

Taxodioxyton-like charcoal from the Late Miocene of western Bulgaria

DIETER UHL^{1, 2}, MARTINA DOLEZYCH³ and MADELAINE BÖHME²

¹Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; e-mail: dieter.uhl@senckenberg.de

²Senckenberg Centre for Human Evolution and Palaeoenvironment, Fachbereich Geowissenschaften, Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany; e-mail: dieter.uhl@uni-tuebingen.de; m.boehme@ifg.uni-tuebingen.de

³Senckenberg Naturhistorische Sammlungen Dresden, Königsbrücker Landstr. 159, 01109 Dresden, Germany; e-mail: martina.dolezych@senckenberg.de

Received 6 February 2014; accepted for publication 28 April 2014

ABSTRACT. We present the first anatomical description and taxonomic interpretation of macroscopic charcoal from the Late Miocene of the Staniantsi Coal Basin in western Bulgaria. The charcoal closely resembles the wood genus *Taxodioxyton* and thus can most likely be assigned to taxodioid Cupressaceae. This group of plants was part of the peat-forming swamp vegetation during generally drier periods, as shown by previous studies on palynomorphs from the basin. Our report presents the first solid evidence indicating which group of plants and probably which type of vegetation were affected by wildfires during deposition of the peat, although taxodioid Cupressaceae certainly were not the only group of plants affected by these fires; it also represents the first record of taxonomically identifiable palaeobotanical macroremains from the Staniantsi Basin.

KEYWORDS: charcoal, palaeowildfire, swamp vegetation, Miocene, Bulgaria

INTRODUCTION

The presence of charcoal (including pyrogenic inertinites, a group of coal macerals) as well as certain pyrogenic polyaromatic hydrocarbons in sediments can be regarded as direct evidence for the occurrence of wildfires during the geological past (Scott 2000, 2010). The oldest evidence of wildfires consuming plant biomass comes from Silurian deposits (Glasspool et al. 2004), and since then wildfires have played an important role in the Earth system (Bowman et al. 2009). A large number of studies have focussed on Palaeozoic, Mesozoic and Quaternary wildfires (cf. Scott 2000, 2010, Conedera et al. 2009 and references therein), but although charcoal occurs frequently in Tertiary sediments (Scott 2000, 2010) there are far fewer detailed studies on Tertiary wildfires.

The majority of studies dealing at least broadly with Tertiary charcoal have a palyno-

logical focus, reporting only the occurrence of fossil microcharcoal (e.g. Masselter & Hofmann 2005, Martin 2006, Utescher et al. 2009). There are also a few studies focussing directly on microcharcoal in sediments (e.g. Dodson et al. 2005). Generally the material investigated in those works is too small to allow for a reliable taxonomic interpretation, leaving it unclear which ecosystems or vegetation types were influenced by wildfires. The few studies that deal with macrocharcoal in more detail have demonstrated the potential of such investigations to provide additional information about the vegetation influenced by fire during the Tertiary (e.g. Figueiral et al. 1999, 2002, Olivares et al. 2004, Holdgate et al. 2007, Cheng et al. 2011, Uhl et al. 2011).

The occurrence of charcoal as evidence of palaeowildfires within lignites of the Belozem

Formation from the Bulgarian part of the Staniantsi Basin at the Bulgarian-Serbian border has been reported (Utescher et al. 2009, Zdravkov et al. 2011) without anatomical or even taxonomical details of this material being given. Our report thus presents the first solid evidence of which plant groups and probably vegetation types (probably amongst others) were affected by wildfires during deposition of the peat; it also represents the first record of taxonomically identifiable palaeobotanical macroremains from the Staniantsi-Masgosh Basin in western Bulgaria.

This information comes from a German-Bulgarian field project begun in 2010 to investigate several small Neogene basins in western Bulgaria.

