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ORIGINAL PAPER

Diversity dynamics of ammonoids during the latest Bajocian and Bathonian (Middle Jurassic) in the epicratonic Polish Basin

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Abstract Results of the analysis of Middle Jurassic (latest Bajocian–Bathonian) ammonoid diversity patterns in the Polish Basin are reported. The data used in this study are based on a large number of ammonoid specimens, collected bed-by-bed, from the Polish Jura in south-central Poland, as well as on existing literature. The ammonoid diversities, both at the genus and species levels, have been calculated for particular ammonite zones and subzones and compared with the regional transgressive–regressive cycles for the Polish Lowlands and Hallam's global sea-level curve. The patterns of ammonoid diversity dynamics seem to be well correlated with global sea-level fluctuations. Particular diversity peaks correspond with major transgressive episodes. Three main regional bio-events related to transgressions have been distinguished for the Polish Basin: (1) the Latest Bajocian (Bomfordi Subchron) bio-event is related to a short-lasting immigration of Tethyan ammonoids; (2) a late Early Bathonian (Tenuiplicatus Chron) bio-event corresponds to a proliferation of *Asphinctites tenuiplicatus* (Brauns), most probably as a result of transgression-driven eutrophication of a shallow-marine environment; during this time, the immigration (passive dispersion?) of some single Tethyan species is also observed; and (3) a Late Bathonian (Hodsoni and Orbis chrons) bio-event corresponds to the highest ammonoid species diversity peaks and most probably is related to the major transgression during the Bathonian, which allowed easy migration of several species via several newly opened sea-ways.

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Introduction

Factors controlling the changes in ammonoid assemblage composition may be both biotic and abiotic in nature (e.g., Sandoval et al. 2002). Even slight perturbations in a marine environment may significantly influence shallow-water, stenotopic organisms (e.g., Kauffman 1977, 1984; Hallam and Wignall 1999), including ammonoids (Kennedy and Cobban 1976; Hallam 1996; Westermann 1996; Sandoval et al. 2001). The relationship between ammonoid diversity patterns and sea-level changes has been demonstrated by several workers (see Wiedmann 1973, 1988; Kauffman 1977, 1984; Saunders and Swan 1984; Marcinowski and Wiedmann 1988; Kutek et al. 1989; Hoedemaeker 1995; Kutek and Marcinowski 1996; Wiedmann and Kullmann 1996; O'Dogherty et al. 2000; Sandoval et al. 2001, 2002; Westermann 2001; Marcinowski and Gasiński 2002; Ruban 2007). Sandoval et al. (2002) confirmed such a relationship during their analysis of the Middle Toarcian–Lower Bajocian ammonoids of France, Spain, Morocco and Italy. Such a phenomenon may also be observed amongst Palaeozoic (Namurian) ammonoids in which not only diversity but also disparity (variety of morphological forms) changes were observed (Saunders and Swan 1984). Recently, Ruban (2007) investigated the diversity of different Jurassic faunal groups and found that only ammonites seem to have been influenced by transgressions and regressions in the Caucasus Mountains (see also Ruban 2010).

Generally, during transgressions, the increase of eco-space favoured the development of new taxa inhabiting new areas (Wiedmann 1973; Hallam 1987; Hoedemaeker 1995). During regressions, changes in temperature and salinity (increasing environmental stress) in shallow epicontinental seas drove several stenotopic taxa to extinction (see Wiedmann 1973, 1988; Kauffman 1977, 1984; Hallam 1987, 1996; Hoedemaeker 1995; Vermeij 1995; Hallam and Wignall 1999; O'Dogherty et al. 2000; Sandoval et al. 2001, 2002; Twitchett 2006). Also, importantly, transgressions and regressions changed palaeogeographic and palaeotopographic situations by opening or closing sea-ways enabling or disabling the migrations of several species (e.g., Dommergues et al. 2009). Interestingly, Ruban (2010) recently found that, in the Bajocian of the Caucasus, the transgressions coincided with impoverishments of ammonite assemblages, whereas regressions coincided with their diversification. The patterns observed by Ruban (2010), however, need further research. Thus, sea-level changes may have operated both directly and indirectly on different taxa, and it seems that ammonoids are very useful tracers of transgressions and regressions on both regional and global scales. They may have far richer utility than other, especially benthic, groups of marine invertebrates (cf. Ruban 2007).

In this paper, the relationship of ammonoid diversity patterns and transgressive–regressive cycles in the Middle Jurassic Polish Basin during the latest Bajocian and Bathonian is described, and ammonoid diversity dynamics during particular chrons and subchrons are discussed in the context of the sea-level-related environmental and palaeobiogeographic changes.

Palaeogeography, geology and palaeoenvironments

Palaeogeographic background

During the Middle Jurassic, the Polish Basin was located at ca. 40°N latitude as a part of the Laurasian continent (Golonka 2000) (Fig. 1a). As the easternmost extension of the large Mid-European Epicontinental Basin, the Polish Basin was bordered by the Fennoscandian land to the north, Belorussian and Ukrainian lands to the east, Bohemian land to the west and pre-Carpathian land to the south (see Dadlez 1989; Ziegler 1990; Feldman-Olszewska 1997) (Fig. 1a).

The basin was undoubtedly connected with the Tethys, and all transgressive pulses from the Aalenian through Bathonian were related to this ocean (Dayczak-Calikowska et al. 1997). However, their main pathways are still unclear in Poland. Dayczak-Calikowska and Moryc (1988) suggested the East-Carpathian Gate in the south-east via the Mid-Polish Trough as the main path. Świdrowska (1994), on the other hand, suggested that the Aalenian transgression, at least, entered from the west (see also Feldman-Olszewska 1997). The Moravian Gate, situated in the south-west, is considered to have been closed at least to the Late Bathonian transgression (Dayczak-Calikowska and Moryc 1988; see also Feldman-Olszewska 1997).

