

## A record of climatic changes in the Triassic palynological spectra from Poland

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Based on quantitative and qualitative analyses of Triassic miopore assemblages from different regions of Poland, climatic changes have been documented. The material came from published and archival works of Orłowska-Zwolińska and of the present author. It comprises ten palynological zones distinguished in the Triassic of Poland. Two different palynological methods were applied in this study – palyno-palaeoclimatic (PPC) model and sporomorph ecogroup (SEG) model – to obtain palaeoclimatic and palaeoenviromental data. The PPC model is based on the percent ratio of xerophytic and hygrophytic elements in miopore assemblages. Dominance of xerophytic elements (spores and pollen grains of xerophytic plants) indicates dry climate conditions, and a higher ratio of hygrophytic forms (spores and pollen grains of hygrophytic plants) reflects humid phases. A significant dominance of xerophytic elements in majority of the analysed assemblages suggests a dry climate during most of the Triassic. An increase of the number of hygrophytic elements is observed in the assemblages found in the Middle Buntsandstein, Upper Muschelkalk, Lower Keuper (Sulechów Beds), Schilfsandstein, Jarkowo Beds and Wielichowo Beds. It marks climate humidification in the Olenekian, Ladinian, Middle Carnian, Late Norian and Rhaetian, respectively. The SEG model, connecting dispersed spores and pollen with the floristic palaeocommunities that occupied determined ecological niches, was applied for palaeoenviromental interpretation. Four SEGs were recognized in the Triassic spore-pollen assemblages: Upland, Lowland and River, Coastal, and not attributed. The Upland SEG dominates in these assemblages with exception of the spectra found in the Lower and Middle Buntsandstein, Upper Muschelkalk, Lower Keuper, Schilfsandstein, Jarkowo Beds and Wielichowo Beds, where the Lowland and River SEG occur more numerously.

Key words: miopores, climate, Triassic, palyno-palaeoclimatic (PPC) model, sporomorph ecogroup (SEG) model.

### INTRODUCTION

Analysis of palynomorph assemblages in palaeoecological and palaeoclimatic studies is a common research tool. Despite effects of external factors, such as transportation or depositional environment, the palynomorphs assemblages reflect the composition of plant communities and, indirectly, the environmental changes caused by climatic fluctuations. Based on the analysis of assemblages from Carnian evaporites and coals, Visscher and Van der Zwan (1981) presented a palaeoclimatological model based on hygrophytic and xerophytic elements (spores and pollen), characteristic for humid and arid climates. Predominant xerophytic elements indicate an arid climate, prevailing hygrophytic ones – a humid climate. The xerophytic or hygrophytic character of miopores is determined by their botanical affinity (Table 1) and palaeoecology of the parent plants. Advanced studies on both these issues enabled to develop the model of Visscher and Van der Zwan (1981) (see Jelen and Kušej, 1982; Heunisch, 1990; Kustatscher et al., 2010). Since 1994, I have used this method in palynological studies of Triassic

deposits from Poland (Fig. 1) and proposed to call it the palyno-palaeoclimatic (PPC) model. This paper summarizes the results of application of the PPC model as well as the sporomorph ecogroup (SEG) model of Abbink (1998; Abbink et al., 2004a, b) for the Triassic miopore assemblages described by Orłowska-Zwolińska and the present author from epicontinental deposits of Poland. The author consistently uses the palynozonation after Orłowska-Zwolińska (1985) as it is the most suitable for the miopore assemblages from the Polish epicontinental basin. Differences in relation to the zones proposed by Kürschner and Hemgreen (2010) for Central and NW Europe may result from the influences of the Siberian palaeofloristic province (see Dobruskina, 1994).

### GEOLOGICAL SETTING

During the Triassic, the Polish part of the epicontinental Southern Permian Basin was temporally connected to the Boreal Sea and the Tethys (e.g., Feist-Burkhardt et al., 2008; Bachmann et al., 2010). The Early Triassic sedimentation of the Buntsandstein took place in fluvio-lacustrine environments influenced by short-time marine incursions of the Boreal Sea in the Early Induan and Early Olenekian (Kopik and Senkowiczowa, 1973; Pieńkowski, 1991; Szyperko-Teller, 1997; Dadlez et al., 1998; Beutler and Szulc, 1999; Feist-Burkhardt et al., 2008; Bachmann et al., 2010; Figs. 2 and 3). In the Middle Tri-

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Table 1

## Quantitatively important Triassic miospore genera in the Polish assemblages and their botanical affinity

Miospore genera	Botanical affinity
<i>Acanthotriletes</i>	Filicales (Balme, 1995)
<i>Accinctisporites</i>	Unknown botanical affinity
<i>Alisporites</i>	Coniferales: Podocarpaceae, Voltziaceae (Grauvogel-Stamm, 1978; Balme, 1995), Pteridosperms (De Jersey, 1962; Van Konijnenburg-Van Cittert, 1971; Balme, 1995)
<i>Anapiculatisporites</i>	Lycopodiales (Balme, 1995)
<i>Angustisulcites</i>	Coniferales (Kürschner and Herngreen, 2010)
<i>Apiculatisporis</i>	Filicales (Balme, 1995)
<i>Aratrisporites</i>	Lycopodiales: Izoetaceae, Selaginellaceae (Helby and Martin, 1965; Grauvogel-Stamm, 1978; Grauvogel-Stamm and Düringer, 1983; Orłowska-Zwolińska, 1979, 1983; Mader, 1990b, 1997; Ruckwied, 2009; Kürschner and Herngreen, 2010)
<i>Aulisporites</i>	Equisetales (Orłowska-Zwolińska, 1983); Cycadales (Balme, 1995; Kustatscher et al., 2012)
<i>Baculatisporites</i>	Filicales: Osmundaceae (Balme, 1995; Van Konijnenburg-Van Cittert, 2002)
<i>Brachysaccus</i>	Coniferales (Orłowska-Zwolińska, 1979)
<i>Calamospora</i>	Equisetales (Orłowska-Zwolińska, 1979; Kelber and Van Konijnenburg-Van Cittert, 1998)
<i>Camerozonosporites</i>	Lycopodiales (Orłowska-Zwolińska, 1979)
<i>Camerosporites</i>	Pteridosperms (Balme, 1995); Coniferales: Cheirolepidaceae (Scheuring, 1970; Visscher et al., 1994; Roghi, 2004)
<i>Carnisporites</i>	Filicales (Roghi, 2004)
<i>Cedripites</i>	Coniferales: Cedraceae (Potonié, 1967)
<i>Cerebropollenites</i>	Coniferales: Taxodiaceae (Larsson, 2009)
<i>Chasmatosporites</i>	Cycadales (Tralau, 1968; Kürschner et al., 2014), Ginkgoales (Balme, 1995)
<i>Conbaculatisporites</i>	Filicales: Dipteridaceae (Pedersen and Lund, 1980; Roghi, 2004)
<i>Concavisporites</i>	Filicales: Dicksoniaceae (Balme, 1995), Matoniaceae (Van Konijnenburg-Van Cittert, 1993; Roghi, 2004)
<i>Concentricisporites</i>	Filicales (Kustatscher et al., 2010)
<i>Corollina (Classopolis)</i>	Coniferales: Cheirolepidiaceae (Van Konijnenburg-Van Cittert, 1987; Balme, 1995)
<i>Cycadopites</i>	Cycadales, Pteridosperms (Balme, 1995), Bennettitales (Kürschner et al., 2014)
<i>Cyclotriletes</i>	Filicales: Osmundaceae (Mädler, 1964; Orłowska-Zwolińska, 1979, 1983)
<i>Cycloverrutriletes</i>	Filicales (Orłowska-Zwolińska, 1979)
<i>Deltoidospora (Cyathidites)</i>	Filicales: Cyathaeaceae, Dicksoniaceae, Dipteridaceae, Marattiaceae, Matoniaceae, Schizeaceae (Douglas, 1973; Van Konijnenburg-Van Cittert, 1989, 1993; Balme, 1995)
<i>Densoisporites</i>	Lycopodiales: Pleuromeiaceae (Knox, 1950; Lundblad, 1950; Yaroshenko, 1975; Orłowska-Zwolińska, 1979; Meyen, 1987; Raine et al., 1988; Wang and Wang, 1990; Abbink, 1998; Looy et al., 2005)
<i>Densosporites</i>	Lycopodiales: Selaginellaceae (Balme, 1995)
<i>Dictyophyllidites</i>	Filicales: Dipteridaceae, Matoniaceae (Van Konijnenburg-Van Cittert, 1989, 1993; Balme, 1995)
<i>Duplicisporites</i>	Coniferales: Cheirolepidiaceae (Visscher et al., 1994; Roghi, 2004)
<i>Echinisporites</i>	?Filicales (Scheuring, 1970)
<i>Ellipsovelatisporites</i>	Coniferales (Mader, 1997)
<i>Endosporites</i>	Lycopodiales (Kürschner and Herngreen, 2010)
<i>Enzonalasporites</i>	Coniferales (Balme, 1995; Visscher et al. 1994; Roghi, 2004)
<i>Equisetumsporites</i> <i>Eucommiidites</i>	Equisetales (Balme, 1995), Cycadales (Van Konijnenburg-Van Cittert, 1987; Balme, 1995), Erdtmannithecales (Pedersen et al., 2013), ?Gnetales (Pedersen et al., 1989)
<i>Gleicheniidites</i>	Filicales: Gleicheniaceae (Potonié, 1967)
<i>Granuloperculatipollis</i>	Coniferales: Cheirolepidiaceae (Orłowska-Zwolińska, 1983; Roghi, 2004)
<i>Heliosaccus</i>	Coniferales: Cheirolepidiaceae (Orłowska-Zwolińska, 1979)
<i>Heliosporites</i>	Lycopodiales: Selaginellaceae (Orłowska-Zwolińska, 1979)
<i>Illinites (Succinctisporites)</i>	Coniferales: Lebachiaceae (Orłowska-Zwolińska, 1979, 1983; Balme, 1995), Voltziaceae (Grauvogel-Stamm and Grauvogel, 1973), Pteridosperms (Kürschner and Herngreen, 2010)
<i>Infernopollenites</i>	Coniferales (Visscher et al., 1994; Roghi, 2004)
<i>Keuperisporites</i>	Unknown botanical affinity
<i>Klausipollenites</i>	Coniferales: Voltziaceae (Potonié, 1967)

Tab. 1 cont.

Miospore genera	Botanical affinity
<i>Kraeuselisporites</i>	Lycopodiales (Balme, 1995; Roghi, 2004; Kürschner and Herengreen, 2010)
<i>Kugelina</i>	Coniferales: Cheirolepidaceae (Roghi, 2004)
<i>Labiisporites</i>	Coniferales: ?Voltziaceae (Orłowska-Zwolińska, 1983)
<i>Leschikisporis</i>	Filicales: Marattiaceae (Orłowska-Zwolińska, 1983; Balme, 1995)
<i>Lunatisporites</i>	Coniferales: Podocarpaceae (Clement-Westernhof, 1974; Visscher et al., 1994; Balme, 1995), Pteridosperms (Looy et al., 2005)
<i>Lundbladispora</i>	Lycopodiales: Pleuromeiaceae (Yaroshenko, 1975; Orłowska-Zwolińska, 1979; Kürschner and Herengreen, 2010; Looy et al., 2005)
<i>Lycopodiadidites</i>	Lycopodiales (Filatoff, 1975; Abbink, 1998)
<i>Lycopodiumsporites</i>	Lycopodiales (Filatoff, 1975)
<i>Marattisporites</i>	Filicales: Marattiaceae (Orłowska-Zwolińska, 1983)
<i>Microcachrydites</i>	Coniferales: Podocarpaceae (Balme, 1964, 1995)
<i>Minutosaccus</i> ( <i>Protodiploxypinus</i> )	Coniferales: Voltziaceae (Kürschner and Herengreen, 2010)
<i>Monosulcites</i>	Cycadales, Bennettitales (Potonié, 1967; Van Konijnenburg-Van Cittert, 1971; Boutler and Windle, 1993), Ginkgoales (Van Konijnenburg-Van Cittert, 1971)
<i>Nevesisporites</i>	Lycopodiales (Kustatscher et al., 2010)
<i>Osmundacidites</i>	Filicales: Osmundaceae (Van Konijnenburg-Van Cittert, 1978)
<i>Ovalipollis</i>	Coniferales: Voltziaceae (Scheuring, 1970; Orłowska-Zwolińska, 1979; Roghi, 2004)
<i>Palaeospongisporis</i>	Unknown biological affinity
<i>Parillinites</i>	Coniferales (Balme, 1995)
<i>Partisporites</i> ( <i>Paracirculina</i> )	Coniferales: Cheirolepidaceae (Orłowska-Zwolińska, 1979, 1983; Visscher et al., 1994; Roghi, 2004)
<i>Perinopollenites</i>	Coniferales: Taxodiaceae/Cupressaceae (Balme, 1985; Van Konijnenburg-Van Cittert and Van der Burgh, 1989; Van Konijnenburg-Van Cittert, 2002; Larsson, 2009)
<i>Perotrilites</i>	Unknown biological affinity
<i>Platysaccus</i>	Coniferales: Podocarpaceae (Balme, 1995)
<i>Podosporites</i>	Coniferales: Podocarpaceae (Orłowska-Zwolińska, 1983; Balme, 1995; Kürschner and Herengreen, 2010)
<i>Polypodiumsporites</i>	Filicales: Polypodiaceae (Balme, 1995)
<i>Porcellispora</i>	Mosses (Mader, 1997; Reinhardt et Ricken, 2000; Roghi, 2004)
<i>Praecirculina</i>	Coniferales: Cheirolepidaceae (Kürschner and Herengreen, 2010)
<i>Protohaploxypinus</i>	Coniferales (Orłowska-Zwolińska, 1983), Pteridosperms (Balme, 1995)
<i>Puntatisporites</i>	Filicales: Marattiaceae, Osmundaceae (Grauvogel-Stamm and Grauvogel, 1980)
<i>Rhaetipollis</i>	Coniferales (Larsson, 2009)
<i>Riccisporites</i>	Mosses: Marchanteaceae (Lundblad, 1954; Balme, 1995), Gymnosperms (Orłowska-Zwolińska, 1979, 1983), Conifers (Rhotwell et al., 2000; Vajda et al., 2013), ?Bennettitales (Mander et al., 2012; Kürschner et al., 2014)
<i>Sphaeripollenites</i>	Coniferales: Taxodiaceae, Cheirolepidaceae (Abbink, 1998)
<i>Sphagnumsporites</i>	Mosses (Filatoff, 1975)
<i>Striatoabietites</i>	Coniferales (Scheuring, 1970; Meyen, 1981, 1987), ?Pteridosperms (Kustatscher et al., 2010)
<i>Todisporites</i>	Filicales: Osmundaceae (Orłowska-Zwolińska, 1983; Balme, 1995)
<i>Toroisporis</i>	Filicales (Roghi, 2004)
<i>Trachysporites</i>	Filicales (Bonis, 2010)
<i>Triadispora</i>	Coniferales: Albertiaceae, Voltziaceae (Grauvogel-Stamm, 1969, 1978; Orłowska-Zwolińska, 1979, 1983; Balme, 1995; Brugman, 1986; Visscher et al., 1994; Kürschner and Herengreen, 2010)
<i>Tsugaepollenites</i>	Pteridosperms (Kürschner and Herengreen, 2010)
<i>Uvaesporites</i>	Filicales (Roghi, 2004), Lycopodiales: Pleuromeiaceae (Looy et al., 2005)
<i>Verrucosisporites</i>	Filicales: Marattiaceae, Osmundaceae (Orłowska-Zwolińska, 1979; Balme, 1995)
<i>Vitreisporites</i>	Ginkgoales: Caytoniaceae (Van Konijnenburg-Van Cittert, 1971; Balme, 1995); Bennettitales (Van Konijnenburg-Van Cittert, 2008), Pteridosperms (Mander et al., 2011)
<i>Voltziacaesporites</i>	Coniferales: Voltziaceae (Balme, 1995)
<i>Zembrasporites</i>	Filicales (Petersen et al., 2013)

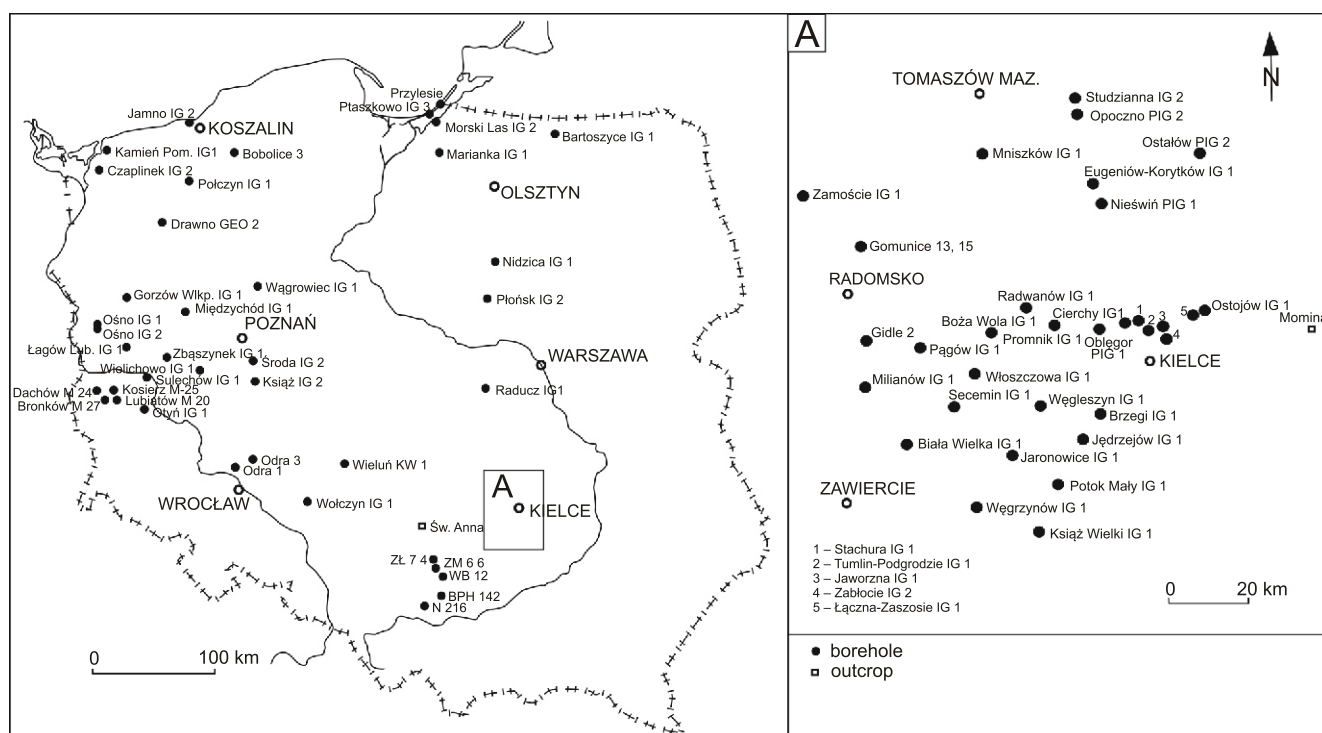


Fig. 1. Location of the studied boreholes and outcrops

assic the Polish Basin was open toward the south and temporally connected with the Tethys, which resulted in marine sedimentation of the Röt and Muschelkalk in the Anisian and Early Ladinian (Figs. 4 and 5). The author correlates the Röt deposits to Early Anisian based on the occurrence of the Anisian pollen *Stellapollenites thergartii* (Mädler) Brugman in miospore assemblages found in the Röt deposits (see also Feist-Burkhardt et al., 2008; fig. 13.1; Lucas, 2010; fig. 3). In the Late Ladinian, the marine basin was replaced by an alluvial plain with lakes and swamps, where the Lower Keuper Sulechów Beds (Lettenkohle) originated, surrounded by areas with fluvial sedimentation (Fig. 6). The latest Ladinian transgression resulted in deposition of the Grenz dolomit. Subsequently, the Polish Basin lost definitely its connection to the Tethys, and deposition of the Lower Gipskeuper occurred in hypersaline lagoon, sabkha and playa environments (Gajewska et al., 1985; Dadlez et al., 1998; Feist-Burkhardt et al., 2008; Bachmann et al., 2010; Fig. 7). During the Middle Carnian (Julian), the Schilfsandstein sedimentation took place in fluvial, deltaic and lacustrine environments (Gajewska, 1977; Szulc, 2000; Fig. 8). In the latest Carnian, evaporitic sedimentation of the Upper Gipskeuper was restricted to the central part of the Polish Basin, whereas fluvial deposition dominated in the adjacent areas (Dadlez et al., 1998). The later, Norian marine incursion resulted in deposition of the lowest part of the Jarkowo Beds. The upper part of the Jarkowo Beds and the Zbąszynek Beds were deposited in varied continental environments – mudflats, lakes, swamps and ephemeral streams with weak marine influences especially in the upper part of the Zbąszynek Beds (Deczkowski, 1997; Dadlez et al., 1998; Fig. 9). Similar sedimentation in fluvial and lacustrine environments continued in the Rhaetian (Feist-Burkhardt et al., 2008; Bachmann et al., 2010; Fig. 10).

