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Early Jurassic dinosaur-dominated track assemblages, floristic and environmental changes in the Holy Cross Mountains region, Poland

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The Early Jurassic succession of the Holy Cross Mountains region in Poland offers a rare opportunity to study ecosystem complexity during the evolution and diversification of early dinosaurs, especially herbivorous ones. The section consists of continental and coastal deposits containing fossil assemblages spanning nearly 25 My of changes in terrestrial plants and some groups of invertebrates and tetrapods. Based on macrofossils and pollen and spores, the broader characteristics of the flora in this succession are presented. The floral assemblages show typical Early Jurassic characteristics and contain lycopsids, sphenopsids, ferns, cycadaleans, bennettitaleans, gnetaleans and ginkgoaleans, as well as conifers, and are similar to other Hettangian–Toarcian floral successions in Europe, showing the presence of a vast coniferous forest dominated by *Hirmeriella* in the early Hettangian, replaced by ginkgophyte-dominated floras in younger stages and araucarian conifer-dominated forests in the late Pliensbachian. Dinosaurs are documented mainly from their trace fossils (tracks and coprolites). Six distinct track assemblages (stratigraphically separated ichnoassemblages) of different ages can be identified. Current evidence indicates that while *Anomoepus* tracks are abundant throughout the long Hettangian–late Pliensbachian interval, medium-sized to large ornithischian tracks do not occur below the lower–middle Hettangian transition zone, associated with the first major marine transgression in the region. Hettangian strata with different theropod tracks (*Grallator*, *Anchisauripus*, *Eubrontes*, *Kayentapus,* cf. *Megalosauripus*), small *Anomoepus* tracks*,* numerous medium-sized *Anomoepus*-like tracks, *Moyenisauropus* tracks, tetradactyl tracks of sauropodomorphs (cf. *Pseudotetrasauropus*) and oval-shaped tracks of sauropods (*Parabrontopodus*) significantly contrast with the higher part of the Lower Jurassic succession (upper Pliensbachian Drzewica Formation and middle–upper Toarcian Borucice Formation) containing new types of medium-sized to large theropod tracks (*Therangospodus*), small and medium-sized bird-like tridactyl tracks (cf. *Trisauropodiscus*, cf. *Anomoepus*), exceptionally large, oval-shaped sauropod tracks (Sauropoda indet.), and new types of medium-sized and large ornithischian tracks (cf. *Deltapodus,* cf. *Anomoepus*). This points to a noticeable difference between the Hettangian and late Pliensbachian–Toarcian dinosaur ichnofaunas and may facilitate the study of regional and global changes and correlations. Both the palaeofloras and dinosaur trace fossils document ecosystem diversity and ecosystem changes, presented here in review form. The nature of these changes requires more detailed study, but preliminary results suggest the occurrence of rather complex and pronounced transformations in the dinosaur communities of the Holy Cross Mountains region. Based on our observations, the most significant event in Early Jurassic ecosystems took place within the Hettangian (change in floristic composition, the emergence of new groups of dinosaurs), but we also found what we believe to be a record of a major faunal turnover across the late Pliensbachian–middle–late Toarcian interval.

Key words: Mesozoic, ecosystems, tetrapod tracks, plant macrofossils, palynomorphs, trace fossils.

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INTRODUCTION

The Early Jurassic (201–180 Ma) records more derived Mesozoic terrestrial ecosystems following the end-Triassic mass extinction, which are dominated by various specialized groups of dinosaurs and early crocodylomorphs (Brusatte et al., 2008; Benton et al., 2014; Pol et al., 2020; Singh et al., 2021). Several major evolutionary advances of the terrestrial biota took place during the Early Jurassic, including the evolutionary radiation of ornithischians, the diversification of sauropods, the origin of advanced mammals and crocodilians, as well as the proliferation of some groups of plants (e.g., Anderson et al., 2007; Brusatte et al., 2008; Pol et al., 2020). The causes and precise timing of these key floral and faunal changes, as well as the changes in dinosaur-dominated ecosystems, have remained unclear, mainly due to the paucity of the fossil record from that time.

There are too few known geological sections containing a comprehensive fossil record of the plants, invertebrates and vertebrates of Early Jurassic terrestrial ecosystems, and most publications describing them focus on particular fossils or specimens. To understand the complexity of past ecosystems we need multidisciplinary reports dealing with the mutual connections between various organisms preserved as fossils of the same stratigraphic age collected in the same bed, section, site or area. Unique palaeontological windows such as the Anina (Steierdorf Formation, Popa, 1999, 2005; Popa et al., 2003; Popa and van Konijnenburg-van Cittert, 2006; Pieńkowski et al., 2009; Barbacka et al., 2016b), Morrison Formation (Chure et al., 2006; Foster, 2007), Daohugou (Pott et al., 2012; Sullivan et al., 2014; Pott and Jiang, 2017), Jehol (Zhonghe, 2006; Chang, 2011; Pan et al., 2013) and Hell Creek (Johnson, 1997; White et al., 1998) provide a fossil record of diversified animals and an exceptionally rich record of plant micro- and macrofossils, and are the subject of multidisciplinary and palaeoecological studies. Other windows, though famous for certain fossils, do not contain a complete set of fossils representing all the elements that originally occurred in their respective ecosystems. For example, the Upper Cretaceous Djadochta, Barun Goyot and Nemegt formations of the Gobi Desert, Mongolia, which preserve numerous fossil vertebrates (mainly skeletons but also tracks of dinosaurs), are poorer in invertebrates and very poor in plants (only barely identifiable petrified wood or rare macrofossils of leaves; Krassilov and Makulbekov, 1995, 1996; Benton et al., 2003). The Yorkshire area is widely known for its Middle Jurassic fossil plants, but vertebrate bones are practically absent and only an ichnological record of invertebrates and vertebrates exists there (Harris, 1961; Harris and Miller, 1974; van Konijnenburg-van Cittert and Morgans, 1999; Romano and Whyte, 2003).

The terrestrial and marginal-marine sedimentary successions of the Holy Cross Mountains (HCM) region (more precisely, the northern Mesozoic margin of the HCM or HCM subbasin of the Early Jurassic Polish basin) in southern Poland document the Early Jurassic interval of plant and dinosaur evolution of the northern part of Pangea (Fig. 1). Although separated, the numerous natural or artificial exposures located in the HCM provide a rich fossil record spanning a nearly 25 My long history different ecosystems (Figs. 2 and 3). Dinosaurs and other tetrapods (crocodylomorphs, eucynodonts, mammals) are documented mainly from trace fossils (tracks and coprolites), as well as from dinosaur nest structures and eggs (Pieńkowski, 1998, 2008). Body fossils are represented mainly by rare specimens of fish, fish scales and tetrapod teeth or other fragmentary tetrapod bone finds (Niedźwiedzki, 2011). Nearly complete fish fossils are extremely rare (Maślankiewiczowa, 1965; Niedźwiedzki, 2011) but their activity is well documented from swimming and feeding traces (*Undichna*, *Osculichnus*: Pieńkowski, 1985). Invertebrates are known from body fossils (e.g., bivalves and gastropod egg capsules, horseshoe crabs) and diverse trace fossils; locally they are abundant (Karaszewski and Kopik, 1970; Pieńkowski, 2004a; Zatoń et al., 2009), especially in the shallow-marine successions. The rich record of plant macro- and microfossils (e.g., Makarewiczówna, 1928; Samsonowicz, 1929; Grabowska, 1963; Reymanówna, 1963a, b; Karaszewski, 1965; Grabowska et al., 1970; Reymanówna, 1992; Ziaja, 2006; Barbacka et al., 2007, 2010; Pacyna, 2013, 2021a, b) spurred palaeobotanic studies of

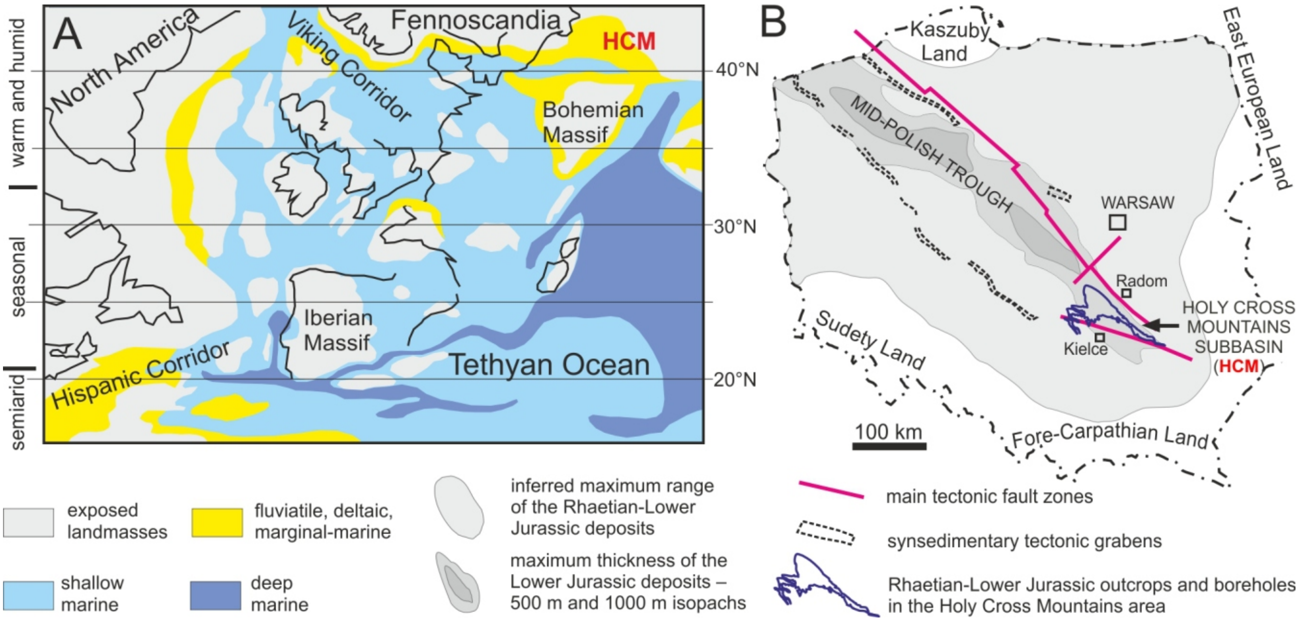

Fig. 1A – palaeogeographical map of Europe in the Early Jurassic (after Thierry et al., 2000); B – Polish Lower Jurassic basin with location of the Holy Cross Mountains (HCM) subbasin (after Pieńkowski et al., 2020, amended)

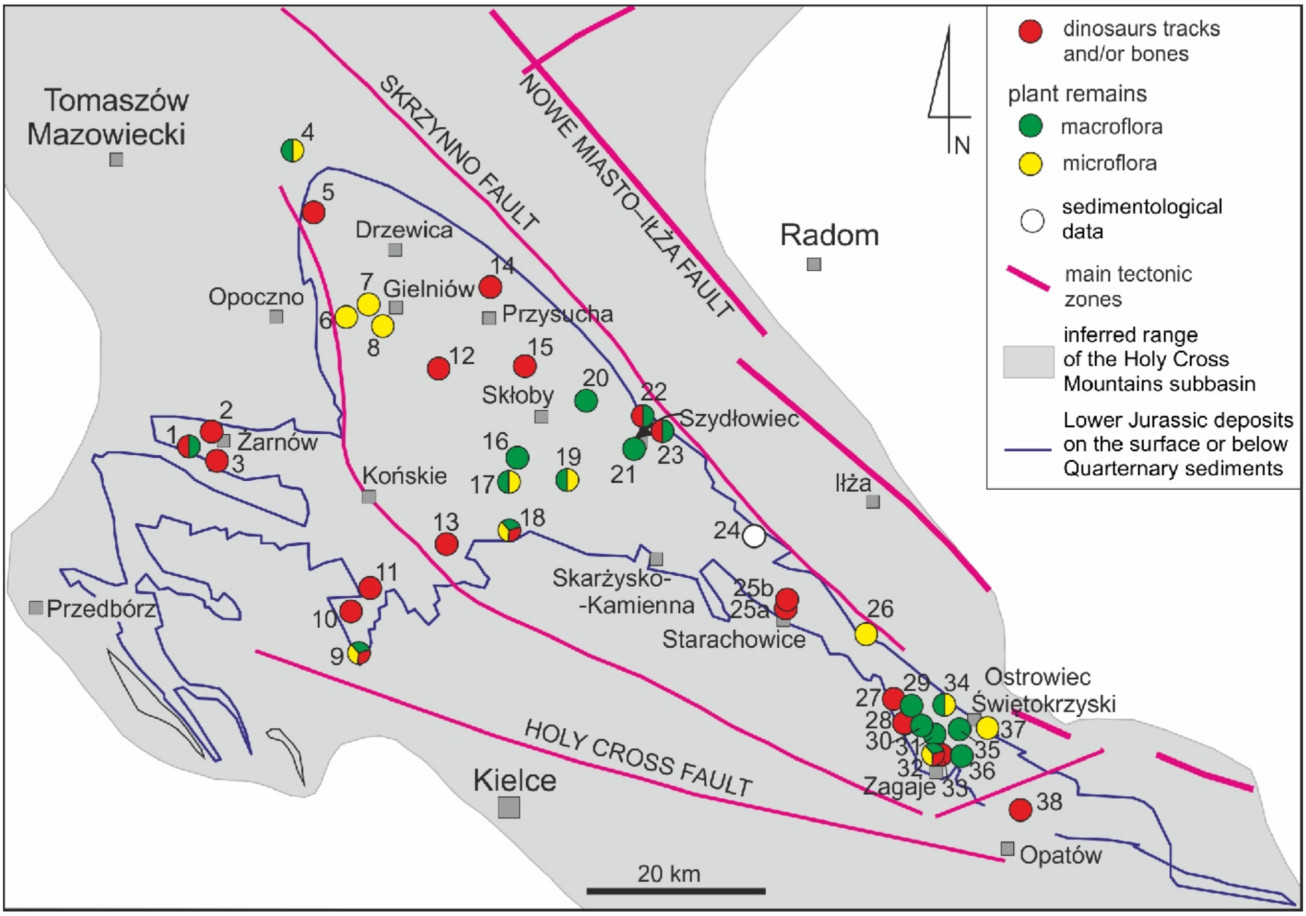

Fig. 2. Early Jurassic localities with plant remains and vertebrate fossils discussed in the text

1 – Dąbie outcrop (tracks, bones, macroflora); 2 – Żarnów outcrop (tracks); 3 – Paszkowice outcrop (tracks); 4 – Studzianna borehole (macroflora, microflora); 5 – Idzikowice outcrop (tracks); 6 – Mroczków Gościnny borehole (microflora); 7 – Mroczków-Kraszków 160 borehole (microflora); 8 – Rozwady borehole (microflora); 9 – Gliniany Las outcrop, Gliniany Las 1 borehole, Gliniany Las 2 borehole (tracks, macroflora, microflora); 10 – Chyby outcrop (tracks); 11 – Kontrewers outcrop (tracks); 12 – Zapniów outcrop (tracks); 13 – Hucisko outcrop (dinosaurian bones); 14 – Jakubów outcrop (tracks); 15 – Borkowice outcrop (tracks, bones); 16 – Dźwiertnia outcrop (macroflora); 17 – Niekłań PIG 1 borehole (macroflora, microflora); 18 – Sołtyków (Odrowąż) outcrop, borehole (tracks, bones, macroflora, microflora); 19 – Huta OP-1 borehole (macroflora, microflora); 20 – Chlewiska outcrop (macroflora); 21 – Szydłowiec outcrop (macroflora); 22 – Szydłówek outcrop (tracks, bones, macroflora); 23 – Śmiłów outcrop (tracks, macroflora); 24 – Jagodne borehole (sedimentological data); 25a – Starachowice a outcrop, Przysucha Ore-bearing Fm. (tracks); 25b – Starachowice b outcrop, Ostrowiec Fm. (tracks); 26 – Brody-Lubienia borehole (microflora); 27 – Kunów outcrop (tracks); 28 – Szwarszowice outcrop (tracks); 29 – Jędrzejowice outcrop (macroflora); 30 – Mychów (Mnichów) outcrop (macroflora); 31 – Podszkodzie outcrop (macroflora); 32 – lower outcrop in Gromadzice (tracks, macroflora, microflora); 33 – upper outcrop in Gromadzice (tracks); 34 – Chmielów outcrop (macroflora, microflora); 35 – Szewna outcrop (macroflora); 36 – Miłków outcrop (macroflora); 37 – Gutwin borehole (microflora); 38 – Podole outcrop (tracks)

Lower Jurassic fossil plants as early as at the end of the 19th century (Raciborski, 1891a, b, 1892a, b). Research on invertebrate trace fossils also has a long history (e.g., Karaszewski, 1962; Pieńkowski, 2004a; Pieńkowski and Niedźwiedzki, 2009; Pieńkowski and Uchman, 2009), and preliminary identification of trace fossil assemblages indicated the enormous variety and complexity of the invertebrate fauna. Dinosaur tracks were first recognised in this region in the 1960s (Karaszewski, 1969) and began to be studied at the end of the 1980s (Pieńkowski and Gierliński, 1987); this continued in the 1990s (Gierliński, 1991; Pieńkowski, 1998, 1999; Gierliński and Pieńkowski, 1999) and into the 21st century (e.g., Gierliński et al., 2000, 2001, 2004; Niedźwiedzki and Niedźwiedzki, 2004; Niedźwiedzki et al., 2009; Niedźwiedzki, 2011; Niedźwiedzki and Pieńkowski, 2016; Pieńkowski and Niedźwiedzki, 2021 and ongoing studies). We currently know of about a dozen sites with plant fossils, dinosaur- and other vertebrate traces from the HCM region (Fig. 2). Some recently discovered sites are still under investigation (Pieńkowski and Niedźwiedzki, 2021), and new material has been found in many of the locations already reported (ongoing study). These sites reveal rich floral assemblages and a diverse range of dinosaur tracks, which confirm the existence of a complex Early Jurassic biota dominated by small to gigantic theropods, medium-sized to large sauropodomorphs/sauropods, and small to large early ornithischians (Fig. 4).

Based on material from drill cores, we were able to detect local environmental changes in landscape and plant cover, which must have had an impact on the occurrence of dinosaurs. Fossil assemblages representing different time intervals from the Hettangian to the Toarcian also allow us to recognize ecosystem changes caused by environmental factors, and to register some changes in the floristic and faunistic assemblages. The Early Jurassic is an especially important time of dinosaur evolution. Many major clades that dominated later in the Middle–Late Jurassic evolved during this time. Herbivorous clades including early ornithischians and sauropodomorphs di-

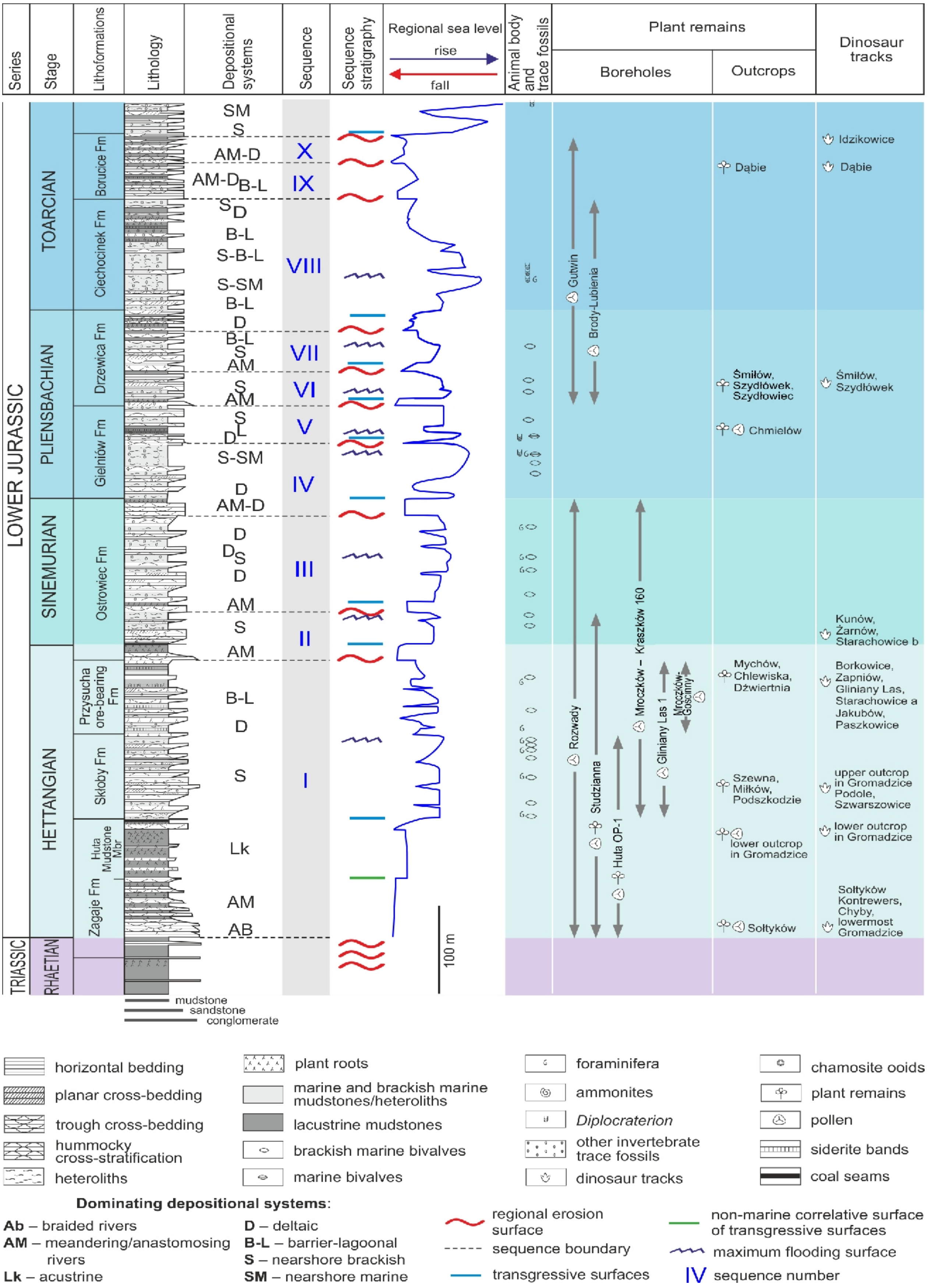

Fig. 3. Lithologic section of Lower Jurassic deposits of the Holy Cross Mountains (HCM), with source strata of the discussed material indicated

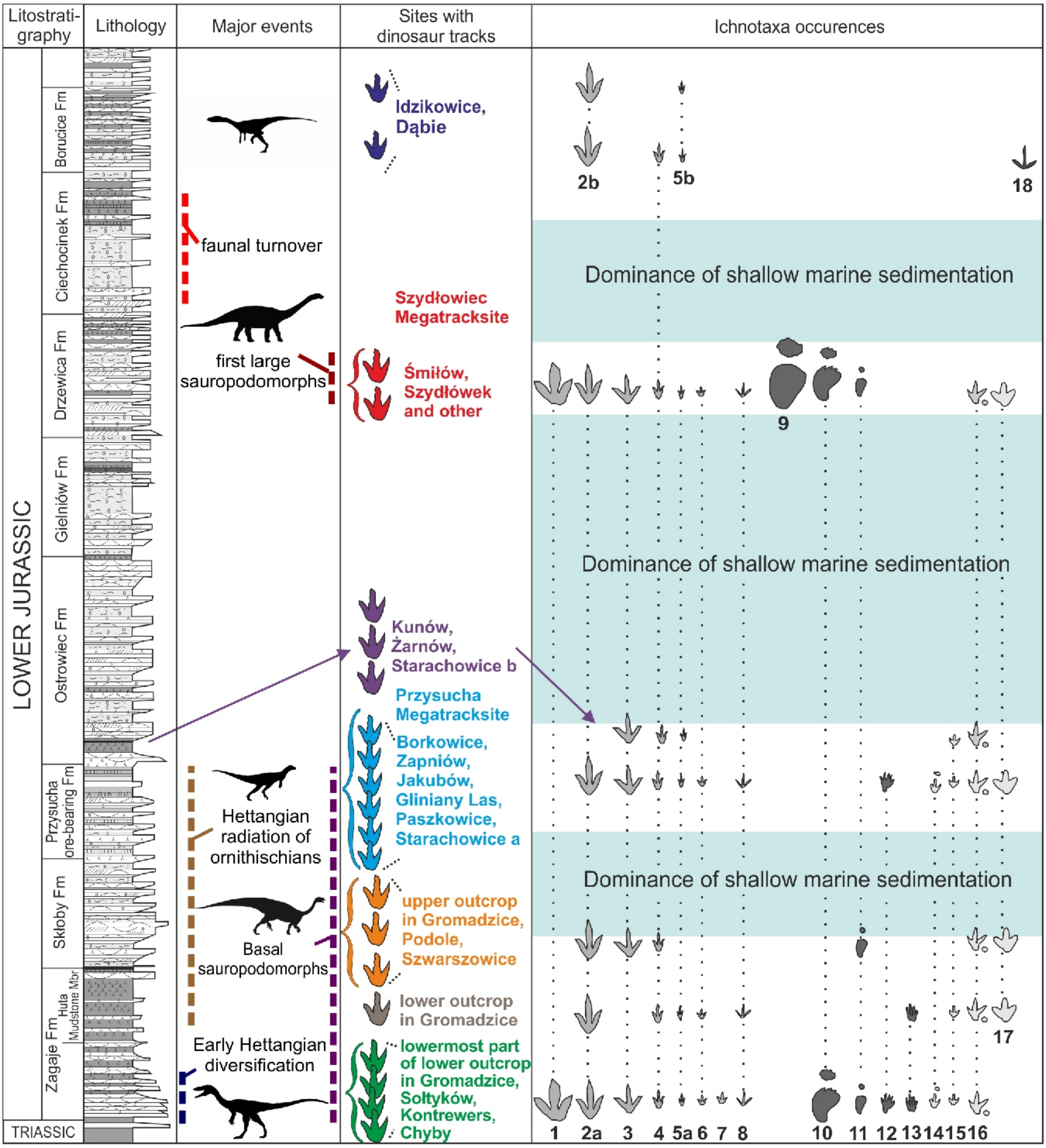

Fig. 4. Stratigraphic positions of track-bearing sites and ranges of dinosaur ichnotaxa in the generalized lithological profile of the Lower Jurassic of the Holy Cross Mountains (HCM), Poland (based on Pieńkowski, 2004a; Niedźwiedzki et al., 2009; Niedźwiedzki, 2011; Niedźwiedzki and Pieńkowski, 2016; Pieńkowski and Niedźwiedzki, 2021)

1 – gigantic theropod tracks, cf. *Megalosauripus* isp.; 2a – large theropod tracks, *Eubrontes* isp./cf. *Eubrontes* isp.; 2b – large theropod tracks, *Therangospodus* isp./cf. *Therangospodus* isp.; 3 – large theropod tracks, *Kayentapus* isp./cf. *Kayentapus* isp.; 4 – medium-sized theropod tracks, *Anchisauripus* isp.; 5a – small theropod tracks, *Grallator* isp.; 5b – small theropod tracks, cf. *Grallator* isp.; 6 – small theropod tracks, cf. *Stenonyx* isp.; 7 – small theropod tracks, Theropoda indet.; 8 – small theropod tracks, *Plesiornis* isp./cf. *Plesiornis* isp.; 9 - large sauropodomorph tracks, Sauropoda indet.; 10 - large sauropod tracks, *Parabrontopodus* isp.; 11 - small sauropod tracks, *Parabrontopodus* isp.; 12 - sauropodomorph tracks, cf. *Tetrasauropus* isp.; 13 - sauropodomorph tracks, cf. *Otozoum* isp.; 14 – small ornithischian tracks, cf. *Atreipus* isp./*Delatorrichnus* isp.; 15 – small ornithischian tracks, *Anomoepus* isp.; 16 – medium ornithischian tracks, *Anomoepus* isp.; 17 – large ornithischian tracks, *Moyenisauropus* isp.; 18 – small to medium dinosaur (?theropod) tracks, *Trisauropodiscus* isp.

versified, and some anatomical innovations evolved (e.g., dental adaptations, increase in body size) which helped them to exploit plant tissues more efficiently (Barbacka et al., 2022 coprolite paper).

After more than forty years of detailed study of the Lower Jurassic floras and dinosaur ichnofaunas of the HCM, and the acquisition of important new material, there is an obvious need for a review article that updates and summarizes the published results. The purpose of this paper is to revise all the documented fossils and characterize all the abiotic/biotic events registered in the succession. We also discuss the co-occurrence of different plant associations and dinosaur faunas, as well as their mutual relationships and their development across the Early Jurassic. We try to determine whether there is any detectable correlation between the composition of the fossil flora and the diversification of herbivorous and predatory dinosaurs.

