

Agora Paleobotanica

The extinct tree fern *Tempskya* Corda from the Albian of Spain: palaeophytogeographical and palaeoenvironmental implications

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ABSTRACT: New evidence of the extinct tree fern of the genus *Tempskya* Corda from Albian deposits in western Eurasia (northeastern Spain) is presented. These plant fossil remains consist of several silicified false trunks measuring up to 1.20 m long, some of which still preserve the apex. Rhizomes and petioles are more abundant in the apical zone of the false trunk. Some false trunks preserve charcoaled tissues that can be interpreted as evidence that palaeo-wildfires affected the false trunks several times from mostly the same direction. Sedimentological evidence suggests that the fern habitat was close to coastal, tidally influenced environments. These new fossils from the Albian of Spain fill the chronological and distributional gap of *Tempskya* that existed in Eurasia during the Early Cretaceous. Temporal and spatial changes in *Tempskya* distributions are proposed on several palaeogeographical maps.

KEY WORDS: charcoal, early cretaceous, Eurasia, palaeoenvironment, palaeophytogeography, wildfires.

The genus *Tempskya* Corda is a group of extinct ferns composed of species that are characterised by a false trunk, which consists of numerous intermingled rhizomes and a large number of adventitious roots coming out from the rhizomes. This false trunk can reach up to 50 cm in diameter and 6 m high (Taylor *et al.* 2009). Due to the unique morphology of this false trunk, *Tempskya* represents an extinct monotypic family Tempskyaceae Read & Brown ex L.C.A. Martínez, 2015.

However, the systematic affinity of the family has remained unclear to date because of the lack of attached leaves and reproductive organs (Tidwell & Ash 1994). Recently, Martínez & Olivo (2015) emended the Tempskyaceae family based on exceptionally well-preserved silicified false trunks, which included possible frond segments and attached sori with sporangia containing spores. The characters of these reproductive remains allowed the authors to attribute this family to the Cyatheales. Some other *Tempskya* remains have also been compared to the Anemiaceae, although no direct evidence supporting this affinity exists (Tidwell & Ash 1994).

The genus *Tempskya* has been recorded exclusively in Cretaceous deposits from the Valanginian (Barale & Viera 1989; Martínez & Olivo 2015) to the Santonian (Nishida 1986). Records of *Tempskya* are found in both Lower and Upper Cretaceous deposits from the Laurasia domain, including North America, but the genus has also been reported from the Lower Cretaceous of Argentina and Australia within the Gondwana realm (see Section 2.4). The remains of this fern

are generally represented in Eurasia by silicified fragments of false trunks that have been recorded in the Lower and ‘Middle’ Cretaceous from the Valanginian–Hauterivian (Barale & Viera 1989) and Hauterivian–Barremian (Puente-Arauzo *et al.* 2014) in Spain, the ‘Wealden Beds’ in England (Seward 1894; Stopes 1915; Austen & Batten 2011), Germany (Jung 1983) and France (Corda 1845; Carpentier 1923), and from the Cenomanian in the Czech Republic (Corda 1845; Velenovsky 1888). Nevertheless, this taxon has not previously been recorded from Albian deposits in western Eurasia.

Here, we describe the first Albian remains of *Tempskya* false trunks in western Eurasia from middle to upper Albian deposits in Spain. These consist of several false trunks of differing sizes, some of which also present possible evidence of palaeo-wildfire damage. These new findings fill the temporal gap of this genus in Eurasia, providing new evidence for inferring the palaeoenvironment and distribution patterns of this genus during the Cretaceous.

1. Material and methods

1.1. Geographical and geological setting

The fossil plants studied in this paper were collected at the ‘Carretera-1’ fossil site near the village of Escucha in Teruel Province (Aragón, NE Spain; Fig. 1). This village is situated 70 km N of Teruel city and 5 km E of Utrillas village, which is a well-known reference locality for both Albian geology



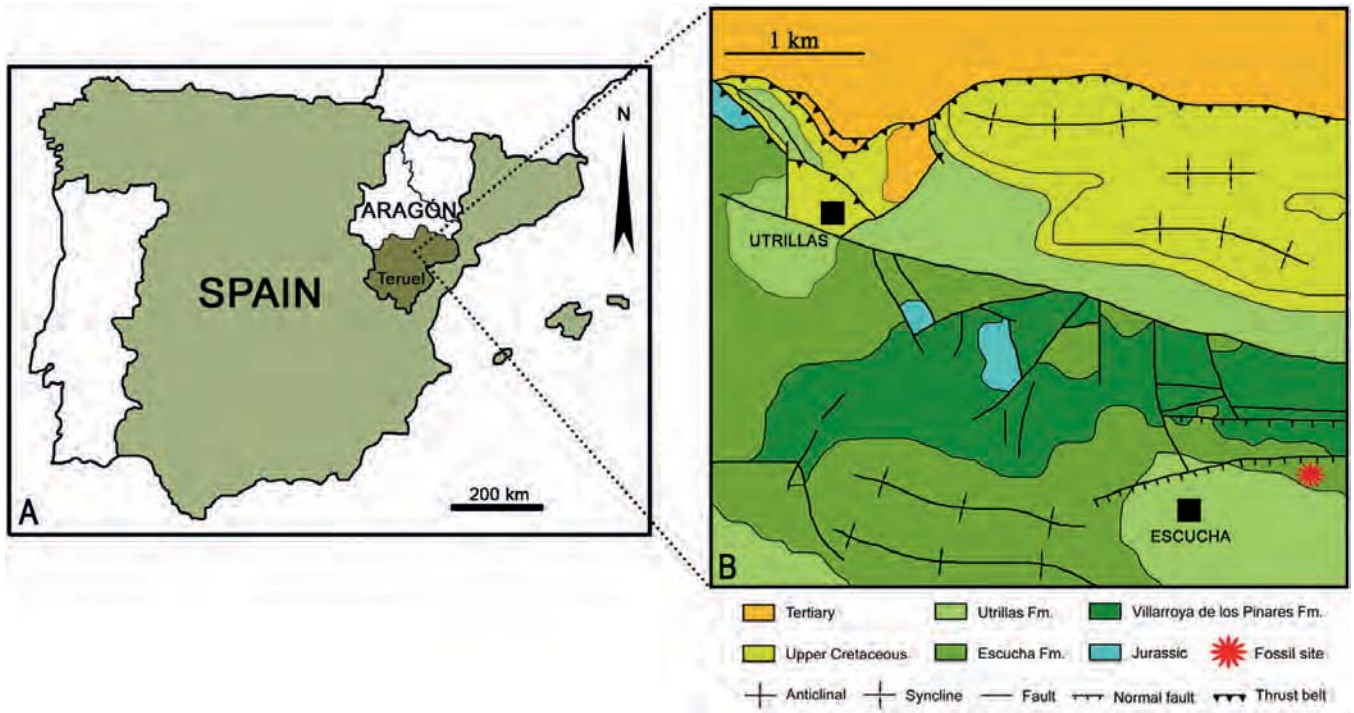


Figure 1 (A) Geographical location of the plant fossil site. (B) Geological map of the fossil site near Escucha village.