## MATERIAL AND METHODS

The analysis covered 172 miospore assemblages in 605 samples from 71 boreholes and two outcrops (Figs. 1–10; Appendix 1\*). They represent 10 miospore zones distinguished in the Triassic deposits of Poland by Orłowska-Zwolińska (1985; Fig. 11). In majority of samples, 100 sporomorphs have been counted for quantitative analyses. The palaeoclimatic interpretation of palynomorph assemblages was done with the slightly modified palaeoclimatological model of Visscher and Van Der Zwan (1981) (I proposed the term “palyno-palaeoclimatic model” – PPC model). In this model, sporomorphs are divided into the following 18 morphogroups: A – alele and monoalele spores, B – trilete laevigate and apiculate spores, C – trilete verrucate, reticulate and murornate spores, D – trilete zonate and cingulate spores (excluding *Densoisporites* specimens), E – *Aratrisporites* spp., and F – *Porcellispora* spp., which represent hygrophytic elements; H – monosulcate pollen, I – *Illinites* spp., *Parillinites* spp., and J – asaccate pollen (excluding circumpollen), which are intermediate elements; K – *Ovalipollis* spp., L – alele bisaccate pollen, M – taeniate bisaccate pollen, N – *Triadispora* spp., O – trilete bisaccate pollen, P – vesiculate pollen, R – monosaccate pollen, and S – circumpollen, which represent xerophytic elements. There is one “problematic” group G consisting of the Early Triassic spores of *Densoisporites* produced by lycopsid *Pleuromeia*, a succulent bushy quillwort (Orłowska-Zwolińska, 1979; Meyen, 1987; Grauvogel-Stamm, 1999) characterized by wide environmental tolerance (Mader, 1990a). Van der Zwan and Spaak (1992), Galfetti et al. (2007) and Hochuli and Vigran (2010) included it to xerophytic forms, whereas Yaroshenko (1977) considered it to be a hygrophytic element. To solve this problem, group G was placed into intermediate elements in the PPC model.

\* Supplementary data associated with this article can be found, in the online version, at doi: 10.7306/gq.1239

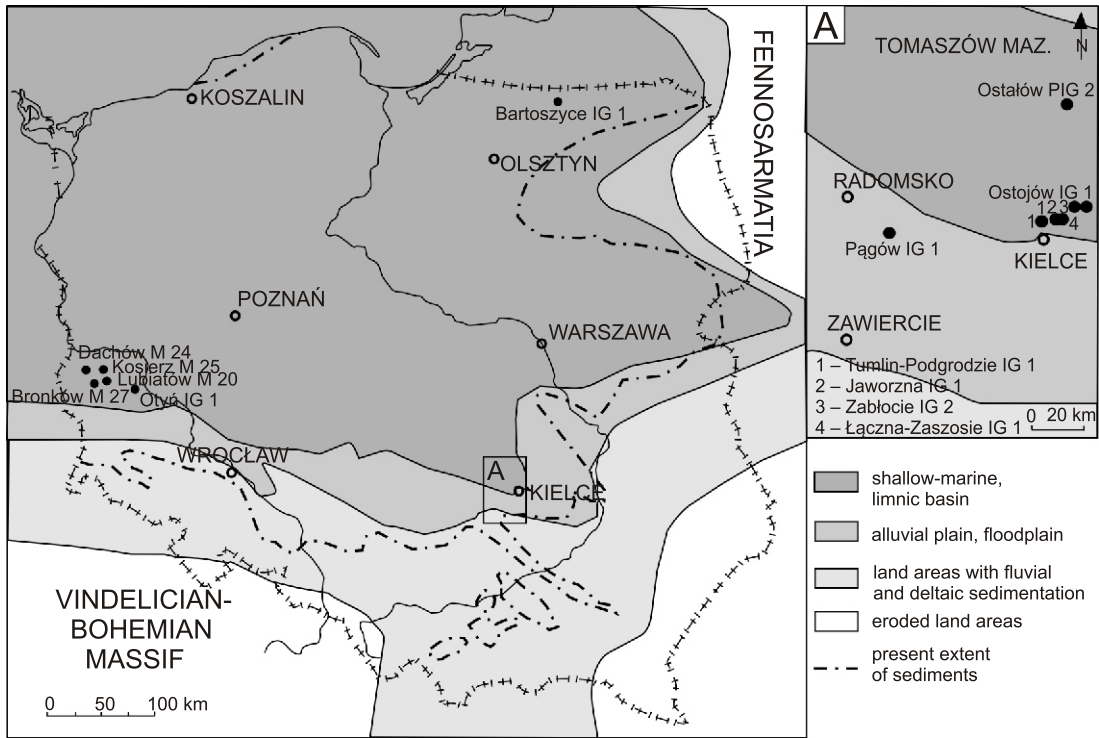


Fig. 2. Palaeogeographic map of the Lower Buntsandstein basin (after Szyperko-Teller, 1977; Dadlez et al., 1998; Kuleta and Zbroja, 2006; Feist-Burkhardt et al., 2008) with location of the boreholes containing miospore assemblages of the *obsoleta-pantii* zone

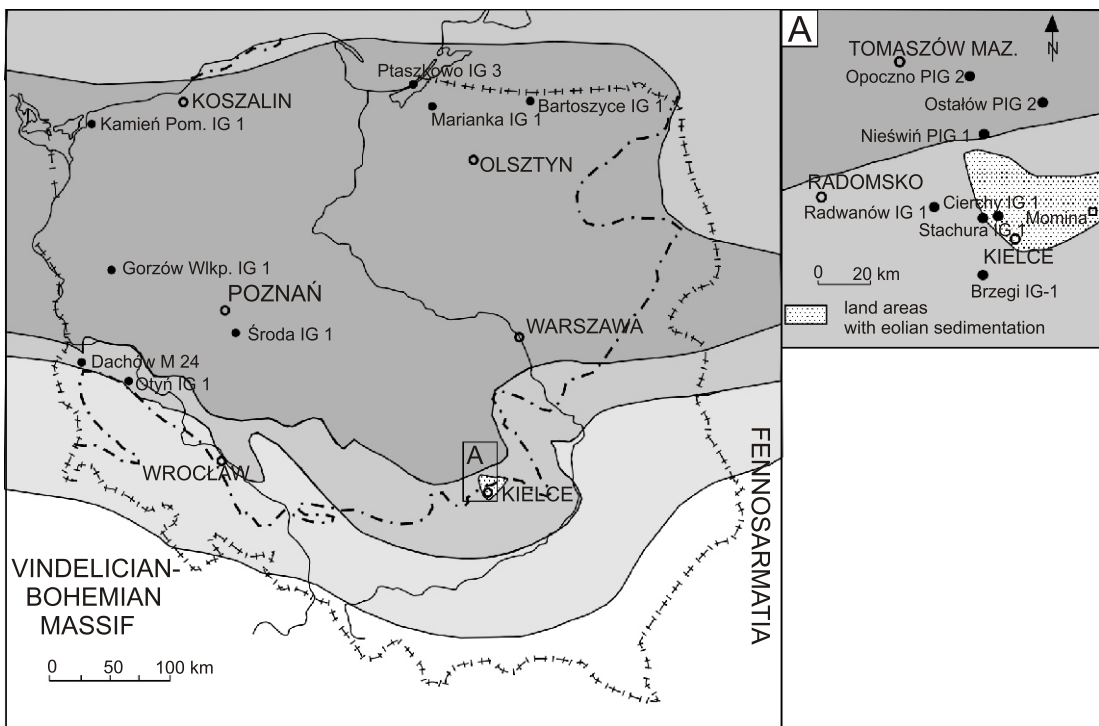


Fig. 3. Palaeogeographic map of the Middle Buntsandstein basin (after Dadlez et al., 1998) with location of the boreholes containing miospore assemblages of the *nejburgii* zone

Other explanations as in Figure 2

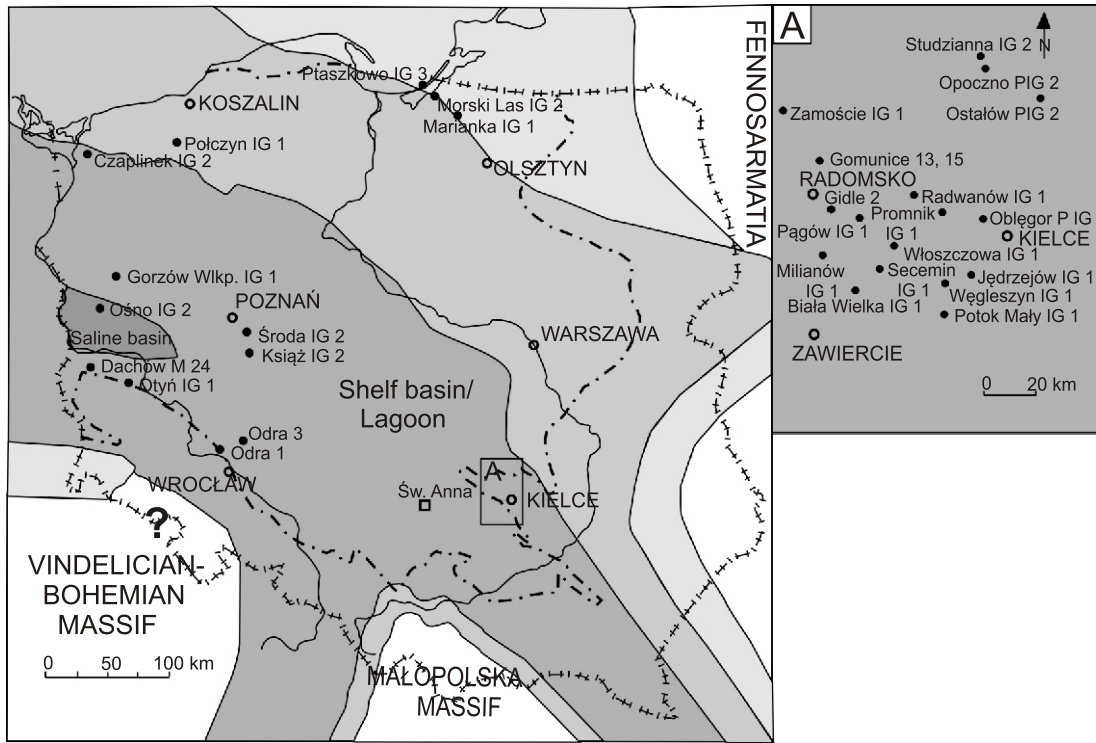


Fig. 4. Palaeogeographic map of the Röt basin (after Dadlez et al., 1998; Feist-Burkhardt et al., 2008) with location of the boreholes containing miospore assemblages of the *heteromorphus* zone

Other explanations as in Figure 2

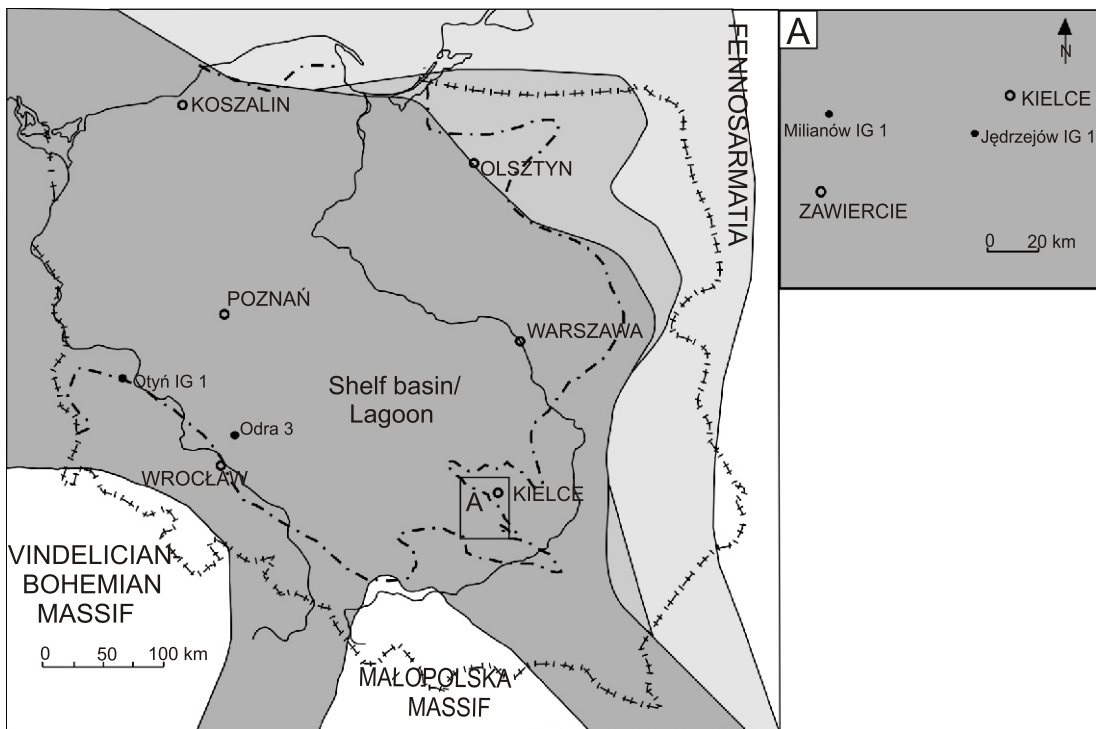


Fig. 5. Palaeogeographic map of the Lower Muschelkalk basin (after Szulc, 2000; Feist-Burkhardt et al., 2008) with location of the boreholes containing miospore assemblages of the *minor* zone

Other explanations as in Figure 2

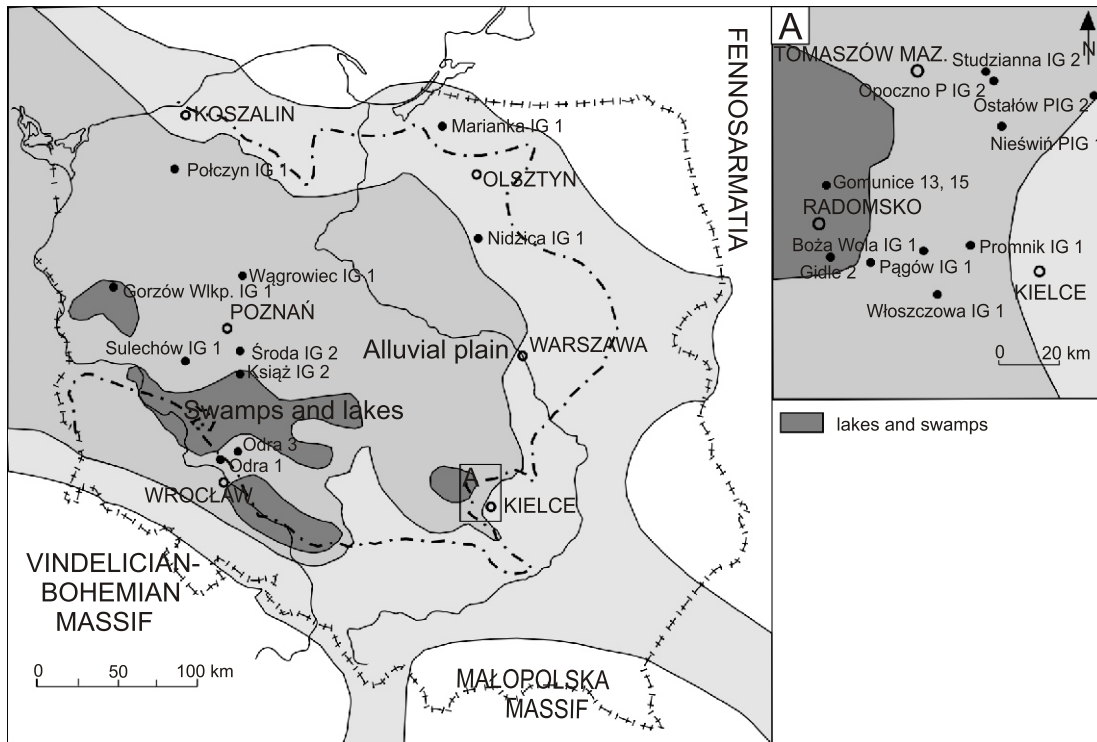


Fig. 6. Palaeogeographic map of the Lower Keuper basin (after Dadlez et al., 1998) with location of the boreholes containing miospore assemblages of the *dimorphus* zone

Other explanations as in Figure 2

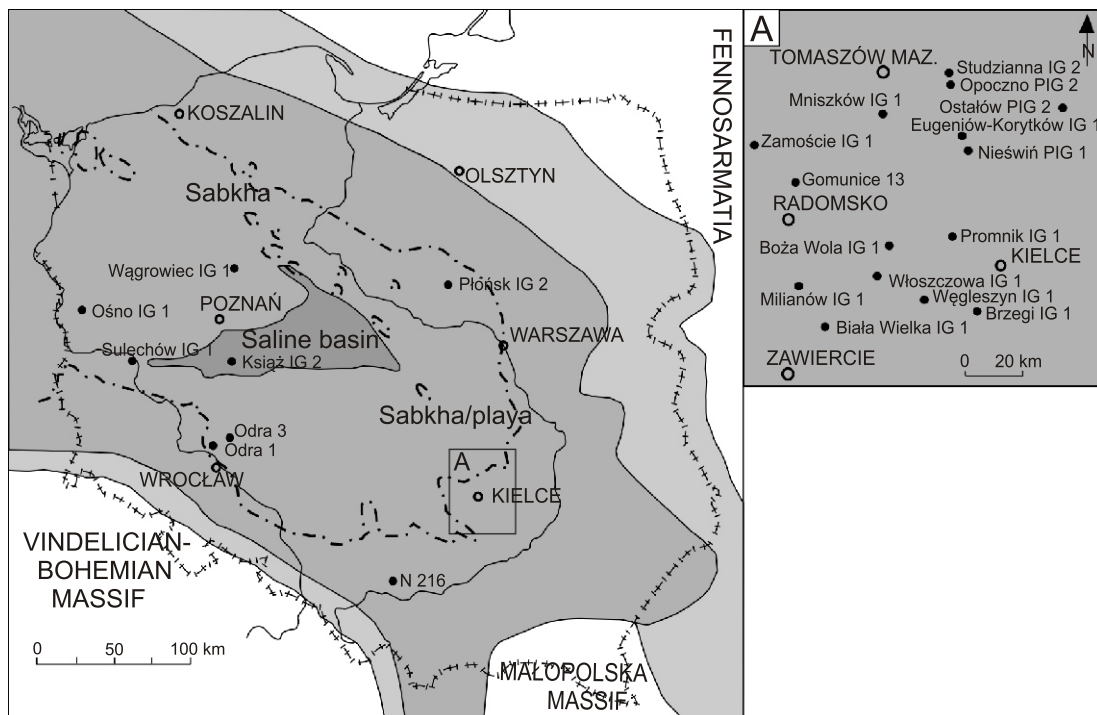


Fig. 7. Palaeogeographic map of the Lower Gipskeuper basin (after Dadlez et al., 1998; Feist-Burkhardt et al., 2008) with location of the boreholes containing miospore assemblages of the *longdonensis* zone

Other explanations as in Figure 2

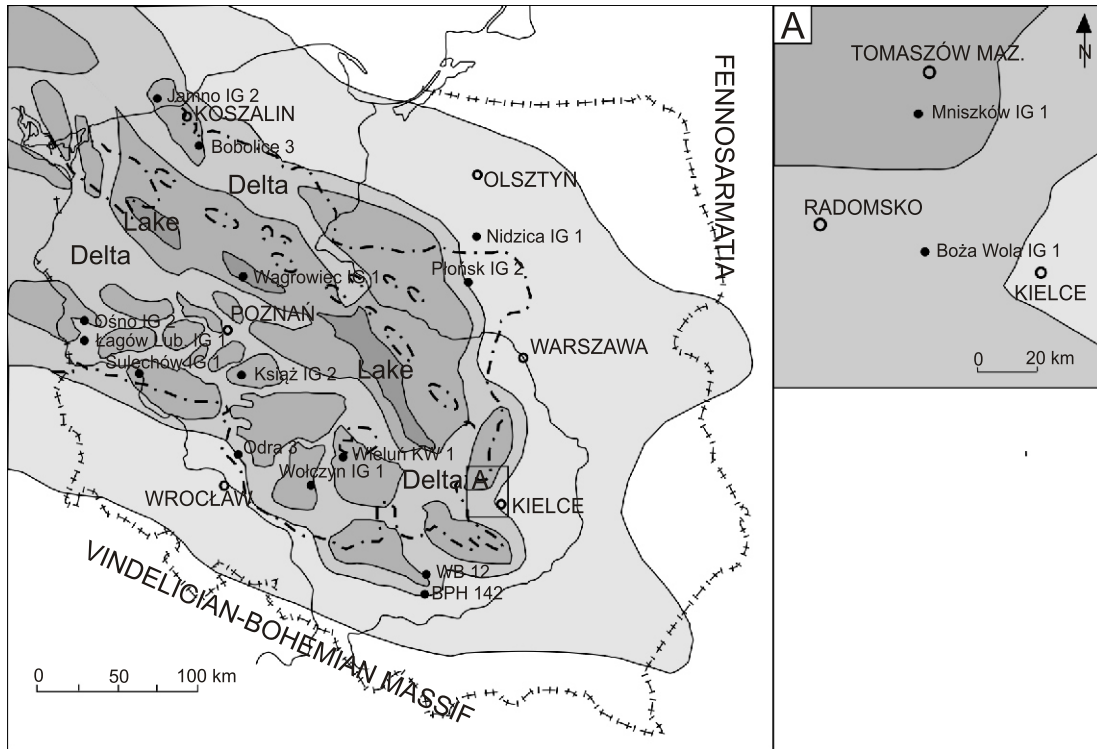


Fig. 8. Palaeogeographic map of the Schilfsandstein basin (after Dadlez et al., 1998) with location of the boreholes containing miospore assemblages of the *astigosus* zone

