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Inoceramids and biostratigraphy at the Turonian/Coniacian boundary; based on the Salzgitter-Salder Quarry, Lower Saxony, Germany, and the Słupia Nadbrzeżna section, Central Poland

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ABSTRACT:

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The candidate Global Standard Stratotype-section and Point for the base of the Coniacian Stage, the Salzgitter-Salder section, Germany, and the Słupia Nadbrzeżna section, central Poland, provide together a continuous record of the inoceramid succession and events across the Turonian/Coniacian boundary interval, that can be correlated throughout Europe and beyond. The Turonian/Coniacian boundary interval marks a radical change from the Upper Turonian, *Mytiloides*/*Inoceramus*-dominated fauna to the *Cremnoceramus*-dominated fauna of the topmost Turonian and Lower Coniacian. The *Cremnoceramus* clade is basically composed of three lineages: *waltersdorfensis*, with subspecies *waltersdorfensis* (ANDERT) and *hannovrensis* (HEINZ); *deformis*, with subspecies *erectus* (MEEK), *dobrogensis* (SZASZ) and *deformis* (MEEK); and *crassus*, with subspecies *inconstans* (WOODS) and *crassus* (PETRASCHECK). Rare *Inoceramus* species range throughout the boundary interval, and in the middle Lower Coniacian representatives of the genus *Tethyoceramus* SORNAY (*non* HEINZ) appear. Twelve species and/or subspecies of these genera are described and illustrated. The inoceramids provide the basis for the subdivision of the uppermost Turonian – Lower Coniacian boundary interval into 7 inoceramid zones. The upper Upper Turonian is divided into the *Mytiloides scupini* Zone and the *Cremnoceramus waltersdorfensis* Zone. In the Lower Coniacian the following zones are distinguished, in ascending order: *Cremnoceramus deformis erectus*, *C. waltersdorfensis hannovrensis*, *Cremnoceramus crassus inconstans*, *Cremnoceramus crassus* + *C. deformis deformis* and *Inoceramus gibbosus*. The inoceramid marker proposed for the base of the Coniacian, formerly referred to as *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE) is a synonym of *Cremnoceramus erectus* (MEEK), and its first appearance marks the base of the *deformis erectus* Zone and the base of the Coniacian Stage. The Salzgitter-Salder section, despite some problems concerning a possible hiatus or condensation at the boundary represents the best available potential stratotype for the Turonian/Coniacian boundary.

INTRODUCTION

SCOTT & COBBAN (1964) and subsequently KAUFFMAN & *al*. (1978) and KAUFFMAN (1978, and *in*: HERM & *al*. 1979) pointed out the synchronous appearance of the early cremnoceramids and Coniacian ammonites. Consequently, in inoceramid terms, they placed the Turonian/Coniacian boundary at the base of the *Cremnoceramus rotundatus* Zone (*see also* SEIBERTZ 1979). Such placing of the Turonian/Coniacian boundary, i.e. at the first appearance datum (FAD) of the inoceramid species *C. rotundatus* (TRÖGER *non* FIEGE), or at the slightly lower *Didymotis* II/*C. waltersdorfensis hannovrensis* Event (*sensu* ERNST & *al*. 1983; WOOD & *al*. 1984), acquired wide acceptance following the First Symposium on the Cretaceous Stage Boundaries, Copenhagen 1983 (ERNST & *al*. 1983; MATSUMOTO 1984; WOOD & *al*. 1984; CECH 1989, KÜCHLER & ERNST 1989; WALASZCZYK 1988, 1992; KOPAEVICH & WALASZCZYK 1990). During the Second Cretaceous Stage Boundaries Symposium, Brussels 1995, the FAD of *C. rotundatus* (*sensu* TRÖGER *non* FIEGE) was formally proposed as the basal boundary marker of the Coniacian Stage. By a majority vote, the Salzgitter-Salder Quarry in Lower Saxony, Germany, was proposed as the Global Standard Stratotype Section and Point (GSSP) (*see* KAUFFMAN & *al*. 1996 and references therein).

Subsequent studies of the inoceramid fauna from the basal boundary stratotype, as well as other European and North American faunas showed that the basal Coniacian boundary inoceramid marker, commonly referred to in the literature of the last decade as *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE), should be referred to its senior synonym, the North American taxon *Cremnoceramus erectus* (MEEK) (*see* WALASZCZYK & COBBAN, *in press*). In addition, the cremnoceramids, the inoceramid group dominating the assemblages of the boundary interval, are shown to be represented by a small number of species exhibiting rapid phyletic evolution.

This paper provides systematic descriptions of the inoceramid fauna and biostratigraphy of the topmost Turonian and lowermost Coniacian succession that is superbly exposed in the proposed standard section of the Salzgitter-Salder Quarry. This section provides a continuous faunal record (*see* WOOD & *al*. 1984; KAUFFMAN & *al*. 1996) allowing bed-by-bed collecting of abundant inoceramid material through the boundary interval. However, the material from this locality suffers from being to some extent deformed as the result of tectonism. This study is also based, to an equal extent, on material from the Vistula section, Central Poland. Although much less well exposed than the German section, this section yields particularly well preserved and largely undeformed material, allowing rigorous palaeontological

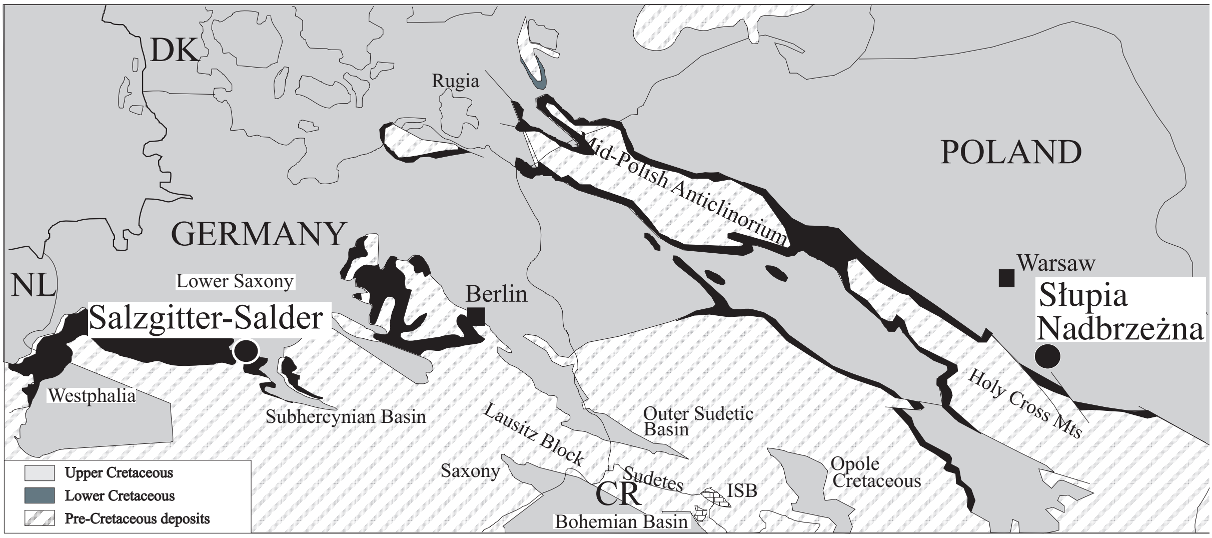


Fig. 1. Location of the Salzgitter-Salder and Słupia Nadbrzeżna sections on a geological sketch map of Central Europe; ISB – Inner Sudetic Basin

analysis of the inoceramid succession across the boundary. For a map to show the positions of the sections studied *see* Text-fig. 1.

This study spans an interval from the *Didymotis* I Event, near the top of the Upper Turonian, to the *inconstans* Event in the middle Lower Coniacian (*see* Text-fig. 2).

SECTION DESCRIPTIONS

The Salzgitter-Salder Quarry, Lower Saxony, Germany

Location: Ca. 750 m long limestone quarry of the Fels-Werke Peine Salzgitter GmbH, located south of the Autobahn 39 between Braunschweig and the Autobahn junction Salzgitter, near the exit to Salzgitter-Salder.

The Salzgitter-Salder Quarry (Text-figs 2-3) is situated near the village of Salzgitter-Salder in the southern part of the Lesse Syncline. This syncline is an asymmetrical structure with shallow dips on its northern flank and steep, up to 70° dips on its southern margin, adjacent to the Lichtenberg inversion structure. The asymmetry of the syncline results from the halokinetic movements of the Broistedt-Wendeburg salt-diapir and the contemporaneous uplift of the Lichtenberg structure. Across the syncline there is a rapid facies change within a very short distance from (predominantly calcisphere) soft chalk sediments on its northern margin to hard, marly limestones facies on its southern margin. The facies differentiation is linked to marked thickness differences in the greater part of the Turonian, with relatively thin successions on the northern flank of the syncline and much thicker successions on the southern flank. Linked to the facies differences are changes in faunal characteristics. The chalk succession is characterized by low-diversity faunas, this being partly an effect of the low preservation potential of aragonite-shelled fossils in chalk facies. The marly limestone sequence, in contrast, yields an abundant, much higher-diversity assemblage.

The quarry exposes a ca. 220 m thick succession of well-bedded carbonate rocks dipping N at 70^0, which can be subdivided into 6 lithostratigraphic units: (1) equivalent of the higher Rotpläner; (2) Lower Limestone Unit; (3) 'Grauweiße Wechselfolge'; (4) Upper Limestone Unit; (5) an un-named transitional unit; and (6) Emscher Marl (*cf.* MORTIMORE & *al.* 1998). The succession extends from the upper Middle Turonian to high in the Lower Coniacian. The Turonian/Coniacian boundary lies near the top of the 'Grauweiße Wechselfolge' at the base of bed MK 47 (Text-fig. 2). The highest beds, belonging to the Emscher Marl, are no longer exposed.

Turonian/Coniacian boundary interval

Details of this interval were given by WOOD & *al.* (1984) and by KAUFFMAN & *al.* (1996, p. 92 and Fig. 4). However, new field observations made in June 1998 have necessitated extensive revision of these details, particularly in respect of the First Appearance Datum (FAD), in the highest part of the Upper Turonian, of the inoceramid genus *Cremnoceramus*, and the correct horizon of the *Didymotis* II Event

The following succession of event beds and fossil occurrences falls within the 'Grauweiße Wechselfolge', a distinctive and highly conspicuous unit of rhythmically alternating dark marls and paler marly limestones.

Didymotis I Event. The event, in limestone MK 39b, is characterized by a flood occurrence of weakly ornamented forms of the thin-shelled bivalve *Didymotis*, associated with a *Mytiloides scupini* Zone inoceramid assemblage comprising *M. herbichi*, *M. scupini*, and *Inoceramus lusatiae*.

Limestone bed MK 41c has the same *M. scupini* inoceramid zonal assemblage as in *Didymotis* I, but so far without any records of *Didymotis*.

The middle and top parts of the limestone Bed MK 43a are characterized by a flood occurrence of *M. herbichi*, which is herein designated as a distinctive *herbichi* Event. This bed has also yielded a single specimen of *Didymotis*, which represents the only known record of this genus between the two *Didymotis* events. The inoceramids were previously (WOOD & *al.* 1984) erroneously attributed to *M. labiatoidiformis* (TRÖGER) and *M. labiatoidiformis* (*sensu* KELLER), taxa which appear to characterize somewhat lower levels in the Upper Turonian.

The overlying, thick (0.95 m) conspicuous marl bed MK 44, has yielded neither inoceramids nor *Didymotis*. However, the friable nature of the sediment hinders the recovery of any macrofossil material that it may contain, and it is possible that

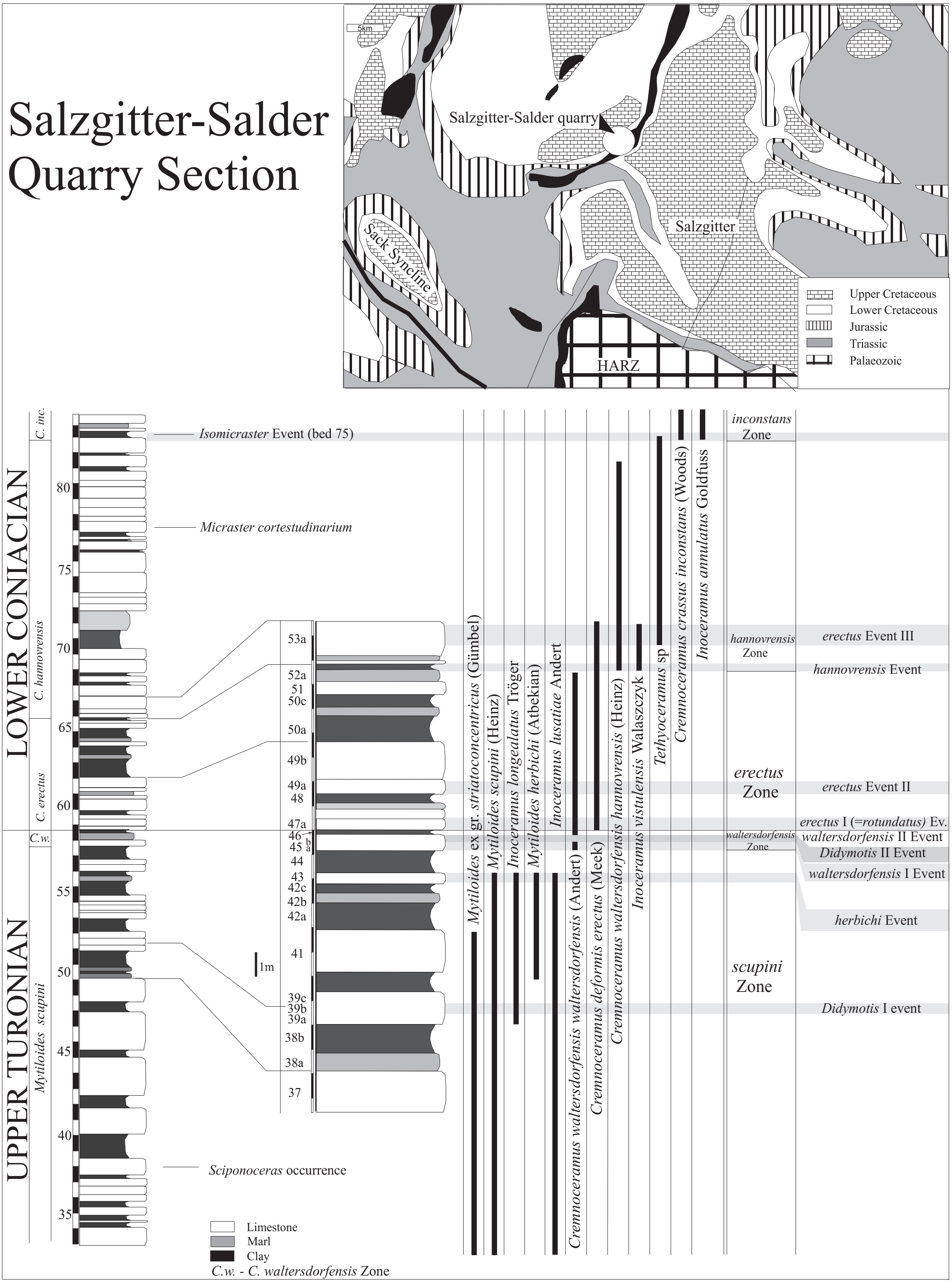
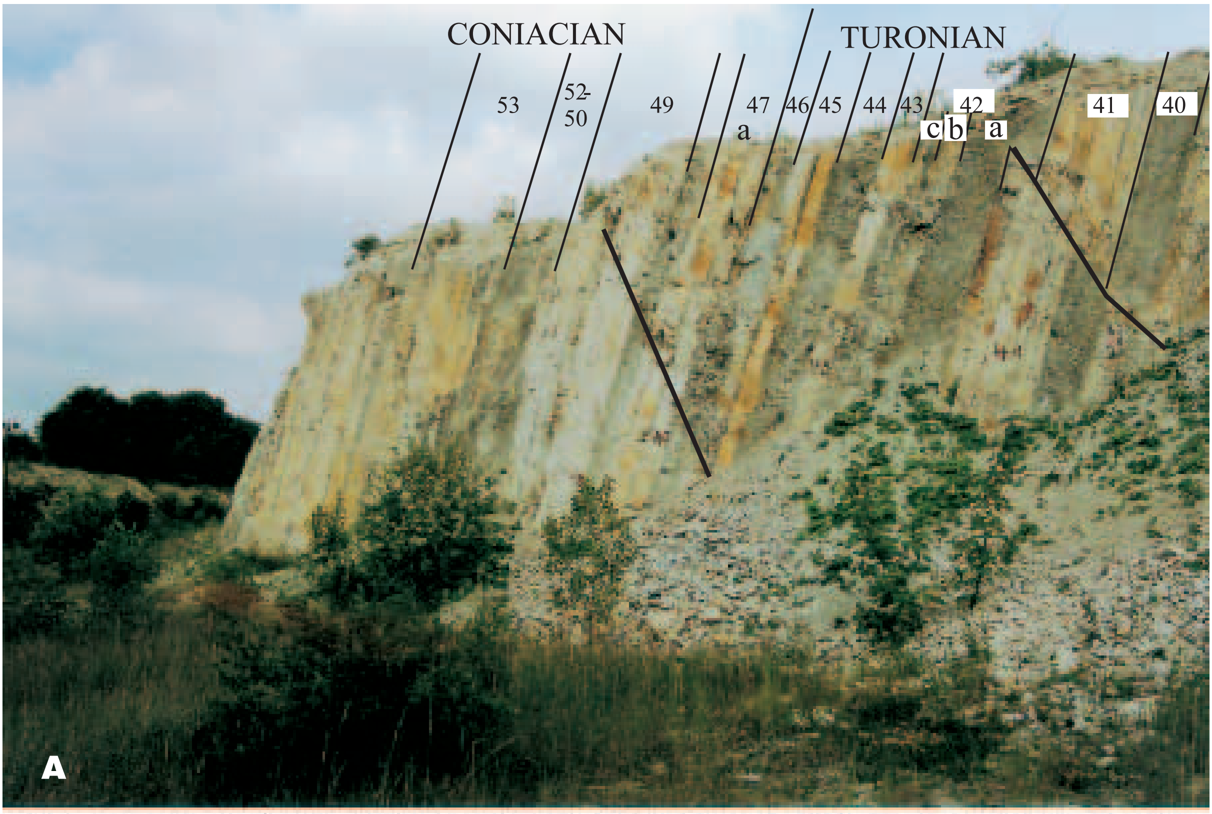


Fig. 2. Geological column, bio- and event stratigraphy, and inoceramid distribution in the Salzgitter-Salder section



Turonian/Coniacian boundary succession of the Salzgitter-Salder section

A – General view; B – Close-up of the boundary interval the apparent barren nature of this bed may result from collection failure.