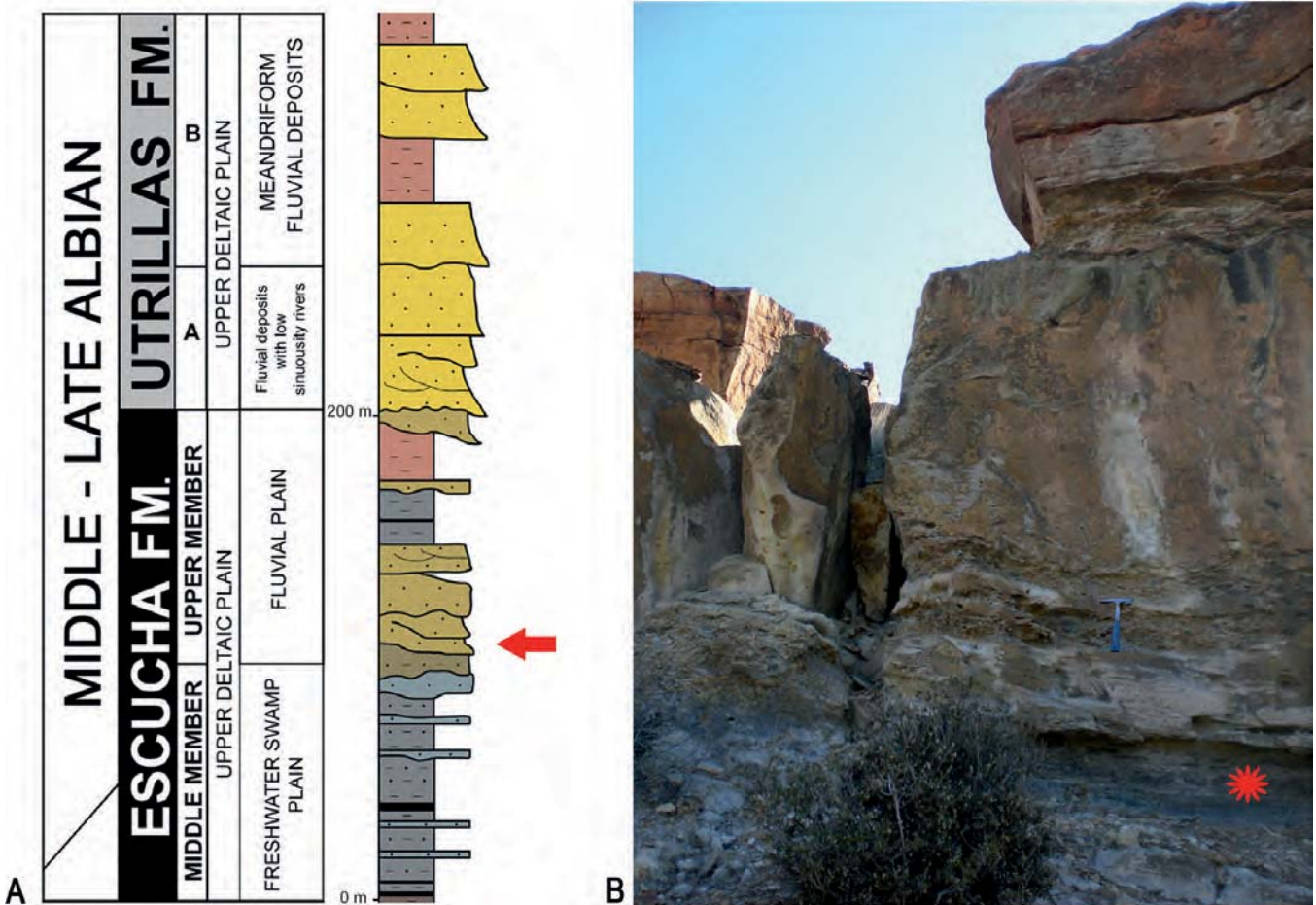


Figure 2 (A) Synthetic stratigraphic section of part of the Escucha and Utrillas Formations, indicating depositional environments and sub-environments (modified from Villanueva-Amadoz 2009). The stratigraphic level bearing *Tempusky* is indicated by an arrow. (B) Fossil site image with the layer containing *Tempusky* indicated by an asterisk. See a hammer for scale (28 cm long), to the left above the asterisk.

and palaeobotany in the region. The fossil locality is in the Cuencas Mineras district, and the stratigraphic level containing *Tempskya* (Fig. 2a) belongs to the Upper Member of the Escucha Formation (Aguilar *et al.* 1971). This formation is mainly a continental detrital unit that consists of alternate sandstones and clays intercalated with coal seams and sporadic marine limestones, which were deposited in a tidally influenced delta-estuary system (Pardo 1979; Pardo & Villena 1979; Querol 1990; Pardo *et al.* 1991; Querol *et al.* 1992; Salas *et al.* 2001).

The Escucha Formation in this area is limited at the base by the carbonated marine deposits of the Villarroya de los Pinares Formation (Aptian in age) and is overlain by sandy fluvial deposits of the Utrillas Formation (middle–late Albian). The most recent palynological studies in the area, where the remains of *Tempskya* were found, indicate a middle to late Albian age for the Upper Member of the Escucha Formation (Villanueva-Amadoz 2009). The lithology of the stratigraphic interval in the Escucha locality bearing the studied fossils exhibits white cross-bedded sandstones intercalated with shales and grey-coloured clays (Fig. 2b) deposited in a fluvio-tidal environment (Pardo *et al.* 1991; Querol *et al.* 1992).

1.2. Studied material

Fragments of permineralised false trunks (24 pieces) possibly represent 14 individual plants. The largest specimen measures 1.20 m long (Fig. 3a). All false trunks are preserved as silicified remains, although they have undergone both recrystallisation and weathering, causing some alteration of internal structures (Fig. 4a). In addition, some samples exhibit compressional deformation. Three false trunks contain some charcoalfied remains preserved within the surrounding silicified tissues (Figs 4b, c, 6, 7).

Fossils were first cleaned with fresh water and then five fragments of fossil trunks were cut transversally in order to obtain polished and thin sections. Photographs of the false trunks and the polished sections were taken using a Nikon D90 camera with an AF-S Micro Nikkor 60 mm macro lens. Thin sections of less deformed false trunks were prepared at the Hard Materials Preparation Service at the University of Zaragoza (Spain). Images of these thin sections were obtained using a Leica DM 2000 LED stereomicroscope with an attached Leica ICC50 W digital camera at the University of Vigo (Spain). Small pieces of charcoalfied roots were extracted from the interior of the false trunks using small needles, and were then mounted on a stub and covered with gold. These charcoalfied remains were photographed using a FESEM Carl Zeiss MERLIN electron microscope at the Microscopy Imaging Service at the University of Zaragoza.