Other explanations as in Figure 2

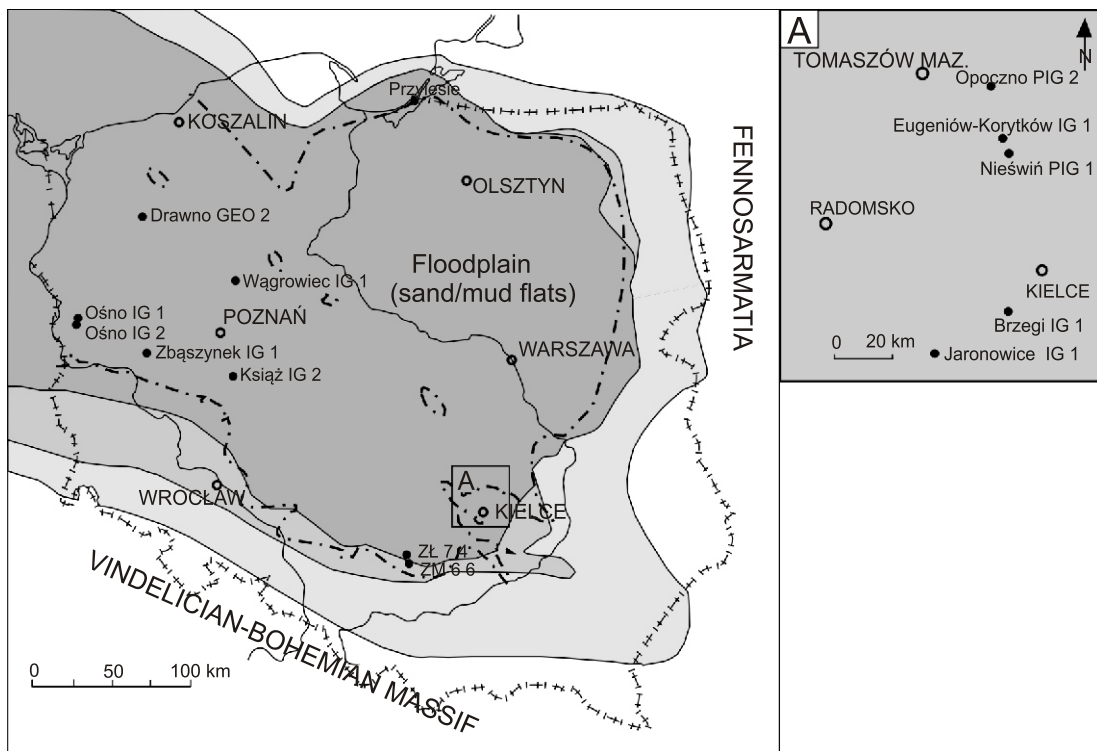


Fig. 9. Palaeogeographic map of the Jarkowo Beds basin (after Dadlez et al., 1998) with location of the boreholes containing miospore assemblages of the *meyeriana* zone

Other explanations as in Figure 2



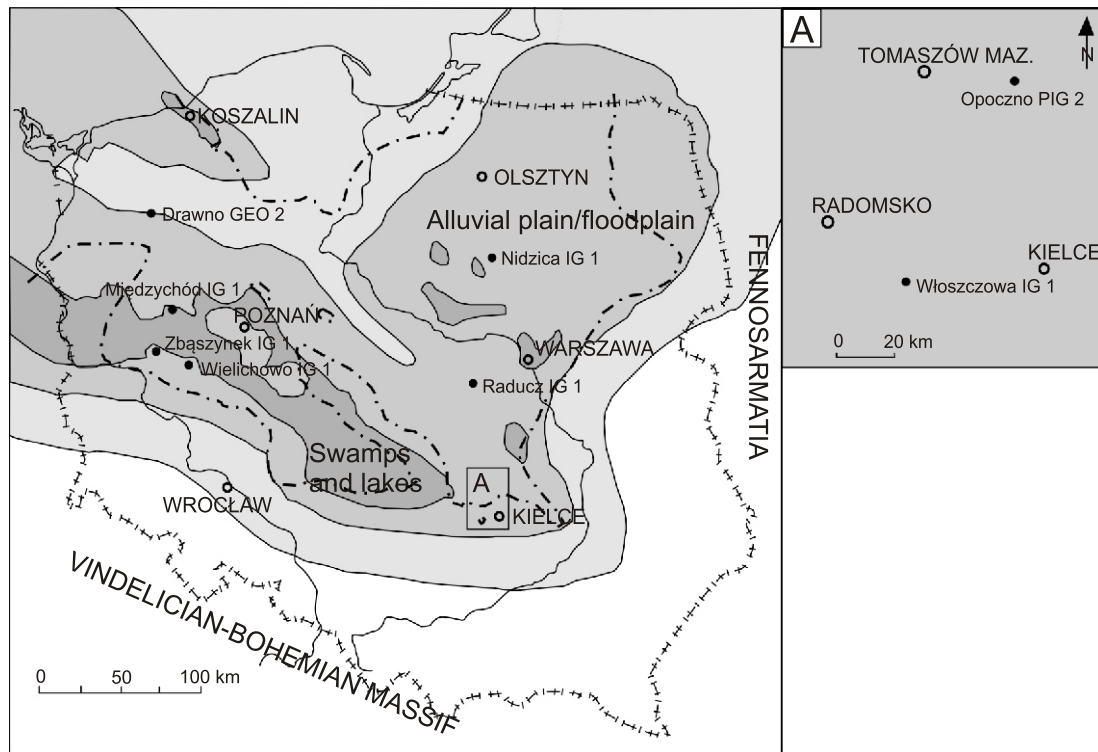


Fig. 10. Palaeogeographic map of the Wielichowo Beds basin (after Dadlez et al., 1998) with location of the boreholes containing miospore assemblages of the *tuberculatus* zone

Other explanations as in Figure 2

Palaeoclimatic interpretations were obtained from the ratio of xero- and hygrophytic forms.

Moreover, the SEG model presented by Abbink (1998; Abbink et al., 2004a, b), which connects dispersed spores and pollen with the floristic palaeocommunities that occupied specific ecological niches, was applied for palaeoenvironmental interpretation. The model is based on the ecological preferences of extinct parent plants determined after actualistic principles as well as features of sediments in which the sporomorphs were found. Four SEGs were recognized in the Triassic spore-pollen assemblages: Upland (U.S.), Lowland and River (L.R.+R.S), Coastal (C.S.), and not attributed (n.a.). Attribution of the sporomorph genera to the different SEGs is presented in Table 2. The Coastal and Land SEGs (c/l) ratio was counted. In addition, the particular miospore species and genera in the Lowland SEG indicate palaeoenvironmental conditions such as "dry" or "more wet", "warmer" or "cooler". In case of the Triassic miospores, these taxa indicators can be applied to determine a wet and/or dry environment (w/d ratio). According to Abbink (1998; Abbink et al., 2004a: p. 20–21), changes that occur especially within the Lowland SEG reflect climatic changes, whereas variations between the SEGs are related to sea level changes, small-scale lateral shifts or tectonic activity. Finally, the marine and terrestrial palynomorphs ratio (m/t) was presented. It provides information on sea level changes and is related to the c/l indicator. The following relationships are observed: when the sea level rises during a transgressive phase, the Lowland SEGs and the c/l indicator decreases whereas the value of the Upland SEG and the m/t ratio are relatively high. In contrast, when the sea level falls in a regressive phase, the Lowland SEGs and the c/l ratio increase and the m/t ratio is low.

Although the outcomes of using the PPC and SEG models depend on the distance from land area, where miospores were

produced, the general trends in climatic changes obtained at their basis coincide with those resulted from other factors like facies, clay minerals or isotope analyses (e.g., Abbink, 1998).

#### APPLICATION OF THE PPC AND SEG MODELS TO MIOSPORE ASSEMBLAGES

##### OBSOLETA-PANTII ZONE

Miospore spectra of the *obsoleta-pantii* zone were found in Lower Buntsandstein deposits of 13 boreholes concentrated in two regions – Western Poland and Holy Cross Mountains (Fig. 2; Appendix 1). The PPC model shows that (except in the Holy Cross Mts.) they are dominated by taenioid pollen of M group (*Protohaploxypinus*, *Striatoabietites* and *Lunatisporites*), which represent xerophytic conifers, reaching even >70% in some samples (Figs. 12–14; Appendix 2). These are accompanied by hygrophytic and intermediate elements: fern (group B – mainly *Cyclotriletes*) and lycopsid spores (group D – mainly *Lundbladispora*, and group G – *Densoisporites*) as well as cycadalean pollen (group H – *Cycadopites* and *Gnetacaepollenites*) reaching an average abundance of 20%. In assemblages from the Holy Cross Mts. (except in the Jaworzna IG 1 borehole, Fig. 15) the dominance of hygrophytic elements of groups D and B is evident. *Densoisporites* spores (group G) and cycadalean pollen (group H) are relatively abundant.

Applying the SEG model (Figs. 12–14; Appendix 2) evidences a marked dominance of the Upland SEG in W and NE Poland, and of the Lowland and River SEGs in the Holy Cross Mts (Fig. 15; Appendix 2). Coastal SEG is generally low and shows the c/l ratio in average of <1. Only in few samples, the

LITHOSTRATIGRAPHY W part of the Polish Basin (Szulc, 2000; Feist-Burkhardt et al., 2008; Wagner, 2008)		PALYNOSTRATIGRAPHY					
		POLAND (Orłowska-Zwolińska, 1985)	CENTRAL AND NW EUROPE (Kürschner and Herrgreen, 2010)				
TRIASSIC	KEUPER	UPPER	Wielichowo Beds	<i>tuberculatus</i>	germanicus	<i>lundbladii</i>	
		MIDDLE	Zbąszynek Beds	----- c		meyeriana	rudis
			Jarkowo Beds	b			
			Upper Gipskeuper	----- ? ----- a			
			Stuttgart Fm.	----- ?	secatus		
		Lower Gipskeuper	<i>long.</i> <i>verrucata</i> <i>iliacoides</i>	<i>verrucata</i>			
		L.	Sulechów Beds	<i>dimorphus</i>	dimorphus	dimorphus	
		MUSCHELKALK	UPPER	Boruszowice Beds			<i>Tasmanites</i>
			MIDDLE	Wilkowice Beds			----- ?
				Tarnowice Beds	oriens	Institisporites	
	Diplopora Beds						
	Karchowice Beds						
	Terebratula Beds						
	LOWER	Gogolin Beds	<i>minor</i>	thiergartii	<i>doubingeri</i>		
	BUNTSANDSTEIN	UPPER	Röt Fm.		<i>heteromorphus</i> <i>fastidiosus</i> <i>heteromorphus</i>	<i>leschiki</i>	
		MIDDLE	Polczyn Fm.	----- ? ----- <i>presselensis</i>	<i>crassa-Verrucosisporites</i>		
				<i>nejburgii</i> <i>nejburgii</i>	<i>nejburgii</i>		
	acritarchs			acritarchs			
	LOWER	Pomorska Fm.	obsoleta-pantii	obsoleta-pantii			
	Bałtyk Fm.						

Fm. – formation, L. – lower, *long.* – *longdonensis*

Fig. 11. Comparison of the Triassic palynological zonation applied in Poland with that of Central and Northwestern Europe

Coastal SEG exceeds 20%. Analysing in detail the composition of lowland flora, merely cycadalean pollen indicate “drier” climate conditions (Abbink, 1998; Abbink et al., 2004a, b). As they are a quantitatively important component of most miospore spectra, the w/d ratio is generally low – in average of <2 (Figs. 12–15; Appendix 2). This “drier” climate is confirmed also by the high amount of taeniate pollen in the spectra (see Meyen, 1987). In addition, *Cycadopites* pollen are suggested indicators of a “warmer” climate (Abbink, 1998; Abbink et al., 2004a, b). The low m/t ratio (0–0.5) evidences a weak Early Triassic transgressive impulse in the Polish Basin.

The following picture of Early Triassic plant communities appears from the sporomorph assemblages: bushy conifers have grown on dry uplands whereas lycopsids, ferns and mosses concentrated in the moist to wet inland floodplain and river banks. Cycads and lycopsids occupied seaside and inland like/playa coasts. These former could be an equivalent of the present mangrove communities (see Visscher et al., 1993). Both dry and wet areas with lower or higher salinity were overgrown by the pioneer lycopsid *Pleuromeia*.

Table 2

## Attribution of the miospore genera to the SEGs

SEG	Sporomorph genera
Upland	<i>Accinctisporites</i> , <i>Alisporites</i> , <i>Angustisulcites</i> , <i>Brachysaccus</i> , <i>Cedripites</i> , <i>Ellipsovelatisporites</i> , <i>Enzonasporites</i> , <i>Heliosaccus</i> , <i>Infernopollenites</i> , <i>Klausipollenites</i> , <i>Kugelina</i> , <i>Labiisporites</i> , <i>Lunatisporites</i> , <i>Microcachrydites</i> , <i>Minutosaccus</i> , <i>Ovalipollis</i> , <i>Parillinites</i> , <i>Partitisporites</i> , <i>Platysaccus</i> , <i>Praecirculina</i> , <i>Protohaploxylinus</i> , <i>Rhaetipollis</i> , <i>Striatoabietites</i> , <i>Triadispora</i> , <i>Tsugaepollenites</i> , <i>Voltziacaesporites</i>
Lowland and River	<i>Acanthotriletes</i> , <i>Anapiculatisporites</i> , <i>Apiculatisporis</i> , <i>Aulisporites</i> , <i>Baculatisporites</i> , <i>Calamospora</i> , <i>Camarozonosporites</i> , <i>Carnisporites</i> , <i>Chasmatosporites</i> , <i>Concavisporites</i> , <i>Conbaculatisporites</i> , <i>Concentricisporites</i> , <i>Cycadopites</i> , <i>Cyclotriletes</i> , <i>Cycloverrutriletes</i> , <i>Deltoidospora</i> , <i>Dictyophyllidites</i> , <i>Echinisporites</i> , <i>Endosporites</i> , <i>Equisetumsporites</i> , <i>Eucommiidites</i> , <i>Gleicheniidites</i> , <i>Heliosporites</i> , <i>Keuperisporites</i> , <i>Leschikisporis</i> , <i>Lycopodiacidites</i> , <i>Lycopodiumsporites</i> , <i>Marattisporites</i> , <i>Monosulcites</i> , <i>Nevesisporites</i> , <i>Osmundacidites</i> , <i>Palaeospongisporis</i> , <i>Perinopollenites</i> , <i>Perotriletes</i> , <i>Porcellispora</i> , <i>Punctatisporites</i> , <i>Riccisporites</i> , <i>Todisporites</i> , <i>Toroisporis</i> , <i>Trachysporites</i> , <i>Sphagnumsporites</i> , <i>Uvaesporites</i> , <i>Verrucosissporites</i> , <i>Vitresporites</i> , <i>Zebraasporites</i>
Coastal	<i>Aratrisporites</i> , ? <i>Cerebropollenites</i> , <i>Classopollis</i> , <i>Densoisporites</i> , <i>Densosporites</i> , <i>Duplicisporites</i> , <i>Granuloperculatipollis</i> , <i>Illinites</i> , <i>Kraeuselisporites</i> , <i>Lundbladispota</i> , <i>Podosporites</i> , <i>Protodiploxylinus</i>
Not attributed	<i>Camerosporites</i> , <i>Cerebropollenites</i> , <i>Polypodiumsporites</i> , <i>Sphaeripollenites</i>

## NEJBURGII ZONE

Spore-pollen spectra of the *nejburgii* zone were found in Middle Buntsandstein deposits of 16 boreholes and one outcrop (Fig. 3; Appendix 1). The PPC model shows that they are more differentiated than in the *obsoleta-pantii* zone. The assemblage of the ***nejburgii* and *acritarchs* subzone** from the Gorzów Wielkopolski IG 1 borehole consists almost exclusively of *Sphaeripollenites* pollen (intermediate element not attributed to any SEG) and acritarchs (Fig. 16). Fern spores (group B – *Cylotriletes*) represent hygrophytic elements, and spores of *Densoisporites nejburgii* (Schulz) produced the by lycopsid *Pleuromeia rossica* Neuburg (Yaroshenko, 1975; Orłowska-Zwolińska, 1979) – intermediate forms (group G). In the Opoczno PIG 2 borehole, the assemblage of this subzone is strongly dominated by intermediate elements – *Densoisporites nejburgii* (group G) and cycadalean pollen (group H). The ratio of the xero- and hygrophytic elements is similar to that in the *oboleta-pantii* zone. Lycopsid spores of *Endosporites* genus (group D) and fern spores of *Cyclotriletes* (group C) are the main hygrophytic elements. Conifer pollen of *Angustisulcites* (group O) and *Klausipollenites* (P group) prevail among xerophytic forms (Fig. 17).

The SEG model evidences a marked dominance of Lowland SEG. The low value of the w/d ratio indicates a dry climate. The presence of acritarchs (m/l ratio 0.5–5) and the low c/l indicator (Figs. 16 and 17; Appendix 3) are related to the Early Olenekian transgression in the Polish Basin.

Though a quantitative increase of the hygrophytic elements – mainly lycopsid spores *Endosporites* and *Lundbladispota* (group D) as well as fern spores *Cyclotriletes* and *Punctatisporites* (group B) – the *Densoisporites* spores (group G) remained dominant (on average >40%; in some samples even 80%) in the assemblages of the ***nejburgii* subzone** (Figs. 12, 14 and 16–19; Appendix 3). Xerophytic elements are dominated by conifer/gingko pollen *Protohaploxylinus*, conifer pollen *Lunatisporites* (M group) and *Platysaccus* (group O).

The SEG model is dominated by the Lowland and River SEG as well as Coastal SEG (Figs. 12, 14, 16, 17 and 19; Appendix 3). The c/l ratio, higher than in older assemblages, evidences the Middle Olenekian regression. The w/d ratio is also higher than in older spectra and varies from 2 to 26 (Figs. 12, 14 and 16–19; Appendix 3), reflecting a gradual humidification of climate.

In spite of the further increase of the number of hygrophytic elements (group B – mainly fern spores *Cycloverrutriletes*,

group D – lycopsid spores *Lundbladispota*, and group O – caytonian pollen *Vitresporites*), group D still dominates in the assemblages of the ***presselensis* subzone** (Figs. 12 and 16F; Appendix 3). Conifer taeniate pollen (M group) and vesiculate pollen (group P) are the main xeromorphic forms.

The high value of the w/d indicator (from several to 50) is a characteristic feature of analysed assemblages (Figs. 12 and 16–21; Appendix 3) and marks the humid phase in the Late Olenekian.

The SEG model shows a marked dominance of Coastal SEG with exception of the Holy Cross Mts., where the Lowland and River SEG prevails. A relatively high c/l ratio, with a maximum value of 25 in some samples, evidences the Late Olenekian regressive trend in the Polish Basin.

Distribution of the plants in the Olenekian was similar to that in the Induan: lycopsids – mainly *Pleuromeias* – and ferns occupied moist to wet inland floodplains as well as marine coastal and deltaic environments (Mader, 1990a; Visscher et al., 1993; Abbink, 1998; Grauvogel-Stamm, 1999; Abbink et al., 2004a, b). Caytoniales, which produced *Vitresporites* pollen (Balme, 1995), were associated with a fluvial environment, whereas other gingkoales and conifers overgrew dry uplands.

Compared to the Induan, the Olenekian miospore assemblages show a higher number and diversity of specimens. A trend of declining dominance of lycopods and rising prevalence of woody gymnosperms is observed. This phenomenon has a global character and reflects the recovery of diverse plant ecosystems after the end-Permian biotic crisis (e.g., Looy et al., 1999; Galfetii et al., 2007; Lindström and McLoughlin, 2007; Hermann et al., 2010, 2011a, b).

## HETEROMORPHUS ZONE

The material comes from Upper Buntsandstein (Röt) deposits of 21 boreholes and one outcrop (Fig. 4; Appendix 1).