In the Middle Jurassic, the Polish Basin broadened gradually, attaining its greatest area in the Late Bathonian, when nearly the whole of the Polish Lowlands was covered by the sea (Matyja and Wierzbowski 2006). During the Bajocian and Bathonian, the sedimentation in the Polish Basin was dominated by siliciclastics, derived primarily from the Fennoscandian and Bohemian lands (Dadlez 1997; Marynowski et al. 2007).

Geology and stratigraphy

The classic area where the Middle to Upper Jurassic deposits are exposed in a large number of localities is the so-called Polish Jura. Polish Jura is a monoclinally extended structure spreading from south-east to north-west of the Cracow-Wieluń Upland in southern and south-central Poland (Fig. 1b-c). Generally, the Middle Jurassic deposits in that area may directly rest upon Palaeozoic and Lower Jurassic deposits, and are directly overlain by Upper Jurassic carbonates or thin Quaternary cover (e.g., Różycki 1953; Dayczak-Calikowska et al. 1997; Kopik 1998).

The Upper Bajocian through Bathonian epicratonic sediments under study consist of a monotonous sequence of dark-grey to black and poorly consolidated siliciclastics with a variable content of a coarser fraction. They are intercalated by massive siderites, as well as carbonate concretions, occurring as single bodies and more or less continuous horizons. This complex in the Polish Jura is known as the Ore-bearing Częstochowa Clay Formation (e.g., Dayczak-Calikowska et al. 1997; Kopik 1998; Majewski 2000; Matyja and Wierzbowski 2000; Zatoń and Marynowski 2006; Szczepanik et al. 2007), and the sediments under discussion are usually simply referred as to clays. They rest nearly horizontally or dip very gently toward the north-east. They are often capped by condensed Callovian limestones, sandstones, sandy-limestones or marls (e.g., Dayczak-Calikowska et al. 1997; Dembicz and Praszkier 2003).

The Middle Jurassic ore-bearing clays are widely exposed in several brick-yards scattered in the southern to northern part of the Polish Jura (see Matyja et al. 2006a, b, c; Marynowski et al. 2007; Wierzbowski and Joachimski 2007; Zatoń et al. 2009). On the basis of lithology, thicknesses and stratigraphic completeness of the ore-bearing clays, the Polish Jura area was divided into northern and southern sedimentary regions by Różycki (1953). The northern sedimentary region (the area north of Ogrodzieniec up to the Wieluń area; see Fig. 1c), unlike the southern one (the Ogrodzieniec and southern areas), is

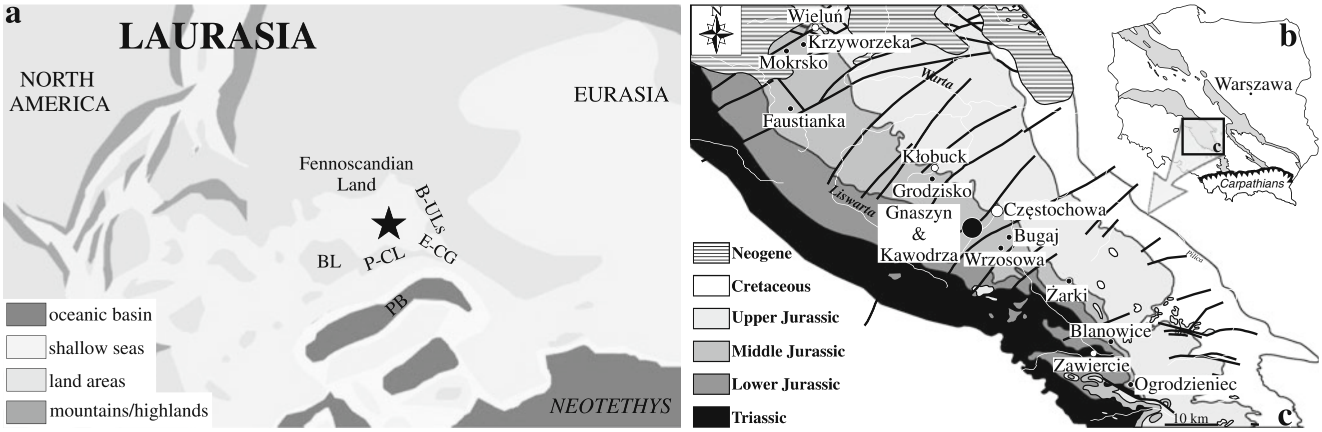

Fig. 1 **a** Location of the Polish Basin (*star*) on the background of the Middle Jurassic palaeogeography (simplified and modified after Golonka 2000). *BL* Bohemian land, *B-Uls* Belorussian and Ukrainian lands, *E-CG* East-Carpathian Gate, *P-CL* Pre-Carpathian land, *PB* Pieniny Basin. **b** Map of Poland with Jurassic deposits indicated (*shaded areas*) after removal of the Cenozoic cover. **c** Geological map of the Polish Jura area with sampled localities indicated (*black circles*) (modified after Zatoń and Taylor 2009a)

characterised by a more fully developed and thicker sequence of the ore-bearing clays.