The specimens are housed at the Museo de Ciencias Naturales de la Universidad de Zaragoza (Natural Sciences Museum of the University of Zaragoza) in Zaragoza city (Spain) under the designations MPZ2009/345–MPZ2009/347 and MPZ2017/531–MPZ2017/541.

2. Results and discussion

2.1. Taxonomic description

Division Pteridophyta
Family Tempskyaceae Read &
Brown ex L.C.A. Martínez, 2015
Genus *Tempskya* Corda emend. Kidston &
Gwynne-Vaughan, 1911
Tempskya sp.
(Figs 3–7)

The false trunks measure up to 1.20 m long in the largest specimen (Fig. 3a), with an average diameter of 10 cm, and consist of thick root mantles (adventitious roots) and embedded rhizomes (Figs 3, 4). Most specimens are somewhat compressed laterally, resulting in an oval outline in cross-sectional view of the false trunk (Fig. 4a, b).

The rhizomes are clearly visible on the surface of both medial and apical parts of the false trunks (Fig. 3b, d), but are often protruded or obscured by root mantles in the basal part (Fig. 3c). The rhizomes are distributed randomly in the false trunks (Fig. 3b–e) and proceed distally from the base to the apex. Interval dichotomisation of rhizomes is *ca.* 5 cm on average, with the next order of rhizomes also dividing dichotomously at approximate intervals of 1.5–2 cm (Fig. 3d, e). In cross section, rhizomes are oval-shaped and arranged randomly in the false trunks (Fig. 4). The leaf traces depart from the dorsal side of the rhizomes, either singly or as part of aggregations of several traces, with shorter internodes in most rhizomes (Figs 5a, b, d). One specimen (MPZ2017/540) shows leaf petiole scars arranged in a definite interval of nearly 0.7 cm on the ventral side of the rhizome (Fig. 3f). Histological details are best preserved in specimen MPZ2017/532 (Fig. 5a), although the preservation is still insufficient to observe tissue details.

Thin sections of the rhizomes show their structure from the centre outwards, consisting in this order of the pith, the vascular cylinder, the cortex and the epidermis. The different tissues can be recognised as concentric areas preserved differently both in colour and in structure (Fig. 5b, d). The cortex is composed of the outer layer, which is preserved as a pale-coloured zone that is probably parenchymatous, and the inner layer, which consists of a dark-coloured band and is possibly sclerenchymatous (Fig. 5b). The vascular cylinder is amphiphloic, with a central ring of scalariform tracheids (Fig. 5h). Possible phloem is observed as more recrystallised, light-coloured areas. The pith is poorly preserved, but as with the outer cortex, is probably parenchymatous. Some rhizomes preserve circular-shaped cells in the xylem and inner cortex, although these cells are usually crushed due to deformation during diagenesis (Fig. 5c).

The leaf traces are V-, C- or U-shaped depending on the orientation of the thin sections (Fig. 5b, d), although they usually present crescent morphologies due to deformations that also caused poor tissue preservation (Fig. 5e). The adaxial margins of the leaf traces are slightly incurved (Fig. 5d).

Roots are the most abundant and best-preserved elements in the false trunks, and form a compact mesh between the rhizomes and departing leaf bases (Fig. 5a, b, d). In cross section, the roots are circular to oval-shaped (Fig. 5f, g), 400–500 μ m in diameter, or, if deformed, 600–800 μ m in maximum dimensions, and consist of central diarch xylem, poorly preserved phloem and a cortex composed of two layers (Fig. 5f). Root metaxylem tracheids show scalariform thickening in longitudinal section (Fig. 5h).

2.2. Affinities

The external part of the false trunks is well preserved, showing some morphological features characteristic of the family Tempskyaceae Read & Brown ex L.C.A. Martínez – namely, three-dimensional networks of slender rhizomes embedded in a thick matrix of adventitious roots. The rhizomes are solenostelic, departing petioles have a single V-, C- or U-shaped vascular bundle and the diarch roots also confirm the family diagnosis.

Detailed histological structures of most specimens have been altered or even destroyed due to recrystallisation. However, partially preserved portions of false trunks provide some internal features. Due to the limited number of taxonomically valid