MATERIAL AND METHODS

This review of ecosystem composition and changes in the Early Jurassic of the HCM was compiled from earlier-published (e.g., Gierliński and Pieńkowski, 1999; Wcisło-Luraniec and Barbacka, 2000; Barbacka et al., 2010; Niedźwiedzki, 2011; Pacyna, 2013; Niedźwiedzki and Pieńkowski, 2016) and new results (see Pieńkowski and Niedźwiedzki, 2021). A substantial portion of the data was revised and supplemented for this summary; for this we made a search of material collected in several institutions, museums and private collections. The most numerous fossil material is available for the Hettangian and Pliensbachian stages. The other two Early Jurassic stages (Sinemurian and Torcian) have a rather weaker but still adequate record for environmental interpretation and initial reconstruction of biotas (Fig. 3). To better understand the stratigraphic sequence of dinosaur ichnofaunas, we also carried out additional field work and made several prospecting trips (2018–2021), the purpose of which was to study the occurrence of fossils in poorly known sites or parts of sections. Fossil data and sedimentological observations from more than 50 outcrops are supplemented by information from several boreholes, especially by palynological data to complement the plant macrofossils (Figs. 2 and 3). The botanical affinity of palynomorphs was determined mainly following classic palaeobotanical studies (Couper, 1958; van Konijnenburg-van Cittert, 1971; Filatoff, 1975; Balme, 1995; Batten and Koppelhus, 1996; Koppelhus and Batten, 1996; Abbink, 1998; Kelber and van Konijnenburg-van Cittert, 1998). Data on the spatial and temporal distribution of plant macrofossils were taken from Pacyna (2013: tabs. 1–5), with some additions and corrections from later reports (Barbacka et al., 2014, 2016a; Pacyna, 2021a, b). We made an integrated analysis of the material from the outcrops and boreholes in order to better understand the depositional systems, depositional sequence development, and the composition of the biota. As an outcome we created lithofacies models which were then combined with the palaeontological results. The total studied area covers ~6000 km^2 and represents a geographically compact area with a well-known Jurassic geology.

The environmental maps portray the time-tuned palaeogeography of the HCM subbasin. The maps were constructed based on analysis of coeval depositional systems at chosen time horizons inferred from correlative bounding surfaces (sequence stratigraphy boundaries correlated by biostratigraphic and chemostratigraphic methods: Pieńkowski, 2004a; Hesselbo and Pieńkowski, 2011; Barth et al., 2018; Pieńkowski et al., 2020). The maps show the subbasin expanding and shrinking in response to supra-regional sea-level changes and modified by local tectonics and sediment delivery.

ECOSYSTEM EVOLUTION IN THE EARLY JURASSIC OF THE HOLY CROSS MOUNTAINS

In the Early Jurassic, the HCM area was located at the central-western margin of a large Pangea landmass, at roughly 45° N palaeolatitude (Fig. 1). During Early Jurassic times, siliciclastic, continental, marginal-marine and marine sediments up to 1400 m thick were deposited in a large epeiric basin extending across Poland as a part of the Central European Basin (Pieńkowski, 1983, 1991, 2004a, 2006; Marek and Pajchlowa, 1997; Pieńkowski et al., 2014; Barth et al., 2018). The sediments are named the Kamienna Group (Pieńkowski, 2004a), subdivided into several lithologic formations showing regional facies differentiation (Fig. 3). The transformation of continental environments of the Late Triassic towards the marginal to fully marine environments of the Early and Middle Jurassic was accompanied by significant environmental and biotic changes. Early Jurassic sedimentation in the Polish epicontinental basin was chiefly controlled by supra-regional sea-level changes, allowing the use of sequence stratigraphy to correlate the whole Lower Jurassic series with biostratigraphically constrained West European sections (Pieńkowski, 2004a; Barth et al., 2018). Recently, the sequence stratigraphy correlation has been supported by chemostratigraphy based on the correlation of ^{13}C curves (Pieńkowski et al., 2020). Humid subtropical climate predominated; seasonality was rather moderate, as shown by palynological and clay mineral studies (Marcinkiewicz, 1962, 1971, 1989; Pieńkowski and Waksmundzka, 2003, 2009; Brański, 2009, 2012; Pieńkowski et al., 2012, 2014, 2016, 2020; Marcinkiewicz et al., 2014).

HETTANGIAN, ZAGAJE FORMATION, SEQUENCE I

Depositional sequence I is the best documented of all sequences of the Lower Jurassic deposits in the HCM region and in all of Poland. It falls within the *Nathorstisporites hopliticus* megaspore zone (Hettangian–Early Sinemurian: see Marcinkiewicz, 1971; Marcinkiewicz et al., 2014). Its Hettangian age is indicated by occurrences of the pollen species *Pinuspollenites minimus* and other characteristic sporomorphs of the *Pinuspollenites*–*Trachysporites* Zone (including *Cerebropollenites thiergartii* defining the earliest Hettangian: see Pieńkowski et al., 2012, 2020) beginning of through the whole sequence. Occurrences of some bivalve species (*Cardinia follini* and *C. ingelensis*) are restricted to this sequence (Pieńkowski, 2004a).

EARLIEST HETTANGIAN, LOWER PART OF ZAGAJE FORMATION, PARASEQUENCE IA, SOŁTYKÓW OUTCROP AND ITS EQUIVALENTS FROM BOREHOLES

ENVIRONMENTAL CONTEXT

The Sołtyków outcrop is an abandoned clay pit in the central-northern margin of the HCM (Karaszewski, 1975; Pieńkowski, 2004a, b). Studies of tetrapod and invertebrate trace fossils and of plant fossils were done separately, sometimes using different names for this locality (Odrowąż in palaeobotanical studies, Sołtyków in geological and palaeontological papers). During the early Hettangian, the Sołtyków site was located some 600–700 km away from the epicontinental sea of Western Europe (Pieńkowski, 2004a; Pieńkowski et al., 2014). The Sołtyków outcrop shows a succession with a record of an earliest Hettangian terrestrial ecosystem and is the best-documented site in the region (see Pieńkowski, 2004a, b; Niedźwiedzki, 2011; Pieńkowski et al., 2014). Earliest Hettangian age of exposed beds is indicated by sequence stratigraphic correlation (Pieńkowski, 2004a), a flora dominated by the conifer *Hirmeriella muensteri* (Reymanówna,1992; Wcisło-Luraniec, 1991; Barbacka et al., 2010), palynomorphs (Ziaja, 2006) and isolated finds of conchostracans *Bulbilimnadia kilianorum* Kozur, Weems *et* Lucas, 2010, the latter known only from the lowermost Hettangian (Kozur and Weems, 2010).

The Sołtyków section shows the lowest part of the first depositional sequence (Ia according to Pieńkowski, 2004a). The interpretation of the lithofacies and depositional system is based both on the exposure and on shallow boreholes (Sołtyków IG 1; Niekłań PGI 1) that penetrated the Lower Jurassic/Rhaetian deposits down to the boundary with the Upper Triassic redbeds, probably of upper Norian age. The lowermost part of sequence Ia shows features of braided river deposits; probably all or at least a significant part of these deposits is of uppermost Rhaetian age. A low-sinuosity stream depositional system gave way to an anastomosing and high-sinuosity stream depositional system due to climatic changes, base level rise and a gradually diminishing geomorphological gradient. The exposure revealed an anastomosing to sinuous stream alluvial plain depositional system dominated by avulsion processes, interbedded with lacustrine deposits. Several depositional subsystems can be distinguished within the anastomosing stream alluvial plain depositional system: a channel-fill subsystem, levee deposits, floodplain–lacustrine, and very numerous and diversified crevasse splays (Pieńkowski, 2004a). Coal-bearing dark grey lacustrine mudstone lithofacies and the anastomosing pattern of the streams indicate a relatively well-blanced water support with a relatively high water table. Together they point to a humid climate, possibly with some seasonality. On the other hand, a record of wildfires (indicated by charcoal occurrences and biomarkers – Marynowski and Simoneit, 2009) suggests drier climate or at least a drier season.

The richest assemblages of tetrapod tracks occur in several beds of crevasse splay–channel deposits within an anastomosing–sinuous river depositional system in the lower and upper parts of the exposure. The location of many different tracks in the lowermost part of the Hettangian strata shows that rapid evolution of dinosaurs occurred shortly after the end-Triassic biota extinction (Pieńkowski et al., 2014; possibly two-phased: see Wignall and Atkinson, 2020). Plant remains (macroremains, spores, pollen grains) were found in alluvial plain–lacustrine deposits just beneath and slightly above the track-bearing interval.

PLANT COVER

Judging from the fossil macroremains (Reymanówna et al., 1987; Wcisło-Luraniec, 1992a; Reymanówna, 1992; Barbacka et al., 2010) and sporomorphs (Ziaja, 1992, 2006; Krupnik et al., 2014), the plant cover in Sołtyków was only moderately diverse but included all plant groups (Figs. 5–8). Reconstruction of the floral communities is hindered by the allochthonous character origin of most plant remains. However, the relatively good state of fossil preservation suggests that water transport was rather short and of low to moderate low energy. Similarly composed plant communities with the dominant conifer *Hirmeriella* were widespread in Europe during the earliest Hettangian, providing a solid base for comparisons (Hörhammer, 1933; Hirmer and Hörhammer, 1934; Wood, 1961; Lewarne and Pallot, 1957; Harris, 1957; Jung, 1968; Weber 1968; Muir and van Konijnenburg-van Cittert, 1970; Barale, 1987; Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Wcisło-Luraniec, 1991b; Thévenard, 1993). The dominant conifer in Sołtyków, arborescent *Hirmeriella muensteri* producing *Classopollis torosus* pollen grains and possessing leaves with a thick cuticle, probably formed the forest canopy (Figs. 6K, 7A, B and 8U), while the other abundant taxon, *Podozamites* sp. with leaves having a fine cuticle, probably grew as a large shrub in the understory (Fig. 6I, J). The forest floor was most probably covered by bryophytes, known from their spores *Rogalskaisporites cicatricosus* and *Foraminisporis jurassicus*, and lycophytes producing spores *Foveotriletes* sp., *Lycopodiacidites rugulatus*, *Lycopodiumsporites cerniidites*, *Lycopodiumsporites semimuris*, *Lycopodiumsporites* sp., *Uvaesporites argenteaeformis* and cf. *Uvaesporites* sp. (Fig. 8A–D).

The other dominant plant was the sphenophyte *Neocalamites lehmannianus*, which is thought to have formed monotypic stands along open waterbodies (lakes) and/or along streams and in patches on fluvial plains, an inference supported by monospecific accumulations of its shoots and root remains preserved *in situ* (Fig. 6A). Dispersed sphenophyte spores *Calamospora tener* are also present (Fig. 8G). The most diverse were the ferns, as confirmed by frond fragments and dispersed spores: Dipteridaceae (macroremains *Thaumatopteris brauniana*, *Goepertella microloba*; spores *Dictyophyllum* sp. and *Deltoidospora*), Osmundaceae (*Todites princeps* leaves, *Todisporites minor* spores), and Matoniaceae (*Phlebopteris angustiloba* leaves, *Matonisporites* spores). Large fragments of rhizomes indicate that some ferns like *Todites princeps* grew *in situ* (Schweitzer, 1978); others are preserved as small, fragmented leaf remains, which points to substantial water transport (Fig. 5B–H). Other fern groups are represented only by their spores: for example, Gleicheniaceae (*Plicifera delicata*), Marattiaceae (*Marattisporites* spp.), Cyatheaceae or Dicksoniaceae (*Cyathidites minor*, *Cyathidites australis, Cyathidites* sp., *Cibotiumspora jurienensis*) and a leptosporangiate of uncertain systematic position (*Concavisporites toralis* spores) (Fig. 8H–M). Ferns are known to grow usually in humid conditions such as in the understory or shaded places along river levees (Raciborski, 1894; Popa, 1999; Popa et al., 2003; Taylor et al., 2009). This is highly probable in regard to the herbaceous Dipteridaceae and Matoniaceae; tree-habit Osmundaceae might have occurred in more open areas (Barbacka, 2011).

Lycophytes are very rare in the macrofossil record (sporophylls *Odrolepis liassica*) but are more frequent in the palynological spectrum (*Aratrisporites minimus* microspores known also from the Skarżysko Kamienna IG 1 borehole (Fijałkowska, 1989), *Nathorstisporites hopliticus* megaspores) probably populated shallow ponds or lakes, like modern *Isoetes* (Figs. 5A and 8E, F). Others lycophytes known from their spores (*Foveotriletes, Lycopodiacidites*, *Lycopodiumsporites*, sellaginellaceous *Uvaesporites*) grew in wet places like river or stream banks (Fig. 8A–D).

The stream banks possibly were also covered by the shrubby seed fern *Pachypteris lanceolata* and the bennettitalean *Otozamites brevifolius* (Fig. 6B, D, E), leaves of which developed secreting trichomes interpreted as of hydatode type, confirming their adaptation to a humid environment (Barbacka et al., 2010). Seed ferns were also represented by *Alisporites robustus, A. thomasii, A.* cf. *diaphanus* and cf. *A.*

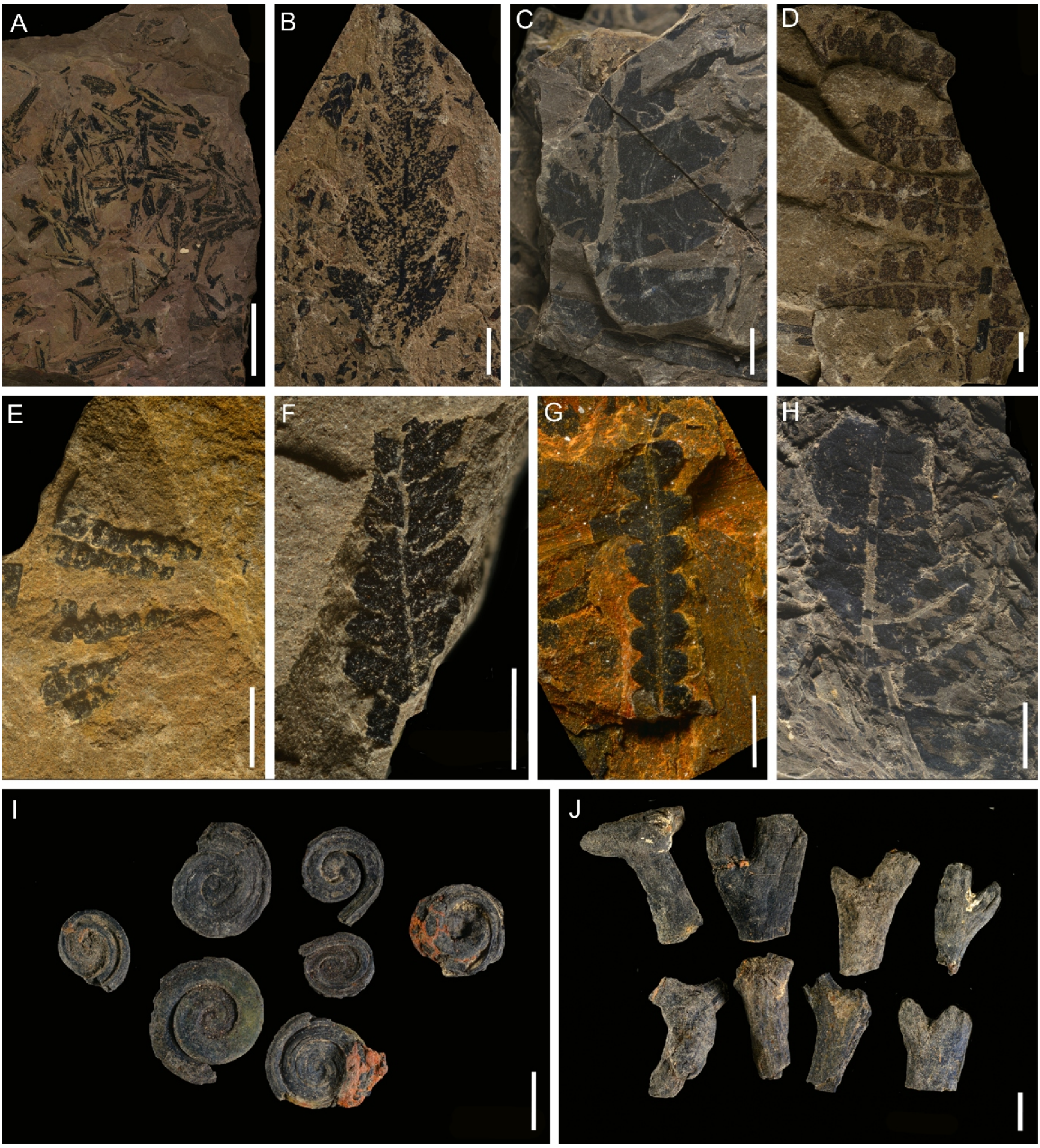

Fig. 5. Macrofossil plant assemblage form Sołtyków outcrop, lower Zagaje Formation, lowest Hettangian

A – *Odrolepis liassica*, KRAM P PM 68/119/I; **B** – *Cladophlebis* sp. 1, KRAM P PM 68/390/I; **C** – *Cladophlebis* sp. 2, KRAM P PM 68/389; **D** – *Todites princeps*, KRAM P PM 68/135; **E** – *Phlebopteris angustiloba*, KRAM P PM 68/1059; **F** – *Goeppertella microloba*, KRAM P PM 68/1007; **G** – *Thaumatopteris brauniana*, KRAM P PM 68/140; **H** – *Dictyophyllum* sp., KRAM P PM 68/1210; **I** – charcoalified fern crosiers, unnumbered, field photo; **J** – charcoalified dichotomously branching probably fern stipes, unnumbered, field photo; scale bars: A – 20 mm, B, C, D, I, J – 5 mm, E, F, G – 3 mm, H – 6 mm

Fig. 6. Macrofossil plant assemblage form Sołtyków outcrop, lower Zagaje Formation, lowest Hettangian (continued)

A – *Neocalamites lehmannianus*, KRAM P PM 68/1120; **B** – *Pachypteris lanceolata*, KRAM P PM 68/2; **C** – *Paracycas minuta*, KRAM P PM 68/283; **D** – *Otozamites brevifolius* leaf, KRAM P PM 68/1; **E** – *Otozamites brevifolius* isolated pinna, KRAM P PM 68/284; **F** – *Pterophyllum* sp., KRAM P PM 68/12; **G** – *Schmeissneria microstachys* male cone, KRAM P PM 68/1226; **H** – *Piroconites kuespertii*, KRAM P PM 68/232; **I** – *Podozamites* sp. shoot with leaves, KRAM P PM 68/141; **J** – *Podozamites* sp. accumulation of isolated leaves, KRAM P PM 68/1078; **K** – *Hirmeriella muensteri* female cone scale, KRAM P PM 68/43; scale bars: A, B, F, G, I – 10 mm, C, E, K – 5 mm, D, J – 20 mm, H – 3 mm

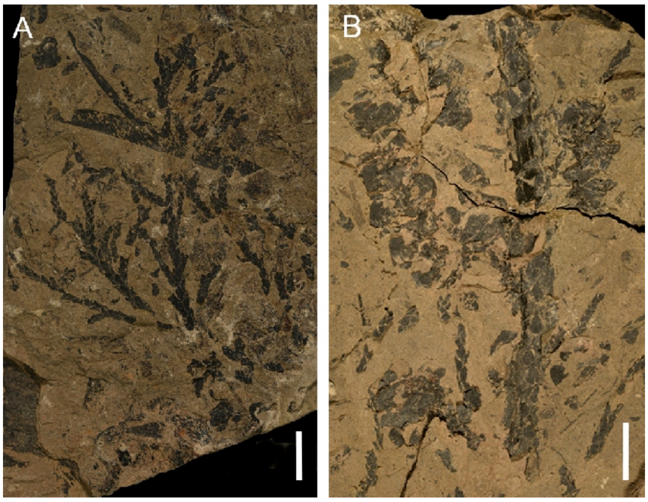

Fig. 7. Macrofossil plant assemblage form Sołtyków outcrop, lower Zagaje Formation, lowest Hettangian (continued)

A, **B** – *Hirmeriella muensteri*, **A** – leafy shoots, KRAM P PM 68/396; **B** – branch with female cones still attached, KRAM P PM 68/278; scale bar – 10 mm

microsaccus pollen grains (Fig. 8N, O). Other seed ferns belonging to Caytoniales, known from seeds *Caytonia* sp. and pollen grains *Vitreisporites pallidus*, probably preferred shaded habitats (Fig. 8P). Among the rest of the flora were bennettitaleans (*Pterophyllum* sp.) and cycads (*Paracycas minuta* macroremains; pollen grains *Chasmatosporites apertus*, *C. hians*, *C. major*, *C.* cf. *elegans* and *C.* cf. *rimatus*), also shrubby in form, most likely adapted to drier conditions within crevasse splays or on levees (Figs. 6C, F and 8R–T). The occurrence of some plants was confirmed only by single cones and dispersed pollen grains: the ginkgoalean female cone *Schmeissneria microstachys* (Fig. 6G) and *Monosulcites minimus* pollen grains, the ?gnetalean male cone *Piroconites kuesperti* (Fig. 6H) and *Ephedripites tortuosus* pollen grains, and the conifer cone *Swedenborgia* sp. (Wcisło-Luraniec, 1992b; Ziaja, 2006). Pollen grains belonging to araucariaceous *Araucariacites australis* and cf. *Araucariacites* sp., pinaceous *Pinuspollenites minimus* and taxodiaceous *Perinopollenites elatoides* suggest that these plants grew in the surroundings (Fig. 8V–X).

The area around Sołtyków was occasionally damaged by fire events, indicated by charred *Hirmeriella* shoots found in the outcrop as well as numerous charcoal clasts in sandstone or mudstone, as well as numerous particles in palynological samples (Ziaja and Wcisło-Luraniec, 1999). It has even been suggested that seed dispersal of *Hirmeriella* depended on cone charring (Ziaja and Wcisło-Luraniec, 1999). In that respect, the thick cuticle of *Hirmeriella* leaves might further support the adaptation of *Hirmeriella* to drier, fire-prone conditions, but the presence of leaf papillae points rather to elevated air humidity (Barbacka et al., 2007).

A mass of charred fern crosier-like fronds was found slightly higher in the Sołtyków section, in alluvial plain–lacustrine deposits (Fig. 5I, J). This record suggests a fern meadow colonizer assemblage, prone to fire incidents. The numerous traces of forest fires in the HCM region (charcoal, polycyclic aromatic hydrocarbons – PAHs) in Sołtyków and in slightly younger localities (Gromadzice and Podole sites, discussed later) point to a sufficiency of oxygen in the earliest Hettangian, sustaining the forest fire window (Marynowski and Simoneit, 2009).

In the highest part of the outcrop, numerous crevasse splay–levee deposits host a rich assemblage of invertebrate and vertebrate tracks and three-dimensionally preserved casts of *Neocalamites lehmannianus*. Here, this sphenopsid formed an autochthonous assemblage associated with riverbank levees. Unidentifiable plant debris containing large (up to 1 m long) log fragments (stem fragments and branches of *Hirmeriella*?) are present in the channel deposits.

Dinosaur coprolites from Sołtyków revealed some additional plants from the vicinity (Barbacka et al., 2022). The seed fern *Komlopteris* sp., cycad *Nilssonia* sp. and indet. ginkgophytes and conifers *Brachyphyllum* sp. and *Podozamites* sp. were typically associated with the humid conditions of flood plains. Another seed fern, *Ptilozamites* cf. *cycadea*, and the bennettitalean cf. *Pterophyllum* sp., both of shrubby habit, were adapted to the drier conditions found in places like levees. Based on these new data, the seed fern *Pachypteris papillosa*, so far known as a coastal halophyte, can be also related to saline/alkaline soils developed on nearby source areas built of exposed Triassic redbeds, surrounding the Early Jurassic sedimentary basin. Alternatively, these halophyte plants could grow in places where alkaline brines were delivered from eroded older rocks.The most frequent plants species determined from the coprolite material were trees and shrubs having relatively large leaves, which supplied proper food for herbivorous dinosaurs and made this area a good place for them to forage.

Close to Sołtyków, the Niekłań PGI 1 borehole exposed the alluvial part of sequence I (parasequence Ia) containing numerous sandstone layers deposited in fluvial channels. Plant fossils are rare; they confirm the occurrence of the tree fern *Todites princeps*, the conifer *Hirmerella muensteri* and an *incertae sedis* gymnosperm, *Desmiophyllum* sp. In the same region, ~10 km NE of Sołtyków, parasequence Ia in the Huta OP-1 borehole is dominated by sandy–muddy lithofacies of a meandering–anastomosing river depositional system. The recorded plant assemblage resembles those in Sołtyków and is composed mainly of horsetails (*Neocalamites lehmannianus*, which also grew in Sołtyków in a monospecific association), the ferns *Phlebopteris angustiloba* and *Coniopteris hymenophylloides*, believed to have preferred drier habitats, and the conifer *Brachyphyllum* sp. (Barbacka et al., 2014). Sporomorphs confirmed quite successively developed community with bryophytes, sphenophytes, lycophytes, ferns, seed ferns, ginkgoaleans, cycads and conifers (Taxodiaceae, Pinaceae, Araucariaceae, Cheirolepidiaceae). The high percentage of *Classopollis* pollen grains (~70% of all sporomorphs per sample from Huta-OP-1 and Studzianna, ~50 km NW of Huta) suggests that Cheirolepidiaceae (e.g., *Hirmeriella*) forests extended along the northern margin of the HCM locally (Rozwady, 30 km NW of Sołyków), transitioning into podocarpaceous woods (Rogalska, 1956; Krupnik et al., 2014).

INVERTEBRATE BODY AND TRACE FOSSILS

Fragmentary insect body fossils have been found in Sołtyków along with plant fossils (Popov, 1996; Węgierek and Zherikhin, 1997). The most diversified are the coleopterans; other insect groups such as heteropterans and cockroaches are rare. Among the crustaceans, freshwater ostracods *Darwinulla* sp. (Karaszewski and Kopik, 1970) and isolated carapaces of conchostracans (Niedźwiedzki, 2011) were found. Numerous specimens of bivalves probably representing

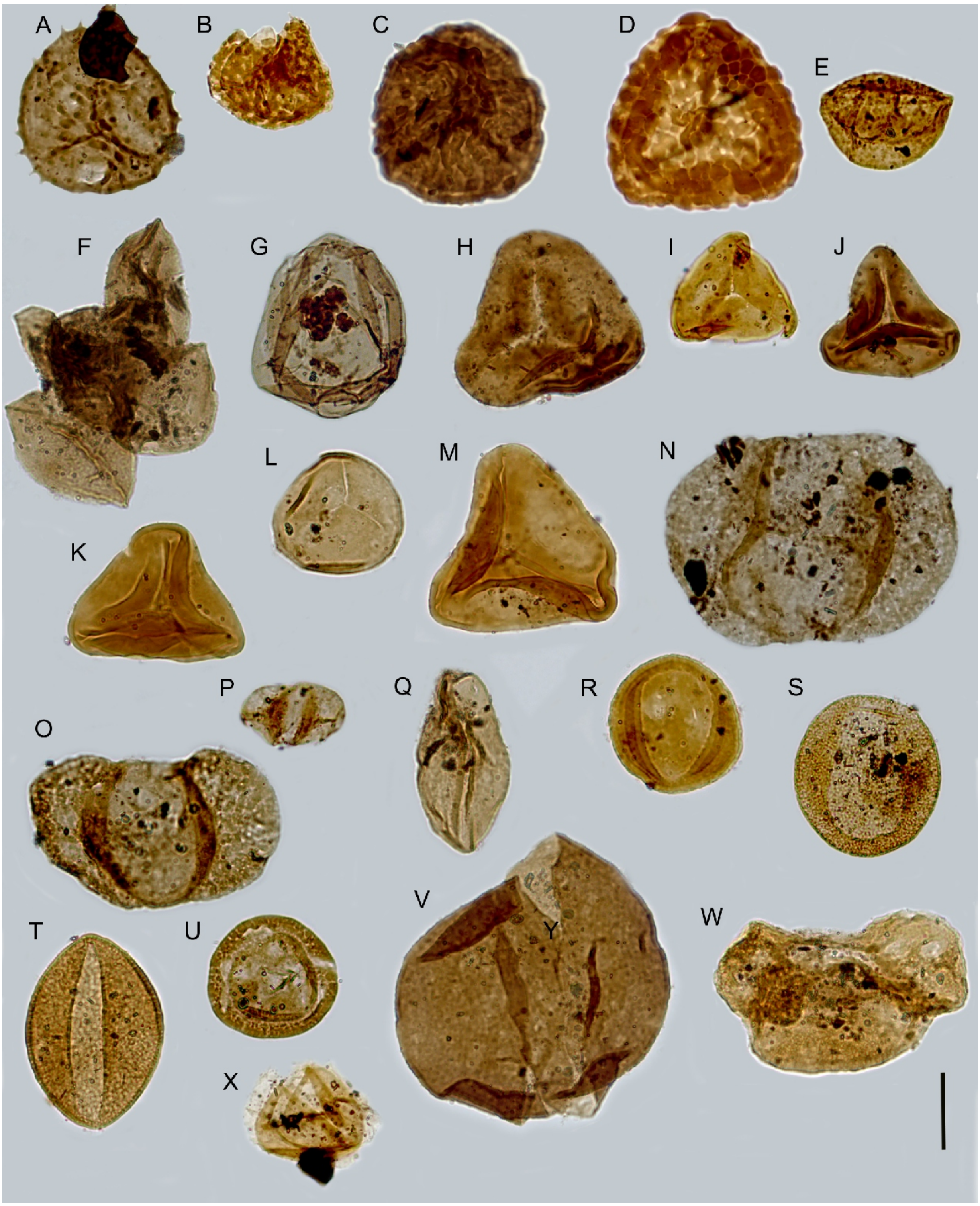

Fig. 8. Selected palynomorphs from Sołtyków outcrop, lower Zagaje Formation, lowest Hettangian

A – *Foraminisporis jurassicus* – bryophyte spore, KRAM P PM 68/8/58/95; **B** – *Foveotriletes* sp. – lycophyte spore, KRAM P PM 68/5/10/9; **C** – *Lycopodiumsporites cerniidites* – lycophyte spore, KRAM P PM 68/8/59; **D** – *Uvaesporites argenteaeformis* – lycophyte spore, KRAM P PM 68/6/1/6; **E** – *Aratrisporites minimus* – isoetalean lycophyte microspore, KRAM P PM 68/5/11/95; **F** – *Aratrisporites minimus* – group of isoetalean lycophytes microspores, KRAM P PM 68/8/5; **G** – *Calamospora tener* – sphenophyte spore, KRAM P PM 68/9/2/8; **H** – *Cyathidites minor* – leptosporangiate fern spore, KRAM P PM 68/10/1; **I** – cf. *Deltoidospora* sp. – leptosporangiate fern spore, KRAM P PM 68/6/2; **J** – *Concavisporites toralis* – leptosporangiate fern spore, KRAM P PM 68/10/1; **K** – *Matonisporites sp.* – matoniaceous fern spore, KRAMP PM 68/6/1/6; **L** – *Todisporites minor* – osmundaceous fern spore, KRAMP PM 68/8/3; **M** – *Plicifera delicata* – gleicheniaceous fern spore, KRAM P PM 68/8/2; **N** – *Alisporites robustus* – seed fern pollen grain, KRAM P PM 68/5/14; **O** – *Alisporites thomasii* – seed fern pollen grain, KRAM P PM 68/8/2; **P** – *Vitreisporites pallidu*s – caytonialean pollen grain, KRAM P PM 68/10/1; **Q** – *Monosulcites subgranulosus* – ginkgoalean/bennettitaleans/cycadalean pollen grain, KRAM P PM 68/8/62; **R** – *Chasmatosporites apertus* – cycad pollen grain, KRAM P PM 68/8/18; **S** – *Chasmatosporites hians* – cycad pollen grain, KRAM P PM 68/9/2/8; **T** – *Chasmatosporites major* – cycad pollen grain, KRAM P PM 68/9/1/1; **U** – *Classopollis torosus* – cheirolepidiaceous conifer pollen grain, KRAM P PM 68/6/1/6; **V** – cf. *Araucariacites* sp. – araucariaceous conifer pollen grain, KRAM P PM 68/9/2/6; **W** – *Pinuspollenites minimus* – conifer pollen grain, KRAM P PM 68/5/10/95; **X** – *Perinopollenites elatoides* – taxodiaceous conifer pollen grain, KRAM P PM 68/8/2; scale bar – 20 µm

Unionoidea were also collected in the channel and lake deposits but have not yet been studied in detail (Pieńkowski and Niedźwiedzki, 2008; Niedźwiedzki and Skawina, 2009).