The FAD, and coincident first flood occurrence of *Cremnoceramus waltersdorfensis waltersdorfensis* occurs at the base of the overlying limestone, bed mK 45a. The inoceramids extend up to the middle of the bed and into the overlying *Didymotis* II Event (*see below*). This first *Cremnoceramus* event, spanning the base and middle of bed mK 45a, is herein designated the *waltersdorfensis* I Event, to distinguish it from the *waltersdorfensis* II Event in the marl KM 46. As first recognized by BRÄUTIGAM (1962), the replacement at this level of the terminal Turonian *Mytiloides*-dominated assemblages by near monospecific *Cremnoceramus* assemblages marks a striking and dramatic faunal change that is readily identifiable, both here and in correlative sections.

The top of bed mK 45a, immediately below the thin detrital marl separating it from the overlying bed MK 45b, and about 0.70 m below the T/C boundary, is marked by the *Didymotis* II Event. This event is characterized by a flood occurrence of strongly ornamented *Didymotis* cf. *costatus* (FRIC) and a nearly monospecific inoceramid assemblage dominated by *C. waltersdorfensis waltersdorfensis*. The latter were previously (WOOD & *al*. 1984) erroneously attributed to small forms of *C. waltersdorfensis hannovrensis* (HEINZ), and the event was accordingly also known as the *Didymotis* II/*waltersdorfensis hannovrensis* Event. The single specimen of *C.* cf. *rotundatus* (*sensu* TRÖGER *non* FIEGE), recorded by WOOD & *al*. (1984), is now believed by us to fall into the range of variation of *C. waltersdorfensis waltersdorfensis*. Contrary to earlier statements (*e.g.* WOOD & *al*. 1984, KAUFFMAN & *al*. 1996), this event does not fall in the limestone MK 45b; this latter bed appears to contain few fossils apart from limonitized sponges, and may mark a reduction in the sedimentation rate, or even a short-term stillstand. The recognition of the true position of the event result from the much better exposure condition in the dip section, illustrated here (Text-fig. 3), compared with the now extremely degraded and overgrown strike section in the western part of the quarry, where this event was first identified.

The overlying marl, MK 46, is marked by a flood occurrence of small *C. waltersdorfensis waltersdorfensis*, constituting the *waltersdorfensis* II (previously *waltersdorfensis waltersdorfensis* I) Event. The inoceramids are very well preserved, albeit somewhat distorted due to compaction, commonly retaining large parts of the shell and the hinge plate.

The FAD of *C. deformis erectus* [previously attributed to *C. rotundatus* (TRÖGER *non* FIEGE)], marking the base of the Coniacian stage, falls at the base of the limestone bed MK 47a. The FAD and simultaneous flood occurrence of this taxon constitutes the *erectus* I (formerly *rotundatus*) Event. The index taxon, *C. deformis erectus*, occurs in abundance, exhibiting a wide range of variation, and associated with subordinate numbers of the ancestral form, *C. waltersdorfensis waltersdorfensis*, and rare *Didymotis*.

The next horizon with a flood occurrence of *C. deformis erectus*, designated herein the *erectus* II Event, occurs in bed mK 49a. It is the horizon corresponding to the *brongniarti* Event as originally recognized in the Słupia Nadbrzeżna section (WALASZCZYK 1992). Thus the supposed hiatus at this stratigraphical level, as suggested in KAUFFMAN & *al*. (1996), does not actually exist.

Above the interval with regular occurrence of *C. deformis erectus* (MEEK), in bed MK 52d, there occurs an ecoevent with flood occurrence of *Cremnoceramus waltersdorfensis hannovrensis* (HEINZ), referred to the *hannovrensis* Event (= *waltersdorfensis hannovrensis* Event of WOOD & *al*. 1984). The marly character of the rock in bed MK 52d results in rather poor preservation of the inoceramid fauna which, as indicated by the material from the Słupia Nadbrzeżna section, is very variable at this level. Starting with the *hannovrensis* Event, the inoceramid record in the Salzgitter-Salder section starts to diversify albeit still always dominated by *C. waltersdorfensis hannovrensis*.

In the overlying limestone bed MK 53a very common *C. waltersdorfensis hannovrensis* (HEINZ) are accompanied by larger forms of the *deformis* lineage, and numerous and variable representatives of the genus *Tethyoceramus* SORNAY (*non* HEINZ). This is designated herein the *erectus* III Event (*erectus* Event of WOOD & *al*. 1984).

Distinctly higher, in bed MK 75, there is a flood occurrence of *Micraster* (*Isomicraster*) sp. associated with inoceramids, represented mostly by *C. waltersdorfensis hannovrensis*, *C. crassus inconstans* and forms transitional between *C. waltersdorfensis hannovrensis* and *C. crassus* *inconstans*. It is the level regarded as the origin level of the *C. crassus* lineage and the base of the *inconstans* Zone. WOODS' species *C. crassus inconstans* dominates in bed 85a, where it occurs in flood abundance. This horizon was designated by WOOD & *al*. (1984) the *inconstans* Event.

Słupia Nadbrzeżna section, Central Poland

Location: Natural exposure in the high, west bank of the river Vistula, in the village of Słupia Nadbrzeżna, about 160 km south of Warsaw (*see* Text-fig. 1).

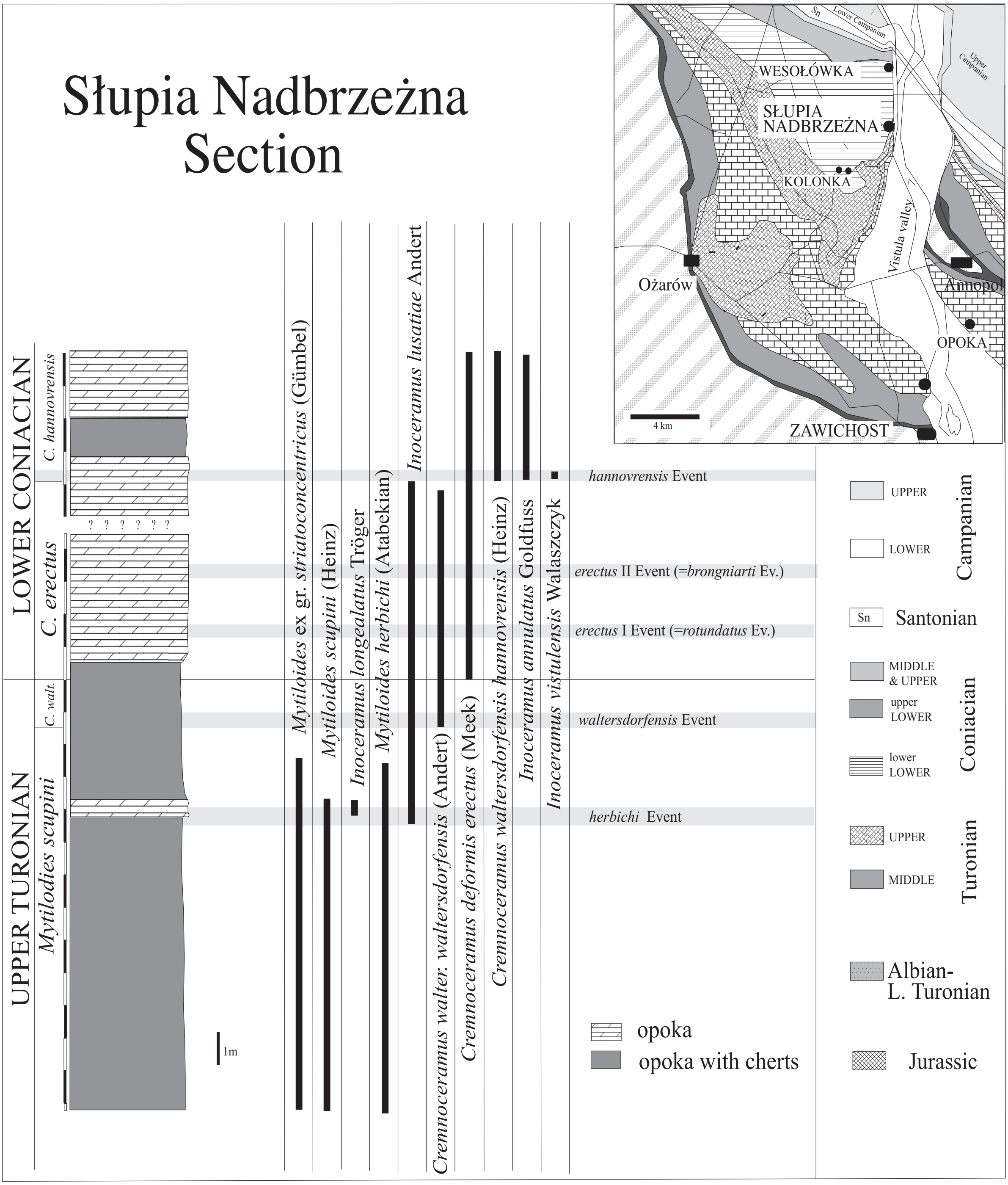


Fig. 4. Geological column, bio- and event stratigraphy, and inoceramid distribution in the Słupia Nadbrzeżna section

The exposure falls within the regularly dipping Albian – Upper Cretaceous succession of the Middle Vistula. This is situated on the southern flank of the Border Synclinorium, the large geotectonic unit that extends from NW to SE throughout the entire territory of Poland (Text-fig. 1). The Upper Cretaceous strata dip gently (2-3^0) to the NE, so that progressively younger deposits crop out in this direction (*see* Text-fig. 4). The succession is best exposed along the middle Vistula River valley. Starting in the Middle Turonian, almost the entire Upper Cretaceous succession is monotonously developed in opoka (=siliceous marls) facies. To the east, this facies passes gradually into chalky facies, while to the SW, the opoka facies passes into marls.

The Turonian/Coniacian boundary succession is best exposed in the village of Słupia Nadbrzeżna, in the steep western bank of the Vistula, north of the entrance to the main valley in which the village is situated (*see* Text-fig. 4). The exposure starts with topmost Turonian strata (top of the *Mytiloides scupini* Zone) and extends to a high level in the Lower Coniacian (Text-fig. 4). The section continues northward, albeit indifferently exposed, to the next village, Wesołówka, where exposures of opokas with black flints are found that already belong to the upper Lower Coniacian, *Cremnoceramus crassus/deformis* Zone.

The succession exposed in Słupia Nadbrzeżna is developed in opoka facies, comprising rhythmically bedded alternations of more and less silicified units. The part of the section investigated starts in the upper part of the *Mytiloides scupini* Zone, in the *Mytiloides herbichi* Event, an extremely fossiliferous bed just below the *waltersdorfensis* Event.

Turonian – Coniacian boundary interval

In the lower part of the exposure occur beds of chertified opoka with a sparse fauna, representing the topmost part of the monotonous, ca.

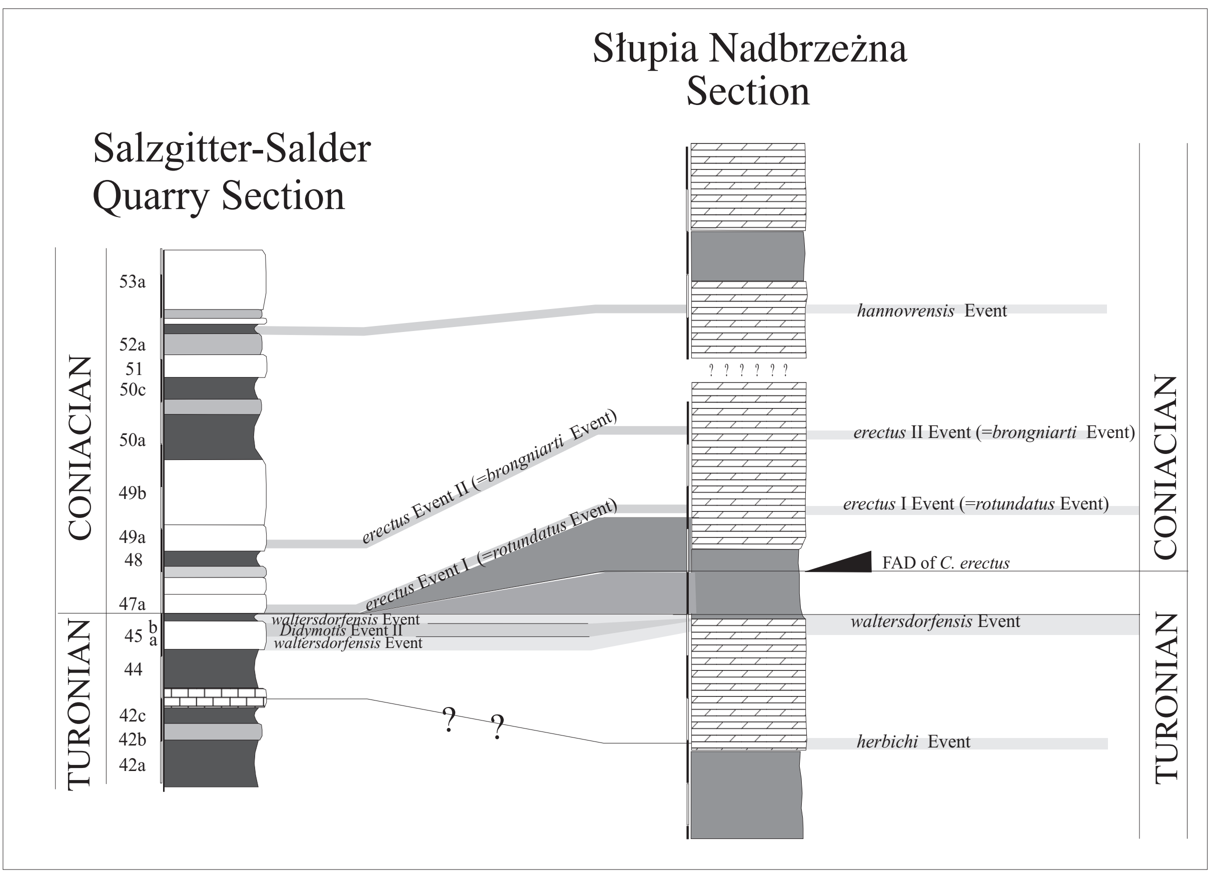


Fig. 5. Bio- and event stratigraphical correlation between Salzgitter-Salder and Słupia Nadbrzeżna sections; *see* Text-figs 2 and 4 for details

50 m thick Upper Turonian succession. These beds are mostly exposed in the steep bank south of the entrance to the main valley, in the village of Słupia Nadbrzeżna (*see* Text-fig. 4). The fauna first appears in strength in the *Mytiloides herbichi* Event, a bed 0.2 m thick, ca. 3.2 m below the T/C boundary. This event-bed contains common Late Turonian mytiloids, referred mostly to *Mytiloides herbichi* (ATABEKIAN), associated with subordinate *M. scupini* (HEINZ) and *Inoceramus lusatiae* ANDERT. Also occurring at this horizon are representatives of the bivalve genus *Didymotis*. The associated groups, which are distinctly rarer in occurrence, comprise ammonites, oysters and pectinacean bivalves, brachiopods (small terebratulids) and echinoids. This level is probably the time-equivalent of bed 41 in the Salzgitter-Salder succession.

Above the *herbichi* Event follows a 2.5 m thick unit of cherty opoka, extending up to the *C. waltersdorfensis waltersdorfensis* Event, and containing rare fossils (*see* Text-fig. 4). This interval is characterized by the same inoceramids as in the *herbichi* Event.

The succeeding *waltersdorfensis* Event, is here regarded as equivalent to the *Didymotis* II and *waltersdorfensis* I and II events of the Salzgitter-Salder section. However, it is impossible here to separate the two events. As in the German section, the *waltersdorfensis* Event is characterized by a mass occurrence of the nominate subspecies of ANDERT's *C. waltersdorfensis*. *Didymotis* is also relatively common

In the succeeding interval, between the *waltersdorfensis* Event and the *erectus* (=*rotundatus*) Event, inoceramids are distinctly rarer. The basal part of this interval is characterized exclusively by *C. waltersdorfensis waltersdorfensis* (ANDERT). The first *C. deformis erectus* (MEEK)[= *C. rotundatus* (*sensu* TRÖGER *non* FIEGE)] was found about 0.7 m above the *waltersdorfensis* Event. However, the level of its mass-occurrence, i.e. the *erectus* Event, is situated about 1.6 m higher. This interval is markedly expanded in comparison with its development in the Salzgitter-Salder section, where the *waltersdorfensis* II Event in bed 46 [*waltersdorfensis waltersdorfensis* Event of WOOD & *al*. 1984] is directly followed by the *erectus* Event. The situation in Salzgitter-Salder may be the result of condensation and/or actual hiatus (see also discussion of this problem by WIESE 1998).

The *erectus* Event is a 0.1-0.15 m thick interval with much more common representatives of the marker species. The inoceramids constitute an almost monospecific assemblage of *C. deformis erectus* with rare *C. waltersdorfensis waltersdorfensis* (ANDERT). The same assemblage extends up to the next inoceramid event, the *erectus* II Event (Text-fig. 4). At this horizon *Didymotis* of an exceptionally large size occur compared to material from lower parts of the succession.

The succeeding part of the succession up to the *hannovrensis* event, some distance above the *erectus* II event (Text-fig. 4), is badly exposed and has therefore not been investigated in detail. The *hannovrensis* event corresponds to the event of the same name in the Salzgitter-Salder section (bed MK 52d). This event marks the first level of distinct increase in inoceramid diversity. It is also the level where *C. waltersdorfensis hannovrensis* first appears. In the sections studied, at least, this change may be readily used for biostratigraphical purposes. Besides the zonal index, the subspecies *hannovrensis*, which is the dominant form in the inoceramid assemblage, the event is characterized by, inter alia, *Inoceramus vistulensis* WALASZCZYK, *I. lusatiae* ANDERT, *Inoceramus annulatus* GOLDFUSS, and *C. deformis erectus* (MEEK). Some other morphotypes in the assemblage are of uncertain taxonomic position and require further study.

THE INOCERAMID RECORD ACROSS THE TURONIAN – CONIACIAN BOUNDARY

General remarks

In and above the *Didymotis* I Event, inoceramids are extremely common in the Turonian/Coniacian boundary interval. They occur within discrete event-accumulations, commonly comprising a monospecific mass-occurrence, but are also common in the intervals between the events. The lower part of the succession, comprising an interval extending up to (but excluding) the *waltersdorfensis* I and *Didymotis* II events, is characterized by the Late Turonian *Mytiloides – Inoceramus* assemblage, representing a single time-slice at a rather late stage in the development of the Upper Turonian inoceramids. Upper Turonian inoceramid faunas are insufficiently well understood to propose here a taxonomic system for them that would be based on their inferred phylogeny. Consequently our approach, and the description of those forms presented here, is wholly typological. Although some of them may represent members of a single phyletic lineage, all of the morphotypes discussed in this paper are referred here to separate species, in order to avoid any possible evolutionary inferences.