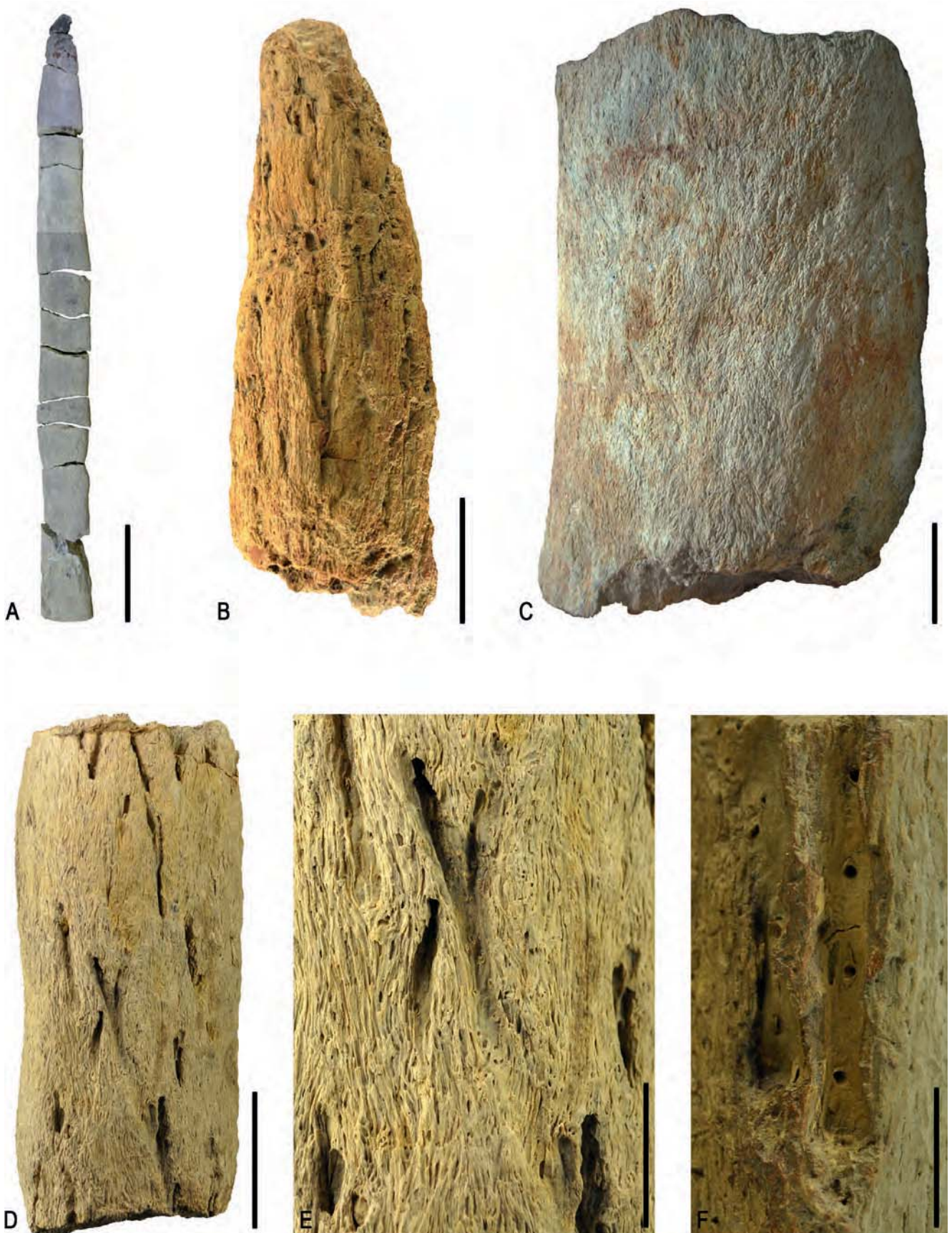


Figure 3 (A) Most complete specimen of *Tempuskya* sp. (MPZ2017/538), measuring 1.2 m long. (B) Apical part of false trunk (specimen MPZ2017/541) presenting abundant surface moulds of rhizomes. (C) Basal part of *Tempuskya* (specimen MPZ2017/539) almost completely covered by adventitious roots. Old rhizomes are covered and obscured by root mantle. (D) Central part of a false trunk (specimen MPZ2017/533) showing well-marked external moulds of dichotomising rhizomes ascending the false trunk. (E) Detail of central area of (D) enlarged, showing the contour of rhizomes. (F) A linear sequence of equally spaced circular marks corresponding to leaf scars (specimen MPZ2017/540). Scale bars = 20 cm (A); 5 cm (B–D); 2 cm (E); 1 cm (F).



Figure 4 Polished transverse sections of false trunks of *Tempskya* sp. (A) Many elliptical to round rhizomes are dispersed randomly within a root mass. Difference in colour is due to weathering caused by water percolation from cracks in the middle of the sample (specimen MPZ2017/535). (B) Specimen MPZ2017/534, showing hollows corresponding to dissolution of the interior part of rhizomes. Red dashed lines indicate positions of charcoalified remains, which comprise three concentric curves parallel to the false-stem external surface. (C) Upper-right area of (B) enlarged, showing black charcoalified roots (arrows). Scale bars = 1 cm (A, C); 2 cm (B).

characters, it is not possible to assign our fossils to a definite species or to designate them as a new taxon within the genus, and it is thus only possible to describe them as *Tempskya* sp. Despite these limitations, it is notable that the short internodes observed in most stem cross sections (Figs 4a, 5a) differ from the long internodes observed in specimen MPZ2017/540 (Fig. 3f), which suggests the presence of false trunks showing different morphologies that could represent two species. However, we do not have sufficient histological information to confirm this hypothetical taxonomic assertion.

2.3. Palaeoenvironmental implications

The presence of abundant remains of larger pieces of false trunks, some of which still preserve the apex (Fig. 3a, b), and the spindle-like original shape would seem to indicate short-distance transportation from the growing habitat. The sedimentological evidence of the fossil-containing deposits near

the Escucha locality (Pardo *et al.* 1991; Querol *et al.* 1992) suggests that the *Tempskya* plants studied here would have grown near the tidally influenced fluvial channels that developed on the western coast of the Tethys Ocean on the Iberian Plate during the middle–late Albian.

A very interesting preservation feature exhibited by three specimens (MPZ2017/533, MPZ2017/534 and MPZ2017/537) is the presence of coalified tissues embedded in the false trunks. The polished section of specimen MPZ2017/534 shows some black-coloured charcoalified roots that seem to be arranged in a circular pattern forming three nearly concentric sequences of incomplete rings parallel to the external contour of the false trunk (Fig. 4b, c). Moreover, these circular sequences of black roots are confined to one side, accounting for nearly one third of the false trunk (Fig. 4b). These roots show a different type of preservation to the surrounding tissues, because they are charcoalified whereas all other elements in the false trunks are silicified. This can also be observed in thin sections as a distinct compositional difference between the charcoalified roots and other silicified roots (Fig. 6a, b), as well as the broken cell walls only present in the former (Fig. 6d). The charcoalification process in these roots is also identifiable under a scanning electron microscope (SEM), showing cell lamellae that are partially fused (Fig. 7c, d) due to the possible influence of high temperatures on the cell walls (Scott 2000, 2010).

The presence of charcoalified plant tissues, which are arranged in three parallel lines on the same side of transverse sections of specimen MPZ2017/534, suggests the possible influence of fire on some of the false trunks, from the same direction. Nevertheless, only a limited number of tissues were affected by fire, while the other surrounding roots remain unaltered (non-charcoalified) (Fig. 6a–c).

One possible explanation for the localised presence of charcoalified roots in some false trunks is that several direction-orientated wind–fire events may have occurred various times during tree fern growth (Fig. 8). Multiple occurrences of such fire events that could have damaged the local plant community have been previously inferred from burnt plant leaves and charcoalified wood remains from the Albian deposits of the Escucha Formation in this area (Villanueva-Amadoz *et al.* 2010, 2015; Sender 2012; Sender *et al.* 2015). In our case, it is possible that the fire only affected a specific part of the plant surface – those dead and/or dried roots, leaving major parts – most living and/or humid roots – intact. It could be also possible that most burnt roots were eroded or washed away before the fire-affected surface was covered again by new roots, leaving limited numbers of charcoalified roots in the false trunk.

Wildfire effects have been documented both in extant plants (Gutsell & Johnson 1996; Scott *et al.* 2000; Stambaugh *et al.* 2017 and references therein) and in fossil plants (Scott 2000, 2010; Scott *et al.* 2000; Brown *et al.* 2012 and references therein). However, in our case, we hypothesise that only the hot winds produced by these fires, and not direct flames, would have affected the false trunks, thus burning only some of the tissues; both the number and position of the charred roots contained within the false trunks are selective, and this could be due to the respective differences in the humidity of the roots within the false trunk. Partially burnt and charred plant tissues caused by wildfires have been documented previously in several extant (Scott 2010) and fossil records, including gymnosperm and angiosperm remains (Jones *et al.* 1993; Scott 2010; Degani-Schmidt *et al.* 2015), and similar effects of fire have been reported in experiments on living lycopods and ferns (Walker & Boneta 1995; Vogel *et al.* 2011).

