Acta Geologica Polonica, Vol. 51 (2001), No. 2, pp. 121-136

Early Cenomanian (Cretaceous) inoceramid bivalves from the Kronsberg Syncline (Hannover area, Lower Saxony, Germany): stratigraphic and taxonomic implications

MARKUS WILMSEN[1], BIRGIT NIEBUHR[1] & CHRISTOPHER J. WOOD[2]

[1] *Institut für Paläontologie der Universität, Pleicherwall 1, D - 97070 Würzburg.*
E-mail: m.wilmsen@mail.uni-wuerzburg.de; niebuhr@mail.uni-wuerzburg.de;
[2] *Scops Geological Services Ltd., 20 Temple Road, Croydon, Surrey, CR0 1HT, UK.*

ABSTRACT:

WILMSEN, M., NIEBUHR, B. & WOOD, C.J. 2001. Early Cenomanian (Cretaceous) inoceramid bivalves from the Kronsberg Syncline (Hannover area, Lower Saxony, Germany): stratigraphic and taxonomic implications. *Acta Geologica Polonica*, **51** (2), 121-136. Warszawa.

An Early Cenomanian inoceramid bivalve assemblage collected from material excavated from a temporary exposure in the Kronsberg Syncline east of Hannover (northern Germany) is described. It consists of *'Inoceramus' crippsi* MANTELL, 1822, *'I.' hoppenstedtensis* TRÖGER, 1967, *Inoceramus virgatus scalprum* BÖHM, 1914 and *I. virgatus virgatus* SCHLÜTER, 1877, as well as transitional forms between *I. virgatus virgatus* and *I. virgatus scalprum* and an apparently undescribed sulcate form. The inoceramid fauna is well preserved and very rich in individuals. Many of the inoceramids occur either as double-valved individuals or with the valves in close association and appear to be concentrated in distinct layers. Co-occurring ammonites are *Mantelliceras dixoni* SPATH, *Mantelliceras* sp., *Schloenbachia varians* (J. SOWERBY), *Hypoturrilites gravesianus* (D'ORBIGNY) and *Scaphites obliquus* J. SOWERBY.

Using event stratigraphy, the stratigraphic interval of the collected fauna can be assigned to the lower part of the Lower Cenomanian *Mantelliceras dixoni* ammonite Zone. It predominantly comprises material from the *Inoceramus virgatus* acme-event (the *Schloenbachia/virgatus* event of German event stratigraphy) at the top of the lower subzone (*Mantelliceras dixoni & M. saxbii* Subzone) of the *dixoni* Zone, which is known from the Lower Saxony, Cleveland (eastern England) and Anglo-Paris basins, where it invariably occurs in carbonate-rich rocks with low diversity faunas. The lithofacies and geochemistry of the strata are documented and the *'Inoceramus' crippsi* and *Inoceramus virgatus* groups are discussed, including the problematic provenance of the type series of *Inoceramus virgatus scalprum*.

Key words: Inoceramid bivalves, Ammonites, Cretaceous, Cenomanian, Northern Germany, Event stratigraphy, Taxonomy.

INTRODUCTION

Despite the wide distribution of Upper Cretaceous rocks in the environs of Hannover, there are virtually no outcrops in this area and the main exposures are provided by large cement quarries in Lower and Upper Campanian sediments. The lower Upper Cretaceous (Cenomanian - Turonian) was formerly worked at only two localities: the so-called HPCF II Quarry east of Hannover (Text-fig. 1), and at Wunstorf Quarry, ca. 25 km west of Hannover. The HPCF II Quarry was abandoned more than 10 years ago and is now partly filled with building waste; the former excellent sections in this stratigraphically important locality are now largely obscured. Therefore, the lower Upper Cretaceous is currently not exposed in the area east of Hannover and the Cenomanian sections in the Wunstorf Quarry are rapidly deteriorating.

In connection with the international exhibition EXPO 2000, subway line D from Laatzen to Wülferode, east of Hannover, was extended. In the course of construction of a new entrance to the subway west of the Autobahn A7 during 1998 - 1999, fossiliferous Lower Cenomanian rocks (Text-fig. 1) were worked and the excavated material was transported to the TEUTONIA cement works in Misburg and dumped there for cement production. The dump of pale coloured Cenomanian limestones was particularly conspicuous in a section exposing relatively dark grey coloured Campanian marly sediments. The fossils and sediments described in this paper were collected by two of us (MW and BN) from this dump.

The aim of this contribution is the illustration of the rich and relatively well preserved Early Cenomanian inoceramid bivalve assemblage collected from this material and the application of event stratigraphy to infer the stratigraphic interval represented. It must be emphasized that no stratigraphic log of the subway excavation is available and that, since the collected material is effectively loose, it cannot be used for population variability studies or for biometric analysis. The lack of exposures in this part of the Lower Saxony Basin and the scarcity of data on Early Cenomanian inoceramids (the last paper on Early Cenomanian inoceramids from the Hannover area - Wunstorf Quarry - dates back to HEINZ 1928) makes this paper an important contribution to palaeontology and regional geology. The palaeontologic data are supplemented with information on the stratigraphy, lithology, and geochemistry of the sediments as well as on the associated fossil groups.

GEOLOGICAL SETTING

During the Mid-Cretaceous, the Hannover area was situated near the centre of the Lower Saxony Basin (e.g. KEMPER 1984; MUTTERLOSE 1984; FRIEG & *al.* 1989). Following the basinal 'Flammenmergel' (spiculitic marls and limestones) of Late Albian age, the Cenomanian succession started - after an hiatus comprising the latest Albian/earliest Cenomanian - with a fossiliferous glauconitic transgression horizon (*ultimus*/*Aucellina* transgression of ERNST & *al.* 1983). However, it is possible that in the Hannover area, near the former basin centre, a continuous boundary succession was deposited. Up-section, claystones, marls and marly limestones developed, characterizing the lower part of the Lower Cenomanian succession ('Liegende Mergelserie' of KAPLAN & *al.* 1984). The upper part of the Lower and the lowermost part of the Middle Cenomanian show a predominance of marls and marly limestones/limestones, which are commonly arranged in rhythmical ABAB successions ('marl/chalk couplets'). This lithostratigraphic unit corresponds to the 'Flaserkalk-Serie' of KAPLAN & *al.* (1984) (the 'Cenoman-' or '*Varians*-Pläner' of former authors), and is very rich in fossils (especially inoceramid bivalves and cephalopods). The succeeding rocks are white, homogeneous coccolith limestones ('Arme *rhotomagense*-Kalke') with relatively scarce fossils and mean carbonate contents well above 90% $CaCO_3$. The facies development of the Cenomanian reflects deepening of the depositional environment and concomitant withdrawal of terrigenous sediment sources during the course of the Cenomanian transgression. The palaeo-coastline was situated in the south: contemporaneous successions in the Subhercynian area (HORNA 1997) and Sack Syncline (KELLER 1982) show a more proximal character and a much higher siliciclastic influx.

The Kronsberg Syncline, east of Hannover, comprises a primary rim syncline of the Lehrte salt structure filled with Albian to Turonian sediments (Text-fig. 1). According to BETTENSTEDT & DIETZ (1957), the thickness of the Cenomanian succession here is ~130 m. The only Cenomanian exposure in the Kronsberg Syncline is the abandoned HPCF (Hannoversche Portland-Cement-Fabrik) II Quarry near Misburg, where a Cenomanian - Middle Turonian section could formerly be seen, overlain with erosive contact by transgressive Santonian sediments (for details see ERNST & *al.* 1997; ERNST & REHFELD 1997, fig. 5). Here some 15 m of Lower Cenomanian marls and marly limestones belonging to the *Mantelliceras dixoni* Zone were formerly exposed at the base of the ca. 85 m Cenomanian section. The *dixoni* Zone succession included two key inter-regional biostratigraphic events: in ascending order the *Schloenbachia*/*virgatus* event and the *Orbirhynchia*/*Schloenbachia* event of ERNST & *al.* (1983).

The subway excavation discussed in this paper was also located in the Kronsberg Syncline, but 7.5 km to the south of the HPCF II Quarry. The only other extensive Cenomanian section in the Hannover area, the Wunstorf Quarry, is situated in the Wunstorf Cretaceous Syncline, which is a rim syncline associated with the Bokeloh salt diapir. Here some 120 m of Cenomanian sediments were formerly exposed (see MEYER 1990, GALE 1995, WOOD & ERNST 1998 for details), of which at least 70 m can be attributed to the Lower Cenomanian. The greater part of the exposed

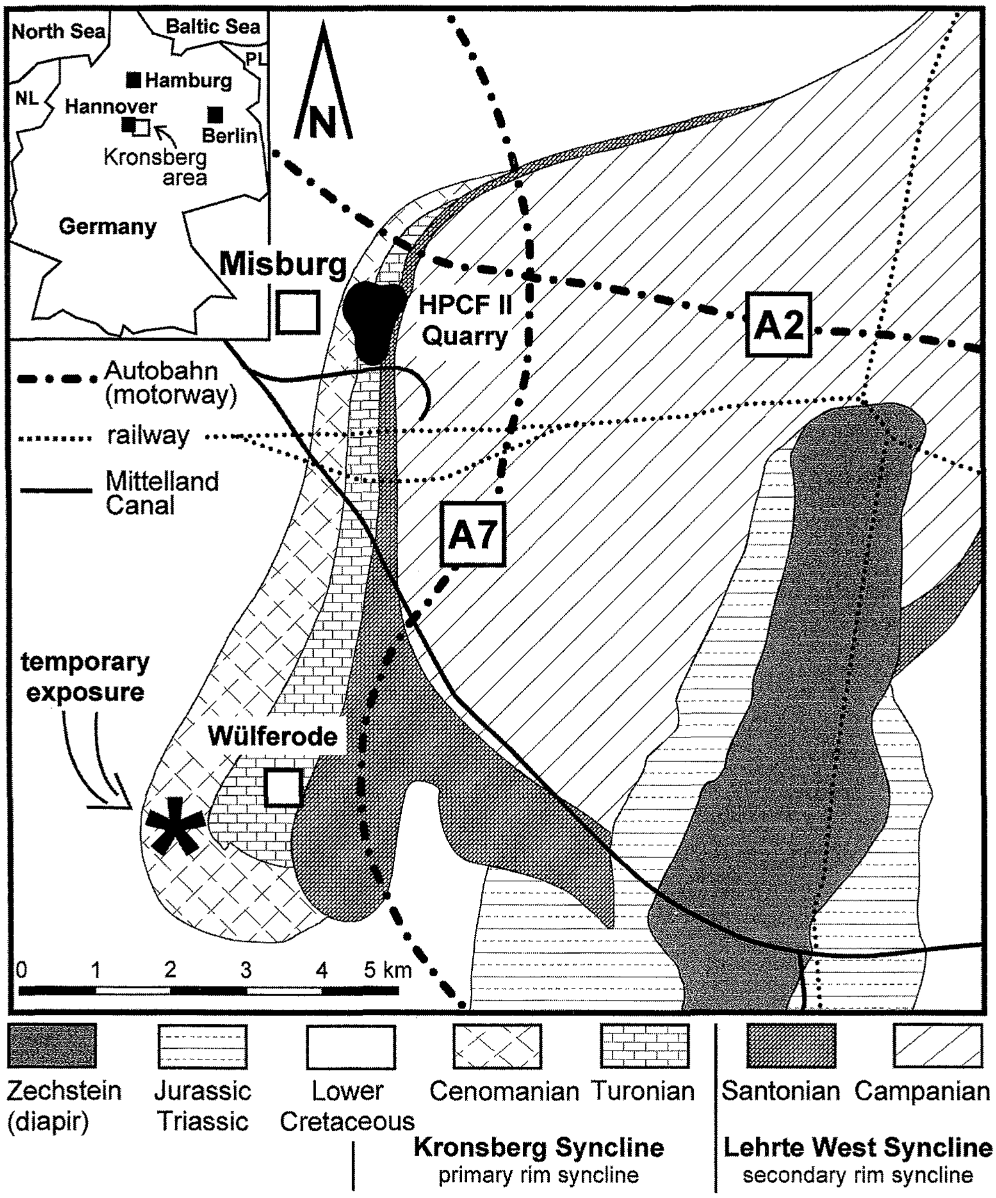


Fig. 1. Geological map of the area east of Hannover with indication of the fossil locality (asterics). Inset: Regional overview

Lower Cenomanian succession appears to belong to the *Mantelliceras dixoni Zone*. The enormous Cenomanian thicknesses in both the Kronsberg and Wunstorf Cretaceous Synclines can be attributed to sedimentation in developing rim synclines adjacent to rising salt diapirs. These thicknesses contrast with the thin Lower Cenomanian successions in the Innerste Syncline, north of the Harz Mountains, where the thickness of the entire Lower Cenomanian in the Flöteberg section is of the order of 28 m and the *Mantelliceras dixoni Zone* at the Baddeckenstedt Quarry is 12 m thick (see ERNST & REHFELD 1997, figs 1 and 2). This latter section was critical in the development of the event stratigraphical framework of the Cenomanian (see ERNST & REHFELD 1997, 1998 and WOOD & *al.* 1997 for details).