The situation in the upper part of the succession is completely different. This interval, starting at the *waltersdorfensis* I and *Didymotis* II events, is marked by the appearance of the first cremnoceramids (*C. waltersdorfensis waltersdorfensis*) and extends almost to the top of the Lower Coniacian, thus spanning almost the entire history of the group. The material at our disposal from this interval has provided us with a very precise record of the stratigraphical succession of inoceramid assemblages. Consequently, based on the inferred sequence of morphotypes, belonging to more than one lineage, it has proved possible to present a taxonomic scheme (Text-fig. 6) that, we believe, truly reflects evolutionary changes.

Phylogenetic patterns

In terms of inoceramid phylogeny, the main boundary in the interval studied is the level of appearance of the first *Cremnoceramus*, with the simultaneous virtual disappearance of representatives of the *Mytiloides* – *Inoceramus* assemblage that characterizes the Euramerican Upper Turonian. This level, which is situated close to the top of the Upper Turonian, is conspicuously marked by a mass-occurrence of the first, small-sized, representatives of the *Cremnoceramus waltersdorfensis* lineage, referred here to *Cremnoceramus waltersdorfensis waltersdorfensis* (ANDERT). The *waltersdorfensis* lineage is considered in this paper to be the basic, ancestral lineage to the complex of forms of inoceramids belonging to the genus *Cremnoceramus*, which we interpret as a clade, herein designated the *Cremnoceramus* clade. During the Early Coniacian, the ancestral lineage gave rise iteratively to two other lineages, namely the *deformis* lineage, at the Turonian/Coniacian boundary and, later in the Coniacian, to the *crassus* lineage (*see* Text-fig. 6). It is very probable that it also gave rise to the *Platyceramus mantelli* lineage at the Early/Middle Coniacian boundary (see also discussion in KAUFFMAN 1977a and NODA & TOSHIMITSU 1990). However, this last inferred phylogeny requires further investigation.

The *waltersdorfensis* lineage was relatively conservative and the phyletic change was mostly the result of allometric size increase. This increase in size, at least in the sections studied, occurred abruptly at the level of the *hannovrensis* Event. The abrupt nature of this change may reflect an acceleration in the rate of phyletic change within the lineage but, on the other hand, it may also be the result of an uneven or incomplete geological record, and have no evolutionary significance.

At a very early stage, the *deformis* lineage branched off from the ancestral *waltersdorfensis* lineage. This side branch comprises the sequence of *deformis erectus* – *deformis dobrogensis* – *deformis deformis* chronosubspecies (*see* Text-fig. 6), spanning almost the whole Lower Coniacian. The chronosubspecies *deformis erectus* comprises forms referred hitherto to *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE), as well as forms referred commonly to *Cremnoceramus inconstans lueckendorfensis* (TRÖGER). Contrary to our previous view (cf. Walaszczyk 1992) we are unclear whether or not *Inoceramus brongniarti* MANTELL, 1822 (Pl. 27, fig. 8; refigured WOODS 1912, Text-fig. 68; BMNH 4751) belongs to the deformis lineage. Clearly if this were the case, the earlier name *brongniarti* would have priority. Although it is highly probable that MANTELL's type comes from the Lower Coniacian, to judge from the type of flint in which it is preserved, it could equally well fall within the morphological plasticity of representatives of the genus *Tethyoceramus* SORNAY. We therefore consider it to be unsafe at present to use the name *brongniarti* for the *deformis* lineage.

There has always been a problem with the correct interpretation of MEEK's species, *Inoceramus erectus*, due to insufficient knowledge. Nevertheless, this taxon has been commonly interpreted both in North America and in Europe as the intermediate member in the *C. rotundatus* (*sensu* TRÖGER *non* FIEGE) – *C. erectus* – *C. deformis* (MEEK) lineage (*see* KAUFFMAN 1979, ERNST & *al.* 1983, WOOD & *al.* 1984). Restudy of the type material (*see* WALASZCZYK & COBBAN, *in press*) has shown, however, that *C. erectus* corresponds to the form that, at least in Europe, was subsequently taken as the basal Coniacian boundary marker, i.e. *C. rotundatus* (*sensu* TRÖGER *non*

FIEGE). The forms corresponding to type *C. erectus* occur already in the basal "*rotundatus*" Event in Salzgitter-Salder, and even forms referred by KAUFFMAN (1977b, also KAUFFMAN & *al.* 1978) to *C. erectus*, late form, occur regularly in bed 49, but may be found as low as the basal "*rotundatus*" Event of that quarry (see discussion in the systematic part of this paper, and also the discussion and description of *C. erectus in* WALASZCZYK & COBBAN, *in press*).

Still higher originates the *crassus* lineage, comprising the chronosubspecies *crassus inconstans* (WOODS) and *crassus crassus* (*see* Text-fig. 6). This branching takes place in the *Isomicraster* Event, Salzgitter-Salder bed MK 75. Because of poor exposure it was not possible to study this level in the Vistula section. The lineage starts with small-sized *Cremnoceramus crassus inconstans* (WOODS), which pass gradually upwards into the subspecies *crassus*. The tendency within *C. waltersdorfensis hannovrensis* towards increased obliquity and change in the surface ornament, with the appearance of regular, round-topped concentric

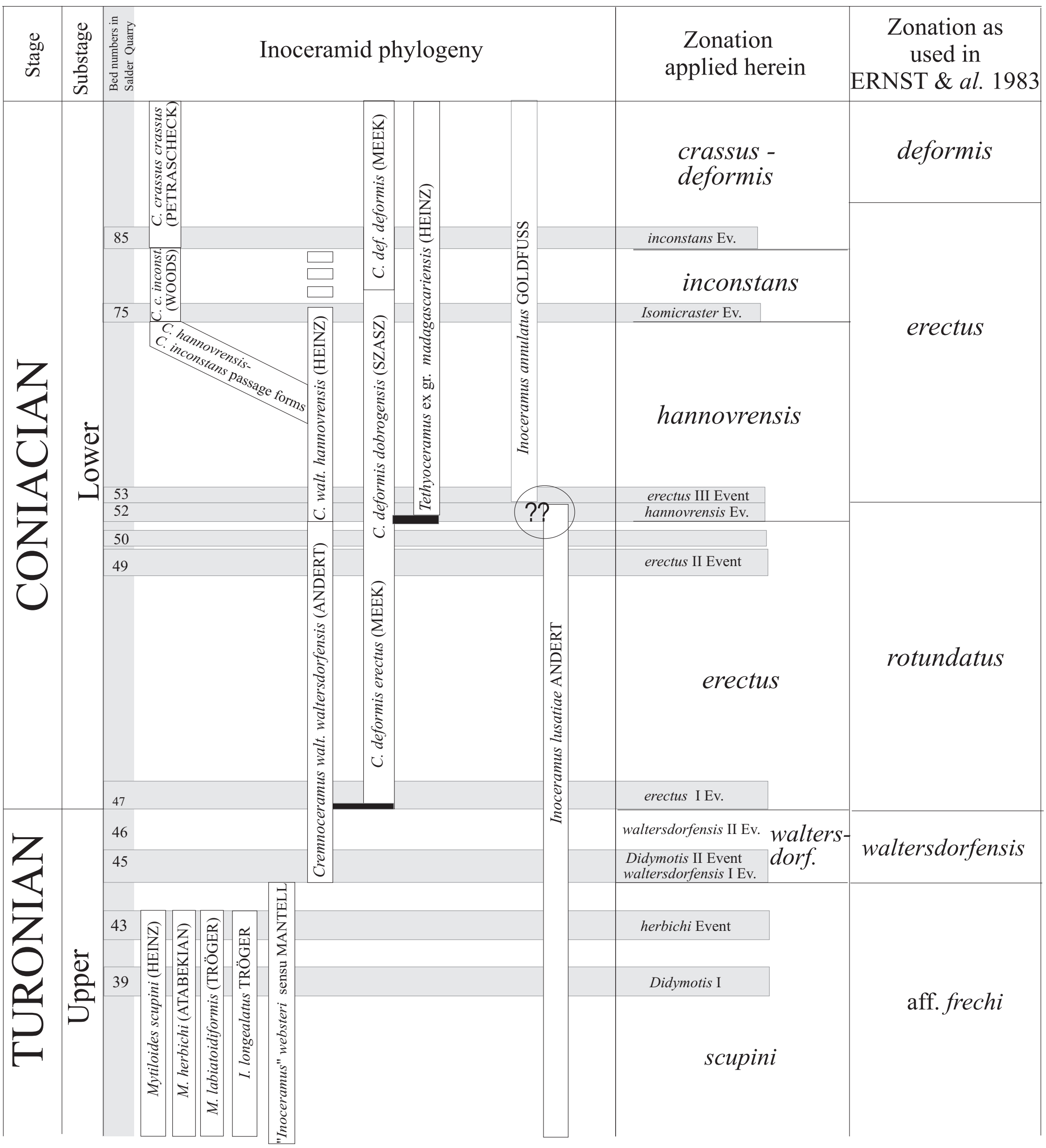


Fig. 6. Stratigraphical ranges, biozonation, and inferred phylogeny of inoceramids across the latest Turonian and early Coniacian

ribs, can actually be observed earlier in the history of the clade, namely in the *hannovrensis* Event, where morphotypes apparently transitional between *hannovrensis* and *inconstans* have been observed within the population (*see* WALASZCZYK 1992, Pl. 19, Figs 1-3). However, these never led to the development of the true *inconstans* morphotype.

Starting in Salder bed 52/53 (the former *waltersdorfensis hannovrensis* Event of WOOD & *al*. 1984), appears a morphologically variable group of large-sized, *lamarcki*-like forms with an ornament-type that is characteristic of advanced cremnoceramids (widely spaced, sharply-edged concentric ribs, with flat-floored interspaces, and with growth marks). These forms were often referred hitherto to the *lamarcki* group. Based on the ornament-type, stratigraphical range, and the fact that the group is accompanied by typical representatives of the *lamarcki* group (*Inoceramus annulatus* GOLDFUSS), we regard it as a separate phylogenetic unit evolving from cremnoceramids at some point in the middle Early Coniacian. The resemblance in outline to representatives of the *lamarcki* group represents only a homeomorphic similarity (convergence) and does not indicate a phylogenetic connection between the two groups. We follow here the interpretation of SORNAY (1980) and refer this distinctive group to the separate genus *Tethyoceramus* SORNAY (*non* HEINZ, 1932). Although SORNAY's concept corresponds to the original concept of HEINZ (1932b), HEINZ's name is formally a *nomen nudum*.

The sudden appearance in numbers of the tethyoceramids with a remarkable degree of specific variability in the sections studied, suggests that they immigrated into the northern European area, rather than evolving rapidly in place. It is worthy of note, in this context, that HEINZ (1932b) strongly emphasized the "southern character" of the *Tethyoceramus* fauna.

STRATIGRAPHY

Evaluation of biostratigraphical potential of particular inoceramid groups from the Turonian/Coniacian boundary

All of the forms occurring commonly in the Turonian/Coniacian interval may be divided into three groups:

(i) "Background group", composed of the cremnoceramids, which occurred in abundance, commonly in mass-accumulations, evolved quickly and apparently in place.

(ii) "Conservative group", comprising the long-ranging forms, already well established in the Upper Turonian and ranging through the whole Lower Coniacian. These comprise *Inoceramus lusatiae* ANDERT, and some rather rarely occurring representatives of the *lamarcki* group (*I. annulatus*? GOLDFUSS, *I. hercules* HEINZ).

(iii) "?Immigrants", probably represented by the tethyoceramids.

Of the three group mentioned above, the zonation should be based on the "background' cremnoceramid inoceramids, in which all transitions are believed to be evolutionary in nature. The cremnoceramids, consequently, constitute the most suitable group for stratigraphical purposes in the area studied. This group provides a complete or virtually complete record in the studied stratigraphical interval. Moreover, zonal boundaries related to evolutionary events should theoretically be isochronous throughout the whole geographical area investigated. We place these boundaries at the three key branching points, i.e. at the cladogenetic origination of particular lineages. In ascending order, these are (*see* Text-fig. 6):

1. The base of the *waltersdorfensis* Zone;
2. The origination point of the *deformis* lineage, *i.e.* the FAD of *Cremnoceramus deformis erectus* (MEEK); and
3. The appearance level of the *crassus* lineage, *i.e.* at the FAD of *Cremnoceramus crassus inconstans* (WOODS).

Further zonal (subzonal) subdivision may be based on members of particular lineages, but the boundaries, being based on subjective taxonomic concepts, will of necessity be drawn at different levels and give the appearance that they are diachronous, rather than more or less isochronous. Since no other group of fossils permits the level of stratigraphical precision in the Turonian/Coniacian boundary interval that is provided by inoceramids, it is extremely difficult to test the isochroneity of a zonation based on the subdivision of phyletic lineages. Basing the boundaries on a single lineage, as in the traditional Lower Coniacian scheme, requires, moreover, that the characteristics of the whole population be taken into account, and not merely that of a single or a small number of specimens, as is often the case. The traditional zonation, based on the *deformis* lineage, i.e. *rotundatus – erectus – deformis*, was particularly imprecise, providing only an approximate position within the Lower Coniacian. The other problem with this zonation was the rather poor taxonomic and morphological definition of almost all members of the lineage. Consequently this traditional Lower Coniacian zonation should not be used as a primary zonal scheme and should be regarded at best as merely a secondary subdivision of the Lower Coniacian zonal scheme.

The base of the Coniacian stage

The base of the Coniacian Stages, as proposed during the Second Cretaceous Stage Boundaries Symposium, Brussels 1995 is defined by the FAD of *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE), which according to the recent revision by WALASZCZYK & COBBAN (*in press*) falls into the synonymy of *Cremnoceramus deformis erectus* (MEEK). In phylogenetic terms, this FAD is the branching point of the *deformis* lineage (*see* Text-fig. 6). The nature of this event thus implies its isochroneity throughout the area of its regular occurrence.

In the area studied, the main turnover point of the inoceramid fauna around the T/C boundary marks the appearance datum of the *Cremnoceramus* clade below the boundary. The dating of this level, and the nature of cremnoceramid appearance is, however, still unclear. In most of the well studied Central European sections, the origin point of cremnoceramids is recorded at or just below the level of the *Didymotis* II Event, where they occur in flood abundance. In the United States Western Interior cremnoceramids appear in a similar manner, also in flood abundance (WALASZCZYK & COBBAN 1999, and *in press*). This sudden appearance of new taxon, with no apparent precursors, is distinctive feature of the Turonian/Coniacian transition in both areas. It could represent either an evolutionary or an immigration event. However, in our view (contrary to published statements by other workers – *see e.g.* KÜCHLER 1998, WIESE 1998), there are so far no unequivocal records of *Cremnoceramus waltersdorfensis* below this level.

Inoceramid zonation of the Turonian/Coniacian boundary interval and of the Lower Coniacian

Following the arguments summarized above, the inoceramid zonal scheme proposed here is constructed using the *Cremnoceramus* clade, and is based primarily on the branching points within this clade, *i.e.* the levels of the cladogenetic appearance of particular cremnoceramid lineages (*see* Text-fig. 6). The proposed zonal scheme thus comprises, in ascending order: the *Mytiloides scupini* Zone and the *Cremnoceramus waltersdorfensis* Zone in the terminal Upper Turonian; and the *C. deformis erectus* Zone, *C. waltersdorfensis hannovrensis* Zone, *C. crassus inconstans* Zone and *C. crassus – deformis* Zone in the Lower Coniacian (*see* Text-fig. 6).

As is well shown by the material from the Staffhorst shaft section, Germany, cremnoceramids actually disappear almost completely before the end of the Early Coniacian (defining the base of the Middle Coniacian by the FAD of *Volviceramus koeneni*). Instead, the inoceramid fauna of the highest Lower Coniacian is dominated by sulcate, *lamarcki*-like forms with only sporadic large *Cremnoceramus*. These forms are provisionally referred to *Inoceramus gibbosus* SCHLÜTER and they form a distinct biozone, referred to the *I. gibbosus* Zone, in the topmost Lower Coniacian (WALASZCZYK & WOOD *in* NIEBUHR & *al.*, *in press*).

Mytiloides scupini Zone

This zone is not discussed here at length, but some qualifying remarks are necessary. The *scupini* Zone (= *Inoceramus* aff. *frechi* Zone of WOOD & *al.* 1984) is defined as a partial range zone, with its base marked by the first appearance of the index taxon, *M. scupini* (HEINZ). Its upper boundary is defined by the appearance of the first representatives of the *C. waltersdorfensis* lineage. The zonal index is relatively uncommon and tends to characterize the lower part of the zone; the higher part of the zone is marked by a relative abundance of the associated species *M. herbichi*. The zone is well represented in the United States Western Interior (*see* WALASZCZYK & COBBAN 1999, and *in press*).

Cremnoceramus waltersdorfensis Zone

The base of the Zone is placed at the FAD of the index taxon, *C. waltersdorfensis waltersdorfensis* (ANDERT). The upper boundary marks the cladogenetic appearance of the *deformis* lineage, with the FAD of its oldest member, *C. deformis erectus* [= *C. rotundatus* (*sensu* TRÖGER *non* FIEGE)]. It is, thus, the terminal zone of the Turonian.

The base of the zone is marked by the main turnover point in inoceramid evolution in the Turonian/Coniacian boundary interval, namely the appearance of the *Cremnoceramus* clade, which will thereafter dominate the inoceramid fauna throughout the Early Coniacian. The zone is characterized by an almost monospecific assemblage composed of small *C. waltersdorfensis waltersdorfensis*, of which those occurring in the basal part of the zone at Salder (*i.e.* in the *Didymotis* II Event) were earlier incorrectly attributed by WOOD & *al.* (1984) to small forms of *C. waltersdorfensis hannovrensis* (cf. KAUFFMAN & *al.* 1996). Some of the morphotypes in this zone from the Vistula section are comparable with *Cremnoceramus websteri* (MANTELL) or with *C. globosus* (SIMIONESCU) (*see* WALASZCZYK & SZASZ 1997), but the phylogenetic and taxonomical status of these two taxa is unclear (see also discussion in the systematic part of this paper). Besides cremnoceramids, the zone yields rare *Inoceramus lusatiae*. The thin-shelled bivalve *Didymotis* cf. *costatus* (FRIC) [=*D.* cf. *uermosensis* (SIMIONESCU) *in* WOOD & *al.* (1984)] is also a characteristic element of the zonal assemblage, with a mass-occurrence in the *Didymotis* II Event.