The invertebrate trace fossil assemblages from alluvial plain deposits of Sołtyków represent three terrestrial ichnofacies: the *Mermia* (entirely aquatic), *Scoyenia* and *Coprinisphaera* ichnofacies (Pieńkowski, 1985; Pieńkowski and Niedźwiedzki, 2008). They span environments from shallow lacustrine to different subaerial fluvial environments. The diversity of invertebrate trace fossils is supported by the strongly mosaic character of the local environments. Bivalve burrows and surface locomotion traces and annelid, insect and crayfish traces and burrows are present. The following ichnotaxa have been recognized (Pieńkowski and Niedźwiedzki, 2008; Pieńkowski and Uchman, 2009; Niedźwiedzki, 2011): *Lockeia siliquaria, L. amygdaloides, L. czarnockii, Calceoformites uchmani*, *Ptychoplasma conica*, *Scalichnus* isp. (produced by bivalves); *Scoyenia* isp., *Spongeliomorpha* isp., *Spongeliomorpha carlsbergi*, *Cruziana problematica*, cf. *Cruziana* isp., *Rusophycus* isp., *Diplichnites* isp., cf. *Kouphichnium* sp., cf. *Xylonichnus* isp., *Linckichnus terebrans* (produced by arthropods); and *Planolites* isp., *Palaeophycus* isp., *Cochlichnus* isp. and cf. *Helminthoidichnites* isp. (produced by *incertae sedis* worm-like organisms). Bivalve burrows reflect highly diversified behaviour in response to changing environmental conditions: in particular, to anastrophic burial during flood events. Commonly, these hypichnial forms are preserved on the underside of crevasse splay sandstone. Also recognised were various other structures attributed to arthropod burrows (vertical to subvertical tunnels), chambered insect nests of Pallichnidae affinity or other nests with septa (likely produced by cicadas), possible earthworm burrows, as well as enigmatic, intriguing radial chambers, likely made by crayfishes (although insect affiliation cannot be excluded as the chambers lack characteristic meniscate infilling). Insects played an important role in the Sołtyków ecosystem; they were relatively abundant and their interaction with wood material is indicated by wood borings and traces of gnawing, such as cf. *Xylonichnus* isp., *Linckichnus terebrans* and *Helminthoidichnites* isp. (Pieńkowski and Niedźwiedzki, 2008). The Sołtyków terrestrial ichnocoenoses were quite diversified, chiefly because of a changing water table and food availability. The trace fossil assemblages suggest that the Early Hettangian invertebrate fauna of Sołtyków was much more diversified than the preserved body fossils would indicate (Zatoń et al., 2009). The makers of all these trace fossils played important roles in soil-forming processes and were key elements of the food chain – for small vertebrates as well, including dinosaurs. Certainly their interaction with the plants was significant but it has not been documented so far.

VERTEBRATE TRACKS, BONE REMAINS, NESTS AND COPROLITES

The Sołtyków outcrop provided one of the most diversified dinosaur track assemblages in the Polish Jurassic (e.g., Pieńkowski and Gierliński, 1987; Gierliński and Pieńkowski, 1999; Gierliński et al., 2004; Niedźwiedzki, 2011; Fig. 9). In the lower part of the outcrop an extensive horizon bearing dinosaur tracks was recognised (Gierliński and Pieńkowski, 1999; Gierliński et al., 2004, Niedźwiedzki, 2011). This horizon lies between layers from which plant macro- and microfossils were collected. Dinosaur tracks are also numerous in the beds exposed in the upper part of the outcrop, where they occur on several palaeosurfaces. Many of the track specimens were found in loose blocks, in several published papers these tracks were referred to only as originating from the upper or lower part of the Sołtyków outcrop without detailing the level of origin. This approach is even more justified because the ichnotaxonomic composition of the tracks is uniform across outcrop levels (see Gierliński et al., 2004; Niedźwiedzki, 2006). However, in the lowermost part of the exposure (Fig. 3) there are horizons with numerous tracks of non-dinosaurian tetrapods (dominated by cf. *Brasilichnium* and small mammal-like tracks cf. *Ameghinichnus*), which may suggest that they represent an ichnoassemblage slightly different from these registered in the beds exposed above.

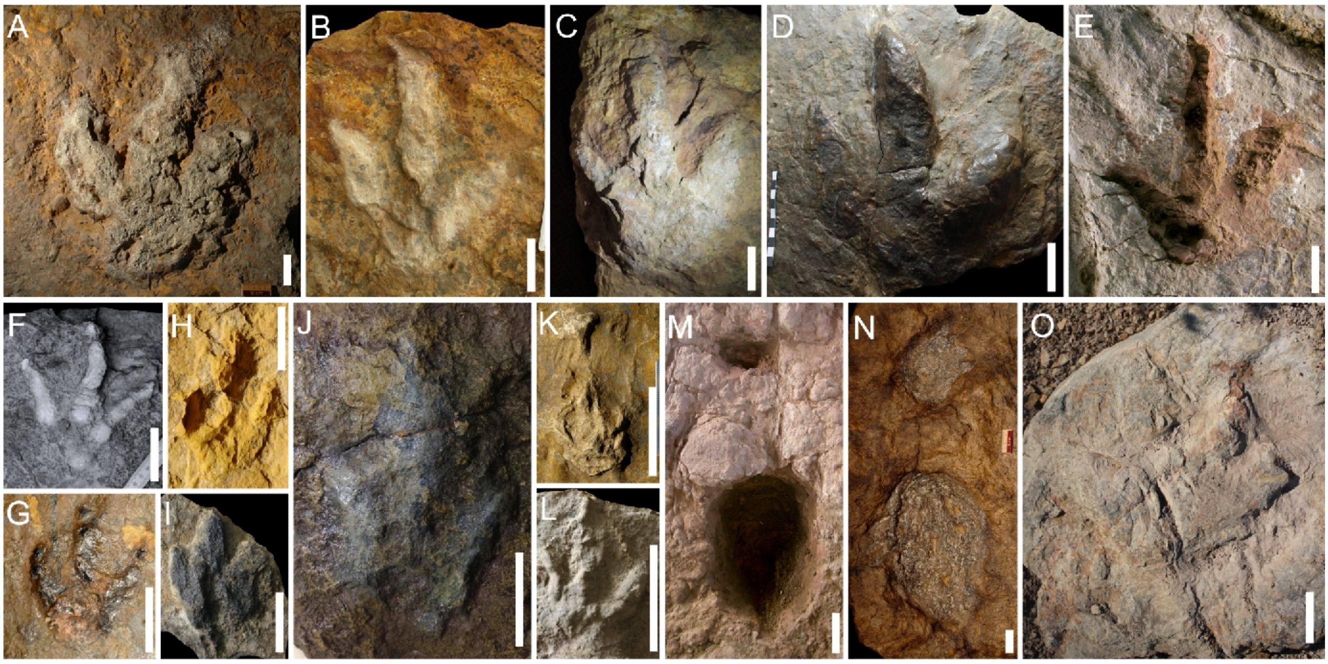

Fig. 9. Dinosaur track association from Sołtyków, Zagaje Formation, lower Hettangian

A – cf. *Megalosauripus* isp.; **B** – cf. *Eubrontes* isp.; **C–E** – *Kayentapus* isp; **F, G** – *Anomoepus* isp.; **H** – *Grallator* isp.; **I** – cf. *Stenonyx* isp.; **J** – *Anchisauripus* isp.; **K** – *Delatorrichnus* isp.; **L** – cf. *Kayentapus* isp.; **M** – small *Parabrontopodus* isp.; **N** – large *Parabrontopodus* isp.; **O** – *Tetrasauropus* isp.; scale bar – 5 cm

The assemblage typical for an alluvial plain environment is characterised by the presence of medium-sized to large sauropod trackmakers (*Parabrontopodus*; Fig. 9M, N) and medium-sized to large predators (theropod trackmakers of *Anchisauripus, Eubrontes* and *Kayentapus*; Fig. 9B–E, J) (Gierliński and Pieńkowski, 1999; Niedźwiedzki, 2011). The theropod tracks are the most abundant (Niedźwiedzki, 2006, 2011). Tracks of small and medium-sized theropods belong to *Stenonyx*, *Grallator* (two types; Fig. 9H, I); these tracks are thought to have been left by early theropods (Gierliński and Niedźwiedzki, 2002). The most numerous small/medium-sized to large theropod tracks, referred to *Kayentapus* (Fig. 9C–E, L), are supposed to have been left by an early large theropod like *Dilophosaurus* Welles, 1970 (Gierliński, 1991, 1994, 1996; Gierliński and Ahlberg, 1994). Some medium-sized tracks of theropods have metatarsal impressions preserved that may have some behavioural implications (Gierliński, 1994; Niedźwiedzki and Niedźwiedzki, 2001, 2004). Of note are peculiar theropod traces (parallel scratches), corresponding in size with *Kayentapus*, left by swimming animals (Gierliński et al., 2004; Niedźwiedzki, 2011). The discovery of very large (50–65 cm long) tridactyl theropod tracks (cf. *Megalosauripus*; Fig. 9A) is especially interesting, as such large theropods are not known from the bone record of the Early Jurassic of northern Pangea (Gierliński et al., 2001; Niedźwiedzki, 2006, 2011). These tracks provide palaeoichnological evidence for the occurrence of a gigantic predatory theropod in the earliest Jurassic. The intriguing tracks are more similar to the largest tracks left by Middle–Late Jurassic theropods than to those from the Early Jurassic (Gierliński et al., 2001; Niedźwiedzki, 2006, 2011). A large theropod *Cryolophosaurus* which could have produced tracks of similar size has been described from the Lower Jurassic Hanson Formation of Antarctica (Hammer and Hickerson, 1994), but this unique find represents a southern Pangean dinosaur and is dated to the Sinemurian–Pliensbachian interval (Elliot et al., 2017).

There are numerous tracks of sauropodomorphs and sauropods in Sołtyków, especially on the palaeosurfaces in the lower part of the outcrop. Basal sauropodomorphs are represented by tetradactyl pes tracks: cf. *Otozoum* and cf. *Tetrasauropus* (Fig. 9O; Niedźwiedzki, 2011). The most intriguing tracks are those of early sauropods, and small and mostly large narrow-gauge *Parabrontopodus* are present in the Sołtyków ichnorecord (Gierliński and Sawicki, 1998; Gierliński and Pieńkowski, 1999). Most of the sauropod tracks were found on the main track-bearing palaeosurface in the lower part of the outcrop. This surface covers ~100m^2; it comprises two parallel trackways of large individuals heading south and four parallel trackways of juveniles heading north. All the sauropod trackways with oval-shaped manus and pes imprints, without distinct digit impressions, show a narrow-gauge pattern and indicates an advanced type of quadrupedality of their producer. The four parallel trackways of the small individuals suggest herding behaviour among juveniles (Gierliński and Pieńkowski, 1999). Interestingly, the steps of juvenile trackmakers become longer along the exposed stretch of the trackways and their trackways synchronously turn north-west. Thus, it seems likely that the group of juveniles were escaping from the large theropod (*Kayentapus* trackmaker – these tracks are visible on the same surface), which was moving towards the sauropod herd (Gierliński and Pieńkowski, 1999).

Ornithischian and putative ornithischian tracks are rare in the Sołtyków ichnoassemblage. Small and medium-sized tracks referred to *Anomoepus* and *Delatorrichnus* are present (Fig. 9F, G, K), of putative early ornithischian/early thyreophoran and heterodontosaurid origin, respectively (Gierliński et al., 2004; Niedźwiedzki, 2011). We cannot confidently claim that all of the *Anomoepus*-like specimens (especially the poorer-quality specimens) were produced by ornithischians, even though the parameters and the features (length/width ratio, mesaxony, interdigital angle) do indeed suggest an ornithischian origin. The ornithischian trace fossil record from Sołtyków is poorer than that of other middle–late Hettangian sites in the HCM (see below), where ornithischian tracks are relatively abundant and at some sites they dominate.

Pieńkowski (1998) described dinosaur nests with diagenetically altered eggs (Pieńkowski, 1998; see also discussion: Sabath et al., 1999; Pieńkowski, 1999). Dinosaur eggs and nests from Sołtyków occur within a single bed in the lower part of the section and probably represent a larger nesting area. Excavated clutches (Pieńkowski, 1998, 1999) typically contain 10 to 20 eggs that range from 7 to 12 cm across and are stacked in sandstone layers, arranged in semicircular patterns. In part of the nesting area in the egg-bearing interval, thin crevasse splay sandstone lenses cover the nests, and the egg-bearing bed is laterally continuous but varies in substrate composition from sandstone to siltstone/mudstone. Sedimentological studies and analyses of nests and egg structures are in progress.

Based on ichnological data (tracks) from the Sołtyków outcrop, Gierliński and Pieńkowski (1999) recognized a characteristic dinosaur ichnoassemblage distinctive for the lower part of the Zagaje Formation (Fig. 10). This ichnoassemblage is associated with an inland humid habitat with both low- and high-growing vegetation, dominated by relatively large herbivores (sauropod trackmakers of *Parabrontopodus)* and medium-sized to large predators (theropod trackmakers of *Anchisauripus, Eubrontes* and *Kayentapus*). There are also other sauropodomorph tracks (cf. *Otozoum*, cf. *Tetrasauropus*), and giant theropod tracks (cf. *Megalosauripus*) in this ichnoassemblage. Theropod and sauropod track finds from the lowermost Gromadzice section (another locality of the lower part of the Zagaje Formation exposed in the Kamionka River valley and located at the base of the lower outcrop in Gromadzice and another neighbouring outcrop) support the view that saurischians dominated in the HCM during the earliest Hettangian (ongoing study). Most abundant in the lowermost Gromadzice record are theropod tracks similar to *Kayentapus* and *Eubrontes.* Possibly the presence of ornithischians is indicated by two isolated occurrences of small *Anomoepus*-like tracks but the remains are rather sparse. The sauropod tracks from the lowermost Gromadzice belong to large animals that left oval-shaped pes prints (perhaps *Parabrontopodus*) with manus imprints much smaller than the pes imprints. The assemblage is strictly similar to those in Sołtyków and also contains small to medium-sized theropod tracks (*Grallator* and *Anchisauripus*) as well basal sauropodomorph tracks (cf. *Evazoum* or juvenile *Tetrasauropus* tracks). The track record from the lower part of the Zagaje Formation at the lowermost Gromadzice is important because it supplements the scant ichnological record of this age in this HCM region.

The Sołtyków section yielded ichnological data valuable for determining the biodiversity of not only the early Hettangian dinosaur fauna but also other terrestrial tetrapods: mammal-like reptiles (cf. *Brasilichnium*), early mammals (cf. *Ameghinichnus*), lepidosauromorphs (*Rhynchosauroides*), pterosaurs (Pterosauria indet.) and early crocodylomorphs (*Batrachopus*, Protosuchidae indet.; Gierliński et al., 2004; Niedźwiedzki,

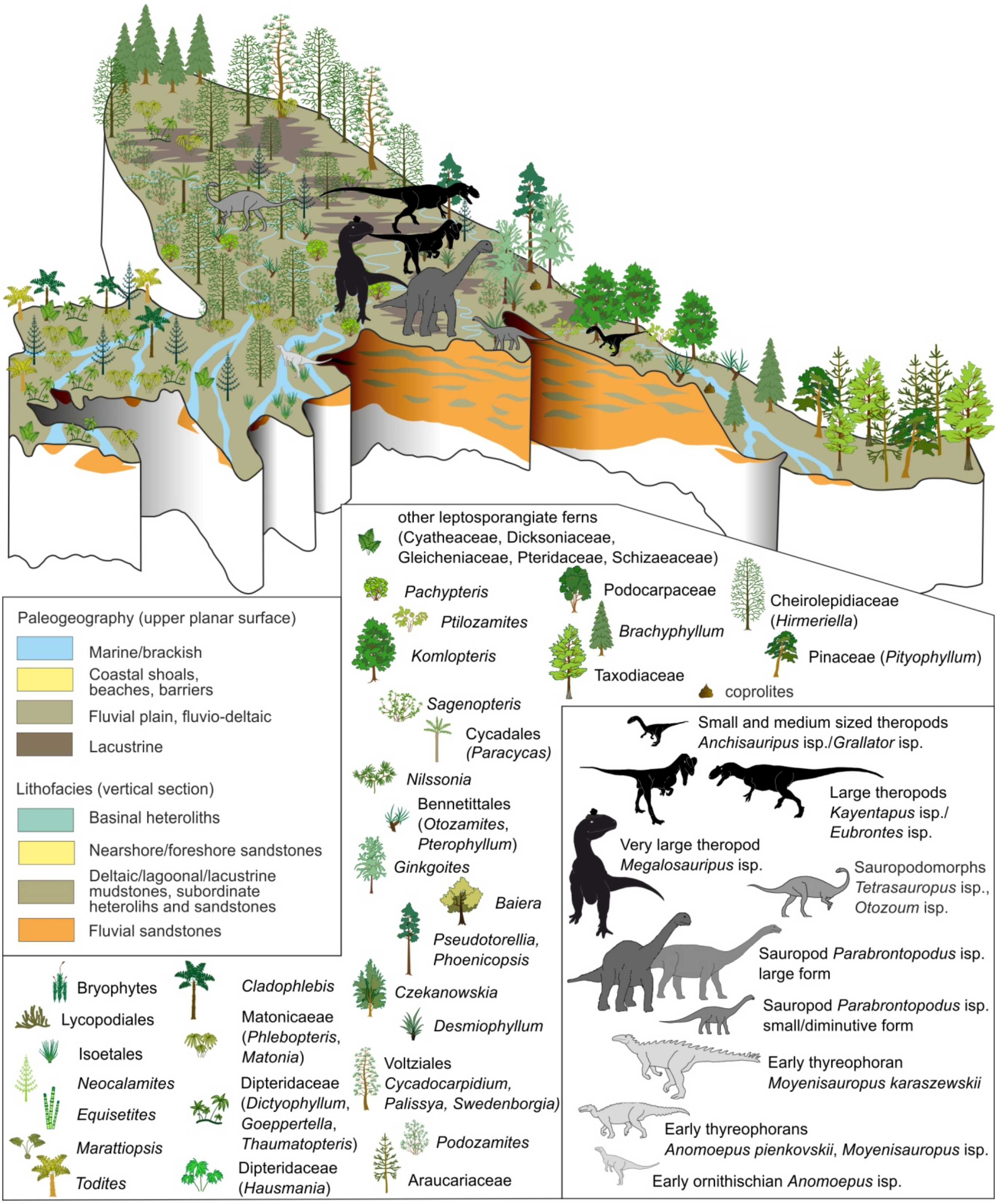

Fig. 10. Reconstruction of the Holy Cross Mountains (HCM) sedimentary subbasin, lower part of the Zagaje Formation (lowest Hettangian, parasequence Ia), with reconstructed plant cover and the most characteristic dinosaurs. Reconstruction, silhouettes and other graphic elements of dinosaurs courtesy of Karol Sabath and based on the authors' sources

2011; Niedźwiedzki et al., 2009). The diversity and affinity of small to tiny tetrapod traces from this site are currently the subject of additional studies. Many still-unpublished finds show that many different small reptiles and mammal-like reptiles ran under the feet of dinosaurs in the earliest Hettangian of the HCM.

Four fossil-bearing intervals in the Sołtyków section also contain numerous vertebrate coprolites (Niedźwiedzki, 2011; Barbacka et al., 2022). They were produced by fish, small tetrapods and in large part by dinosaurs. The coprolites, numbering >500 specimens, are among the most frequent vertebrate trace fossils in the Zagaje Formation of Sołtyków. Fossilized faeces of both predators and herbivorous dinosaurs were recognized from the site. This coprolite collection is the subject of ongoing studies, and some results are being published (Barbacka et al., 2022).

Vertebrate body fossils are very rare at the Sołtyków locality. Only a few bone fragments (fragmental caudal vertebrae, dorsal vertebrae, ischium and pubis fragments, limb bone fragments) and one tooth with serrations have been found, all belonging to theropods (Niedźwiedzki, 2011; Pieńkowski et al., 2014). Isolated scales, fish vertebrae and teeth have also been found (Karaszewski and Kopik, 1970; Niedźwiedzki, 2011). Two specimens, complete fish body fossils strongly “carbonatized” during early diagenesis, were found in lacustrine deposits (Niedźwiedzki, 2011). Recently, fragments of bones of large dinosaurs (Theropoda indet., Sauropodomorpha indet.) were found in rocks probably representing the basal part of the Zagaje Formation and exposed at the Hucisko clay-pit, ~40 km W of Sołtyków. This find, not yet published, enriches the picture of the Zagaje Formation fauna and is an important addition to research on vertebrate skeletal remains from the Lower Jurassic of Poland.

LATEST EARLY HETTANGIAN, UPPER PART OF ZAGAJE FORMATION, PARASEQUENCE IB, LOWER OUTCROP IN GROMADZICE AND ITS EQUIVALENTS FROM BOREHOLES

ENVIRONMENTAL CONTEXT

The meandering–anastomosing river depositional system exposed in Sołtyków and the lowermost part of the Gromadzice section was replaced by mudstone/claystone coal-bearing lithofacies with palaeosols of a lacustrine–backswamp depositional system, particularly well developed in the subbasin depocentre (upper part of the Huta OP-1 borehole: Pieńkowski, 2004a; Barbacka et al., 2014; Niekłań PGI 1 borehole: Barbacka et al., 2016a). This sedimentary event, related to the correlative transgressive surface (Pieńkowski, 2004a), forms an easily identifiable parasequence boundary (Ia/Ib) across the whole HCM region. Lacustrine sedimentation of parasequence Ib predominates in the subbasin centre (Huta OP-1 borehole, northern margin of HCM); river deposit areas become limited to the periphery of the subbasin (lower outcrop in Gromadzice, on bank of Kamionka stream, north-eastern margin of HCM). The abrupt change of depositional systems at the parasequence Ia/Ib boundary can be explained by the rapid rise of the base level, which had a pronounced effect on sedimentation in the continental basin. Alluvial deposition was rapidly replaced by lacustrine deposition. The advancing transgression subsequently led to marine flooding and a nearshore environment developed, forming a step-wise (delayed) retrogradational encroachment of the transgression onto the continental area. This step-wise progress of the transgression is well visible in the lower outcrop in Gromadzice.

The lower outcrop in Gromadzice is situated in the marginal part of the sedimentary subbasin and represents the uppermost part of the Zagaje Formation. The outcrop reveals a sequence of an alluvial depositional system and an upper delta plain depositional subsystem (Pieńkowski, 2006). The change of depositional system from alluvial plain to delta plain is gradual. The lower part of the outcrop comprises a typical meandering (high-sinuosity) alluvial channel subsystem with trough cross-bedded sandstone filling channels deeply incised into fluvial plain mudstone. The sandstone is rich in unidentifiable plant detritus (sometimes represented by log fragments up to 1 m long); it contains dinosaur tracks preserved at the channel’s bottom and sandstone beds representing crevasse splay deposits. The overlying complex is composed of grey laminated mudstone, siltstone and grey fine-grained sandstone, and contains a very rich dinosaur track ichnoassemblage. Its features point to a delta plain (upper delta plain depositional system), where the muddy overbanks were at least periodically flooded by brackish water with a bay bivalve association. The sandstone/siltstone layers represent deltaic, basinward prograding crevasse splay deposition. These features are consistent with rapid aggradation during which crevassing, lacustrine/marsh sedimentation and avulsion dominated the delta plain/floodplain. The bivalve assemblage contains both freshwater Unionoidea and rare brackish-water Cardiniidae and Mytilidae (Pieńkowski, 2004a, 2006).

PLANT COVER

Most plant macrofossils from the lower outcrop in Gromadzice are preserved in crevasse splay deposits (Figs. 11–13). This assemblage is dominated by leaves of ginkgoaleans (*Sphenobaiera*; Fig. 11J), czekanowskialeans (*Czekanowskia*) and an enigmaitic gymnosperm *Desmiophyllum* (Fig. 8K), probably shed during dry seasons (Pacyna et al., 2018). Conifers are the next most numerous group, with frequent *Podozamites* and *Pityophyllum* and rare *Brachyphyllum* and *Stachyotaxus* (Fig. 12B). Numerous lax female and male cones and seeds, produced by the abovementioned taxa, have been found among accumulations of leaves; they belong to the cone taxa *Leptostrobus, Stachyopitys, Cycadocarpidium, Sorosaccus* and *Ixostrobus* (Figs. 11L and 12A). A poorer assemblage dominated by numerous ferns *Marattiopsis* and with rare gymnosperms *Podozamites* have been found in dark mudstone deposited in floodplains. The lack of preserved cuticle details hampers determination of the true taxonomical diversity of the linear-leaved gymnosperms. Based on gross morphology alone, *Pseudotorellia* and *Phoenicopsis* probably were also present.