Baker & Dugan (2013) recorded the distribution, size and shape of fire scars on trunks of an extant conifer, and they found that the scar orientations were usually aligned towards

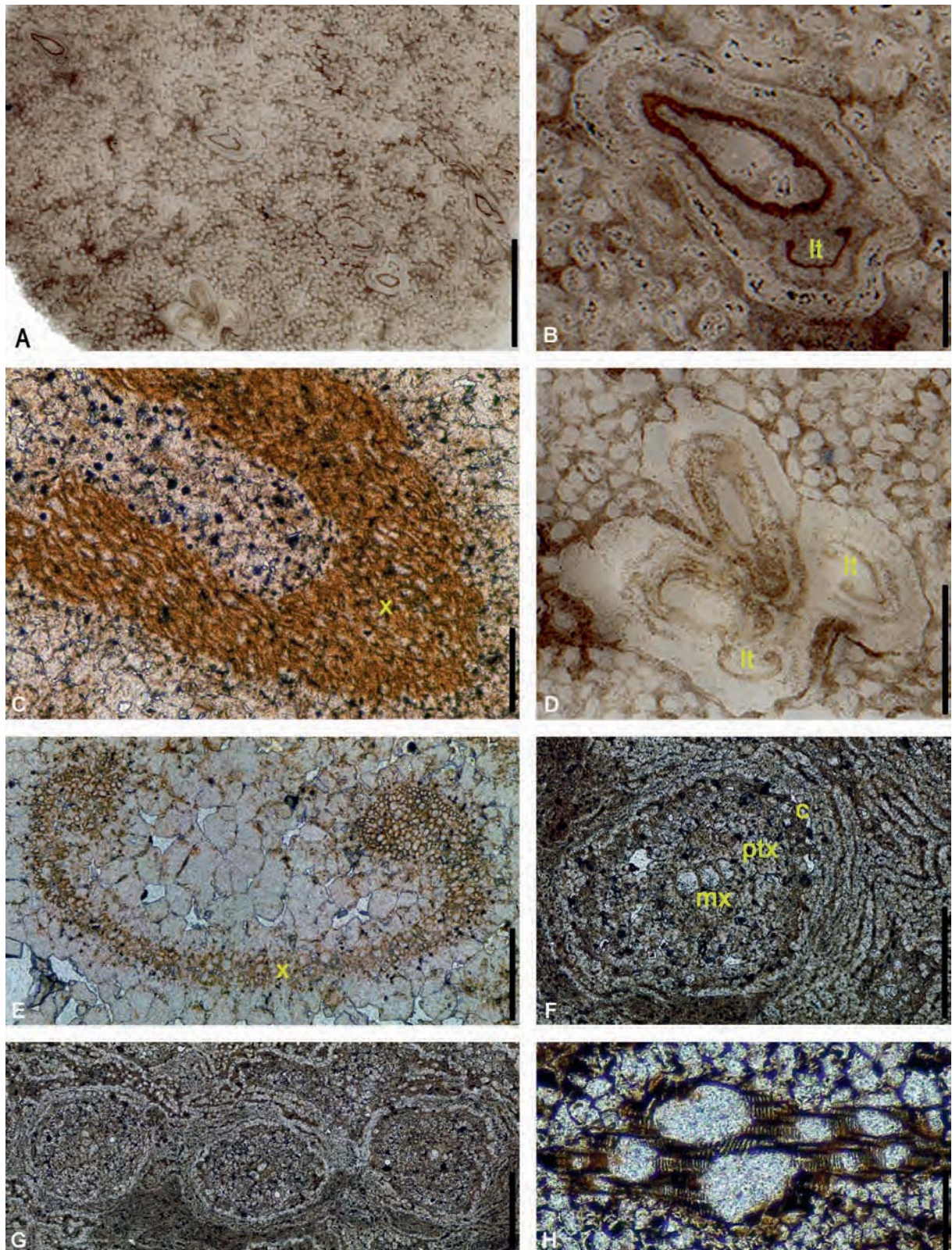


Figure 5 Transverse thin sections of false trunks of *Tempuskyia* sp.. (A) Nearly oval-shaped rhizomes with departing petiole bases, showing dorsoventrally oriented rhizome (specimen MPZ2017/532). (B) Upper-left part of (A) enlarged, showing a rhizome departing a C-shaped leaf trace. Notice a leaf trace in preparation on the upper-left side of the rhizome. (C) Specimen MPZ2017/532, with part of a rhizome xylem cylinder and surrounding tissues cut slightly oblique, showing deformed xylem cells between other recrystallised tissues. (D) Lower part of (A) enlarged, showing a dichotomising rhizome having formed two solenosteles, each developing leaf traces. (E) Close-up of a petiolar leaf trace with a distorted C-shape and only xylem cells preserved. (F) Specimen MPZ2017/535, showing a single root preserving the cortex, protoxylem and the metaxylem in the centre. (G) A group of three roots in transverse section from the same specimen as in (F). (H) Root tracheids showing scalariform thickenings in an oblique longitudinal section. Abbreviations: c = cortex; lt = leaf trace; mx = metaxylem; ptx = protoxylem; x = xylem. Scale bars = 1 cm (A); 1 mm (B), 200 μ m (C); 3 mm (D); 400 μ m (E, F); 500 μ m (G); 100 μ m (H).