Based on ammonite faunas, it is clear that the exposed ore-bearing clays range from the Parkinsoni Zone of the Upper Bajocian up to the Orbis Zone of the Upper Bathonian (Kopik 1998; Matyja and Wierzbowski 2000; Matyja et al. 2006a, b, c; Zatoń 2007a, 2010a, b). The basal Middle Bathonian Progracilis Zone was documented north of Częstochowa (see Matyja and Wierzbowski 2000), but so far no guide ammonites have been presented, so its position within the clays is still unknown. Poulsen (1998), based upon dinocysts, assumed that the higher zone of the Upper Bathonian—the Discus Zone—may be present in the northern part of the Polish Jura. Quite recently, Barski et al. (2004), also using dinocysts, confirmed the presence of the Discus Zone in the southern part of the area. However, this zone has so far not been recognised from ammonites. It must also be noted that, in the past, even older (Lower Bajocian) deposits were exposed in the Polish Jura area (e.g., Kopik 1967).

Remarks on palaeoenvironments

During the Bajocian and Bathonian, the Polish Basin was characterised by a monotonous sedimentation regime consisting mainly of siliciclastic clays and muds. The sedimentation of the ore-bearing clays in the northern sedimentary region was basically continuous and has been interpreted to have proceeded in a quiet marine environment, generally below the storm wave-base (Matyja et al. 2006a, b, c). However, in some intervals of the Upper Bajocian and Bathonian, signs of sedimentation pauses and/or erosion occur in a form of exhumed concretions (hiatus concretions) that were intensively bored and encrusted (Zatoń et al. 2006; Zatoń and Taylor 2009a). The concretions are also characterised by deeply truncated borings indicating that a strong hydrodynamic conditions (likely storms) influenced them episodically on the sea-bottom. In the southern sedimentary region, sedimentation had taken place in shallower environments. According to Różycki (1953), the southern region represented a shallower, marginal marine facies zone where a reduction of thickness, hiatuses and coarser grain fractions are evident. The strong water agitation is not only evidenced by hiatus concretions (Zatoń et al. 2006) but also from heavily encrusted, large oncoids (see Zatoń and Taylor 2009b, 2010).

Geochemical and petrographical investigation of the Upper Bajocian and Bathonian clay deposits of both the northern and southern sedimentary regions indicated that during sedimentation the bottom waters were oxygenated and any evidence of anoxia, both at the bottom and in the water column, is lacking (Marynowski et al. 2007; Szczepanik et al. 2007). This is well-supported by the diverse benthic fauna (e.g., foraminifers, various molluscs, echinoderms, arthropods, bryozoans, annelids) and trace fossils (see Różycki 1953; Matyja et al. 2006a, b, c; see also Zatoń et al. 2009 for a short review). Recent stable isotopic studies of calcareous biota (Wierzbowski and Joachimski 2007) indicate that bottom water palaeotemperatures ranged from 7.4 to 10.1°C and that surface waters were warmer but probably below 18°C (but see Marynowski et al. 2007) in the Late Bajocian–Bathonian epicratonic sea of south-central Poland. Such palaeotemperature values are rather low for the generally warm Jurassic period (e.g., Hallam 1985), but in agreement with a palaeoclimatic study of Price (1999) who suggested a global cooling in the Bajocian and Bathonian.

Materials and methods

Amongst the macroinvertebrate groups inhabiting the Late Bajocian–Bathonian Polish Basin, ammonoids are the beststudied, being the subject of several palaeontological and biostratigraphical works (e.g., Różycki 1953, 1955; Potocki 1972; Korcz 1973; Dayczak-Calikowska et al. 1988, 1997; Majewski 1997; Kopik 1974, 1979, 1998, 2006; Kopik et al. 1980; Matyja and Wierzbowski 2000, 2001, 2003; Matyja et al. 2006a, b, c; Zatoń and Marynowski 2006; Zatoń 2007a, b, 2008, 2010a, b). They thus provide excellent material for study of diversity dynamics.

For this research, ammonites have been gathered from the Polish Jura, an area situated in south-central Poland where the exposures of Middle and Upper Jurassic sedimentary rocks are abundant and easily accessible. Thus, in light of this research, the area of the Polish Jura may be considered as a reference point for studying the Upper Bajocian–Bathonian ammonoids of the epicratonic Polish Basin.

In order to provide accurate data, the number of genera and species for each of the Upper Bajocian–Bathonian ammonite zones and subzones have been counted. To do so, the data about the ammonoid genera/species number were selected from the works of Zatoń (2007a, 2010a, b), where the ammonoids studied were collected from stratigraphically well-defined horizons. All the indeterminable specimens were excluded from the analysis. If the correspondence of macro- and microconchs of particular species is known, as in the case of the Middle Bathonian *Morrisiceras morrisi* (Oppel) (see Zatoń 2008), they are treated as the same species. Since there are different approaches to the taxonomy of ammonoids (see discussion in, e.g., Sandoval et al. 2001), the author has not used data presented in the form of just species lists (with no figured specimens) included in comprehensive works (e.g., Kopik et al. 1980; Dayczak-Calikowska et al. 1988, 1997; Kopik 1998). Nor were the species names provided for particular zones or subzones with no figured specimens in some recent papers (e.g., Matyja et al. 2006a, b, c) considered for the present study. Such an exclusion of listed but not figured species is crucial to avoid overestimating the number of species, which in fact, in some circumstances, might have been synonyms. The exception to this procedure, however, is the use of only those genera that have not been documented by Zatoń (2007a, 2010a, b). This is because genera, in contrast to species, are usually assigned with greater objectivity by the ammonite workers. Each additional genus derived from the published lists is considered as an additional species. However, in the case where a listed genus is represented by two or more species, it is counted as one species to avoid any further species overestimation. Also, the ammonite species of uncertain or not exact stratigraphic provenance (e.g., Dayczak-Calikowska et al. 1988; Kopik 1974; Kopik et al. 1980) have been disregarded. The additional taxonomic data mentioned above were derived from the works of Kopik (1998, 2006), Matyja and Wierzbowski (2000, 2003) and Matyja et al. (2006a, b, c). Using such a methodology for data gathering may exclude some true ammonoid species not listed by Zatoń (2007a, 2010a, b), but it avoids species overestimation within particular ammonite zones/subzones.