This assemblage is strikingly similar to North Asian Jurassic floras dominated by *Czekanowskia, Phoenicopsis, Pseudotorellia, Ginkgoites, Pityophyllum* and *Nilssonia*, which also formed extensive leaf mats after shedding spur-shoots with leaves (Krassilov, 1975, 2003). Considering this similarity to well known and widespread Asiatic floras, it is possible to draw some conclusions about the plant cover during sedimentation of the upper Zagaje Formation around the lower outcrop in Gromadzice. *Czekanowskia* was an early colonizer of the delta-plain to floodplain habitat, where it formed woody wetland forests. *Czekanowskia* was accompanied or locally replaced by a needle-leaved conifer *Pityophyllum* or a narrow-leaved gymnosperm *Pseudotorellia*. *Czekanowskia* forest may have been

Fig. 11. Macrofossil plant assemblage from the lower outcrop in Gromadzice, upper Zagaje Formation, uppermost lower Hettangian

A – *Marattiopsis muensteri* sterile and fertile leaves, *Matonia braunii* sterile leaf (lower right corner), A-III-25/28; **B** – *Cladophlebis* sp., PC IB UJ 106/47; **C** – *Todites williamsoni*, A-III-25/1; **D** – *Todites princeps*, A-III-26/14; **E** – *Matonia braunii* fertile leaf, PC IB UJ 106/54b; **F** – *Dictyophyllum nilssoni*, PC IB UJ 106/40a; **G** – *Neocalamites lehmannianus*, PC IB UJ 106/60; **H** – *Equisetites muensteri*, A-III-26/3; **I** – *Taeniopteris tenuinervis*, A-III-25/5; **J** – *Sphenobaiera* sp., PC IB UJ 106/69; **K** – accumulation of isolated leaves, mainly *Desmiophyllum harrisii*, PC IB UJ 106/74; **L** – *Ixostrobus siemiradzkii* male cone, A-III-25/15; scale bars: A, B, E, F – 6 mm, C, D, G, H, I – 10 mm, J – 5 mm, K – 20 mm, L – 3 mm

Fig. 12. Macrofossil plant assemblage form the lower outcrop in Gromadzice, upper Zagaje Formation, uppermost lower Hettangian (continued)

A – *Cycadocarpidium* sp., PC IB UJ 106/18; **B** – *Stachyotaxus septentrionalis*, A-III-25/2; **C** – *Schizolepis* sp., isolated winged seed, PC IB UJ 106/20; **D** – *Schizolepis follini* cone, A-III-25/10; scale bars: A – 4 mm, B –5 mm, C – 6 mm, D – 10 mm

replaced by *Phoenicopsis*-dominated forests through the course of plant succession stages and also along a gradient of disturbed to relatively stable habitats (Krassilov, 2003). *Czekanowskia* and *Phoenicopsis* forests were peat-forming (Krassilov, 1975, 2003), so they may have contributed significantly to the coal seams occurring in the Zagaje and Skłoby formations.

Two other plant communities may also have contributed to the lower outcrop in Gromadzice assemblage: *Baiera–Sphenobaiera* peat-bog forest and *Nilssonia–Podozamites* willow-like riparian thickets. Sphenopsids (*Neocalamites* macroremains and *Calamospora tener* spores; Figs. 11G and 13A), ferns (leaves *Cladophlebis, Phlebopteris, Dictyophyllum*, spores *Matonisporites* sp., *Concavisporites toralis*, *Cyathidites minor* and *Deltoidospora* sp.; Figs. 11B, E, F and 13B–F), seed ferns (*Sagenopteris, Pachypteris* leaves and bisaccate pollen grains), bennettitaleans (*Otozamites*) and cycads (*Nilssonia*) are rare in the lower outcrop in Gromadzice and preserved as rather small fragments, probably transported over a long distance from communities growing along a river flowing from the hinterland. Palynological data supplement our knowledge about the vegetation. Bennettitales or Ginkgoales (*Monosulcites* sp.), Cycadales (cf. *Chasmatosporites elegans*) and Taxodiaceae (*Perinopollenites elatoides*) occurred in marshy, wetter places, while conifers producing bisaccate pollen grains (e.g. *Pinuspollenites minimus*) are believed to have grown in drier habitats (Fig. 13G–M). For Erdtmanithecales (*Eucommiidites troedssonii*; Fig. 13N, O) there is no data about their ecological preferences. Forest fires were frequent, inferred from charcoal and biomarkers (Marynowski and Simoneit, 2009). A more taxonomically diversified plant assemblage was described from the Gromadzice area by Raciborski (1891a, b, 1892a, b) and Makarewiczówna (1928), also from the upper part of the Zagaje Formation, but those specimens lack detailed location data (Pacyna, 2013, 2021a). In contrast to the plant remains gathered recently from the lower outcrop at Gromadzice, this collection is fern-dominated (Pacyna et al., 2018). Plant fossils originated from several different lithological types representing separate sedimentological environments. In sandy mudstone of fluvial origin, the following ferns were mainly found: dipteridaceous *Dictyophyllum nilssonii* and *Thaumatopteris brauniana,* matoniaceous *Phlebopteris angustiloba*, marattiaceous *Marattiopsis muensteri* and sphenopsids *Neocalamites lehmannianus* and *Equisetites muensteri* (Fig. 11A, G, H). Among the gymnosperms, the czekanowskialean male cone *Ixostrobus siemiradzkii* is moderately frequent (Wcisło-Luraniec and Barbacka, 2000; Pacyna and Zdebska, 2011), and the conifers *Schizolepis follinii* and *Stachyotaxus septentrionalis* are rare (Fig. 12B–D). Sometimes complete large gymnosperm leaves are preserved in mudstone, belonging, for example, to the cycadophytes (*Nilssonia orientalis, Taeniopteris superba, T. tenuinervis*; Fig. 11I) and ginkgophytes (*Czekanowskia rigida*, *Ginkgo* aff. *whittbyensis*). In fine clay, probably of lacustrine origin, the fossils are much rarer and are represented by small segments of compound leaves belonging to ferns (*Todites princeps*, *Matonia braunii* and *Goeppertella microloba*) and a seed fern (*Sagenopteris rhoifolia*). Large fragments of fern leaves (especially *Dictyophyllum nilssonii*) and equisetalean shoots point to rather short transport from a riparian community before burial; the rarer gymnosperms may have originated from surrounding forests (Fig. 11D).

The composition of the flora known from outcrops is supplemented with borehole data. The Huta OP-1 borehole, located ~60 km NW of Gromadzice, penetrated a thick package of lacustrine plant-bearing strata (Huta Mudstone Member of Zagaje Formation, parasequence Ib). Most of the fossils originate from laminated or massive mudstone and claystone deposited in a lacustrine/backswamp depositional system. Based on such random data from a single borehole it is difficult to reconstruct the plant communities. Similarly to Gromadzice, probably there were monotypic stands of sphenopsids (*Neocalamites lehmannianus*), fern brake (*Coniopteris hymenophylloides*, *Cladophlebis nebbensis, Todites princeps, ?Thaumatopteris* sp.) and gymnosperm forests dominated by ginkgophytes (*Baiera furcata,* cf. *Baiera* sp., *Pseudotorellia* sp., *Ixostrobus groenlandicus*, *Podozamites distans*, *Desmiophyllum harrisii*) (Barbacka et al., 2014). In the palynological record, besides fern spores (*Matonisporites* spp.) and cycadalean pollen grains (*Monosulcites minimus, Chasmatosporites apertus*, *Chasmato-*

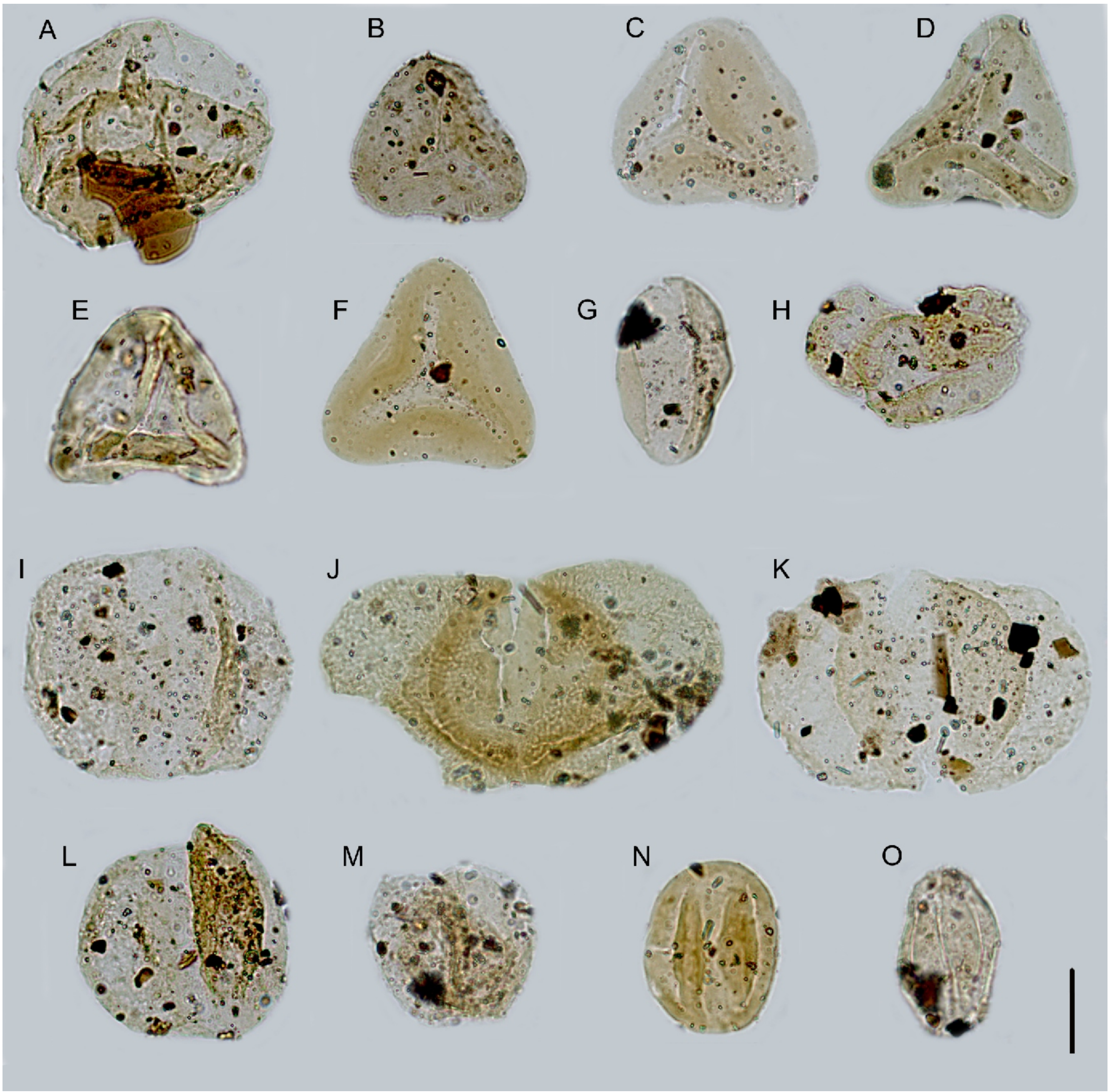

Fig. 13. Selected palynomorphs from the lower outcrop in Gromadzice, upper Zagaje Formation, uppermost lower Hettangian

A – *Calamospora tener* – sphenophyte spore, KRAM P PM 84/1/3/3; **B** – *Cyathidites minor* – leptosporangiate fern spore, KRAM P PM 84/1/3/3; **C** – *Deltoidospora* sp. – leptosporangiate fern spore, KRAM P PM 84/1/2/1; **D** – *Concavisporites toralis* – leptosporangiate fern spore, KRAM P PM 84/1/2/2/97; **E** – *Concavisporites toralis* – leptosporangiate fern spore, KRAM P PM 84/1/2/10; **F** – *Matonisporites sp.* – matoniaceous fern spore, KRAM P PM 84/1/2/1; **G** – *Chasmatosporites elegans* – cycad pollen grain, KRAM P PM 84/1/3/3; **H** – *Pinuspollenites minimus* – conifer pollen grain, KRAM P PM 84/1/1/9; **I** – *Alisporites robustus* – seed fern pollen grain, KRAM P PM 84/1/3/3; **J** – bisaccate pollen grain of seed fern or conifer, KRAM P PM 84/1/3/3; **K** – bisaccate pollen grain of seed fern or conifer, KRAM P PM 84/1/3/3; **L** – bisaccate pollen grain of seed fern or conifer, KRAM P PM 84/1/3/3; **M** – *Perinopollenites elatoides* – taxodiaceous conifer pollen grain, KRAM P PM 84/1/2/7; **N** – *Eucommiidites troedssonii* – erdtmanithecalean pollen grain, KRAM P PM 84/1/1/3; **O** – *Eucommiidites troedssonii* Erdtman – erdtmanithecalean pollen grain, KRAM P PM 84/1/2/10; scale bar – 20 µm *sporites* sp.), *Perinopollenites elatoides* pollen grains indicate the occurrence of taxodiaceous conifers, and *Classopolis* pollen grains point to the presence of cheirolepidiaceous conifers in the surroundings (Krupnik et al., 2014).

In the nearby Niekłań PGI 1 borehole, the fern *Matonia braunii* was preserved in laminated claystone of floodplain–backswamp origin. Their habitat was probably the shore of a small floodplain lake, where this fern was an opportunistic species colonizing a disturbed environment (Barbacka et al., 2016a). Other plant remains from this borehole belong to the same gymnosperm assemblage as in the lower outcrop at Gromadzice: numerous leaves of *Desmiophyllum harrisi*, accompanied by *Podozamites*, *Phoenicopsis* and *Pseudotorellia*.

A slightly different picture of late early Hettangian vegetation comes from data of the Studzianna borehole >100 km NW of Gromadzice and ~60 km NW of Huta OP-1 (Barbacka et al., 2014). Only ginkgoaleans and czekanowskialeans are present. One of the likely explanations for this impoverishment may be a difference in plant composition in the source area resulting from climatic/topographic/edaphic conditions. The Studzianna area received sediment supply from the north-east, while the area occupied by today's Huta OP-1 borehole was supplied by rivers mostly from the south (Pieńkowski, 2004a). The presence of *Ginkgoites* cf. *marginatus*, *Pseudotorellia nordenskioeldii*, *Czekanowskia hartzi*, *Czekanowskia rigida* and *Phoenicopsis insolita* indicate a forested environment. *Czekanowskia* was an early colonizer of wetlands characteristic for waterlogged alluvial to peat-bog facies. This riparian vegetation was successionally replaced by *Phoenicopsis* forests in less disturbed lowland places. Lower slope woody assemblages may be represented by *Pseudotorellia.*

VERTEBRATE TRACKS

Numerous dinosaur tracks were found in the upper part of the lower outcrop in Gromadzice (Figs. 14A–E and 15). They represent the *Moyenisauropus*–*Anomoepus*–sauropodomorph/sauropod–*Kayentapus*–Eubrontes–*Anchisauripus*–*Grallator* ichnoassemblage, which is more typical for the mid and late Hettangian (Skłoby and Przysucha Ore-bearing formations). The tracks were left by small to medium-sized, low-browsing dinosaurs belonging to basal ornithischians (*Anomoepus, Moyenisauropus*; Fig. 14C–E), which fell prey to small to medium-sized theropods. This assemblage is regarded as a typical ichnofacies of delta plain and barrier–lagoon deposits as defined by Gierliński and Pieńkowski (1999) and Pieńkowski (2004a). The most numerous tracks of *Moyenisauropus* show digit length ratios very close to those of the early thyreophoran skeleton (Gierliński and Pieńkowski, 1999; Niedźwiedzki and Niedźwiedzki, 2001, 2004; Galton and Upchurch, 2004). Wide, robust *Moyenisauropus* cf. *natator* tracks with a large pentadactyl manus point to the trackmaker's adaptation to an unstable surface, such as the boggy terrain of delta plains or coastal zones of lagoons, lakes and rivers. A few sauropodomorph and sauropod tracks (?*Parabrontopodus* isp.,*Otozoum* cf. *pollex* and cf. *Evazoum*; Fig. 14B) were also found (Gierliński, 1997; Gierliński and Niedźwiedzki, 2005).

MIDDLE HETTANGIAN, SKŁOBY FORMATION, PARASEQUENCES IC–IF, UPPER OUTCROP IN GROMADZICE

ENVIRONMENTAL CONTEXT

During the middle Hettangian (Pieńkowski, 2004a; Krupnik et al, 2014), deltaic depositional systems prevailed on the margins of the HCM subbasin, while the subbasin centre was dominated by nearshore and barrier-lagoon depositional systems (Pieńkowski, 2004a). The transgressive surface of depositional sequence I occur at the base of parasequence Ic is commonly associated with the development of a barrier-lagoon depositional system in the subbasin centre, which slightly preceded the transgression on the subbasin's margins. The transgressive barrier-lagoon depositional system probably was associated with detachment of beach ridges from the mainland by a rise in sea level and inundation of the lower areas. The deltaic depositional system was developed particularly along the eastern and northern edges of the subbasin, with the characteristic joint occurrence of bivalves representing both Unionoidea and the non-freshwater Cardiniidae and Mytyloida (upper outcrop in Gromadzice and outcrop in Podole). Delta depositional systems in these regions were represented by two types: one characterized by stronger reworking of waves and coastal currents, which resulted in the formation of long-shore barriers and lagoons–marshes creating a more complex cyclicity of sedimentation (Gromadzice type); and simple Gilbert-type, fluvial-dominated deltas with simple upward-coarsening cyclicity (Podole type; Pieńkowski, 2004a).

The upper outcrop in Gromadzice shows deltaic and nearshore facies of depositional parasequences Ic and Id of the Skłoby Formation (Fig. 16). The stratigraphic pattern is of small-scale, "composed" delta complexes. The upper outcrops in Gromadzice show three coal/clastic sediment contacts in one deltaic progradational cycle. Coal seams are present in marginal-marine settings and herald a local/regional sea-level rise. The presence of the flanking barrier facies and a restricted interdistributary bay/interdeltaic lagoon with very long plant roots at the top points to sedimentation proceeding in tandem with plant growth. Plant roots and plant debris are abundant but identifiable plant remains have not yet been found.

PLANT COVER

Neighbouring the upper outcrop in Gromadzice, localities in Szewna and Podszkodzie villages, belonging to the same depositional systems, provided some plant remains. In Szewna only ferns were found: *Dictyophyllum(?) rydzewskii* and *Phlebopteris* sp. (Makarewiczówna, 1928). In nearby Podszkodzie, plants are preserved in sandstone, but indeterminate plant detritus predominates, which may indicate long-distance/high-energy transport (Makarewiczówna, 1928). The most frequent species are *Neocalamites lehmannianus, Nilssonia orientalis* and *Podozamites distans.* Among the rarer species are the cycadophytes *Nilssonia inouyei* and *Pterophyllum nathorsti,* ginkgophytes *Ginkgo sibirica*, *Ginkgoites taeniata* and *Ixostrobus siemiradzkii*, and conifer *Pityophyllum longifolium*. Ferns are absent. *Nilssonia* and *Podozamites* probably formed willow-like riparian thickets. The presence of *Ginkgoites* may indicate lush upslope forests (Krassilov, 2003). Accompanying the plant remains, hybodontid shark egg capsules (*Palaeoxyris muensteri*) suggest brackish environment and point to marine connections (Makarewiczówna, 1928).

In general, the Skłoby Formation deposits show marine/brackish marine influences. The Gliniany Las 1 borehole yielded dinoflagellate cysts (e.g., *Dapconidium priscum*). The Gliniany Las 1 and Mroczków-Kraszków 160 boreholes show a taphonomically biased predominance of bisaccate pollen grains over spores, characteristic for marine influenced sediments (Pieńkowski and Waksmundzka, 2009). Spores were produced by lycophytes (*Carnisporites spiniger, Apiculatisporis ovalis*, *A. parvispinosus*), including Sellaginellaceae (*Uvaesporites argenteaeformis*), and ferns (families

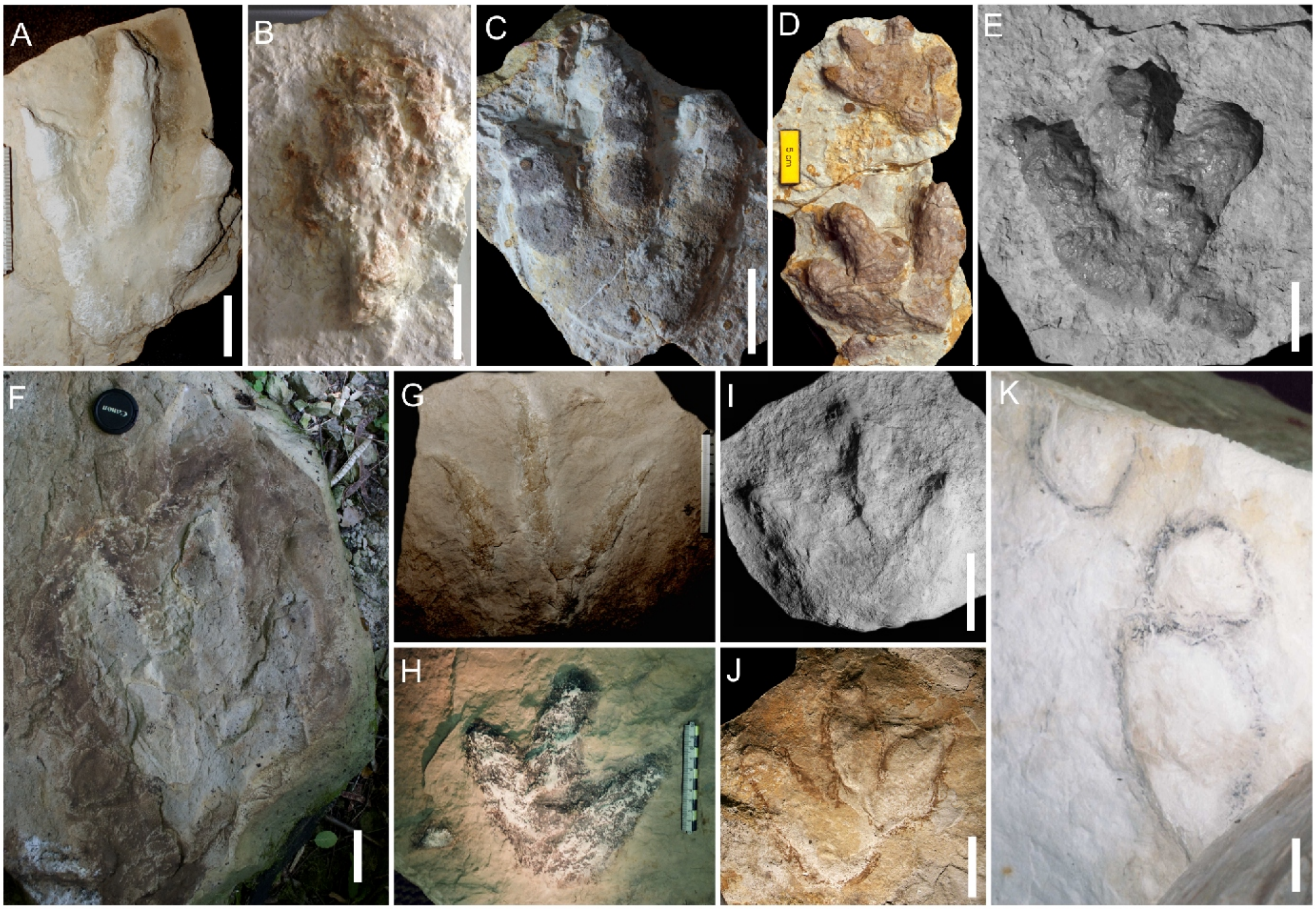

Fig. 14. Dinosaur track associations from the lower outcrop in Gromadzice, upper part of the Zagaje Formation, lower Hettangian (A–E) and Podole (F), upper outcrop in Gromadzice (G, H, K) and Szwarszowice site (I, J), Skłoby Formation, mid Hettangian

A – cf. *Eubrontes* isp.; **B** – *Otozoum* cf. *pollex;* **C–E** – *Moyenisauropus* isp.; **F** – cf. *Eubrontes* isp.; **G** – *Kayentapus* isp.; **H–J** – *Moyenisauropus* isp.; **K** – cf. *Parabrontopodus* isp.; scale bars: A–F, I, K – 5 cm; G, H – 10 cm

Cyatheaceae, Dipteridaceae, Dicksoniaceae, Matoniaceae, Schizaeaceae or Pteridaceae) preferring a humid habitat (Gliniany Las 1 borehole, Waksmundzka, 2014). In the Rozwady borehole (Rogalska, 1956) ~40 km N of Gliniany Las, spores confirmed the occurrence of bryophytes and of ferns (Matoniaceae, Osmundaceae, Marattiaceae). The registered gymnosperm pollen grains belong to Cheirolepidiaceae, Caytoniales, Ginkgoales and Cycadales. Bisaccate pollen grains of Podocarpaceae and other conifers are believed to have originated from local vegetation on higher terrain.

VERTEBRATE TRACKS

In the upper outcrop in Gromadzice, small sauropod tracks (small *Parabrontopodus*) were found in loose blocks and *in situ* (Fig. 14K), which represent distributary channel facies (Pieńkowski, 2006). Their presence in a deltaic environment is intriguing; perhaps the small size of the trackmaker is due to environmental constraints. Larger sauropod tracks are absent from this stratigraphic interval. It is also possible that their trackmaker was a diminutive form of early sauropod similar to *Ohmdenosaurus,* with an estimated length of 3–4 m, known from the Toarcian of Germany (Wild, 1978). Medium-sized semibipedal ornithischian tracks referred to *Moyenisauropus* (Fig. 14H–J) and small *Anomoepus*-like tracks are also present (Gierliński et al., 2001). Poorly preserved small to medium-sized (*Grallator*, *Anchisauripus*) and medium-sized to large (cf. *Eubrontes, Kayentapus*; Fig. 14) theropod tracks were also found in the Skłoby Formation exposure at the upper outcrop in Gromadzice (Gierliński and Niedźwiedzki, 2005; Niedźwiedzki, 2006).

The deltaic deposits of the Skłoby Formation exposed at Podole near Opatów (eastern part of HCM) revealed specimens of four dinosaur ichnotaxa: *Anchisauripus*, *Kayentapus*, small *Parabrontopodus*, and cf. *Anomoepus*. These finds confirmed that the deltaic (delta-plain) association of dinosaurs is characterized by the dominance of low-browsing thyreophorans accompanied by juvenile sauropods and medium-sized to large theropods (Niedźwiedzki and Pieńkowski, 2004). Recently collected dinosaur track material from the Podole site, containing a few theropod tracks (*Kayentapus*, cf. *Eubrontes*), is still under study (Fig. 14F).

Ornithischian dinosaur tracks similar to *Moyenisauropus* were also found in the Skłoby Formation at Szwarszowice near Ostrowiec Świętokrzyski (Niedźwiedzki et al., 2009). A few theropod tracks (*Grallator*, *Anchisauripus*) were also collected

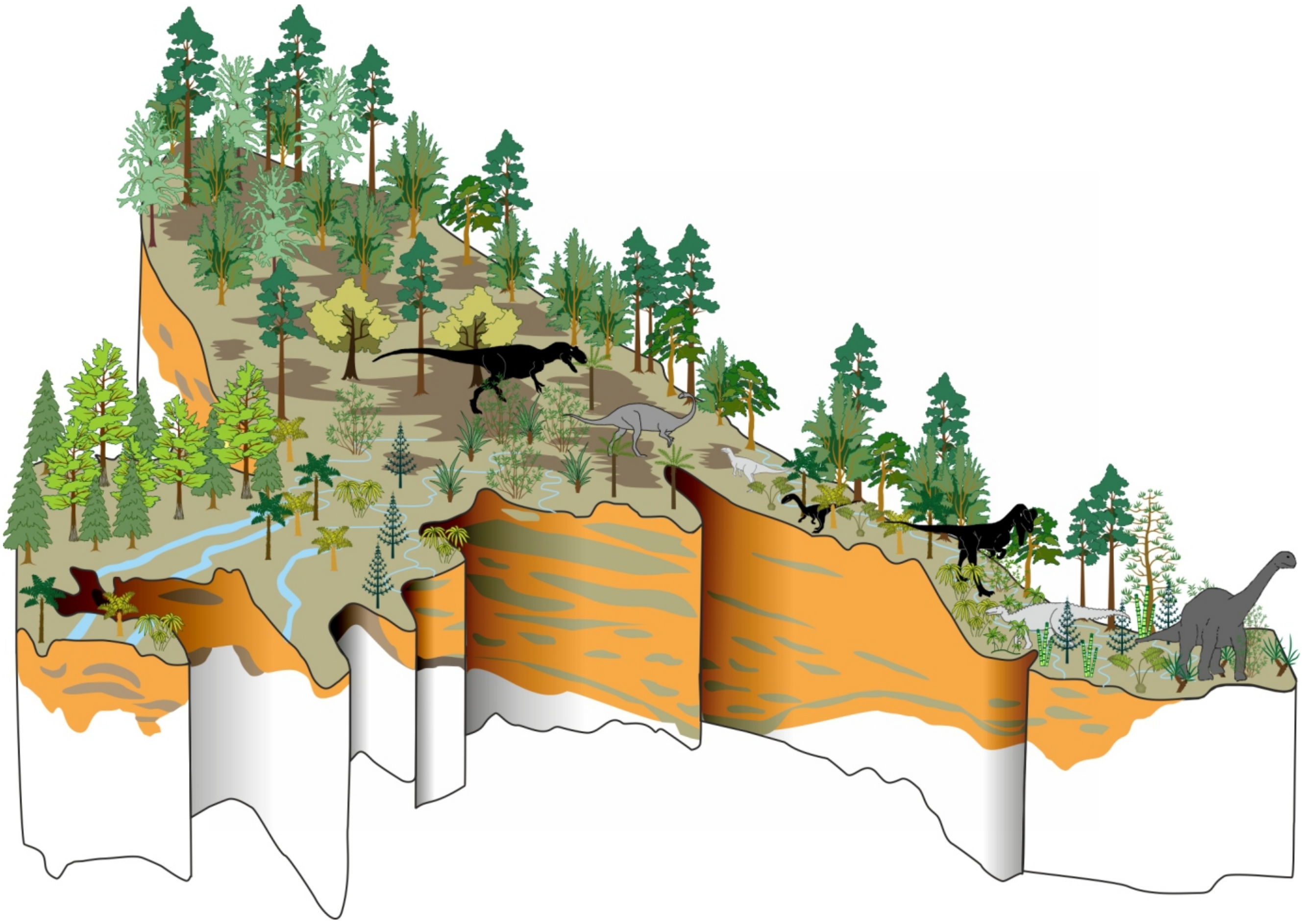

Fig. 15. Reconstruction of the Holy Cross Mountains (HCM) sedimentary subbasin, upper part of the Zagaje Formation (upper part of lower Hettangian, parasequence Ib), with reconstructed plant cover and the most characteristic dinosaurs

at the same locality. Both the lithological character and trace fossil content suggest that the Szwarszowice dinosaur ichnorecord is similar to track assemblage the upper outcrop in Gromadzice (Fig. 14I, J).