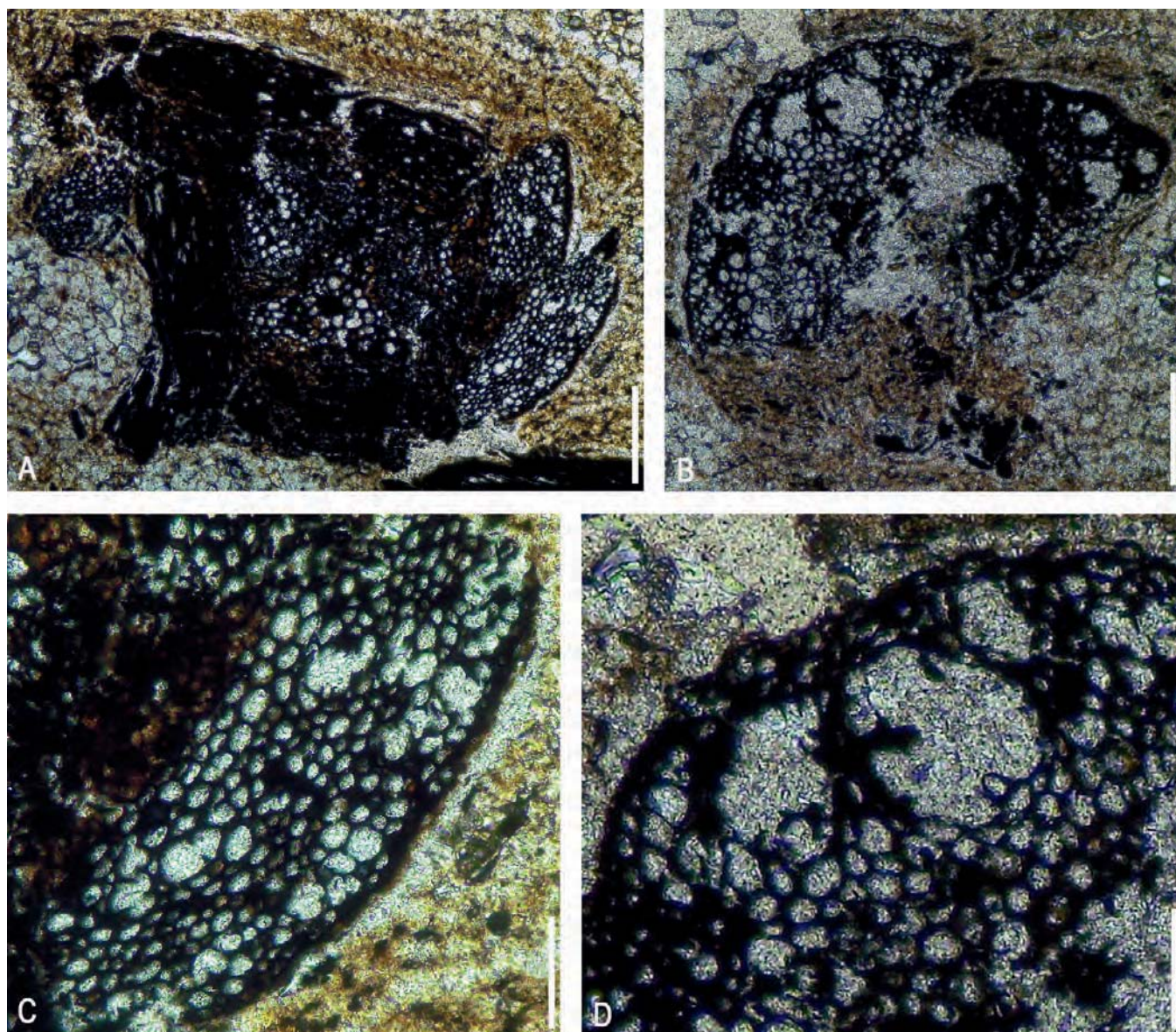


Figure 6 Thin sections of charcoalfied roots from specimen MPZ2017/534 in Figure 4b. (A, B) Two charcoalfied roots partially fused or cracked by probable fire influence. (C) Detail of (A), showing distinct type of preservation between charcoalfied tissues (in black) and silicified tissues (yellow to ochre). (D) Detail of (B). Some charcoalfied cells are broken, resulting in large holes due to recrystallisation. Scale bars = 500 µm (A, B); 200 µm (C, D).

the direction of the fire. In our case, only charred tissues but not fire scars were preserved; although the anatomy of tree ferns precludes a classical fire scar, we can also estimate the direction of the fire based on the distribution pattern of the charcoalfied roots in the false trunk. Following the distribution of charcoalfied remains, at least three fire events that could have influenced the plant community of the *Tempskya* from Spain have been identified (Fig. 4b, c). After each event, subsequent plant regrowth covered the charcoalfied roots, embedding them within the false trunk. It is also noteworthy that this is the first report worldwide of the possible effects of wildfire on false trunks of *Tempskya*.

Another possibility concerning the explanation for the selective charcoalfication of roots in the studied false trunks of *Tempskya* could be a result of low-intensity surface fire, causing charring on the leeward side of the false trunk. In this process, the char would detach from the false trunks due to both the brittle nature of charcoal and the less dense nature of the *Tempskya* tissue compared to true trunks. This may have been followed by growth of new roots over the injured

face (Dr Tamara Fletcher, personal communication). However, we did not find any base of preserved *Tempskya* and, therefore, we are not able to check the possible charcoalfied remains in the area, which would indicate the action of a surface fire.

2.4. Palaeophytogeographical dispersal of genus *Tempskya* during the Cretaceous

To date, the genus *Tempskya* has been found in both hemispheres and on all continents except Africa and Antarctica (Table 1). The fossils occur most abundantly in Albian–Cenomanian deposits from western regions of the US (Ash & Read 1976), but this abundance could be due to extensive palaeontological field campaigns and excavations carried out at the beginning of the 20th Century by a number of North American scientists. Nevertheless, *Tempskya* has also been recovered from many other locations worldwide in the last three decades.

Some articles on *Tempskya* have tried to map its distribution patterns during the Cretaceous (Tidwell & Wright 2003; Clifford & Dettmann 2005). Unfortunately, these attempts

Table 1 Data of *Tempskya* species, indicating their geographic distribution and age.

Species	Geographic location	Age
1. <i>Tempskya dernbachii</i> Tidwell & Wright emend. Martínez, 2015	Neuquen province (Argentina)	Valanginian
2. <i>Tempskya dernbachii</i> Tidwell & Wright, 2003	Neuquén province (Argentina)	Valanginian (formerly assigned to Albian deposits but emended by Martínez & Olivo, 2015)
3. <i>Tempskya riojana</i> Barale & Viera, 1989	La Rioja and Soria provinces (Spain)	Valanginian–Hauterivian
4. <i>Tempskya</i> aff. <i>riojana</i> Puente-Arauzo <i>et al.</i> , 2014	Burgos province (Spain)	Upper Hauterivian–Lower Barremian
5. <i>Tempskya</i> sp. Carpentier, 1923	Glageon (France)	Barremian–Aptian?
6. <i>Tempskya schimperi</i> Corda, 1845	Germany, Czech Republic, England and France	Hauterivian–Barremian?
7. <i>Tempskya</i> sp. Jung, 1983	Bavaria state (Germany)	Hauterivian–Barremian?
8. <i>Tempskya erosa</i> Stopes, 1915	Brighstone, Wigh Island (England)	Aptian–Albian
*<i>Tempskya</i> sp. (this paper)	Escucha, Aragón region (Spain)	Middle–Upper Albian
9. <i>Tempskya whitei</i> Berry, 1911	Maryland (USA)	Middle–Upper Albian
10. <i>Tempskya superba</i> Arnold, 1958	Nebraska, Nevada and Utah (USA)	Aptian–Albian?
11. <i>Tempskya reesidei</i> Ash & Read, 1976	Nuevo México (USA)	Upper Albian
12. <i>Tempskya zelleri</i> Ash & Read, 1976	Nuevo México and Utah (USA)	Upper Albian
13. <i>Tempskya minor</i> Read & Brown, 1937	New Mexico, Utah, Wyoming, Nevada and Idaho (USA)	Upper Albian
14. <i>Tempskya readii</i> Tidwell & Hebbert, 1992	Utah (USA)	Albian
15. <i>Tempskya stichkae</i> Tidwell & Hebbert, 1992	Utah (USA)	Albian
16. <i>Tempskya wyomingensis</i> Arnold, 1945	Utah and Wyoming (USA)	Upper Albian
17. <i>Tempskya grandis</i> Read & Brown, 1937	Utah and Wyoming (USA)	Upper Albian
18. <i>Tempskya wessellii</i> Arnold, 1945	Utah, Montana, Idaho and Oregon (USA)	Upper Albian
19. <i>Tempskya knowltoni</i> Seward, 1924	Utah and Montana (USA)	Upper Albian–Lower Cenomanian
20. <i>Tempskya jonesii</i> Tidwell & Hebbert, 1992	Utah (USA)	Albian and Cenomanian
21. <i>Tempskya judithae</i> Clifford & Dettmann, 2005	Winton, Queensland (Australia)	Upper Albian
22. <i>Tempskya pulchra</i> Corda, 1845	Bohemia region (Czech Republic)	Cenomanian?
23. <i>Tempskya varians</i> Velenovsky, 1888	Pecínov, Bohemia region (Czech Republic)	Upper Cenomanian
24. <i>Tempskya cretacea</i> Hosius & von der Marck, 1880	Westfalia state (Germany)	Senonian?
25. <i>Tempskya rossica</i> Kidston & Gwynne-Vaughan, 1911	Karaganda River basin, Aktobe Region (Kazakhstan)	Santonian?
26. <i>Tempskya iwatensis</i> Nishida, 1986	Iwate prefecture (Japan)	Santonian?
27. <i>Tempskya uemurae</i> Nishida, 2001	Iwate prefecture (Japan)	Santonian

have failed to show chronological phytogeographical changes because they only used one palaeogeographical map for a given age. Here, we present five palaeogeographical maps from Scotese (2013), on which we have plotted the locations of *Tempskya* at five age intervals, i.e., the Valanginian, Hauterivian–Barremian, Aptian–Albian, Cenomanian and Santonian (Fig. 9).

