Inoceramid bivalves at the Turonian/Coniacian boundary: biostratigraphy, events and diversity trend

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ABSTRACT:

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The Turonian/Coniacian boundary marks one of the main turnover levels in the Late Cretaceous history of the inoceramid bivalves. The change from the *Mytiloides*-dominated Late Turonian fauna to the *Cremnoceramus*-dominated Early Coniacian fauna was a dramatic experience for the group, with a series of successive assemblages interrupted by their almost total elimination, and with intervening short-term expansions of the bivalve *Didymotis*. The taxonomic diversity dropped to a few species per interval calculated and marks the lowest level in their Late Cretaceous history, comparable to the trough around the Cenomanian/Turonian boundary. The whole change must have taken no longer than a quarter of a million years and its duration could have been as short as some tens of thousand years.

Key words: Turonian, Coniacian, Bio- and Event stratigraphy, Inoceramids, Taxonomic diversity.

INTRODUCTION

The inoceramid bivalves from the Turonian/Coniacian boundary interval of the Euramerican biogeographical region possess one of the most complete and richest records among Late Cretaceous invertebrate groups. Abundant material from the area permits refined bio- and event stratigraphical studies as well as detailed analysis of diversity trends and evolutionary patterns. For a long time the extraordinary richness of inoceramid faunas during this interval marked one of the main peaks in the published graphs of Late Cretaceous inoceramid taxonomic diversity (PERGAMENT 1967, TRÖGER 1976, VOIGT 1995, 1996; ZONOVA & YAZYKOVA 1999) and was interpreted in terms of particularly favourable environmental conditions. Recent restudy of classic material from Europe and North America, as well as detailed investigation of selected successions throughout the Euramerican region, showed, however, that the inferred Turonian/Coniacian boundary inoceramid diversity peak in no way reflected the existence of taxonomically rich inoceramid fauna inhabiting the latest Turonian and Early Coniacian seas. Besides taxonomic over-splitting, which has considerably effected the interpretation of previous diversity trends, this peak is a result of a time-cumulative effect due to the highly accelerated evolutionary rate of the group during the latest Turonian and Early Coniacian. The actual standing diversity at the boundary interval remained, however, for a long time at a very low level.

This report briefly summarises recent developments in the bio- and event stratigraphy of the Turonian – Coniacian boundary of the Euramerican biogeographical region and presents a new interpretation of the taxonomic diversity trend of the inoceramid fauna across the boundary. The latter is based on actual sections, although the taxonomy and distribution patterns of the inoceramids in question have been taken from the standardised literature-based data-bank.

GEOGRAPHICAL SETTING

The discussions presented in this paper refer to the area of the Euramerican Biogeographical Region, using
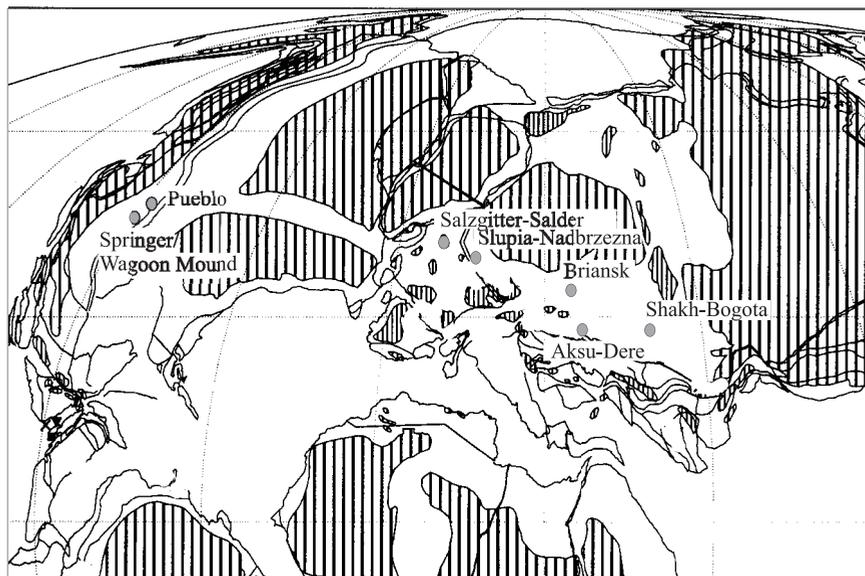
Fig. 1. Palaeogeographical location of studied sections; palaeogeography after HAY & *al*. (1999)