Middle Hettangian deltaic sediments exposed at the upper outcrop in Gromadzice, Podole and Szwarszowice sites yield many specimens of ornithischian tracks and a diverse assemblage of dinosaur tracks. These three tracksites reveal a very similar and characteristic deltaic/coastal dinosaur ichnofauna and confirm the existence of the characteristic ichnoassemblage (Gierliński and Pieńkowski, 1999) dominated by *Moyenisauropus* and *Anomoepus*, with small sauropod and various theropod tracks (*Moyenisauropus–Anomoepus–Parabrontopodus–Kayentapus–Eubrontes* ichnoassemblage). A few of the *Moyenisauropus* trackways from the upper outcrop in Gromadzice indicate both bipedal and quadrupedal locomotion.

LATE HETTANGIAN, PRZYSUCHA ORE-BEARING FORMATION, PARASEQUENCES IG–IK

ENVIRONMENTAL CONTEXT

Above the maximum flooding surface in the Skłoby Formation, a progradational, regressive highstand system tract (HST) is developed, comprising five parasequences (Ig, Ih, Ii, Ij Ik) belonging to the Przysucha Ore-bearing Formation of a late Hettangian age, as indicated by sequence stratigraphy and palynomorph assemblage (Pieńkowski 2004a; Krupnik et al. 2014). These parasequences are generally characterized by lower-energy, more shallow-water depositional systems than parasequences Ic–f of the Skłoby Formation. Barrier-lagoon depositional cycles dominate, for example in the Gliniany Las and Zapniów exposures (Pieńkowski and Gierliński, 1987; Pieńkowski 2004a; Niedźwiedzki and Pieńkowski, 2016) and recently discovered Borkowice tracksite (Pieńkowski and Niedźwiedzki, 2021). Fluvial-dominated deltaic cycles are also common, particularly on the eastern and northern margins of the subbasin (Pieńkowski, 2004a). An offshore, open-basin depositional subsystem is restricted to the narrow central part of the HCM subbasin. Particularly widespread are lagoonal and embayment deposits represented by mudstone containing sideritic clay forming characteristic ore-bearing horizons. The lagoons were broad but shallow. Iron compounds were delivered from vast marsh/swampy areas developed around lagoonal shores. In the past these ore-bearing horizons were mined for of iron ore, and clay and mudstone are still exploited in places as sources of clay minerals (e.g., Zapniów, Borkowice). In the HCM subbasin there are usually three ore-bearing horizons, pointing to three episodes of widespread development of lagoonal depositional subsystems. In places closer to the subbasin centre, connections with the open basin situated to the north-west were wider, which led to the formation of wider embayments, observed in the upper parts of the Zapniów and Borkowice exposures (Niedźwiedzki and Pieńkowski, 2016; Pieńkowski and Niedźwiedzki, 2021). In these embayments,

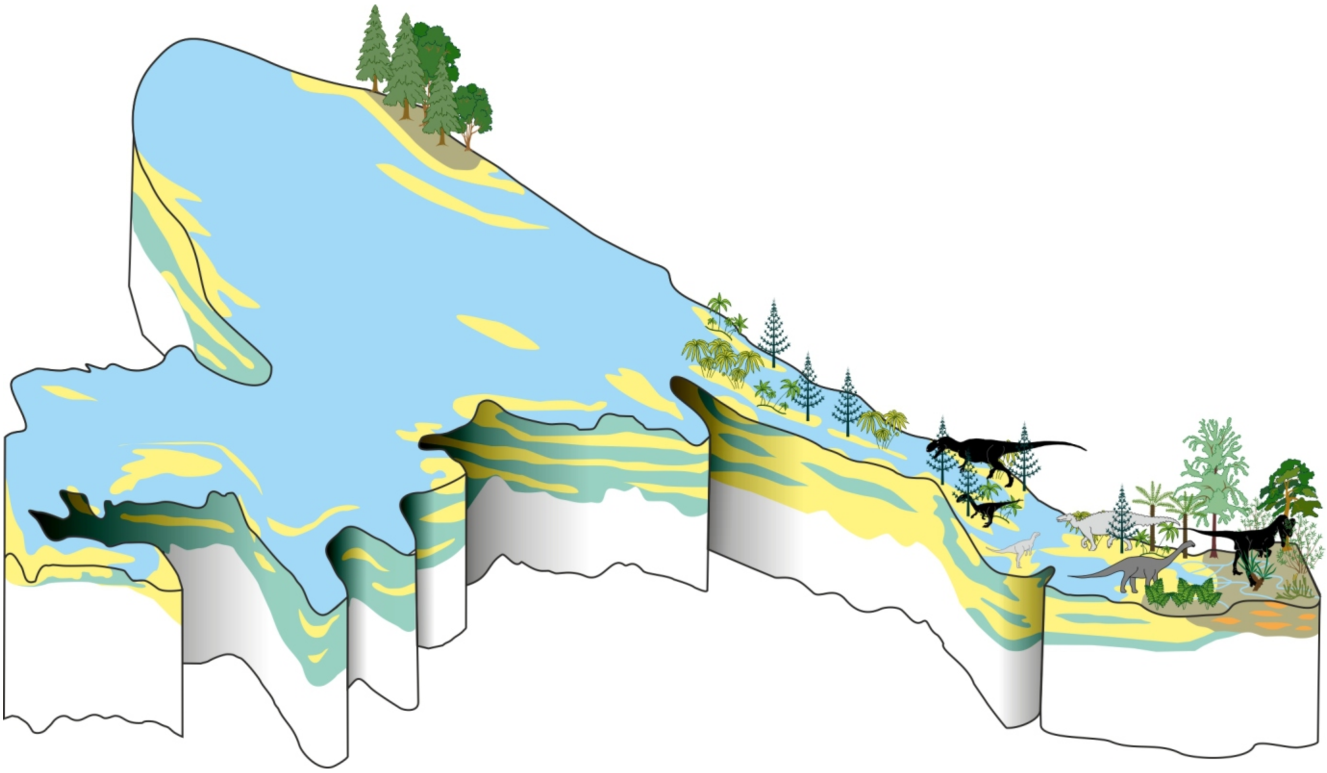

Fig. 16. Reconstruction of the Holy Cross Mountains (HCM) sedimentary subbasin, Skłoby Formation (middle Hettangian, parasequences Ic–If), with reconstructed plant cover and the most characteristic dinosaurs

wave-generated structures are more common, siderite bands and palaeosoils are less frequent, and the marine influence is more prominent, supported by brackish-marine fauna (Pieńkowski, 2004a). On the other hand, temporarily emerged barriers and periodically drying lagoonal clays provided a good environment both for dinosaur activity and for the preservation of their tracks (Pieńkowski and Niedźwiedzki, 2021). The lagoons and embayments were subject to dynamic sedimentation processes, during which they quickly filled with sediment of migrating barriers or deltas at river mouths. The Przysucha Ore-bearing Formation occurs only in the HCM subbasin, pointing to the general isolation of this subbasin in the late Hettangian.

PLANT COVER

Rare late Hettangian plant fossils were recorded from the northeastern margin of the HCM. Raciborski (1891a) described single shoots of *Neocalamites lehmannianus* from sideritic nodules from Mychów, and a huge accumulation of this species from gray shale above a thin coal seam in Miłków, which suggests that this species was a coal generator. The trace fossil *Helminthoidichnites* isp. on decaying shoots may indicate the presence of waterbodies with which sphenopsids were associated.

Plant remains are better known from the northern margin of the HCM, but the collected specimens were never properly documented and are lost. Only cycadophyte remains (*Bennettites raciborskii*) were reported from the lowest third ore-bearing horizon at Chlewiska near Szydłowiec (Kuźniar, 1924). More plant remains were found in the second ore-bearing horizon at this locality. Sphenopsid *Neocalamites lehmannianus*, matoniaceous ferns *Phlebopteris braunii* and *P. muensteri*, the dipteridaceous fern *Dictyophyllum acutilobum,* gingkophyte *Baiera muensteriana* and conifer *Palissya sphenolepis* correspond well with the floras of banks of numerous shallow water basins. A similar assemblage was recorded from Dźwiertnia near Niekłań, also from the same horizon. Here, besides *Neocalamites lehmannianus*, matoniaceous ferns *Phlebopteris brauni* and *P. muensteri*, the dipteridaceous fern *Dictyophyllum exile* and cycadophyte *Nilssonia elongata* were found (Kuźniar, 1923). This colonizing assemblage, enriched with some ginkgophytes like *Czekanowskia* sp. (Gielniów-Skarżysko area: Karaszewski and Kopik, 1970) and *Ginkgoites* sp. and *Czekanowskia hartzii* (Studzianna borehole: Barbacka et al., 2014), probably was associated with deltaic and coastal environments.

The importance of ferns in the late Hettangian vegetation is indicated by the palynological record. The lower part of the Przysucha Ore-bearing Formation is rich in ferns, as attested by data from the northern margin of the HCM subbasin (Gliniany Las 1, Mroczków-Kraszków 160 boreholes, see Pieńkowski, 2004a; Waksmundzka, 2014; Mroczków Gościnny borehole, see Rogalska, 1956; Studzianna borehole, see Krupnik et al., 2014). The spores confirm the occurrence of bryophytes (*Stereisporites* sp., *Rogalskaisporites cicatricosus*), lycophytes or bryophytes (*Limbosporites lundbladii*), lycophytes (*Apiculatisporis parvispinosus*, *Uvaesporites argenteaeformis*, *Lycopodiacidites* spp., *Densosporites* spp.), sphenophytes (*Calamospora tener*, *Concentrisporites* spp.), and ferns from the families Cyatheaceae and/or Dicksoniaceae and/or Dipteridaceae (*Deltoidospora australis, D. crassexina, D. toralis, Cyathidites* sp.), ?Hymenophyllaceae (*Foraminisporis* spp.), Dipteridaceae (*Conbaculatisporites mesozoicus*), ?Schizaeaceae (*Contignisporites problematicus*), Marattiaceae (*Marattisporites* spp.), Matoniaceae (*Concavisporites tumidus, C. toralis*, *C. polygonalis*) and Osmundaceae (*Osmundacidites* sp.). Gymnosperms were less diverse; noted were pollen grains of Caytoniales (*Vitreisporites* spp.), Ginkgoales (*Monosulcites minimus*), Cycadales (*Cycadopites* sp., *Chasmatosporites*

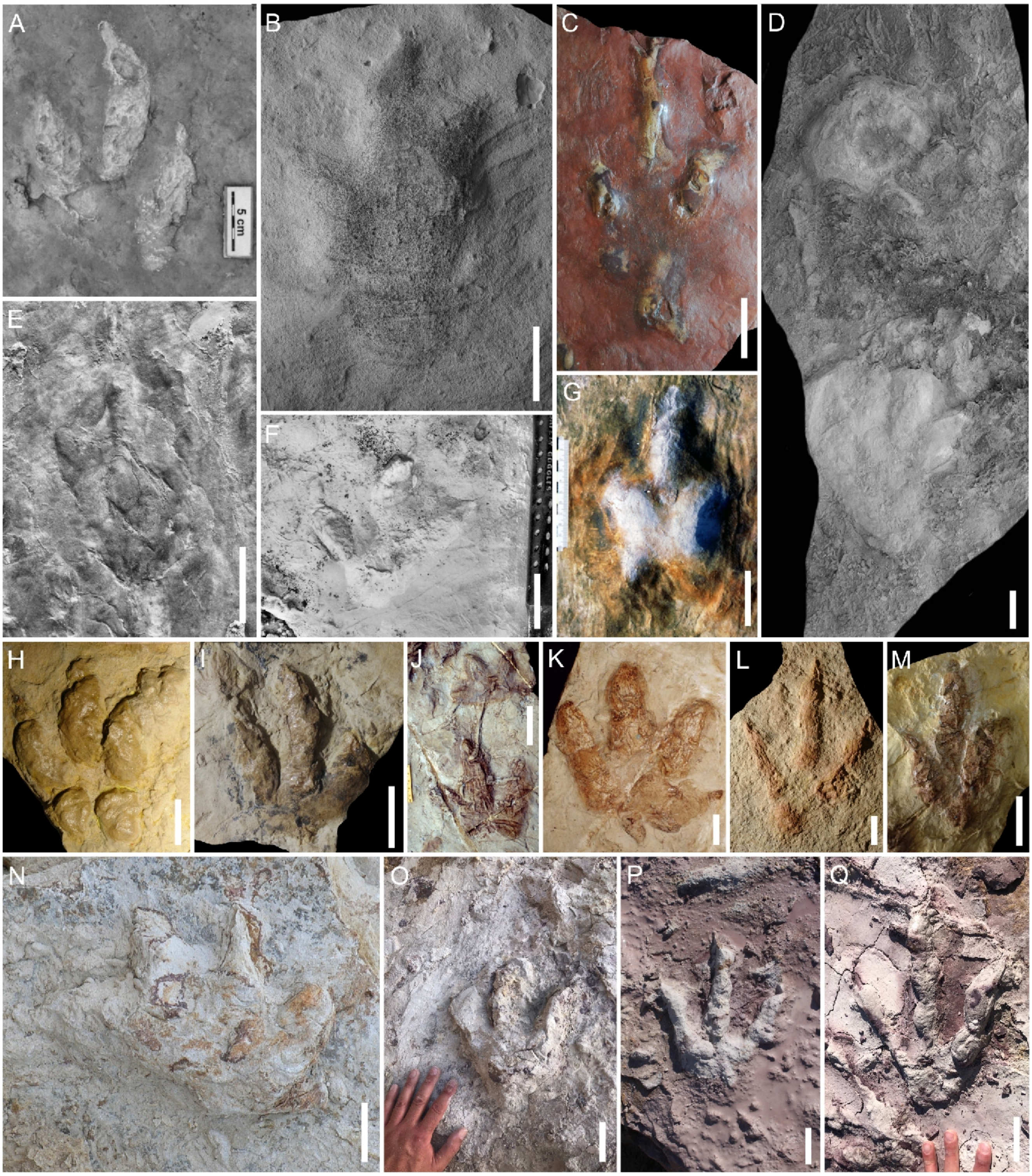

Fig. 17. Dinosaur track associations from the Jakubów (A), Zapniów (B–G), Gliniany Las (H–M) and Borkowice (N–Q) sites, Przysucha Ore-bearing Formation, upper Hettangian

A – cf. *Anchisauripus* isp.; **B**, **C**, **G** – *Anchisauripus* isp.; **D** – cf. *Tetrasauropus* isp.; **E** – *Grallator* isp.; **F** – *Anomoepus* isp.; **H** – cf. *Atreipus* isp.; **I**, **J** – *Anomoepus* isp.; **K** – *Moyenisauropus* isp.; **L** – *Kayentapus* isp.; **M** – *Grallator* isp.; **N** – *Moyenisauropus* isp. (manus); **O** – *Moyenisauropus* isp. (pes); **P**, **Q** – cf. *Kayentapus* isp.; scale bar – 5 cm *apertus*), Podocarpaceae and other conifers or seed ferns (bisaccate pollen grains).

In the Gliniany Las 1 (Pieńkowski and Waksmundzka, 2009), Mroczków-Kraszków 160 (Pieńkowski, 2004a; Waksmundzka, 2014) and Studzianna (Krupnik et al., 2014) boreholes the upper Hettangian palynofacies are characteristic for wide shallow bays or lagoons, confirmed by the presence of acritarchs.

VERTEBRATE TRACKS

Most of the known dinosaur tracks of the upper Hettangian Przysucha Ore-bearing Formation come from a small quarry of a farmer situated in Gliniany Las village near Mniów (Gierliński and Pieńkowski, 1999) and from the recently discovered, much richer Borkowice clay pit exposure (Fig. 17; Pieńkowski and Niedźwiedzki, 2021). The first Polish dinosaur tracks were described from Gliniany Las more than fifty years ago (Karaszewski, 1969). Sandstone with mudstone and claystone intercalations occurring at both the Zapniów and Borkowice sections have been assigned to the middle–upper part of the Przysucha Ore-bearing Formation (specifically to a barrier sediments, separating the middle and upper siderite-bearing horizons). In slightly younger or coeval Gliniany Las (below the upper siderite-bearing horizon), most of the dinosaur tracks come from two (1–3 cm thick) sandstone beds of back-barrier origin, several centimetres above a sandstone bed indicating the top of the barrier. Tracks occur as true tracks, undertracks as well as natural casts preserved on the bottom surface of the overlying bed; they include an *Anomoepus–Moyenisauropus–Eubrontes–Kayentapus–Anchisauripus–Grallator* ichnoassemblage (Gierliński and Pieńkowski, 1999). Similar track assemblages have been described from Jakubów (Fig. 17A; Gierliński and Pieńkowski, 1999) and Zapniów (Fig. 17B–G; Niedźwiedzki and Pieńkowski, 2016), the latter also containing prosauropod footprints. A recently discovered dinosaur track assemblage from Borkowice (located 6 km east of Zapniów and representing the same stratigraphic horizon) represents the best-preserved the Early Jurassic dinosaur tracks described so far from Poland (Fig. 17N–Q). The quality of preservation of the tracks from Borkowice is equal to that of the best-known discoveries from North America, South Africa, Greenland, and China (personal observ.). They are in such good condition that most of them show three-dimensional natural casts of dinosaur feet, on which anatomical features and impressions of scaly skin are preserved in unusual detail. For such a state of preservation to be possible, a very special sequence of sedimentary/taphonomic events had to take place in a very short time. The collection also includes an ethological record of dinosaurs. So far, several hundred dinosaur tracks representing at least seven different species of these animals have been collected and secured, ongoing studies are in progress, and the prospect of discovering new finds is high (Pieńkowski and Niedźwiedzki, 2021). The Zapniów and Borkowice assemblages are similar to those older ones known from the lower and upper outcrops in Gromadzice (upper Zagaje and Skłoby formations, although they show traces of somewhat more derived ornithischian and theropod and sauropodomorph traces (cf. *Tetrasauropus*), absent from Gromadzice. *Tetrasauropus*-like track was found in a small, no longer existent artificial outcrop of the Przysucha Ore-bearing Formation in the town of Starachowice (G. Gierliński, 2021, personal comm.). The described cf. *Tetrasauropus* from Zapniów (Fig. 17D) and Starachowice (present also in Borkowice) is the first unequivocal evidence of basal sauropodomorphs in the late Hettangian of the HCM, and is a new record of this ichnotaxon in the Early Jurassic of Poland (see Niedźwiedzki, 2011). Interestingly, in Borkowice there are two different assemblages of dinosaur footprints, separated by several-metre-thick barrier deposits (Pieńkowski and Niedźwiedzki, 2021). The lower assemblage is similar to the one observed in the upper outcrop in Gromadzice, while the upper one is closer to the assemblage known from Gliniany Las. At the current state of knowledge, it is difficult to decide whether this difference is related to evolutionary changes; if so, it occurred in a relatively short time (probably no more than 100–200 ky, assuming the inferred duration of the late Hettangian: Hesselbo et al., 2020). Alternatively, these changes could be related to local environmental factors, although all those deposits generally represent a similar deltaic-lagoonal shoreline habitat which was invaded by low-browsing herbivores such as ornithischian trackmakers of *Anomoepus* and *Moyenisauropus,* and predators such as theropod trackmakers of *Grallator, Anchisauripus, Eubrontes* and *Kayentapus.* In general, the track-bearing strata of the Przysucha Ore-bearing Formation are dominated by various ornithischian tracks (Fig. 17H–K). The smallest were referred to *Anomoepus* sp., *Anomoepus curvatus* and *A. scambus*. They were left by early, clearly bipedal ornithischians, probably similar in size and body proportions to *Lesothosaurus*. The assemblage also has medium-sized quadrupedal trackways described as *Anomoepus pienkovskii* (some specimens with metatarsal impressions: Niedźwiedzki and Niedźwiedzki, 2001, 2004; Niedźwiedzki, 2003) and the large bipedal *Moyenisauropus karaszevskii* (Gierliński, 1991; Gierliński and Pieńkowski, 1999), both of supposed thyreophoran origin (Gierliński, 1999). The pedal pattern of *A. pienkovskii* allowed its trackmaker to be sought among the moderate-sized, early thyreophorans such as *Emausaurus*, although this dinosaur comes from the lower Toarcian strata of NE Germany (Haubold, 1990). Gierliński (1995a) also entertained the idea that *A. pienkovskii* may have been left by juvenile trackmakers of *M. karaszevskii.* Other tracks, rare in this assemblage, such as cf. *Atreipus* (Fig. 17H), are suspected to be of ornithischian origin and made by a heterodontosaurid (Gierliński and Niedźwiedzki, 2002). Theropod dinosaur tracks in the Przysucha Ore-bearing Formation are relatively rare in Gliniany Las and Zapniów (Fig. 17L, M) but abundant in Borkowice (Fig. 17P, Q). Small theropod tracks have been identified as *Grallator*, left by a theropod similar to *Syntarsus*. Medium-sized to large *Anchisauripus*- or *Eubrontes*-like and *Kayentapus* forms (including large ichnites ~40 cm long) were also found (Gierliński, 1990; Gierliński and Niedźwiedzki, 2005; Niedźwiedzki and Pieńkowski, 2016; Pieńkowski and Niedźwiedzki, 2021). Numerous probable theropod tracks have only the distal part of the digits appearing in the impression (subdigitigrade); they were referred to *Carmelopodus*, tracks of a small theropod dinosaur (=*"Grallator* (*Grallator*) *zvierzi"* according to Gierliński, 1991). Other very small prints presumably left by a diminutive or baby theropod were determined as cf. *Stenonyx* (Gierliński and Niedźwiedzki, 2002). The maker of small tracks *Plesiornis pilulatus* may have been of avian affinity (Gierliński, 1996; Gierliński and Pieńkowski, 1999).

The finds from Zapniów and Borkowice suggest similarities between dinosaur associations living in marginal-marine environments (delta-plain and foreshore-barrier/lagoon lithofacies), containing low-browsing thyreophorans accompanied by sauropodomorphs and theropods (usually small to mid-sized, but sometimes also larger ones). The presence of ornithischian tracks (*Anomoepus, Moyenisauropus*) suggests their prominent role as a major component of middle–late Hettangian dinosaur faunas in marginal-marine environments dominating in the region (Figs. 18 and 19). Specifically, during late Hettangian times, dinosaur tracks occur in foreshore-barrier-lagoon litho-

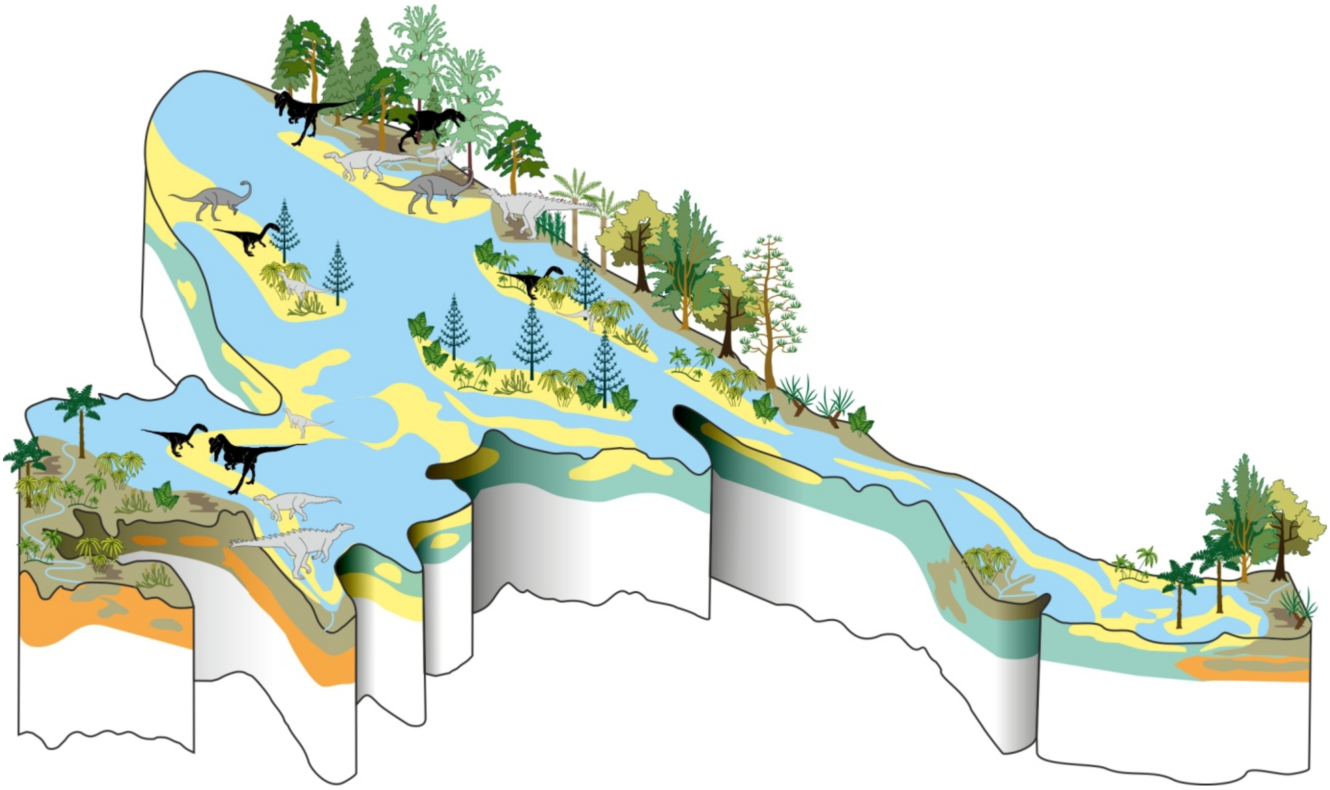

Fig. 18. Reconstruction of the Holy Cross Mountains sedimentary subbasin, lower part of the Przysucha Ore-bearing Formation (upper Hettangian, parasequences Ig–Ik), with reconstructed plant cover and the most characteristic dinosaurs

facies, which probably represented an environment frequented by these animals roaming (likely long-shore wandering) and feeding opportunities (Niedźwiedzki and Pieńkowski, 2016; Pieńkowski and Niedźwiedzki, 2021).

EARLY SINEMURIAN, LOWER OSTROWIEC FORMATION, SEQUENCE II

ENVIRONMENTAL CONTEXT

The end of progradational sedimentation of the highstand system tract of depositional sequence I (Przysucha Ore-bearing Formation) is followed by a regional erosion surface. In certain places (particularly in the east), erosion removed sediments of the underlying parasequences. This erosional surface is associated with a substantial fall in sea level, and forms a sequence boundary.

Initial sediments above the sequence boundary forming parasequence IIa are represented by medium- to coarse-grained, trough cross-bedded sandstone lithofacies. The next parasequence, IIb, starts from the transgressive surface (ravinement) of depositional sequence II. The transgression was rapid; in the whole area, facies of a nearshore depositional system overlie parasequence IIa. Parasequence IIb and subsequent parasequence IIc are composed of deposits representing a nearshore depositional system, so these sediments are not promising for studies of terrestrial fossils.

PLANT COVER

The environment was not favourable for the development of a later succession stage vegetation (Fig. 20). Two fern species, *Hausmania forchhammeri* and *Phlebopteris* sp. (Makarewiczówna, 1928), from Jędrzejowice (northeastern margin of HCM subbasin) probably colonized disturbed habitats. More stable associations developed at Studzianna during this time, with *Neocalamites* sp., *Cladophlebis* sp. *Pachypteris* sp. *Pseudotorellia nordenskioeldii* and *Phoenicopsis insolita*. *Pachypteris* could be associated with an estuarine zone (Barbacka et al., 2014). The occurrence of *Phoenicopsis* may indicate a lowland climax forest (Krassilov, 2003).