These mapped distributions show that the first presence of *Tempskya* in the Hauterivian was recorded in two very distant areas, namely Spain (Barale & Viera 1989) and Argentina (Martínez & Olivo 2015) (Fig. 9e). Another interesting point deduced from the maps is the constant presence of *Tempskya* from the Valanginian to Albian in the area occupied today by the Iberian Peninsula (Fig. 9c–e), and a possible distributional shift of the genus from the central Atlantic Ocean area to the Far East during the Cenomanian–Santonian (Fig. 9a, b). These data suggest that the area occupied by the Iberian Peninsula during the Valanginian–Albian may have been a

dispersal pathway for this genus, at least to North America, as the distribution of land masses and seas changed, developing land bridges and barriers to dispersal. This hypothesis regarding the possible dispersal of plant taxa between North America and the islands that constituted the Iberian Plate during the Early Cretaceous was presented recently by Sender *et al.* (2012, 2016) based on similar distributional patterns of angiosperm taxa in both areas. Therefore, it is also possible that *Tempskya* could have dispersed along the same route, probably through Greenland and islands that once connected North America and the Iberian Plate during the Albian.

3. Conclusions

- The first record of the genus *Tempskya* from the Albian of western Eurasia is reported based on silicified false trunks found in the Upper Member of the Escucha Formation in NE Spain.

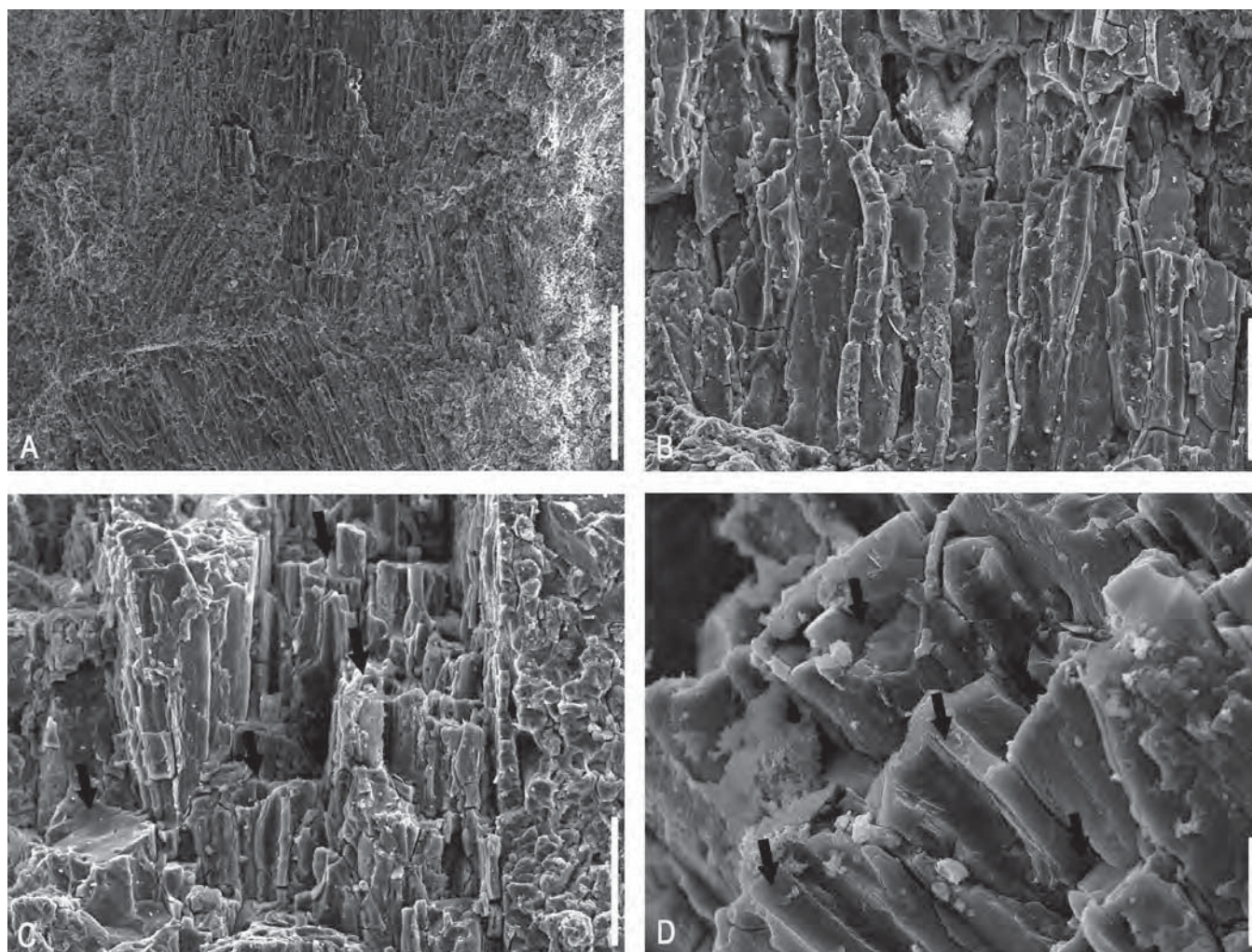


Figure 7 SEM images of charcoaled roots from specimen MPZ2017/534 in Figure 4b. (A) general view of a root fragment with oriented arrangement of grouping tracheids. (B) Detail of (A), showing tracheids. (C) Broken cells with fused lamellae (arrows). (D) detail of some of the broken cells (tracheids), showing fused lamellae due to the influence of fire (arrows). Scale bars = 200 μm (A); 50 μm (B); 25 μm (C); 5 μm (D).