KAUFFMAN's (1973) palaeobiogeographical division. The compiled results are based on a number of sections already studied in detail, as well as on a whole series of additional ones used for comparison purposes or currently under study (Text-fig. 1). The critical sections include (from east to west): Shakh-Bogota, Western Kazakhstan (MARCINOWSKI & *al*. 1996, MARCINOWSKI 1996); Słupia Nadbrzeżna, Central Poland (WALASZCZYK 1992, WALASZCZYK & WOOD 1999a); Salzgitter-Salder, Lower Saxony, northern Germany (WOOD & *al*. 1984, KAUFFMAN & *al*. 1996, WOOD & ERNST 1997, WALASZCZYK & WOOD 1999a); and two North American sections, i.e. Springer and Wagon Mound in New Mexico and Pueblo in Colorado, both from the US Western Interior (SCOTT & COBBAN 1966, PRATT & *al*. 1985, WALASZCZYK & COBBAN 1999, 2000). Also of importance are a section from the vicinity of Briansk, SW of Moscow (WALASZCZYK, ALFIRIEV & KOPAEVICH, in prep.), the Aksu-Dere section in SW Crimea (KOPAEVICH & WALASZCZYK 1991) and the Opole section in SW Poland (WALASZCZYK 1988, 1992).

Some provisional reports suggest that the inoceramids from the Turonian/Coniacian boundary probably formed a uniform record over a much broader area than the Euramerican biogeographic region. Virtually the same boundary inoceramid assemblage has already been reported from the adjacent areas of the Tethyan Realm (Caribbean Province – KAUFFMAN 1965, 1978; Gosau Cretaceous – HERM & *al*. 1979, TRÖGER & SUMMESBERGER 1994; Sardinia – WALASZCZYK & FANTIN, in prep.) and the same forms are also listed from Brazil, representing the South-Atlantic subprovince of the South Temperate Realm (KAUFFMAN & BENGTSON 1985).

STRATIGRAPHICAL FRAMEWORK

Boundary recommendation

The Turonian – Coniacian boundary concept applied here follows the recommendation at the Symposium on Cretaceous Stage Boundaries in Brussels in 1995 (KAUFFMAN & *al*. 1996). The boundary is accordingly placed at the appearance level of the inoceramid species *Cremnoceramus deformis erectus* (MEEK), the correct name for forms referred hitherto to *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE), the species proposed in Brussels as the boundary marker taxon (see WALASZCZYK & WOOD 1999a, WALASZCZYK & COBBAN 2000).

The entrance level of *C. deformis erectus* does not mark the main turnover level in inoceramid faunas in the boundary interval. This took place slightly lower, at the base of the terminal Turonian *Cremnoceramus waltersdorfensis waltersdorfensis* Zone, marking the main change from the typically Turonian *Inoceramus* – *Mytiloides* fauna, to the typically Coniacian *Cremnoceramus* fauna. At first sight this latter bioevent might seem to be a more suitable stage boundary marker than the one chosen in Brussels. The problem, however, is that the appearance of the first cremnoceramids is still unclear. Although it is interpreted herein as coeval with the lower *waltersdorfensis* Event, some published records of isolated occurrences of forms apparently close to, or even conspecific with, *Cremnoceramus waltersdorfensis* from below this level throw doubt on this interpretation and require further investigation (TRÖGER 1989). On the other hand, the entrance of *Cremnoceramus deformis erectus* is a well

defined cladogenetic evolutionary event, well recorded e.g. in the Słupia Nadrzeżna section in Central Poland (see WALASZCZYK & WOOD 1999a) and in the Pueblo section.

Biostratigraphy

The Turonian-Coniacian boundary and the boundary interval possesses a well-defined biostratigraphical framework (Text-fig. 2) based primarily on inoceramids (WOOD & *al*. 1984, KAUFFMAN & *al*. 1996, WALASZCZYK & WOOD 1999a). Throughout the topmost Turonian and the lowermost Coniacian, a uniform zonation may be applied to the whole Euramerican region, comprising, from bottom upwards, the zones of *Mytiloides scupini*, *Cremnoceramus waltersdorfensis waltersdorfensis*, and *Cremnoceramus deformis erectus* (Text-fig. 2). Because of the relatively rare occurrence of *Cremnoceramus waltersdorfensis hannovrensis* (HEINZ) and of *Cremnoceramus crassus inconstans* (WOODS), forms that are common in Europe, the zones based on these taxa in Europe are difficult to apply in the US Western Interior. Instead, it is more convenient to distinguish there the zone of *Cremnoceramus deformis dobrogensis* (SZÁSZ) (Text-fig. 2). The succeeding *Cremnoceramus crassus crassus* Zone is well represented both in Europe and in the US Western Interior.