EVENT STRATIGRAPHICAL FRAMEWORK

In the Lower Cenomanian *Mantelliceras dixoni* Zone, several inter-regional bioevents and/or marker horizons can be identified. These comprise, in ascending order (Text-fig. 2):

I. The *Mariella* event, near the base of the *dixoni* Zone,

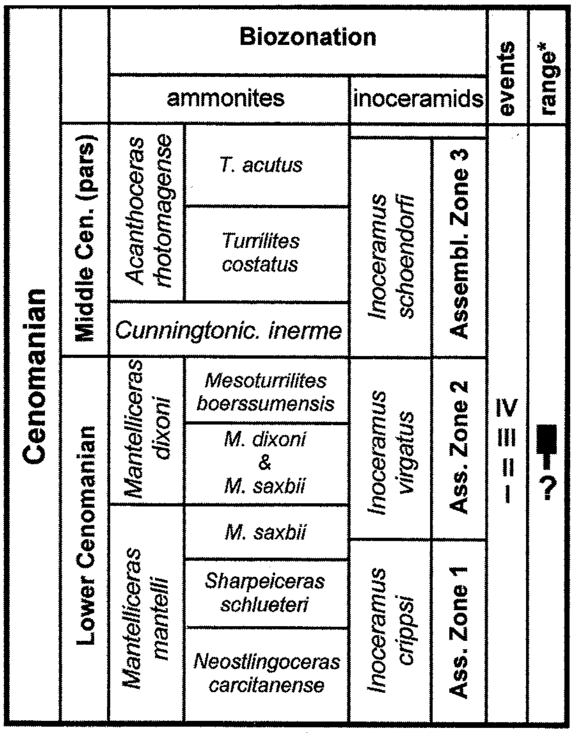


Fig. 2. Biostratigraphic subdivision of the Lower and lower Middle Cenomanian in northern Germany (compiled after KAPLAN & *al.* 1998; TRÖGER 1989) (I = *Mariella* event; II = the 'rib'; III = group of six limestones (marker 'A' of MITCHELL & *al.* 1996) including the *Schloenbachia/virgatus* event; IV = *Orbirhynchia/Schloenbachia* event; *inferred stratigraphic range of the macrofossils collected from the temporary exposure in the Kronsberg Syncline)

consists of a concentration of large, relatively poorly preserved turriliticone heteromorph ammonites (*Hypoturrilites*, *Mariella*), associated with common '*Inoceramus*' *crippsi* MANTELL. The event is seen in eastern England (the 'turrilitoid plane' of JEANS 1980), Westphalia (KAPLAN & *al.* 1998), Lower Saxony (Wunstorf Quarry, MEYER 1990; Baddeckenstedt Quarry, ERNST & REHFELD 1997, figs 2, 4) and also at Hoppenstedt Quarry in the Subhercynian Cretaceous Basin, Saxony-Anhalt (ERNST & REHFELD 1997, fig. 4). It is typically located a short distance above coarse-grained, inoceramid shell detrital sediments and/or sponge beds. In Westphalia, the first specimens of the zonal index, *Mantelliceras dixoni* SPATH, are recorded from this horizon.

II. The so-called 'rib', a thin conspicuous prominent limestone, containing common *Inoceramus* ex gr. *virgatus* SCHLÜTER associated with '*Inoceramus*' *crippsi* and *Mantelliceras dixoni*. This is the first horizon in which *I.* ex gr. *virgatus* and *M. dixoni* are relatively common. This marker horizon can be traced from the Anglo-Paris Basin, via the Cleveland Basin in eastern England (Speeton cliff section) to Baddeckenstedt Quarry and also to the relatively condensed succession at Hoppenstedt Quarry in the Subhercynian Cretaceous Basin (cf. GALE 1995, fig. 4).

III. A group of six, closely spaced, carbonate-rich, pale coloured limestones of generally similar thickness containing shell debris and complete shells of *I.* ex gr. *virgatus* (marker horizon A of MITCHELL & *al.* 1996, fig. 2 and p. 14). The lowest four limestones contain common well preserved bivalved *I.* ex gr. *virgatus*, with the acme (*Schloenbachia/virgatus* event of ERNST & *al.* 1983; see Text-fig. 3) in the top two of these. The highest (sixth) limestone of the group contains ammonites including *Mantelliceras dixoni* (the *dixoni* event recognized in Westphalia by KAPLAN & *al.* 1998). In some localities, e.g. Baddeckenstedt Quarry and (A. S. GALE, pers. comm.) Wunstorf Quarry, *M. dixoni* is also well represented in the fourth limestone. As in the case of the 'rib', this marker group can be used for long-range correlation between England and northern Germany.

IV. Marker horizon III, with its associated *Schloenbachia/virgatus* and *dixoni* events, is overlain in England and northern Germany (Lower Saxony, Saxony-Anhalt and [U. KAPLAN: pers. comm] Westphalia) by an unit of more marly sediments containing the rhynchonellid brachiopod *Orbirhynchia mantelliana* (J. DE C. SOWERBY) associated with an ammonite fauna including *Acompsoceras* spp., *Mantelliceras dixoni* and *Mesoturrilites boerssumensis* (SCHLÜTER). In northern Germany, this event-occurrence of *O. mantelliana* constitutes the *Orbirhynchia/Schloenbachia* event of ERNST & *al.* (1983): it equates with the lowest of the three *Orbirhynchia mantelliana* bands in English successions.

Mesoturrilites boerssumensis is the index-fossil of the higher of the two subzones of the *dixoni* Zone recognized in Westphalian successions (see KAPLAN & *al.* 1998). In Westphalia, the lowest occurrence of *M. boerssumensis* is in the *dixoni* event and the base of the subzone is accordingly drawn at this level. The underlying *dixoni* Zone succession down to the *Mariella* event and the basal sponge beds was assigned by KAPLAN & *al.* (1998) to the *Mantelliceras dixoni* and *M. saxbii* Subzone. In Lower Saxony (Baddeckenstedt Quarry) the approximate position of the base of the *boerssumensis* Subzone can be inferred from the co-occurrence of *Orbirhynchia* and *Acompsoceras* in the *Orbirhynchia/Schloenbachia* event. The Westphalian zonal scheme is applied in this paper to all of the northern German Cenomanian localities discussed rather than the scheme used by previous workers.

LITHOFACIES

Lithostratigraphically, the rocks encountered correspond to the Flaserkalk-Serie (*sensu* KAPLAN & *al.* 1984). In the absence of a detailed stratigraphic log, their main characteristics are briefly described below.

Macrofacies: The sediments are medium-bedded, yellowish-brown to buff coloured marly limestones and limestones with thin partings of dark marl; porosity is still very high. Some of the beds are crowded with inoceramids (Text-fig. 3). Bioturbation is evident from the slightly darker colour of the burrow infills and the concentration of macrofossil debris. Inoceramid bivalves, some of which occur double-valved, dominate the faunal spectrum, followed by ammonites and rare brachiopods (see Section: Fauna).

Microfacies: Thin sections revealed calcisphere pack- and wackestones with inoceramid and echinoderm debris, few thin-shelled ostracods, small planktic (hedbergellids) and benthic foraminifera (*Lenticulina* sp.,

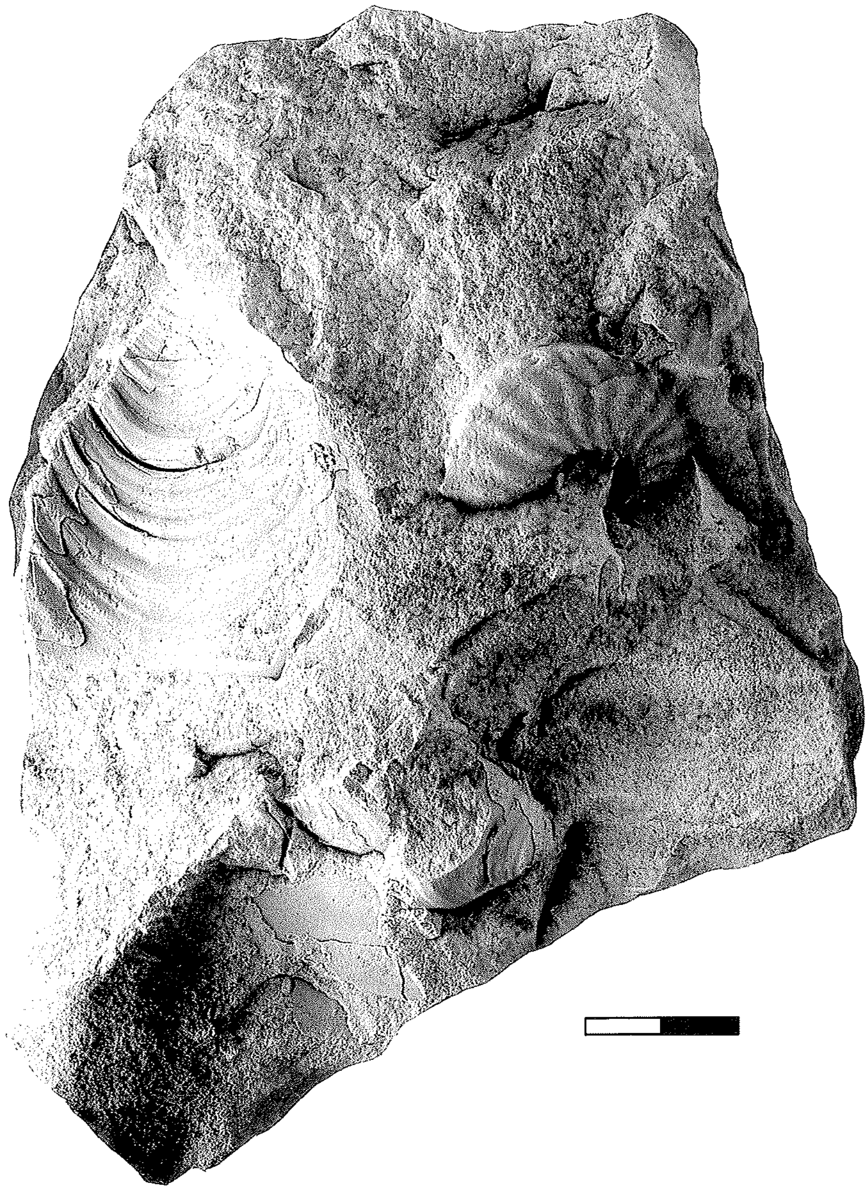


Fig. 3. Limestone slab with *Schloenbachia varians* (J. SOWERBY) and two valves of *Inoceramus virgatus* SCHLÜTER, 1877 (*Schloenbachia*/*virgatus* event; scale bar is 2 cm; specimen PIW2001I 62)

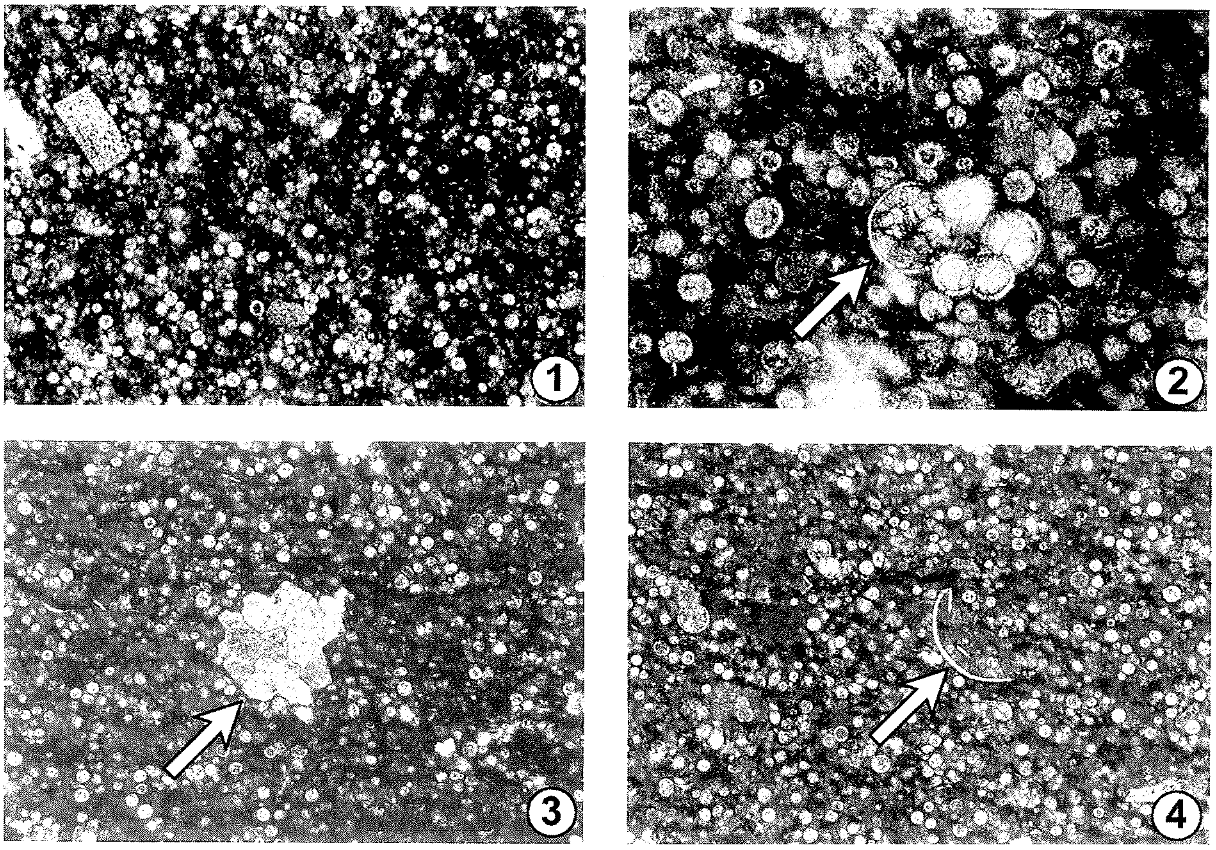


Fig. 4. Microfacies of the fossiliferous sediments. 1. Calcisphere packstone (× 40); 2. Calcisphere packstone with hedbergellid foraminifer (arrowed) (× 70); 3. Calcisphere wackestone with inoceramid prisms in cross-section (arrowed) (× 40); 4. Thin-shelled ostracod (arrowed) (× 40)