In the Salzgitter-Salder section, the zone comprises bed 45 (including the *waltersdorfensis* I and *Didymotis* II events) and bed 46 (*waltersdorfensis* II Event). It is distinctly more expanded in the Vistula section.

Cremnoceramus deformis erectus Zone

The base of the zone is defined by the appearance of *Cremnoceramus deformis erectus* [=*Cremnoceramus rotundatus* (TRÖGER *non* FIEGE)], the oldest member of the *deformis* lineage. In evolutionary terms, it is a branching point, and marks the cladogenetic appearance of a new lineage. The root, *waltersdorfensis* lineage, is interpreted, however, as surviving and remaining unchanged in its ancestral form. At and above the branching point, it thus co-occurs in the basal Lower Coniacian with its daughter species (*see* Text-fig. 6). The base of the zone is the base of the Coniacian Stage. The upper boundary of the zone is marked by the anagenetic appearance of *C. waltersdorfensis hannovrensis*. The *deformis erectus* Zone, as here defined, corresponds to the *rotundatus* Zone as recognized in the Salzgitter-Salder quarry by WOOD & *al.* (1984) and to the *Cremnoceramus brongniarti* Zone in the Vistula section as postulated by WALASZCZYK (1992). In general, the zone approximates to the *rotundatus* Zone as traditionally recognized in the Euramerican palaeobiogeographical region.

Cremnoceramus waltersdorfensis hannovrensis Zone

The zone starts at the *hannovrensis* Event and extends to the first appearance of *Cremnoceramus crassus inconstans*. Its base is thus defined on anagenetic transformation within the *waltersdorfensis* lineage, namely by the appearance of *C. waltersdorfensis hannovrensis*. This level almost coincides with the appearance of representatives of the distinctive and separate genus *Tethyoceramus* SORNAY (*non* HEINZ). At least within the geographical extent of the localities studied, the tethyoceramids may well be taken as a complementary taxon characterizing the *hannovrensis* Zone. Starting with the *hannovrensis* Zone, there is a marked increase in the taxonomic diversity of the inoceramid assemblages. Together with the tethyoceramids, there are the first regular occurrences of large-sized representatives of the genus *Inoceramus*, referred here mostly to *Inoceramus annulatus*. In the Vistula section, this is also the level of occurrence of *Inoceramus vistulensis* WALASZCZYK, which bears some similarity to the Japanese Lower Coniacian species *Inoceramus uwajimensis* NAGAO & MATSUMOTO and may possibly be related to, or even conspecific with, *Inoceramus websteri* sensu MANTELL. Rare specimens compared to *I. vistulensis* are known from Bed 50c/51a and Bed 52 at Salder, *i.e.* at more or less the same stratigraphical level. It is, in fact, interesting to speculate that these stratigraphically restricted occurrences may possibly represent an immigration event, approximately coincident with the overall increase in taxonomic diversity (see section on taxonomic diversity).

Cremnoceramus crassus inconstans Zone

The base of the zone is marked by the FAD of *Cremnoceramus crassus inconstans*, the earliest representative of the *crassus* lineage (Text-fig. 6). The upper boundary is placed in the appearance level of either *C. deformis deformis* or *C. crassus crassus*.

Cremnoceramus crassus crassus/C. deformis deformis Zone

The base of the zone is marked by the appearance of *C. crassus crassus* (PETRASCHECK), and the coincident, but usually less regular occurrence, of *C. deformis deformis* (MEEK) Both index forms of the zone are members of phyletic lineages, and the lower boundary of the zone may consequently be relatively difficult to define, due the imprecise delimitation of both subspecies from their respective phyletic ancestors, i.e. *C. deformis erectus* and *C. crassus inconstans* (Text-fig. 6). The cremnoceramids are accompanied by large representatives of *Inoceramus* ex gr. *lamarcki*, referred here to *Inoceramus annulatus* GOLDFUSS, but their taxonomy needs further investigation. In addition, the zone is still characterized by tethyoceramids, but these are poorly known.

"Inoceramus gibbosus" Zone

The highest Lower Coniacian zone is the *Inoceramus gibbosus* Zone, recognized recently in the material from the Staffhorst mine-shaft, Germany (*see* WALASZCZYK & WOOD *in* NIEBUHR & *al.*, *in press*). The zone is characterized by an almost complete lack of cremnoceramids and the occurrence of sulcate representatives of the *lamarcki* group. These forms are provisionally referred to SCHLÜTER's *I. gibbosus*, although there are three other species that are related to, or even conspecific with SCHLÜTER's *gibbosus*, *I. russiensis* NIKITIN, *I. lezennensis* DECOCQ, and *I. percostatus* MÜLLER (see also discussion *in* WALASZCZYK & WOOD *in* NIEBUHR & *al.*, *in press*).

Correlation

Text-fig. 7 presents the correlation of the zonation proposed herein with the published

<table>
<tr><th rowspan="2">Stage</th><th rowspan="2">Substage</th><th colspan="7">INOCERAMID ZONATIONS</th></tr>
<tr><th>This paper</th><th>KAUFFMAN & al. 1978</th><th>TRÖGER 1989</th><th>WOOD & al. 1984</th><th colspan="3">WALASZCZYK 1992</th></tr>
<tr><td rowspan="4">CONIACIAN</td><td rowspan="4">LOWER</td><td>crassus/ deformis</td><td></td><td rowspan="3">21
? ? ? ?</td><td>C. deformis</td><td rowspan="5">CONIACIAN</td><td rowspan="3">MIDDLE</td><td>C. crassus</td></tr>
<tr><td>inconstans</td><td>37. I. deformis + I. inconstans</td><td rowspan="2">C. erectus</td><td rowspan="2">C. deformis</td></tr>
<tr><td>hannovrensis</td><td>36. I. deformis deformis</td></tr>
<tr><td>erectus</td><td>35. I. erectus n. ssp.
34. I. erectus erectus
33. I. rotundatus</td><td>20</td><td rowspan="2">C.? rotundatus</td><td rowspan="2">LOWER</td><td>C. brongniarti</td></tr>
<tr><td rowspan="2">TURONIAN</td><td rowspan="2">UPPER</td><td>waltersdorfensis</td><td rowspan="2">32. Mytilodies lusatiae</td><td rowspan="2">19</td><td>C. waltersdorfensis</td></tr>
<tr><td>scupini</td><td>I. aff. frechi</td><td>TURON.</td><td>UPPER</td><td>M. incertus</td></tr>
</table>

Fig. 7. Correlation of the zonation proposed here with the published schemes of KAUFFMAN (*in* KAUFFMAN & *al.* 1978a), TRÖGER (1981, 1989), WOOD & *al.* (1984), and WALASZCZYK (1992)

schemes of KAUFFMAN (*in* KAUFFMAN & *al.* 1978a), TRÖGER (1981, 1989), WOOD & *al.* (1984), and WALASZCZYK (1992). In case of KAUFFMAN's and TRÖGER's schemes, which are based on assemblage zones, we took for correlation the taxa that we use in our own zonal scheme, although differences in the taxonomic concepts concerned make the correlation rather approximate. Some of these "assemblages", according to our data, comprise faunas from very wide stratigraphical intervals.

Event stratigraphy

ERNST & *al.* (1983) and WOOD & *al.* (1984) recognized a set of events around the Turonian/Coniacian boundary in Northern Germany, thereby markedly increasing the stratigraphical resolution of that interval (*see* Text-figs 2, 4-5). Subsequently it was found that most of these events could be recognized in many sections throughout Europe (CECH 1989; KÜCHLER & ERNST 1989; WALASZCZYK 1988, 1992; WIESE 1997; KÜCHLER 1998), extending even as far as the western limits of central Asia (MARCINOWSKI & *al.* 1996), allowing very refined correlation of the Turonian-Coniacian boundary beds throughout the continent. Some of these events were recently recognized in the Western Interior of the United States (WALASZCZYK & COBBAN, *this volume*) The events in question are named after the dominant faunal element(s) (these are usually inoceramids). However, the taxonomic revision of many of the index inoceramids presented here has also necessitated changing the nomenclature of the corresponding events, in spite of the fact that some of them *e.g.* the *rotundatus* Event) have already become widely used stratigraphical terms. Below, in ascending order, the original individual events are discussed, starting with the new name, followed by the old name in square brackets, and a short characteristic of the event. The stratigraphical position of all events is shown in Text-figs 2, 4-5.

Didymotis I Event. This event is characterized by common occurrence of poorly ornamented *Didymotis*, associated with *M. herbichi*, *M. scupini*, and *Inoceramus lusatiae*.

herbichi Event. This event in Salder bed 43 was not previously recognized and is characterized by a flood occurrence of *M. herbichi*.

waltersdorfensis I Event. This event has not been previously recognized. It is characterized by the FAD and simultaneous flood occurrence of *C. waltersdorfensis waltersdorfensis*, in the lower part of bed 45a, immediately beneath the *Didymotis* II Event.

Didymotis II Event [old name: *Didymotis* II Event]. The event is characterized by a flood occurrence of the bivalve *Didymotis* cf. *costatus*, associated with common *C. waltersdorfensis waltersdorfensis*.

waltersdorfensis II Event [old name: *waltersdorfensis waltersdorfensis* Event]. The event is characterized by small-sized representatives of *C. waltersdorfensis waltersdorfensis*.

erectus I Event [old name: *rotundatus* Event; the original name referred to the species *C. rotundatus* (*sensu* TRÖGER *non* FIEGE). This species was shown recently (*see* WALASZCZYK & COBBAN, *in press*), and also the systematic part of this paper) to be a junior synonym of *C. deformis erectus* (MEEK)]. As in the case of the *erectus* Event II, this event is characterized by common occurrence of the index taxon and small representatives of *C. waltersdorfensis waltersdorfensis*

erectus II Event [old name: *brongniarti* Event; this event was recognized originally by WALASZCZYK (1992) in the Słupia Nadbrzeżna section, and was later found in the Salzgitter-Salder section]. This event is characterized by flood occurrence of the index taxon and small representatives of *C. waltersdorfensis waltersdorfensis*

hannovrensis Event [old name: *hannovrensis* Event]. This event is characterized by a flood occurrence of the index taxon, with rare occurrences of *C. deformis erectus*, *Inoceramus vistulensis* WALASZCZYK and, only in the Słupia Nadbrzeżna section, *Inoceramus lusatiae* ANDERT.

erectus III Event [old name: *erectus* Event – the name *erectus* is retained, with the addition of the Roman numeral III to indicate the occurrence of two other *erectus* events lower in the succession]. This event is characterized by commonly occurring *Cremnoceramus waltersdorfensis hannovrensis* but its most conspicuous elements are relatively common large-sized representatives of the genus *Tethyoceramus*. *C. deformis erectus* also occurs, but is rare.

CONCLUDING REMARKS

Cremnoceramus deformis erectus (MEEK), according to the recent revision of the type material by WALASZCZYK & COBBAN (*in press*), exactly matches the characters of forms referred hitherto to *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE). Consequently it is the appropriate name for the inoceramid marker of the base of the Coniacian stage. Based on the North American record of the *deformis* lineage it can be demonstrated that the main phyletic change within it took place at the level approximately corresponding to the level of the *hannovrensis* and *erectus* III events of the European record. All forms of the lineage below this level down to its evolutionary appearance form a relatively homogenous assemblage and are referred to *C. deformis erectus*. All members of the lineage occurring above this level are actually closer in its characters to the nominate subspecies. Two subspecies, *dobrogensis* (SZASZ), and the nominative subspecies *deformis* (MEEK), distinguished mainly through their ribbing pattern may, however, be further distinguished in that part of the lineage (*see* WALASZCZYK & COBBAN, *in press*) (*see* Text-fig. 6).

The comparison with the Słupia Nadbrzeżna section has shown that the Turonian/Coniacian boundary succession of Salzgitter-Salder, at the boundary itself, is most probably condensed or else is interrupted by a small gap. The *waltersdorfensis* II and *erectus* I events, which are situated here in direct superposition, are separated by a 2.3 m-thick succession in the Słupia Nadbrzeżna section (Text-fig. 5, *see also* discussion by WIESE, *in press*). This latter interval contains the record of the evolutionary appearance of the boundary marker, *Cremnoceramus deformis erectus* (MEEK), the FAD of which in the Słupia Nadbrzeżna section falls markedly below (Text-figs 4-5), and not (as at Salzgitter-Salder) in the *erectus* I Event.

SYSTEMATIC PALAEONTOLOGY

Taxonomic concepts

The state of preservation of the material studied here, which is mostly internal moulds, does not allow use of the complex set of characters often called for by inoceramid taxonomists. In fact, we use only the morphology (general shape and ornament), as that is all that we can observe in this material. In this context, two very important points must be made concerning not only the material studied for this paper, but most of the available inoceramid material in general. Firstly, in spite of the repeated requirement to use internal characters such as musculature in taxonomy, these characters, in practice, in all of the material available hitherto from all over the world, are known only in single, exceptionally preserved specimens. Even where apparent muscle insertions have been observed by some workers, those workers' conclusions have been doubted or, at least, questioned by others. Secondly, the more conspicuous internal or structural characters, such as details of the ligament, display, as in the case of the external shell morphology, a marked variability within populations (*see* CRAMPTON 1996, WALASZCZYK 1997). Determination of the variability of the ligament requires the study of numerous specimens, exceptionally preserving the shell and ideally collected from a single horizon, a situation that rarely obtains. Until such data become available, the inferences regarding inoceramid phylogeny and their taxonomy, must be based on thorough studies of the sections with the best inoceramid record.

The taxonomy of the inoceramid bivalves presented here reflects an inferred phylogenetic interpretation, with a clear distinction being made between cladogenesis and phyletic transformation within lineages. The separate morphotypes within a lineage are referred to as subspecies, this term being used here in the sense of a chronosubspecies and not as a biological (i.e. geographical) subspecies. The evolutionary, cladogenetic point may represent either a doubling of species or a branching pattern, with the surviving, ancestral species co-occurring with the newly evolved one. The interpretation of selected lineages presented here is based on a very detailed biostratigraphical analysis of two geographically widely separated (1000 km), but readily correlated successions, in different facies

(Salzgitter-Salder and Słupia Nadbrzeżna); (*see* Text-fig. 1). The high resolution biostratigraphical documentation has also allowed a more realistic genus-level taxonomy of the topmost Turonian and Lower Coniacian inoceramid faunas than hitherto.

The measurements, made mainly on the material from Słupia Nadbrzeżna section, were published recently (WALASZCZYK 1992) and are omitted here.

Morphologic features of inoceramid shells

All of the basic morphological terminology and morphometric parameters used here are taken from HARRIES & *al*. (1996) and illustrated in Text-fig. 8. In case of the surface ornament, we use, when needed, the term concentric ribs for concentric elements that are subordinate to rugae.

Location of the specimens

This is indicated by the following abbreviations: FU – Institut der Paläontologie der Freie Universität, Berlin; UW – Museum of the Geological Department of Warsaw University, Warsaw; BMNH – The Natural History Museum, London; BGS – Museum of the British Geological Survey, Keyworth; FGI – Geologisches Institut Bergakademie Freiberg; MU – Museum of Moscow University, Moscow; NHMP – Natural History Museum, Paris; MMG – State Museum of Mineralogy and Geology, Dresden; USNM – National Museum of Natural History,

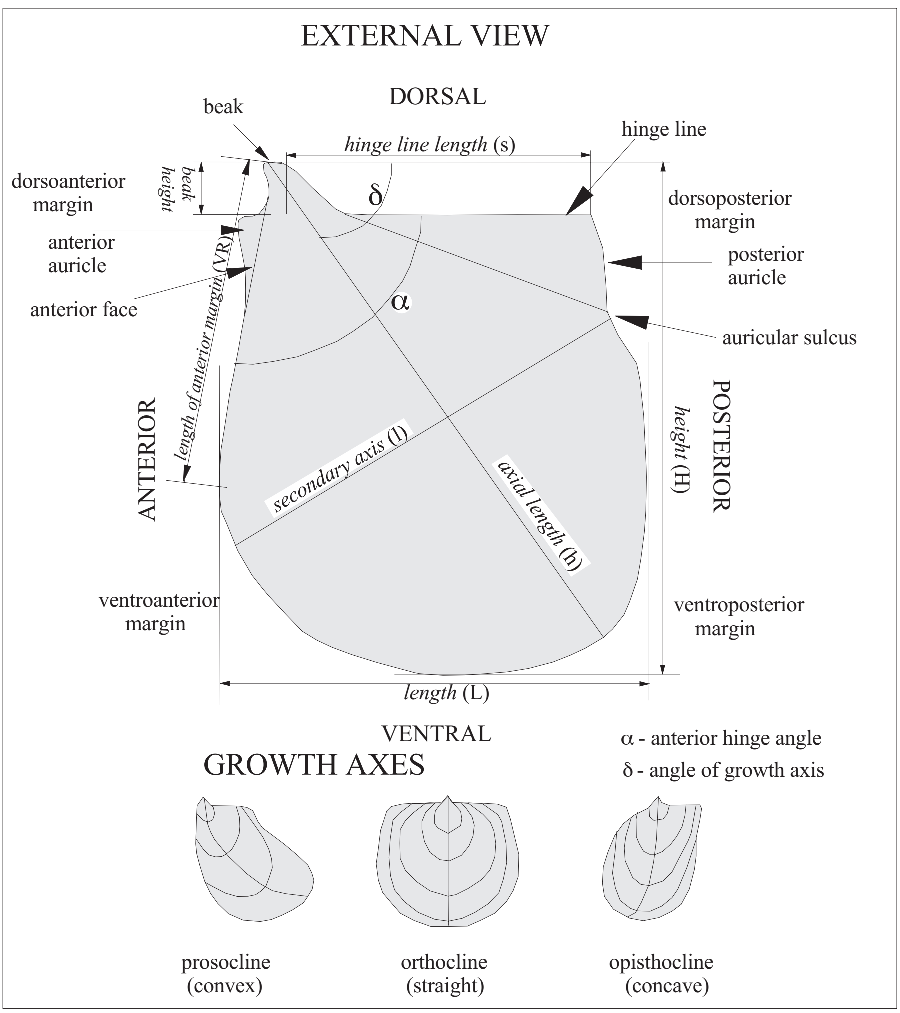


Fig. 8. Key external morphological features of the inoceramid shell as used in the present paper (modified *after* HARRIES & *al*. 1996)

Washington; GS – Museum of the Polish Geological Survey.