Stage	Substage	Inoceramid zones	
		Europe	US Western Interior
CONIACIAN	Middle	*Platyceramus* ex gr. *mantelli* + *Volviceramus koeneni*	
CONIACIAN	Lower	*Inoceramus gibbosus*	?? ??
CONIACIAN	Lower	*Cremnoceramus crassus crassus* + *Cremnoceramus deformis deformis*	
CONIACIAN	Lower	*Cremnoceramus crassus inconstans*	*Cremnoceramus deformis dobrogensis*
CONIACIAN	Lower	*Cremnoceramus waltersdorfensis hannovrensis*	*Cremnoceramus deformis dobrogensis*
CONIACIAN	Lower	*Cremnoceramus deformis erectus*	
TURONIAN	Upper (part)	*Cremnoceramus waltersdorfensis waltersdorfensis*	
TURONIAN	Upper (part)	*Mytiloides scupini*	

Fig. 2. Inoceramid zonation of the topmost Turonian and Lower Coniacian of the Euramerican Biogeographical Region (compiled after: WOOD & *al*. 1984, WALASZCZYK & WOOD 1999a, WALASZCZYK & WOOD *in* NIEBUHR & *al*. 1999, WALASZCZYK & COBBAN 2000)

As was demonstrated in the Staffhorst shaft section, northern Germany (WALASZCZYK & WOOD *in* NIEBUHR & *al*. 1999) cremnoceramids do not range to the top of the Lower Coniacian, the topmost part of the substage being dominated by a radially sulcate *Inoceramus* taxon, referred provisionally to *Inoceramus gibbosus* SCHLÜTER. A similar succession was found in the Lower Coniacian of the Briansk section, SW of Moscow (WALASZCZYK, OLFIRIEV & KOPAEVICH, in. prep.). It seems probable that occurrences of the basal Middle Coniacian *Platyceramus* ex gr. *mantelli* – *Volviceramus koeneni* fauna directly above the last cremnoceramids, as is usually observed in the European and North American sections, results from a large-scale interregional gap, presumably associated with a distinct sea-level rise at that time (see e.g. HANCOCK 1990).

The ammonites in the interval concerned were much less sensitive to environmental change than the inoceramids and consequently they do not allow the application of a uniform zonation to the whole Euramerican region (KENNEDY & COBBAN 1991, WALASZCZYK & COBBAN 2000). Moreover, the application of the standard ammonite zonation to European sections (KENNEDY 1984a, b) is hampered by the rarity of the zonally diagnostic taxa (KAPLAN & KENNEDY 1994, 1996).

The main transition from the typically Turonian to the typically Coniacian ammonites took place already in the topmost Turonian *Mytiloides scupini* Zone, which, in Europe, broadly corresponds to the *Prionocyclus germari* ammonite Zone. This is clearly demonstrated by rich material from the US Western Interior (KENNEDY & COBBAN 1991, WALASZCZYK & COBBAN 1999), but was also recently confirmed in Europe, by a single find of *Forresteria* cf. *petrocoriensis* (Coquand) in the topmost *scupini* Zone of the Vistula section, Central Poland (determination by W.J. KENNEDY).

Event stratigraphy

The Turonian – Coniacian boundary interval is set in a well defined event stratigraphical framework (Text-fig. 3). This scheme, originally worked out by WOOD & *al*. (1984) in the north German succession, is composed of a series of bioevents consisting of acme-occurrences of inoceramid bivalves and *Didymotis*, which mostly represent diversification events (as defined by SAGEMAN & *al*. 1998). Many of the events were subsequently recognised throughout Europe (KÜCHLER & ERNST 1989, ČECH 1989, WALASZCZYK 1992), western Asia (MARCINOWSKI & *al*. 1996) and quite recently also in the US Western Interior (WALASZCZYK & WOOD 1999a; WALASZCZYK & COBBAN 1999, 2000). They thus constitute a series of events on an

interregional or even intercontinental scale, implying a sequence of very rapid environmental changes that were synchronous over a large part of the Northern Hemisphere.