GEOLOGICAL BACKGROUND

The Staniantsi Basin, located in eastern Serbia (where it is known as Masgosh Basin) and western Bulgaria (Fig. 1), is a NW–SE-trending intramontane graben 10 km long and 3 km wide (Vatsev 1999).

The Staniantsi Basin is 50 km north-northwest of Sofia. It is a northwest-southeast trending intramontane basin ca 6 km long, covering the Bulgarian-Serbian border. The Staniantsi Brown Coal Mine exposes a >50 meter thick section (referred to the Belozem and Zainitsa Formations by Vatsev 1999), showing several erosional hiatuses and a great variety of sedimentary facies (e.g. lignite, xylite, lignitic/xylitic clay, marl, lacustrine chalk, travertine, caliche, fine sand, conglomerate, breccia). A main characteristic of the overall swampy (coal) sedimentation of the Belozem Formation is the cyclic change. Each lignite cycle



Fig. 1. Map of Bulgaria. Star indicates location of Staniantsi Coal Basin in western Bulgaria



Fig. 2. Field photograph of the contact of two lignite-xylite cycles



Fig. 3. Carbonate-coated roots and caliche at top of a xylite layer

ends with xylites (Fig. 2) containing charcoal layers and/or carbonatic caliche-like horizons (Fig. 3), both suggesting strong climatic forcing of sedimentation. For further details on the geology of the basin, including a rough geological map and a profile, see Utescher et al. (2009) and references therein.

Based on scarce biostratigraphic data (mammal remains, MN13; Nikolov 1985) and (preliminary) paleomagnetic data (Utescher et al. 2009), the basal part of the Belozem Formation, during which peat formation occurred, is presumed to have been deposited during the latest Miocene Pontian regional stage.

MATERIAL AND METHODS

MATERIAL

The material investigated here comes from the top of a lignite-xylite cycle from the Belozem Formation. It was collected during field work in 2012, from

a xylitic horizon in the middle part of the main coal seam. A more detailed publication on the geology, stratigraphy and palaeozoology of the basin is in preparation and will be published elsewhere. The material is housed at the Palaeontological Collection of Tübingen University and stored under accession number GPIT/PL/00766.

METHODS

Samples from a single specimen of charred wood were extracted mechanically from the sediment and mounted on standard stubs with LeitC (Plano GmbH), then examined with a JEOL JSM 6490 LV Scanning Electron Microscope (SEM, acceleration voltage 15 kV) at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Germany).

RESULTS AND DISCUSSION

PRESERVATION

The material described here was identified as charcoal based on the following characteristics considered diagnostic for this type of preservation (Scott 1989, 2000, 2010): black colour and streak, splintery fracture (Fig. 4), silky lustre (Fig. 4), internal anatomy preserved (Pls 1, 2), cell walls homogenised under SEM (Pl. 2, fig. 8).

The three-dimensional preservation of anatomical details is excellent; there are no fractures due to diagenetic compression as seen in many localities with macroscopic fossil charcoal (e.g. Scott 2000, Uhl et al. 2004, 2010, 2011) or in many coals or lignites containing compressed and crushed charcoal remains (known as *Bogenstrukturen* in coal petrography; e.g. Scott 1989, 2000).

The charred wood fragments range in size from microscopic up to specimens several decimeters long and several centimeters wide (Fig. 4). As such large charred wood specimens are extremely susceptible to mechanical stress, it seems unlikely that they had been transported over even short distances prior to burial, as this would have led to fragmentation of these specimens into smaller cuboid blocks of charcoal. The general appearance of several of the charcoal-rich layers on top of xylites (large fragments, no indication of abrasion) probably indicates an autochthonous origin of these charcoals. Further investigations on the taphonomy of these charcoal-rich layers are currently in progress and will be published elsewhere.