The PPC model shows that miospore assemblages of this zone are strongly dominated by xerophytic elements – conifer pollen with prevalent trilete pollen of *Voltziacaesporites* and *Angustisulcites* (group O), in average of 20–30% (Figs. 12, 16–18, 22 and 23; Appendix 4). Vesiculate pollen *Microcachrydites* and *Klausipollenites* (group P), taeniate pollen *Protohaploxylinus* and *Striatoabietites* (group M) as well as *Triadispora* (group N) occur abundantly. *Illinites chitonoides* Klaus (*al. Succinctisporites grandior* Leschik *sensu* Mädlar)

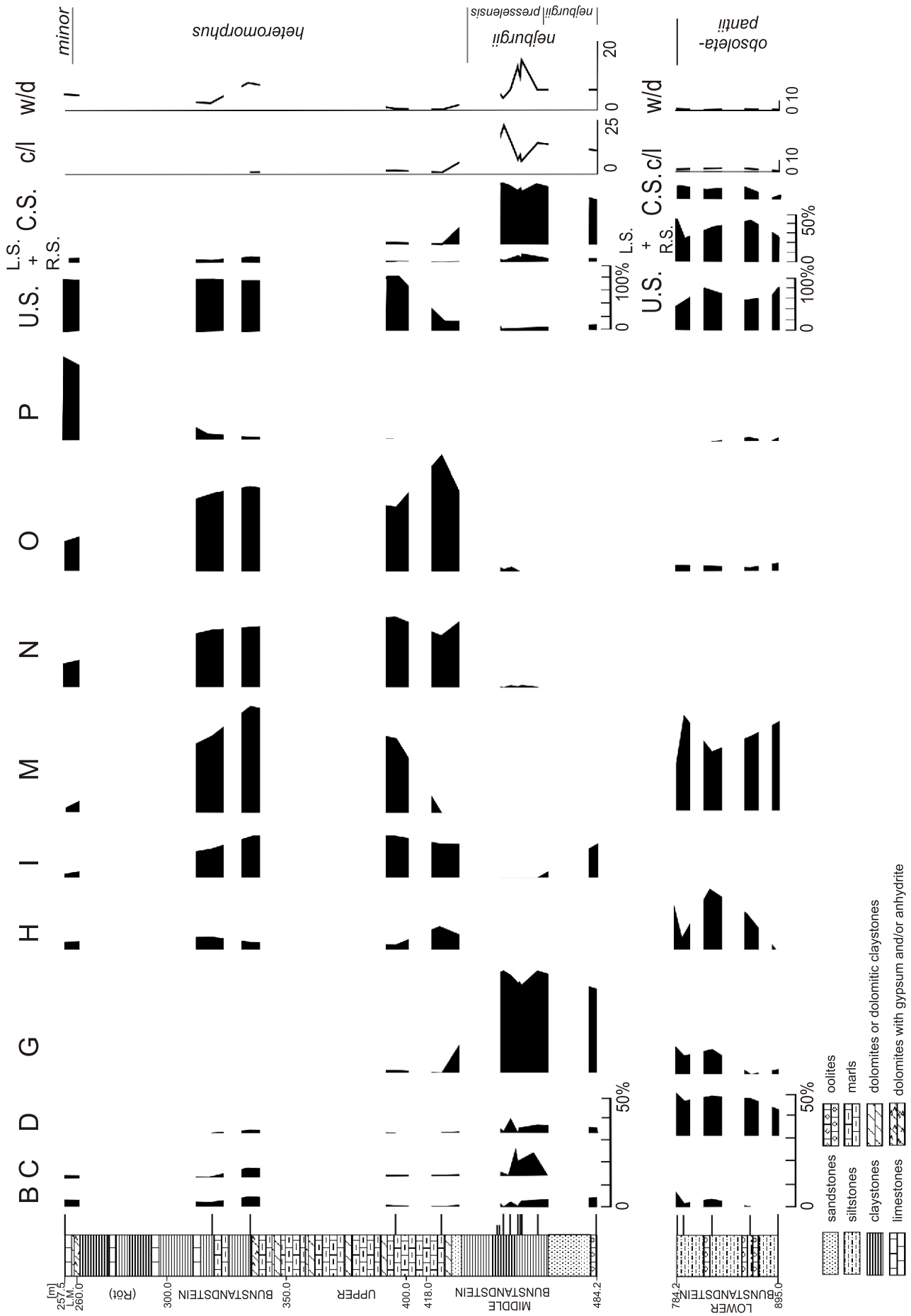


Fig. 12. Application of the PPC and SEG models to the assemblages of the *obsolete-pantii*, *neburgii* and *heteromorphus* zones from the Dachów M 24 borehole (based on Ortowska-Zwołńska, 1984)

L.M. – Lower Muschelkalk

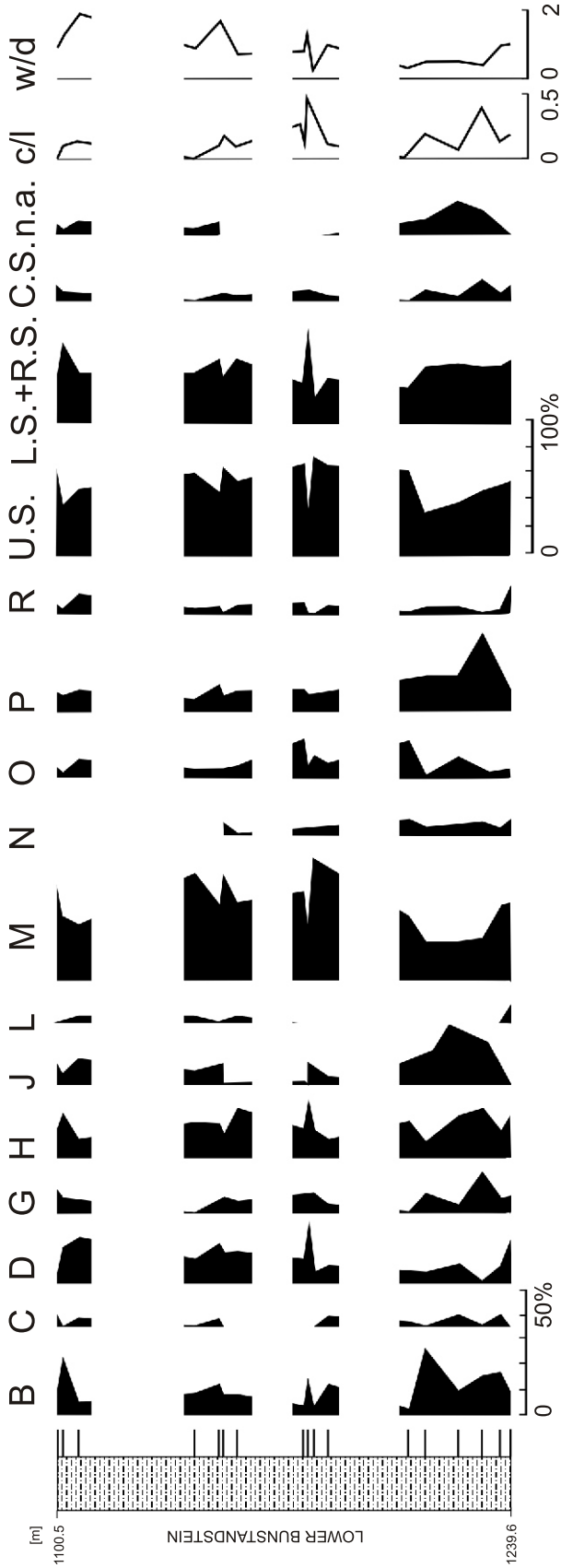


Fig. 13. Application of the PPC and SEG models to the assemblage of the *obsoleta-pantii* zone from the Kosierz M 25 borehole (based on Fijałkowska, 1995)

Explanations as in Figure 12

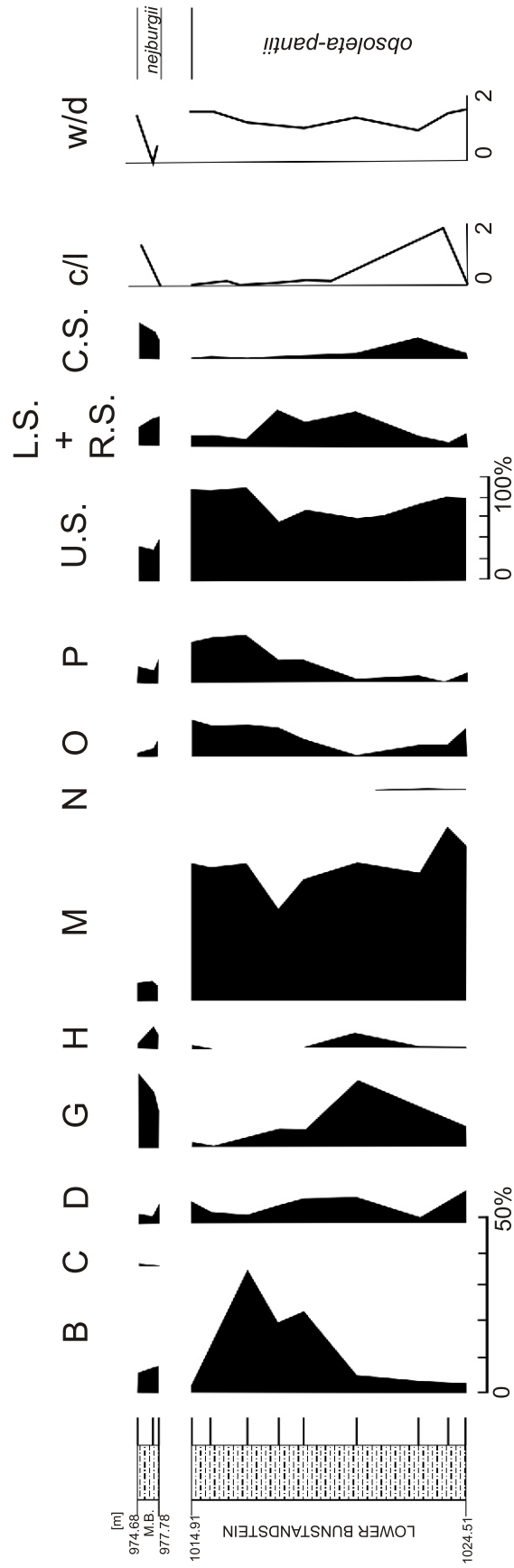


Fig. 14. Application of the PPC and SEG models to the assemblages of the *obsoleta-pantii* and *nejburgii* zones from the Bartoszyce IG 1 borehole

Explanations as in Figure 12; M.B. – Middle Buntsandstein

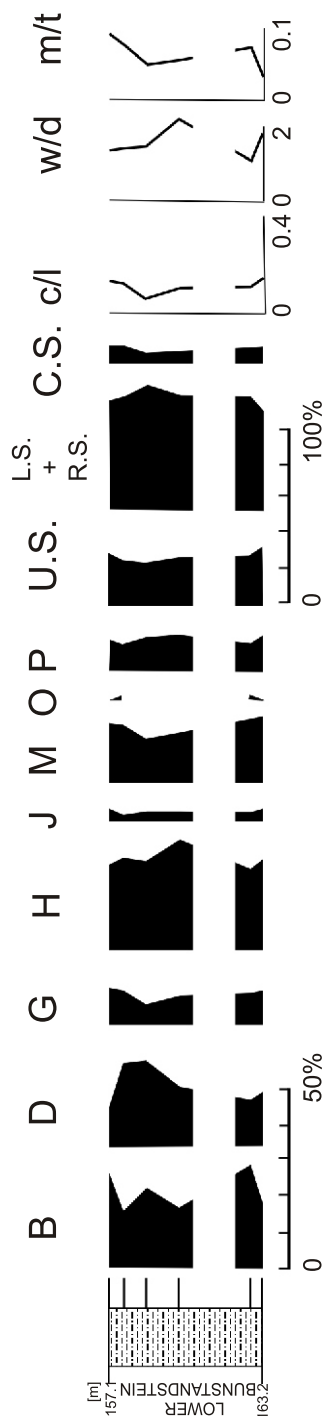


Fig. 15. Application of the PPC and SEG models to the assemblage of the *obsoleta-pantii* zone from the Jaworzna IG 1 borehole (based on Fijałkowska, 1994a)

Explanations as in Figure 12

(group I), produced by the ruderal herbaceous conifer *Aethophyllum stipulare* (Brongniart) (Grauvogel-Stamm, 1978; Rothwell et al., 2000), is a characteristic element of the Early Anisian spectra. Fern spores *Cyclotriletes* (group B) and *Verrucosisporites* (group C), cycadalean pollen (group G) and lycopid spores *Aratrisporites* (group E) prevail among the hygromorphic components.

The w/d indicator curve has a marked "arid" pick in the assemblages representing the upper part of the *heteromorphus* zone, distinguished as the *fastidiosus* subzone (Figs. 18, 22 and 23), which corresponds to the arid climate in Early Anisian.

The SEG model shows a remarkable dominance of the Upland SEG (in average of >80%) (Figs. 12, 16–18, 22 and 23; Appendix 4) consisting most exclusively of conifers. The Lowland SEG is relatively poor and represented by rare lycopids, ferns and horsetails. The low c/l ratio – in average of <1 (Figs. 16 and 18; Appendix 4) and the presence of acritarchs mark the Early Anisian transgression in the Polish Basin. Strong dominance of conifer pollen in the Early Anisian spectra evidences the next phase of forestation during the Triassic (e.g., Kürschner and Hergreen, 2010). Taxonomically diverse conifer forests and bushfields occupied not only dry uplands but also marine/lagoon coasts, where *Aethophyllum stipulare* formed reed-like belts (Grauvogel-Stamm, 1978; Mader, 1990a; Visscher et al., 1993). This plant was an important element of wetland communities during the Middle Triassic (Brugman et al., 1994; Rothwell et al., 2000).

#### MINOR ZONE

Miospore assemblages of the *minor* zone were found in Lower Muschelkalk deposits of 10 boreholes (Fig. 5; Appendix 1). In majority of the studied samples they are strongly dominated by xerophytic conifer pollen *Microcachrydites* (group P) with average abundance of >20% (Figs. 12, 16 and 18; Appendix 5). Conifer pollen *Angustisulcites* (group O) and *Triadispora* (group N) occur less frequently. Lycopod spores *Aratrisporites* (E group), spores *Perotriletes* of unknown botanical affinity (group D), fern spores *Cyclotriletes* and horsetail spores *Equisetumsporites* (group B) represent the hygrophytic forms.

The SEG model shows that Upland SEG, composed most exclusively of conifers, prevails in all analysed samples (in average of >80%; Figs. 12, 16 and 18; Appendix 5) which could partly result from the distance to land areas. Only in few samples, a higher abundance of the Lowland and River SEG is observed (Appendix 5). The low c/l ratio results from transgression of the Muschelkalk sea documented by the presence of acritarchs (see m/t indicator). A rise of the w/d ratio is observed in relation to the *heteromorphus* zone, which is >7 in some samples and reflects wet climate conditions.

Distribution of palaeoflora was similar to that known from the Early Anisian. Visscher et al. (1993) suggested, based on the palynomorph spectra from Southern Germany, a recessive palaeoflora migration from coastal areas towards inland.

#### ORIENS ZONE

Assemblages of the *oriens* zone were found in Middle Muschelkalk deposits of nine boreholes (Appendices 1 and 6). They consist almost entirely of xerophytic elements that include conifer pollen *Triadispora* (group N), *Microcachrydites* (group P) and *Angustisulcites* (group O) (Figs. 24 and 25; Appendix 6). Dominance of *Triadispora* pollen is also observed in spectra from Southern Germany (Visscher et al., 1993; Kürschner and Hergreen, 2010).

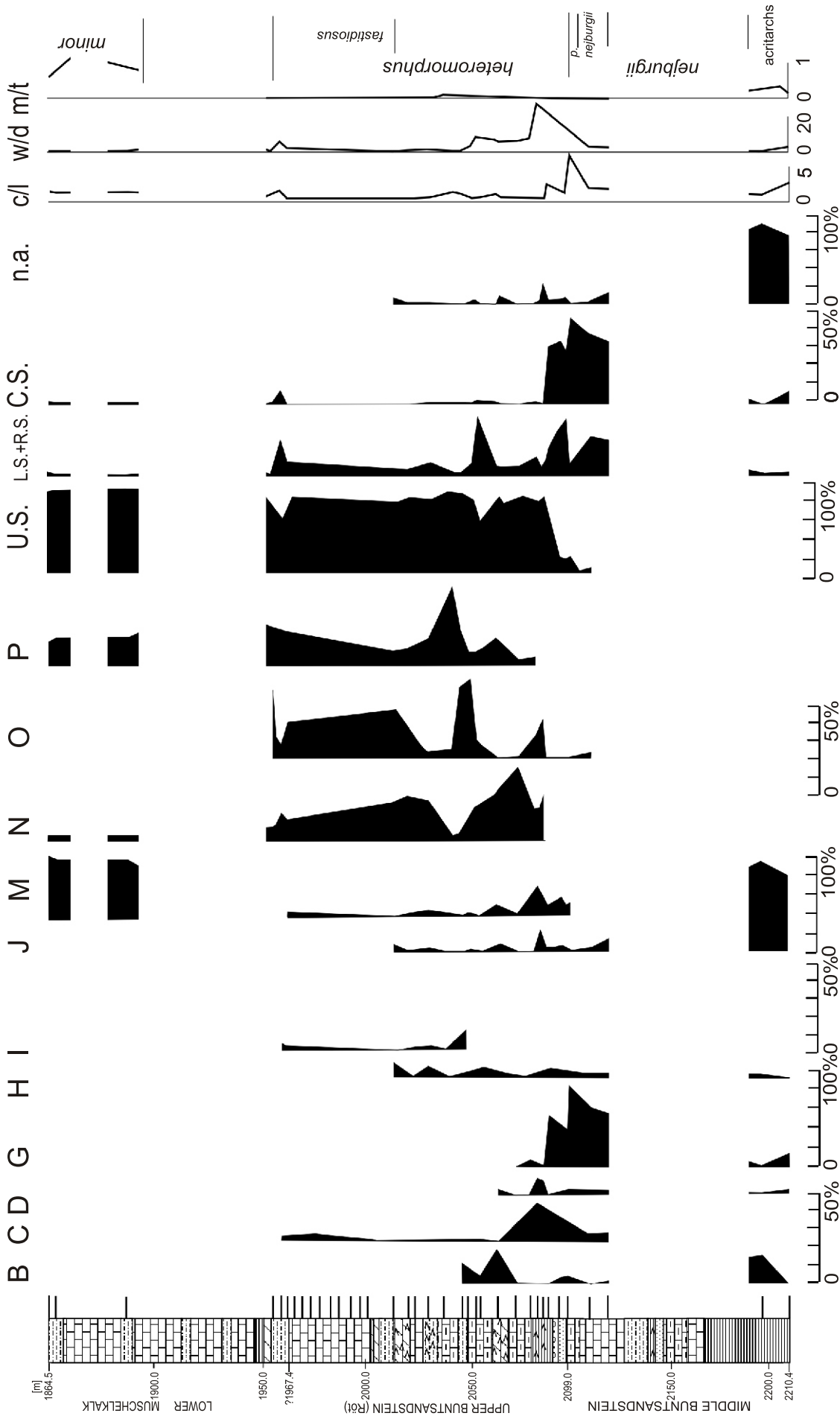


Fig. 16. Application of the PPC and SEG models to the assemblages of the *nejburgii*, *heteromorphus* and *minor* zones from the Gorzów Wielkopolski IG 1 borehole (based on Ortowska-Zwoińska, 1977)

Explanations as in Figure 12: *p.* – *presselensis*

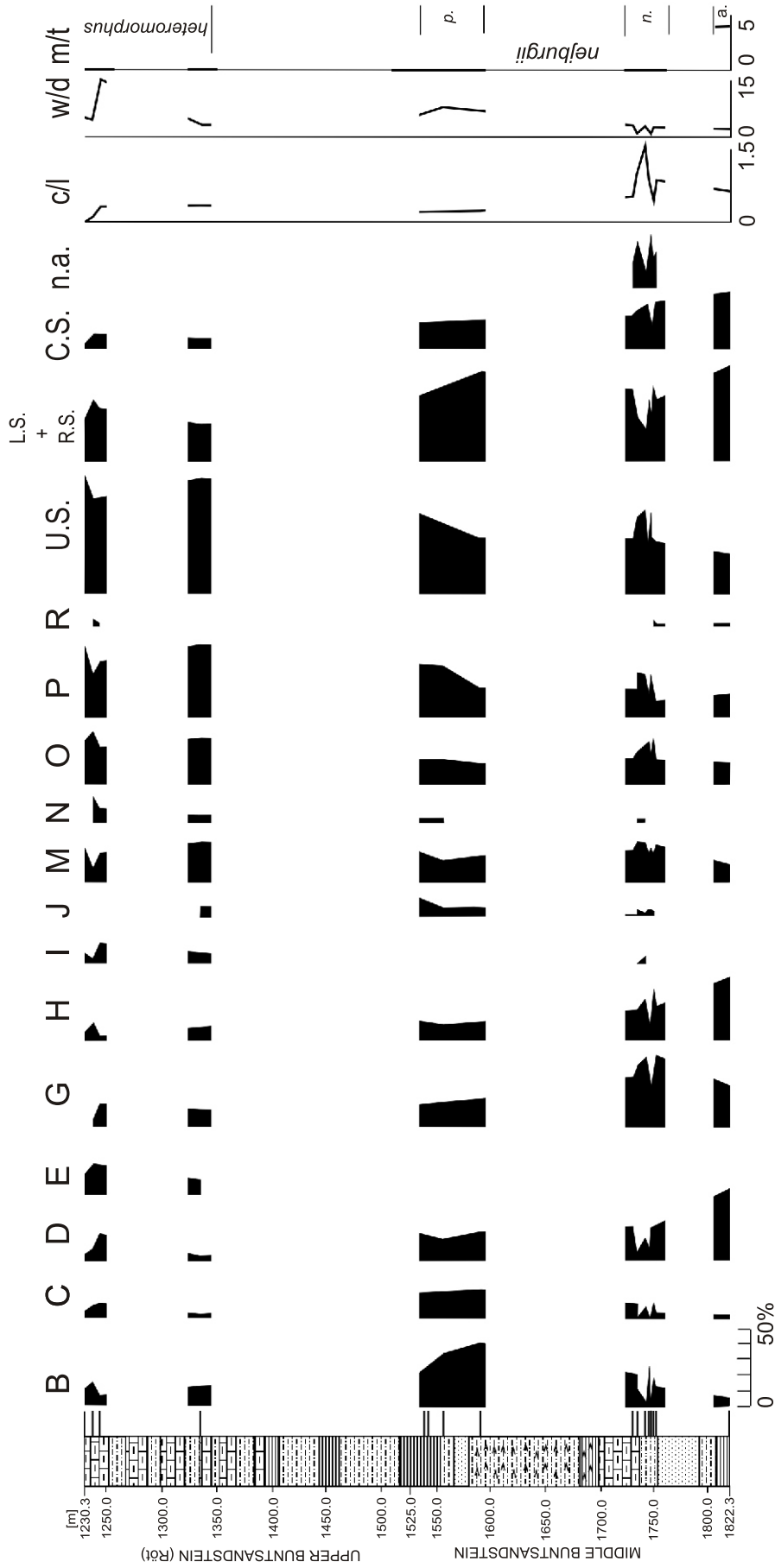


Fig. 17. Application of the PPC and SEG models to the assemblages of the *neburgii* and *heteromorphus* zones from the Opočno PIG 1 borehole (based on Fijałkowska, 1993, 2006a)