textulariids) as well as rare brachiopods (see Text-fig. 4). Inoceramid shell fragments are up to 5 mm long and relatively thin. The high carbonate content (see Table 1) is probably related to the mass-occurrence of calcispheres. The fabric of the sediment is inhomogeneous due to bioturbation.

The fine-grained fabric and a predominance of planktic components such as calcispheres and planktic foraminifera is inferred to indicate a hemipelagic setting well below fair-weather wave-base.

Geochemistry: The content of seven main elements in 19 samples was investigated in the laboratory of the TEUTONIA cement works in Misburg (see Table 1). The sediments show a relatively high carbonate content with a mean of nearly 86% $CaCO_3$ (values vary between about 80% and almost 92%) compared to contemporaneous deposits (e.g. Sack syncline, cf. KELLER 1982; Wunstorf Quarry, MEYER 1990; Baddeckenstedt, BARTELS 1993). The terrigenous influence is low, reflected by the low SiO_2 (mean ca. 8%) and Al_2O_3 (mean ca. 3.2%) contents, and shows only minor variations.

analysis	**SiO_2** (%)	**Al_2O_3** (%)	**Fe_2O_3** (%)	**$CaCO_3$** (%)	**MgO** (%)	**SO_3** (%)	**K_2O** (%)
1	10.16	3.65	1.20	81.94	0.37	0.39	0.47
2	8.99	3.67	1.20	84.30	0.40	0.19	0.49
3	7.54	3.14	1.05	86.19	0.31	0.04	0.37
4	11.42	3.60	1.25	80.89	0.40	0.07	0.50
5	7.77	3.35	1.09	86.17	0.32	0.12	0.41
6	10.81	3.55	1.19	81.19	0.37	0.40	0.45
7	8.49	3.61	1.16	84.74	0.37	0.16	0.45
8	6.35	2.85	0.91	88.95	0.31	0.15	0.33
9	7.20	3.12	0.98	87.17	0.33	0.09	0.37
10	11.01	4.24	1.32	80.37	0.38	0.13	0.53
11	9.25	3.28	1.09	83.64	0.37	0.27	0.43
12	10.80	3.62	1.20	81.48	0.41	0.08	0.46
13	5.89	2.69	0.89	90.10	0.22	0.06	0.29
14	8.49	2.72	0.90	86.46	0.22	0.04	0.32
15	5.73	2.72	0.90	90.24	0.23	0.05	0.31
16	6.33	2.67	0.90	89.13	0.25	0.04	0.32
17	7.27	3.41	1.06	87.13	0.33	0.01	0.41
18	4.96	2.54	0.93	91.67	0.23	0.02	0.29
19	7.13	2.70	0.74	89.17	0.33	0.04	0.31
mean:	**8.19**	**3.22**	**1.05**	**85.83**	**0.32**	**0.12**	**0.39**

minimum:	4.96	2.54	0.74	80.37	0.22	0.01	0.29
maximum:	11.42	4.24	1.32	91.67	0.41	0.40	0.53

Table 1. Geochemistry of the fossiliferous Lower Cenomanian beds in the Kronsberg Syncline

FAUNA

The collected fauna is of extremely low diversity and mainly comprises inoceramid bivalves (ca. 130 specimens). The accompanying fauna is very poor in individuals and includes subordinate numbers of ammonites, oysters, brachiopods, sponges and bryozoa.

Inoceramid bivalves: The taxa collected comprise *'Inoceramus' crippsi* MANTELL, *'I.' hoppenstedtensis* TRÖGER, *I.* ex gr. *virgatus* and an undescribed thin-shelled sulcate form of uncertain affinities. The inoceramids of the *virgatus* group predominate (comprising more than 70% of the collected inoceramid bivalves) and include forms referable to *I. virgatus virgatus* SCHLÜTER, *I. virgatus scalprum* BÖHM and to posssible transition forms between the two taxa. The inoceramids of this group are three-dimensionally preserved, often retaining their shell, in pale coloured limestones, commonly occurring as bivalved individuals or with the two valves closely associated. The preservation of this group is unusually good, including details of the juvenile umbonal ornament in some cases. The inoceramid bivalves are briefly described below in a separate systematic section.

Ammonites: This faunal group is relatively poorly represented (Text-fig. 5). The commonest species is *Schloenbachia varians* (J. SOWERBY), of which 6 specimens were collected. The zonal index-species, *Mantelliceras dixoni*, is represented by 2 specimens; poorly preserved, specifically indeterminate *Mantelliceras* are also present. The heteromorph ammonites *Scaphites obliquus* J. SOWERBY and *Hypoturrilites gravesianus* (D'ORBIGNY) are each represented by single occurrences.

Brachiopods: Brachiopods are rare faunal elements. The samples yielded only single specimens of the long-ranging *Terebratulina protostriatula* OWEN and the more stratigraphically restricted *Monticlarella* cf. *brevirostris* (ROEMER), a synonym of *M. rectifrons* (PICTET & CAMPICHE). The latter species ranges in the Anglo-Paris Basin from the *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone up to the *boerssumensis* Subzone of the *dixoni* Zone, being particularly common in the *dixoni* Zone. Interestingly, representatives of the genus *Orbirhynchia* are missing, giving indirect evidence for the stratigraphic position of the inoceramid assemblage (see following section).

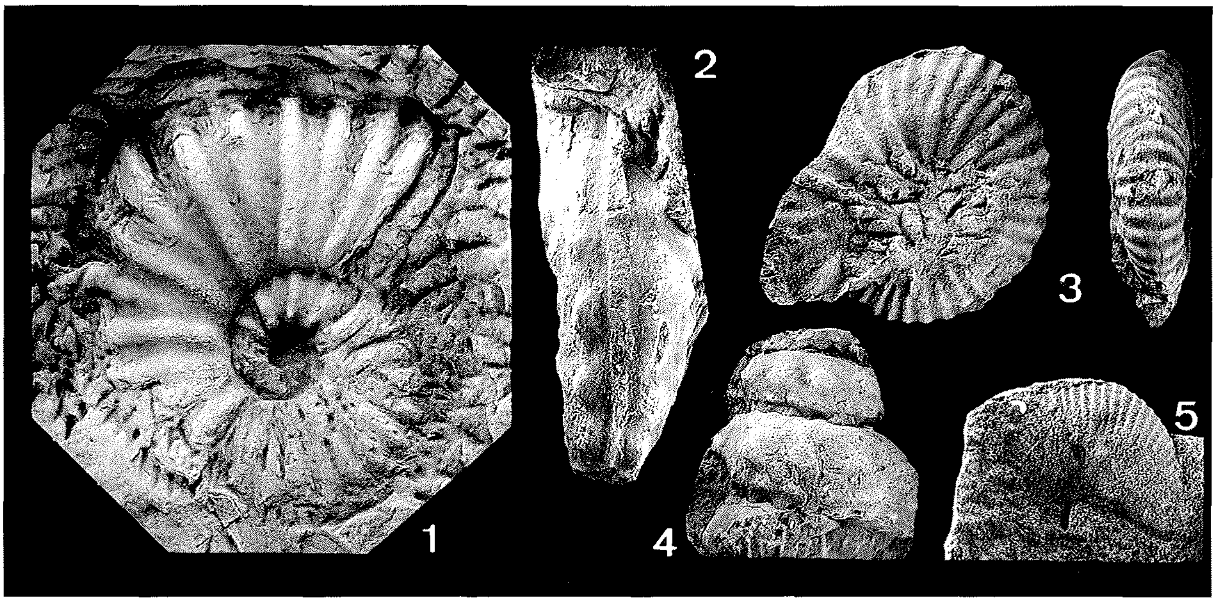


Fig. 5. Ammonites; 1 – *Mantelliceras dixoni* SPATH; specimen PIW2001I 1; lateral view (× 1); 2 – *Schloenbachia varians* (J. SOWERBY); specimen PIW2001I 2; ventral view (× 1); 3 – *Mantelliceras* sp.; specimen PIW2001I 3; left: lateral view; right: ventral view (× 1); 4 – *Hypoturrilites gravesianus* (D'ORBIGNY); specimen PIW2001I 4; lateral view (× 1); 5 – *Scaphites obliquus* J. SOWERBY; specimen PIW2001I 5; lateral view (× 2)

Non-inoceramid bivalves: Three very small (juvenile) oysters belonging to the genus *Pycnodonte* were collected.

Sponges: Only a single specimen of a hexactinellid sponge, tentatively ascribed to *Eurete,* was found.

Bryozoa: Bryozoans (order Cheilostomata) are recorded as relatively poorly preserved epizoic overgrowth on inoceramid shells, but no attempt was made to determine them.

INTERPRETATION OF THE STRATIGRAPHIC POSITION OF THE INTERVAL COLLECTED

Application of event stratigraphy (see Section: Event stratigraphical framework) enables the stratigraphic position of the collected material to be inferred with a high degree of confidence.

The occurrence of abundant, well-preserved inoceramid bivalves of the *Inoceramus virgatus* group in pale coloured, carbonate rich limestones points unequivocally to the *Schloenbachia*/*virgatus* event of German event stratigraphy (ERNST & *al.* 1983), the equivalent of the six limestones constituting inter-regional Cenomanian marker horizon A of MITCHELL & *al.* (1996). This interpretation is supported by the extremely low diversity of the associated fauna and the high carbonate content of the rocks.

The absence of common large *Mariella* sp. and *Hypoturrilites* sp. (indicative of the *Mariella* event) and of common *Orbirhynchia mantelliana* associated with ammonites including *Acompsoceras* sp. and *Mesoturrilites boerssumensis* (indicative of the *Orbirhynchia*/*Schloenbachia* event near the base of the *M. boerssumensis* Subzone) constrains the interval to the greater part of the *Mantelliceras dixoni* and *M. saxbii* Subzone of the *M. dixoni* Zone (see Text-figs 2, 6). The single small specimen of *Hypoturrilites gravesianus* (Text-fig. 5) cannot safely be regarded as indicative of the *Mariella* event, and the specimens of *Mantelliceras dixoni* (Text-fig. 5) are more likely to have come from the equivalent of the 'rib' or the *Schloenbachia*/*virgatus* event rather than from the underlying succession. The only fossils that might point to the lower part of the *Mantelliceras dixoni* and *M. saxbii* Subzone, i.e. the interval between the *Mariella* event and the 'rib', are the finds of large '*Inoceramus*' ex gr. *crippsi* (Pl. 1, Fig. 6), as well as of '*Inoceramus*' *crippsi* and '*I.*' *hoppenstedtensis*, but both of these latter taxa are relatively long-ranging.