DESCRIPTION AND TAXONOMIC AFFINITY (PLATES 1, 2)

Growth rings. Growth rings vary in width (Pl. 1, fig. 1). Growth ring boundaries are distinct (Pl. 1, figs 1, 2). The transition from early- to latewood seems to be abrupt (Pl. 1, figs 1, 2). Latewood is characterised by radially flattened tracheids. The thin-walled latewood is only 1 cell wide in most cases (Pl. 1, figs 1, 2), only occasionally 2 and rarely 3 cells wide.

Tracheids. The lumina are \pm squared to polygonal in cross section (Pl. 1, figs. 1, 2).

Bordered pits. Bordered pits in the radial walls of the tracheids occur in two or three adjacent vertical rows (Pl. 1, figs 6, 8; Pl. 2, figs 2–7). Crassulae are sometimes present (Pl. 2, figs 5, 6). In the tangential walls of the tracheids the pits are considerably smaller (Pl. 1, figs 3–7; Pl. 2, fig. 10).

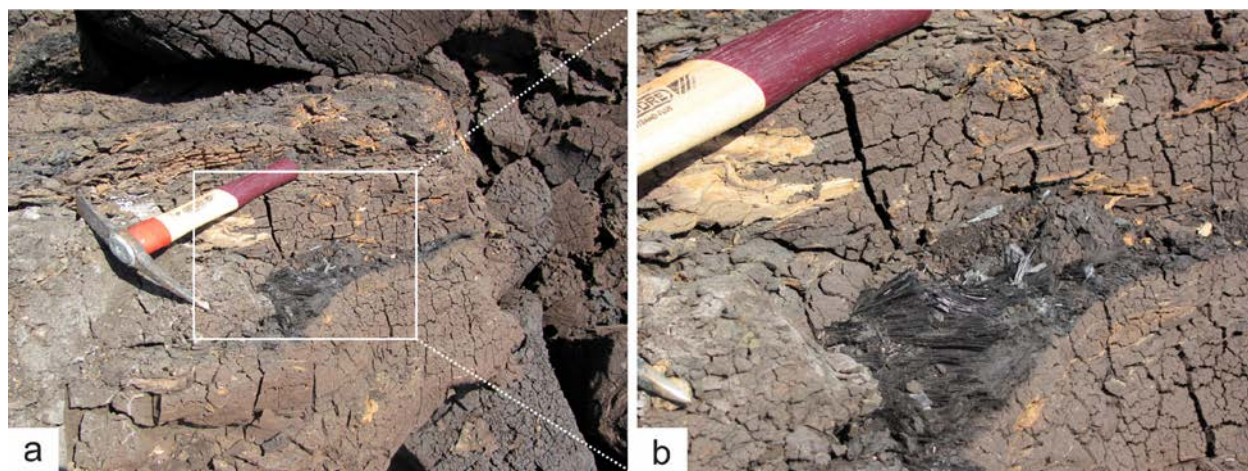


Fig. 4. **a** – Large fragment of charcoal near top of a xylite layer; **b** – enlargement of **a**, showing silky lustre and splintery fracture of charcoal

Axial parenchyma. Not observed.

Rays. Unicellular rays are 2–21 cells high (Pl. 1, figs 3–7; Pl. 2, fig. 9). The horizontal walls are thin, ca 2 µm thick; they appear to be unpitted (Pl. 2, fig. 7). The tangential walls are up to ca 2 µm thick and appear to be smooth (Pl. 2, fig. 7). The cross-fields have three to four taxodioid pits (Pl. 2, figs 1, 2) (however, the habitus of cross-field pits is easily altered during charring; Gerards et al. 2007).

Anatomical details of the charcoal point to the fossil genus *Taxodioxyton* sensu Gothan 1905 (see e.g. Dolezych 2011) but some caveats remain (i.e. no axial parenchyma has been observed) and a specific affiliation to any known species of this genus is not possible, due to taphonomic changes which affect the appearance and size of diagnostically important features such as pits on tracheid walls or cross-field pitting during charring (e.g. Jones & Chaloner 1991, Gerards et al. 2007). Specific affiliations of charred woods generally are problematic, mostly due to these diagenetic alterations of diagnostic features; as a rule, such material can be determined only to generic level.

