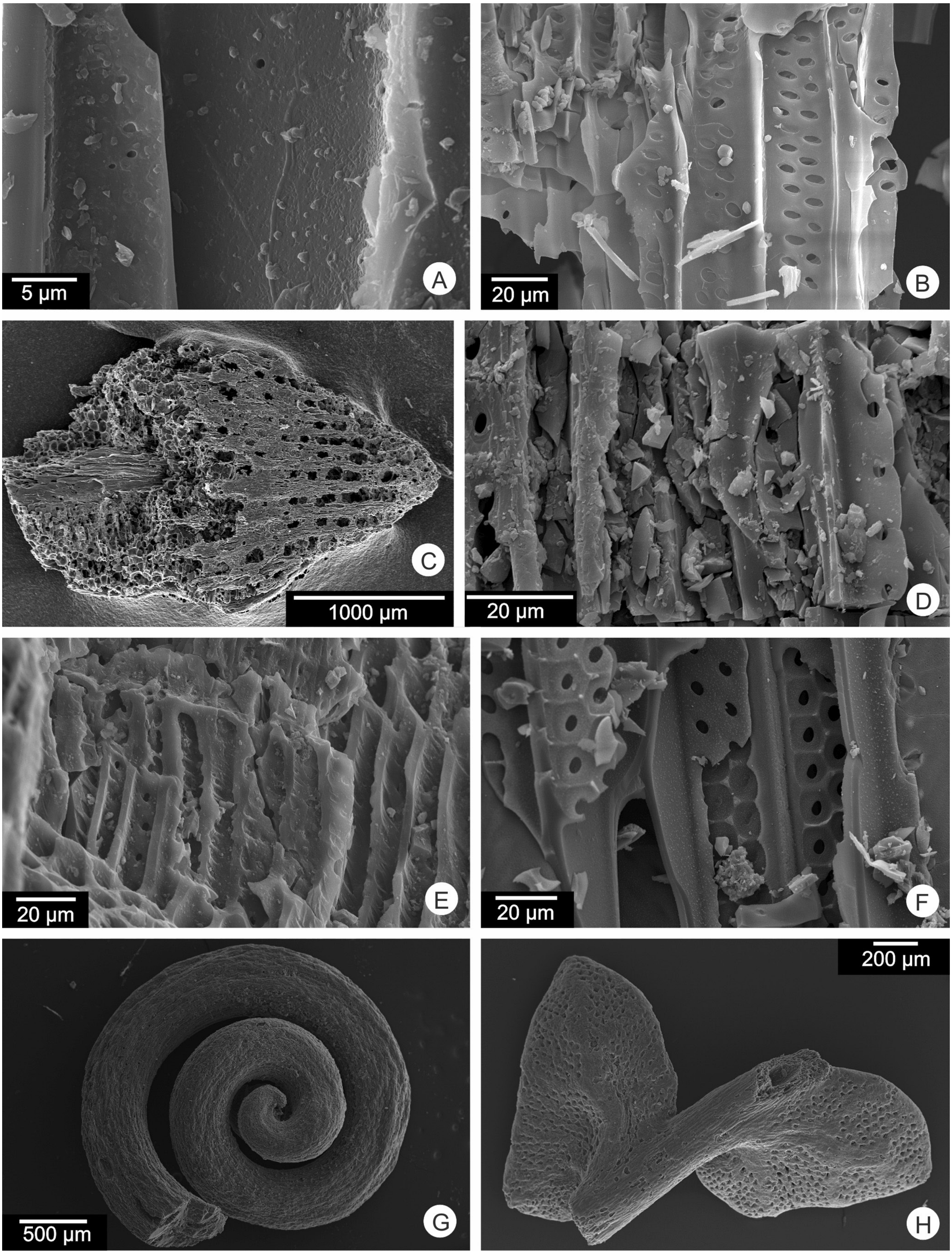

PLATE 1

still rather small (62 occurrences of palaeo–wildfire evidence for a period of 60 million years) making it difficult, to draw undoubtable conclusions; a fact that is still also true for most other periods of Earth's history.