Explanations as in Figure 12; a. – acritarchs, n. – *neburgii*, p. – *presselensis*



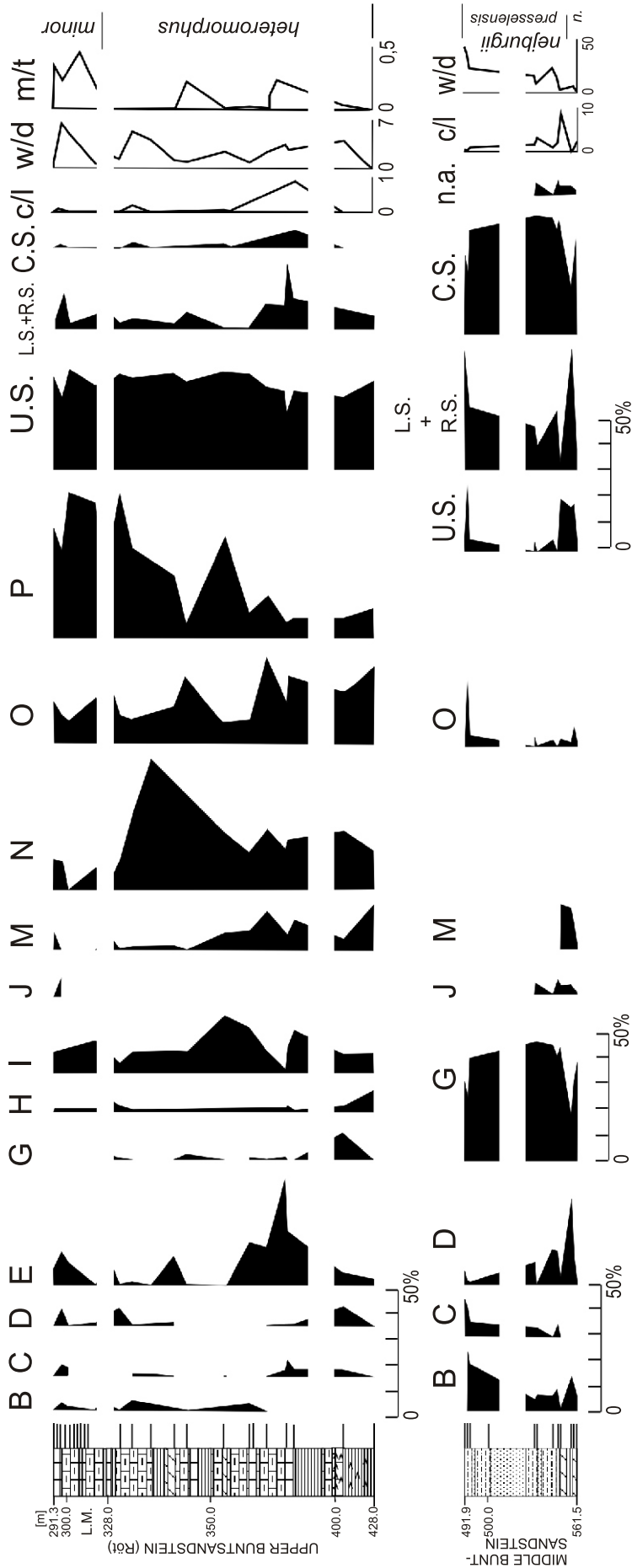


Fig. 18. Application of the PPC and SEG models to the assemblages of the *nejburgii*, *heteromorphus* and *minor* zones from the Otyń IG 1 borehole (based on Ortowska-Zwolińska, 1984)

Explanations as in Figure 12; L.M. – Lower Muschelkalk, n. – *nejburgii*

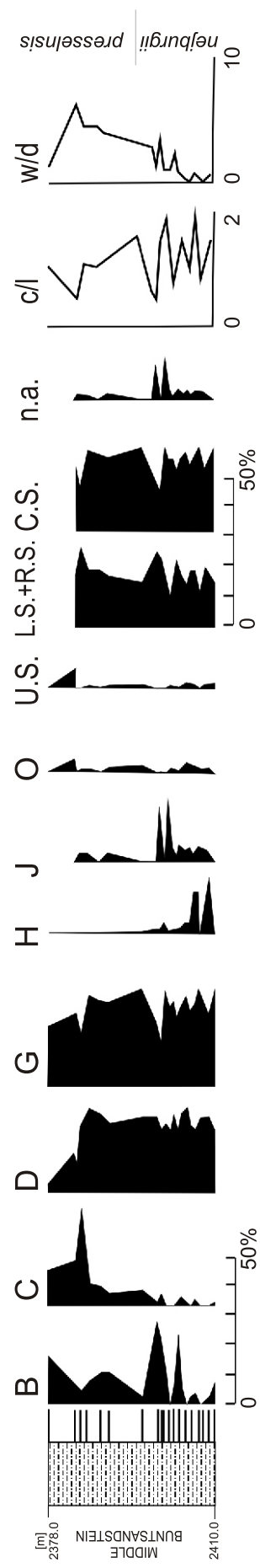


Fig. 19. Application of the PPC and SEG models to the assemblages of the *nejburgii* zone from the Środa IG 2 borehole (based on Ortowska-Zwolińska, 1977, 1982, 1984)

Explanations as in Figure 12

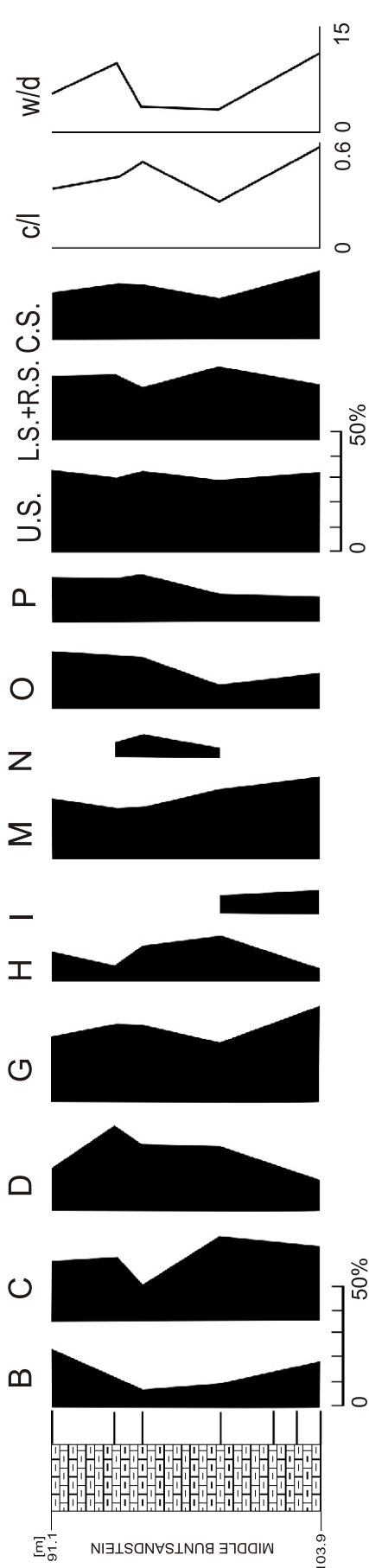


Fig. 20. Application of the PPC and SEG models to the assemblages of the *neiburgii* zone from the Cierchy IG 1 borehole (based on Fijałkowska, 1994a)

Explanations as in Figure 12

The very low w/d indicator – in average of <1 (Figs. 24 and 25; Appendix 6) marks dry climate conditions in the Late Anisian.

The Upland SEG shows the highest values among the Triassic miospore spectra, with an average of 90%. The Coastal SEG is highly reduced, even to 0 in some samples, which implies a very low c/l ratio related to the transgressive trend in the Polish Basin.

#### DIMORPHUS ZONE

##### TASMANITES SUBZONE

The material comes from Upper Muschelkalk deposits of seven boreholes (Appendices 1 and 7).

The PPC model evidences significant differences in the spectra from the lower part of the *dimorphus* zone – **Tasmanites subzone** – between the individual regions of Poland. In general, the assemblages from NE Poland and the Nida Basin are dominated by xerophytic elements (P group), whereas those from eastern and western Poland as well as the Holy Cross Mts – by hygrophytic forms (groups E and B; Figs. 24–30; Appendix 7).

Conifer pollen *Minutosaccus* (*al. Protodiploxylinus*; group P), *Triadispora* (group N), *Illinites* (group I) and monosaccate pollen *Heliosaccus* (group R) are the main xerophytic elements. Taeniate pollen of *Striatoabietites* and *Protohaploxylinus* (group M) occur less frequently. Lycopside spores *Aratrisporites* (group E), fern spores *Todisporites* (group B) and *Verrucosporites* (group C) prevail among hygrophytic forms.

The w/d ratio value is variable and relatively high: 30–70 in N–NW Poland and the Holy Cross Mts., 11–30 in E–NE Poland and the Nida Basin (Figs. 24–30; Appendix 7), indicating a wet climate in the Early Ladinian.

The SEG model shows a remarkable dominance of the Lowland and River SEG in western Poland and the Holy Cross Mts. (in average of >65%) and of the Upland SEG in NE Poland and the Nida Basin. The Coastal SEG varies from 4 to 17% and the c/l ratio is 0.1–0.8 (Figs. 24–30; Appendix 7). Low m/t ratio indicates a weak influence of the Early Ladinian transgression in the Polish Basin.

Conifers overgrown not only dry uplands but also occurred as pioneers in the xerophytic marine coastal palaeobiocenosis. An important component of these plant communities was Voltziales producing pollen *Minutosaccus gracilis* (Scheuring) Orłowska-Zwolińska and *Podosporites amicus* Scheuring (Visscher et al., 1993; Kürschner and Hengreen, 2010). Lycopside and ferns represented wetter lowland floras.

##### DIMORPHUS SUBZONE

Miospore assemblages representing the upper part of the *dimorphus* zone – **dimorphus subzone** were found in the Sulechów Beds (Lettenkeuper) deposits from 18 boreholes (Fig. 6; Appendix 1). They are dominated by hygrophytic elements: equisetale spores *Calamospora*, fern spores *Todisporites* and *Cyclotriletes* (group B) (in average of >30%) and taxonomically diverse *Aratrisporites* spores (group E) (4–50%) (Figs. 24, 25 and 28–32; Appendix 8). Conifer pollen *Minutosaccus* and *Brachysaccus* (group P) (10–40%) are the main xerophytic components.

The w/d ratio varies widely from 0.5 to 58, but is generally high (in average of >20) with a decreasing trend in the upper

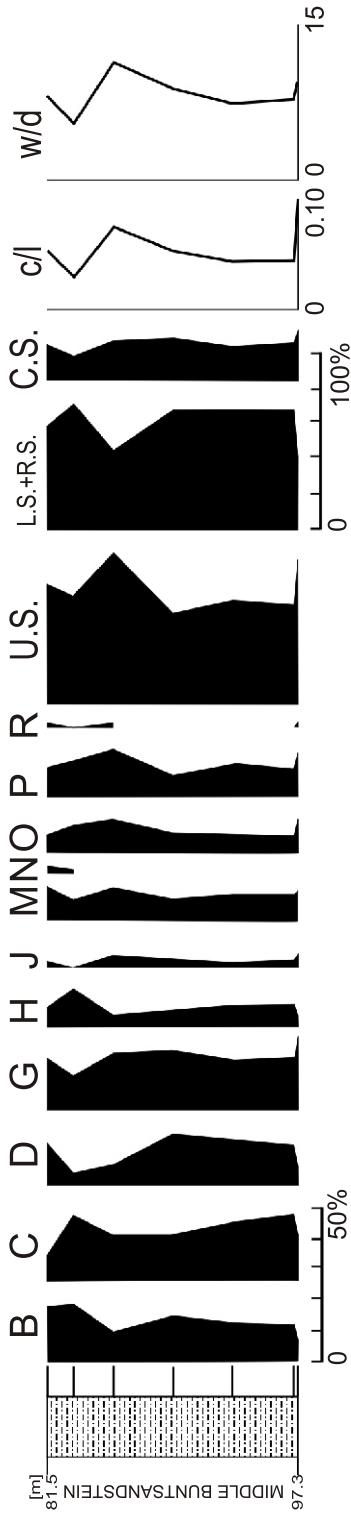


Fig. 21. Application of the PPC and SEG models to the assemblages of the *presseleensis* subzone of the *nejburgii* zone from the Stachura IG 1 borehole (based on Fijałkowska, 1994a)

Explanations as in Figure 12

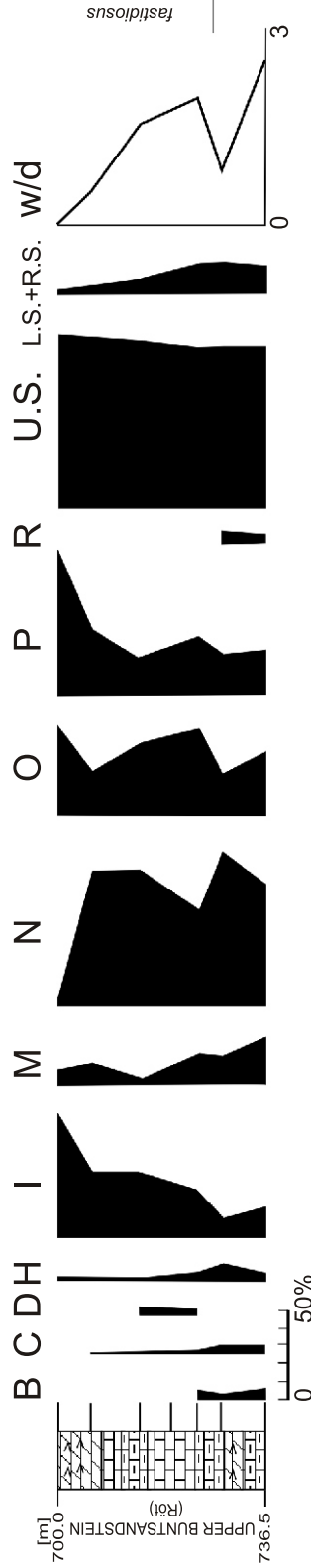


Fig. 22. Application of the PPC and SEG models to the assemblages of the *heteromorphus* zone from the Odra 3 borehole (based on Orłowska-Zwolińska, 1988)

Explanations as in Figure 12

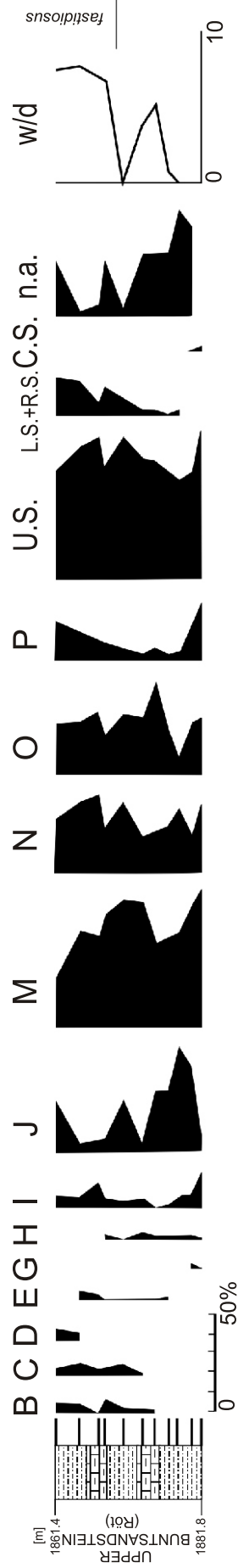


Fig. 23. Application of the PPC and SEG models to the assemblages of the *heteromorphus* zone from the Polczyn IG 1 borehole (based on Orłowska-Zwolińska, 1977, 1984)

Explanations as in Figure 12

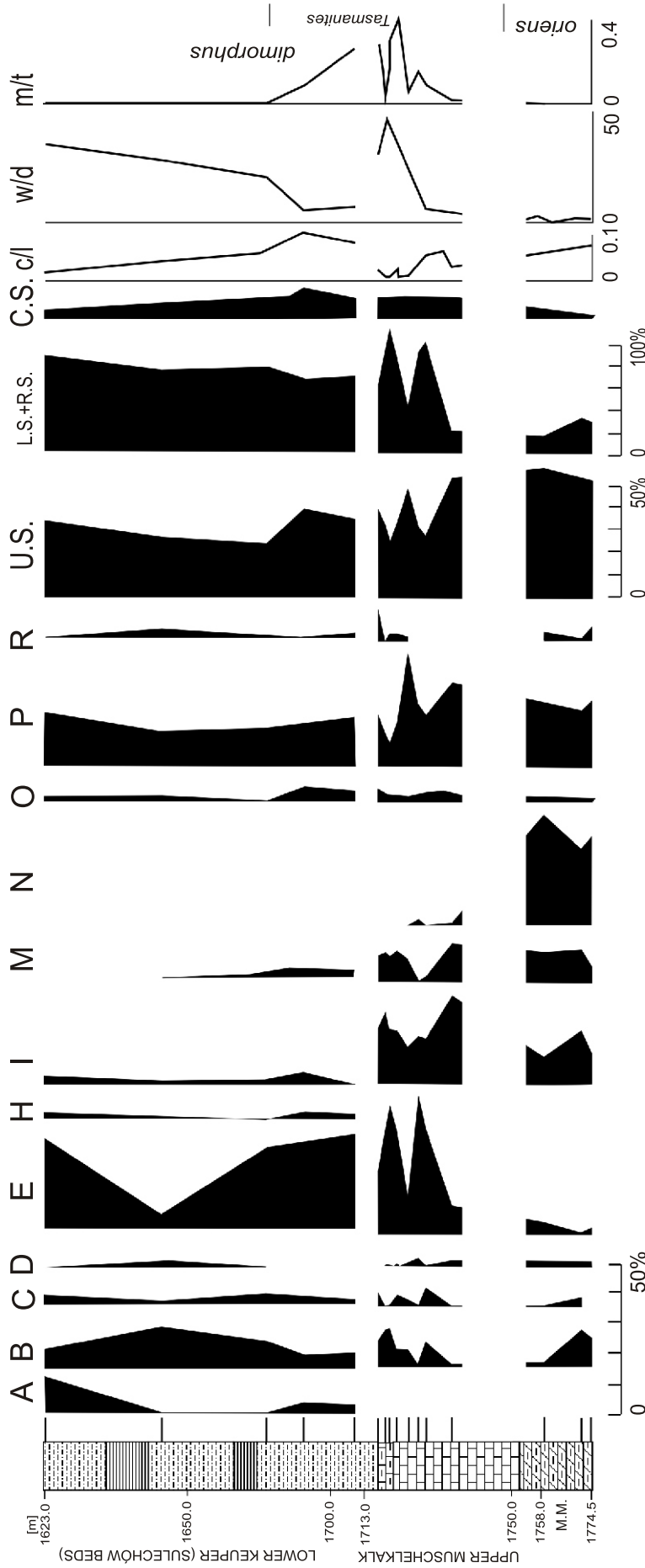


Fig. 24. Application of the PPC and SEG models to the assemblages of the *oriens* and *dimorphus* zones from the Gorzów Wielkopolski IG 1 borehole (based on Orłowska-Zwołńska, 1977, 1983)

Explanations as in Figure 12; M.M. – Middle Muschelkalk

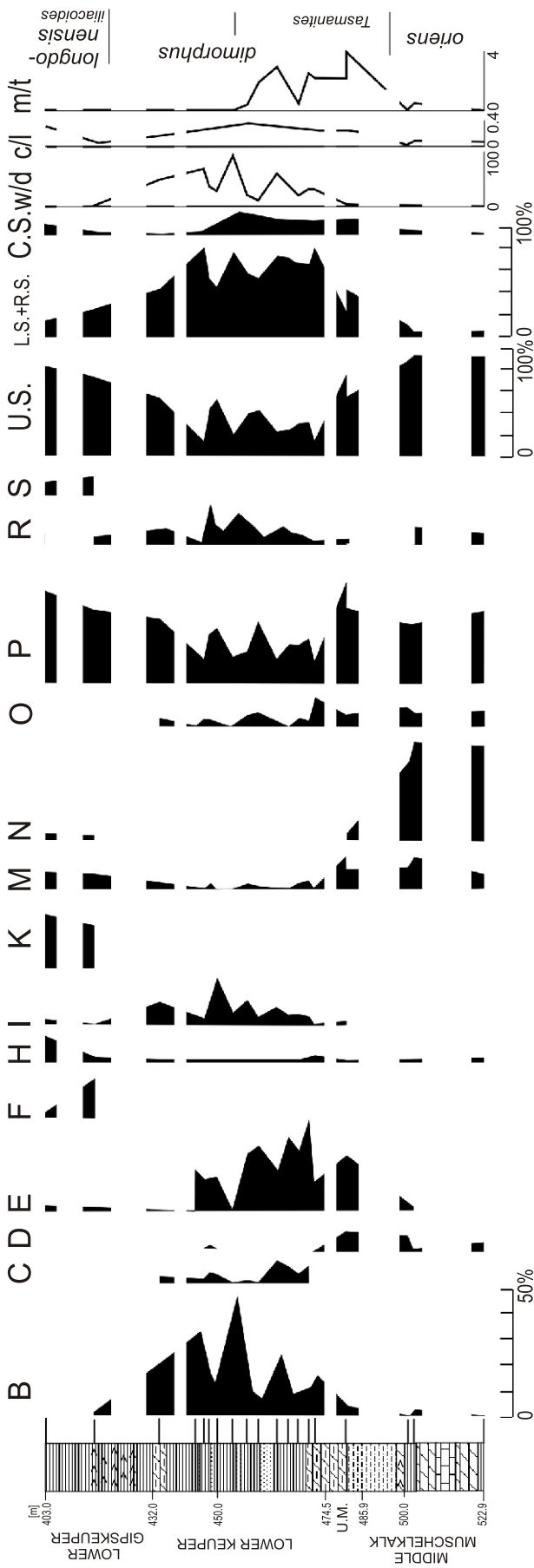


Fig. 25. Application of the PPC and SEG models to the assemblages of the oriens, dimorphus and longdonensis zones from the Odra IG 3 borehole (based on Ortowska-Zwolińska, 1988)