The source plants for *Taxodioxyton* and related taxa may be different members of the taxodioid Cupressaceae, such as *Sequoia* and *Taxodium*, but it is not clear which of these taxa was the source of the material studied here. Palynological data from the same locality only point to the occurrence of Cupressaceae/Taxodiaceae at relatively low abundance, without giving more specific determinations (Ivanov et al. 2008, Utescher et al. 2009).

PALAEOECOLOGICAL SIGNIFICANCE

Fires are regular disturbances in a number of modern (e.g. Yin et al., 1993, Jones et al. 2013) as well as Tertiary (e.g. Demchuk 1993, Figueiral et al. 2002) peatforming wetlands inhabited by taxodioid Cupressaceae. Based on palynological data, Ivanov et al. (2008) and Utescher et al. (2009) suggested that taxodioid Cupressaceae were autochthonous elements in the Late Miocene peat bogs of the Staniantzi-Masgosh Basin. Our results, together with previous observations by Utescher et al. (2009) and Zdravkov et al. (2011), demonstrate that fires occurred in these peat bogs during phases of peat accumulation. Utescher et al. (2009) interpreted these phases as generally drier

phases with a lower water table, as contrasted with wetter phases characterised by sedimentation of lignitic marls. At Staniantzi it can be assumed that the lignite-xylite alternation is controlled by precessional dry-wet cyclicity similar to more or less contemporaneous sections in the Florina–Ptolemais–Servia Basin, NW Greece (e.g. Steenbrink et al. 2006). Water stress during peat formation is further indicated by carbonate accumulation and carbonate-coated roots in the xylitic part of the lignite-xylite cycles (see Fig. 3). Relatively dry climatic conditions (e.g. seasonality-related) may have favoured the ignition and spread of wildfires within mires in the Staniantzi Basin. Fires can occur during irregular or regular dry spells even in such wetland habitats (e.g. Johnson 1984, Flannigan et al. 2009), and macroscopic as well as microscopic fossil charcoal (including pyrogenic inertinites) are known from other peatforming environments, not only from the Tertiary (e.g. Demchuk 1993, Figueiral et al. 2002, Diessel 2010) but also from other periods of Earth's history (e.g. Scott 2000, Diessel et al. 2010, Jasper et al. 2011, 2013).

Possible indicators of some kind of seasonality are the thin latewood zones observed in the charcoal. The transition from earlywood to latewood is abrupt, as also seen for example in *Taxodioxyton megalonissum* described by Süß & Velitzelos (1997) from the late Oligocene/early Miocene deposits of the island of Lesbos (Greece). However, this character cannot be given much diagnostic value as it can be controlled by ecological and environmental factors (IAWA Committee 2004).

Possible factors explaining such an abrupt transition from earlywood to latewood are marked seasonality or regularly occurring changes of certain environmental conditions. At the moment it is not clear which climatic or environmental parameters may have caused the growth interruptions. From studies on modern taxodiaceous Cupressaceae it is known that these plants can produce such clear growth rings not only in response to seasonally changing climate parameters but also in response to changes in hydrological regimes (i.e. the water table) (e.g. Ewel & Parende 1984, Young et al. 1993, 1995).

In the particular case of Staniantzi, Zdravkov et al. (2011) speculated that fire may have been one of the reasons for the termination of peat formation in the Staniantzi

Basin, due to the occurrence of a centimetre-thick charcoal layer at the top of the seam, but this layer was obviously restricted to a relatively small area near the centre of the basin and probably represents a xylitic phase of the lignite-xylite cycle as described here. Unfortunately these authors did not provide detailed information about this interesting but anecdotal observation; thus their interpretation concerning the termination of peat formation in the Staniantsi Basin due to a large fire event must be considered speculative at this point.