The ammonoid diversity has been presented as both genera and species numbers for each ammonite zones/subzones investigated. The diversity curve of the latest Bajocian–Bathonian ammonoid faunas from the Polish Basin was then compared to the transgressive–regressive cycles distinguished for the Polish Lowlands by Feldman-Olszewska (1997) and the sea-level curve of Hallam (1988, 2001) The latter, in contrast to the sea-level curve constructed by the Exxon group (Haq et al. 1987), was established on the basis of classic European sections having well-recognised stratigraphy and located on a relatively stable craton (see also Hallam 1992).

The ammonoid diversity patterns in the Polish Basin

Following rather poor and monotonous ammonoid diversity, on both the genus and species levels (mainly the ammonites of the genus *Parkinsonia*), within the Upper Bajocian Parkinsoni Subzone, the first peak of ammonoid diversity is observed higher up in the Bomfordi Subzone, attaining seven genera and 12 species (Fig. 2; Table 1). Apart from ammonoids that are characteristic for the extra-Mediterranean areas, such as *Parkinsonia*, *Strigoceras* or *Vermisphinctes*, the ammonoids whose diversity and abundance is greatest in the Tethyan areas, such as *Phylloceras*, *Nannolytoceras* and *Lissoceras* (see, e.g., Galácz 1980), also occur and constitute a characteristic component of the whole assemblage.

During the Early Bathonian (Zigzag Chron), the ammonoid diversity drops (Fig. 2; Table 1). The lowest (two genera and five species) is noted for the Convergens Subchron dominated by *Parkinsonia* and *Planisphinctes* (Kopik 1998; Matyja and Wierzbowski 2000; Zatoń and Marynowski 2006; Zatoń 2007a). Somewhat higher, but still low (five genera and five species), diversity is noted for the Yeovilensis Subchron (Fig. 2; Table 1). The latter is characterised by the presence of oppeliids (*Oxycerites*), morphoceratids (*Asphinctites*, *Berbericeras*) and stephanoceratids (*Cadomites*) (Matyja and Wierzbowski 2003; Kopik 1998; Zatoń 2007a). Kopik (2006) has allegedly stated that true *Tulites* representatives, as *Tulites cadus* Buckman which he described, come from the Lower Bathonian of the Polish Jura. However, as the specimens mainly represent an old collection without any indication of the horizon they were collected from, their stratigraphic provenance is uncertain.

Yet higher ammonoid diversity (six genera and ten species) is noted in the uppermost part of the Lower Bathonian–Tenuiplicatus Zone (Fig. 2; Table 1). Especially interesting is a mass occurrence of dimorphic pairs of the

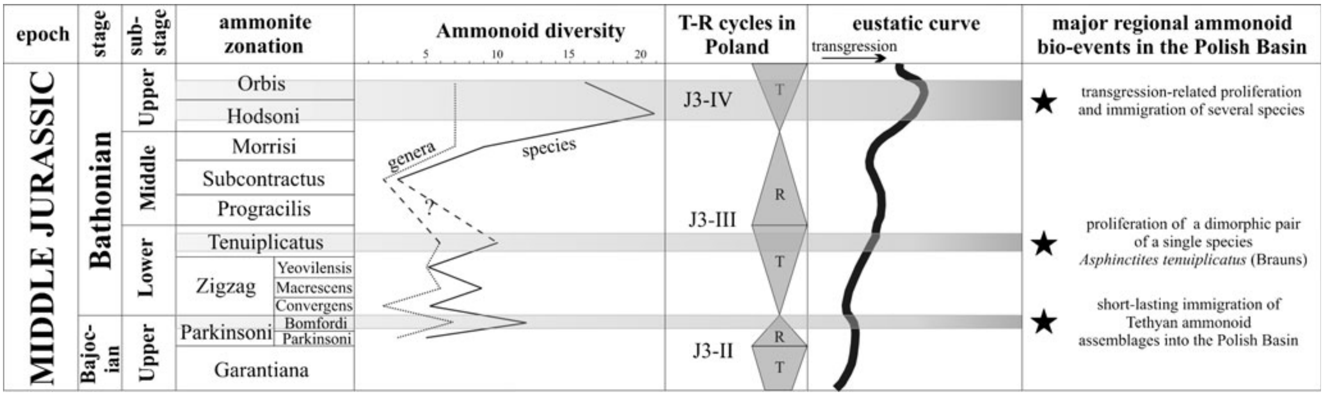

Fig. 2 Ammonoid diversity on the genus (*dotted line*) and species (*solid line*) level within particular ammonite zones and subzones, compared with the transgressive–regressive (*T-R*) cycles distinguished for the Polish Lowlands (slightly modified after Feldman-Olszewska 1997) and eustatic curve of Hallam (1988, 2001), together with major regional, transgressive-driven ammonoid bio-events for the Polish Basin

morphoceratid species *Asphinctites tenuiplicatus* (Brauns) [=*Asphinctites tenuiplicatus* (Brauns) [M] and *Polysphinctites secundus* (Wetzel) [m]; see Matyja and Wierzbowski 2000, 2001) that occur both in Kawodrza Górna and Faustianka, the latter site located ca. 40 km north (Fig. 1c; see also Matyja and Wierzbowski 2000, 2001 for details). Apart from *Asphinctites* assemblages, oppeliids [*Oxycerites* (*O.*) *yeovilensis* Rollier [M & m], *Oxycerites* (*O.*) *seebachi* (Wetzel), *Oxycerites* (*Paroecotraustes*) *formosus* (Arkell)] (see also Matyja and Wierzbowski 2000) and perisphinctids (*Procerites* [M & m] and *Wagnericeras* [M]) occur, but in much smaller quantity. Single phylloceratid *Calliphylloceras disputabile* (Zittel) as phragmocones of large individuals, and again *Lissoceras solitarium* Zatoń & Marynowski [m] known from the uppermost Bajocian Bomfordi Subzone also occur. However, the latter two species represent an insignificant component of the whole ammonoid assemblage here.