Explanations as in Figure 12; U.M. – Upper Muschelkalk

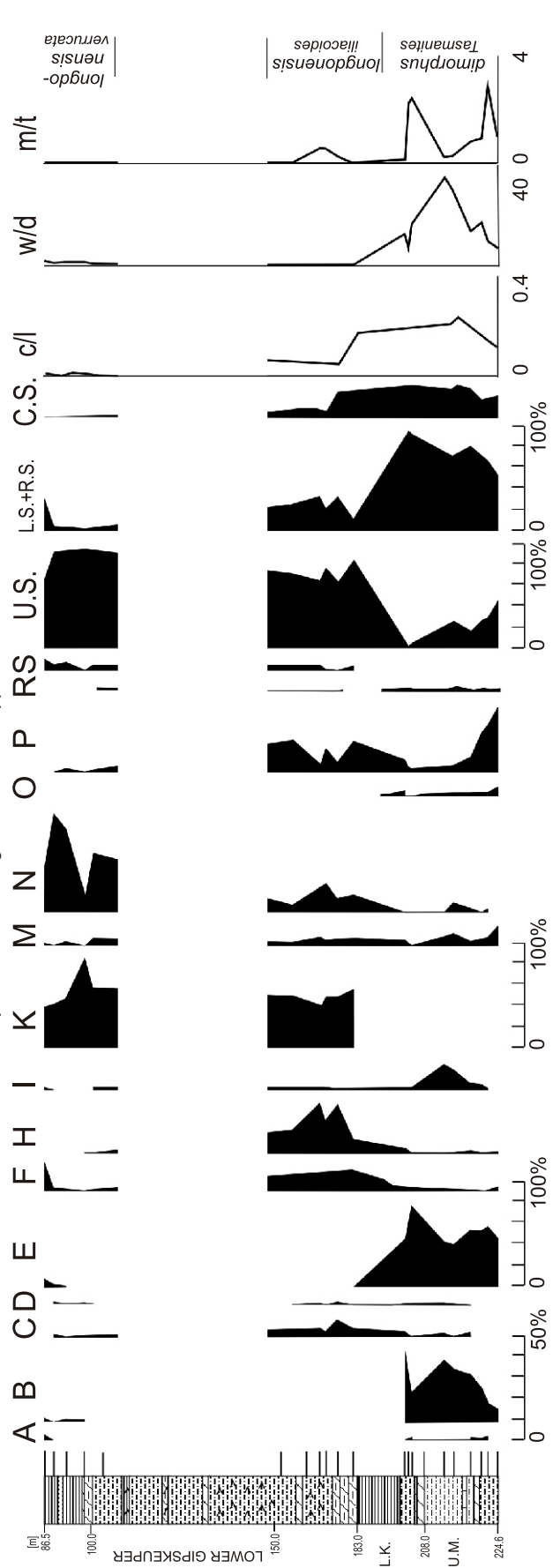


Fig. 26. Application of the PPC and SEG models to the assemblages of the dimorphus and longdonensis zones from the Odra 1 borehole (based on Ortowska-Zwolińska, 1988)

Explanations as in Figures 12 and 25; L.K. – Lower Keuper

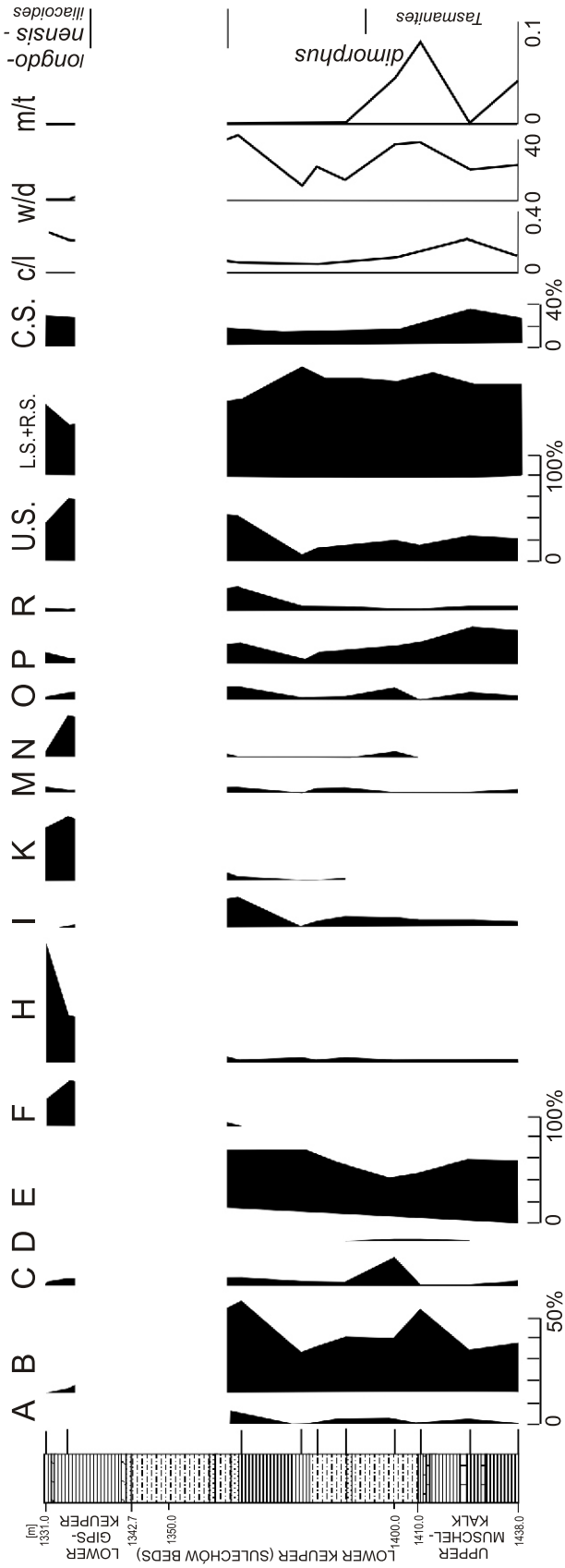


Fig. 27. Application of the PPC and SEG models to the assemblages of the *dimorphus* and *longdonensis* zones from the Książ IG 2 borehole (based on Ortowska-Zwolińska, 1983)

Explanations as in Figure 12

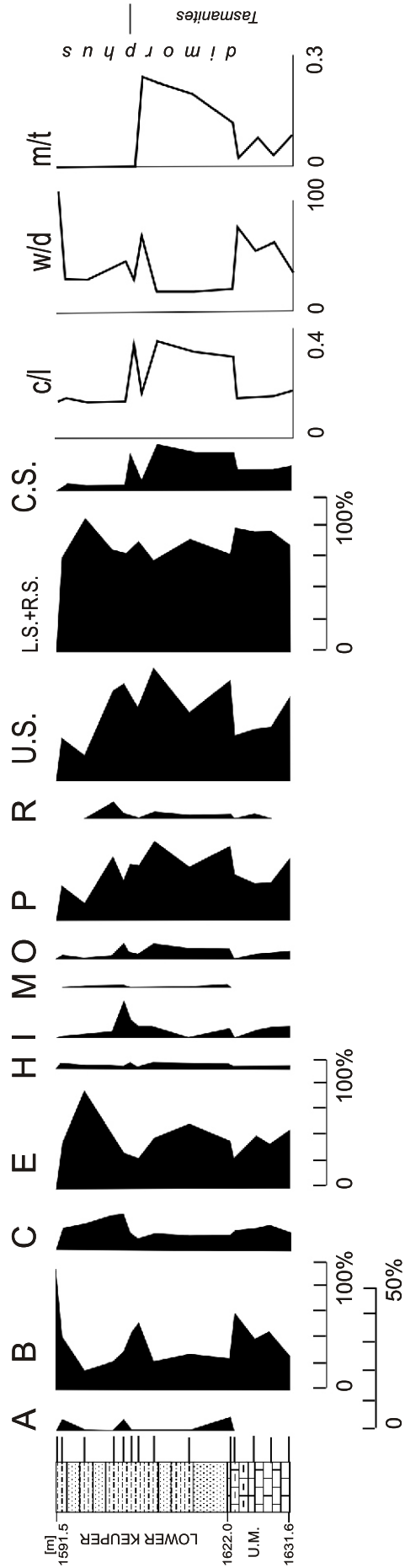


Fig. 28. Application of the PPC and SEG models to the assemblages of the *dimorphus* zone from the Polczyn IG 1 borehole (based on Ortowska-Zwolińska, 1983)

Explanations as in Figures 12 and 25

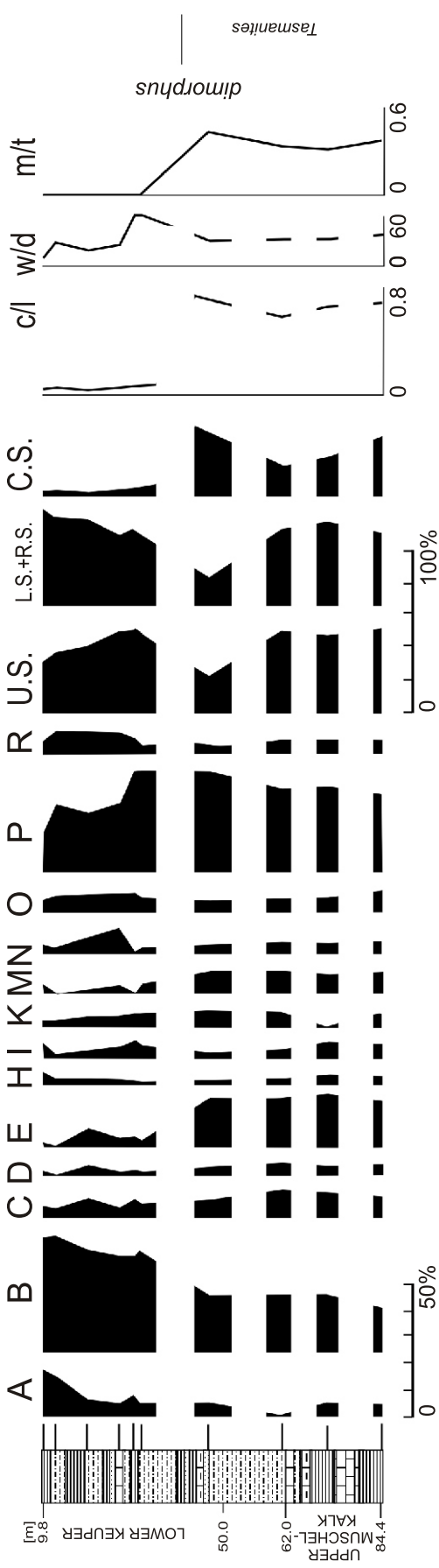


Fig. 29. Application of the PPC and SEG models to the assemblages of the *dimorphus* zone from the Promnik IG 1 borehole

Explanations as in Figure 12

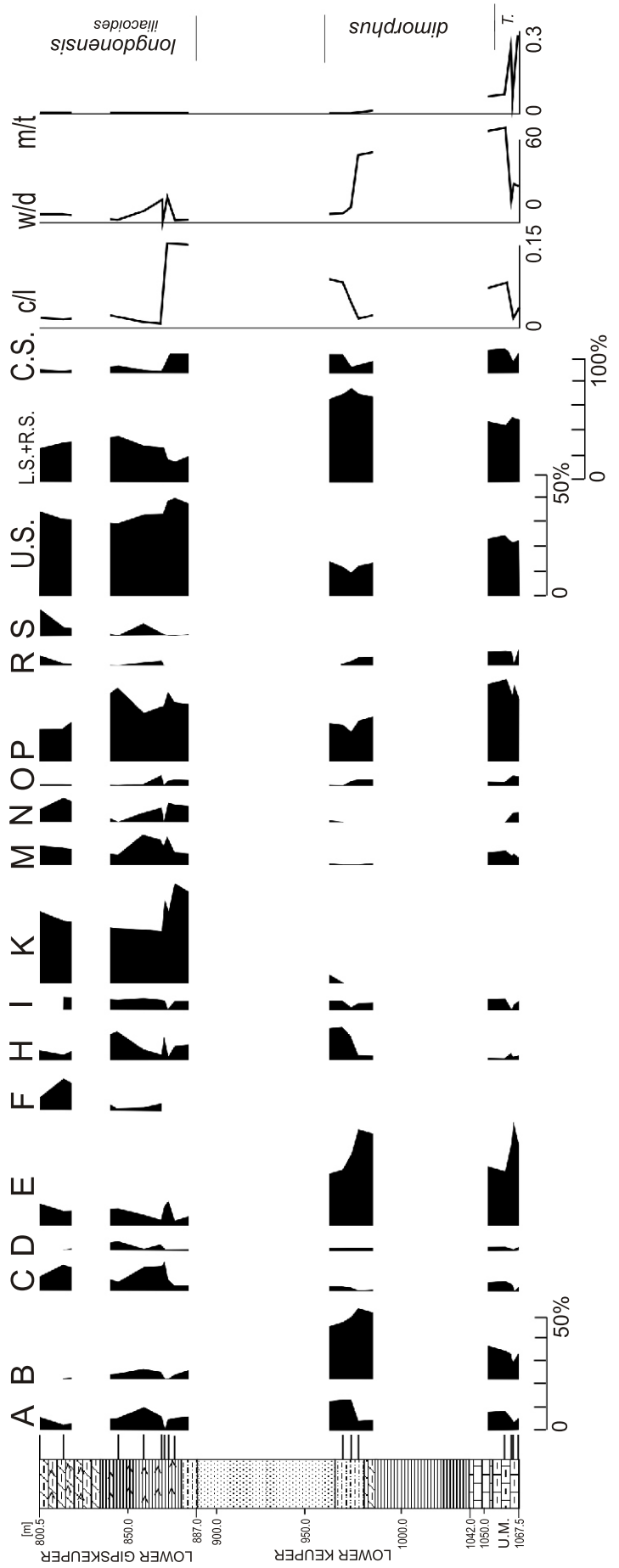


Fig. 30. Application of the PPC and SEG models to the assemblages of the *dimorphus* and *longdonensis* zones from the Nieswiń PI1 borehole (based on Fijałkowska, 1991)

Explanations as in Figures 12 and 25; T. – *Tasmanites*

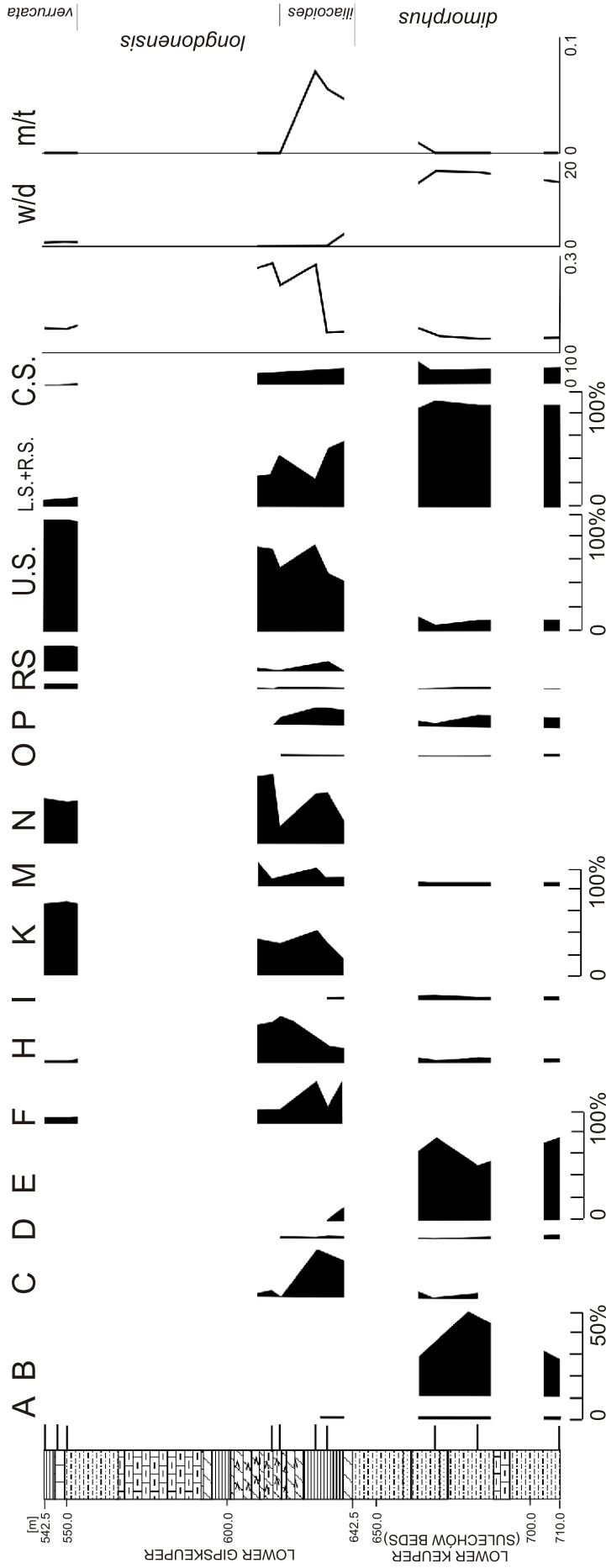


Fig. 31. Application of the PPC and SEG models to the assemblages of the *dimorphus* and *longdonensis* zones from the Sulechów IG 1 borehole (based on Ortowska-Zwolińska, 1972b, 1983)

Explanations as in Figure 12



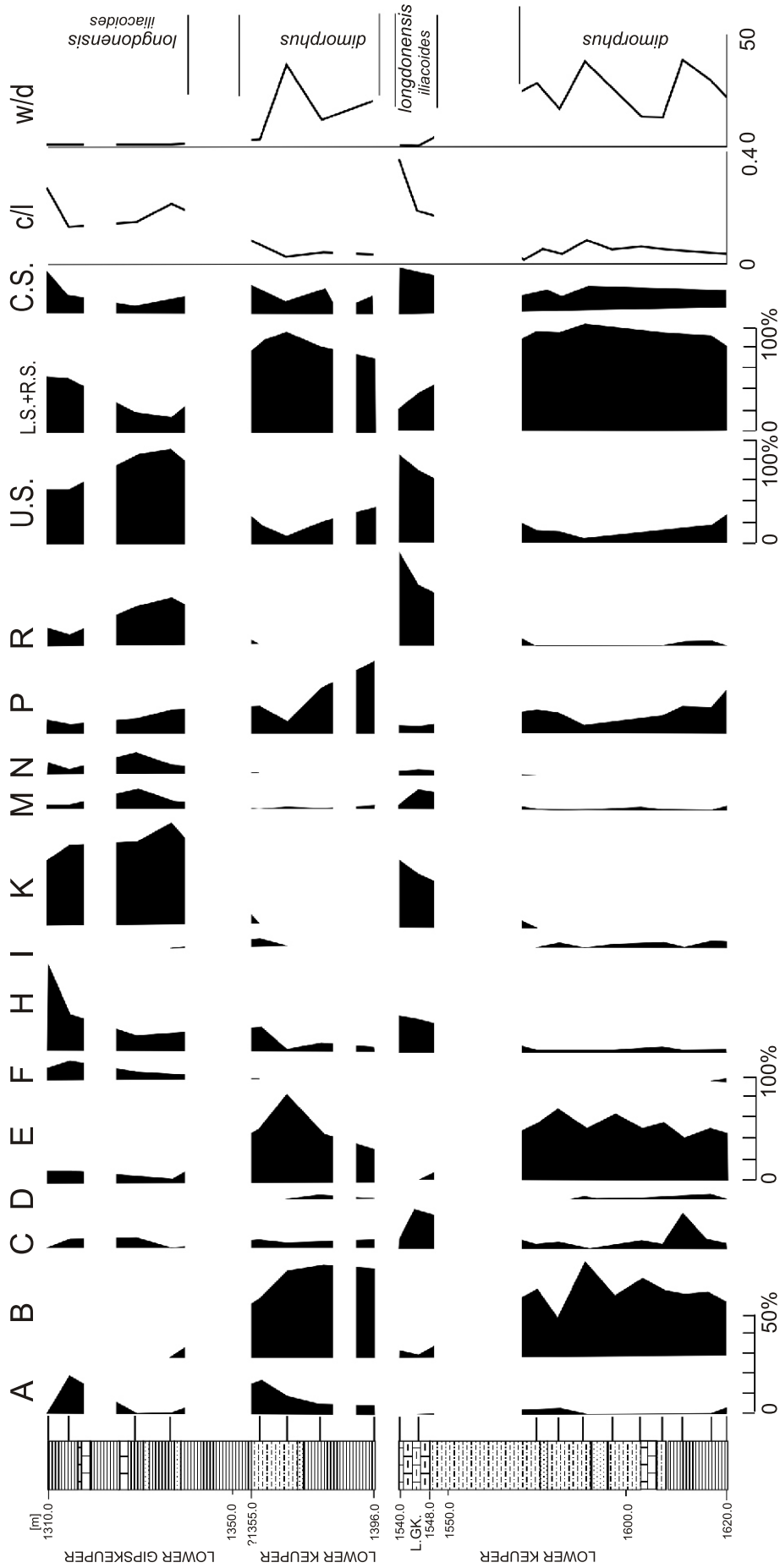


Fig. 32. Application of the PPC and SEG models to assemblages of the *dimorphus* and *longdonensis* zones from the Boża Wola IG 1 borehole (based on Ortowska-Zwolińska, 1972a)  
 Explanations as in Figure 12; L.G.K. – Lower Gipskeuper