Based on geochemical results, Zdravkov et al. (2011) and Stefanova et al. (2011) concluded that the vegetation of the mires within the Staniantsi Basin was dominated by angiosperms, and that conifers were only accessory elements, whereas Utescher et al. (2009) inferred dominance of pteridophytes, with Taxodiaceae as accessory elements. Further taxonomic analysis of more charcoals from this and additional xylitic horizons from the Staniantsi Basin, which will be part of an ongoing project, may help to unravel these puzzling results on the composition and dominance patterns within the Late Miocene mire system of this basin.

ACKNOWLEDGMENTS

We thank Claudia Franz (Senckenberg Forschungsinstitut und Naturmuseum Frankfurt) for technical assistance with SEM facilities, Nade Ognianova (Sofia), Manuela Aiglstorfer, Jerome Prieto, Philippe Havlik, and Davit Vasilyan (all Tübingen) for assistance during field work, and two anonymous reviewers for their useful comments and suggestions.

REFERENCES

- BOWMAN D.M.J.S., BALCH J.K., ARTAXO P., BOND W.J., CARLSON J.M., COCHRANE M.A., D'ANTONIO C.M., DEFRIES R.S., DOYLE J.C., HARRISON S.P., JOHNSTON F.H., KEELEY J.E., KRAWCHUK M.A., KULL C.A., MARSTON J.B., MORITZ M.A., PRENTICE I.C., ROOS C.I., SCOTTA.C., SWETNAMT.W., VANDERWERFG.R. & PYNE S.J. 2009. Fire in the Earth System. *Science*, 324: 481–484.
- CHENG Y., JIANG X., LI C.S. & WANG Y.F. 2011. Pliocene charcoals from Shanxi Province of China and their application to studies of prehistoric wildfires. *Sci. China Earth Sci.*, 54: 509–518.
- CONEDERA M., TINNER W., NEFF C., MEURER M., DICKENS A.F. & KREBS P. 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quat. Sci. Rev.*, 28: 555–576.
- DEMCHUK T.D. 1993. Petrology of fibrous coal (fusain) and associated inertinites from the Early Paleocene of the central Alberta Plains. *Int. J. Coal Geol.*, 24: 211–232.
- DIESSEL C.F.K. 2010. The stratigraphic distribution of inertinite. *Int. J. Coal Geol.*, 81: 251–268.
- DODSON J.R., ROBINSON M. & TARDY C. 2005. Two fine-resolution Pliocene charcoal records and their bearing on pre-human fire frequency in south-western Australia. *Austr. Ecol.*, 30: 592–599.