Carboniferous

Charcoal as direct evidence for wildfires, is frequent and ubiquitous in many continental but also some marine deposits from the Carboniferous (Fig. 2), and already 20 years ago there was an extensive record of publications on this subject (Scott, 2000, and citations therein). Since than a large number of additional publications has dealt with fossil evidence for palaeo–wildfires during this period, not only dealing with wildfires from the widespread coal measures of the northern hemisphere, but also from the drier hinterland (e.g. Falcon–Lang & Bashforth, 2005; Scott *et al.*, 2010; Zodrow *et al.*, 2010, 2012; Clack *et al.*, 2019; Uhl & Jasper, 2021).

So far almost all studies on Carboniferous wildfires come from the northern hemisphere, probably due to more extensive studies on the Carboniferous strata on this hemisphere, as well as a lack of fossil bearing sediments on Gondwana. The later was caused by widespread glaciations and by a scarcity or even lack of biomass/vegetation in large periglacial areas that would produce large quantities of charcoal which could have entered the fossil record.

Only recently Pennsylvanian macro–charcoal was described by Benício *et al.* (2019b) from Western Gondwana. An assemblage of fragmentary macro–charcoal remains originating from the Itararé Group, from the southern part of the Paraná Basin, Brazil, remains the so far only published direct evidence of wildfires for the entire continent during the Carboniferous (Benício *et al.*, 2019b; Jasper *et al.*, 2020).

Permian

When Scott (2000) wrote his review there were only very few published records dealing with fossil charcoal from the Permian. Although it was known for a long time, that many Permian coals from Gondwana had very high inertinite contents, it was not clear at this time, whether these inertinites were of pyrogenic origin or not. Due to several studies dealing with such inertinites in greater details in the last two decades a huge amount of evidence has accumulated that such inertinites are mostly of pyrogenic origin (e.g. Scott, 2000, 2010; Scott & Glasspool, 2007, Glasspool & Scott, 2010).

During the last decades our knowledge about Permian wildfires has increased considerably, not only with regard to pyrogenic inertinites, and a short review of the literature demonstrates that today more studies on Permian palaeo–wildfires have been published than for any other part of the Palaeozoic and Mesozoic (Fig. 2). Since 2000 large number of studies has dealt with previously unknown or undescribed occurrences of fossil charcoal from almost all parts of the world, including Western and Southern Europe (e.g. Uhl & Kerp, 2003; Uhl *et al.*, 2004, 2012a), North–America (e.g. DiMichele *et al.*, 2004), Russia (e.g. Hudspith *et al.*, 2012) and China (e.g. Xiao *et al.*, 2020), but also large parts of the former supercontinent Gondwana, like the Middle East (e.g. Uhl *et al.*, 2007), Brazil (e.g. Jasper *et al.*, 2008, 2011a, 2013, Degani–Schmidt *et al.*, 2015; Manfroi *et al.* 2015b; Kauffmann *et al.*, 2016; Benício *et al.*, 2019a; Kubik *et al.*, 2020), India (e.g. Jasper *et al.*, 2012, 2013, 2016a, b, 2017; Murthy *et al.*, 2021); South Africa (e.g. Glasspool, 2000, 2003a, b) and Antarctica (e.g. Holdgate *et al.*, 2005; Slater *et al.*, 2015) (Fig. 3). A number of these studies dealt with macro–charcoal and inertinites from coal deposits (e.g. Hudspith *et al.*, 2012; Jasper *et al.*, 2017; Benício *et al.*, 2019a) adding further convincing evidence that the inertinites in these coals represent fossil charcoal that has been produced by wildfires (Fig. 4).