A regional comparison with Wunstorf (MEYER 1990) and Baddeckenstedt (ERNST & REHFELD 1997; see Text-fig. 6) shows that the thickness of the stratigraphic interval in the Kronsberg Syncline corresponds to a maximum 30 m in the expanded Wunstorf Quarry section and less than 6 m in the highly condensed Baddeckenstedt Quarry section in the Salzgitter area to the south. The interval comprising the 'rib' and the group of six limestones is approximately three times as thick at Wunstorf (A. S. GALE unpublished section,

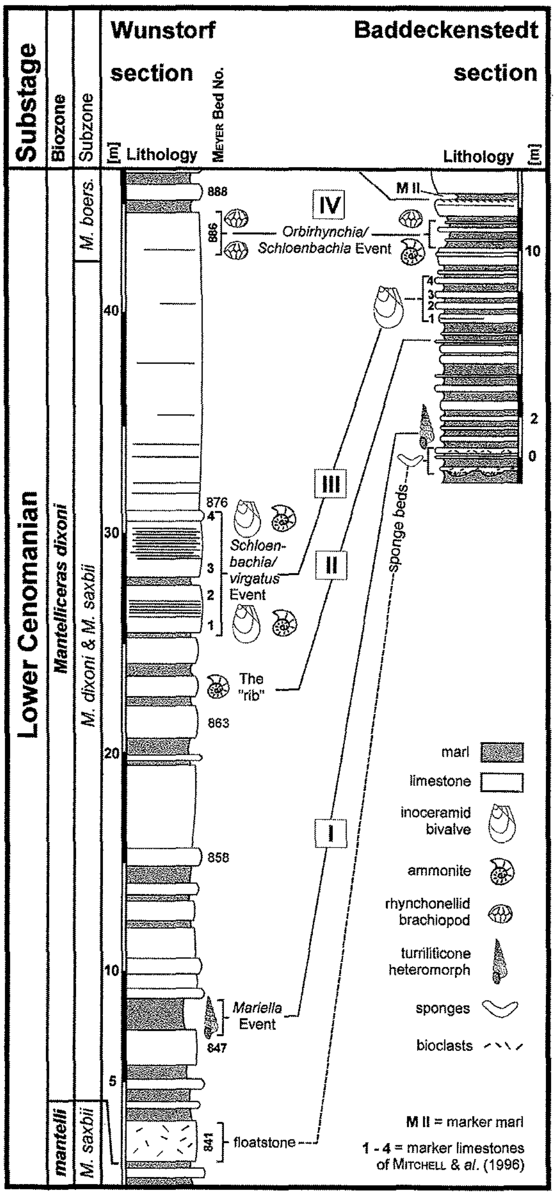


Fig. 6. Stratigraphic interval of the fossil beds calibrated against Wunstorf (section modified after MEYER 1990 and WOOD & ERNST 1998) and Baddeckenstedt (section from ERNST & REHFELD 1997); Roman numbers refer to the events mentioned in Fig. 2; *M. boers.* = *Mesoturrilites boerssumensis*; note the great difference in thickness between the two localities

MITCHELL & *al.* 1996, fig. 2) as at Baddeckenstedt (see GALE 1995, fig. 4).

SYSTEMATIC PALAEONTOLOGY

The herein figured and additional material is stored at the Institute for Palaeontology of Würzburg University (repository PIW2001I).

Class Bivalvia LINNAEUS, 1758
Subclass Pteriomorphia BEURLEN, 1944
Order Pterioida NEWELL, 1965
Family Inoceramidae GIEBEL, 1852

Genus *Inoceramus* J. SOWERBY, 1814

TYPE SPECIES: *Inoceramus cuvierii* J. SOWERBY, 1814.

DIAGNOSIS: Medium-sized to large, equivalve to moderately inequivalve, ovate, trapeziform or suborbicular; posterior wing variably developed; ligamental area concave transversely.

'*Inoceramus*' *crippsi* MANTELL, 1822
(Pl. 1, Fig. 1)

* 1822. *Inoceramus crippsi* MANTELL, p. 133, pl. 27, fig. 11.
1911. *Inoceramus crippsi* MANTELL, 1822; WOODS, p. 273-278, text-figs 33 and 34, pl. 48, fig. 2 (non fig. 3?).
1962. *Inoceramus crippsi* MANTELL, 1822; BRÄUTIGAM, p. 188, pl. 1, figs 1-2.
1967. *Inoceramus crippsi crippsi* MANT., 1822; TRÖGER, p. 24, pl. 2, figs 4-5.
1982. *Inoceramus crippsi crippsi* MANTELL, 1822; KELLER, p. 44-47, pl. 1, fig. 5 (see for extensive synonymy).
?1995. *Inoceramus crippsi* MANTELL 1822 forma indet; LEHMANN, p. 43, pl. 2, fig. 5.

MATERIAL: Only one specimen (PIW2001I 6).

REMARKS: Following the indications given by KAUFFMAN (1976) and MATSUMOTO & *al.* (1987), we consider that *Inoceramus crippsi* and related forms do not belong to the genus *Inoceramus* sensu stricto and have accordingly placed the generic name in quotation marks to indicate this. The distinctive triangular ligament plate with the closely-spaced and vertically elongate ligament pits is quite different from that of *Inoceramus* s.s. and resembles that of the much younger (Coniacian - Santonian) genus *Platyceramus.* The flange-like anterior margin of '*Inoceramus*' *crippsi* is also somewhat reminiscent of that seen in *Platyceramus.* Professor E. G. KAUFFMAN (pers comm. to CJW) has suggested that the key diagnostic feature of the *crippsi* group is the presence of a weak radial rib on the interior of the shell delimiting the edge of the posterior auricle.

'*Inoceramus*' *crippsi* is characterized by an initially subcircular growth-trace, regularly developed thick rugae, an oblique and slightly concave growth axis and a rather thick shell with a massive ligament plate. The rugae continue across the disc without weakening. The co-occurring taxon, '*Inoceramus*' *hoppenstedtensis,* in contrast, has a dorsoventrally elongate growth trace, a more or less straight growth axis and a much thinner shell with more irregularly developed rugae. Excellent illustrations of steinkerns of '*I.*' *crippsi* from marly limestones in southern England were given by WOODS (1911, text-fig. 33 [the holotype from Offham, near Lewes] and text-fig. 34 [a better preserved specimen similar to the holotype from another locality]). In addition, WOODS (1911, pl. 48, fig. 2) illustrated an exceptionally well preserved bivalved individual, retaining the ligament plate and much of the shell, from the basal Cenomanian Rye Hill Sands near Warminster. Typical examples in marly limestone preservation from the former Kalkwerk Nordharz Quarry at Hoppenstedt (Saxony-Anhalt) were figured by TRÖGER (1967, pl. 2, figs 4 and 5) and a well preserved steinkern retaining some shell was illustrated by KELLER (1982, pl. 1, fig. 5) from the Sack Syncline. In southern England, forms close to the holotype are common in and characterize the inoceramid fauna of the *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone, which is accordingly generally presumed by English stratigraphers to correspond to the horizon of the holotype.

The figured specimen attributable to '*I.*' *crippsi* from the Kronsberg Syncline material (Pl. 1, Fig. 1) has the regularly developed rugae of this species but the growth trace trends more towards that of '*I.*' *hoppenstedtensis*. TRÖGER (1967, p. 27) noted that there appeared to be intermediate forms between his subspecies *I. crippsi hoppenstedtensis* (see remarks under '*I.*' *hoppenstedtensis*), but that in the latter the umbonal regions was commonly compressed because of the thin shell.

OCCURRENCE: '*Inoceramus*' *crippsi* ranges in Europe and western Asia from the Lower Cenomanian into the lower Middle Cenomanian (KELLER 1982; KAPLAN & *al.* 1984; TRÖGER 1989). Published records outside these areas, e.g. from North and South America, need to be re-evaluated. In the type area in southern England, this taxon characterizes the *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone, in which it is common, dominating the inoceramid assemblage. The specimen from the Kronsberg Syncline is of Early Cenomanian (*M. dixoni* Zone) age.

'Inoceramus' hoppenstedtensis TRÖGER, 1967
(Pl. 1, Figs 2-5)

* 1967. *Inoceramus crippsi hoppenstedtensis* n. ssp.; TRÖGER, p. 26-28, pl. 1, figs 9-10.
1982. *Inoceramus crippsi hoppenstedtensis* TRÖGER, 1967; KELLER, p. 47-49, pl. 2, fig. 3.
1984. *Inoceramus crippsi hoppenstedtensis* TRÖGER; KAPLAN, KELLER & WIEDMANN, pl. 8, fig. 6.
1996. *Inoceramus crippsi hoppenstedtensis* TRÖGER; MARCINOWSKI, WALASZCZYK & OLESZEWSKA-NEJBERT, p. 25, pl. 16, fig. 3.

MATERIAL: 7 specimens, mostly isolated valves (PIW2001I 7-13).

REMARKS: *Inoceramus crippsi hoppenstedtensis* was erected by TRÖGER (1967) as a separate subspecies of *Inoceramus crippsi* on the basis of morphometric analysis. It was stated to differ from the nominate subspecies, *I. crippsi crippsi,* mainly in shape (dorso-ventrally elongate, i.e. oval, rather than rounded growth-trace), form of beak, a growth axis at right angles to the hinge-line and a comparatively thin shell. TRÖGER (1967) considered that there were transitional forms between *I. crippsi hoppenstedtensis* and *I. crippsi crippsi*.

The holotype is the original of TRÖGER (1967, pl. 1, fig. 9), from the 'Unteres Cenoman' of the former Kalkwerk Nordharz Quarry at Hoppenstedt (Saxony-Anhalt). The exact horizon was not given, but Professor K.-A. TRÖGER (Freiberg) has informed us (pers. comm., 2001) that the holotype came from the *Mantelliceras saxbii* Subzone of the *Mantelliceras mantelli* Zone. *'I.' hoppenstedtensis* is also relatively common in the *M. dixoni* Zone at this locality.

Specimens attributed to this species from the Kronsberg Syncline material (Pl. 1, Figs 2-5) are all incompletely preserved, but exhibit the characteristic straight growth axis, thin shell and irregular development of the rugae.

The relationship between *'Inoceramus' crippsi* and *'I.' hoppenstedtensis* is unclear and requires further investigation. Despite the fact, as noted by TRÖGER (1967) that the two forms appear to intergrade in respect of overall morphological features (outline, shape of growth trace, etc), *'I.' crippsi* is invariably a much thicker shelled form with a massive ligament plate (cf. the specimen from the Rye Hill Sands figured by WOODS 1911, pl. 48, fig. 2), which appears earlier in the Cenomanian than *'I.' hoppenstedtensis*. Because it is thicker shelled, *'I.' crippsi* is typically preserved with only minimal distortion due to compaction. In any case, since the two taxa appear to occur together in the same locality and in the same part of the succession, e.g. at Hoppenstedt as well as in southern England, *'I.' hoppenstedtensis* cannot be regarded as an eastern geographical subspecies, as originally suggested, and should be accorded full specific status within the *crippsi* group. Professor TRÖGER (pers. comm., 2001) supports this taxonomic change, and has additional records of the species throughout northern Europe from France, Bornholm, the Münsterland Cretaceous Basin, Lower Saxony, the Subhercynian Cretaceous Basin, the north Thuringia Basin and from borehole cores in Mecklenburg and Brandenburg. He also has seen it in Poland, the Crimea (TRÖGER 1978), Dagestan, the Kopet Dag and Mangyschlak.

OCCURRENCE: *'I.' hoppenstedtensis* ranges from the Lower Cenomanian into the lower Middle Cenomanian (KELLER 1982; KAPLAN & *al.* 1984; TRÖGER 1989). It is common in the *Mantelliceras saxbii* Suzone of the *M. mantelli* Zone and in the overlying *M. dixoni* Zone, as well as in the lower Middle Cenomanian *Turrilites costatus* Subzone of the *Acanthoceras rhotomagense* Zone, and it is widely distributed in northern Europe and western Asia. TRÖGER (1989, text-fig. 1) showed it to range up into the *Turrilites acutus* Subzone. However, it is unclear how many of these records actually relate to the taxon established by TRÖGER (1967). The specimens from the Kronsberg Syncline are of Early Cenomanian (*M. dixoni* Zone) age.

'Inoceramus' ex gr. *crippsi* MANTELL, 1822 (large form)
(Pl. 1, Fig. 6)

?1997 large inoceramid; ERNST & REHFELD, pl. 3, fig. 5.

MATERIAL: 3 incomplete specimens (PIW2001I 14-16).

REMARKS: The specimen illustrated from the Kronsberg Syncline material (Pl. 1, Fig. 6) is larger and flatter than the other inoceramids attributed to the *'Inoceramus' crippsi* group. It is an incompletely preserved steinkern retaining some shell on the anterior and posterior margins. The umbonal region and hinge-line are obscured by matrix. The growth trace is subcircular, as in *'I.' crippsi*, but the growth axis appears to be relatively straight. The rugae (as seen on the steinkern) are rather irregularly developed and weaken towards the ventral margin.

This form is of uncertain taxonomic position, seeming to share some of the characters of both *'I.' crippsi* (subcircular growth trace) and *'I.' hoppenstedtensis* (thin shell, irregular development of rugae, straight growth axis). On the other hand it is larger than typical examples of either taxon. A similar form, but with much more regularly developed rugae, was figured from the *Mesoturrilites boerssumensis* Subzone of the Künsebeck Quarry, Westphalia, by KELLER (1982, Pl. 2, Fig. 3) as *I. crippsi hoppenstedtensis*. Further similar forms were figured by ERNST & REHFELD (1997) and NIEBUHR & *al.* (subm.) from the lower and upper *dixoni*-Zone of the Salzgitter area (Baddeckenstedt and the Konrad 101 borehole, respectively). In southern England, forms comparable to the Kronsberg Syncline example range from the *Sharpeiceras schlueteri* Subzone up to the higher part of the *M. dixoni* Zone.