- DOLEZYCH M. 2011. Taxodiaceous woods in Lusatia (Central Europe), including curiosities in their nomenclature and taxonomy, with a focus on *Taxodioxylon*. *Japanese J. Hist. Bot.* 19: 25–46.
- EWEL K.C. & PARENDES L.A. 1984. Usefulness of annual growth rings of cypress tress (*Taxodium distichum*) for impact analysis. *Tree-ring Bull.*, 44: 39–43.
- FIGUEIRAL I., MOSBRUGGER V., ROWE N.P., ASHRAF A.R., UTESCHER T. & JONES T.P. 1999. The Miocene peat-forming vegetation of northwestern Germany: an analysis of wood remains and comparison with previous palynological interpretations. *Rev. Palaeobot. Palynol.*, 104: 239–266.
- FIGUEIRAL I., MOSBRUGGER V., ROWE N.P., UTESCHER T., JONES T.P. & VON DER HOCHT F. 2002. Role of charcoal analysis for interpreting vegetation change and paleoclimate in the Miocene Rhine Embayment (Germany). *PALAIOS*, 17: 347–365.
- FLANNIGAN M.D., KRAWCHUK M.A., DE GROOT W.J., WOTTON B.M. & GOWMAN L.M. 2009. Implications of changing climate for global wildland fire. *International J. Wildland Fire*, 18: 483–507.
- GERARDS T., DAMBLON F., WAUTHOZ B. & GERIENNE P. 2007. Comparison of cross-field pitting in fresh, dried and charcoalified softwoods. *IAWA J.*, 28: 49–60.
- GLASSPOOL I.J., EDWARDS D. & AXE L. 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology*, 32: 381–383.
- HOLDGATE G.R., CARTWRIGHT I., BLACKBURN D.T., WALLACE M.W., GALLAGHER S.J., WAGSTAFF B.E. & CHUNG L. 2007. The Middle Miocene Yallourn coal seam – The last coal in Australia. *Int. J. Coal Geol.*, 70: 95–115.
- IAWA Committee 2004. IAWA list of microscopic features for softwood identification. *IAWA J.*, 25: 1–70.
- IVANOV D., UTESCHER T., ASHRAF A.R., MOSBRUGGER V., SLAVOMIROVA E., DJORGOVA N. & BOZUKOV V. 2008. Vegetation structure and dynamics in the late Miocene of Staniantsi Basin (W Bulgaria). *Compt. Rend. Acad. bulg. Sci.* 61(2): 223–232.
- JASPER A., UHL D., GUERRA-SOMMER M., BERNARDES-DE-OLIVEIRA M.E.C. & MACHADO N.T.G. 2011. Upper Paleozoic charcoal remains