Based on the large number of records and the abundance of charcoal in individual deposits it emerged that the Permian, was indeed a high–fire phase of Earth's history (e.g. Jasper *et al.*, 2013; 2020). One of the reasons for this, was a very high atmospheric pO_2 during most of the Permian (e.g. Glasspool & Scott, 2010). With such an elevated atmospheric pO_2, probably exceeding 28% in some stages (Glasspool & Scott, 2010), even wet plant parts could easily be ignited and very large fires could be sustained in a wide range of terrestrial habitats (e.g. Jasper *et al.*, 2017; Benício *et al.*, 2019a).

During the latter part of the Permian atmospheric pO_2 dropped according to geochemical modelling, and Abu Hamad *et al.* (2012), in their review of Permian and Triassic wildfire occurrences, showed a kind of correlation between changes in pO_2 and wildfire evidence. Although not yet clear, in the last few years there is increasing evidence that fires were involved in the widespread destruction and finally collapse of continental ecosystems during the P/T extinction event. At the moment it is nonetheless clear that wildfires occurred more or less regularly or even increased in certain terrestrial ecosystems just prior to the Permian–Triassic boundary event(s) (e.g. Shen *et al.*, 2011; Yan *et al.*, 2016, 2019; Arzadún *et al.*, 2017; Shivanna *et al.*, 2017; Sun *et al.*, 2017; Feng *et al.*, 2020; Vajda *et al.*, 2020; Cai *et al.*, 2021).

Triassic

Scott (2000) stated that there are relatively few records of Triassic charcoal, citing only a few occurrences from the Rhaetian–Liassic, as well as from Chinese coal seams and the "Petrified Forest" in Arizona. Also for this period, again sparked by the seminal review of Scott (2000), the number of published records of fossil charcoal increased during the following decade (Fig. 2).

Abu Hamad *et al.* (2012) published a review of published evidence for Triassic wildfires demonstrating that there are considerably less reports on intertinites from Triassic coals