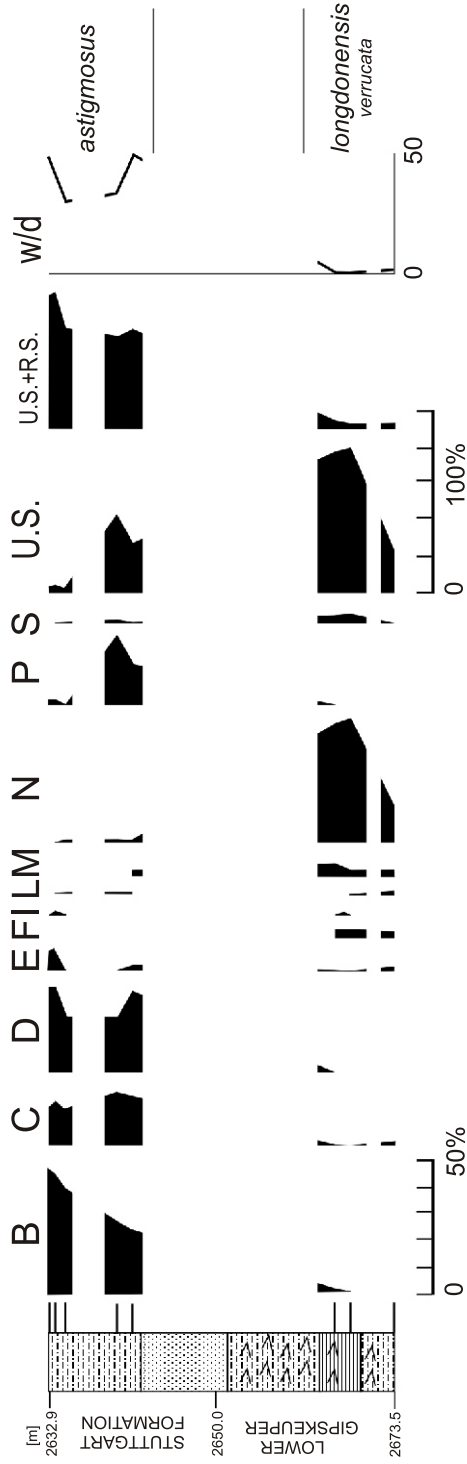


Fig. 33. Application of the PPC and SEG models to the assemblages of the *longdonensis* and *astigmus* zones from the Płotńsk IG 2 borehole (based on Ortowska-Zwolińska, 1983)

Explanations as in Figure 12

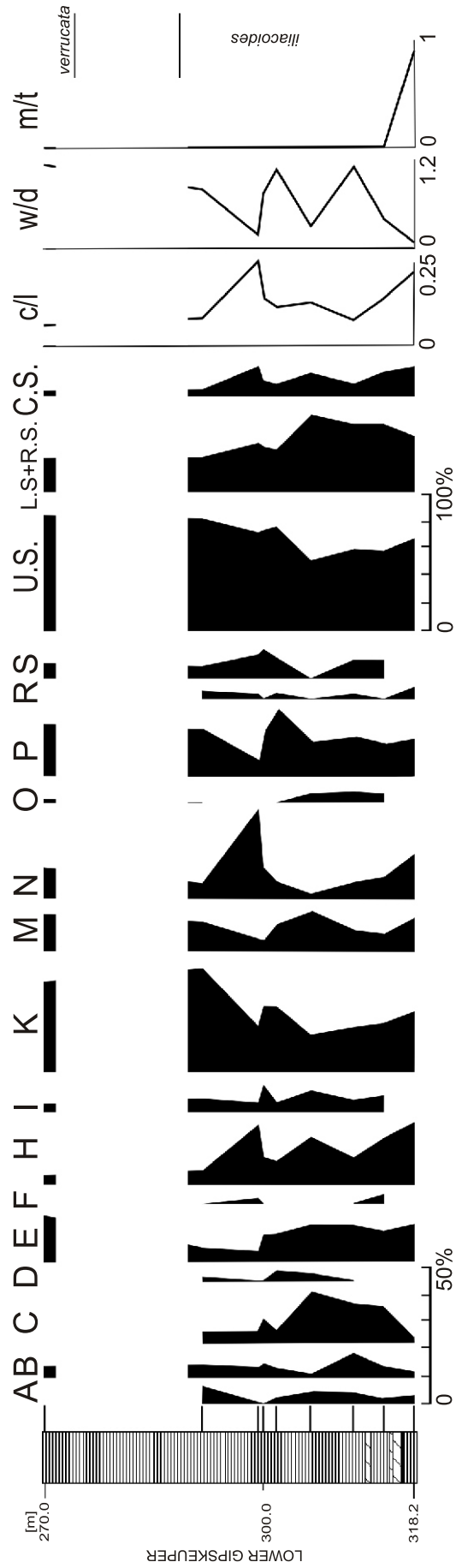


Fig. 34. Application of the PPC and SEG models to the assemblages of the *longdonensis* zone from the Eugeniów-Korytków IG 1 borehole (based on Fijałkowska, 1992)

Explanations as in Figure 12

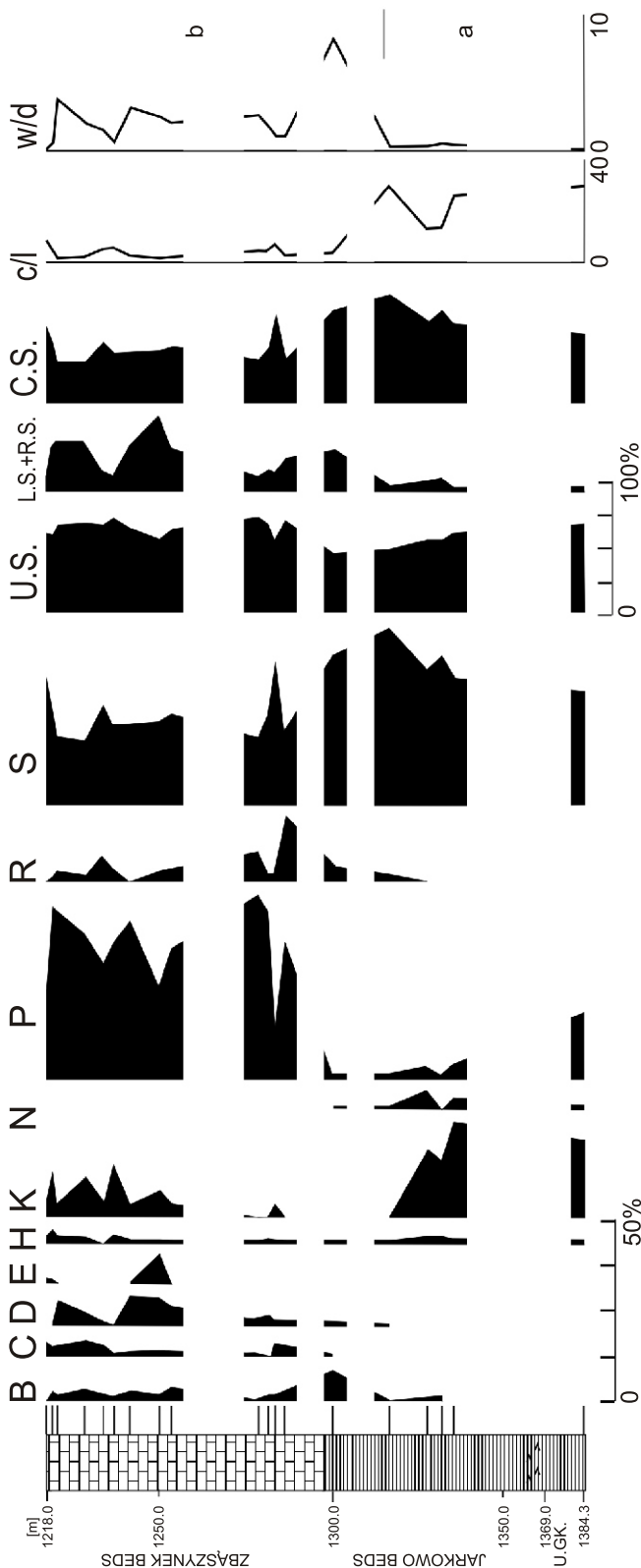


Fig. 35. Application of the PPC and SEG models to the assemblages of the *meyeriana* zone from the Drawno GEO 2 borehole (based on Orłowska-Zwolińska, 1983). Explanations as in Figure 12; U.G.K. – Upper Gipskeuper

part of the zone (Figs. 24, 25 and 28–32; Appendix 8), suggesting a gradual aridification of the Late Ladinian climate.

Lowland and River SEG strongly dominates in the SEG model with a maximum of 92%. The Coastal SEG varies from 4 to 13% and the c/l ratio – from 0.1 to 0.4.

A marked change is observed in the composition of palaeoflora. Lycopsids (*Lycostrobus* and *Annalepis*), showing a wide environmental tolerance (Grauvogel-Stamm, 1978; Orłowska-Zwolińska, 1979; Mader, 1990b, 1997), dominated in deltaic and lake coastal palaeobiocenoses (Visscher et al., 1993; Brugman et al., 1994). The wet hinterland was overgrown mainly by horsetails and ferns. *Equisetites* formed reed colonies along rivers and lake banks (Mader, 1990b, 1997). The dry hinterland, distant from sedimentary basins, was occupied by shrubby and arborescent conifers (Kustatscher and Van Konijnenburg-VanCittert, 2005).

#### LONGDONENSIS ZONE

Miospore spectra of the *longdonensis* zone were found in Lower Gipskeuper deposits from 23 boreholes (Fig. 7; Appendix 1).

The PPC model evidences that assemblages of the *iliacoides* subzone are strongly dominated by xerophytic elements: conifer pollen *Ovalipollis* (K group) reaching even 80%, *Minutosaccus*, *Labiisporites* and *Cedripites* (group P; Figs. 16, 17, 25–27 and 30–34; Appendix 9). Fern spores *Leschikisporis* (group A), *Todisporites* and *Cyclotriletes* (group B), *Verrucosisporites*, *Anapiculatisporites* and *?Echinisporites* (group C), equisetalean spores *Calamospora* (group B), and bryophyte spores *Porcellispora* (group F) are the main hygrophytic components. Cycadalean pollen (group H) prevail among intermediate elements.

The PPC model shows marked dominance of the Upland SEG – in average >60%.

Compared to the *dimorphus* zone, a significant decrease of the w/d ratio is observed. It varies from 0 to 7 (Figs. 16, 17, 25–27 and 30–34; Appendix 9) and indicates arid conditions in the latest Ladinian and earliest Carnian.

A general decrease of the Coastal SEG and c/l ratio is observed in the *dimorphus* zone. The low c/l ratio and presence of acritarchs in the Grenzdolomite deposits mark the latest Ladinian transgression in the Polish Basin. Assemblages of the *verrucata* subzone are composed most exclusively of xerophytic elements: conifer pollen *Ovalipollis* (group K), *Triadispora* (group N), *Minutosaccus*, *Labiisporites*, *Cedripites* (group P), *Infernopollenites* and *Striatoabietites* (group M) (Figs. 26, 31, 33 and 34; Appendix 9).

The very low w/d ratio, in average of <0.5 (Figs. 16, 17, 25–27, 30–32 and 34; Appendix 9), suggests a very dry climate in the Early Carnian.

In the SEG model, strong dominance of the Upland SEG – in average of >80% – is observed.

Conifers occupied not only uplands but also, together with ferns, equisetals and cycads, moist to wet inland floodplains. Areas of higher salinity on the

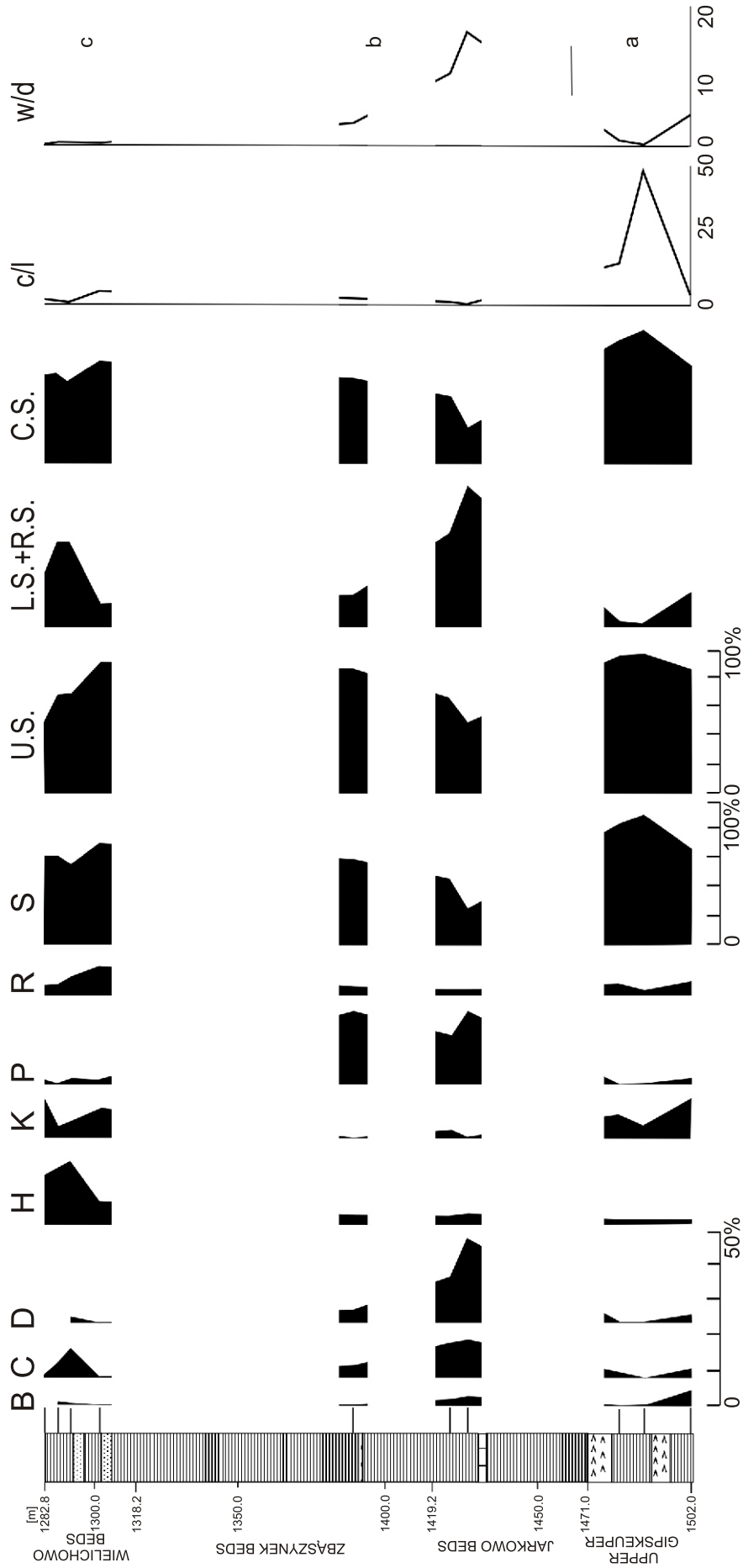


Fig. 36. Application of the PPC and SEG models to the assemblages of the *meyeriana* zone from the Wagrowiec IG 1 borehole (based on Orłowska-Zwolińska, 1983)

Explanations as in Figure 12

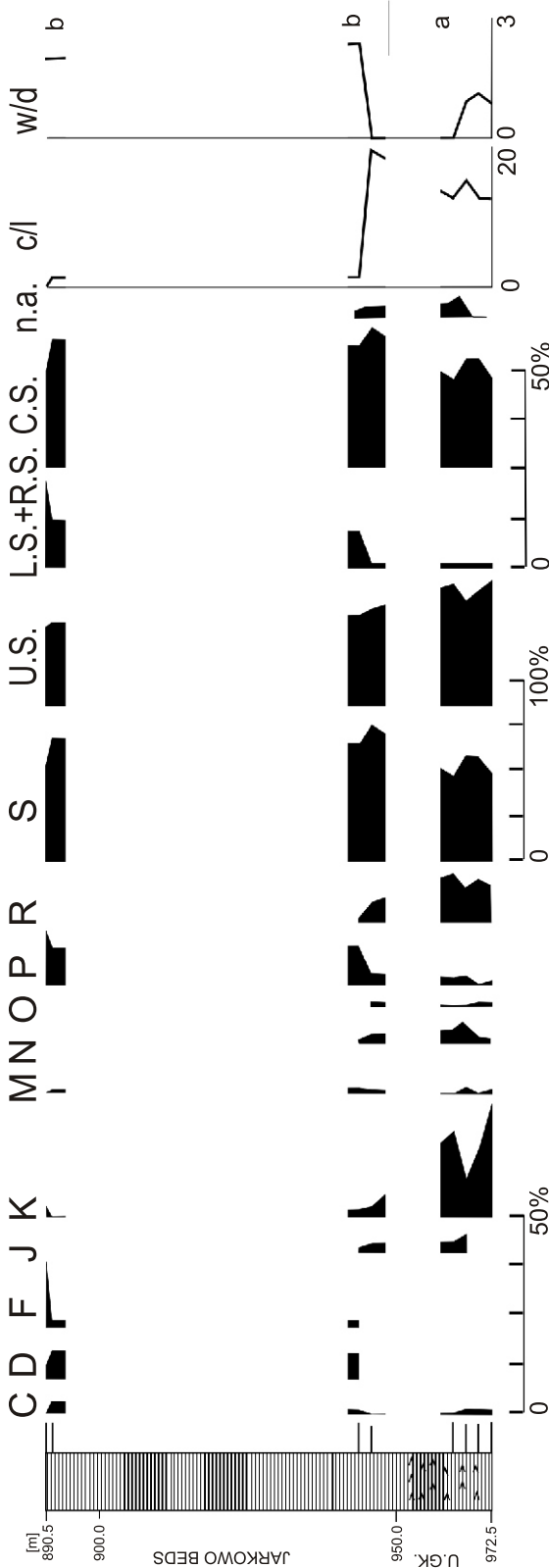


Fig. 37. Application of the PPC and SEG models to the assemblages of the *meyeriana* zone from the Ośno IG 1 borehole (based on Orłowska-Zwolińska, 1983)

Explanations as in Figures 12 and 35

sabkha/playa coast, were overgrown by pioneer halophyte lycopsids.

#### ASTIGMOSUS ZONE

The material comes from Schilfsandstein (Stuttgart Formation) deposits of 13 boreholes (Fig. 8; Appendix 1).

Assemblages of the *astigmosus* zone are strongly dominated by hygrophytic elements (in average of >80%): ?equisetalean spores *Aulisporites*, equisetalean spores *Calamospora*, fern spores *Todisporites* (B group), fern spores *Leschikisporites* (A group), lycopsid spores *Anapiculatisporites* and fern spores *Verrucosisporites* (group C) as well as lycopsid spores *Camarozonosporites* (group D) and *Aratrisporites* (group E; Fig. 33; Appendix 10). Xerophytic elements are represented mainly by conifer pollen *Ovalipollis* (group H), *Brachysaccus* and *Labiisporites* (group P).

The high w/d ratio >70 in some samples (Fig. 33; Appendix 10), indicates a humid climate and corresponds with the "Carnian pluvial event" (e.g., Kozur and Bachman, 2010; Roghi et al., 2010; Arche and Lópoez-Gómez, 2014).

The SEG model shows a strong dominance of the Lowland and River SEG and Coastal SEG. Ferns, equisetales, lycopsids and cycads inhabited moist to wet floodplains, areas of retarded drainage and those located at different distances from channels and lakes. Conifers colonised drier uplifted areas, with enhanced drainage and/or those located at greater distances from streams and pools, preferentially in basin margins or even on the flanks of erosional highlands (Mader, 1997).

#### MEYERIANA ZONE

Miospore assemblages of the *meyeriana* zone were found in the Upper Gipskeuper, Jarkowo Beds and the lower part of the Zbąszynek Beds, as well as their equivalents, in 13 boreholes (Fig. 9; Appendix 1).