The ammonoid diversity for the basal Middle Bathonian Progracilis Zone is unknown. In the literature, the Progracilis Zone is either omitted (Kopik 1998) or united with the successive Subcontractus Zone (see Kopik 2006). A

Table 1 Ammonoid genera and their species number (in parentheses) in particular ammonite zones and subzones of the Polish Jura area

Substage/zone/subzone	Ammonite taxa	References
Upper Bathonian/Orbis Zone	*Oxycerites* (4), *Prohecticoceras* (2), *Procerites* (2), *Choffatia* (5), *Epistrenoceras* (1), *Cadomites* (1), *Bullatimorphites* (1),	Kopik (1998); Zatoń (2007a, b, 2010a, b)
Upper Bathonian/Hodsoni Zone	*Calliphylloceras* (1), *Oxycerites* (4), *Cadomites* (2), *Procerites* (6), *Wagnericeras* (2), *Choffatia* (3), *Bullatimorphites* (3)	Kopik (1998, 2006); Zatoń (2007a, 2010a, b)
Middle Bathonian/Morrisi Zone	*Calliphylloceras* (1), *Oxycerites* (3), *Prohecticoceras* (1), *Procerites* (1), *Choffatia* (1), *Bullatimorphites* (1), *Morrisiceras* (1)	Kopik (2006); Zatoń (2007a, 2008)
Middle Bathonian/Subcontractus Zone	*Oxycerites* (2), *Tulites* (1)	Zatoń (2007a, b, 2010a, b)
Lower Bathonian/Tenuiplicatus Zone	*Calliphylloceras* (1), *Oxycerites* (3), *Lissoceras* (1), *Procerites* (3), *Wagnericeras* (1), *Asphinctites* (1)	Matyja and Wierzbowski (2000, 2001); Zatoń and Marynowski (2006); Zatoń (2007a, 2010a, b)
Lower Bathonian/Zigzag Zone/Yeovilensis Subzone	*Oxycerites* (1), *Cadomites* (1), *Berbericeras* (1), *Morphoceras* (1), *Asphinctites* (1)	Kopik (1998); Matyja and Wierzbowski (2003); Zatoń (2007a, 2010a, b)
Lower Bathonian/Zigzag Zone/Macrescens Subzone	*Oxycerites* (1), *Cadomites* (1), *Procerites* (1), *Zigzagiceras* (1), *Parkinsonia* (2), *Morphoceras* (3)	Kopik (1998); Zatoń (2007a, 2010a, b)
Lower Bathonian/Zigzag Zone/Convergens Subzone	*Parkinsonia* (4), *Planisphinctes* (1)	Kopik (1998); Zatoń (2007a, 2010a, b)
Upper Bajocian/Parkinsoni Zone/Bomfordi Subzone	*Phylloceras* (1), *Nannolytoceras* (1), *Lissoceras* (2), *Strigoceras* (1), *Oxycerites* (2), *Vermisphinctes* (1), *Parkinsonia* (4)	Matyja and Wierzbowski (2000); Zatoń and Marynowski (2006); Zatoń (2007a, 2010a, b)
Upper Bajocian/Parkinsoni Zone/Parkinsoni Subzone	*Cadomites* (1), ?*Leptosphinctes* (1), *Parkinsonia* (3)	Matyja and Wierzbowski (2000); Zatoń (2007a, 2010a, b)

potential site where deposits of the Progracilis Zone may be present is Faustianka. There, the lower part of the exposure is definitely dated as the uppermost Lower Bathonian Tenuiplicatus Zone (e.g., Matyja and Wierzbowski 2000). Matyja and Wierzbowski (2000) have stated they have found ammonites (mainly *Procerites*) characteristic of the Progracilis Zone at Faustianka; however, they are not yet either described or illustrated. Therefore, for the time being, the characteristics of the Progracilis Zone together with its ammonite content are not known in the Polish Jura area.

The ammonoid diversity in the following Subcontractus Zone is very low (two genera and three species) (Fig. 2; Table 1). In Blanowice (Fig. 1c), only two species (*Tulites subcontractus* Buckman [M] and *Oxycerites* (*O.*) sp. ex gr. *yeovilensis* Rollier [M]) have been documented (Zatoń 2007a, b, 2010a, b), and from the Częstochowa environs (Gnaszyn Dolny) just one, *T. cadus* Buckman [M], although the *Oxycerites* species may also occur there. Besides *T. cadus* Buckman and *T. tulotus* (Buckman), the species *T. subcontractus* (Morris & Lycett) was also mentioned by Kopik (1998, 2006) from the Częstochowa environs.

This impoverishment of ammonoid diversity during the Subcontractus Chron may result from insufficient sampling, as the deposits of this zone were not well exposed in the Częstochowa area during fieldwork conducted by Zatoń (2007a), or are very reduced in the Blanowice locality (Zatoń 2007b). However, as we brought together the data obtained by Zatoń (2007a, b, 2010a, b) and that selected from the literature, it seems that during this chron the overall ammonite diversity was indeed low.