OCCURRENCE: This large, flat form of *'Inoceramus'* ex gr. *crippsi* MANTELL, 1822 seems to be restricted to the higher part of the *mantelli* and the *dixoni* Zone of the Early Cenomanian. So far it is only known from southern England and northern Germany.

Inoceramus virgatus virgatus SCHLÜTER, 1877
(Pl. 2, Figs 2-7; Pl. 3, Figs 2a, 2b, 3; Pl. 4, Figs 3a, 3c)

1834-1840. *Inoceramus lamarcki* SOWERBY; GOLDFUSS, pl. 111, fig. 2.

*1877. *Inoceramus virgatus* sp. n.; SCHLÜTER, p. 257-260.

pars 1962. *Inoceramus virgatus* SCHLÜTER, 1877; BRÄUTIGAM, p. 189-190, pl. 1, figs 3-5 (non 6-8 = *I. virgatus scalprum*).

1967. *Inoceramus virgatus* SCHLÜTER, 1877; TRÖGER, p. 29-33, pl. 1, figs 1-2, 5, ?3, ?4 ('längliche Variante').

1978. *Inoceramus virgatus* SCHLÜTER; SORNAY, p. 510-511, pl. 2, fig. 4.

1982. *Inoceramus virgatus virgatus* SCHLÜTER, 1877; KELLER, p. 51-54, pl. 1, fig. 1 (see for extensive synonymy).

1983. *Inoceramus virgatus virgatus* SCHLÜTER; TRÖGER, fig. 1a.

1984. *Inoceramus virgatus virgatus* SCHLÜTER; KAPLAN, KELLER & WIEDMANN, p. 323, pl. 8, fig. 4 (non fig. 3 = *I. virgatus scalprum*).

1987. *Inoceramus virgatus* SCHLÜTER, 1877; MATSUMOTO, ASAI & HIRANO, p. 157, text-figs 6-8.

1995. *Inoceramus virgatus* SCHLÜTER 1877 forma virgatus; LEHMANN, p. 44, pl. 2, fig. 3.

1997. *Inoceramus virgatus virgatus* SCHLÜTER; WILMSEN, p. 71, pl. 41, figs 1-2.

MATERIAL: 26 specimens (PIW2001I 17-42) commonly occurring as bivalved individuals or with the two valves closely associated.

REMARKS: The species comprising the *virgatus* group are retained in the genus *Inoceramus* sensu stricto in this paper, pending future revision by inoceramid workers. *I. virgatus virgatus* is rather common in the Kronsberg Syncline material and is readily recognizable from the distinctive radial striae on internal moulds (e.g., Pl. 2, Fig. 7). The nominate subspecies differs from *I. virgatus scalprum* in the short, straight, rather than broadly rounded, anterior margin. The overall outline is correspondingly subrectangular rather than subcircular. Some transitional forms to *I. virgatus scalprum* (e.g. Pl. 4, Fig. 1) occur. For discussions of this taxon and its relationship to *I. virgatus scalprum* see last section.

OCCURRENCE: According to TRÖGER (1989, text-fig. 1), *I. virgatus virgatus* ranges from the middle part of the Lower Cenomanian (*Mantelliceras saxbii* Subzone) into the middle part of the Middle Cenomanian (*Turrilites acutus* Subzone.). It is widely distributed in the northern hemisphere (cf. DHONDT 1992; VOIGT 1996), albeit absent from North America, and it is also recorded from South America and the Pacific Realm (e.g. Japan - MATSUMOTO & *al.* 1987).

Inoceramus virgatus scalprum BÖHM, 1914
(Pl. 3, Figs 4-7; Pl. 4, Figs 2, 3a, 3b)

1881. *Inoceramus convexus*, ETHERIDGE; R. ETHERIDGE, p. 143, pl. 2, figs 6, 5a.

1911. *Inoceramus etheridgei* nov. nom; WOODS, p. 278-279, pl. 49, fig. 3.

*1914. *Inoceramus scalprum* nov. nom.; BÖHM, p. 599.

pars 1962 *Inoceramus virgatus* SCHLÜTER, 1877; BRÄUTIGAM, p. 189-190, pl. 1, figs 6-8 (non 3-5 = *I. virgatus virgatus*).

1967. *Inoceramus virgatus* SCHLÜTER, 1877; TRÖGER, p. 29-33, pl. 1, figs 6-7 ('cycloide Variante').

1978. *Inoceramus virgatus scalprum* J. BÖHM; SORNAY, p. 510-511, pl. 2, figs 2, 5.

1982. *Inoceramus virgatus scalprum* BÖHM, 1914; KELLER, p. 54-57, pl. 1, fig. 2 (see for extensive synonymy).

1983. *Inoceramus virgatus virgatus* SCHLÜTER (cycloid variant); TRÖGER, fig. 2a.

1984. *Inoceramus virgatus virgatus* SCHLÜTER; KAPLAN, KELLER & WIEDMANN, p. 323, pl. 8, fig. 3 (non fig. 4 = *I. virgatus virgatus*).

MATERIAL: 13 specimens (PIW2001I 43-55), many of which occur double-valved.

REMARKS: *I. virgatus scalprum* was established as a subspecies of *Inoceramus virgatus* by SORNAY (1978) and is fairly common in the Kronsberg Syncline material. The early ontogenetic stages are particularly well preserved in some specimens (e.g. Pl. 3, Figs 6 and 7). Furthermore, transition forms to *I. virgatus virgatus* are recorded (e.g. Pl. 3, Fig. 8) and it should be stressed that the two subspecies are obviously occurring in the same bed (Pl. 4, Figs 3a-c). This observation indicates that the two forms could not be regarded as geographically separate subspecies. For further discussion of the *Inoceramus virgatus* group see section below.

OCCURRENCE: According to TRÖGER (1989, text-fig. 1) *I. virgatus scalprum* ranges from the middle part of the Lower Cenomanian (*M. saxbii* Zone) well into the Middle Cenomanian (*Turrilites costatus* Subzone). It occurs throughout Europe and western Asia (cf. DHONDT 1992; VOIGT 1996) and it is also recorded from Far East Russia (PERGAMENT, 1966), albeit (Dr. I. WALASZCZYK, Warsaw, pers. comm., 2001) from the Upper Cenomanian rather than from the Lower and lower Middle Cenomanian. Both *I. virgatus scalprum* and *I. virgatus virgatus* are reported to co-occur in the Cenomanian of Japan (MATSUMOTO & *al.* 1987). Records from outside these areas need to be re-evaluated.

Undetermined inoceramid bivalve with well-developed dorso-ventral sulcus (Pl. 4, Figs 4, 5)

MATERIAL: Two specimens (PIW2001I 58-59).

REMARKS: This sulcate taxon is very tentatively compared to *Inoceramus* aff. *arvanus* STEPHENSON from the Lower Cenomanian *Forbesiceras brundettei* Zone of Trans-Pecos Texas, USA as figured by KENNEDY & *al.* 1989, fig. 32, A-C, E, F), although these lack the distinctive sulcus of the later *I. arvanus* - *I. rutherfordi* WARREN evolutionary lineage and of the Kronsberg Syncline specimens. There are sulcate inoceramids in the Natural History Museum from the lower Middle Cenomanian of southern England that were attributed by KAUFFMAN (unpublished) to an early subspecies of *I. rutherfordi*. The only conspicuously sulcate published Cenomanian taxon from northern Europe is '*Inoceramus*' *longobardicus* (HEINZ), i.e. the form from the traditional Upper Cenomanian *Holaster subglobosus* Zone (inferred *Calycoceras guerangeri* ammonite Zone) of southern England figured by WOODS (1911, pl. 48, fig. 4) as *I. crippsi* var. *reachensis* R. ETHERIDGE; however, this taxon is stratigraphically much younger than the level of the Kronsberg Syncline specimens and possesses an extremely thin shell with laminae instead of rugae. It is therefore possible that this form from the Kronsberg Syncline represents an undescribed Lower Cenomanian species. Professor TRÖGER has unpublished records (pers. comm., 2001) of similar forms with a weak dorso-ventral sulcus from the former Görke Quarry near Birgte (Westphalia), the former Kalkwerk Nordharz Quarry at Hoppenstedt (Saxony-Anhalt) and from Sachsenthal near Worbis in the northern Thuringian Basin. These specimens are preserved in the collections of the Geological Institute of the Academy of Mining and Technology (Technical University), Freiberg.

NOTE: Additional material of the '*Inoceramus*' *crippsi* group (5 specimens) and of the *I. virgatus* group (28 specimens not determinable to subspecies level) are kept in the collections of the Institute for Palaeontology of Würzburg University under repository PIW2001I 60 and PIW2001I 61, respectively.

OBSERVATIONS ON THE *INOCERAMUS VIRGATUS* GROUP

SORNAY (1978) recognized two subspecies in the *Inoceramus virgatus* group, namely *I. virgatus virgatus* and *I. virgatus scalprum*. *I. virgatus virgatus* is based on an excellent description by SCHLÜTER (1877), who referred to a figure of *Inoceramus lamarcki* (GOLDFUSS 1834-40, pl. 111, fig. 2). It is unclear whether or not the original of this figure, which becomes the holotype by monotypy, still exists. The stratigraphic and locality data (Cenomanian Varians-Pläner of Siddinghausen near Büren, Westphalia as interpreted by SCHLÜTER 1877, p. 259) are inadequate to identify the exact horizon.

Inoceramus scalprum is a replacement name introduced by BÖHM (1914) for *I. etheridgei* WOODS, 1911, *non* ETHERIDGE jr., 1901, which was itself a replacement name for *I. convexus* R. ETHERIDGE, 1881 *non* HALL & MEEK, 1855. *I. etheridgei* may well be conspecific with the French Cenomanian taxon *I. laevigatus* LEYMERIE, 1842, *non I. laevigatus* GOLDFUSS, 1840 (a species from the Lias). The (lecto)type (effectively designated by SORNAY 1978) of *Inoceramus scalprum* is the specimen in the Sedgewick Museum, Cambridge, registration number SMC B.297, originally figured by R. ETHERIDGE (1881, pl. 2, fig. 6) as *Inoceramus convexus*, and subsequently refigured as *I. etheridgei* by WOODS (1911, pl. 49, fig. 3). This was chosen as the (lecto)type by SORNAY (1987) on the basis of it being the only one out of the original two figured specimens of *I. convexus* that was refigured by WOODS. This was not entirely a valid choice, because WOODS clearly stated that the original of his plate 49, fig. 3 was *one of the types, not the type* (our italics). In fact, the second of the two specimens, figured by ETHERIDGE (1881, pl. 2., fig. 6a), but not subsequently refigured by WOODS, has an equal, if not better claim to be selected as the lectotype of *Inoceramus scalprum*. Not only is it a bivalved specimen with most of the shell preserved, including the ligament plate of both valves, but it is clear that part of ETHERIDGE'S original description was based on it. Furthermore, in the paragraph where he discussed plaster casts of the types, SORNAY actually appears to be referring to the bivalved specimen with the preserved hinge as the type, for it is on this specimen and not on the original of WOODS (1911, pl. 49, fig. 3), that the striae can be seen on part of the *right* valve where the shell is missing. The type horizon of the original two specimens, as well as another specimen figured by WOODS (1911, pl. 49, fig. 4) and the type of *Inoceramus convexus* var. *quadratus* ETHERIDGE (ETHERIDGE 1881, pl. 2, fig. 7), was given as the Totternhoe Stone of Burwell, Cambridgeshire, England.

Inoceramus virgatus virgatus and *I. v. scalprum* are respectively subquadratic and subcircular in outline, with the latter being distinguished by its short, curved anterior margin and the nominate subspecies by a long, straight anterior margin and (as emphasized by SCHLÜTER 1877) conspicuous raised radial striae on the steinkern. These striae are particularly well seen in the bivalved specimen figured by KAPLAN & *al.* (1984, pl. 8, fig. 4) from the *M. saxbii* Zone of Rheine-Waldhügel, Westphalia, which closely resembles SCHLÜTER'S holotype, and in the specimen figured herein on Pl. 2, Fig. 7. SORNAY (1978) noted that the distinction based on the presence of the radial striae breaks down, in that WOODS' specimens of *I. etheridgei* also show traces of radial striae on the steinkern. Excellent illustrations of specimens assigned to these two forms were given by SORNAY (1978, pl. 2, figs 5 and 2) and by KELLER (1982, pl. 1, figs 1 and 2). In both sets of figures the two forms are clearly morphologically distinct, although the shell ornament of the specimens of *I. v. scalprum* appears to be much more strongly developed. However, it may be significant that both specimens of *I. v. scalprum*, particularly that figured by KELLER, are well preserved and retain most of the shell.