In the context of chronostratigraphy as well as environmental interpretation, the synchroneity of particular events over the whole area of their recognition remains open to question. Whereas claims relating to the time-equivalency of a single event over a distance of some thousands of kilometres require independent dating, the Turonian – Coniacian boundary interval is marked by a series of events (about 10 well-defined horizons) occurring with an identical pattern in different areas. The possibility that such a repeated pattern could be heterochronous is inconceivable. The problem lies in the correct identification of particular events. This may be especially difficult in the case of those events that are represented by recurring single taxon accumulations, e.g. acme-occurrences of the bivalve] *Didymotis* (see discussion in WIESE 1999) or of *Cremnoceramus deformis erectus* (MEEK).The definitive identification of any one bioevent requires careful assessment of the accompanying fauna as well as its precise location in the succession.

TURONIAN – CONIACIAN BOUNDARY EVENTS – A COMPILATION

Text-fig. 3 compiles the stratigraphical position of most of the events encountered hitherto in the uppermost Turonian and lowermost Coniacian in all of the analysed sections, although it is based primarily on the Salzgitter-Salder and Słupia Nadbrzeżna sections. Details of the diagnostic features of these events are to be found in WOOD & *al*. (1984), WOOD & ERNST (1997), WALASZCZYK & WOOD (1999a) and in WALASZCZYK & COBBAN (1999, 2000).

The analysed succession, starting at the base of the *Mytiloides scupini* Zone, is clearly three-fold in respect of faunal content and diversity levels Almost directly above the level with abundant occurrence of *M scupini* at the base of the *scupini* Zone is found the expanded and poorly fossiliferous Late Turonian "barren interval" (see HATTIN 1975), which ranges approximately to the level of the *Didymotis* I Event. This interval is very poorly known indeed, and very little may be said about it besides the fact that it has been recognised throughout the Euramerican Region (Text-fig. 3). In the succeeding interval, comprising the Turonian/Coniacian boundary transition, inoceramids become extraordinary abundant, although the standing diversity is very low. A sudden increase in diversity, with still remarkably high numbers of individuals, begins at the *erectus* III Event, marking the lower boundary of the third interval.

The Inoceramids underwent two main turnovers at the very top of the Turonian, at two horizons which seem to be critical: the appearance of the '*websteri*' fauna; and a slighly younger one, the entrance level of cremnoceramids (Text-fig. 3). The '*websteri*' fauna is very poorly known, being reported so far only from the Słupia Nadbrzeżna and the Pueblo sections. The assemblage comprises forms comparable to *Inoceramus lusatiae* ANDERT, *Inoceramus glatziae* FLEGEL (sensu ANDERT 1911, 1934), as well as *Inoceramus websteri* (sensu WOODS *non* MANTELL), but its actual composition requires further taxonomic study. The entrance of cremnoceramids, appearing as a mass-occurrence of a small *Cremnoceramus waltersdorfensis waltersdorfensis* (ANDERT), is very much more clearly defined. Where this form came from is still unclear. It may have been derived from a member of the '*websteri*' fauna or it could have had a progenitor taxon lower in the *scupini* Zone.

Cremnoceramids reigned through most of the Early Coniacian. In contrast to previous opinions, however, it seems that they disappeared some time before the entrance of the Middle Coniacian *Volviceramus – Platyceramus* assemblage, giving way to the radially sulcate *Inoceramus gibbosus* fauna of WALASZCZYK & WOOD (*in* NIEBUHR & *al*. 1999).

TAXONOMIC DIVERSITY

The most characteristic aspect of the inoceramid fauna observed in actual sections spanning the Turonian – Coniacian boundary is, despite its exceptional richness in numbers of individuals, a very low taxonomic diversity. This applies to the assemblages from the topmost Turonian and lowermost Coniacian, up to the *erectus* III Event. Some of the assemblages, e.g. in the *Cremnoceramus waltersdorfensis waltersdorfensis* Zone, are almost monospecific.