More diverse assemblages were confirmed by spores from the Mroczków-Kraszków 160 borehole (Pieńkowski, 2004a, Waksmundzka, 2014): Bryophytes (*Retusotriletes mesozoicus*), lycopsids (*Apiculatisporis ovalis, A. parvispinosus*) and ferns from the families Cyatheaceae/Dipteridaceae/Dicksoniaceae (*Deltoidospora australis*, *D. crassexina*, *D. toralis*), Cyatheaceae (*Zebrasporites interscriptus*), Dipteridaceae (*Conbaculatisporites mesozoicus, C. spinosus*), Dicksoniaceae (*Cibotiumspora jurienensis*), Matoniaceae (*Dictyophyllidites crassexinius* = *Concavisporites crassexinius*, *Dictyophyllidites mortoni*) and Osmundaceae (*Osmundacidites wellmanii*, *Baculatisporites opressus*).

Like the ferns, Taxodiaceae (*Cerebropollenites*) may reflect a type of vegetation associated with an unstable and early developing ecospace (Abbink, 1998). Other conifers or seed ferns having bisaccate pollen grains indicate a marine influence due to their quantitative predominance over spores. Marine acritarchs and dinoflagellate cysts were also noted (Pieńkowski, 2004a). The palynofacies are characteristic mainly for a shoreface-foreshore complex mixed with lagoon, or for shoreface-foreshore mixed with an offshore brackish marine environment (Pieńkowski and Waksmundzka, 2009). It should be noted that the lowermost part of the Ostrowiec Formation, of inferred latest Hettangian/earliest Sinemurian age, is built of sandstone of fluvial origin (Pieńkowski, 2004a) and that no palynomorphs have been described from this part of the section.

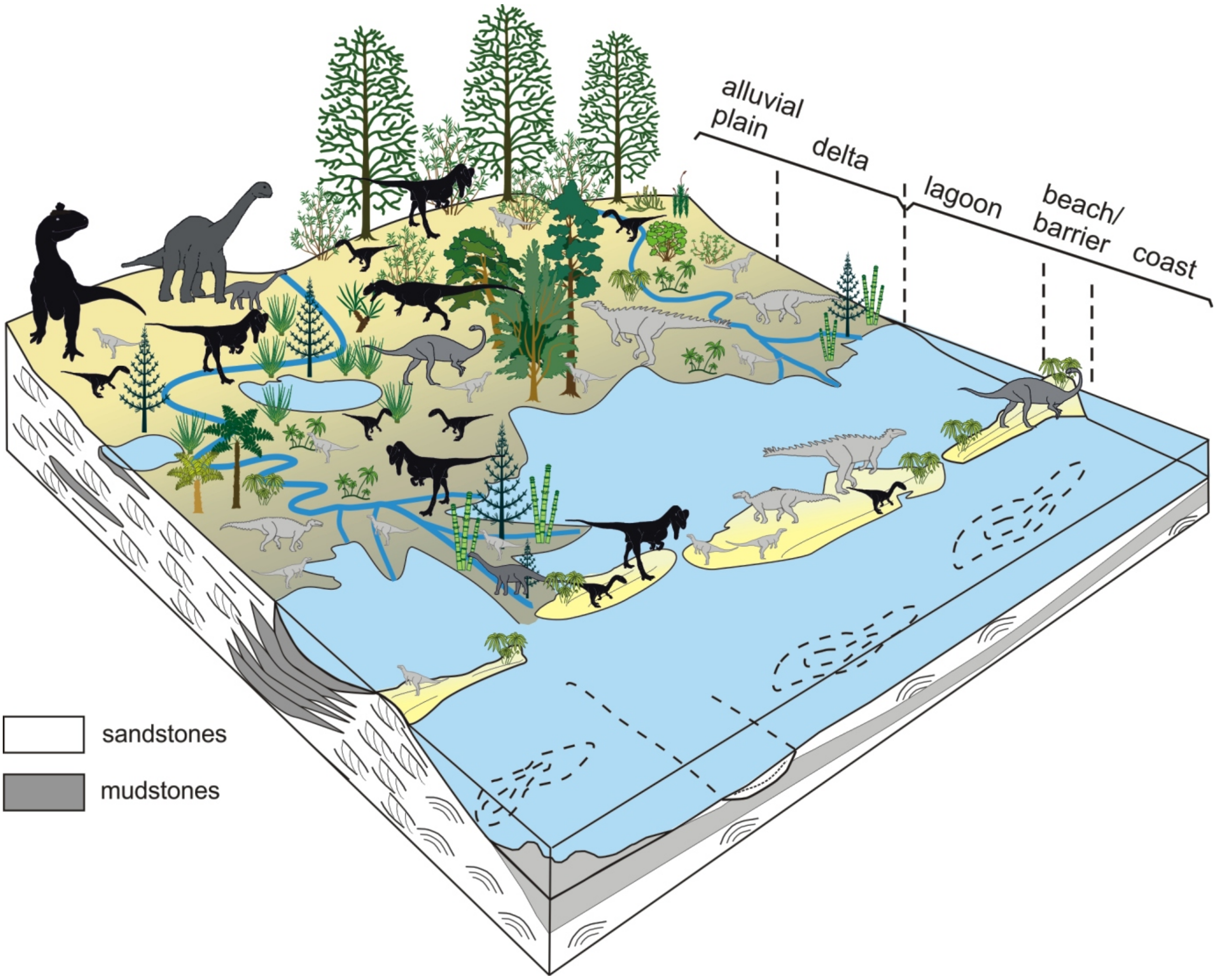

Fig. 19. Spatial distribution of dinosaur ichnoassemblages in the Hettangian of the Holy Cross Mountains, *Parabrontopodus–Anchisauripus–Eubrontes–Kayentapus–Megalosauripus* ichnoassociation typical for meandering river plain and *Anomoepus–Moyenisauropus–Kayentapus–Eubrontes–Anchisauripus–Grallator* ichnoassociation typical for deltaic-lagoonal shoreline habitats, both associated with different types of plant cover

VERTEBRATE TRACKS

Tracks are rare in the Ostrowiec Formation, known only from the lowermost, alluvial/deltaic part (Fig. 20). In the lower Sinemurian deposits exposed in the Starachowice outcrop, three poorly preserved tracks of small to medium-sized theropods, assigned to cf. *Grallator* and cf. *Anchisauripus*, were found (Niedźwiedzki et al., 2009). In another locality with a relatively large exposure of the Ostrowiec Formation, an active sandstone quarry near Żarnów ("Żarnów II"), a few isolated theropod tracks (cf. *Kayentapus*, *Anchisauripus*) and ornithischian tracks (cf. *Anomoepus*) were observed and collected, but only one, the first specimen from this site, has been described so far (see Niedźwiedzki et al., 2009). Two new sites with dinosaur tracks were discovered in 2017 and 2018 in the Old Kunów quarry near Ostrowiec Świętokrzyski, where the marginal-marine lower part of the Ostrowiec Formation is exposed. The Kunów tracksite is dominated by small tridactyl tracks (length 10–15 cm) that are approximately as long as wide and have characteristic high divarication angles between the outer digits. They are temporarily classified as indeterminate early ornithischian tracks (cf. *Anomoepus*); they add to the dinosaur ichnodiversity of the Ostrowiec Formation.

LATE SINEMURIAN–EARLY PLIENSBACHIAN, UPPER OSTROWIEC FORMATION–GIELNIÓW FORMATION, SEQUENCES III–V

ENVIRONMENTAL CONTEXT

Higher in the profile, in the younger Lower Jurassic strata of the HCM subbasin, three sequences (III, IV, V) of transgressive/regressive deposits represent a variety of coastal (barrier-lagoon, deltaic, foreshore) and shallow marine sediments. In the lower Pliensbachian part of this profile, the so-called Chmielów clays that contain a rich macroflora are located (Karaszewski, 1960, 1965).

Depositional sequence III, belonging still to the Ostrowiec Formation, begins with conspicuous erosion (sequence boundary) and ensuing fluvial sedimentation. In some places, a significant portion of underlying parasequence IIc has been eroded.

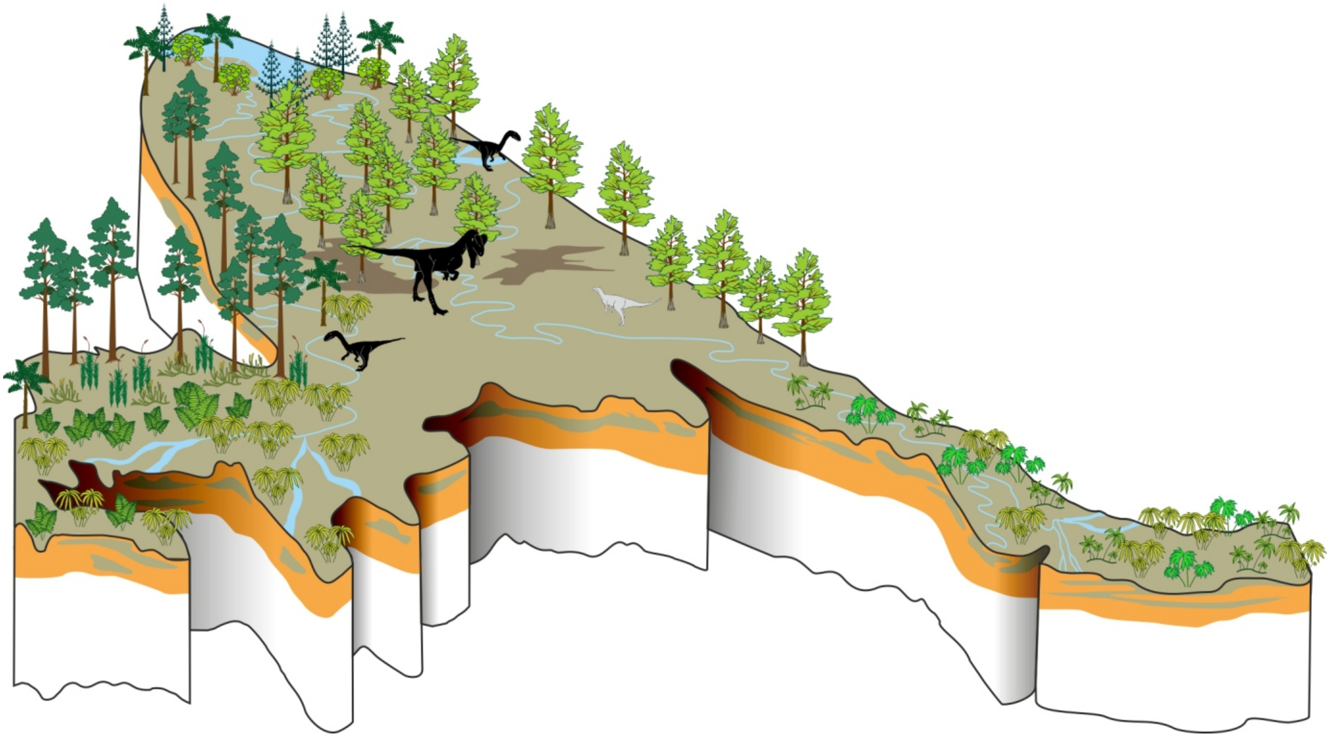

Fig. 20. Reconstruction of the Holy Cross Mountains (HCM) sedimentary subbasin, lower part of the Ostrowiec Formation (lower Sinemurian, sequence II), with reconstructed plant cover and the most characteristic dinosaurs

The development of the transgressive surface of depositional sequence III depended on the local sedimentation. In areas influenced by intense river discharge, the transgressive sediments of parasequence IIIb commence with a delta depositional system. In areas with no or low river discharge the transgression almost immediately induced a nearshore depositional system at the base of parasequence IIIb. The maximum extent of the subbasin (maximum flooding surface) and highest share of the offshore depositional subsystem are associated with parasequence IIIc. This parasequence is built largely of brackish-marine deposits (a mostly heterolithic facies) with a very abundant and diverse ichnofauna. Above the maximum flooding surface is the highstand system tract composed of the upper part of parasequence IIIc and parasequences IIId and IIIe. Sequence III falls within the *Horstisporites planatus* megaspore zone (late Sinemurian–Pliensbachian age: Marcinkiewicz, 1971; Marcinkiewicz et al., 2014); based on sequence stratigraphy correlation, its age can be narrowed to the late Sinemurian.

Depositional sequence IV forms part of the Gielniów Formation and is dominated by the following depositional systems: brackish-marine, nearshore, deltaic, barrier-lagoon, and in the lowermost part alluvial. Initial parasequence IVa (still of a latest Sinemurian age) is preceded by erosion (sequence boundary) associated with regional regression. Alluvial and deltaic deposits dominate. The next parasequence, IVb, starts with rapid and widespread transgression traceable in the entire Polish Basin (Pieńkowski, 2004a; Barth et al., 2018), which created a ravinement or quickly inundated the area. This parasequence is generally built of offshore-shoreface deposits, but later in some areas a very conspicuous and rapid delta progradation occurred. Development of the delta system ended deposition of parasequence IVb. The flooding surface of parasequence IVc reinstated basinal conditions in the HCM subbasin and led to the development of the marine offshore-shoreface depositional subsystems. The maximum flooding surface of sequence IV occurs in this parasequence. Offshore mudstone and heterolithic strata near this surface show a marine character associated with the appearance of marine bivalves and trace fossils such as *Teichichnus* and *Diplocraterion parallelum*, indicating marine or almost marine salinity (mesohaline conditions). Also in the western margin of the HCM, marine or brackish-marine deposits with foraminifera mark pronounced marine influences within the succession identified as lower Pliensbachian (Jurkiewiczowa, 1967). The strata associated with the maximum flooding surface are followed by a progradational nearshore depositional succession, but no facies shallower than a shoreface subsystem were recorded. Development of the shoreface depositional system was soon interrupted by the next flooding surface of parasequence IVd, which briefly reinstated offshore basinal conditions in the whole area, again soon followed by a shoreface or lagoonal-deltaic depositional system. Sequence IV marks the most pronounced marine influence in the HCM subbasin. Sequence IV deposits still fall within the *Horstisporites planatus* megaspore zone (late Sinemurian–Pliensbachian age, Marcinkiewicz, 1971; Marcinkiewicz et al., 2014).

The beginning of deposition of sequence V is associated with a widespread fall in sea level associated with subaerial erosion at the IV/V sequence boundary. The erosional, regressive period must have been quickly followed by transgression, as the overlying deposits are generally thin and represent not an alluvial but a delta-distributary depositional subsystem. The distributary facies are covered by the transgressive surface of sequence V. The rapid transgression quickly reinstated marine sedimentation, with rich and diversified trace fossils. The transgressive system tract (TST) deposits are very thin, and the sequence V maximum flooding surface is situated several metres above the transgressive surface across the whole HCM subbasin. The maximum flooding sediments contain an assemblage of relatively rich and diversified marine bivalves such as *Pleuromya forchhammeri*, *Nuculana (Dactryomya) zieteni* and

Pronoella cf. *elongata* found in the Szydłowiec borehole (Kopik, 1962, 1964). The maximum flooding sediments also contain *Diplocraterion parallelum*, pointing to marine influences. There is lateral replacement of marine facies by embayment/deltaic facies in sequences IV and V in part of the subbasin (Jagodne–Szydłowiec–Budki section; Pieńkowski, 2004a). Above the maximum flooding surface, continuous regression of parasequence Vb led to the development of a barrier-lagoon depositional system topped by a delta depositional system. The age of depositional sequence V deposits falls within the *Horstisporites planatus* megaspore zone (late Sinemurian–Pliensbachian age; Marcinkiewicz, 1971; Marcinkiewicz et al., 2014). The bivalves found in this sequence point to early Pliensbachian age (Kopik, 1962, 1964). The sequence V deposits belong to the upper part of the Gielniów Formation.

PLANT COVER

Clay pits in the Chmielów area provided a diverse assemblage of fossil plants (Figs. 21–23; Raciborski 1891a, b, 1892a, b; Makarewiczówna, 1928). Unfortunately, these artificial exposures are now overgrown, and their exact collection sites and stratigraphic horizons can only be inferred. Assuming the significant thickness of ceramic clays (most likely subsequently kaolinized during the Paleogene), lithological characteristics and content of the flora, the Chmielów clays should be correlated with a thick, relatively homogenous succession of lagoonal clays containing floral remains, belonging to the upper part of the lower Pliensbachian (sequence V), which are known from the Jagodne 1 borehole, located ~30 km NW of Chmielów (Pieńkowski, 2004a). Consequently, the stratigraphic horizon of plant-bearing clay lies probably within the uppermost part of the lower Pliensbachian (Gielniów Formation, sequence V: Pieńkowski, 2004a). The preliminary palynological analysis of the Chmielów clays presented here does not contradict this age estimation. In some beds, detritus of numerous indeterminable plants predominates and may indicate high-energy or long-distance transport of plant remains, but among the detritus are also some better-preserved single specimens. Hybodontid shark egg capsules (*Palaeoxyris muensteri*) accompany the plant remains (Makarewiczówna, 1928), pointing to marine influences in a lagoonal environment (Pieńkowski, 2004a).

Different plant communities from various environments contributed to the fossil plant assemblage deposited in a lagoonal basin of the Chmielów area (Raciborski, 1891a, 1892a; Makarewiczówna, 1928). The macrofloristic data are supplemented and expanded by recent palynological study of these clays. Gymnosperms predominate, particularly *Czekanowskia rigida* and *Podozamites lanceolatus*. Woody wetland forests of *Czekanowskia* trees (*C. rigida, C. setacea*, *Ixostrobus siemiradzkii*) probably dominated the community in surrounding deltaic settings (Figs. 21J and 22A). In some areas *Czekanowskia* was accompanied or locally replaced by conifers of *Pityophyllum* (*P. angustifolium, P. longifolium*), forming bog forests. *Nilssonia– Podozamites (N. acuminata, N. orientalis, N. simplex, P. angustifolius, P. distans, P. gramineus, P. lanceolatus, P. stobieckii*), willow-like riparian thickets, likely occurred along banks of distributary channels (Figs. 21D, G and 22B). The presence of upslope mesic forests is confirmed by the occurrence of ginkgoaleans (*Ginkgo digitata, G. sibirica, Ginkgoites* sp.; Fig. 21H, I). Conifers *Brachyphyllum* sp. (Fig. 22D), *Cycadocarpidium erdtmanii* (Fig. 22C), *Palissya* sp., *Schizolepis braunii, S.* cf. *moelleri* and *S. follinii* probably formed mesophytic woodland to shrubland. Known only from pollen, the conifers Cheirolepidiaceae (*Classopollis torosus*; Fig. 23T), Taxodiaceae (*Perinopollenites elatoides*; Fig. 23X) and Pinaceae (*Pinuspollenites minimus*; Fig. 23U) may also belong here. Shrubland was composed of diversifed seed ferns – macroremains: *Sagenopteris nilssoniana, S. phillipsi, S. rhoifolia*, *Pachypteris* sp. (Fig. 21B); pollen grains: *Alisporites* cf. *thomasii*, *Alisporites* spp. (Fig. 23R, S) and cycadaleans (macroremains: *Ctenis fallax*; pollen grains: *Chasmatosporites elegans*, *C. major*, *C. rimatus*; Fig. 23N–P). Leaves of *Pterophyllum* preserved as relatively large fragments indicate that they were bog plants and grew near rivers or on delta plain (Fig. 21E–G). Pollen *Cerebropollenites thiergartii* (Taxodiaceae) according to Abbink (1998) was characteristic for places submerged by the sea for longer periods (Fig. 23Y). Limnic-brackish, planktonic, colonial green algae *Botryococcus* sp. confirm such a habitat type (Fig. 23Z). Bisaccate pollen grains from Podocarpaceae (*Podocarpidites ellipticus* and *Podocarpidites* spp.) represent upland vegetation (Fig. 23V, W).

A diverse range of spore-producing plants occurred. The affinity of some of them is unknown (e.g., for tetrad of fern spores; Fig. 23K). Bryophytes (*Retusotriletes* sp.; Fig. 23A) and lycophytes are only in the palynomorph record (*Uvaesporites* spp., *Lycopodiacidites rugulatus*, *Lycopodiumsporites reticulumsporites, Lycopodiumsporites vilhelmii*; Fig. 23B–D). Sphenophytes (macroremains *Neocalamites lehmannianus*, spores *Calamospora tener*; Fig. 23E) probably formed monotypic stands along open waterbodies. Many fern taxa are present in the macrofossil and palynological record: osmundaceous (*Cladophlebis denticulata, C. haiburnensis*, *Todites princeps*; spores *Baculatisporites comaumensis*, *Osmundacidites* sp.; Fig. 23I, J), dipteridaceous (*Clathropteris meniscoides, Dictyophyllum acutilobum, D. exile, Hausmania crenata*; Fig. 21A), matoniaceous (*Phlebopteris muensteri, P. angustiloba*; spores *Matonisporites* sp.; Fig. 23L), Cyatheaceae/Dipteridaceae/Dicksoniaceae (spores *Cyathidites concavus*, *Cyathidites* spp., *Deltoidospora* spp.; Fig. 23F, G), Cyatheaceae (spores *Zebrasporites interscriptus*; Fig. 23H) and Gleicheniaceae (spores *Gleicheniidites* spp.; Fig. 23M), but among the macrofossils only *Dictyophyllum acutilobum* is common, the rest of the taxa being sparse. Ferns probably occurred along river/distributary channel banks, on levees, on floodplains, forming fern marshes or the understorey of gymnosperm forests.

VERTEBRATE TRACKS

No data for the vertebrate track record from the Gielniów Formation (lower Pliensbachian) are available. Exposures of the Gielniów Formation are rare, and those still accessible represent marine and shallow marine sedimentation (Pieńkowski, 2004a; Niedźwiedzki et al., 2009).

LATE PLIENSBACHIAN, DRZEWICA FORMATION, SEQUENCES VI–VII

ENVIRONMENTAL CONTEXT

Depositional sequence VI rests on an extensive erosional surface in the Polish Basin (Pieńkowski, 2004a). The sediment overlying the erosional sequence boundary (parasequence VIa) occurs uniformly as sandy, sometimes coarse fluvial deposits.

The ensuing late Pliensbachian transgression was associated with the development of foreshore/shoreface/barrier deposits or lagoonal deposits. The marine transgression led to rapid inundation of the alluvial valleys and coastal plains, producing an embayed coastline with detached beach/barrier

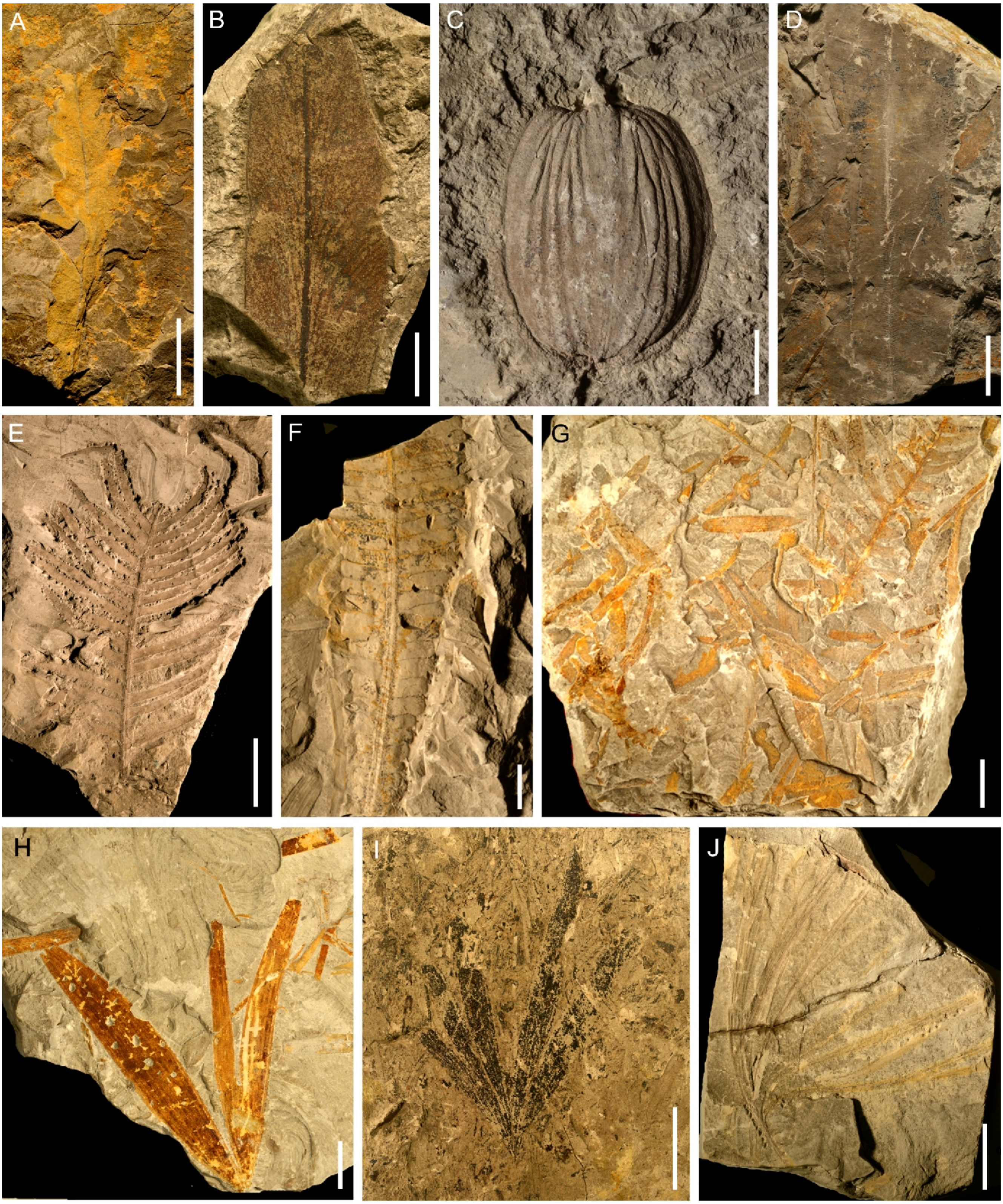

Fig. 21. Macrofossil plant assemblage form Chmielów outcrop, upper Gielniów Formation, lower Pliensbachian

A – *Dictyophyllum exile*, A-III-26/25; **B** – *Sagenopteris nilssoniana*, A-III-26/65; **C** – *Sacculotheca* sp. A-III-26/60; **D** – *Nilssonia* sp., PC IB UJ 107/5; **E** – *Pterophyllum polonicum*, PC IB UJ 107/1 ; **F** – *Pterophyllum* sp. 1, A-III-26/61; **G** – *Pterophyllum* sp. 2 and isolated leaves of *Podozamites* sp., PC IB UJ 107/6; **H** – *Sphenobaiera* sp., PC IB UJ 107/3; **I** – *Ginkgoites* sp., A-III-26/63; **J** – *Czekanowskia setacea*, A-III-25/7; scale bars: A, D, F, G, H, J – 10 mm, B – 6 mm, C – 5 mm, E, I – 20 mm

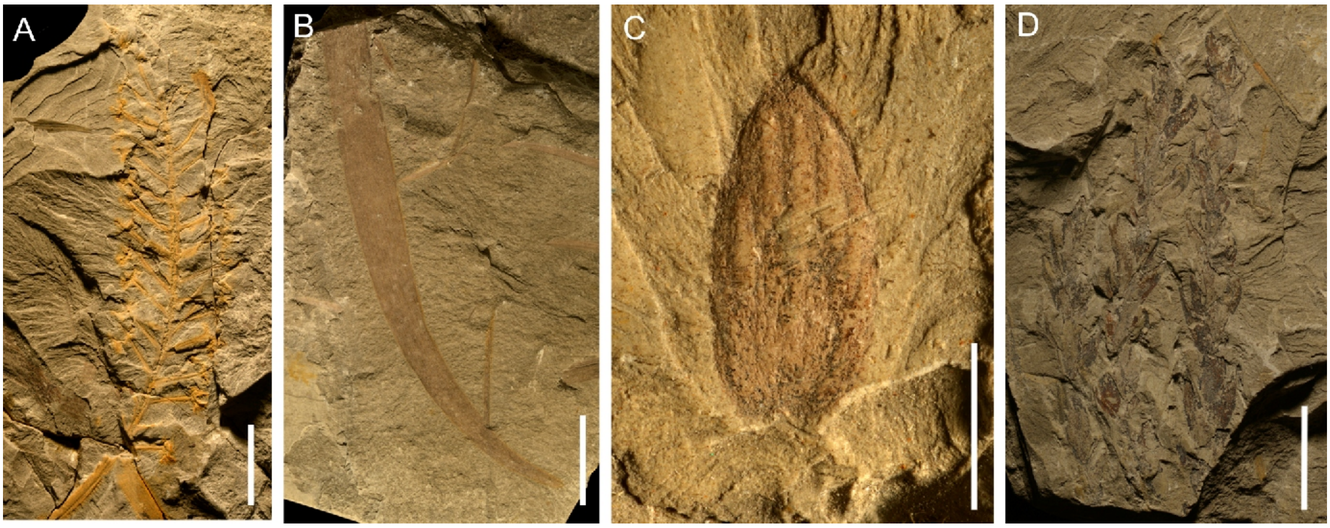

Fig. 22. Macrofossil plant assemblage form Chmielów outcrop, upper Gielniów Formation, lower Pliensbachian (continued)

A – *Ixostrobus* sp. male cone, A-III-26/66; **B** – *Desmiophyllum* sp., A-III-26/51a; **C** – *Cycadocarpidium erdmannii*, A-III-26/53; **D** – *Brachyphyllum* sp., A-III-26/62; scale bars: A, C – 10 mm, B – 20 mm, D – 5 mm

ridges. Further sea-level rises formed successions of extensive sandy shoreface deposits. These point to an enduring equilibrium between sea level, subsidence and a relatively high rate of sediment supply. The maximum flooding surface of depositional sequence VI occurs in the middle part of parasequence VIb. These TST–HST transitional deposits are represented by very well sorted sandstone lithofacies with hummocky cross stratification and horizontal bedding, known as Szydłowiec sandstone, praised for its value for construction since medieval times. This quartz sandstone occurs in the Szydłowiec area, specifically in the lower part of the Szydłowiec, Szydłówek and Śmiłów exposures. Higher up in the sequence, a regressive trend associated with the highstand system tract is developed, starting from a coastal eolian dune depositional subsystem associated with coastal lagoons. The Śmiłów exposure reveals well-developed foreshore facies with preserved seaward-dipping clinoforms and coastal eolian deposits, with plants buried in the life position and dinosaur footprints. The coastal dunes are associated with lagoonal mudstone containing palaeosol horizons. These marginal-marine deposits are covered with fluvial sandstone representing both deltaic/distributary and fluvial depositional systems, commencing the next depositional sequence, VII (Pieńkowski, 2004a).