The relatively well preserved material of the *Inoceramus virgatus* group from the Kronsberg Syncline includes forms that are apparently transitional between the two subspecies *I. virgatus virgatus* and *I. virgatus scalprum* (e.g., Pl. 3, Fig. 8, Pl. 4, Fig. 1), introducing the possibility that the subspecific separation between these two taxa is rather artificial and perhaps should not be maintained. This conclusion had previously been reached by MATSUMOTO & *al.* (1987), who noted that the two forms could not be regarded as separate (geographical) subspecies since (in Japan) they occurred in the same region and at the same horizon. This is also indicated by the Kronsberg material as the two subspecies apparently occur in the same bed (e.g., Pl. 4, Figs 3a-c). LEHMANN (1995) accordingly treated the two forms merely as varieties of *I. virgatus*. Also TRÖGER (1967, 1983) recognized a rare 'cycloid variant' in populations of *I. virgatus* from former Kalkwerk Nordharz Quarry at Hoppenstedt. TRÖGER (1967) noted that the cycloid variant could be distinguished morphometrically from the normal subrectangular form by the Na (Nebenachse)/Ha (Hauptachse) ratio. He later (TRÖGER 1983, figs 1a and 2a) clearly illustrated the differences in the umbonal region and the shape of the growth trace between the two forms using specimens from Hoppenstedt, and introduced a new subspecies, *I. virgatus poloniae*, from the Cenomanian of Poland. His illustration of the 'cycloid variant' (TRÖGER 1983, fig. 2a) matches the particularly well preserved specimens from the Kronsberg Syncline (Pl. 3, Figs 6 and 7) which show details of the ornament of the umbonal region. TRÖGER (1967) regarded the *scalprum* form (his 'cycloid variant') as rare (in eastern Germany) whereas SORNAY (1978) considered that this was the predominant form in France and, particularly, in England. Because of this difference in the geographical distribution of the two forms, SORNAY (1978) stated that the *scalprum* form should be treated as an independent subspecies, *Inoceramus virgatus scalprum*.

The Kronsberg Syncline material does not help to resolve the relationship between the *virgatus* and *scalprum* forms. Unfortunately, as noted above, the collected material is effectively loose and it therefore cannot safely be used for population variability studies or for biometric analysis. In any case, both of the taxa in question are relatively ill-defined. In fact, the lectotype of *I. virgatus scalprum* (WOODS, 1911, pl. 49, fig. 3) is closer to forms figured here as questionably transitional than it is to the form from the Cenomanian of Le Mans (France) figured by SORNAY (1978, pl. 2, fig. 2) or to the superbly preserved subcircular form figured by KELLER (1982) from the Cenomanian near Goslar, Germany. It is actually possible that *I. virgatus virgatus* and *I. v. scalprum* (in the sense of the lectotype and type series) may fall within the variability of a single species. However, this variable species is not necessarily conspecific with the extreme subcircular forms that have been assigned to *I. v. scalprum*. It also must be emphasized that all of the English forms attributed to *I. v. scalprum* have more weakly developed striae on the steinkern than *I. virgatus virgatus*.

The problem of speciation within the *Inoceramus virgatus* group can be resolved only by morphometric analysis of successive populations. The problem is further complicated by the fact that there is considerable uncertainty regarding the stratigraphic provenance of the type series of *I. virgatus scalprum*. The specimens are unequivocally, albeit surprisingly, recorded as coming from the Totternhoe Stone of Burwell. The Totternhoe Stone is a calcarenite of Middle Cenomanian (*Acanthoceras rhotomagense* Zone, *Turrilites costatus* Subzone) age that is developed in an area from the Chiltern Hills to eastern England (East Anglia, Lincolnshire, Yorkshire). The fauna of the Totternhoe Stone is essentially that associated with the (*Praeactinocamax*) *primus* event of German event stratigraphy (ERNST & *al.* 1983) and does not normally include *Inoceramus* of the *virgatus* group. Furthermore, the matrix inside the valves of the type series is a tough marly chalk that is quite unlike the distinctive coarse-grained Totternhoe Stone. The Totternhoe Stone is developed in a 'shelf' and a 'channel facies' (HOPSON & *al.* 1996). In the case of the shelf facies the bed consists of a single unit of calcarenite, typically less than one metre thick, with a basal concentration of reworked glauconitized and phosphatized chalk pebbles. The channel facies, on the other hand, is several metres thick, and may incorporate many separate units of calcisiltites and calcarenites stacked one above the other. In both cases the base of the stone is strongly erosive, usually resting somewhere in the *Mantelliceras dixoni* Zone, but locally (e.g. at the type locality, Totternhoe in the Chiltern Hills) as low as the *Sharpeiceras schlueteri* Subzone or even lower (SHEPHARD-THORN & *al.* 1994).

It is known that Totternhoe Stone channels were developed at Burwell, from which it follows that the type series of *I. virgatus scalprum* could have come from a biostratigraphically complex channel fill. This interpretation is reinforced by the fact that all of the specimens are more or less iron-stained and are exceptionally well preserved, retaining the greater part of the shell without any adherent matrix. In fact, they have the appearance of pebble-fossils that where originally incorporated in a *soft* matrix. This type of preservation does not compare well with that of the *virgatus* acme-event, or with the material from the Kronsberg Syncline. Until the stratigraphical relationships at Burwell are clarified, and the exact stratigraphic provenance of material comparable to the type series of *I. virgatus scalprum* is determined, it will be difficult to apply this taxonomic concept in the sense of the type series with confidence.

Acknowledgements

Professor A. S. GALE (University of Greenwich, UK) kindly provided an unpublished log of the Wunstorf Quarry section and A. KEYDEL (Hannover, TEUTONIA cement works) the geochemical analyses. H. SCHÖNIG and R. SCHRÖDER (both Würzburg) are thanked for photographic work and L. THÜMLER (Würzburg) for the developing of fossils. C. NIEBUHR (Würzburg) helped to compile the references. We are particularly grateful to one of the journal referees, Professor K.-A. TRÖGER (Freiberg), for valuable and stimulating discussion of inoceramid taxonomy and for allowing us to use some of his unpublished records. Dr. I. WALASZCZYK (Warsaw) also provided helpful comments on taxonomy and on the geographical distribution of the inoceramids in a global context. Further valuable remarks by another anonymous journal referee are appreciated.

REFERENCES

BARTELS, H. 1993. Mikropaläontologische-statistische Untersuchungen in den untercenomanen Plänern von Baddeckenstedt und Flöteberg (Niedersachsen). Ruhr-Universität Bochum, 46pp. Bochum. [unpubl. diploma thesis]

BETTENSTEDT, F. & DIETZ, C. 1957. Tektonische und erdölgeologische Untersuchungen im Raum Lehrte östlich Hannover. *Geologisches Jahrbuch*, **74**, 463-522. Hannover.

BEURLEN, K. 1944. Beiträge zur Stammesgeschichte der Muscheln. *Bayerische Akademie der Wissenschaften, Sitzungsberichte*, **1-2**, 133-145. München.

BÖHM, J. 1914. Zusammenstellung der Inoceramen der Kreideformation (Nachtrag). *Jahrbuch der königlich preussischen geologischen Landesanstalt*, **35**/1, 3. 595-599. Berlin.

BRÄUTIGAM, D. 1962. Zur Stratigraphie und Paläontologie des Cenomans und Turons im nordwestlichen Harzvorland. Technische Universität Braunschweig, 261pp. Braunschweig. [unpubl. PhD-thesis]

DHONDT, A.V. 1992. Cretaceous inoceramid biogeography: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **92**, 217-232. Amsterdam.

ERNST, G., SCHMID, F. & SEIBERTZ, E. 1983. Event-Stratigraphie im Cenoman und Turon von NW-Deutschland. *Zitteliana*, **10**, 531-554. München.

ERNST, G. & REHFELD, U. 1997. Transgressive development in the Early Cenomanian of the Salzgitter area (northern Germany) recorded by sea level controlled eco- and litho-events. *Freiberger Forschungsheft*, **C468**, 79-107. Leibzig.

ERNST, G. & REHFELD, U. 1998. C 2.8 Cenomanian-Turonian of Baddeckenstedt. In: MUTTERLOSE, J., BORNEMANN, A., RAUER, S., SPAETH, C. & WOOD, C.J. (*Eds*), Key localities of the Northwest European Cretaceous. *Bochumer geologische und geotechnische Arbeiten*, **48**, 91-94. Bochum.

ERNST, G., NIEBUHR, B. & REHFELD, U. 1997. 2.10. HPCF II quarry at Misburg. In: MUTTERLOSE, J., WIPPICH, M.G.E., & GEISEN, M. (*Eds*), Cretaceous Depositional Environments of NW Germany. *Bochumer geologische und geotechnische Arbeiten*, **46**, 77-82. Bochum.

ETHERIDGE, R. 1881. Appendix A. Palaeontology. In: PENNING, W.H. & JUKES-BROWNE, A.J. (*Eds*), Geology of the neighbourhood of Cambridge. *Memoir of the Geological Survey (England and Wales), HMSO*, 132-148. London.

FRIEG, C., KEMPER, E. & BALDSCHUHN, R. 1989. Mikropaläontologische Gliederung und Abgrenzung von Ober-Alb und Unter-Cenoman in Nordwestdeutschland. *Geologisches Jahrbuch*, **A 113**, 73-193. Hannover.

GALE, A.S. 1995. Cyclostratigraphy and correlation of the Cenomanian stage in Western Europe. In: HOUSE, M.R. & GALE, A.S. (*Eds*), Orbital forcing timescales and cyclostratigraphy. *Geological Society, Special Publication*, **85**, 177-197. London.

GIEBEL, C.G. 1852. Deutschlands Petrefacten. Ein systematisches Verzeichnis aller in Deutschland und den angrenzenden Ländern vorkommenden Petrefacten nebst Angabe der Synonyme und Fundorte. 329-441. Leipzig.

GOLDFUSS, A. 1834-1840. Petrefacta Germaniae, **II**, 106-118. Düsseldorf.

HALL, J. & MEEK, F.B. 1855. Descriptions of new species of fossils from the Cretaceous Formations of Nebraska with observations on *Baculites ovatus* and *B. compressus* and the progressive development of the septa in *Baculites*, *Ammonites* and *Scaphites*. *Memoir of the American Academy of Arts and Sciences*, N.S. **5** (for 1854), 379-411.

HEINZ, R. 1928. Über Cenoman und Turon bei Wunstorf westlich von Hannover (zugleich Beiträge zur Kenntnis der oberkretazischen Inoceramen II). *Jahresberichte der niedersächsischen geologischen Versammlung*, **21**, 18-38. Hannover.

HOPSON, P.M., ALDISS, D.T. & SMITH, A. 1996. Geology of the country around Hitchin. *Memoir of the British Geological Survey, Sheet 221 (England and Wales), HMSO*, 152pp. London.

HORNA, F. 1997. Die Cenomantransgression von Langenstein: Alter und eventstratigraphische Position. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **203** (1), 47-56. Stuttgart.

JEANS, C.V. 1980. Early submarine lithification in the Red Chalk and Lower Chalk of eastern England: a bacterial control model and its implications. *Proceedings of the Yorkshire Geological Society*, **43**, 81-157. Leeds.

KAPLAN, U., KELLER, S. & WIEDMANN, J. 1984. Ammoniten- und Inoceramen-Gliederung des norddeutschen Cenoman. *Schriftenreihe der Erdwissenschaftlichen Kommission*, **7**, 307-347. Wien.

KAPLAN, U., KENNEDY, W.J., LEHMANN, J. & MARCINOWSKI, R. 1998. Stratigraphie und Ammonitenfaunen des westfälischen Cenoman. *Geologie und Paläontologie in Westfalen*, **51**, 1-236. Münster.

KAUFFMAN, E.G. 1976. British Middle Cretaceous inoceramid biostratigraphy. *Annales du Muséum d'Histoire Naturelle de Nice*, **4**, IV, 1-12. Nice.

KELLER, S. 1982. Die Oberkreide der Sack-Mulde bei Alfeld (Cenoman - Unter-Coniac): Lithologie, Biostratigraphie und Inoceramen. *Geologisches Jahrbuch*, **A 64**, 3-171. Hannover.

KEMPER, E. 1984. Ober-Alb und Unter-Cenoman in Nordwestdeutschland. *Geologisches Jahrbuch*, **A 75**, 465-487. Hannover.

KENNEDY, W.J. COBBAN, W.A., HANCOCK, J.M. & HOOK, S.C. 1989. Biostratigraphy of the Chispa Summit Formation at its type locality: a Cenomanian through Turonian reference section for Trans-Pecos Texas. *Bulletin of the Geological Institutions of the University of Uppsala, New Series*, **15**, 39-119. Uppsala.