Systematic account

Genus: *Cremnoceramus* COX, 1969 [non *Cremnoceramus* HEINZ, 1932 (*nomen nudum*)]

TYPE SPECIES: By original designation the type species is *Inoceramus inconstans* WOODS, 1912, from the Upper Chalk of Lewes, southern England.

REMARKS: The genus was characterized by KAUFFMAN (*in* HERM & *al*. 1979), WALASZCZYK (1992) and recently discussed at length by CRAMPTON (1996). Therefore only brief comment is necessary here.

It is not easy to diagnose the genus *Cremnoceramus*, and to list a set of unique characters common to all its members. When comparing the three European lineages of the genus, i.e. *C. waltersdorfensis*, *C. deformis*, and *C. crassus*, they differ in the general outline and pattern of surface ornament, as well as in the characteristics of the ligament plate. On the other hand, all members of the genus, can be placed in a common evolutionary framework (Text-fig. 6). What is common to all cremnoceramids is the geniculation (although this character is variably developed) with an associated change in the surface ornament. Although the geniculation may occur sporadically in almost all inoceramid groups (*see* SEITZ 1967, TRÖGER 1981), in the genus *Cremnoceramus* it occurs regularly, and is most probably genetically controlled (WALASZCZYK 1992, CRAMPTON 1996).

OCCURRENCE: Topmost Turonian and Lower Coniacian, world-wide.

Cremnoceramus waltersdorfensis (ANDERT, 1911) lineage

The species appears, most probably, at the level of the *waltersdorfensis* I Event (Bed 45a in the Salzgitter-Salder section) and the *waltersdorfensis* Event in the Vistula section, and apparently ranges through the whole Lower Coniacian.

Within the species, two remarkably different, stratigraphically successive morphotypes can be distinguished, interpreted here as two chronosubspecies, and referred to *C. waltersdorfensis waltersdorfensis* (ANDERT) and *C. waltersdorfensis hannovrensis* (HEINZ)(*see* Text-fig. 6).

The nominate subspecies is characterized by small size, subquadrate shape of the juvenile part and usually well developed adult part. Juvenile ornamentation is composed of closely spaced, rounded or angular growth lines and narrow, slightly irregular rugae. The adult parts are smooth or with irregular rugae. Most specimens are geniculated, with the adult part usually making a relatively high angle with the juvenile part. This morphotype agrees with the original characteristics of the species *C. waltersdorfensis* as given by ANDERT (1911) (*see also* WALASZCZYK 1996 for recent re-description and illustration), and is referred here to the nominate subspecies *C. waltersdorfensis waltersdorfensis* (ANDERT).

The younger morphotype is characterized by larger size, generally less closely spaced juvenile ornamentation with much better developed rugae, and a more projected umbonal part. This morphotype agrees with the characteristics of HEINZ' (1932a) species *Inoceramus hannovrensis* as interpreted and described by TRÖGER (1967), and is referred to here as *C. waltersdorfensis hannovrensis* (HEINZ).

In the sections studied both subspecies are relatively clearly separated stratigraphically. *C. w. hannovrensis* has its FAD in the *hannovrensis* Event (= *waltersdorfensis hannovrensis* Event of WOOD & *al*. 1984). In Salzgitter-Salder it is bed 52.

At this point it must be clearly stated that the concepts of the subspecies *waltersdorfensis* and *hannovrensis* as understood here assumes both of them to represent two chronosubspecies, and differs from the hitherto applied concepts, in which both taxa were treated strictly typologically (TRÖGER 1967, KAUFFMAN 1978a, KELLER 1982).

PHYLOGENETIC REMARKS: The *C. waltersdorfensis* lineage is the ancestral group for all Early Coniacian cremnoceramids (*see also* KAUFFMAN *in* HERM & *al*. 1979), with the successive evolutionary appearance of the *Cremnoceramus deformis* lineage (*erectus – dobrogensis – deformis*) at the Turonian/Coniacian boundary, and of the *Cremnoceramus crassus* lineage (*inconstans – crassus*) in the mid-Early Coniacian. It is possible that at the Lower/Middle Coniacian boundary the lineage gave rise to the *Platyceramus mantelli* lineage, the characteristic group of the Middle Coniacian.

The phylogenetic precursor of *C. waltersdorfensis* (ANDERT) is unknown. KAUFFMAN (*pers. comm.*) regards *Inoceramus dimidius*, the small, commonly geniculated forms from the Upper Turonian, as a possible ancestor. However, *I. dimidius* as traditionally interpreted appears to represent juvenile ontogenetic stages only, the species actually being a medium to large sized form (WALASZCZYK & COBBAN, *in press*), markedly distinct from the morphotype of *C. waltersdorfensis* (ANDERT).

OCCURRENCE: *C. waltersdorfensis* (ANDERT) first appears in the topmost Turonian, most probably at the level of the *waltersdorfensis* I Event, and ranges through the whole Lower Coniacian.

Cremnoceramus waltersdorfensis waltersdorfensis (ANDERT, 1911)
(Pl. 5, Figs 1, 3-7, 9-13, 15-18; Pl. 15, Figs 1-3; Pl. 17, Fig. 3)

1899. *Inoceramus transilvanicus*, J. SIMIONESCU, p. 2 (pars).
1911. *Inoceramus waltersdorfensis* n.sp.; H. ANDERT, p. 53, Pl. 5, Figs 2 and 5.
1911. *Inoceramus sturmi* n.sp.; H. ANDERT, p. 58, Pl. 2, Fig. 5.
1911. *Inoceramus protractus* SCUPIN; H. ANDERT, p. 61, Pl. 3, Fig. 2.
1967. *Inoceramus waltersdorfensis waltersdorfensis* ANDERT; K.-A. TRÖGER, pp. 114-117, Pl. 12, Figs 1-2; Pl. 13, Figs 1-5.
1967. *Inoceramus inconstans inconstans* WOODS; K.-A. TRÖGER, pp. 101-102, Pl. 13, Fig. 19.
1978a. *Inoceramus waltersdorfensis waltersdorfensis* ANDERT; E.G. KAUFFMAN, Pl. 5, Figs 6-7.
1992. *Cremnoceramus waltersdorfensis* (ANDERT); I. WALASZCZYK, pp. 41-46, Pls 16-17, Pl. 18, Figs 1-3.
1996. *Cremnoceramus waltersdorfensis* (ANDERT); I. WALASZCZYK, pp. 374-376, Fig. 3C-F; 4F-G.
1997. *Cremnoceramus waltersdorfensis* (ANDERT); I. WALASZCZYK & L. SZASZ, p. 783, Fig. 3b-d.

TYPES: The lectotype is an unregistered MMG specimen, the original of ANDERT (1911, Pl. 5, Fig. 5 and reillustrated subsequently by WALASZCZYK 1996, Fig. 3E-F) by subsequent designation of WALASZCZYK (1992). The paralectotype is the second specimen of ANDERT (1911, Pl. 5, Fig. 2; reillustrated by WALASZCZYK 1996, Fig. 3C-D), also housed in MMG.

MATERIAL: There are large uncatalogued collections from both the Salzgitter-Salder and Słupia Nadbrzeżna sections housed in the Institute of Palaeontology of the Free University of Berlin and in the Institute of Geology of the Warsaw University. Additional specimens from Polish Geological Survey and Natural History Museum London.

DESCRIPTION: Equivalve or subequivalve, inequilateral, of small size for the genus. Juvenile part subquadrate to ovate in outline. Anterior margin straight or slightly convex, passing into broadly convex ventral margin. Posterior auricle large; either clearly distinct from disc, with well developed auricular sulcus (Pl. 5, Figs 11, 17-18), or joining disc without any visible boundary (Pl. 5, Figs 13, 15-16). Umbonal part variably developed; ranging from flat, indistinct (e.g. Pl. 5, Fig. 16) to markedly inflated, pointed (Pl. 5, Figs 11-12, 17-18), projecting only rarely above hinge line. Adult part usually much lower than juvenile, but specimens with extraordinary high adults are noted (*see* WALASZCZYK 1992, Pl. 17, Fig. 4). Associated slope change varies from very indistinct and gradual to right angle.

Juvenile part ornamented with raised, asymmetrical growth lines and variably developed concentric rugae. They range from flat, widely spaced, regular (Pl. 5, Figs 15-16) to irregularly spaced and strong (Pl. 5, Fig. 17). Adult part smooth or with irregular, low rugae.

REMARKS: *Cremnoceramus waltersdorfensis waltersdorfensis* (ANDERT) represents the stratigraphically oldest member of the *waltersdorfensis* lineage and, at the same time, the oldest representative of Euramerican cremnoceramids (KAUFFMAN *in* HERM & *al.* 1979). In the present state of knowledge of Upper Turonian inoceramids it is impossible to indicate, or even to suggest an ancestral group. The form appears suddenly and in almost monospecific assemblages, at least within the limits of the Euramerican Palaeobiogeographical Region.

From its phyletic successor, *C. waltersdorfensis hannovrensis* (HEINZ), *C. walt. waltersdorfensis* differs in its smaller size and in the development of the umbonal part. In Heinz's form the pointed umbonal part projects markedly above the hinge line. The outline of the valve is markedly height-elongated, with a long and steep anterior face.

Conspecific with *C. waltersdorfensis waltersdorfensis* (ANDERT) are many of the forms from the English Chalk, housed in the Natural History Museum, London, and referred to MANTELL's *Inoceramus striatus* (*see* Pl. 15, Figs 1-3, Pl. 17, fig. 3), including the specimen referred to *I. striatus* and illustrated by WOODS (1912, Pl. 52, Fig. 1). This does not apply, however, to the type of the species (MANTELL 1822, Pl. 51, Fig. 5), the characters of which are more equivocal. MANTELL's specimen (BMNH 4768) is a highly and evenly inflated, small-sized shell, which, although very similar to the more uniformly ornamented specimens of *C. waltersdorfensis waltersdorfensis*, does not show the change in the ornament associated with change in the growth direction. Even forms without well developed geniculation, similar in outline to the type of *I. striatus* possess clearly separated juvenile and adult ornament types (*e.g.* the specimen illustrated here from the English Chalk – see Pl. 17, Fig. 3). Moreover, there is also a problem regarding the horizon of this specimen. Taking into account the small difference and the uncertainty regarding the horizon of the type of *I. striatus*, these two species are not synonymised (in which case MANTELL's species would have priority), despite the fact that the other forms referred to *I. striatus* (at least those illustrated by WOODS 1912) clearly represent forms that are conspecific with ANDERT's *C. waltersdorfensis waltersdorfensis*.

OCCURRENCE: *C. waltersdorfensis waltersdorfensis* appears in the topmost Turonian, at the level of *waltersdorfensis* I Event, and ranges up to (but excluding) the *hannovrensis* Event of the Lower Coniacian; known from Europe, western Asia and North America.

Cremnoceramus waltersdorfensis hannovrensis (HEINZ, 1932)
(Pl. 5, Figs 2, 8; Pl. 9, Fig. 2; Pl. 11, Figs 2; Pl. 12, Figs 1-4; Pl. 13, Figs 2-7)

1932a. *Inoceramus hannovrensis* n.sp.; R. HEINZ, p. 29.
1959. *Inoceramus striato-concentricus* GÜMBEL; S.A. DOBROV & M.M. PAVLOVA, p. 135, Pl. 2, Fig. 2.
1967. *Inoceramus waltersdorfensis hannovrensis* HEINZ; K.-A. TRÖGER, pp. 117-120, Pl. 12, Figs 3-4; Pl. 13, Figs 6-9.
1989. *Inoceramus* (?*Cr.*) *waltersdorfensis hannovrensis* HEINZ; T. KÜCHLER & G. ERNST, Pl. 4, Figs 2-4.
1992. *Cremnoceramus waltersdorfensis* (ANDERT); I. WALASZCZYK, pp. 41-46 (pars), Pl. 18, Figs 4-7, Pl. 19, Pl. 30, Fig. 1).

TYPE SPECIMEN: The lectotype is the specimen No. 914, illustrated and designated subsequently by TRÖGER (1967, Pl. 12, Fig. 3). The specimen is housed in the Museum of the Niedersächsiches Landesamt für Bodenforschung, in Hannover. It should be noted that, although TRÖGER (1967) gave the locality as Lüneburg-Zeltberg, the specimen actually came from the St. Petersberg section, east of Goslar.

This taxon was introduced as a species by HEINZ (1932a, p. 29) with only a short description, and without illustration or designation of a type. TRÖGER (1967) assigned the taxon to subspecific status, giving a full description and selecting as lectotype a specimen labelled by HEINZ as *Inoceramus hannovrensis*.

MATERIAL: Numerous specimens from Salzgitter-Salder and Słupia Nadbrzeżna housed in the Institute of Palaeontology of the Free University of Berlin and in the Institute of Geology of the Warsaw University.

DESCRIPTION: Small to moderate in size, inequilateral, equivalved. Umbonal part usually well developed with beak projecting markedly above hinge line. Anterior margin straight, long, or slightly convex. Ventral margin rounded. Hinge line long and straight. Adult part most often only poorly separated from juvenile part.

Shell ornamented with closely spaced, raised growth lines, covering whole juvenile part, and with superimposed, more or less regular, rugae. In adults growth lines are no longer distinct or surface of rugae is completely smooth.

REMARKS: *C. waltersdorfensis hannovrensis* (HEINZ) represents the stratigraphically younger member of the *waltersdorfensis* lineage. From the nominate subspecies it differs in the characters of the umbonal region, which possesses a well differentiated beak, projecting markedly above the hinge line, and more or less distinctly curved inward. Moreover, on average, it possesses less closely spaced concentric rings, and, in adults, distinctly developed, concentric rugae. It is also of larger size.

Starting in the *erectus* Zone, parallel to the typical morphotype of *C. waltersdorfensis*, appear forms with very regular ornament, composed mainly of lamellate growth lines, and usually without superimposed rugae (*see* Pl. 11, Fig. 4; Pl. 15, Figs 4-5; Pl. 17, Fig. 5). Such forms, referred by WALASZCZYK (1992) to *Cremnoceramus denselamellatus* (KOTSYUBINSKY, 1965), are particularly common in the *hannovrensis* Event, and are known from all over Europe. They were also reported from Afghanistan by SORNAY (1974) and referred by him to the new subspecies *Inoceramus waltersdorfensis afghanicus*, which is conspecific with KOTSYUBINSKY's *C. denselamellatus*. This form is very close to *C. waltersdorfensis*, and it may represent only an extreme morphological variant within ANDERT's species.

OCCURRENCE: *C. waltersdorfensis hannovrensis* (HEINZ), as interpreted here, appears in the *hannovrensis* Event and ranges probably through the rest of the Lower Coniacian. Within and above the *hannovrensis* Event (*hannovrensis* Zone) it dominates inoceramid assemblages, at least in Central Europe. Known from Europe and North America.

Cremnoceramus deformis (MEEK, 1871) lineage

REMARKS: *Cremnoceramus deformis* is interpreted here as an evolutionary unit starting with the appearance of *C. deformis erectus* (MEEK) and ranging to the extinction of *C. deformis deformis* (MEEK) (*see* Text-fig. 6). It comprises orthocline, geniculated forms, covered, in the juvenile part, with more or less regularly spaced concentric rugae, with increasing interspaces in phyletically younger members. The adult part is smooth or with irregular rugae.

The adult part may occasionally attain extraordinary large size (including the next geniculation). Such forms were often referred to a separate species, *Cremnoceramus browni* CRAGIN (*see e.g.* KAUFFMAN 1977b, and KAUFFMAN & *al.* 1978), but extremely large adult size may be found in almost every *Cremnoceramus* species and it has rather no taxonomic value (discussion *in* WALASZCZYK & COBBAN, *in press*; and also CRAMPTON, *this volume*).

OCCURRENCE: Lower Coniacian, possibly extending into the basal Middle Coniacian.

Cremnoceramus deformis erectus (MEEK, 1877)
(Pl. 5, Fig. 14; Pl. 6, figs 1-6, 8; Pls 7-8; Pl. 9, Figs 1, 3-6; Pl. 10, Figs 1-4, 6; Pl. 11, Figs 1, 3, 5-7; Pl. 13, Fig. 1; Pl. 15, Fig. 6)

1877. *Inoceramus erectus* MEEK; F.B. MEEK, p. 145, Pl. 13, Fig. 1; Pl. 14, Fig. 3.
1893. *Inoceramus deformis* MEEK; T.W. STANTON, p. 85 (*pars*), Pl. 15, Fig. 1 [non Fig. 2].
1912. *Inoceramus inconstans* sp.n.; H. WOODS, pp. 285-291 (*pars*), Text-fig. 44 [only].
1911. *Inoceramus Cuvieri* var. *planus* MÜNSTER (ELBERT); H. ANDERT, p. 45, Pl. 1, Fig. 2; Pl. 7, Fig. 8.
1911. *Inoceramus subquadratus* SCHLÜTER; H. ANDERT, pp. 60, Pl. 5, Fig. 7.
1930. *Inoceramus inconstans rotundatus* em.; K. FIEGE, pp. 43-44 (*pars*), Pl. 8, Fig. 31.
1934. *Inoceramus inconstans* WOODS em. ANDERT; H. ANDERT, pp. 102-106 (*pars*), Text-fig. 7C.
1955. *Inoceramus sowerbyi* sp.n.; M.M. PAVLOVA, p. 169, Pl. 4, Fig. 3.
1958. *Inoceramus labiatus* var. *latus* SOWERBY; S.P. KOTSYUBINSKY, p. 10 (*pars*), Pl. 1, Fig. 8.
1959. *Inoceramus inconstans* WOODS; S.A. DOBROV & M.M. PAVLOVA, pp. 137-138, Pl. 5, Fig. 1.
?1959. *Inoceramus weisei* ANDERT; S.A. DOBROV & M.M. PAVLOVA, p. 138, Pl. 7, Fig. 3.
1959. *Inoceramus schloenbachi* BÖHM; S.A. DOBROV & M.M. PAVLOVA, p. 152, Pl. 8, Figs 1, ?2.
1962. *Inoceramus rotundatus* FIEGE; Z. RADWAŃSKA, pp. 147-149, Pl. 1-2, Figs 4-?5.
1967. *Inoceramus rotundatus* FIEGE; K.-A. TRÖGER, pp. 110-113, Pl. 12, Figs 5-6; Pl. 13, Figs 10-13.
1967. *Inoceramus inconstans lueckendorfensis* n.ssp.; K.-A. TRÖGER, pp. 102-105, Pl. 11, Figs 1-2.
1968. *Inoceramus brongniarti* MANTELL; S.P. KOTSYUBINSKY, pp. 124-125, Pl. 18, Figs 6-8.
1978a. *Inoceramus waltersdorfensis* ANDERT n. subsp. transitional to *I. rotundatus* FIEGE; E.G. KAUFFMAN, Pl. 5, Fig. 16.
1978. *Inoceramus erectus erectus* MEEK; E.G. KAUFFMAN & *al.*, Pl. 15, Figs 3-4.
1978. *Inoceramus erectus* MEEK n.subsp. (late form); E.G. KAUFFMAN & *al.*, Pl. 15, Fig. 6.