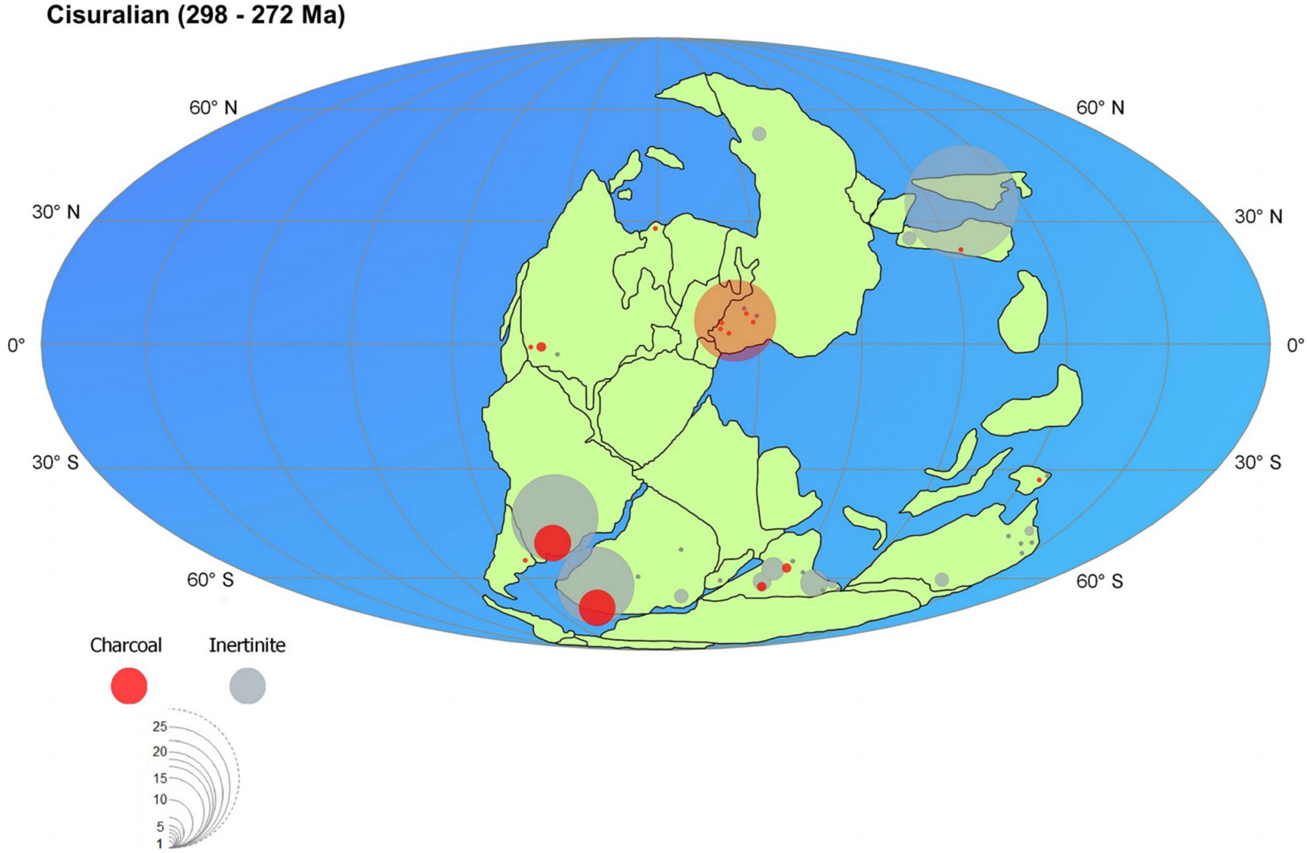

Fig. 3—Global distribution of sedimentary charcoal and inertinites during the Cisuralian. Dots represent the number of described charcoal occurrences by basin and diameter varies according to scale (from Benício *et al.*, 2019a, Fig. 5).

than from Permian coals, but approximately the same number of studies on charcoal from clastic sediments. This is not surprising, as there are considerably less Triassic than Permian coal deposits, with even a global coal–gap lasting from the earliest Induan up to the Carnian (e.g. Retallack *et al.*, 1996). There seems to be an earliest Triassic (i.e. Induan) charcoal gap and a more or less steady increase of the published evidence for micro–as well as macro–charcoal in clastic sediments from the Olenekian onwards, especially during the Middle and Late Triassic (e.g. Belcher & McElwain, 2008; Abu Hamad *et al.*, 2012). The so far oldest post–Permian macro–charcoal (being of coniferous affinity) is known from the Anisian *Voltzia*–sandstone of SW–Germany (Uhl *et al.*, 2010). These strata are well known to include the first diverse fossil macro–flora after the Permian–Triassic mass–extinction event (e.g. Grauvogel–Stamm & Ash, 2005).

Since this overview by Abu Hamad *et al.* (2012) a number of additional studies on macro–charcoal has been published from Europe (e.g. Havlik *et al.*, 2013; Uhl *et al.*, 2014; Kubik *et al.*, 2015; Philipe *et al.*, 2015), the Middle East (e.g. Abu Hamad *et al.*, 2013, 2014), Antarctica (e.g. Kumar *et al.*, 2011) and South America (e.g. Cardoso *et al.*, 2018). These studies demonstrate that charcoal occurs globally in Triassic deposits, which are suitable for the preservation of this kind of fossil. However, charcoal seems to be extremely rare or completely absent in the globally widespread Early and Middle Triassic red–beds, which formed during this period in several regions on the supercontinent Pangaea. It is, however, difficult to assess whether this is due to a real rarity of wildfires during this period, or (more likely in the view of the authors) to various taphonomic factors. Such factors include, amongst others, a low preservation potential of charcoal in such red beds (e.g. Skjemstad *et al.*, 1996; Uhl *et al.*, 2004, 2010), a low amount of combustible biomass (=fuel) and human bias, i.e. neglecting charcoal as an interesting type of fossil evidence (cf. Uhl *et al.*, 2010; Abu Hamad *et al.*, 2012).