LEHMANN, J. 1995. Die Genese des Münsterländer Kiessandzuges unter Berücksichtigung des Geröllbestandes und der Fossilinhalt der Oberkreidekalke. *Geologie und Paläontologie in Westfalen*, **41**, 27-53. Münster.

LEYMERIE, A. 1842. Sur le terrain crétacé du departement de l'Aube (2nd part). *Mémoire de la Société géologique de France*, **5**, 34 pp. Paris.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 1, Laurentii Salvii, Holmiae, 824pp.

MANTELL, G. 1822. Fossils of the South Downs, or illustrations of the geology of Sussex. 320pp. London.

MARCINOWSKI, R., WALASZCZYK, I. & OLSZEWSKA-NEJBERT, D. 1996. Stratigraphy and regional development of the mid-Cretaceous (Upper Albian through Coniacian) of the Mangyshlak Mountains, Western Kazakstan. *Acta Geologica Polonica*, **46** (1-2), 1-60. Warszawa.

MATSUMOTO, T., ASAI, A. & HIRANO, H. 1987. Some inoceramids (Bivalvia) from the Cenomanian (Cretaceous) of Japan. II. Three species from Hokkaido, well known abroad but hitherto undescribed in Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **147**, 146-164. Tokyo.

MEYER, T. 1990. Biostratigraphische und sedimentologische Untersuchungen in der Plänerfazies des Cenoman von Nordwestdeutschland. *Mitteilungen aus dem Geologischen Institut der Universität Hannover*, **30**, 114pp. Hannover.

MITCHELL, S.F., PAUL, C.R.C. & GALE, A.S. 1996. Carbon isotopes and sequence stratigraphy. In: HOWELL, J.A. & AITKEN, J.F. (*Eds*), High Resolution Sequence Stratigraphy: Innovations and Applications. *Geological Society of London, Special Publication*, **104**, 11-24. London.

MUTTERLOSE, J. 1984. Die Unterkreide-Aufschlüsse (Valangin - Alb) im Raum Hannover. *Mitteilungen aus dem*

Geologischen Institut der Universität Hannover, **24**, 1-61. Hannover.

NEWELL, N.D. 1965. Classification of the Bivalvia. *American Museum Novitates*, **2206**, 1-25. New York.

NIEBUHR, B., WIESE, F. & WILMSEN, M. The cored borehole Konrad 101 (Salzgitter area, Germany): A key section for the Cenomanian to Lower Coniacian in eastern Lower Saxony. *Cretaceous Reserach*, London. [submitted].

PERGAMENT, M.A. 1966. Zonal stratigraphy and inocerams of the lower-most Upper Cretaceous on the Pacific coast of the USSR. *Transactions of the Geological Institute of the Academy of Sciences of the USSR*, **146**, 80pp. Nauka, Moscow. *[In Russian]*

SCHLÜTER, C. 1877. Kreide-Bivalven. Zur Gattung *Inoceramus*. *Palaeontographica*, **24**, 249-288. Stuttgart.

SHEPHARD-THORN, E.R., MOORLOCK, B.S.P., COX, B.M., ALLSOP, J.M. & WOOD, C.J. 1994. Geology of the country around Leighton Buzzard. *Memoir of the British Geological Survey, Sheet 220 (England and Wales), HMSO*, 127pp. London.

SORNAY, J. 1978. Précisions palaéontologiques et stratigraphiques sur divers Inocérames cénomaniens et, en particulier, sur ceux de la Sarthe figurés par E. GUÉRANGER en 1867. *Géobios*, **11** (4), 505-515. Lyon.

SOWERBY, J. 1814. The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals and shells, which have been preserved at various times and depths in the earth. 609pp. London.

TRÖGER, K.-A. 1967. Zur Paläontologie, Biostratigraphie und faziellen Ausbildung der unteren Oberkreide (Cenoman bis Turon). I: Paläontologie und Biostratigraphie der Inoceramen des Cenomans bis Turons Mitteleuropas. *Abhandlungen des staatlichen Museums für Mineralogie und Geologie*, **12**, 13-207. Dresden.

TRÖGER, K.-A. 1978. Probleme der Paläontologie, Biostratigraphie und Paläobiogeographie oberkretazischer Faunen (Cenoman - Turon) Westeuropas und der Russischen Tafel. *Zeitschrift für geologische Wissenschaften*, **6**, 557-570. Berlin.

TRÖGER, K.-A. 1983. *Inocerasmus virgatus poloniae* n. ssp. aus dem Cenoman von Annopol und Jazwini (Volksrepublik Polen). *Freiberger Forschungsheft*, **C384**, 20-23. Freiberg.

TRÖGER, K.-A. 1989. Problems of Upper Cretaceous inoceramid biostratigraphy and palaeobiogeography in Europe and western Asia. In: WIEDMANN, J. (*Ed*), Cretaceous of the Western Tethys. *Proceedings of the 3rd International Cretaceous Symposium, Tübingen 1987*, 911-930. Stuttgart.

VOIGT, S. 1996. Paläobiogeographie oberkretazischer Inoceramen und Rudisten - ozeanographische und klimatologische Konsequenzen einer neuen Paläogeographie. *Münchner Geowissenschaftliche Abhandlungen*, **A 31**, 101pp. München.

WILMSEN, M. 1997. Das Oberalb und Cenoman im Nordkantabrischen Becken (Provinz Kantabrien, Nordspanien): Faziesentwicklung, Bio- und Sequenzstratigraphie. *Berliner geowissenschaftliche Abhandlungen*, **E 23**, 167pp. Berlin.

WOOD, C.J. & ERNST, G. 1998. C 2.4 Cenomanian-Turonian of Wunstorf. In: MUTTERLOSE, J., BORNEMANN, A., RAUER, S., SPAETH, C. & WOOD, C.J. (*Eds*), Key Localities of the Northwest European Cretaceous. *Bochumer geologische und geotechnische Arbeiten*, **48**, 62-72. Bochum.

WOOD, C.J., ERNST, G. & REHFELD, U. 1997. 2.6 Baddeckenstedt quarry. In: MUTTERLOSE, J., WIPPICH, M.G.E. & GEISEN, M. (*Eds*), Cretaceous depositional environments of NW Germany. *Bochumer geologische und geotechnische Arbeiten*, **46**, 39-45. Bochum.

WOODS, H. 1911. A Monograph of the Cretaceous Lamellibranchia of England, 2: 7. *Inoceramus. Monograph of the Palaeontographical Society*, 262-284. London

Manuscript submitted: 31th January 2001
Revised version accepted: 20th April 2001

PLATES 1- 4

PLATE 1

'Inoceramus' crippsi group

1 – *'Inoceramus' crippsi* MANTELL, 1822; PIW2001I 6.
2 – *'Inoceramus' hoppenstedtensis* TRÖGER, 1967; PIW2001I 7.
3 – *'Inoceramus' hoppenstedtensis* TRÖGER, 196; PIW2001I 8.
4 – *'Inoceramus' hoppenstedtensis* TRÖGER, 1967; PIW2001I 9.
5 – *'Inoceramus' hoppenstedtensis* TRÖGER, 1967; specimen PIW2001I 10.
6 – *'Inoceramus'* ex gr. *crippsi* MANTELL, 1822, subsp. indet (large form); PIW2001I 14.

All figures are natural size

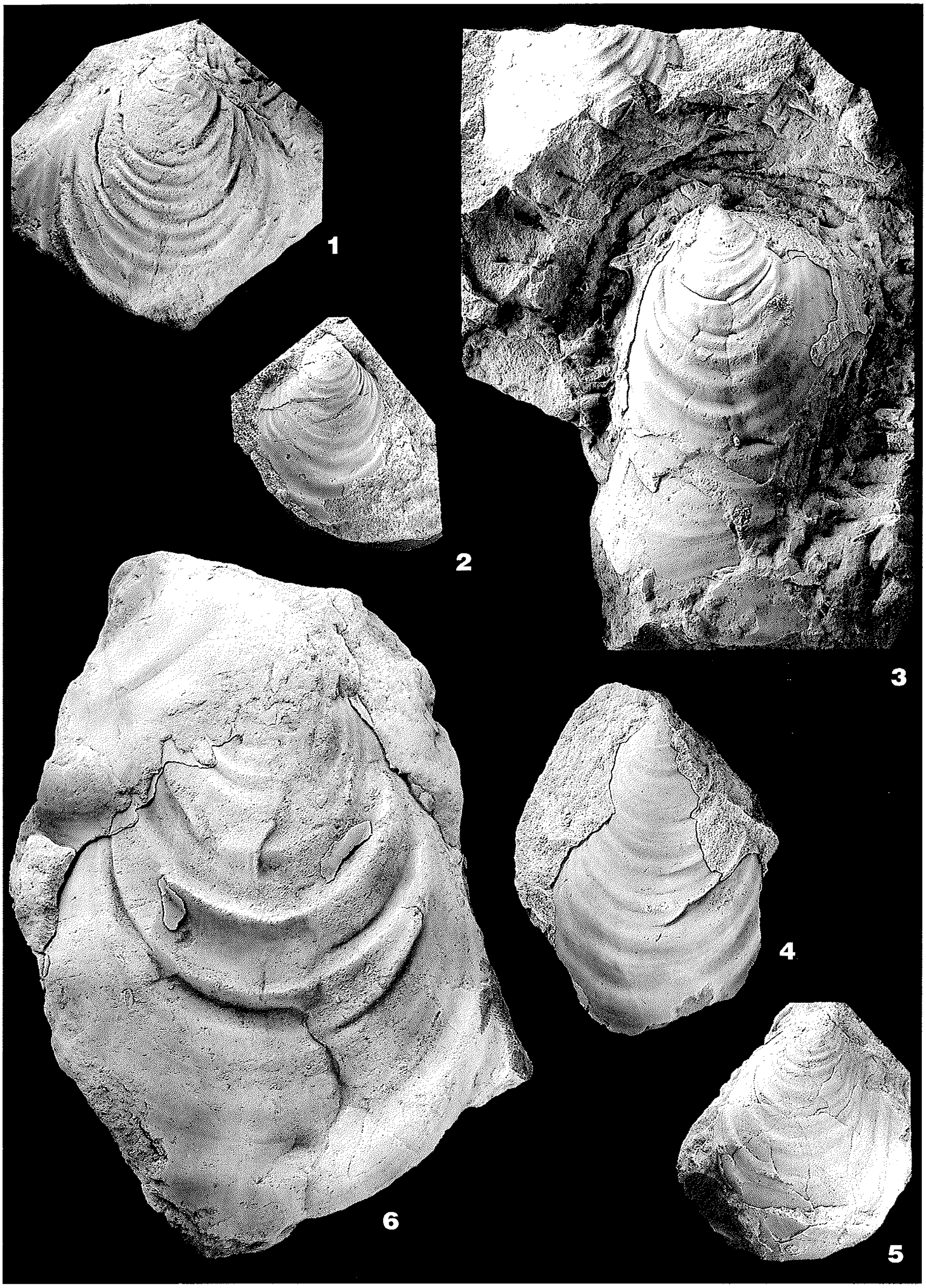

1
2
3
4
5
6

PLATE 2

Inoceramus virgatus group

1 – *Inoceramus virgatus* SCHLÜTER, 1877. subsp. indet.; PIW2001I 61.

2 – *Inoceramus virgatus virgatus* SCHLÜTER, 1877; PIW2001I 17.

3 – *Inoceramus virgatus virgatus* SCHLÜTER, 1877; specimen PIW2001I 18.

4 – *Inoceramus virgatus virgatus* SCHLÜTER, 1877; specimen PIW2001I 19.

5 – *Inoceramus virgatus virgatus* SCHLÜTER, 1877; specimen PIW2001I 20.

6 – *Inoceramus virgatus virgatus* SCHLÜTER, 1877; specimen PIW2001I 21.

7 – *Inoceramus virgatus virgatus* SCHLÜTER, 1877, clearly showing the characteristic radial striae on the steinkern; specimen PIW2001I 22.