Higher up, in the Morrisi Zone, ammonoid diversity on the species level is a little bit higher (nine species) than on the genus level (seven genera), but generally the diversity on both taxonomic levels is quite similar (Fig. 2; Table 2). Among the species recorded, the most abundant is the morphologically widely variable *Morrisiceras morrisi* (Oppel) [M & m] (see Zatoń 2008) and *Oxycerites* (*O.*) sp. ex gr. *yeovilensis* Rollier [M & m]. Although the first is confined only to the Morrisi Zone, the latter species also occurs in the older Subcontractus Zone.

The highest ammonoid diversity is noted in the Upper Bathonian Hodsoni Zone (Fig. 2; Table 1). It must be underlined, however, that the diversity on the species level (21 species) is much higher than that on the genus level (seven genera). There may be fewer ammonite species because our knowledge about the dimorphism of such Late Bathonian species as *Oxycerites* or *Choffatia* is still insufficient, which may result in overestimating the ammonite species in general. During the Hodsoni Chron, apart from the genera mentioned above, there is also the beginning of domination by representatives of the genus *Procerites* and *Choffatia* in the Polish Basin.

In the following Orbis Zone, the number of ammonoid genera remains the same as in the precedent zone (seven genera), and the number of species slightly decreased to 16 species (Fig. 2; Table 1). Generally, however, the species diversity in the Orbis Zone is much higher than in any of the Lower and Middle Bathonian intervals (see Fig. 2).

Diversity dynamics of ammonoids on the background of the sea-level changes during latest Bajocian and Bathonian in the Polish Basin: a discussion

The diversity pattern of uppermost Bajocian and Bathonian ammonoids in the Polish Jura sector of the Polish Basin seems to correspond well with the sea-level changes marked on the eustatic curves of Hallam (1988, 2001), as well as with the majority of transgressive–regressive cycles distinguished for the Polish Lowlands by Feldman-Olszewska (1997) (see Fig. 2). It indicates that the general eustatic trend was not masked significantly by regional tectonics in the Polish Basin. During the Middle Jurassic, intense rifting leading to the gradual break-up of Pangea (e.g., Golonka 2000), and simultaneous eustatic sea-level rise may have significantly weakened the results of regional tectonics in the areas of epicratonic basins.

Diversity dynamics during the latest Bajocian

In the ammonoid assemblages dated as latest Bajocian Bomfordi Subchron, apart from dominating parkinsoniids, representatives of Phylloceratina and Lytoceratina are recorded. Generally, Phylloceratina and Lytoceratina ammonoids are characteristic components of oceanic pelagic environments (e.g., Wiedmann 1973; Ward and Signor 1983; Marcinowski and Wiedmann 1988; Lehmann 1995; Fernández-López and Meléndez 1996; Westermann 1990, 1996; Cecca 1992, 1998, 1999). There is a general agreement among Jurassic and Cretaceous ammonite workers that their maximum dispersion occurred during times of high sea-level (Wiedmann 1973, 1988; Kauffman 1977, 1984; Kennedy and Cobban 1976; Westermann 2001). In northern Europe, the transgressive pulse that begun in the Late Bajocian attained its peak at the Bajocian/Bathonian transition (Hallam 1992, 2001). In the Mediterranean Province, the transgressive phase is dated on the beginning of the Parkinsoni Chron (Sandoval et al. 2001), while in the Polish Basin a decline of the transgression is assumed (transgressive–regressive cycle J3-II of Feldman-Olszewska 1997). However, the presence of *Phylloceras* sp. and abundant *Nannolytoceras tripartitum* (Raspail) points to a regional bio-event corresponding to immigration from Tethyan areas during the Late Bajocian transgressive event (see also Zatoń and Marynowski 2006). It must also be added that the ammonoids mentioned above are represented by juveniles.

Fernández-López and Meléndez (1996; see also Fernández-López and Gómez 2004) also noticed an immigration of juvenile representatives of Phylloceratina and Lytoceratina (including *Nannolytoceras*) during the Late Bajocian transgression. According to them, the juvenile phylloceratids and lytoceratids have not found suitable conditions for both their ontogenetic development and breeding. Although single phylloceratids, such as *Calliphylloceras disputabile* (Zittel), sporadically occur in the Bathonian of the Polish Jura (Zatoń 2007a, 2011a, b), the representatives of *Nannolytoceras* no longer occur. However, *Calliphylloceras* is represented by incomplete phragmocones of large individuals, which may point to necroplanktic drift of their shells, or occasional, passive expansion of particular species (Fernández-López and Gómez 2004). *Nannolytoceras tripartitum* (Raspail) is most abundant in the uppermost Bajocian–Lower Bathonian deposits. In Hungary, this species disappears at the beginning of the Middle Bathonian (Progracilis Chron; see Galácz 1980), and in Spain, the genus *Nannolytoceras* is recorded until the end of the Early Bathonian (Sandoval et al. 2001). The complete absence of this genus in both the lower and higher horizons of the ore-bearing clays, even in the richest ammonite-bearing horizons (e.g., the Tenuiplicatus Zone of Kawodrza Górna and Faustianka), proves that they were short-lasting, transgression-driven immigrants not adapted for living in the epicratonic Polish Basin during those times. This hypothesis may be supported by the pattern of occurrence of the genus *Lissoceras* [M & m], which is also noted as an immigrant in Spain (Fernández-López and Gómez 2004).