This trend is demonstrated here by the two sections from which rich material was collected (each of them provided more than 1000 specimens): the Salzgitter-Salder and the Słupia Nadbrzeżna sections (Text-fig. 3). The sample size effect was correctedby means of modified SANDER's (1968) rarefaction equations (RAUP 1975). These empirical data are verified against the literature-based data bank, comprising the verified stratigraphy and taxonomically standardised literature entries. [The data bank is not included here but is accessible on request from the author. Although it was prepared in the licence-demanding computer program Paleo-Tax (LÖSER 1996) the version prepared on standard Microsoft Office Access program is available.] Taxonomic standardisation of the most important collections was already published,
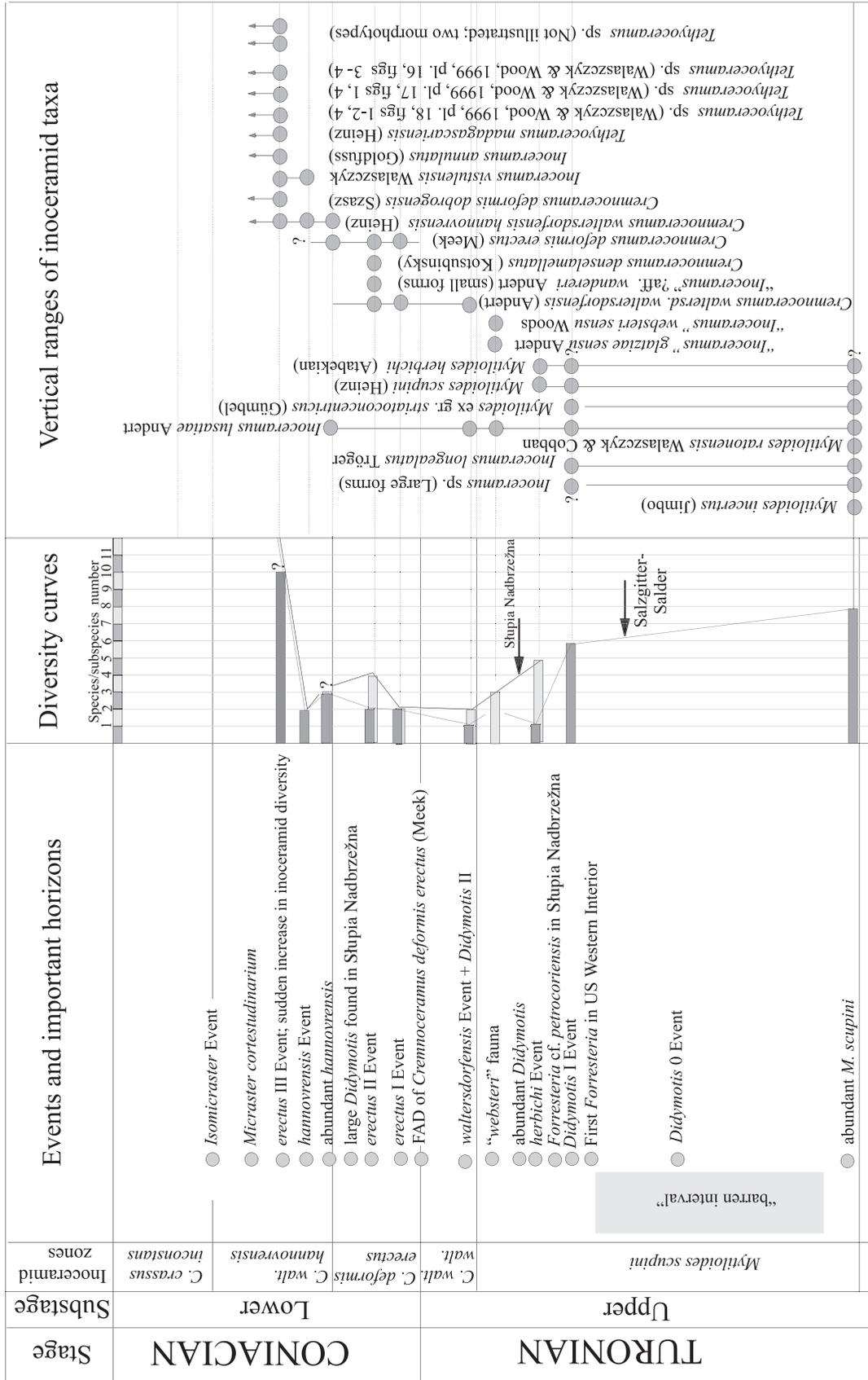
Fig. 3. Compilation of events, important horizons, vertical ranges of inoceramid taxa, and the diversity curves for the topmost Turonian and lowermost Coniacian of the Salzgitter-Salder and Słupia Nadbrzeżna sections
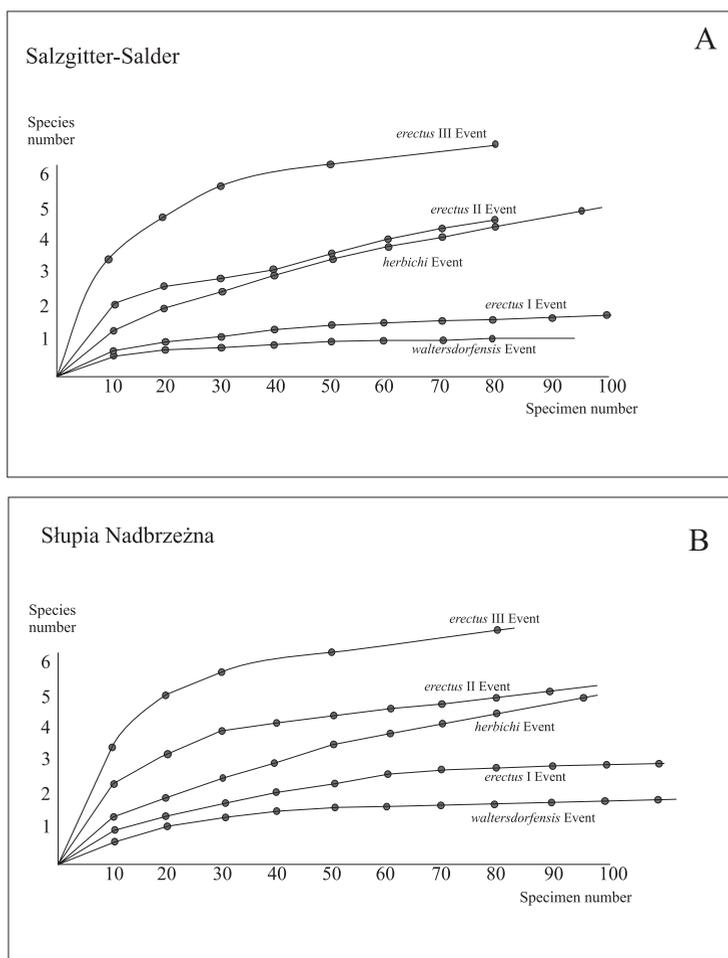
Fig. 4. Rarefaction curves for samples from the Salzgitter-Salder and Słupia Nadbrzeżna sections