A few studies have discussed a potential connection between the end–Triassic mass extinction event, caused by the eruption of the CAMP, and an increase in wildfires during the Triassic–Jurassic transition (e.g. Belcher *et al.*, 2010). However, at the moment it is not yet clear whether these studies can be generalized for larger regions or whether they just report more local changes of fire regimes and/or frequencies.

Jurassic

Already Daubrée (1846) reported charcoal from late Triassic–early Jurassic strata of Sweden, and Scott (2000) summarized a large number of studies, which had already dealt with Jurassic charcoal and wildfires up to this time. Since then, a number of additional studies dealing in more or less detail with Jurassic evidence of wildfires (e.g. Hesselbo *et al.*, 2003; Belcher & McElwain, 2008; Marynowski & Simoneit, 2009; Marynowski *et al.*, 2011; Uhl *et al.*, 2012b, c; Tanner *et al.*, 2012; Yun *et al.* 2020; Zhang *et al.*, 2020).

Interestingly a number of geochemical models reconstructed very low atmospheric pO_2 during large parts of the Jurassic (e.g. Falkowski, 2005; Berner, 2009; Tappert *et al.*, 2013), which would have led to a largely reduced flammability and wildfire activity. The above mentioned frequent and partly abundant fossil evidence for wildfires contradicts these models, highlighting the importance of palaeo–wildfire research for testing the reliability of such models (Belcher & McElwain, 2008).

Cretaceous

From a palaeobotanical point of view, the Cretaceous is regarded as a period of major changes, with the appearance of angiosperms during the Early Cretaceous and their rapid radiation and spread over the entire globe until they dominated many ecosystems worldwide during the Late Cretaceous (e.g. Wing & Tiffney, 1987; Wing *et al.*, 1987; Friis *et al.*, 2011; Coiffard *et al.*, 2012). A large number of studies has dealt with Cretaceous wildfires (cf., Scott, 2000; Brown *et al.*, 2012) (Fig. 2) and in general this period is regarded as one of the high–fire periods of Earth's history (e.g. Brown *et al.*, 2012; Scott *et al.*, 2014). Several workers have studied macro–charcoal in Cretaceous localities otherwise known for their abundance of dinosaurs, also demonstrating that these animals often lived in fiery environments (e.g. Brown *et al.*, 2013; Vajda *et al.*, 2013; El Atfy *et al.*, 2019a; Uhl, 2020; El Atfy & Uhl, 2021).

A review about Cretaceous wildfires by Brown *et al.* (2012) found a bias towards studies on the northern hemisphere. A considerable number of studies has dealt with charcoal and palaeo–wildfires from the northern hemisphere since then, adding more evidence for a ubiquitous occurrence of wildfires on the northern hemisphere (e.g. Falcon–Lang *et al.*, 2012; Girard *et al.*, 2013; Fletcher *et al.*, 2014; Uhl *et al.*, 2019). However, several studies have also demonstrated that fires were probably equally frequent on the southern hemisphere, e.g. Brazil (e.g. dos Santos *et al.* 2016; de Lima *et al.*, 2019, 2021), Jordan (e.g. Abu Hamad *et al.*, 2016a, b), India (e.g. Kumar, 2018; Mohabey *et al.*, 2018), Egypt (e.g. El Atfy *et al.*, 2016, 2019a), South Africa (e.g. Muir *et al.*, 2015) and Antarctica (e.g. Manfroi *et al.*, 2015a; de Lima *et al.*, *in press*).