1979. *Cremnoceramus*? sp. aff. *C.? rotundatus* (FIEGE); E.G. KAUFFMAN *in* HERM & *al*., Pl. 9, Fig. A.
1979. *Inoceramus* sp. aff. *I. ernsti* HEINZ; E.G. KAUFFMAN *in* HERM & *al*., Pl. 9, Fig. B.
1979. *Cremnoceramus*? *rotundatus* (FIEGE); E.G. KAUFFMAN *in* HERM & *al*., pp. 68-71, Pl. 9, Fig. C.
1982. *Inoceramus rotundatus* FIEGE; S. KELLER, pp. 114-116, Pl. 8, Fig. 2.
1985. *Inoceramus rotundatus* FIEGE; L. SZASZ, p. 167, Pl. 10, Fig. 4.
1986. *Inoceramus erectus* MEEK; W.A. COBBAN, Fig. 6B.
1988. *Cremnoceramus rotundatus* (FIEGE); I. WALASZCZYK, Pl. 7, Figs 1-6.
1992. *Cremnoceramus brongniarti* (MANTELL); I. WALASZCZYK, pp. 48-52 (*pars*), Pl. 22, Figs 1-2; Pl. 23, Figs 1-5; Pl. 24, Figs 1-5; Pl. 25, Figs 1-5; Pl. 30, Fig. 2 (non Pl. 22, Fig. 3).
1996. *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE); I. WALASZCZYK, p. 377, Figs 3G-J.

TYPE: The lectotype, designated by WALASZCZYK & COBBAN (*in press*) is the double valved specimen from Chalk Creek, near Upton, Utah (USNM 7850), illustrated by MEEK (1877, Pl. 13, Fig. 1 and Pl. 14, Fig. 3). The second specimen (USNM 7850) of MEEK (1877, Pl. 13, Fig. 1a), from the same locality, is the paralectotype. Both specimens are illustrated and described in detail by WALASZCZYK & COBBAN (*in press*).

MATERIAL: Numerous specimens from the Salzgitter-Salder and Słupia Nadbrzeżna sections housed in the Institute of Palaeontology of the Free University of Berlin and in the Institute of Geology of the Warsaw University. Some additional material from Słupia Nadbrzeżna comes from POŻARYSKI's collection housed in the Museum of the Polish Geological Survey.

DESCRIPTION: Moderate size for genus, inequilateral, equivalve. Juvenile stage subquadrate to subrounded. Its anterior margin straight or slightly convex, passing into widely rounded ventral margin. Hinge line long, straight. Umbonal part usually wide, rather poorly separated from rest of shell. In larger specimens beak projects markedly above hinge line. Posterior auricle moderately large to large, mostly well separated from disc.

Ornament consists of regular concentric rugae, with gradually increasing inter-rugae spaces ventralward. In umbonal part and up to 20-30mm axial length the ornament is composed of both rugae and raised growth lines. The adult part is smooth or bears irregular rugae.

REMARKS: The species is described in detail and discussed by WALASZCZYK & COBBAN (*in press*).

Cremnoceramus erectus was commonly interpreted as the middle member of the *rotundatus – erectus – deformis* lineage (*see e.g.* KAUFFMAN *in* HERM & *al*. 1979), with the earliest member referred to *Cremnoceramus rotundatus* (*sensu* TRÖGER *non* FIEGE). Revision of the types of *C. erectus* showed, however, that MEEK's species is the form corresponding to TRÖGER's *C. rotundatus* and, consequently, that *C. erectus* is the correct name for the basal Coniacian boundary marker. In the phyletic history of the *deformis* lineage it is followed by successive subspecies *deformis dobrogensis* (SZASZ) and *deformis deformis* (MEEK) (WALASZCZYK & COBBAN, *in press*).

The species *Cremnoceramus rotundatus* (FIEGE) does not fall, however, into the synonymy of *C. deformis erectus* (MEEK). The type of FIEGE's species (reillustrated here in Pl. 6, Fig. 7) differs from MEEK's *C. erectus* in the type of ornament, which is already of the type found in stratigraphically much younger species, such as *C. crassus crassus* or *C. deformis deformis*. FIEGE's type actually comes from a much younger stratigraphical interval, where it was found to co-occur with *Inoceramus schloenbachi* (=*C. crassus crassus* as interpreted herein). Two specimens from the Vistula section, Central Poland (Pl. 12, Figs 5-6), from the *hannovrensis* (?*inconstans*) Zone are comparable with FIEGE's type.

Consequently, we interpret *C. deformis erectus* (MEEK) as comprising all forms of the *deformis* lineage with more or less closely spaced concentric rugae, with the inter-rugae spaces being on average smaller than or equal to the width of the rugae; and preceding the appearance of the subspecies *deformis dobrogensis* Szasz. TRÖGER's *Inoceramus inconstans lueckendorfensis*, as well as forms formerly referred to *C. brongniarti* (MANTELL) (*e.g.* KOTSYUBINSKY 1968, WALASZCZYK 1992) fall into the synonymy of *C. deformis erectus* (MEEK).

OCCURRENCE: Lower Lower Coniacian of Europe, N. America and Eastern Asia (Japan).

Cremnoceramus crassus (PETRASCHECK, 1903) lineage

REMARKS: The species *C. crassus* (PETRASCHECK), a senior synonym of *C. schloenbachi* (BÖHM) (*see* WALASZCZYK 1992) is interpreted here as forming a phyletic lineage comprising late Early Coniacian markedly oblique cremnoceramids. Their juvenile parts are ornamented with regularly spaced concentric rugae, with size and spacing increasing in phyletically younger forms. The adult part, even in small and/or the phyletically oldest forms is usually smooth, or with irregular rugae.

The stratigraphically oldest forms are small-sized, with the juvenile part covered with regular, round-topped concentric rugae: these are conspecific with WOODS' (1912) *I. inconstans*, and are referred here to *C. crassus inconstans* (WOODS). Their juvenile ornament closely resembles the ornament of *Mytiloides incertus* (JIMBO). In phyletically more advanced forms, wide, flat-floored concentric ribs with well developed growth marks (*Anwachsmarken* of HEINZ 1928c – the typical ornament element of cremnoceramids apart from the *C. waltersdorfensis* lineage) appear already in the juvenile stage. These forms are typical representatives of PETRASCHECK's (1903) *I. crassus*, and are referred here to *C. crassus crassus* (PETRASCHECK).

C. crassus evolved from *C. waltersdorfensis hannovrensis* (HEINZ), at the level of the *Isomicraster* Event (Bed 75 in Salzgitter-Salder). Such an evolutionary path was suggested earlier by WALASZCZYK (1992), although he placed this evolutionary divergence much earlier, on the basis of remarkably oblique morphotypes (intermediate between *C. waltersdorfensis* and *C. inconstans* – see WALASZCZYK 1992, Pl. 19, Figs 1-3) present already in the *hannovrensis* Event (Bed 52 in Salzgitter-Salder). However, as the material from the Salzgitter-Salder section demonstrates, the actual evolutionary appearance of *C. crassus* was clearly later. The morphotypes very close to the *hannovrensis – inconstans* intermediates were probably a constant form within the populations of *C. waltersdorfensis hannovrensis* (HEINZ), representing a subordinate, extreme morphotype. Their record from the *hannovrensis* Event results simply from the exceptionally rich sample from this level, which is characterized by a flood occurrence of HEINZ' subspecies, giving a statistically higher chance of finding rare morphotypes (the intermediate morphotype in question was represented by 3 specimens out of a sample of more than 100 specimens).

OCCURRENCE: The *C. crassus* lineage appeared at the *Isomicraster* Event (Bed 75 in Salzgitter-Salder) and ranges possibly into the basal Middle Coniacian (KÜCHLER 1998).

Cremnoceramus crassus crassus (PETRASCHECK, 1903) (Pl. 17, Fig. 2)

1843-40. *Inoceramus Cuvieri* SOWERBY; A. GOLDFUSS, p. 114, Pl. 111, Figs 1?a, b, c.

1903. *Inoceramus crassus* nov. spec.; W. PETRASCHECK, pp. 164-165, Pl. 8, Fig. 4.

1911. *Inoceramus crassus* PETRASCHECK; H. ANDERT, pp. 46-47, Pl. 3, Fig. 4; Pl. 6, Figs 1-2.

1911. *Inoceramus Weisei* n.sp.; H. ANDERT, p. 47, Pl. 4, Figs 2-3; Pl. 6, Fig. 3.

1912. *Inoceramus schloenbachi* BÖHM; J. BÖHM, p. 570.

1930. *Inoceramus inconstans Schloenbachi* em. BÖHM; K. FIEGE, pp. 40-42 (*pars*), Pl. 7, Figs 27, ?29; Pl. 8, Figs ?28, 30 [non Pl. 7, Fig. 26].

1930. *Inoceramus inconstans Woodsi* em. FIEGE; K. FIEGE (*pars*), Pl. 26, Fig. 4 [only].

1930. *Inoceramus schloenbachi* var. *rostrata* n.var.; R. HEINZ, p. 28.

1934. *Inoceramus schloenbachi* BÖHM; H. ANDERT, pp. 107-109, Text-fig. 8, Pl. 3, Fig. 2.

1934. *Inoceramus crassus* PETRASCHECK; H. ANDERT, pp. 109-111, Text-fig. 9, Pl. 3, Fig. 3.

1962. *Inoceramus schloenbachi* BÖHM; Z. RADWAŃSKA, pp. 142-145, Pl. 2, Figs 1, 4; Pl. 3, Fig. 1; Pl. 4, Fig. 2.

1967. *Inoceramus deformis* MEEK; K.-A. TRÖGER, pp. 130-132, Pl. 14, Fig. 7.

1969. *Inoceramus inconstans achuraensis* subsp. nov.; R.A. KHALAFOVA, pp. 166-167, Pl. 8, Fig. 7; Pl. 9, Fig. 1.

1969. *Inoceramus quasiinconstans* sp.nov.; R.A. KHALAFOVA, pp. 168-170, Pl. 9, Figs 2-3.

1974. *Inoceramus schloenbachi* BÖHM; K.-A. TRÖGER, pp. 114-118, Pls 1-3.

1974. *Inoceramus schloenbachi* BÖHM; A.A. ATABEKIAN, p. 213, Pl. 103, Fig. 2.

1974. *Inoceramus chosroviensis* ATABEKIAN sp.nov.; A.A. ATABEKIAN, p. 214, Pl. 106, Fig. 1; Pl. 107, Fig. 1.

1985. *Inoceramus schloenbachi* BÖHM; L. SZASZ, pp. 159-161 (*pars*), Pl. 3, Figs 1, ?2; Pl. 15, Fig. 2; Pl. 18, Fig. 3; Pl. 22, Fig. 3; ?Pl. 25, Fig. 3; ?Pl. 27, Fig. 2; ?Pl. 31, Fig. 2; Pl. 35, Fig. 1; ?Pl. 39, Fig. 2 [non Pl. 16, Fig. 2; Pl. 28, Fig. 1; Pl. 30, Fig. 1].

1985. *Inoceramus crassus anderti* n.ssp.; L. SZASZ, p. 158.

1991. *Inoceramus schloenbachi* BÖHM; R. TARKOWSKI, pp. 114-115 (*pars*), Pl. 16, Fig. 1 [non Pl. 14, Fig. 1]

1992. *Cremnoceramus crassus* (PETRASCHECK, 1903); I. WALASZCZYK, pp. 54-55, Text-fig. 17, Pl. 34, Figs 1-4; Pl. 35, Figs 1-2; Pl. 36, Figs 3, 5.

1992. *Cremnoceramus crassus* (ANDERT); S. CECH & L. SVABENICKA, Pl. 1, Fig. 12.

1992. *Cremnoceramus* cf. *schloenbachi*; S. CECH & L. SVABENICKA, Pl. 1, Fig. 13.

1992. *Cremnoceramus crassus* n. subsp.; S. CECH & L. SVABENICKA, Pl. 2, Fig. 7.

1994. *Cremnoceramus crassus* (PETRASCHECK); K.-A. TRÖGER & H. SUMMESBERGER, p. 168, Pl. 1, Figs 4-5.

1996. *Cremnoceramus crassus* (PETRASCHECK, 1903); I. WALASZCZYK, pp. 380-383, Figs 6C, 7A-B.

TYPE SPECIMEN: By monotypy the specimen figured by PETRASCHECK (1903, Pl. 8, Fig. 4), reillustrated by WALASZCZYK (1992, Pl. 34, Fig. 1) from the Lower Coniacian of the Dachsloch quarry near the village Leöne (German: Innozenzidorf), Bohemia, Czech Republic; the specimen is housed in the National Museum, Prague.

MATERIAL: We have not collected specimens from the studied intervals of the sections concerned. There are some specimens in the older collections of the FU Berlin from Salzgitter-Salder and numerous specimens are housed in UW collections from many localities from Poland.

DESCRIPTION: Shells distinctly oblique, medium to large-sized with moderately inflated or almost flat juvenile part. Juvenile part with short, straight or slightly convex anterior margin, passing into widely rounded ventroanterior and ventral margins. Ventroposterior margin narrowly rounded with well developed sulcus at contact of disc and posterior auricle. Hinge line long, straight.

Juvenile part ornamented with widely spaced, sharp-edged concentric rugae, covered in umbonal part with raised, slightly lamellate growth lines. Adult part usually smooth or with irregular concentric rugae.

REMARKS: This is one of the most common late Early Coniacian forms, albeit variously referred to a number of species and subspecies (see synonymy list). Its rather inadequate original illustration by PETRASCHECK (1903) resulted in it being subsequently only rarely recognized [mostly by ANDERT (1911, 1934), who worked on material from PETRASCHECK's original localities]. In Europe, representatives of *C. crassus crassus* were commonly referred to *I. schloenbachi* BÖHM, which was the new name for GOLDFUSS' (1834-40) *Inoceramus cuvieri* (BÖHM 1912). In Eastern Europe, as a result of inadequate knowledge of the type material, the form was referred to a number of new species and subspecies (*I. inconstans achuraensis* KHALAFOVA, *I. quasiinconstans* KHALAFOVA, *I. chosrovensis* ATABEKIAN, *I. crassus anderti* SZASZ), all exactly matching the characters of *C. crassus crassus* (PETRASCHECK). ANDERT's (1911) *Inoceramus weisei* represents deformed specimens of *C. crassus crassus* (see WALASZCZYK 1996).

OCCURRENCE: Late Early Coniacian of Europe, western Central Asia (Kazakhstan, Turkmenistan), and North America (US Western Interior).

Cremnoceramus crassus inconstans (WOODS, 1912) (Pl. 16, Figs 1-2, 5-6)

1822. *Inoceramus* sp.; G. MANTELL, p. 217, Pl. 27, Fig. 9.

1911. *Inoceramus glatziae* FLEGEL; H. ANDERT, p. 52 (*pars*), Pl. 1, Fig. 7; Pl. 7, Fig. 2 [only].

1911. *Inoceramus Cuvieri* var. *planus* (ELBERT); H. ANDERT, p. 45 (*pars*), Pl. 1, Fig. 5.

1912. *Inoceramus inconstans* sp. nov.; H. WOODS, pp. 285-291 (*pars*), Text-figs 42-43; Pl. 51, Fig. 2.

1913. *Inoceramus inconstans* WOODS; H. ANDERT, p. 294.

1912. *Inoceramus inconstans* WOODS; H. WOODS (*pars*), Text-figs 67-68, 71-73.

1930. *Inoceramus inconstans* WOODS em. FIEGE; K. FIEGE, pp. 39-40 (*pars*), Pl. 6, Figs 20-21, 23 [non Figs 22, 24].

1932a. *Inoceramus germanobohemicus* n. sp.; R. HEINZ, p. 43.

1990. *Cremnoceramus inconstans inconstans* (WOODS); L.F. KOPAEVICH & I. WALASZCZYK, Pl. 4, Figs 1-2.

1992. *Cremnoceramus inconstans* (WOODS); I. WALASZCZYK, pp. 53-54, Pl. 35. Fig. 3; Pl. 36, Fig. 1.

1996. *Cremnoceramus inconstans* (WOODS 1911); I. WALASZCZYK, pp. 378-379, Figs 5A-C, 6A-B.

TYPE SPECIMEN: The lectotype is the specimen (BMNH 4765) illustrated by WOODS (1911, Text-fig. 42), from the Upper Chalk of Lewes, southern England, by subsequent designation of TRÖGER (1967).

MATERIAL: Numerous specimens in the FU collections, Berlin, from the Salzgitter-Salder section (particularly from the *inconstans* Event (Bed 85), where this form dominates the assemblage).

DESCRIPTION: Small to medium-sized for the genus, inequilateral, equivalved. It possesses long, straight hinge line passing, with well developed sulcus, into rounded ventral margin, and anteriorwards into widely rounded anterior margin. Juvenile part weakly inflated or almost flat. In most specimens, angle between juvenile and adult parts is almost 90°. Umbonal part small, pointed, extending only slightly above hinge line.

Juveniles ornamented with round-topped, regularly spaced concentric rugae, covered with evenly spaced, sharp-edged growth lines.

REMARKS: The close resemblance in ornament between the subspecies *inconstans* and the species *Cremnoceramus waltersdorfensis*, and the presence of the intermediate forms between these two taxa, is interpreted here as the result of the evolutionary appearance of *C. crassus inconstans* from the *C. waltersdorfensis* lineage (*see* Text-fig. 6). It took place at or close to the *Isomicraster* Event (Bed 75 in the Salzgitter-Salder section). *C. crassus inconstans* is the ancestor of the nominate subspecies *crassus* in the *C. crassus* lineage.

Juveniles of *C. crassus inconstans* and *C. crassus crassus* may be difficult or impossible to distinguish. The latter usually show, even in these very early ontogenetic stages, more widely spaced and sharp-edged rugae.

Less oblique forms of the subspecies *inconstans* may closely resemble representatives of the late Late Turonian *Mytiloides incertus* (JIMBO) group. This could be the explanation for earlier reports of JIMBO's species from the Lower Coniacian.

OCCURRENCE: *Cremnoceramus crassus inconstans* is known from the middle and upper Lower Turonian of Europe and North America.