including the Romanian collections of SIMIONESCU (1899) from Ürmös (WALASZCZYK & SZÁSZ 1997), as well ANDERT's (1911, 1934) material from Saxony and Bohemia (WALASZCZYK 1996, WALASZCZYK & TRÖGER 1996, and WALASZCZYK & WOOD 1999a), which is particularly important for a study of the inoceramid faunas across the Turonian/Coniacian boundary. Also restudied were critical forms from PETRASCHECK (1903), WOODS (1912), HEINZ (1928, 1933), AIRAGHI (1904), and DOBROV & PAVLOVA (1959) with revision and new illustrations (TRÖGER 1967, WALASZCZYK 1992, and WALASZCZYK & WOOD 1999a). The North American inoceramids were recently revised by COLLOM (1998) and WALASZCZYK & COBBAN (2000). WALASZCZYK & WOOD (1999a) provided a monographic description of the inoceramid faunas from the Salzgitter-Salder and the Słupia Nadbrzeżna sections.

The diversity trend across the boundary (Text-fig. 3), revealed by these two sections starts with a moderately diverse assemblage at the bottom of the *Mytiloides scupini*

Zone. A similar diversity is present above the "barren interval", up to the *herbichi* Event. A distinct drop in diversity is observed very close to the boundary, in the terminal Turonian *waltersdorfensis waltersdorfensis* Zone, and continues in the basal Coniacian *deformis erectus* Zone and at the base of the *waltersdorfensis hannovrensis* Zones. It is probable that this drop in diversity starts already at the level of the '*websteri*' fauna, but the present knowledge of that horizon is insufficient to give reliable counts. There is a sudden increase in diversity at the level of the *erectus* III Event. The number of taxa counted at this level is about one order higher than in the interval below. The details of the evolution of the inoceramids at that level are still poorly known, but the actual number of species (or better distinct fans) may be exceptionally high. It is the appearance level of the diverse and rapidly evolving genus *Tethyoceramus* (see discussion in WALASZCZYK & WOOD 1999a) and also the level where most of the Early Coniacian species monographed by KHALAFOVA (1969), IVANNIKOV (1979) and SZÁSZ (1985) first appear [these

authors described some dozens (!) of new species of which a remarkably large number seem to be valid taxa]. The high inoceramid diversity persists through much of the higher Lower Coniacian although details still needs further study.