In the more marginal area, parasequence VIb is developed as partly reworked deltaic deposits. The development of this sequence reflects rapid sea level changes: from low stand at the sequence V/VI boundary to a rapid sea level rise afterwards.

Depositional sequence VI deposits fall within the *Horstisporites planatus* megaspore zone (late Sinemurian–Pliensbachian age; Marcinkiewicz, 1971; Marcinkiewicz et al., 2014). As underlying sequence V is of early Pliensbachian age (bivalve finds), sequence VI is of early late Pliensbachian age. This sequence belongs to the Drzewica Formation.

Depositional sequence VII is known from the marginal part of the subbasin. Its lower, alluvial portion is exposed at Śmiłów Quarry and other quarries located in the same area. The Śmiłów exposure exhibits the sequence VI/VII boundary. It shows that the sea level fall was not as significant as at the base of the previous sequence. The transgressive surface of depositional sequence VII in the Holy Cross Mountains subbasin shows a sea level rise and rapid inundation of the whole area. This was preceded by the development of a delta system/marsh subsystem. Overlying nearshore depositional system sediments indicate that the amplitude of this transgression was quite high.

Depositional sequence VII deposits still fall within the *Horstisporites planatus* megaspore zone (late Sinemurian–Pliensbachian age; Marcinkiewicz, 1971; Marcinkiewicz et al., 2014). This sequence belongs to the Drzewica Formation and is likely of latest Pliensbachian age.

SZYDŁÓWEK QUARRY, DRZEWICA FORMATION, LATE PLIENSBACHIAN, SEQUENCE VI

ENVIRONMENTAL CONTEXT

Szydłówek is a small quarry in the vicinity of Szydłowiec. The Szydłowiec sandstone is a succession (from oldest to youngest) of nearshore–foreshore–backshore/eolian facies covered by fluvial deposits. Fossils include, besides numerous vertebrate tracks, casts of woody trunks, plant roots, brackish bivalves, and limulids.

PLANT COVER

Imprints of wood trunks probably of conifer origin are particularly abundant in this setting, pointing to the occurrence of vast coniferous forests around the tracksite. This is an interesting association of coniferous forest and dinosaur megafauna, suggesting colder and drier climate in late Pliensbachian times.

VERTEBRATE TRACKS

Well-preserved theropod, sauropod and ornithischian dinosaur tracks were discovered in the Szydłówek Quarry (Fig. 24A–C, E–H, J, K) and assigned to the dinosaurian ichnogenera *Anchisauripus, Eubrontes*, cf. *Megalosauripus, Kayentapus*, *Parabrontopodus*, *Moyenisauropus*, *Anomoepus* and cf. *Anomoepus* (Niedźwiedzki and Remin, 2008; Niedźwiedzki et al., 2008, 2009; Gierliński et al., 2009). The non-dinosaurian ichnogenera *Batrachopus* and cf. *Brasilichnium* were also reported (Niedźwiedzki and Remin, 2008). The ichnofauna is similar to some others from the HCM subbasin region and to other classic ichnofaunas of Early Jurassic age in Europe (Gierliński and Pieńkowski, 1999; Gierliński et al., 2004; Niedźwiedzki and Pieńkowski, 2016). Their abundance and ex-

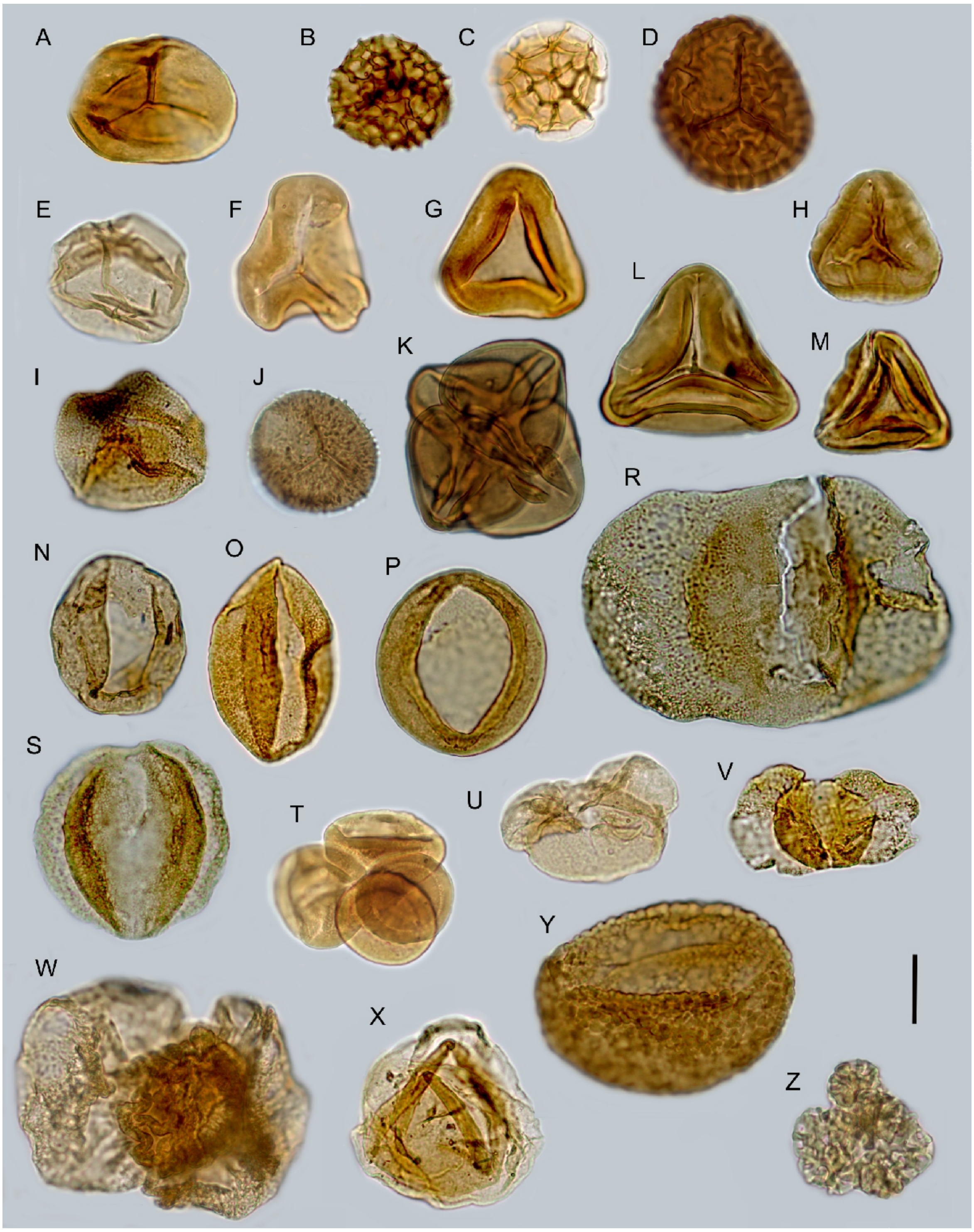

Fig. 23. Selected palynomorphs from Chmielów outcrop, upper Gielniów Formation, lower Pliensbachian

A – *Retusotriletes* sp. – bryophyte spore, KRAM P PM 142/2/5; **B** – *Lycopodiumsporites reticulumsporites* – lycophyte spore, KRAM P PM 142/2/2; **C** – *Lycopodiumsporites vilhelmii* – lycophyte spore, KRAM P PM 142/2/3; **D** – *Lycopodiacidites rugulatus* – lycophyte spore, KRAM P PM 142/2/3; **E** – *Calamospora tener* – sphenophyte spore, KRAM P PM 142/2/5; **F** – *Cyathidites concavus* – leptosporangiate fern spore, KRAM P PM 142/2/3; **G** – *Deltoidospora* sp. – leptosporangiate fern spore, KRAM P PM 142/2/4; **H** – *Zebrasporites interscriptus* – leptosporangiate fern spore, KRAM P PM/142/2/2; **I** – *Osmundacidites* sp. – osmundaceous fern spore, KRAM P PM 142/2/2; **J** – *Baculatisporites comaumensis* – osmundaceous fern spore, KRAM P PM 142/2/4; **K** – Tetrad of fern spores of unknown affinity, KRAM P PM 142/2/4; **L** – *Matonisporites* sp. – matoniaceous fern spore, KRAM P PM 142/2/4; **M** – *Gleicheniidites* sp. – gleicheniaceous fern spore, KRAM P PM 142/2/4; **N** – *Chasmatosporites elegans* – cycad pollen grain, KRAM P PM 142/2/2; **O** – *Chasmatosporites major* – cycad pollen grain, KRAM P PM 142/2/3; **P** – *Chasmatosporites rimatus* – cycad pollen grain, KRAM P PM 142/2/2; **R** – *Alisporites* sp. – seed fern pollen grain, KRAM P PM 142/2/4; **S** – *Alisporites* cf. *thomasii* – seed fern pollen grain, KRAM P PM 142/2/; **T** – *Classopollis torosus* – cheirolepidiaceous conifer tetrad of pollen grains, KRAM P PM 142/2/3; **U** – *Pinuspollenites minimus* – conifer pollen grain, KRAM P PM 142/2/2; **V** – *Podocarpidites ellipticus* – podocarpaceous conifer pollen grain, KRAM P PM 142/2/2; **W** – *Podocarpidites* sp. – podocarpaceous conifer pollen grain, KRAM P PM 142/2/3; **X** – *Perinopollenites elatoides* – taxodiaceous conifer pollen grain, KRAM P PM 142/2/4; **Y** – *Cerebropollenites thiergartii* – taxodiaceous conifer pollen grain, KRAM P PM 142/2/4; **Z** – *Botryococcus* sp. – green algae colony, KRAM P PM 142/2/3; scale bar – 20 μm cellent preservation as shallow natural casts and sometimes as true tracks (some with pad and claw impressions) is worth nothing. Gigantic theropod dinosaur tracks (provisionally named cf. *Megalosauripus*; Fig. 24J) revealed huge metatarsal pad impressions and united pads on digit III (Niedźwiedzki and Remin, 2008). The gigantic tridactyl ichnites from the Szydłówek Quarry are more similar to the large theropod tracks described from the Middle–Late Jurassic sites. These finds furnish new evidence for the occurrence of large predatory dinosaurs in the Early Jurassic, and are the third find of gigantic theropod tracks in the Lower Jurassic of Poland (Niedźwiedzki and Remin, 2008). Other large theropod footprints (30–40 cm long) identified at Szydłówek resemble *Eubrontes* (Fig. 24F), a classic theropod ichnotaxon of the Early Jurassic. Numerous tracks from Szydłówek Quarry show an anomoepodid pattern and a typical functionally tridactyl pes with relatively short and robust digits, and also typical *Anomoepus* or *Moyenisauropus* size (Gierliński, 1991; Lockley and Gierliński, 2006). These specimens were initially described as cf. *Anomoepus* and *Anomoepus* or *Moyenisauropus* but require revision and more detailed study (Fig. 24C).

All these finds suggest that gigantic and medium-sized to large theropods occupied varied environments and coexisted with large herbivorous dinosaurs such as sauropods (*Parabrontopodus* isp; Fig. 24K) and various ornithischians. Tracks of crouching theropods have been reported from this quarry (Gierliński et al., 2009). The palaeogeographic and stratigraphic setting of the tracks suggests a single track-making episode in a foreshore/barrier-fluvial setting. The finds confirm that the barrier-lagoonal association of theropod dinosaurs of the Lower Jurassic of the HCM was dominated by small and medium-sized forms, but it also contains prints made by larger animals.

ŚMIŁÓW QUARRY, LATE PLIENSBACHIAN, DRZEWICA FORMATION, UPPERMOST SEQUENCE VI AND LOWERMOST SEQUENCE VII

ENVIRONMENTAL CONTEXT

The large Śmiłów Quarry exploits fine-grained, very well sorted quartz-cemented sandstone of the lower part of the section, mostly nearshore facies. In the lower part is a shoreface depositional system with domination of hummocky cross-stratification and parallel bedding. In this part of the section trace fossils are numerous, including *Thalassinoides* (= *Spongeliomorpha*), other well-preserved crustacean burrow systems with characteristic outlets, and *Rhizocorallium*. In the nearby quarry a well preserved horseshoe crab was found. Undeterminable bivalve fossils also occur, along with very numerous bivalve resting traces *Lockeia* (Pieńkowski, 2004a). The shoreface deposits pass upwards into sandstone showing giant-scale, low-angle tabular bedding representing seaward-dipping beach clinoforms. Measurements of sedimentary dip in the quarry and the succession of sedimentary environments show that the tabular bedding represents a buried barrier form. This section of the profile shows eolian reworking in the uppermost part and plants buried in growth position by barrier crest eolian dunes. The barrier crest was trending roughly N–S. Large logs of drifted trees and poorly preserved dinosaur footprints are also found here. Next is a lagoonal facies (mudstone with plant roots) that ends the upward-shallowing, prograding part of sequence VI (Pieńkowski, 2006).

The higher, unexploited (due to poor sandstone quality) part of the section is built of fine- to medium-grained, relatively poorly sorted sandstone with trough cross-bedding, floral remains and in places plant roots *in situ*. This sandstone represents an alluvial depositional system (amalgamated meandering channels, i.e. channel fill and point bar deposits) of the lowermost part of sequence VII. The erosional sequence boundary is well visible over the whole quarry area ; it is rather uniform, without conspicuous channelized features. The current flow vector points south-west.

PLANT COVER

The eolian deposits from Śmiłów Quarry contain plants preserved in the life position, similar to the neighbouring Podkowiński Quarry in Szydłowiec (Gierliński et al., 2006; Pacyna, 2021b). Based on the taphonomy and sedimentological data, the environment was interpreted as seashore dune field (Karaszewski, 1962; Karaszewski and Kopik, 1970; Pieńkowski, 2004a). The plants grew in clusters and leaned in one direction; identifiable remains belong to the fern *Matonia braunii* (Pacyna, 2021a). At Śmiłów, moulds of large tree trunks indicate dominance of coniferalean woods, with small shares of ferns.

Sporomorphs confirm the occurrence of a more diverse flora in Gutwin, ~40 km SE of Śmiłów (Rogalska, 1976) and ~30 km SE of Śmiłów in the Brody-Lubienia boreholes (Pieńkowski et al., 2016). Bryophytes (*Stereisporites* sp.) were not abundant but lycophytes (*Densoisporites perinatus, Densoisporites* spp., *Uvaesporites glomeratus*, cf. *Lycopodiumsporites* spp.) were very diverse in this formation. Ferns of both herbaceous and arborescent forms were also diverse: Cyatheaceae, Dipteridaceae, Dicksoniaceae (*Cyathidites* sp.), Gleicheniaceae (*Gleicheniidites senonicus, Gleicheniidites* spp.) and Osmundaceae (*Osmundacidites* sp., *Todisporites minor, T. undans*), which usually are colonizing and riparian plants. Among the gymnosperms, conifers of the families Podocarpaceae (cf. *Podocarpidites* spp.) and Pinaceae (*Piceapollenites alatus*) dominated. A ginkgoalean (*Monosulcites minimus*), bennettitalean (*Exesipollenites tumulus*) and cycadalean (*Cycadopites* sp.) were present and formed shrubs. A similar assemblage extended towards Brody-Lubienia (Pieńkowski et al., 2016). Marine influences are confirmed by palynomorphs *Leiosphaeridia* and limnic–brackish, planktonic, colonial green algae *Botryococcus* sp. (Gutwin borehole, Rogalska, 1976).

VERTEBRATE TRACKS

The footprints in Śmiłów Quarry were left in the siliciclastic foreshore zone, interfingering with backshore dunes (Fig. 24D, I, L). The first dinosaur tracks discovered in Śmiłów belonged to a very small theropod trackmaker (Gierliński and Niedźwiedzki, 2005). Subsequent finds were of larger theropod footprints. They fit the size range of the medium-sized grallatorids (15–25 cm long) labelled *Grallator* or *Anchisauripus*. In total, nine dinosaur tracksites have been identified in the Śmiłów area (ongoing study), one of which is no longer accessible. A survey of undescribed specimens and available ichnological data on these localities shows that the dinosaurs represented by tracks include small bipedal ornithischians (cf. *Anomoepus*), a large ornithischian (cf. *Moyenisauropus*; Fig. 24D), theropods (*Eubrontes, Kayentapus, Anchisauripus, Grallator*) and sauropods (*Parabrontopodus*). Small and medium-sized theropod tracks are most abundant and are present in all localities, followed in abundance by ornithischian tracks. There are two or

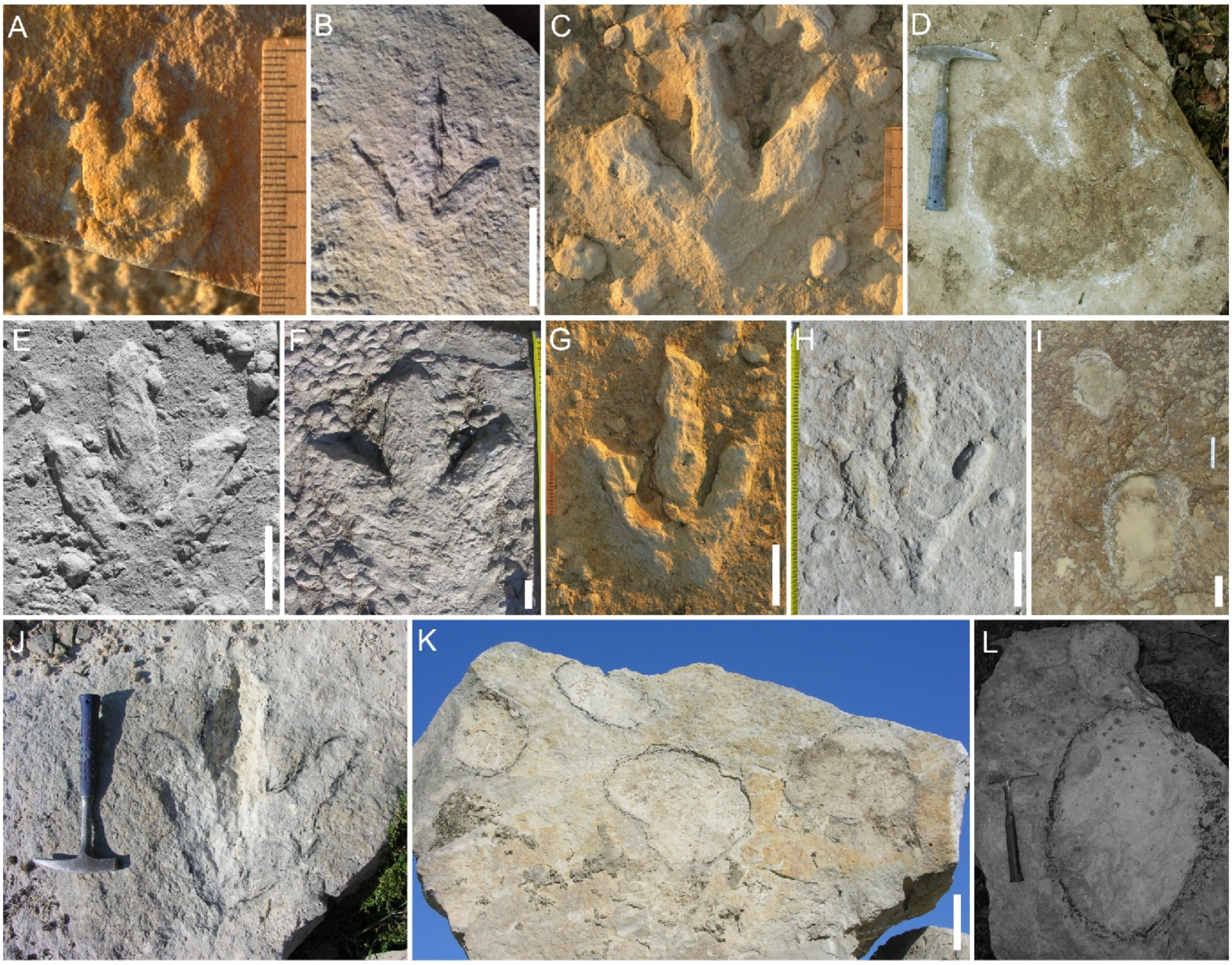

Fig. 24. Dinosaur track associations from the Szydłówek (A–C, E–H, J, K) and Śmiłów (D, I, L) sites, Drzewica Formation, upper Pliensbachian

A – cf. *Stenonyx* isp.; **B** – cf. *Plesiornis* isp.; **C** – *Anomoepus* isp.; **D** – *Moyenisauropus* isp.; **E** – cf. *Anchisauripus* isp.; **F** – cf. *Eubrontes* isp.; **G**, **H** – cf. *Kayentapus* isp.; **I** – small *Parabrontopodus* isp.; **J** – cf. *Megalosauripus* isp.; **K**, **L** – large sauropod tracks, Sauropoda indet.; scale bars: A – 3.5 cm; B, C, E–H – 5 cm; D, J, L – hammer 27 cm; I – 10 cm; K – 20 cm

three morphotypes, perhaps partly related to different ontogenetic stages of the animals that left the large ornithischian tracks. Sauropod tracks occur in two beds in Śmiłów Quarry were registered small as well as gigantic oval-shaped manus and pes ichnites were registered (Fig. 24I, L). There is a strong discrepancy in diversity and composition between the different beds with tracks from the same lithological unit (e.g., beds with theropod tracks, bed with sauropod tracks). This suggests local taphonomical control of trace fossil preservation, or that it is a record of specific animal behaviours in the different environments. Material from the Śmiłów area is currently under study; conclusions about the record of dinosaur ichnofaunas in this sequence will be presented in a separate publication.

Based on this locality and other sites of the Drzewica Formation (e.g., Szydłówek), Niedźwiedzki et al. (2009) indicated that there might be a third type of dinosaur track assemblage in the Lower Jurassic of the HCM subbasin (Figs. 25 and 26). This new foreshore–beach–backshore eolian dune association would be characterized by the presence of small and medium-sized forms (theropods *Grallator*, *Anchisauripus*, *Kayentapus*; thyreophorans *Anomoepus*, *Moyenisauropus*) but it also contains tracks made by large dinosaurs (large sauropods and theropods).

EARLY TOARCIAN, CIECHOCINEK FORMATION, SEQUENCE VIII

ENVIRONMENTAL CONTEXT

Depositional sequence VIII in the HCM subbasin is known only from the Brody-Lubienia borehole and from archival reports from old quarries that no longer exist (Karaszewski, 1962). The erosional surface of the sequence boundary is marked by a thin layer with quartz pebbles. Erosion at the sequence boundary could be significant. Initial sedimentation of parasequence VIIIa proceeded within an alluvial-meandering river depositional system. The nearshore depositional system that developed above contains numerous *Diplocraterion parallelum* vertical burrows, indicating a marine environment. Basinal deposits are developed as grey-green mudstone and lenticular/wavy heteroliths with microhummocky cross-stratifi-

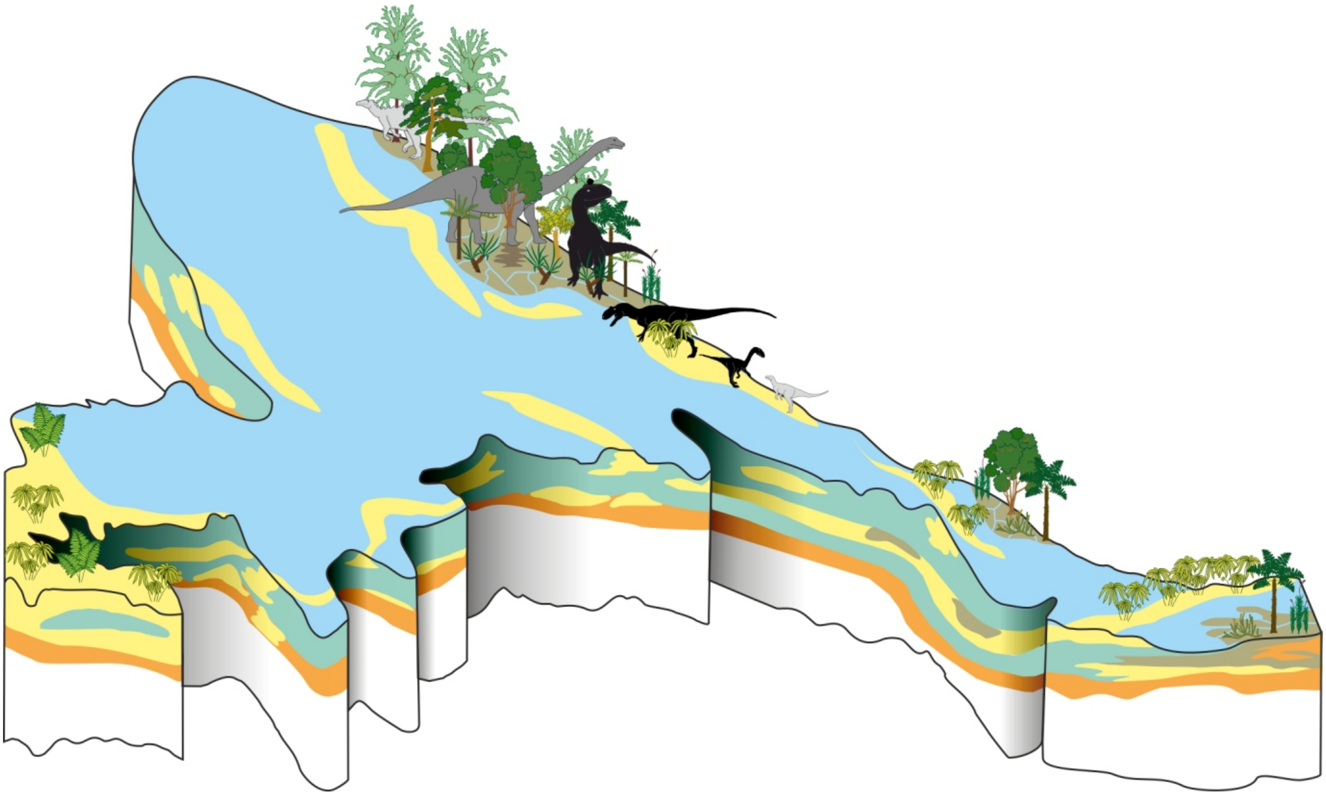

Fig. 25. Reconstruction of the Holy Cross Mountains (HCM) sedimentary subbasin, Drzewica Formation (upper Pliensbachian, sequences VI–VII), with reconstructed plant cover and the most characteristic dinosaurs

cation. The subbasin, though mesohaline in character, was shallow. It may be described as a broad, shallow marine embayment which recurrently emerged, with subsequent development of vegetation and high-water-table palaeosoils. The basinal deposits are thin and quickly pass into deposits of a very shallow lagoonal-marsh depositional subsystem with green/dark grey/reddish mudstone, claystone and heteroliths with conchostracans, numerous plant roots, palaeosoil horizons and desiccation cracks. Sideritic nodules and bands of coaly clay are common. The shallow lagoonal-marshy basin of the uppermost part of sequence VIII was quickly filled in by deltaic deposits ending the sequence.

Depositional sequence VIII deposits fall within the *Paxillitriletes phyllicus* megaspore zone (Toarcian age; Marcinkiewicz, 1971; Marcinkiewicz et al., 2014). We assign this sequence to the early Toarcian which forms part of the characteristic ("green mudstone-bearing") Ciechocinek Formation.