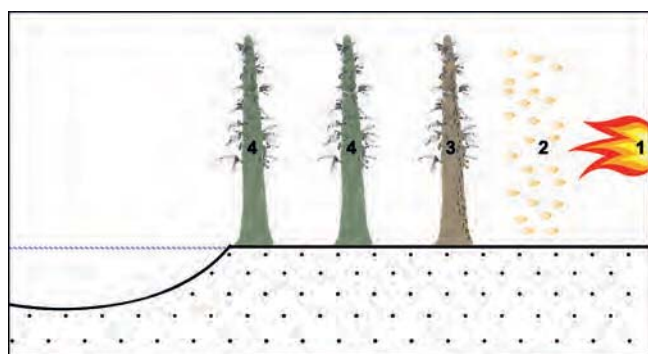


Figure 8 Schematic palaeoenvironmental reconstruction of the hypothetical fire event affecting *Tempskya* sp. plants, which grew near a fluvio-tidal channel close to the coast. (1) Recurrent wildfires occurred in relatively distant neighbouring forests. (2) Hot winds or weak fires coming from main wildfires. (3) The heat from fires partially burnt some *Tempskya* plants or parts of them. (4) More distant coeval *Tempskya* plants remain intact.

- These findings fill the biostratigraphic gap of *Tempskya* between the basal Early Cretaceous and the early Late Cretaceous in western Eurasia.

- The presence of large fragments representing several individuals and the taphonomic data from the fossil-bearing deposits indicate that the plants grew near tidally influenced fluvial channels.
- The remains of charred roots in some false trunks suggest environmental conditions involving recurrent occasional fires.
- Nearby wildfires from the same direction could have caused hot winds that promoted partial charring of some exposed surfaces of the false trunks at several distinct times during plant growth.
- These new records of the *Tempskya* tree fern from the Albian of Spain may support the hypothesis that the genus dispersed from western Eurasia to both North America and eastern Eurasia during the mid-Cretaceous.

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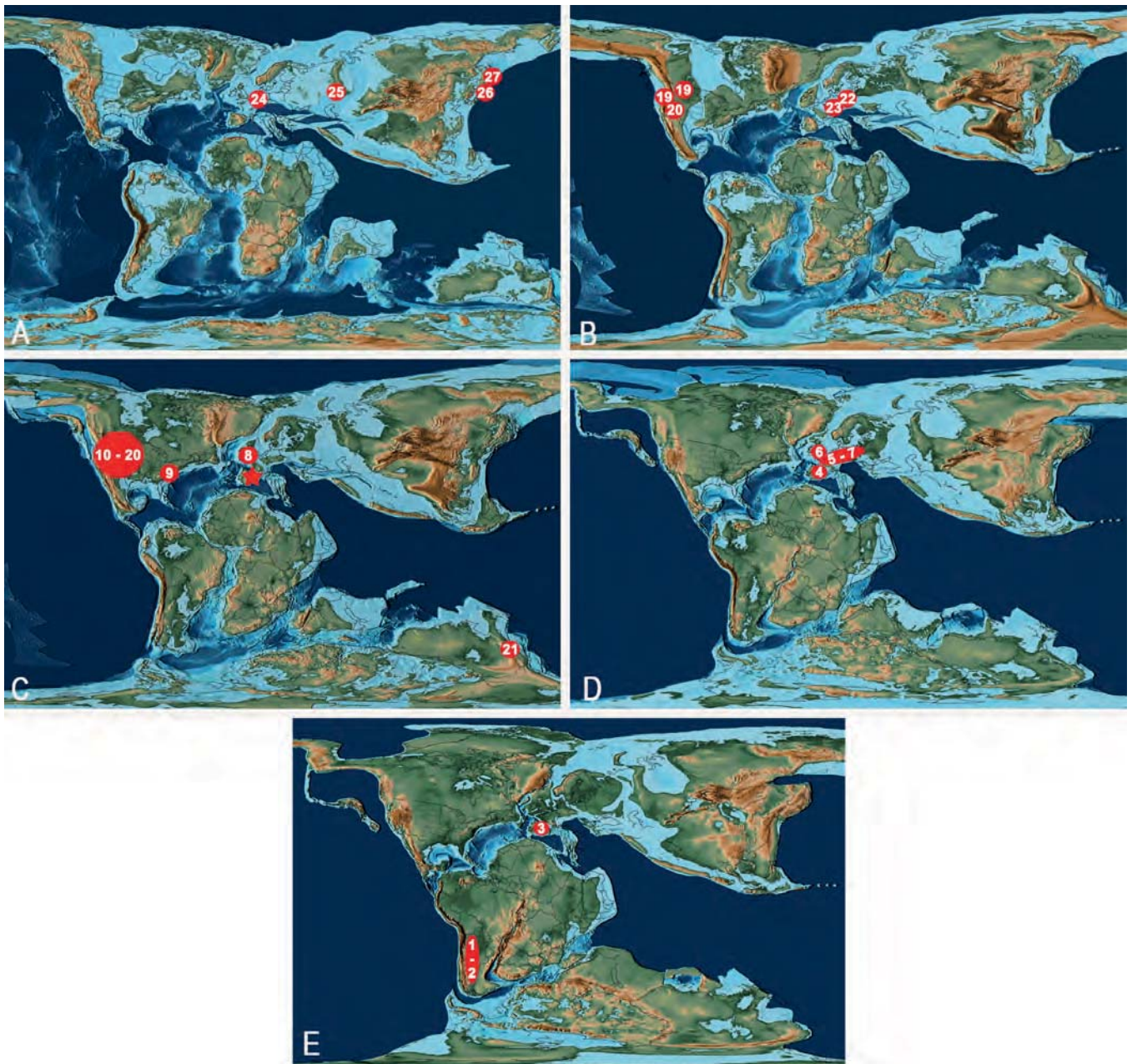


Figure 9 Palaeophytogeographical distribution of *Tempuskyia* in time, based on fossil sites (indicated by red dots) associated with the number referring to the species reported for each site. (A) Santonian. (B) Cenomanian. (C) Albian–Aptian. (D) Barremian–Hauterivian. (E) Valanginian. 1, 2. *Tempuskyia dernbachii* Tidwell & Wright emend. Martínez; 3. *T. riojana* Barale & Viera; 4. *T. aff. riojana* Puente, Arauzo *et al.*; 5. *Tempuskyia* sp. in Carpentier; 6. *T. schimperi* Corda; 7. *Tempuskyia* sp. in Jung; 8. *T. erosa* Stopes; 9. *T. whitei* Berry; 10. *T. superba* Arnold; 11. *T. reesidei* Ash & Read; 12. *T. zelleri* Ash & Read; 13. *T. minor* Read & Brown; 14. *T. readii* Tidwell & Hebert; 15. *T. stichkae* Tidwell & Hebert; 16. *T. wyomingensis* Arnold; 17. *T. grandis* Read & Brown; 18. *T. wessellii* Arnold; 19. *T. knowltoni* Seward (1924); 20. *T. jonesii* Tidwell & Hebert; 21. *T. judithae* Clifford & Dettmann; 22. *T. pulchra* Corda; 23. *T. varians* Velenovsky; 24. *T. cretacea* Hosius & Marck; 25. *T. rossica* Kidston & Gwynne-Vaughan; 26. *T. iwatensis* Nishida; 27. *T. uemurae* Nishida. Palaeogeographical maps modified from Scotese (2013).

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