- from South America: Multiple evidences of fire events in the coal bearing strata of the Paraná Basin, Brazil. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 306: 205–218.
- JASPER A., GUERRA-SOMMER M., ABU HAMAD A.M.B., BAMFORD M., BERNARDES-DE-OLIVEIRA M.E.C., TEWARI R. & UHL D. 2013. The Burning of Gondwana: Permian fires on the Southern Continent – a palaeobotanical approach. *Gondwana Res.*, 24: 148–160.
- JOHNSON B. 1984. The Great Fire of Borneo. World Wild Life Fund, Godalming, Surrey, 24 pp.
- JONES J.W., HALL A.E., FOSTER A.M. & SMITH T.J. 2013. Wetland fire scar monitoring and analysis using archival Landsat data for the Everglades. *Fire Ecol.*, 9: 133–150.
- MARTIN H.A. 2006. Cenozoic climatic change and the development of the arid vegetation in Australia. *J. Arid Env.*, 66: 533–563.
- MASSELTER T. & HOFMANN C.-C. 2005. Palynology and palynofacies of Miocene coal-bearing (clastic) sediments of the Hausruck area (Austria). *Geobios*, 38: 127–138.
- NIKOLOV I. 1985. Catalog of the findings of Tertiary mammals in Bulgaria. *Palaeontology, Stratigraphy and Lithology*, 21: 43–62 (in Bulgarian).
- OLIVARES C.A., ANTÓN M.G., MANZANEQUE F.G. & JUARISTI C.M. 2004. Palaeoenvironmental interpretation of the Neogene locality Caranceja (Reocín, Cantabria, N Spain) from comparative studies of wood, charcoal, and pollen. *Rev. Palaeobot. Palynol.*, 132: 133–157.
- SCOTT A.C. 1989. Observations on the nature and origin of fusain. *Int. J. Coal Geol.*, 12: 443–475.
- SCOTT A.C. 2000. The Pre-Quaternary history of fire. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 164: 297–345.
- SCOTT A.C. 2001. Preservation by fire. In: *Palaeobiology a synthesis II*. Briggs, D.E.G., Crowther, P.R. (eds) Blackwell Scientific Publ., 277–280.
- SCOTT A.C. 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 291: 11–39.
- STEENBRINK J., HILGEN F.J., KRIJGSMAN W., WIJBRANS J.R. & MEULENKAMP J.E. 2006. Late Miocene to Early Pliocene depositional history of the intramontane Florina-Ptolemais-Servia Basin, NW Greece: interplay between orbital forcing and tectonics. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 238: 151–178.
- STEFANOVA M., IVANOV D.A. & UTESCHER T. 2011. Geochemical appraisal of palaeovegetation and climate oscillation in the Late Miocene of Western Bulgaria. *Org. Geochem.*, 42: 1363–1374.
- SÜSS H. & VELITZELOS E. 1997. Fossile Hölzer der Familie Taxodiaceae aus tertiären Schichten des Versteinerten Waldes von Lesbos, Griechenland. *Feddes Rep.*, 108: 1–30.
- 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). *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 207: 23–35.
- UHL D., JASPER A., SCHINDLER T. & WUTTKE M. 2010. Evidence of paleowildfire in the early Middle Triassic (early Anisian) *Voltzia* Sandstone: the oldest post-Permian macroscopic evidence of wildfire discovered so far. *PALAIOS*, 25: 837–842.
- UHL D., SCHINDLER T. & WUTTKE M. 2011. Paläoökologische Untersuchungen im Oberoligozän von Norcken (Westerwald, Rheinland-Pfalz, W-Deutschland) – Erste Ergebnisse. *Mainzer naturwiss. Archiv*, 48: 115–127.
- UTESCHER T., IVANOV D., HARZHAUSER M., BOZUKOV V., ASHRAF A.R., ROLF C., URBAT M. & MOSBRUGGER V. 2009. Cyclic climate and vegetation change in the late Miocene of Western Bulgaria. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 272: 99–114.
- VATSEV M. 1999. Lithostratigraphy of the Neogene rocks from Staniantsi basin (Central Western Bulgaria). *Ann. Univ. Mining and Geol.*, 42: 35–43 (in Bulgarian).
- YIN Z.Y. 1993. Fire regime of the Okefenokee swamp and its relation to hydrological and climatic conditions. *Int. J. Wildland Fire*, 3: 229–240.
- YOUNG P.J., KEELAND B.D. & SHARITZ R.R. 1995. Growth response of baldcypress [*Taxodium distichum* (L.) RICH.] to an altered hydrologic regime. *Am. Midland Nat.*, 133: 206–212.
- YOUNG P.J., MEGONIGAL J.P., SHARITZ R.R. & DAY F.P. 1993. False ring formation in baldcypress (*Taxodium distichum*) saplings under two flooding regimes. *Wetlands*, 13: 293–298.
- ZDRAVKOV A., BECHTEL A., SACHSENHOFER R. F., KORTENSKI J. & GRATZER R. 2011. Vegetation differences and diagenetic changes between two Bulgarian lignite deposits – Insights from coal petrology and biomarker composition. *Org. Geochem.*, 42: 237–254.