PLANT COVER

The reconstruction of plant cover from the Ciechocinek Formation is based on the palynological record from the Gutwin (Rogalska, 1976) and Brody-Lubienia boreholes (Pieńkowski et al., 2016). The plant assemblage was dominated by spore-producing plants: bryophytes (*Stereisporites* sp.), lycophytes (*Cingulatisporites floridus, Cingulizonates* spp., *Densoisporites perinatus, Densoisporites* spp., *Uvaesporites glomeratus*, cf. *Lycopodiumsporites* spp., *Retitriletes globosus*) and ferns of the families Cyatheaceae/Dipteridaceae/Dicksoniaceae (*Cyathidites* sp.), Gleicheniaceae (*Gleicheniidites senonicus, Gleicheniidites* spp.), Marattiaceae (*Marattisporites scabratus*), Matoniaceae (cf. *Matonisporites* sp., *Concavisporites polygonalis*), Osmundaceae (*Osmundacidites* sp., *Todisporites minor, T. undans*) and Schizaeaceae (*Klukisporites variegatus*). Gymnosperms were not abundant: conifers of cheirolepidiacean affinity (*Classopollis* spp.) and Taxodiaceae (*Perinopollenites elatoides*), together with cycads (*Chasmatosporites rimatus*, *Cycadopites* sp.). The aquatic environment contained both oligohaline (*Botryococcus* sp., *Tasmanites*) and brackish palynomorphs (*Micrhystridium* sp., Dinophyceae, *Leiosphaeridia*), which points to changing salinity.

Based on palynological data from the Brody-Lubienia borehole, the following plant groups were detected in the lower part of the Ciechocinek Formation: bryophytes, lycopsids, ferns, seed ferns, conifers, cycads, bennettitaleans and ginkgophytes (Pieńkowski et al., 2016). The peak of non-bisaccate pollen grains and fern spores is seen slightly above the Pliensbachian/Toarcian boundary. Higher in the section, in the interval representing the Toarcian Oceanic Anoxic Event (T-OAE), there is a marked spike of spore-producing plants, especially ferns, lycopsids, bryophytes and quillworts. The megaspores, such as the most common *Paxillitriletes phyllicus*, and *Minerisporites institus* (Marcinkiewicz, 1962, 1971, 1989; Marcinkiewicz et al., 2014), come from hydrophilous lycopsids (club mosses, quillworts). These data strongly support the inferences made by many authors that the T-OAE negative excursion corresponds to a time of extremely warm and humid climate and very high atmospheric CO_2 (Jenkyns, 2003; Hesselbo and Pieńkowski, 2011; Pieńkowski et al., 2020). Gymnosperms other than seed ferns and conifers were in decline during this time. After this event the diversity of conifers rose, and ferns declined slightly. Other spore-producing plants also decreased in number. Cycads, bennettitaleans and ginkgophytes were rare, as they were during the T-OAE. Increasing temperature during the T-OAE promoted fungal-mediated decomposition of plant litter, specifically in normally resistant woody tissues; numerous

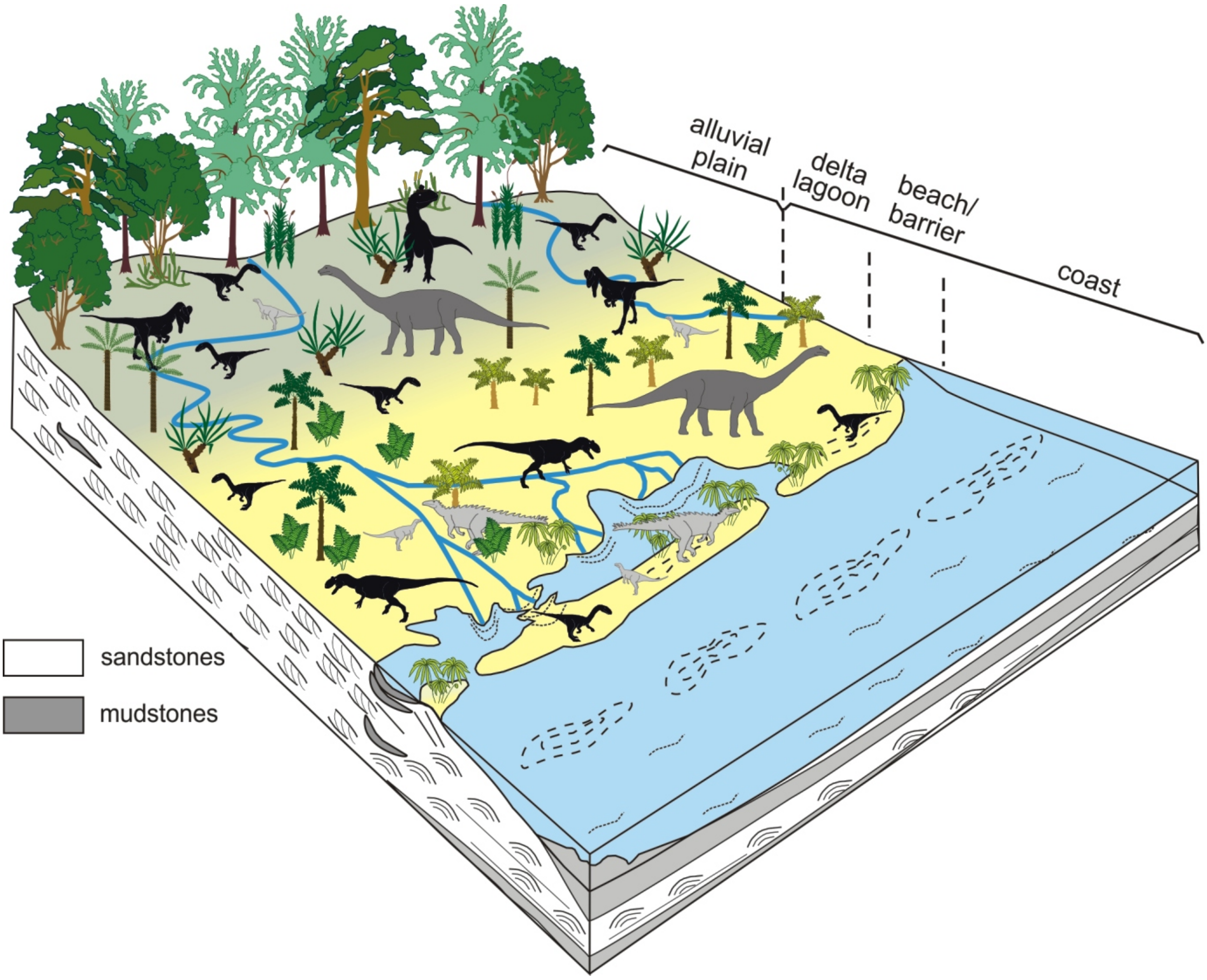

Fig. 26. Spatial distribution of dinosaur ichnoassemblages in the upper Pliensbachian of the Holy Cross Mountains, foreshore–beach–backshore eolian dune association characterized by dominance of small and medium-sized forms (theropod *Grallator*, *Anchisauripus*, *Kayentapus*; thyreophoran *Moyenisauropus*) but also containing large animals (sauropods, theropods) associated with different types of plant communities

fungal spores are recorded in this part of the core from the Brody-Lubienia succession (Pieńkowski et al., 2016).

VERTEBRATE TRACKS

Dinosaur or other tetrapod tracks have not been found in the Ciechocinek Formation strata of the HCM subbasin so far.

MIDDLE–LATE TOARCIAN, BORUCICE FORMATION, SEQUENCES IX AND X

ENVIRONMENTAL CONTEXT

Like depositional sequences VII and VIII, the uppermost Lower Jurassic sequences IX and X in the HCM are known principally from the Brody-Lubienia succession (north-eastern area) and the northwestern part of the HCM subbasin (Idzikowice outcrop, Dąbie Quarry). The bottom of sequence IX is associated with the main erosional surface. In places, erosion removed significant parts of the lower Toarcian deposits down to the *falciferum*-dated deposits, as evidenced by chemostratigraphy (Hesselbo and Pieńkowski, 2011; Pieńkowski et al., 2020). However, in the Brody-Lubienia section much of the lower Toarcian survived the erosional event and a complete T-OAE succession with overlying sediments is preserved (Hesselbo and Pieńkowski, 2011). Sequences IX and X represent uniform, alluvial-deltaic depositional systems (anastomosing river or delta plain depositional systems with a prominent share of progradational crevasse deposits). In the lower parts of parasequences IXb and IXc, an enlarged accommodation space allowed extensive development of a deltaic depositional system (as outcropped in Dąbie Quarry). The whole subbasin was quickly infilled by these deposits. The rest of parasequences IXb and IXc show typical fluvial (deltaic-distributary/alluvial) character. Similarly, the last sequence (X) is represented by alluvial-deltaic deposits. The age of depositional sequences IX and X falls within the *Paxillitriletes phyllicus* megaspore zone (Toarcian age: Marcinkiewicz, 1971; Marcinkiewicz et al., 2014), which confirms middle–late Toarcian age (Pieńkowski, 2004a), although the lower part of sequence IX may still be of early Toarcian age.

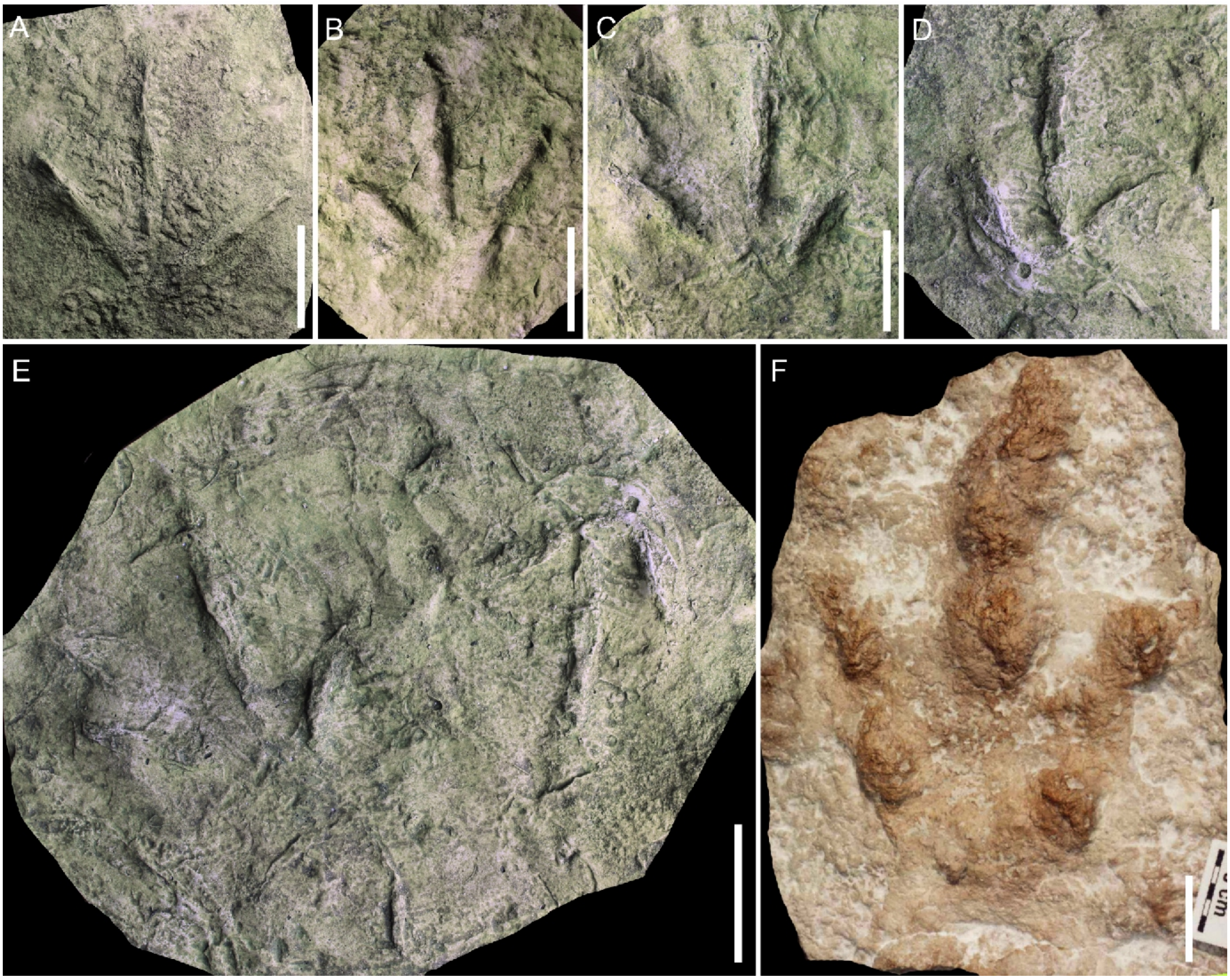

Fig. 27. Dinosaur tracks from the Dąbie Quarry (A–E) and Idzikowice outcrop (F), Borucice Formation, mid–upper Toarcian

A–E – *Trisauropodiscus* isp.; **F** – cf. *Therangospodus* isp.; scale bar – 5 cm

PLANT COVER

Plant remains have recently been discovered in the lower part of the Borucice Formation (depositional sequence IX) in Dąbie Quarry. This quarry exhibits upper Toarcian sandstone and mudstone of deltaic origin. Two deltaic depositional subsystems are present: in the lower part of the section a delta-front subsystem with horizontal layers of sandstone with ripple-drift cross-lamination is exposed, and in the upper part an interval with giant-scale trough cross-bedded sandstone representing distributary channels is visible. The plant fossils occur in the trough cross-bedded sandstone and are preserved as impressions or casts completely devoid of organic matter. Bennettitalean leaf remains dominate the assemblage, and cycads are probably present. The most frequent is a conifer (probably araucarian), represented by leafy shoots and cones. The bennettitalean *Otozamites falsus* was found in the Wyszmontów borehole on the eastern margin of the HCM (Marcinkiewicz, 1973).

According to Rogalska (1976), in the Gutwin borehole 100 km to the south-east, on the other side of the studied region, spores testify the occurrence of bryophytes (*Stereisporites* sp.), lycophytes (*Cingulatisporites floridus, Cingulizonates* spp., *Densoisporites perinatus, Densoisporites* spp., *Uvaesporites glomeratus*, cf. *Lycopodiumsporites* spp., *Retitriletes globosus*) and various ferns from the families Cyatheaceae, Dipteridaceae, Dicksoniaceae (*Cyathidites* sp., *Cyathidites concavus*), Gleicheniaceae (*Gleicheniidites senonicus, Gleicheniidites* spp.), Marattiaceae (*Marattisporites scabratus*), Matoniaceae (cf. *Matonisporites* sp., *Concavisporites polygonalis*), Osmundaceae (*Osmundacidites* sp., *Baculatisporites truncatus*, *Todisporites minor*) and Schizaeaceae (*Klukisporites variegatus*). The gymnosperms of diverse affinity, were mainly arborescent: Ginkgoales (*Monosulcites minimus*), Taxodiaceae (*Perinopollenites elatoides*, *Cerebropollenites* spp.), Cheirolepidiaceae (*Classopollis* spp.) and Podocarpaceae (cf. *Podocarpidites* spp.). The shrub level was less diverse, formed only by bennettitaleans (*Exesipollenites tumulus*) and cycadaleans (*Chasmatosporites magnolioides*). The occurrence of various Araucariaceae (*Callialasporites dampieri, C. segmentatus, C. trilobatus*) is noteworthy because during the Jurassic they usually formed forests in coastal zones (Harris, 1979; Abbink, 1998). Marine influences are documented by aquatic palynomorphs: *Lecaniella* sp., *Leiosphaeridia*, *Schizocystia* and *Tasmanites*.

VERTEBRATE TRACKS

Vertebrate tracks from the Borucice Formation are still poorly known. We are at the stage of initial identification of this ichnofauna (ongoing study) but some information can be presented and commented here (Fig. 27). Theropod tracks left by a relatively large theropod and referred to *Eubrontes* (Gierliński, 1995) or *Megalosauripus sensu lato* (Gierliński et al., 2001) were reported from the Idzikowice outcrop (small old quarry located east of the Idzikowice railway station). Interestingly, the morphology of these tracks points to a similarity with the Middle–Late Jurassic *Therangospodus* ichnotaxon (Fig. 27F). This locality also yielded a few rather poorly preserved small tridactyl tracks tentatively classified here as theropods (cf. *Grallator* isp.). These specimens were found in an alluvial (meandering river) depositional system of sequence IX or X (Pieńkowski, 2004a). A recently discovered new tracksite at Dąbie Quarry represents nearshore–deltaic deposits of the lower part of the Borucice Formation (Pieńkowski, 2006); seven specimens were registered and collected from Dąbie Quarry. This material is still under study but it shows that the terminal Early Jurassic ichnoassemblage is dominated by tracks of theropod dinosaurs (cf. *Grallator*, cf. *Anchisauripus*, *Trisauropodiscus*; Fig. 27A–E) and medium-sized tridactyl theropod tracks of problematic affinity (cf. *Therangospodus*). The dinosaur ichnofauna of the Borucice Formation clearly differs from the other ichnofaunas of Pliensbachian and older formations of the region; it contains elements characteristic of the Middle–Late Jurassic dinosaur ichnoassembalges of Pangea (ongoing study).

ECOSYSTEM CHANGES AND THEIR CAUSES

The changes detected in the flora and dinosaur fauna should be considered in connection with the climatic and local environmental background. After a major climate change in the late Rhaetian (Pieńkowski et al., 2012, 2014), during the Early Jurassic the studied area remained in a relatively stable warm, wet-winter climatic zone. However, there were several climate changes that might have exerted an influence on the local ecosystem as well as the evolution of the flora or dinosaur fauna. Based on inferred Rhaetian–Early Jurassic air temperature trends in the mid-latitudes (Pieńkowski et al., 2020), one can point to several cooling or warming events that might have affected the development of plant cover and the associated biota. After the end-Triassic greenhouse period, punctualed by cool events in the latest Rhaetian (climatic reversals), the beginning of the Hettangian was relatively cooler and drier (parasequence Ia), resulting in the growth of *Hirmeriella* forests associated with meandering and anastomosing rivers and accompanied by a dinosaur megafauna of various sauropodomorphs and medium-sized to large theropods. Warm, humid conditions were established during the early–middle Hettangian (latest *planorbis–liassicus* zones). A base-level rise correlated with the Hettangian transgression led to the development of a lacustrine environment (parasequence Ib), followed by marine flooding associated with the appearance of basinal/coastal environments recognized in parasequence Ic (Pieńkowski, 2004a). *Hirmeriella*-dominated woods gave way to czekanowskialean–ginkgoalean deltaic and coastal forests. Uplands were overgrown by ginkgophyte forests dominated by *Ginkgoites*. This type of environment and vegetation thrived with little change to the early Pliensbachian. In this environment, small and medium-sized theropods, small to medium-sized sauropodomorphs and diverse ornithischians appeared; their tracks dominate in the tetrapod ichnorecord. The Hettangian was a 1.9 My long age (Hesselbo et al., 2020) during which the dinosaur fauna rapidly diversified, as documented by dinosaur footprints from Sołtyków, Gromadzice, Gliniany Las, Borkowice and other sections. In the late Hettangian (*angulata* Zone) there were some fluctuations of climate (Pieńkowski et al., 2020), with presumed cooler periods reflected in some floristic changes), but probably these did not influence the animal biota much. The Sinemurian was a time of rather stable warm and humid climate, with an optimum (higher temperature) in the middle–late Sinemurian (*oxynotum* Zone), and such conditions continued through the early Pliensbachian, with a markedly warmer period in the *davoei* Zone (reflected in the Chmielów flora). Our data do not confirm any significant changes in the local dinosaur faunas through the Sinemurian–early Pliensbachian interval. Cooler and drier conditions prevailed in the late Pliensbachian, expressed in the flora and dinosaur fauna (emergence of megafauna), related to the domination of coniferous forests. The diversified dinosaur ichnorecord from this period includes large sauropod and large theropod footprints. The last major change took place between the Drzewica and Borucice formations, between the latest Pliensbachian and middle–upper Toarcian. Of major significance was the early Toarcian carbon cycle disturbance, associated with a supergreenhouse event and floristic change (Pieńkowski et al., 2016, 2020). However, in Poland there is no dinosaur ichnorecord from the lower Toarcian Ciechocinek Formation deposits separating the Drzewica and Borucice formations. Most likely, here we are dealing with a crisis and subsequent recovery associated with major environmental disturbances during the Toarcian Oceanic Anoxic Event (Jenkyns Event) in the early Toarcian. The reappearance of dinosaur fauna in the HCM subbasin in middle–late Toarcian times points to a recovery promoted by stabilization of the climate. During that period the first large sauropods and new groups of ornithischian dinosaurs appeared. Very large oval-shaped tracks identified in the late Pliensbachian, as well as a new type of tridactyl track (theropods) from the middle–late Toarcian, suggest some faunal changes across the late Pliensbachian–early Toarcian interval. The record of dinosaur assemblages from this period is rather poor worldwide, although a new report from Argentina (Pol et al., 2020) points to an extinction of non-eusauropod lineages and a drastic turnover of the dinosaur fauna with the appearance of eusauropods just after the Toarcian Oceanic Anoxic Event (and concomitant greenhouse event on land). The palynological data from the Brody-Lubienienia drill core (Pieńkowski et al., 2016) confirms marked changes in floristic composition, especially in the early Toarcian. Gymnosperms producing non-bisaccate pollen grains and ferns represented by spores clearly dominated in assemblages located slightly above the Pliensbachian/Toarcian boundary. During the Toarcian Oceanic Anoxic Event (early Toarcian), spore-producing plants, especially ferns, lycopsids, bryophytes and quillworts, occurred in considerable numbers, while gymnosperms other than seed ferns and conifers were in decline. After this event the diversity of conifers increased, and ferns declined slightly. Specific dinosaur ichnoassemblages are strongly connected with a specific environment, climate, and the resulting plant cover. The ichnorecord suggests that the large herbivores (sauropodomorphs) preferred forested areas and that plant-rich alluvial plains developed along the large meandering rivers; in contrast, nearly all small and medium-sized ornithischians preferred delta plains with rather low vegetation. This scenario may have been repeated in the studied area, similar to that seen in the dinosaur turnover in Argentina (Pol et al., 2020).

The other factor to be considered is atmospheric oxygen content. Plant chamber experiments have revealed relationships between carbon isotope discrimination and changing pO_2 (Porter et al., 2017), but this variable in the geological record is interpreted from reconstructions that vary widely, particularly for the Mesozoic and early Cenozoic eras (Glasspool and Scott, 2010). In respect to the geological time interval studied here, these low-resolution models are often controversial, although they confirm the general rule that high rates of organic carbon burial result in subsequent oxygen production (Krause et al., 2018). Following this rule, increased pO_2 pressure should be expected just after intense organic carbon burial events, which are associated with plankton blooms, oceanic anoxia and deposition of black shales. Such events occurred in the early Hettangian and early Toarcian, and on a lesser scale in the early Pliensbachian. Therefore, it is possible that dinosaur evolutionary events (e.g., their diversification and the appearance of megafauna) recorded in the Hettangian, late Pliensbachian and middle–late Toarcian of Poland were connected with these oxygenation events. The frequency of forest fires (Ziaja and Wcisło-Luraniec, 1999; Marynowski and Simoneit, 2009) registered in the lower Hettangian strata tends to support this hypothesis.

CONCLUSIONS

The present review provides, for the first time, a comprehensive characterization of the palaeoenviroments, fossil floras and dinosaur ichnofaunas of the Early Jurassic of the Holy Cross Mountains subbasin (southern Poland). We applied sedimentological, palaeobotanical and palaeoichnological interpretations in order to the reconstruct the vegetation and dinosaur-dominated ecosystems of the HCM and their evolution over the course of the early Hettangian–late Toarcian interval.

The early Hettangian flora from Sołtyków is most similar to coeval floras from Franconia, France and Wales in its dominance of the conifer *Hirmeriella* (compare e.g., Schenk, 1867; Gothan, 1914), but also shows similarities to Scania and Greenland floras, particularly in its fern species (compare e.g., Nathorst, 1878, 1907, 1908, 1910; Lundblad, 1950; Pott and McLoughlin, 2011). The younger floras from Gromadzice and Chmielów (latest early Hettangian–Pliensbachian) are similar to Scania, Bornholm and Greenland floras in their overall composition (compare e.g., Möller 1902; Antevs, 1919; Harris, 1931, 1935, 1937) but are enriched with numerous ginkgophytes taxa of Asiatic–Siberian provenance. The late Pliensbachian and Toarcian coniferous forests dominated by Araucariaceae are similar to those in East Greenland (Lund and Pedersen, 1985) and the Danish subbasin (Dybkjær, 1991). The presence of *Callialasporites dampieri, C. segmentatus* and *C. trilobatus* is noteworthy, because during the Jurassic their source plants usually formed forests in coastal zones (Harris, 1979; Abbink, 1998).

The dinosaur ichnorecord of the Lower Jurassic Kamienna Group of the HCM comprises various ornithischian, theropod and sauropodomorph tracks and coprolites. Dinosaur tracks occur in a variety of terrestrial and coastal environments: alluvial floodplain, fluvial, deltaic-lagoonal and barrier-foreshore coastal deposits. The local environment (e.g., stability of substrate, accessibility to water, food availability), together with vegetation (food sources, hiding opportunities, mobility), are presumed to have influenced the character of the recorded dinosaur ichnofaunas. At least six distinct dinosaur track assemblages were identified: (1) the lower Zagaje Formation (lowermost Hettangian) ichnoassemblage with tracks of small ornithischians, large sauropodomorphs (including early sauropods) and diverse theropods (including gigantic forms); (2) the upper Zagaje Formation (lower Hettangian) ichnoassemblage with tracks of small and medium-sized ornithischians, medium-sized sauropodomorphs and small to medium-sized theropods; (3) the Skłoby Formation (middle Hettangian) ichnoassemblage with tracks of diverse ornithichians, small sauropodomorphs and small to medium-sized theropods; (4) the Przysucha Ore-bearing Formation (upper Hettangian) ichnoassemblage with tracks of diverse ornithichians and small to large theropods; (5) the Drzewica Formation (upper Pliensbachian) ichnoassemblage with tracks of medium-sized to large ornithischians, large sauropods and small to large theropods; and (6) the Borucice Formation (middle–upper Toarcian) ichnoassemblage with tracks of small to large theropods. The Borucice Formation (fluvial and deltaic environment) ichnoassemblages contain some elements typical of Middle Jurassic ichnofaunas (*Therangospodus* and *Trisauropodiscus* tracks).

Some distinct changes in the faunas of Early Jurassic ecosystems of the HCM occurred: (1) in the early Hettangian (difference between ichnoassemblages of the lower and upper parts of the Zagaje Formation) and (2) in the late Pliensbachian–early Toarcian (transition from the Drzewica Formation to the Borucice Formation). The ichnodiversity of the record from the Lower Jurassic of the HCM is higher than in the record of other areas of northern Pangea.

There are signals of evolutionary events in these faunas: (1) the appearance of a megapredator (cf. *Megalosauripus* tracks) in the earliest Hettangian (lower Zagaje Formation); (2) the diversification and size increase of early ornithischian dinosaurs, reflected in *Anomoepus*–*Moyenisauropus* tracks observed successively from the upper Zagaje through the Skłoby to the Przysucha Ore-bearing formations (uppermost lower–middle–upper Hettangian); and (3) the appearance of very large herbivores (large sauropod tracks) in the late Pliensbachian (Drzewica Formation).

The ornithischian tracks (occurring mainly in the Hettangian upper Zagaje, Skłoby and Przysucha Ore-bearing formations) show the most diversified group of dinosaurs from the Lower Jurassic of the HCM; they represent trackmakers that frequented coastal environments such as delta plains, lagoons and beaches. From a behavioural perspective, this observation supports suggestions about the specific habitat preferences of early ornithischian dinosaurs.

The changes in dinosaur ichnofaunas are related to changes in the dominant plant communities. The earliest Hettangian cheirolepidiaceous conifer *Hirmeriella*-dominated forest associated with more inland fluvial environments was replaced by deltaic and coastal ginkgophyte *Czekanowskia*-*Sphenobaiera*-dominated forests in the late early Hettangian, and probably by araucarian conifer-dominated forests in the late Pliensbachian.

The plant fossil and dinosaur ichnorecord emphasizes the importance of the HCM sequence in attempts to reconstruct the complexity and diversity of Early Jurassic terrestrial ecosystems. It also focuses attention on the abundance of unique fossils in the Lower Jurassic deposits of Poland. Viewed as a whole, the Lower Jurassic of the HCM is a stratigraphic interval rich in plant fossils and dinosaur tracks but poor in dinosaur body fossil remains. Indeed, with almost thirty well dated tracksites and sites with numerous plant macrofossils, spread across the lower Hettangian to middle–upper Toarcian interval, this area has become one of the world's best-sampled Lower Jurassic terrestrial sequences.

The present review demonstrates that the Early Jurassic ecosystems of the HCM subbasin show high diversity of the floral assemblages and dinosaur ichnofaunas; the two components formed complex terrestrial and marginal-marine communities. The review also suggests that the changes registered in the dinosaur ichnofaunas of the Early Jurassic of the HCM do not appear to reflect some proposed global patterns, but rather regional ecological/evolutionary events instead. This highlights the need for caution when interpreting global trends based on local fossil records.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or other relationships that could appear to influence the study reported in this paper.

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