During the last decades a number of studies have dealt with the influence of wildfires on the evolution of several plant groups during the Cretaceous, presenting evidence that a number of modern plant lineages and vegetation types, adapted to fire, already originated in the high–fire world of the Cretaceous (e.g. He *et al.*, 2012, 2016; Lamont & He, 2017). However, there is also increasing evidence that wildfires may have influenced the early evolution of angiosperms in general and that the radiation and spread of early angiosperms may have influenced fire regimes (e.g. Bond & Scott, 2010; Brown *et al.*, 2012; Belcher & Hudspith, 2017). Angiosperms can have much higher productivities and reproduction rates than other plant groups, leading to faster accumulation of fuels and thus higher fire frequencies, especially under high atmospheric oxygen conditions and globally warmer temperatures as reconstructed for large parts of the Cretaceous (e.g. Bond & Scott, 2010). Also physical and morphological properties of the radiating and spreading angiosperms altered the ignitability and flammability of potential fuels (e.g. Belcher & Hudspith, 2017). Especially angiosperm shrubs, maybe in connection with fern understoreys, may have contributed to changes of fire behaviour leading to an increased rate of crown fires in gymnosperm canopies, and ultimately to higher mortalities of trees (Belcher & Hudspith, 2017). As fire regimes are characterised by multiple positive and negative feedbacks with a variety of biological and physical parameters within an ecosystem, such changes must have had profound influences not only on angiosperms, but on entire ecosystems (e.g. Bond & Scott, 2010; Belcher, 2010).

But wildfires did not only affect the evolution of angiosperms and ecosystems during the Cretaceous they also preserved pristine evidence for the evolution of angiosperms in form of charred flowers and seeds (e.g. Scott, 2000; Friis *et al.*, 2011, 2014, 2019; Schönenberger, 2005). Such remains provide very significant anatomical evidence for the evolution of early angiosperm clades and new techniques, like synchrotron X–ray microtomography, have provided a wealth of new data about the early evolution of angiosperms in the last decades (e.g. Friis *et al.*, 2014, 2017, 2018). These techniques are, obviously, not restricted to Cretaceous angiosperm remains, but can be applied to charred plant remains, as far back as the Palaeozoic (e.g. Scott *et al.*, 2009).

In the past several studies have suggested that massive wildfires have played a major role in the K/Pg extinction event (e.g. Wolbach *et al.*, 1990; Robertson *et al.*, 2013). However, detailed studies on fossil charcoal (e.g. Scott, 2000; Belcher *et al.*, 2003, 2005), geochemical evidence (e.g. Belcher *et al.*, 2009), as well as experimental (Belcher *et al.*, 2015) and modelling approaches (e.g. Goldin & Melosh, 2009) have questioned such worldwide conflagrations in the immediate aftermaths of the Chixuclub impact.

Fig. 4—Artistic reconstruction of a burning peat–forming landscape based on records from the tuffite layer from the Quitéria Outcrop in S–Brasil (by ©A. Pozzebon–Silva) (from Jasper *et al.*, 2020, Fig. 3).

CONCLUSIONS

During the last 20 years great advances have been made in the research on Palaeozoic and Mesozoic palaeo–wildfires, especially due to increased efforts to document wildfires occurrences, but also due to methodological and methodological advances. However, in several regions, especially on southern hemisphere continents, which were formerly part of the super–continent Gondwana, there are still many regional and temporal gaps where we still have not enough data to provide meaningful syntheses in space and time. Another "problem" are studies which do not sufficiently document evidence for the pyrogenic origin of putative charcoal they are studying, as that cannot be validated by other authors. It is thus strongly recommended to document such evidence (i.e. SEM–images of homogenized cell walls in the case of sedimentary charcoal) and to follow standard protocols for the identification of fossil charcoal (e.g. Scott, 2000, 2010).

Finally we want to conclude this overview with a (highly subjective) selection of some open questions and suggestions for further research directions:

- Increase documentation of additional records for palaeo–wildfires especially for so far understudied regions and periods, using established procedures for the identification of fossil charcoal.
- Increase the database of studies on the taphonomy of charcoal following modern wildfires.
- What were the roles of fires in the mass extinction events at the P/Tr–boundary, the Tr/J–boundary and the K/Pg–boundary?
- Why are there so few published records of charred foliage as compared to wood remains for most periods?
- How to avoid the potential taxa bias in the records caused by more or less resistance to complete plant burning?

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