The PPC model evidences that these assemblages from the upper part of the Upper Gipskeuper are strongly dominated by xerophytic circumpollen, mainly *Classopollis* and *Granuloperculatipollis* (group S) that accounts for 9 to 80% (Figs. 35–37; Appendix 11). Conifer pollen *Ovalipollis* (group K), *Cedripites* and *Labiisporites* (group P) occur less abundantly (in average of >20%). Scarce hygrophytic components consist of cycadalean and bennettitalean pollen of *Cycadopites* and *Monosulcites* (group H) as well as lycopsid spores (groups D and E).

The w/d ratio is distinctly lower in comparison to the *astigmosus* zone and varies from 0 to 12, 3 on average (Figs. 35–37; Appendix 11), and indicates a dry climate in the Early Norian.

The SEG model shows dominance of the Upland SEG (49–78%). The Coastal SEG is high and varies from 8 to 45%. The c/l ratio is also high and reaches even 48, which reflects a regressive trend in the Polish Basin during the Early Norian.

A prominent change is observed in the composition of the palaeoflora, where the conifers Cheirolepidacean, producing pollen *Classopollis*, became a dominant element. They were drought-resistant trees and shrubs that occurred in a wide spectrum of environments: coastal, river, lowland and ?upland (Alvin, 1982; Abbink, 1998). Dry lowland and upland areas and lagoon coastal zones were overgrown by other conifers, whereas lycopsids and cycads concentrated in the marginal zone of floodplains.

The assemblages of the *meyeriana* b subzones, identified in the Jarkowo Beds and the lower part of the Zbąszynek Beds,

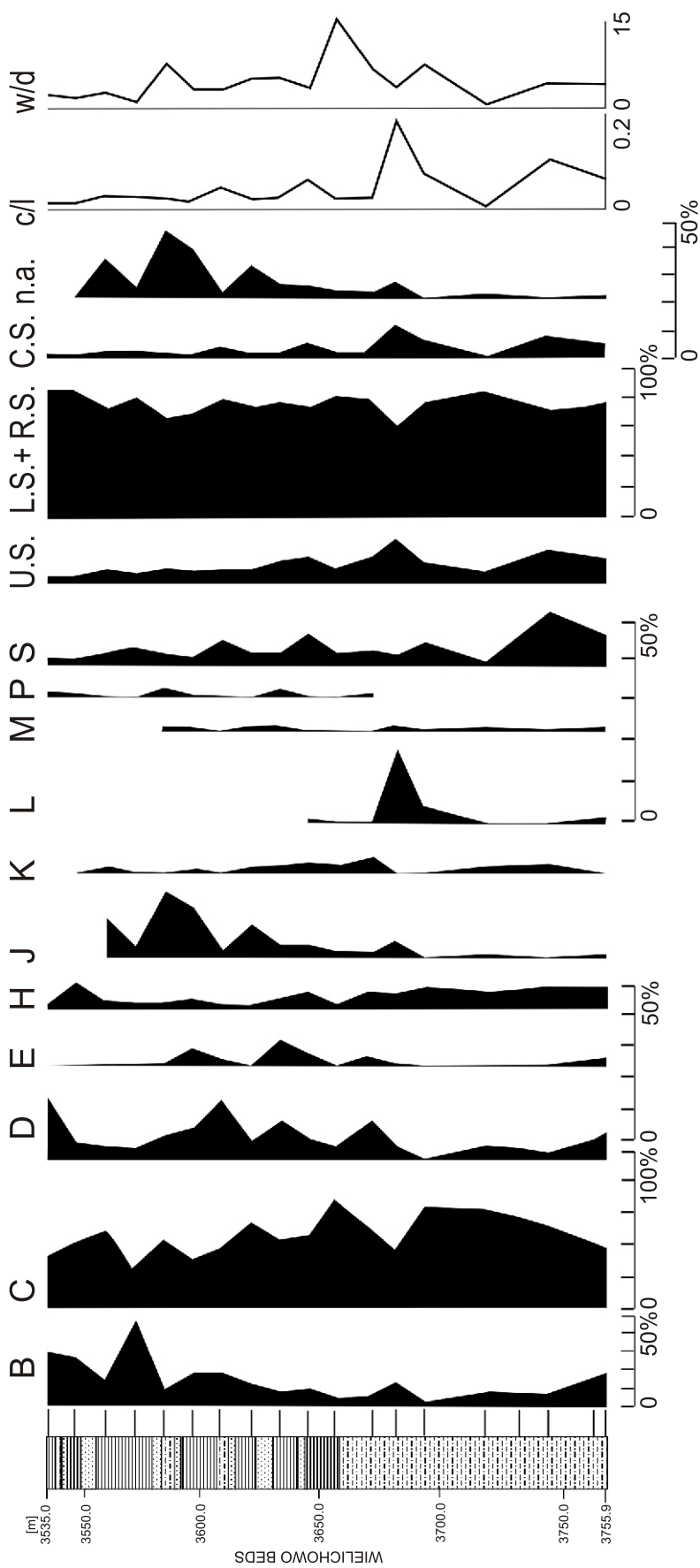


Fig. 38. Application of the PPC and SEG models to the assemblage of the *tuberculatus* zone from the Raducz IG 1 borehole (based on Orłowska-Zwolińska, 1983, 1986)

Explanations as in Figure 12

as well as their equivalents, show an increase in the amount of hygrophytic elements. Conifer pollen *Brachysaccus*, *Cedripites* (group P), *Classopolls* and *Granuloperculatipollis* (group S) still prevail in the miospore spectra (Figs. 35–37; Appendix 11). Hygrophytic components are dominated by lycopsid spores *Densosporites* (group D), *Lycopodiumsporites* (group C) and equisetalean spores *Equisetumsporites* (group B).

The w/d ratio increases even to 18 and suggests the next pluvial event in the Late Norian (e.g., Berra et al., 2010; Preto et al., 2010).

The SEG model shows an increase of the Lowland and River SEG and a marked decrease of the Coastal SEG. The c/l ratio is low – in average of <1.

Moist to wet inland floodplain was occupied by lycopsids and equisetals. Dry uplands were covered with conifer forests consisting mainly of cedars. Cheirolepidacean formed bushfields along river banks and lagoon coastal zones (e.g., Abbink, 1998).

The assemblage of the *meyeriana c* subzone was found in the upper part of the Zbąszynek Beds only in the Wągrowiec IG 1 borehole (Fig. 9). It is strongly dominated by circumpollen (group S; Fig. 36). Pollen *Ovalipollis* (group K) and cycadalean/bennettitalean pollen *Monosulcites* (group H) are abundant.

The w/d ratio (0.5–2) visibly decreases in comparison to the *meyeriana b* subzone and indicates aridification of the Early Rhaetian climate (see Haas et al., 2012).

The SEG model shows an increase of Coastal SEG.

#### TUBERCULATUS ZONE

The material comes from the Wielichowo Beds and their equivalents from 8 boreholes (Fig. 10; Appendix 1).

Assemblages of the *tuberculatus* zone consist mainly of hygrophytic elements (in average more than 50%) – fern spores *Corrugatisporites*, *Marattisporites* and *Osmundacidites* (group B), *Deltoidospora* (al. *Cyathidites*), *Gleicheniidites* and *Todisporites* (group A), lycopsid spores *Camarozonosporites*, *Cingulizonates* and *Densosporites* (group D) as well as intermediate forms such as cycadalean, bennettitalean and ginkgoalean pollen *Cycadopites*, *Chasmatosporites*, *Eucommiidites*, *Monosulcites*, and *Riccisporites* (group H) accounting for up to 87% in some samples (Fig. 38; Appendix 12). Scarce xerophytic forms are represented by conifer pollen *Pinuspollenites* (group M), *Ovalipollis* (group K) and circumpolles *Classopollis* (group S).

The w/d ratio changes from very low and low values (0.1–2) in the spectra from the lower part of the zone, to 8–25 in its upper part. An increase of humidity is due to climate pluvialisation in Late Rhaetian time (e.g., Michalik et al., 2010; Preto et al., 2010; Brański, 2011; Haas et al., 2012; Lintnerová et al., 2013; Pieńkowski et al., 2014; Szulc and Racki, 2015).

The SEG model evidences the strong dominance of the Lowland and River SEG – in average of >80% and even 100% in some samples (Fig. 38; Appendix 12).

Moist to wet inland floodplain, swamps, river banks, margins of lakes and deltas were colonised by ferns, mosses, horsetails and lycopsids (e.g., Abbink, 1998; Van Konijnenburg-Van Cittert, 2002). These plants represented the ground cover habitat. Vegetation of the drier lowlands was composed mostly of cycads, bennettiales, taxodiaceae, ferns (mainly Gleicheniaceae and Cyatheaceae) and seed ferns. These plants together with conifers are included into the mid and upper canopy habitat (Petersen et al., 2013). Scarce Pinaceae and Cheirolepidaceae occurred in dry hinterland and coastal

environments (e.g., Kürschner, 2010; Götz et al., 2011; Bonis and Kürschner, 2012). A significant change in floral composition is observed in relation to the Late Norian biocenoses strongly dominated by gymnosperms Cheirolepidaceae. In the Rhaetian assemblages, spores are accompanied by numerous pollen *Riccisporites tuberculatus* Lundblad produced by ruderal, herbaceous conifers that were able to colonise disturbed habitats (Rothwell et al., 2000; Vajda et al., 2013). Although Kürschner et al. (2014) suggested that parent plants of *R. tuberculatus* preferred probably cooler climatic conditions in comparison to Cheirolepidaceae producing pollen *Classopollis*, this change may be explained rather by a biotic crisis related to volcanic activity in the Central Atlantic magmatic province (e.g., Van de Schootbrugge et al., 2009; Bonis et al., 2010; Kürschner and Hengreen, 2010; Mander et al., 2013; Pálffy and Koscic, 2014; Pieńkowski et al., 2014). On the assumption of Early Rhaetian age of the *meyeriana c* subzone (see Kürschner and Hengreen, 2010), this floral turnover took place in the Early Rhaetian, whereas in literature it is worldwide dated as latest Rhaetian (Hubbard and Boutler, 2000; Hesselbo et al., 2002; Marzoli et al., 2004; Kliti et al., 2005; Deenen et al., 2010; Bonis and Kürschner, 2010, 2012; Blackburn et al., 2013).

#### PALAEOCLIMATIC INTERPRETATION

Dominance of xerophytic miospores and relatively high amount of *Cycadopites* pollen in assemblages of the *obsoleta-pantii* zone indicate a warm, semiarid climate during the Induan (Fijałkowska-Mader, 1999; Fig. 39). This suggestion corresponds with palaeoclimatic reconstructions for the Early Triassic, where Central and Western Europe is located within the subtropical climate zone, between 15 and 25°N (e.g., Frakes, 1979; Van der Zwan and Spaak, 1992; Ziegler et al., 1994; Zharkov and Chumakov, 2001; Chumakov and Zharkov, 2003; Sellwood and Valdes, 2007; Kürschner and Hengreen, 2010; Paul and Puff, 2010). According to Kutzbach and Gallimore (1989) the area of Poland was placed in the northern intertropical convergence zone with the monsoonal circulation characterized by strong seasonality of temperatures and precipitations (see also Parrish, 1993; Hermann et al., 2012). Relatively high temperatures could be explained not only by the palaeogeographical position of Poland but also by the global greenhouse effect which started in the Late Permian (e.g., Dickins, 1993; Racki and Wignall, 2005; Twitchett, 2007; Krassilov and Karsev, 2009; Hochuli et al., 2010; Preto et al., 2010).

Analysis of assemblages of the *nejburgii* and acritarchs subzone indicates that climatic conditions in the Early Olenekian (Early Smithian) remained similar to those in the Induan. Decreasing dominance of xerophytic miospores of the *nejburgii* subzone suggests an increase of humidity and a change from a warm semiarid to a subhumid climate during the Late Smithian (e.g., Dobruskina, 1994; Fig. 39). This humidity increase was suggested also by Yaroshenko (1977) on the basis of the worldwide expansion of Pleuromeiaceae. Other circumstances like the presence of abundant plant fossils, conchostraca and Chirotherium tracks in the Hardegsen Formation and its equivalents may also document the increasing humidity (Paul and Puff, 2010) and contradicts the global character of the “dry” episode at the Middle/Late Smithian boundary (e.g., Hermann et al., 2012). The further increase of humidity is observed in assemblages of the *presselensis* subzone (Spathian) and coincides with a “wet” pick on the climatic curve presented by Paul and Puff (2010). It does not confirm the

CHRONOSTRATIGRAPHY			PALYNOSTRATIGRAPHY (Orłowska-Zwolińska, 1985)	CLIMATE										
				Poland				German Basin (Haas et al., 2012)						
				a	sa	sh	h	a	sa	sh	h			
TRIASSIC	RHAETIAN		<i>tuberculatus</i>											
			----- c -----											
	NORIAN	Sevastian												
		Alaunian		b										
		Lacian		<i>meyeriana</i> ----- ?										
	CARNIAN	Tuvalian		a ----- ?										
		Julian		<i>astigosus</i>										
		Cordevolian		<i>longdo-</i> <i>nensis</i> <i>verrucata</i> <i>iliacoides</i>										
	LADINIEN	Longobardian		<i>dimorphus</i> <i>dimorphus</i> <i>Tasmanites</i>										
		Fassanian		----- ?										
	ANISIAN	Illyrian		<i>oriens</i>										
		Pelsonian		<i>minor</i>										
		Bithynian ----- Aegeian		h. <i>fastidiosus</i> <i>heteromorphus</i>										
	OLENEKIAN	Spathian		n. <i>presselensis</i>										
		Smithian		n. <i>nejburgii</i> <i>acritarchs</i>										
	INDUAN	Dinerian		<i>obsoleta-pantii</i>										
		Griesbachian												

Fig. 39. Main climatic stages of Poland and the German Basin based on palynological data

Climate: a – arid, sh – semiarid, sh – subhumid, h – humid; palynological zones: n. – *nejburgii*, h. – *heteromorphus*, ? – luck of data



change from humid to drier conditions postulated by Hermann et al. (2011a, 2012) at the Smithian/Spathian boundary.

High differentiation of the w/d curves in the Late Olenekian spectra that may result from the climatic change at the Smithian/Spathian boundary (SSB event) from warm and equable conditions into more differentiated with greater temperature oscillations (e.g., Looy et al., 1999; Galfetii et al., 2007; Lindström and McLoughlin, 2007; Preto et al., 2010).

A distinct decrease of humidity to semiarid and arid conditions is observed in pollen assemblages of the *heteromorphus* zone (Early Anisian; Fig. 39).

Relatively low w/d ratio in assemblages of the *minor* zone confirms the semiarid climate of the Middle Anisian (Late Bithynian–Pelsonian) suggested by Frakes (1979), Kürschner and Hergreen (2010) and Haas et al. (2012). There is no evidence for a Bithynian humid episode in the Polish spectra (e.g., Haas et al., 2012; Fig. 39).

Compared to the Early Triassic, the area of Central and Western Europe was slightly moved towards the north between 25 and 30° but still remained within the subtropical climate belt (Frakes, 1979; Ziegler et al., 1994).

The very low w/d indicators in spectra of the *oriens* zone suggest an arid climate in the Illyrian (Fig. 39). A warm and very dry climate may also be proven by strong dominance of *Triadispora* pollen (e.g., Visscher et al. 1993; Kürschner and Hergreen, 2010). There is no evidence in the Polish assemblages for the Late Anisian humid event postulated by Hochuli and Vigran (2010) and Preto et al. (2010).

Based on the high w/d ratio values in assemblages of the *Tasmanites* subzone, the Middle Ladinian (Early Longobardian) climate can be determined as subhumid and humid (e.g., Grodzicka-Szymanko and Orłowska-Zwolińska, 1972; Orłowska-Zwolińska, 1983; Szulc, 1999; Preto et al., 2010; Fig. 39). This suggestion does not coincide with the semiarid climate postulated by Lindström et al. (2009), Hochuli and Vigran (2010) and Kürschner and Hergreen (2010). Preto et al. (2010) correlated the uppermost Muschelkalk and Lettenkeuper (Erfurt Formation) to the uppermost Ladinian and suggested a humid and warm climate for that time. After Feist-Burkhard et al. (2008: fig. 13.1) the Upper Muschelkalk is correlated to the uppermost Illyrian-Lower Longobardian, and the Lettenkeuper to the Lower-Middle Longobardian. Therefore, the warm and humid climate suggested by Preto et al. (2010) should be related rather to the Early than Late Ladinian.

According to Brugman et al. (1994) the high amount of hygrophytic components in the Late Ladinian miospore spectra may result rather from local environmental factors than climate changes but the composition of the Lowland and River SEG, containing mostly “more humid” taxa, suggests rather climatic causation (see also Kustatscher and Van Konijnenburg-Van Cittert, 2005). A gradual decrease of humidity is observed within the *dimorphus* subzone (Late Ladinian) from humid to semiarid conditions.

The very low d/w ratio values in the spectra of the *longdonensis* zone suggest that the latest Ladinian climate was semiarid and became more dry and arid in the Early Carnian (Fig. 39) that agrees with palaeogeographic maps presented by Frakes (1979) and Ziegler et al. (1994) where the area of Central and Western Europe was placed at 30°N within the dry tropical climate belt.

Both the PPC model and the high w/d ratio in the *astigmatosus* zone indicate a humid and warm climate during the Late Julian, which corresponds to the “Carnian Pluvial Event” (Simms and Ruffell, 1989, 1990; Simms et al., 1995; Kozur and Bachmann, 2010; Preto et al., 2010; Roghi, 2004; Roghi et al., 2010; Haas et al., 2012).

The PPC model as well as low w/d ratio in the *meyeriana* a subzone indicate a warm semiarid climate in the Early Norian (Fig. 39), which coincides with observations of the other authors (e.g., Ahlberg et al., 2002; Berra et al., 2010; Preto et al., 2010; Brański, 2011, 2014; Pieńkowski et al., 2014; Szulc and Racki, 2015). Vakhrameev (1981, 1987, 1991) suggested that the high content of pollen *Classopollis* indicates an arid climate. This rule finds also confirmation in microflora from Poland (see Fig. 34).

Both the PPC model and the w/d ratio in the *meyeriana* b subzone indicate an increase of humidity in the Late Norian (Fig. 39), which corresponds to the pluvial event (Berra et al., 2010; Preto et al., 2010; Szulc and Racki, 2015).

The lower w/d ratio in the *meyeriana* c subzone reflects a return to a semiarid climate in the Early Rhaetian.

Predominance of hygrophytic elements in assemblages of the *tuberculatus* zone suggests a subhumid climate in the Late Rhaetian (Fig. 39). The change of climate from dry to wet in the Early Rhaetian was documented in many areas of Europe (e.g., Ahlberg, 2002; Berra et al., 2010; Michalik et al., 2010; Preto et al., 2010; Götz et al., 2011; Brański, 2011, 2014; Haas et al., 2012; Lintnerová et al., 2013; Krupnik et al., 2014; Pieńkowski et al., 2014). The author’s observations do not confirm the decrease of humidity and arid to semiarid climate in the Late Rhaetian suggested by Haas et al. (2012).

During the Rhaetian, the area of Central and Western Europe was placed at 40°N in the subtropical, monsoonal climatic belt (Ziegler et al., 1994; Kent and Tauxe, 2005; Sellwood and Valdes, 2007; Bonis and Kürschner, 2012).

## CONCLUSIONS

1. Application of the PPC model to the miospore assemblages from Poland allowed reconstructing the climate changes during the Triassic. The results obtained by author generally coincide with the palaeogeographical and palaeoclimatic reconstructions for Central and Northwestern Europe with the exception of the Middle Ladinian. The high w/d ratio in the Polish assemblages indicates a subhumid and humid climate.

2. Dominance of xerophytic elements in the palynomorph spectra reflects a persistent subtropical warm dry climate during most of the Triassic. Significant proportions of hygrophytic elements in the microfloral assemblages document humid phases during the Late Olenekian, Middle/Late Ladinian, Middle Carnian, Late Norian and Late Rhaetian.

3. Application of the seg model enabled a rough reconstruction of the changes in palaeofloral communities. In the Induan, a ruderal strategy is observed by the colonisation of habitats destroyed in the Permian/Triassic crisis, mainly by lycopsids (lowland seg). A stress-tolerating strategy related to living in coastal environments (coastal SEG) dominated in the Olenekian. In the Early Anisian, the first significant reforestation after the Permo-Triassic crisis took place, accompanied by the renewal of conifers which dominated not only in the Upland SEG but occurred numerously also in the Lowland and Coastal SEGs. Dry climate and marine transgression in the Middle Anisian caused the strong dominance of the Upland SEG. This situation changed only in the Ladinian when the amount of lycopsids increased, and the Lowland and River SEG prevailed. At the same time, conifers developed a ruderal strategy by colonisation of xerophytic coastal habitats. The conditions favourable for plants deteriorated rapidly in the Early Carnian due to climate aridisation. The “Carnian Pluvial Event” in the Middle Carnian caused an expansion of equisetals – the main component of the Lowland and River SEG. The next arid phase in the

Early Norian contributed to the expansion of xerophytic Cheirolepidacean which occupied a wide range of environments – Upland, Lowland and Coastal SEGs. In the Late Norian, a small humid impulse is marked by an increase of the amount of lycosids and equisetals (Lowland and River SEG). The humid and warm climate of the Late Rhaetian favoured the development of ferns which dominated in the Lowland and River SEG.

4. A significant decrease of the number of saccate pollen in the Rhaetian *tuberculatus* zone, and a simultaneous sudden proliferation of ruderal *Riccisporites tuberculatus* may have occurred due to volcanic activity in the Central Atlantic Magmatic Province.

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