Genus *Tethyoceramus* SORNAY, 1980
(*non* HEINZ 1932)
(Pl. 14, Figs 3-7; Pl. 16, Figs 3-4; Pl. 17, Figs 1, 4; Pl. 18, Figs 1-2, 4; Pl. 19, Fig. 4)

TYPE SPECIES: *Inoceramus* (*Tethyoceramus*) *basseae* SORNAY (1980, Pl. 1, Figs 1, 4, 6; Pl. 2, Figs 1-3), by original designation.

REMARKS: HEINZ (1932b) established the invalid genus *Tethyoceramus* without formal description, selecting as type species *T. emigrans*, which is a *nomen nudum*. SORNAY (1980) validated HEINZ's concept, selecting as type one of two specimens from Madagascar identified by HEINZ as *T.* aff. *emigrans*, renaming the taxon *Inoceramus* (*Tethyoceramus*) *basseae*. We regard *Tethyoceramus* as unrelated to *Inoceramus* and treat it here as independent genus, of which the invalid subgenera *Climacoceramus*, *Proteoceramus* and *Idioceramus*, are synonyms.

EMENDED DIAGNOSIS: The genus is of moderately large size, equivalve to moderately inequivalve; valves moderately to very convex; umbo well developed, inclined inward and anteriorly; posterior auricle usually well developed, extending often distinctly outward; geniculation sometimes well developed; ornamentation consists of rugae and growth-marks, with superimposed growth lines (or crestae); in ontogeny the ornamentation is reduced to rugae; ligamental plate simple, slightly concave, with regularly spaced resilifers being wider than inter-resilifer spaces.

DISCUSSION: The genus embraces a series of forms, most of which are very poorly known, with only tenuous phylogenetic/phyletic links, characterized, in general, by a more or less *lamarcki*-type outline and *Cremnoceramus*-type ornament. The genus corresponds closely to HEINZ' (1932b) concept of the subfamily Tethyoceraminae, and represents one of the most interesting (albeit very poorly known) inoceramid groups of the Early Coniacian. The number of species distinguished is relatively high, in spite of the fact that the existing number of morphotypes seems to be rather limited. The following discussion is a provisional attempt to show the well resemblance of many of these 'species' and their possible synonymy.

In this context, it is noteworthy that, as already emphasized by HEINZ (1932b), the group seems to be out of place in the Central European area, implying its southern origin. It is a very interesting idea and one that, at first glance, actually appears to fit the palaeontological record. These forms constitute a subordinate group within the assemblages in both Salzgitter-Salder and the Vistula section, where they appear suddenly, and already split taxonomically. Moreover, most of the described forms come from more southerly parts of Europe. Consequently, it is very probable that they really were periodic immigrants into Central Europe and that the record here, *i.e.* in the sections studied, does not reflect the evolutionary history of the group.

The rich *Tethyoceramus* fauna from the more southerly areas in Europe (Romania, southern Ukraine, Crimea, Caucasus), at least in those localities that have been studied stratigraphically (Caucasus – WALASZCZYK 1992; Crimea – KOPAEVICH & WALASZCZYK 1990), appears at approximately the same stratigraphical level as in the sections studied here. Moreover, even in the southern areas, the tethyoceramids seem to dominate only in limestone facies, being a subordinate element in marly or clayey facies. Everywhere in Central Europe, in those rare localities where limestone facies is developed in this part of the Lower Coniacian (*e.g.* Polish Jura Chain), tethyoceramids are common (*see also* WALASZCZYK 1992). This suggests that tethyoceramid distribution may be to a large extent facies controlled.

In the Salzgitter-Salder and Vistula sections representatives of the group first appear in bed 53, at the level of the *erectus* III Event.

We are disinclined to give a rigorous taxonomic description of the *Tethyoceramus* fauna from the studied sections while our understanding of the group (it may easily be a polyphyletic taxon) is insufficient. Moreover, the number of forms, apparently representing *Tethyoceramus*, described recently (KHALAFOVA 1969, ROMANOVSKAYA, 1968, IVANNIKOV 1979, SORNAY 1980, SZASZ 1985) is very high and require thorough studies based on much more complete material than we have. Redescription is also needed in the case of classic species, such as *Climacoceramus alpinus* HEINZ, 1932b (by reference to AIRAGHI's 1904, Pl. 4, fig. 9), *Climacoceramus zeltbergensis* (HEINZ 1928a, p. 74; HEINZ 1928c, Pl. 3, Fig. 1), and *Tethyoceramus humboldti* (EICHWALD, 1865).

Best represented in the studied material are forms with the outline of *I. lamarcki* (see Pl. 14, Fig. 7; Pl. 18, Figs 1-2, 4), which have often been referred to *I.* ex gr. *lamarcki* (e.g. SZASZ 1985, WALASZCZYK 1992). They possess, however, the distinctive *Cremnoceramus* ornament-type. Identical forms were reported from the Coniacian chalk of the Ukraine and referred, apparently incorrectly, to *Inoceramus woodsi* or *Inoceramus kleini* by IVANNIKOV (1979, Pl. 16, Fig. 1; Pl. 17, fig. 1; Pl. 31, Figs 2-3; Pl. 32, Fig. 1). Moreover, many such forms were illustrated by SZASZ (1985), from the Lower Coniacian of Dobrogea, eastern Romania. He referred some of them, incorrectly to *I. lamarcki* (even to the subspecies *lamarcki* – e.g. SZASZ 1985, Pl. 12, Fig. 2) but the other specimens, usually those better preserved, he referred to a new species *Inoceramus pseudowandereri* (SZASZ 1985, Pl. 17, Fig. 2; Pl. 25, Fig. 1; Pl. 27, Fig. 1), which should be assigned to *Tethyoceramus pseudowandereri* (SZASZ). This species is most probably conspecific with our forms. Similar specimens from Caucasus were illustrated by KHALAFOVA (1969) and referred by her to a number of new subspecies of *Inoceramus wandereri* ANDERT. Some of these, such as *Inoceramus wandereri alatus* KHALAFOVA, *I. wandereri arpatschajensis* KHALAFOVA, *I. wandereri concinnus* KHALAFOVA, and *I. wandereri polycostatus* KHALAFOVA (*see* KHALAFOVA 1969, Pls 15-16), judging by the illustrations alone, seem to be very close to our specimens and very close if not conspecific with the species *Tethyoceramus pseudowandereri* (SZASZ). Finally, the species that also closely resembles the group in question is EICHWALD's (1865) *Inoceramus humboldti*, which, if all the above-mentioned taxa are conspecific, would have priority.

Less distinctive, and much more rarely represented in the inoceramid literature, are massive, strongly inflated forms from the Salzgitter-Salder section (Pl. 17, Figs 1 and 4). Similar forms were illustrated by SZASZ (1985, Pl. 11, Fig. 5) and referred by him to a new species, *Inoceramus macoveii* SZASZ. This seems to be very close to *Inoceramus kulbakovii*, described by IVANNIKOV (1979, Pl. 1, Fig. 1) from the Coniacian of the Ukraine.

The other specimens from the Salzgitter-Salder section are represented by relatively flat forms characterized by a concave anterior margin and a small, but well separated posterior auricle (Pl. 16, Figs 3 and 4). Of the few similar forms illustrated in the literature, one was referred to *Inoceramus* aff. *angulosus* JIMBO by SZASZ (1985, Pl. 7, Fig. 1) and the others, illustrated by IVANNIKOV (1979, Pl. 4, Figs 2-3), were referred to *Inoceramus brongniarti* MANTELL. Neither of these names is appropriate, and both specimens should probably be referred to a new species.

The massive, markedly inflated forms from Salzgitter-Salder (Pl. 17, Figs 1 and 4) resemble SZASZ' (1985, Pl. 11, Fig. 1) species *Inoceramus macoveii*. A similar form was illustrated from the Ukraine and referred to a new species *Inoceramus kulbakovi* by IVANNIKOV (1979, Pl. 16, Fig. 2; Pl. 17, Fig. 1; Pl. 18, Fig. 1).

From the lower part of the *hannovrensis* Zone (mostly from the *erectus* III Event) come a number of specimens (*see* Pl. 14, above all Figs 3, 5, 7 to some extent also 4 and 6) comparable with *Tethyoceramus madagascariensis* (HEINZ) from Madagascar, as illustrated by SORNAY (1980) and WALASZCZYK (1997). They also resemble forms described earlier from the Vistula section by WALASZCZYK (1992, Pl. 26, Figs 1-6) and referred by him to new species *Inoceramus vistulensis* (see Pl. 14, Figs 1-2).

Genus *Inoceramus* J. SOWERBY, 1814

TYPE SPECIES: *Inoceramus cuvieri* J. SOWERBY, by subsequent designation of COX (1969, p. *N*315).

REMARKS: For description and discussion of the genus *see* HARRIES & *al.* (1996).

Inoceramus lusatiae ANDERT, 1911
(Pl. 1, Fig. 9; Pl. 10, Fig. 5; 13; Pl. 2; Pl. 3, Figs 1, 3-6; Pl. 4)

1911. *Inoceramus lusatiae* n.sp.; H. ANDERT, pp. 54-56 (*pars*); Pl. 2, Fig. 1; Pl. 3, Fig. 3; Pl. 8, Fig. 3 (*non* Pl. 8, Figs 4-5)
1912-13. *Inoceramus lusatiae* ANDERT; H. SCUPIN, pp. 209-210; Text-fig. 34
1934. *Inoceramus lusatiae* ANDERT; H. ANDERT, pp. 126-128 (*pars*); Text-fig. 14a-b; Pl. 7, Figs 2-3 (*non* Pl. 7, Fig. 1)
1934. *Inoceramus dachslochensis* ANDERT; H. ANDERT, pp. 128-129 (*part*); Pl. 7, Fig. 4a-b
non 1955. *Inoceramus lusatiae* ANDERT; V.L. EGOYAN, Pl. 3, Figs 4-5.
non 1955. *Inoceramus lusatiae* ANDERT var. *grata* var. nov.; V.L. EGOYAN, pp. 202-203; Pl. 2, Fig. 7.
non 1959. *Inoceramus lusatiae* ANDERT; S.A. DOBROV & M.M. PAVLOVA, p. 151; Pl. 4, Figs 5-6.
non 1962. *Inoceramus* n. sp. aff. *lusatiae* ANDERT; F. BRÄUTIGAM, pp. 202-203; Pl. 3, Fig. 3.
1967. *Inoceramus lusatiae* ANDERT; K.-A. TRÖGER, pp. 73-76; Pl. 8, Figs 2-3.
non 1968. *Inoceramus lusatiae* ANDERT; S. PAULIUC, pp. 81-82; Pl. 19, Figs 1-3.
non 1969. *Inoceramus lusatiae* ANDERT; R.A. KHALAFOVA, pp. 125-126; Pl. 1, Figs 8-11.
1969. *Inoceramus lusatiae* ANDERT; T. JERZYKIEWICZ, pp. 175-176; Figs 4-5.
? 1971. *Inoceramus lusatiae* ANDERT; M.A. PERGAMENT, pp. 94-95; Pl. 23, Fig. 1.
? 1974. *Inoceramus lusatiae* ANDERT; A.A. ATABEKIAN, pp. 211-212; Pl. 102, Fig. 1.
non 1976b. *Mytiloides* ?sp. aff. *M. lusatiae* (ANDERT); E.G. KAUFFMAN, Pl. 2, Fig. 3.
1976a. *Mytiloides* (?) *lusatiae* (ANDERT); E.G. KAUFFMAN, Pl. 2, Fig. 5; Pl. 4, Fig. 5.
non 1977. *Mytiloides lusatiae* (ANDERT); E.G. KAUFFMAN, Pl. 10, Figs 3, 5; Pl. 9, Figs 17, 23.
non 1982. *Inoceramus lusatiae* ANDERT; S. KELLER, pp. 87-79; Pl. 6, Fig. 3.
non 1985. *Inoceramus lusatiae* ANDERT; L. SZASZ, p. 172; Pl. 4, Figs 2-3.
?non 1991. *Inoceramus lusatiae* ANDERT; K.-A. TRÖGER *in* K.-A. TRÖGER & W.K. CHRISTENSEN, p. 29; Pl. 3, Fig. 6.
?non 1991. *Inoceramus lusatiae* ANDERT; R. TARKOWSKI, p. 113; Pl. 7, Fig. 4.
1992. *Inoceramus lusatiae* ANDERT; I. WALASZCZYK, pp. 32-33; Pl. 27, Figs 1-6.
?1996. *Inoceramus* (*Inoceramus*) *lusatiae* ANDERT; M. NODA, pp. 558-564 (*pars*), Figs 2.1-2 (non Figs 3.1-3).

LECTOTYPE: By subsequent designation of TRÖGER (1967) the specimen illustrated by ANDERT (1911, Pl. 2, Fig. 1 and Pl. 8, Fig. 3) from the topmost Turonian – Lower Coniacian of the Sonnenberg near Waltersdorf, Saxony, SE Germany; housed in the State Museum of Mineralogy and Geology, Dresden.

MATERIAL: 6 specimens from the Salzgitter-Salder section, 18 specimens from the Vistula section, and numerous specimens from the type collection of ANDERT from the Sonnenberg near Waltersdorf, Saxony, SE Germany, housed in the State Museum of Mineralogy and Geology, Dresden.

DESCRIPTION: Small to medium-sized for the genus, inequilateral, inequivalve. Anterior margin straight or slightly convex, relatively short (being well below 50% of relative height in adults). Very characteristic of the species is a clear distinction between anterior and ventroanterior margins, with the latter being long and widely convex (Pl. 2, Fig. 4; Pl. 4, Figs 6-7). This is particularly well developed in LV, RV more uniform, with anterior margin passing continuously into ventral one (Pl. 3, Fig. 6). Ventroposterior margin narrowly rounded, passing with shallow, well-developed sulcus into posterior margin. Hinge line long, straight. Posterior auricle large or very large, well separated from disc, and strongly inflated toward RV (Pl. 2, Fig. 4; Pl. 3, Fig. 5; Pl. 4, Fig. 7). Umbonal part with pointed beak, projecting above hinge line.

Shell inequivalve, as result of differences in growth direction in juvenile parts of RV and LV because of peculiar development of posterior auricle. While RV grows continuously obliquely, LV, in juvenile (up to 35-45 mm axial length), is much less oblique (measured values for δ angle at h=40 mm for RV and LV are 50-55° and 70° respectively). As a result juveniles of LV are subquadrate in outline, massive while RV, even as juveniles, are *Mytiloides*-like (Pl. 3, fig. 5 and Pl. 4, Figs 5, 7a).

Ornament composed of well developed, round-topped concentric rugae and raised, sharp-topped growth lines. In axial part rugae often markedly weaker than in anterior and posterior parts of disc (this is particularly clearly seen in the lectotype – see Pl. 2, Fig. 4). Concentric rugae almost disappear when passing onto posterior auricle, which may be almost smooth. Ornament *lamarcki*-like, most closely resembling that of *Inoceramus annulatus* GOLDFUSS (see Pl. 3, Fig. 2).

REMARKS: The *lamarcki*-like ornament, well separated from the disc and the extended posterior auricle, the slight inequivalveness, shell obliquity, and distinct stratigraphical horizon, makes *I. lusatiae* ANDERT a well defined species, which is well represented in Central Europe (ANDERT 1911, 1934; TRÖGER 1967; JERZYKIEWICZ 1969; KAUFFMAN 1978a; TRÖGER & CHRISTENSEN 1991; WALASZCZYK 1992). The species is also cited from most of the areas of the northern hemisphere, but almost none of the illustrated forms really corresponds to the concept of ANDERT's species presented here. It is absent from the United States Western Interior (*see* WALASZCZYK & COBBAN, *in press*).

Forms referred to *I. lusatiae* and reported from the topmost Turonian – earliest Coniacian of south-eastern Europe (Caucasus, Crimea) usually represent different *Mytiloides* species, or even early cremnoceramids. KHALAFOVA (1969) illustrated four different specimens, of which at least two (KHALAFOVA 1969, Pl. 1, Figs 10-11) represent early *Cremnoceramus erectus* (MEEK). The other two (KHALAFOVA 1969, Pl. 1, Figs 8-9) may represent the same species, or some Late Turonian *Mytiloides*, but without seeing the original specimens it is impossible to give a definitive identification. In addition, the larger specimen illustrated by DOBROV & PAVLOVA (1959, Pl. 4, Fig. 5), with distinct geniculation and even, regular ornament in the early stage, most probably represents the early *Cremnoceramus deformis erectus* (MEEK). Their second specimen (DOBROV & PAVLOVA 1959, Pl. 4, Fig. 6), characterized by much lower inflation, and lamellate, regular ornament, is very close to or conspecific with *Mytiloides turonicus* WALASZCZYK.

The type of surface ornament, character of the posterior auricle and the general outline distinguish the specimens illustrated by EGOYAN (1955, Pl. 3, Figs 4-5) from *I. lusatiae*. EGOYAN's specimens clearly represent two distinct species, but based only on the illustrations it is difficult to give correct determinations. Similarly, his "*I. lusatiae* var. *grata* nov. var." (EGOYAN, 1955, Pl. 3, Fig. 7) is quite far from the concept of *I. lusatiae*, and seems to be much closer to *Mytiloides mytiloidiformis* (TRÖGER)[if this determination was correct, EGOYAN's name would have the priority].

WALASZCZYK (1992, p 32) included into the synonymy of *I. lusatiae* the specimen illustrated by DOBROV & PAVLOVA (1959, Pl. 3, Fig. 1), and referred by those authors to *I. lamarcki* PARKINSON. However, the relatively long anterior margin, low obliquity and the strengthening of the ornament at the axial part of the disc set this specimen apart from the concept of *I. lusatiae*.

Extra-European reports mostly result from different concepts of ANDERT's species. PERGAMENT (1971, Pl. 22, Fig. 1) illustrated a specimen from the *lamarcki* group, but the regular surface ornament, passage of the concentric ribs onto the posterior auricle, low VR/H ratio, and the character of the posterior auricle make this specimen quite distinct from *I. lusatiae* (see also discussion in NODA, 1996).

Similarly, the forms reported by KAUFFMAN (1977, Pl. 9, Figs 17 and 23; *see also* KAUFFMAN & *al*. 1978, Pl. 9, Figs 17 and 23), and referred to *Mytiloides lusatiae* (ANDERT), differ markedly in surface ornament and character of the posterior auricle and represent a quite different species. The smaller specimen (KAUFFMAN 1977, Pl. 9, Fig. 23) is only a juvenile and is impossible to determine.

Inoceramus lusatiae was also listed from South America. KAUFFMAN & BENGTSON 1985 reported it from the Sergipe Basin, Brasil, and VILLAMIL (1991, unpublished report) from Colombia. Without checking the original specimens or at least the photographs, both reports cannot be positively cited.