All figures are natural size

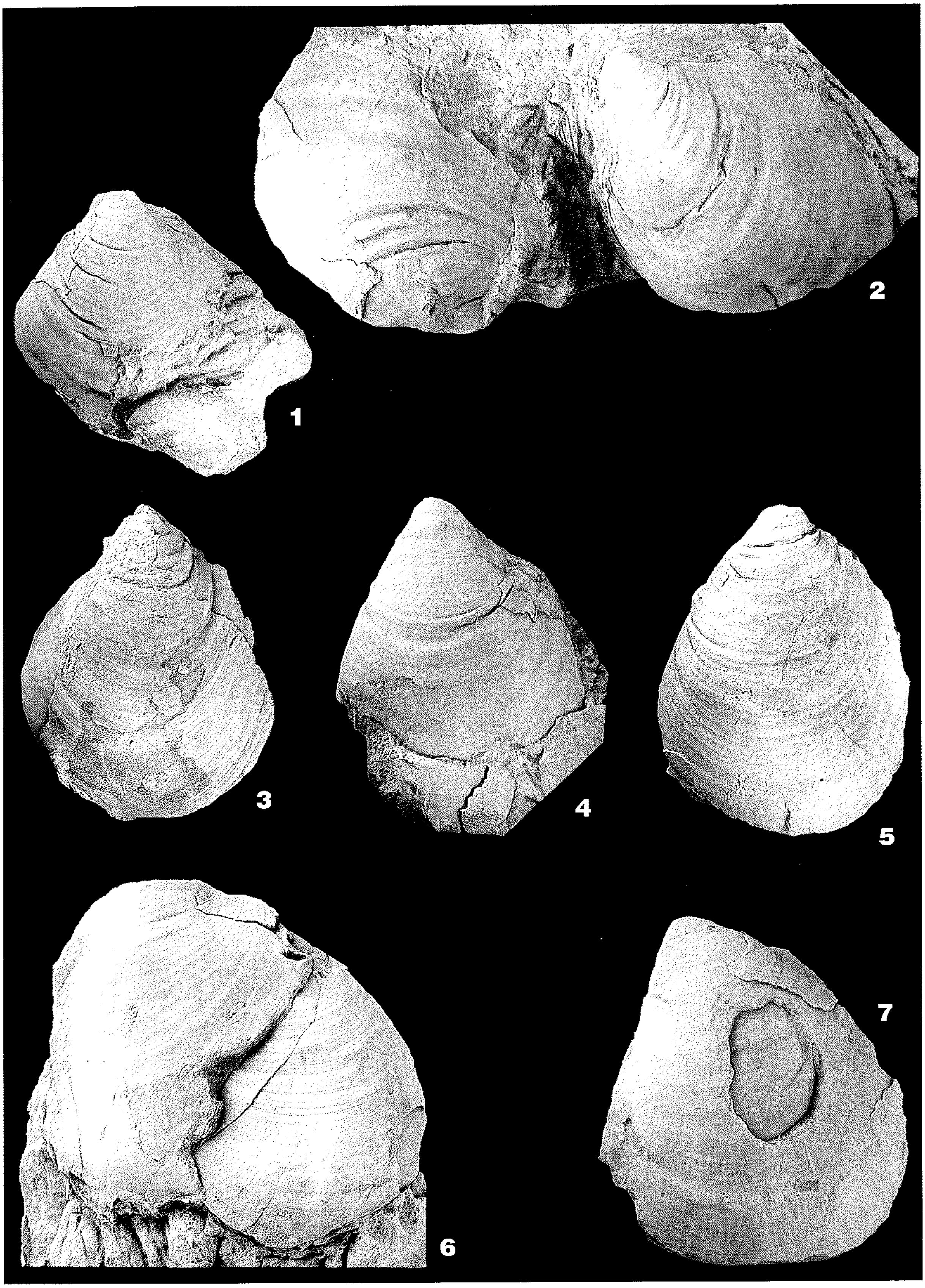

1
2
3
4
5
6
7

PLATE 3

Inoceramus virgatus group

1 – *Inoceramus virgatus* SCHLÜTER, 1877, subsp. indet.; specimen PIW2001I 61.

2a – *Inoceramus virgatus virgatus* SCHLÜTER, 1877, juvenile; specimen PIW2001I 23.

2b – *Inoceramus virgatus virgatus* SCHLÜTER, 1877, juvenile; specimen PIW2001I 23, x 2.0.

3 – *Inoceramus virgatus virgatus* SCHLÜTER, 1877, juvenile; specimen PIW2001I 24.

4 – *Inoceramus virgatus scalprum* BÖHM, 1914; specimen PIW2001I 43.

5 – *Inoceramus virgatus scalprum* BÖHM, 1914; specimen PIW2001I 44.

6 – *Inoceramus virgatus scalprum* BÖHM, 1914, with exceptionally well- preserved juvenile shell ornament; specimen PIW2001I 45.

7 – *Inoceramus virgatus scalprum* BÖHM, 1914, with exceptionally well- preserved juvenile shell ornament; specimen PIW2001I 46.

8 – *Inoceramus virgatus scalprum* BÖHM, 1914, or transitional form to *I. virgatus virgatus* SCHLÜTER, 1877; specimen PIW2001I 56.

All figures natural size (except Fig. 2b)

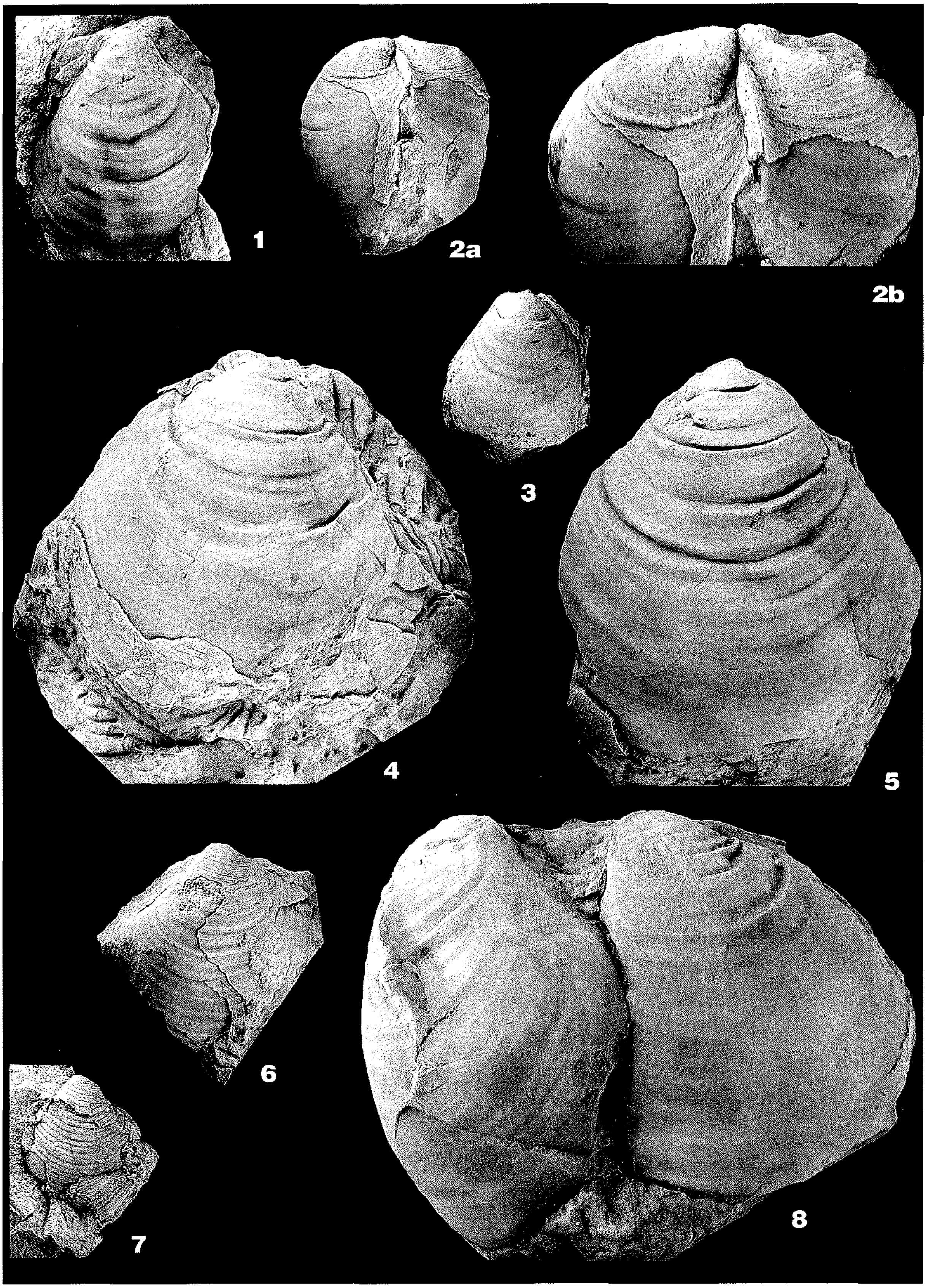

1
2a
2b
3
4
5
6
7
8

PLATE 4

1 – Possible transitional form between *Inoceramus virgatus virgatus* SCHLÜTER, 1877, and *Inoceramus virgatus scalprum* BÖHM, 1914; specimen PIW2001I 57, × 1.0.

2 – *Inoceramus virgatus scalprum* BÖHM, 1914; specimen PIW2001I 47, × 1.0.

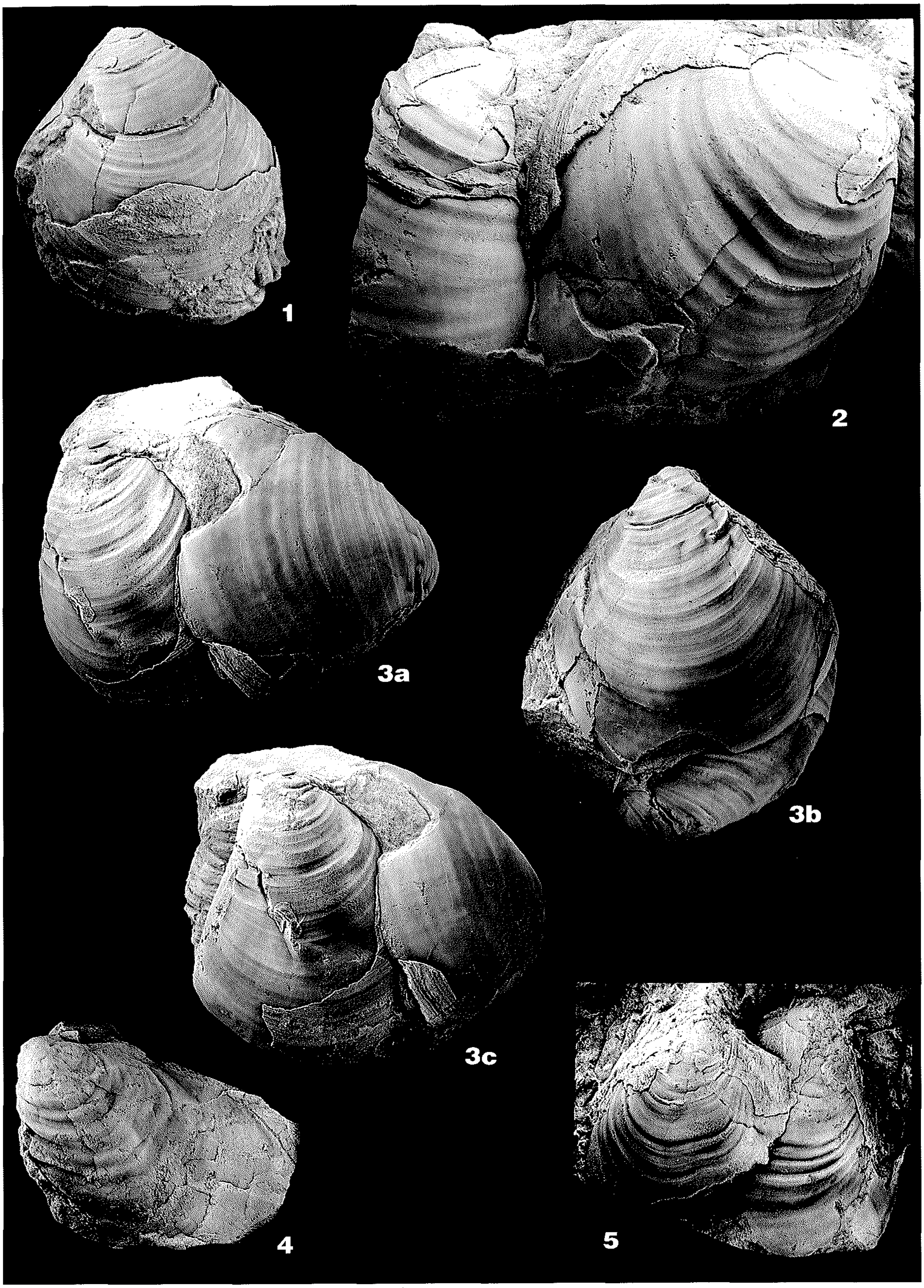
3a – *Inoceramus virgatus scalprum* BÖHM, 1914 and *Inoceramus virgatus virgatus* SCHLÜTER, 1877; note co-occurrence of the two subspecies in one slab of limestone (compare to Figs 3b and 3c); specimen PIW2001I 48, × 0.9.

3b – *Inoceramus virgatus scalprum* BÖHM, 1914; specimen PIW2001I 48, × 1.0.

3c – *Inoceramus virgatus virgatus* SCHLÜTER, 1877; specimen PIW2001I 48, × 0.9.

4 – undetermined inoceramid bivalve with dorso-ventral sulcus; specimen PIW2001I 58, × 1.0.

5 – undetermined inoceramid bivalves with well-developed dorso-ventral sulci; specimen PIW2001I 59, × 1.0.


1
2
3a
3b
3c
4
5