Representatives of the genus *Nannolytoceras*, as well as the Phylloceratina in general, occur abundantly in the southerly located Pieniny Basin (e.g., Wierzbowski et al. 1999; Schlögl et al. 2005). The presence of prosopid crabs associated with small oyster buildups or brachiopod lumachelles in the uppermost Bajocian ore-bearing clays point to a shallow-water environment (Krobicki and Zatoń 2008). Although water-depth may have been one of the factors limiting the development of these oceanic forms (but see Daniel et al. 1997), lower temperatures in northern areas as compared to those in Tethyan regions may have been a more likely ecological barrier for their further development (Fernández-López and Gómez 2004). The temperatures estimated on the basis of stable isotopes derived from belemnite rostra were rather low, ranging from 6 to 10°C during the latest Bajocian Bomfordi Chron in the Polish Jura sector of the Polish Basin (see Wierzbowski and Joachimski 2007: fig. 9). Thus, *Nannolytoceras* and Phylloceratina may have represented parademic populations (Fernández-López 1991; see also Fernández-López and Meléndez 1996) if their dispersion was passive, or miodemic (Fernández-López 1991; see also Fernández-López and Meléndez 1996) if the dispersion was active. There is no indication, however, that they reached the Polish Basin by post-mortem drift as an ademic population (Fernández-López 1991; see also Fernández-López and Meléndez 1996). The probable route of their immigration was by the Mid-Polish Trough via the East-Carpathian Gate which linked the Polish Basin with the Tethys Ocean (Dayczak-Calikowska and Moryc 1988; Feldman-Olszewska 1997) (Fig. 1a). At the Bajocian/Bathonian transition, on the other hand, parkinsoniids are the most numerous in north-western and central Europe (e.g., Galácz 1980; Sandoval et al. 2001), from where they migrated into the Tethyan areas (Galácz 1980). Their presence as both juveniles and adults (e.g., Matyja and Wierzbowski 2000; Zatoń and Marynowski 2006) in the Polish Basin both below and above the transgressive peak indicate that they found optimal biotic conditions favouring their development in the epicratonic Polish Basin. Therefore, they may be regarded as a eudemic population (Callomon 1985; see also Fernández-López and Meléndez 1996).

Diversity dynamics during the Early Bathonian

The low diversity noted in the Lower Bathonian Convergens Subzone correlates with a regressive episode/pulse on the sea-level curve of Hallam (1988, 2001) (see Fig. 2). This episode may have led to a total disappearance of the representatives of *Nannolytoceras* in the Polish Basin, as they are not noted subsequently. Representatives of the subgenus *Parkinsonia* (*Parkinsonia*) also slowly disappear, with only the species *P.* (*P.*) *schloenbachi* Schlippe continuing. However, the subgenus *P.* (*Gonolkites*), represented by the well-known species *P.* (*G.*) *subgaleata* (Buckman), appears for a short time as its occurrence is limited to the Convergens Subzone. On the other hand, *P.* (*Durotrigensia*), a subgenus well known since the Late Bajocian, continued into the earliest Bathonian. The reasons for low ammonoid diversity during the Yeovilensis Subchron are unclear. Despite the documented representatives of *Oxycerites* and *Asphinctites* (Kopik 1998; Matyja and Wierzbowski 2003; Zatoń 2007a, 2010a, b), some single specimens of morphoceratid genera *Morphoceras* and *Berbericeras* have been documented by Matyja and Wierzbowski (2003) and Matyja et al. (2006b). Therefore, the scarcity of ammonoids in the Yeovilensis Subzone may have resulted from taphonomic or lithological factors. In Kawodrza Górna ('Leszczyński' clay-pit; see e.g., Matyja and Wierzbowski 2000 for details), the Yeovilensis Subzone includes a thick clay sequence with a horizon of massive sideritic nodules. Therefore, on the one hand it is difficult to find and retrieve ammonites from soft, unconsolidated clays, while on the other hand, the ammonite fauna is rare in sideritic nodules, so that the overall ammonoid diversity within this subzone is artificially very low.

In the older Macrescens Subzone of the Zigzag Zone, and in the younger Tenuiplicatus Zone, a gradual increase of ammonoid diversity is observed (Fig. 2). In the Macrescens Subzone, six genera and nine species are recorded (Fig. 2), dominated by parkinsoniids of the subgenus *Parkinsonia* (*Oraniceras*) [*P.* (*O.*) *gyrumbilica* (Quenstedt) and *P.* (*O.*) *wuerttembergica* (Oppel)] with characteristic discoidal shells, perisphinctids (*Procerites tmetolobus* Buckman) and morphoceratids. At the end of the subchron, all representatives of *Parkinsonia* and *Morphoceras* disappear (see Sandoval et al. 2001).

Probably, as was mentioned above, the presence of phylloceratids in the Tenuiplicatus Zone may have resulted from their passive dispersion from Tethyan areas during a sea-level rise. The gradual increase in sea-level may have also influenced the re-immigration of *Lissoceras* into the Polish Basin. What is very distinctive for the Tenuiplicatus Zone in the Polish Jura is a proliferation of the two sexual dimorphs of the morphoceratid *Asphinctites tenuiplicatus* (Brauns) which well outnumber the rest of the ammonite species (e.g., Matyja and Wierzbowski 2000, 2001). Moreover, the macroconchs of that species are noted to be much larger in Poland than in other European localities (Matyja and Wierzbowski 2001). This distinct, regional bio-event may have resulted from optimal conditions prevailing in the area, and is probably linked to a greater nutrient supply (eutrophication) during the transgression.