The diversity curves in the present study stand seemingly in disagreement with the hitherto published diversity curves of the Late Cretaceous inoceramids (PERGAMENT 1967, TRÖGER 1976, VOIGT 1995, 1996, ZONOVA & YAZYKOVA 1999), which show the Turonian – Coniacian boundary interval as one of the main diversity peaks. Although, beyond any question, the data bank as well as the taxonomic concepts and stratigraphical distribution of the particular taxa used in this paper and in the cited publications are different, the main cause of this apparent discrepancy lies in a different method of constructing the curves. All of the published curves could be referred to as 'interval' curves, in which particular points on the curve represent counts from shorter or longer time-stratigraphical units. The curve constructed herein assembles counts from approximately single time-planes, thus representing the plot of the standing diversity of the inoceramid fauna in the studied interval. Such an analysis requires very precisely located material. The use of counts from an approximation to a single time-plane avoids a problem pertinent to all analyses of diversity trends in fossil material, namely the time factor involved in the use of data from a stratigraphical interval rather than a plane. The other important factor affecting the measured level of species diversity, i.e. the species/area ratio increase, which is mainly caused by area heterogeneity, plays only a minor role in this analysis, as is shown by the empirical data. Because the data may have been influenced by sampling, sample sizes were corrected using rarefaction equations (Text-fig. 4).

The most important conclusion to be derived from this study is the fact that the peaks from the Turonian – Coniacian boundary as seen on the 'interval curves' do not actually represent times of taxonomically rich inoceramid assemblages resulting from particularly favourable environmental or paleogeographical conditions. Quite the opposite, the Turonian – Coniacian boundary was a very dramatic time for inoceramids. Most of the latest Turonian and part of the Early Coniacian inoceramids of the Euramerican biogeographical region were represented by a few species forced by sudden environmental changes either to rapid evolution or else driven to extinction. The periods of favourable conditions, marked by rapid expansion and abundance increases of single species were, through much of that time, too short to allow for a successful diversification of inoceramid assemblages. Environmental stability did not become established until later, about the time of the *erectus* III Event in the mid-Early Coniacian.

CONCLUSIONS

The abundant and taxonomically rich inoceramid fauna recorded in the literature from the topmost Turonian and Lower Coniacian of the Euramerican palaebiogeographial region never actually formed taxonomically diverse living assemblages. The dozens of inoceramid taxa known from this interval are the result of an extraordinarily high turnover rate at, in general, low or very low standing diversity. Some of the assemblages are almost monospecific. The turnover rate was particularly high close to the boundary, with turnover intervals probably as short as 100 000 years or less. The inoceramids twice experienced a dramatic change (?extinctions): fistly, with the appearance of the '*websteri*' fauna; and secondly with the entrance of cremnoceramids (*waltersdorfensis* Event), the latter marking the main turnover level in their history in this interval. Through the next few hundred thousand years the inoceramids were represented by poorly diversified assemblages. It is not until the *erectus* III Event that the inoceramids started to diversify, with dozens of species appearing at this one level.

The series of events marking the topmost Turonian and lowermost Coniacian and recognisable throughout the Euramerican biogeogaphic region are mostly diversification bioevents (in the terminology of SAGEMAN & *al*. 1998), marked by rapid expansions of particular faunas, due to abrupt changes in environmental conditions and by the evolutionary appearances of new taxa. These accelerated faunal changes are associated with changes in sedimentary record, marked by clear rhythmicity, observed in most of the studied sections ("Grauweiße-Wechselfolge" in German sections), and although the nature of these changes is still very poorly known, they affected the biota of the Turonian/Coniacian boundary seas with a strength comparable to that experienced by the Cretaceous biota during the Cenomanian/Turonian transition.

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