PLATES

Plate 1

SEM images of *Taxodioxyton*-like charcoal from Late Miocene of Staniantsi Coal Basin (Bulgaria)

1. Slightly oblique view of cross section, showing several growth rings
2. Enlargement of 1, showing single growth ring
- 3–5. Tangential view with unicellular rays of varying height
6. Tangential view with large unicellular ray and radial view with bordered pits
7. Enlargement of 4, showing bordered pits on tangential cell walls
8. Tangential view with folded radial cell walls exhibiting bordered pits mostly in 3 rows

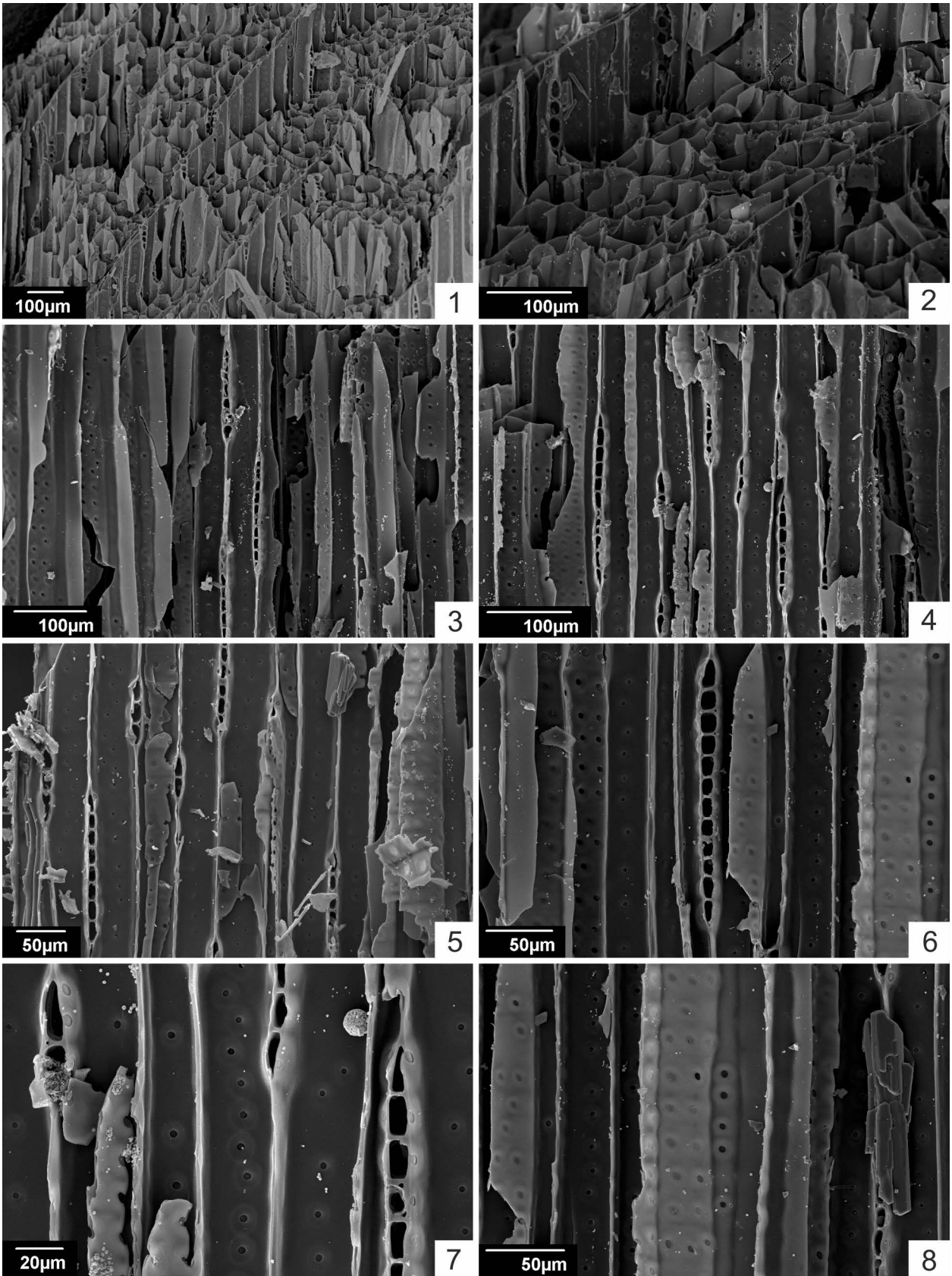


Plate 2

SEM images of *Taxodioxyton*-like charcoal from the Late Miocene of the Staniantsi Coal Basin (Bulgaria)

1. Radial view showing cross-field pitting with 3–4 taxodioid pits
2. Radial view showing cross-field pitting with 3–4 taxodioid pits (left) on cross-field walls and bordered pits on “normal” tracheid walls (right)
3. Tangential view with large area of folded cell walls in radial view
4. Detail of bordered pits on radial cell walls
- 5, 6. Detail of bordered pits, partly with crassulae visible, on radial cell walls
7. Oblique view of broken-up ray cells
8. Enlargement of single homogenised cell wall, typical for charcoal
9. Tangential view with very high ray
10. Enlargement of bordered pits on tangential cell walls