Matyja and Wierzbowski (2000) have pointed out that oppeliids are much rarer than *Asphinctites* in the area of Częstochowa (Kawodrza Górna locality) as compared to the northern area of Faustianka. This may be explained either by a shift of the ammonite faunas from the older (Częstochowa area) to the younger one (Faustianka), or by the different locations of the both areas within the Polish Basin: more peripheral and shallower in the environs of Częstochowa where a contribution of deeper-dwelling oppeliids was smaller than in the Faustianka area (see Matyja and Wierzbowski 2000). It must be taken into account, however, that the oppeliids described by Matyja and Wierzbowski (2000) come exclusively from the Faustianka locality, while in Kawodrza Górna ('Leszczyński' clay-pit) they cited only a single fragment of *Oxycerites* (Matyja and Wierzbowski 2000, p. 195). The ammonite fauna collected from Kawodrza Górna (Majewski 1997; Zatoń 2007a, 2010a, b) indicates that oppeliids occur in similar quantity as in Faustianka, and thus the bathymetric differences between the both areas are insignificant. Therefore, the conclusions put forward by Matyja and Wierzbowski (2000) are based on their insufficient sampling of the Tenuiplicatus Zone at Kawodrza Górna that simultaneously may have been biased towards more common *Asphinctites* specimens.

The gradual increase of ammonoid diversity beginning after the Macrescens Subchron may be related to progressive transgression during these times (transgressive–regressive cycle J3-III of Feldman-Olszewska 1997) (Fig. 2).

Diversity dynamics during the Middle Bathonian

The next transgressive peak occurs in the lower part of the Middle Bathonian (Progracilis Zone) (Fig. 2). The lack of data from epicratonic Poland, however, prevents the discussion of the ammonoid diversity within this interval. In the Subcontractus Zone, the ammonite diversity is very low. As stated above, this low diversity may be related to insufficient sampling. However, using the data in this study and the literature (Kopik 1998, 2006), it is evident that the overall ammonoid diversity during the Subcontractus Chron was low.

On the other hand, this low diversity seems to correlate with the regression phase (Fig. 2). Moreover, according to Feldman-Olszewska (1997), during the transgressive–regressive cycle J3-III during the Subcontractus Chron, a regressive pulse is well discerned in the Polish Lowlands (Fig. 2). It is worth stressing here that all European species of *Tulites* are recorded exclusively from the Subcontractus Zone (see Mangold and Gygi 1997). The exception is *T. tuwaiqensis* Arkell known from the Lower Bathonian of Sicily (Galácz 1999) and Saudi Arabia (Enay and Mangold 1994). However, its taxonomic status is uncertain (Galácz 1999, p. 161). If it actually belongs to the genus *Tulites*, as Mangold and Gygi (1997) stated, its migration toward European areas, although still problematic (see Mangold and Gygi 1997), may have been related to the progressive Early Bathonian transgression which culminated at the beginning of the Middle Bathonian (Fig. 2). The disappearance of all *Tulites* species, and the extinction of the genus itself, on the other hand, may have been related to an overall regression.

In the Morrisi Zone, the transition from regression (lower part of the zone) to transgression (upper part of the zone) is observed on the Hallam's curve (Fig. 2). The genus *Morrisiceras*, known also from England, France, Germany, Switzerland and Middle Asia (see Zatoń 2008), is going to become extinct at the end of the Middle Bathonian (in the sense of the North-European subdivision). Its extinction, similar to the case of *Tulites*, may have been caused by the regression-related strong restriction of shallow-marine habitats (Zatoń 2008). Such a scenario seems to be supported by the absence of *Morrisiceras* representatives in deeper Tethyan settings. An alternative view may be that its disappearance was related to its poor competitive abilities against the new species appearing during the Late Bathonian transgression. It is known that 'invasive' species may contribute to the extinction of native species (e.g., Clavero and García-Berthou 2005; see also Didham et al. 2005; Navarro et al. 2005).

Diversity dynamics during the Late Bathonian

The highest ammonoid diversity on the species level took place during the Late Bathonian (Hodsoni Chron) in the Polish Basin (Fig. 2), which correlates with the highest transgressive peak on the Hallam's (1988, 2001) curve and transgressive pulse in the Polish Lowlands (transgressive–regressive cycle J3-IV of Feldman-Olszewska 1997). In the Orbis chron, the number of species slightly decreases, but the overall ammonoid diversity is still very high (Fig. 2). Therefore, the highest species diversity levels during both the Hodsoni and Orbis chrons seem to be tightly correlated with the largest transgression occurring in the Late Bathonian (Fig. 2). Also, in the Late Bathonian, the Polish Basin attained the greatest width during its entire Bajocian–Bathonian expansion history (see Dayczak-Calikowska and Moryc 1988; Matyja and Wierzbowski 2006). The high levels of species diversity may have been related to the opening of several new sea-ways that enabled migrations.

Conclusions

The ammonoid diversity during the latest Bajocian and Bathonian in the Polish Basin distinctly fluctuated in the course of particular chrons and subchrons. These changes seem to be correlated with global sea-level fluctuations, as well as with the majority of the regional transgressive-regressive cycles for the Polish Lowlands. Three main ammonoid diversity peaks (regional ammonoid bio-events) are found to be correlated with particular transgressive episodes: (1) the Latest Bajocian (Bomfordi Subchron) bio-event is related to the short-lasting immigration of Tethyan ammonoids to the epicratonic Polish Basin; (2) a late Early Bathonian (Tenuiplicatus Chron) bio-event corresponds to the proliferation of a dimorphic pair of a single species *Asphinctites tenuiplicatus* (Brauns), as a probable result of a transgression-driven eutrophication of shallow-marine environment; and (3) a Late Bathonian (Hodsoni and Orbis chrons) bio-event corresponds to the highest ammonoid diversity, most probably as a result of the major transgression episode during the Bathonian that allowed migration via newly opened sea-ways.

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