The only extra-European report which looks really very similar is one of the specimens illustrated by NODA (1996, Pl. 2, Fig. 1). A detailed comparison (based on the plaster cast, kindly sent to us for study by Dr. NODA), with ANDERT's type material shows a high degree of similarity. However, this does not apply to the other specimens illustrated by NODA (1996) and also referred to *I. lusatiae*, which are actually quite distinct.

Although the Japanese sample may represent a uniform, potentially monospecific group, its characters differ from those of larger samples of *I. lusatiae*, such as the one from the type locality of the species (partly illustrated here – Pls 2-4). The resemblance of a single specimen may be only fortuitous, or it may result from some affinity of the Japanese forms to *I. lusatiae*, but not necessarily conspecificity. This single Japanese specimen is cited here in the synonymy with a question mark: new material is needed to show whether the species *I. lusatiae* was actually present in the North Pacific Province, or whether the Japanese form belongs to another species with extreme representatives that are morphologically very close to the European *I. lusatiae*.

The second group of forms, often referred to *Inoceramus lusatiae*, are *lamarcki*-like representatives with an oblique antero-ventral part, which occur at the Middle/Upper Turonian boundary (*e.g.* KELLER 1982, Pl. 6, Fig. 3). At the moment, it is impossible to clearly demonstrate the phylogenetic relationship between such forms and typical *I. lusatiae* from the Turonian/Coniacian boundary interval, but such a link is very probable.

In the upper part of the Lower Coniacian (*C. deformis-crassus* Zone) occur massive forms, similar in general outline to *I. lusatiae*, but with a markedly different ornamentation pattern (*e.g.* SZASZ 1985, Pl. 4, Figs 2-3). Such forms were also found in the upper Lower Coniacian of Poland, and an identical specimen, from the Coniacian of Armenia, was also illustrated and referred to *I. lusatiae* by ATABEKIAN (1974, pp. 211-212; Pl. 102, Fig. 1). All these specimens are conspecific but different from *I. lusatiae*, and they should be referred to a new species.

Incompletely preserved or partly deformed specimens of *Inoceramus lusatiae* are extremely difficult to distinguish from *Inoceramus annulatus* GOLDFUSS. The lectotype of the latter species (the original specimen of GOLDFUSS 1836, Pl. 110, Fig. 7a – lectotype designation of HEINZ, 1926 – *see* Pl. 3, Fig. 2) possesses an identical ornament type and a distinct posterior auricle. It is, however, less oblique (78° compared to about 60° in the RV of *I. lusatiae*) and the concentric ornament elements are symmetrical. *Inoceramus annulatus* seems to occur slightly higher stratigraphically than *I. lusatiae*, in the upper Lower Coniacian.

Based on the external characters *Inoceramus lusatiae* is here referred to the genus *Inoceramus* J. SOWERBY. The type of posterior auricle, valve outline as well as the type of ornament matches the characteristics of the *lamarcki* – group (*see also* TRÖGER 1967, *and* NODA 1996). KAUFFMAN (*in* HERM & *al*. 1979) argued that among specimens illustrated by ANDERT (1911) some, represented by erect morphotypes, should be referred to the genus *Inoceramus*, and others, with curved growth axis, posteriorly flared auricle, somewhat projecting beaks and delicate ligament, should be referred to the genus *Mytiloides*. His interpretation is very hard to follow, while the references to respective figures, given by KAUFFMAN (*in* HERM & *al*. 1979) are clearly mistaken and some of them (Pl. 7, Figs 1-2) refer to other species (*I. glatziae*). On the other hand, however, some of the characters listed by KAUFFMAN in the case of forms he referred to the genus *Mytiloides* are possessed by all the forms referred by ANDERT (1911) to his new species *Inoceramus lusatiae* (Pl. 2, Figs 4-5; Pl. 3, Figs 5-6; Pl. 4, Figs 5-8). However, in contrast to KAUFFMAN's view they all possess *lamarcki*-type ornament, and moreover, none of the characters mentioned by him automatically indicates affiliation to the genus

Mytiloides. Erect forms, occurring in ANDERT's original material, are either small forms (the juveniles of the species are always erect) or deformed specimens. ANDERT's material is represented by sandy moulds, very often remarkably deformed (*see also* discussion *in* WALASZCZYK 1996) due to secondary compression, as *e.g.* in his specimen illustrated here on Pl. 8, Fig. 5.

OCCURRENCE: Topmost Turonian (*M. scupini* and *C. waltersdorfensis* zones) – lowermost Coniacian (*C. erectus* Zone) of Central Europe.

Inoceramus annulatus GOLDFUSS, 1836
(Pl. 3, Fig. 2; Pl. 18, Fig. 3)

part 1836. *Inoceramus annulatus* nobis; A. GOLDFUSS, p. 114, Pl. 110, Fig. 7a [non Fig. 7b].
1926. *Inoceramus* ex aff. *annulatus* GOLDF.; R. HEINZ, p. 99.
1928d. *Inoceramus annulatus* GOLDF., part. HEINZ; R. HEINZ, pp. 73-76, Pl. 5, Fig. 2.
1958. *Inoceramus* cf. *annulatus* GOLDFUSS; S.P. KOTSUBINSKY, pp. 14-15, Pl. 5, Fig. 23.
1962. *Inoceramus annulatus* GOLDFUSS part HEINZ; R. BRÄUTIGAM, pp. 203-204, Pl. 3, Fig. 4.
1962. *Inoceramus annulatus* GOLDFUSS; Z. RADWAŃSKA, pp. 149-150, Pl. 5, Fig. 3; Pl. 6, Figs 1-2.
?1962. *Inoceramus circularis* SCHLÜTER; Z. RADWAŃSKA, pp. 150-151, Pl. 7, Fig. 1, Pl. 8, Fig. 1.
?1965. *Inoceramus annulatus* GOLDFUSS; E.M. ARZUMANOVA, pp. 121-122, Pl. 1, Fig. 3.
1968. *Inoceramus annulatus* GOLDFUSS; S.P. KOTSUBINSKY, pp. 129-130, Pl. 19, Figs 3-4.
1979. *Inoceramus annulatus* GOLDFUSS; A.V. IVANNIKOV, pp. 40-41, Pl. 2, Fig. 3.
?1988. *Inoceramus* cf. *annulatus* GOLDFUSS; K.-A. TRÖGER *in* TRÖGER & CHRISTENSEN, p. 28, Pl. 4, Fig. 1.

TYPE SPECIMEN: By subsequent designation of HEINZ (1926, p. 99) the lectotype is the specimen figured by GOLDFUSS [1836, Pl. 110, Fig. 7a (non 7b)], from the "*Scaphitenschichten*" (?Upper Turonian – ?Lower Coniacian) of northern Germany.

MATERIAL: Plaster cast of the lectotype; 3 specimens from Słupia Nadbrzeżna housed in the Institute of Geology of the University of Warsaw.

DESCRIPTION: Medium to large-sized, orthocline species, inequilateral, ?equivalved. Anterior margin straight, long, passing into widely rounded ventral margin. Anterior face steep. Posterior auricle well developed and well separated from the disc. Umbo massive, projecting above the hinge line.

Valves ornamented with regularly spaced, round-topped concentric rugae, covered by regularly spaced, raised growth lines.

REMARKS: We refer to this species all orthocline forms with very regular *lamarcki*-like ornament, appearing in the *hannovrensis* Zone and ranging to the end of the Lower Coniacian and possibly to the basal Middle Coniacian. Such forms are rather rare in the middle Lower Coniacian, but become increasingly common toward the top of the Lower Coniacian (*see also* WALASZCZYK & WOOD *in* NIEBUHR & *al.*, *in press*). Unfortunately, it is usually found as incomplete specimens (some with a reconstructed height of up to 1 m), with the more complete museum material usually lacking precise stratigraphical information and the forms referred here tentatively to *I. annulatus* may actually be heterogenous.

OCCURRENCE: Middle – upper Lower Coniacian of Europe and Northern America.

Genus: *Mytiloides* BRONGNIART, 1822

TYPE SPECIES: By monotypy the type species is *Ostracites labiatus* SCHLOTHEIM [=*Inoceramus* (*Mytiloides*) *labiatus* (SCHLOTHEIM) *in* COX, 1969, p. *N*320].

REMARKS: Following KAUFFMAN & POWELL (*in* KAUFFMAN & *al.* 1977) and HARRIES & *al.* (1996), we provisionally accept the generic assignment of the Late Turonian mytiloid-like forms to the genus *Mytiloides*. On the other hand, despite close similarity in general outline to the Lower Turonian *Mytiloides*, the Upper Turonian forms (with the exception of *Mytiloides incertus*) possess a different ornament-type. Moreover, there is a large stratigraphical gap between the Lower – lower Middle Turonian forms and the Upper Turonian representatives, and there are many forms in the lowest Upper Turonian which could have evolved into mytiloid-like forms during the Late Turonian. This closely resembles the situation with the Middle Turonian representatives of the genus *Inoceramus* and the upper Lower Coniacian tethyoceramids, discussed above. Very detailed studies of the phylogeny of the Upper Turonian mytiloids are needed to resolve this problem.

Such studies are likewise needed to clear up the taxonomic status of a series of 'morphotypes' distinguished within the Upper Turonian mytiloids. The 'taxa' described here come from the topmost Turonian and constitute a group from a single time slice, albeit with a very poor knowledge of their geological history. These forms are mostly treated in the literature as separate species (or subspecies), but the range of variability and the course of changes over time in particular lineages is largely unknown. Consequently, the taxonomy given here is very speculative. The rough scheme is based on observations in many European sections.

OCCURRENCE: Topmost Cenomanian – Lower/?Middle Coniacian; world-wide.

Mytiloides scupini (HEINZ, 1930)
(Pl. 1, Fig. 10)

1911. *Inoceramus frechi* FLEGEL; H. ANDERT, p. 51, Pl. 1, Fig. 8; Pl. 7, Fig. 6.
1928. *Inoceramus stillei* HEINZ; R. HEINZ, p. 73 (*pars*).
1930. *Inoceramus stillei* var. *scupini* n. var.; R. HEINZ, p. 26.
1934. *Inoceramus frechi* FLEGEL; H. ANDERT, p. 120, Pl. 5, Figs 5-9; Pl. 6, Fig. 1.
1955. *Inoceramus frechi* FLEGEL; V.L. EGOYAN, Pl. 4, Fig. 5.
1982. *Inoceramus frechi* FLEGEL; S. KELLER, pp. 96-98, Pl. 7, Fig. 1.
1986. *Mytiloides* aff. *mytiloidiformis* (TRÖGER); W.A. COBBAN, Fig. 6D.
1996. *Mytiloides scupini* (HEINZ); I. WALASZCZYK & K.-A. TRÖGER, pp. 400-402, Fig. 3C-E.

TYPE SPECIMEN: The holotype, by original designation, is the specimen illustrated by ANDERT (1911, Pl. 1, Fig. 8 and Pl. 7, Fig. 6) (and reillustrated by WALASZCZYK & TRÖGER 1996, Fig. 3C-E) from the Sonnenberg near Waltersdorf in Saxony, Germany. Original in the State Museum of Mineralogy and Geology, Dresden, Germany.

MATERIAL: 5 specimens; 4 from Salzgitter-Salder and a single specimen from the Vistula section. Relatively rare in both studied sections.

DESCRIPTION: Small to moderate sized, slightly oblique *Mytiloides*, with well separated posterior auricle. Umbo pointed, projecting above the hinge line. Anterior face steep. Anterior margin straight or widely convex. Hinge line long, straight. Posterior auricle contacts the disc along more or less developed auricular sulcus.

Ornament very characteristic, consisting of well developed, widely-spaced, sharp-edged concentric rugae, passing onto posterior auricle. Inter-rugae spaces flat-floored.

REMARKS: The species was recently discussed at length by WALASZCZYK & TRÖGER (1996).

In general, *M. scupini* comprises the forms referred in the older literature to *Inoceramus frechi* ANDERT *non* FLEGEL (see synonymy, *and also* WALASZCZYK & TRÖGER 1996). The specimen illustrated by KELLER (1982, Pl. 7, Fig. 1), and referred by him to *Inoceramus frechi* FLEGEL, also most probably belongs to this species. WALASZCZYK (1992) included this specimen questionably in the synonymy of his *Inoceramus vistulensis*, but it possesses a distinctly curved, instead of straight, growth axis and a more slender outline, typical of *M. scupini* (HEINZ) (*see* WALASZCZYK & TRÖGER 1996).

OCCURRENCE: Upper Upper Turonian of the Euramerican Palaeobiogeographical Region.

Mytiloides herbichi (ATABEKIAN, 1968)
(Pl. 1, Figs 3, 5, 7)

1899. *Inoceramus labiatus* SCHLOTHEIM; J. SIMIONESCU, p. 159 (*pars*), Pl. 1, Fig. 9.
1899. *Inoceramus labiatus* SCHL. var. *regularis* SIMIONESCU; J. SIMIONESCU, p. 160, Pl. 2, Fig. 3.
1963. *Inoceramus glatziae* FLEGEL; Z. RADWAŃSKA (*pars*), Pl. 6, Fig. 1.
1968. *Inoceramus sublabiatus* MÜLLER; S. PAULIUC, p. 60 (*pars*), Pl. 5, Figs 1-4, 6.
1969. *Inoceramus herbichi* nom.n.; A.A. ATABEKIAN, p. 11.
1978. *Inoceramus nairicus* sp.n.; R.A. GAMBASHIDZE, p. 179, Pl. 2, Fig. 8.
1992. *Mytiloides carpathicus* (SIMIONESCU); I. WALASZCZYK, p. 26 (*pars*), Pl. 14, Figs 1-6, 8; Pl. 15, Figs 1-3, 5-7.
1997. *Mytiloides herbichi* (ATABEKIAN); I. WALASZCZYK & L. SZASZ, pp. 774-775, Figs 3a, g, h; 5h.

TYPE SPECIMEN: The holotype, by monotypy, is the specimen, UMCN 5851H, illustrated by SIMIONESCU (1899, Pl. 2, Fig. 3), the type of his *Inoceramus labiatus* var. *regularis*; the original is housed in the palaeontological collections of the University Cluj, Romania.

MATERIAL: 5 relatively well preserved and many incomplete specimens from the Salzgitter-Salder section, housed in the Institute of Palaeontology of the Free University, Berlin.

DESCRIPTION: Upright or slightly oblique *Mytiloides* with extended posterior auricle. Anterior margin straight or slightly convex, passing gradually into wide, rounded ventral margin. Hinge line long, straight. Umbo narrow, usually slightly projecting above the hinge line.

Juvenile ornament composed of raised, sharp-edged growth lines. In adult part appear irregular concentric ribs.

REMARKS: The ornament, particularly in the juvenile part, closely resembles that of *Mytiloides striatoconcentricus striatoconcentricus* (GÜMBEL), particularly in the sense of TRÖGER (1967 – *see* Pl. 1, Fig. 11 of this paper). The latter form displays, however, rather uniform ornament throughout ontogeny, and is, moreover, markedly more inflated.

OCCURRENCE: Upper Upper Turonian of Europe, western Asia and North America.

Mytiloides labiatoidiformis (TRÖGER, 1967)
(Pl. 1, Figs 1-2, 6, 8, ?12)

1967. *Inoceramus dresdensis*? *labiatoidiformis* n.sp.; K.-A. TRÖGER, pp. 125-127, Pl. 10, Figs 5-6.

1974. *Inoceramus striatoconcentricus* GÜMB. *sabzakensis* subsp.nov.; J. SORNAY, pp. 32-33, Pl. 2, Figs 5-6.

non 1977. *Inoceramus dresdensis*? *labiatoidiformis* TRÖGER; E.G. KAUFFMAN, Pl. 10, Fig. 2.

non 1982. *Inoceramus labiatoidiformis* TRÖGER; S. KELLER, pp. 100-103, Pl. 5, Figs 5 and 7.

non 1986. *Inoceramus* aff. *labiatoidiformis* TRÖGER; G.R. SCOTT & *al.*, Fig. 6h and j.

1990. *Mytiloides labiatoidiformis* (TRÖGER); L.F. KOPAEVICH & I. WALASZCZYK, Pl. 2, Fig. 4.

?1992. *Inoceramus* (*Mytiloides*) *labiatoidiformis* TRÖGER; G. LOPEZ, pp. 113-115, Pl. 4, Fig. 2.

1992. *Mytiloides labiatoidiformis* (TRÖGER); I. WALASZCZYK, pp. 21-22; Pl. 12, Figs 1-2.

TYPE SPECIES: The holotype, by original designation, is the specimen, F1010, illustrated by TRÖGER (1967, Pl. 10, Fig. 5) from the Upper Turonian limestones of the Dresden-Strehlen Quarry, Germany; the type is housed in the collections of the TU Bergakademie Freiberg, Germany.

MATERIAL: One specimen from the Turonian of Crimea, the types of *M. labiatoidiformis* and of *Inoceramus striatoconcentricus sabzakensis* SORNAY. No specimen referable to TRÖGER's *M. labiatoidiformis* was found in the studied interval.

DESCRIPTION: Medium-sized for genus, inequilateral, ?equivalved. *Mytiloides*-shaped, with gently, anteriorly curved growth axis. Anterior margin long, widely convex, passing into narrowly rounded ventral margin. Hinge line long, straight. Posterior auricle small, sometimes separated from the disc with a distinct auricular sulcus. Valves weakly to moderately inflated, with maximum inflation dorsal. Beak usually does not project above the hinge line.

Ornament, apart from that of umbonal part, uniform throughout ontogeny, composed of regularly spaced, asymmetrical concentric rugae, with steeper ventral margins. In umbonal part it consists of raised, densely spaced growth lines. No change in ornament is observed when passing onto posterior auricle.

REMARKS: This species is one of those Upper Turonian forms that often appear in inoceramid lists from all over the world, although only a few of these citations relate to the type concept of the species. The species has a very simple, regular and uniform ornament, composed of asymmetrical, closely spaced rugae, and possesses only a slightly convex growth axis. *Inoceramus striatoconcentricus sabzakensis*, described by SORNAY (1974) from Afghanistan (illustrated here on Pl. 1, Fig. 6) is conspecific with TRÖGER's species.

KELLER (1982) markedly widened the original concept of *I. labiatoidiformis* TRÖGER, by distinguishing two variants (a and b) that differed in the ornament pattern. However, none of the illustrated specimens may be referred to TRÖGER's species. His variant *a* (KELLER 1982, Pl.5, Fig. 7) most probably represents a RV of *Mytiloides striatoconcentricus* (GÜMBEL), which is markedly less inflated than the LV. His variant b possesses a quite distinct and very peculiar ornament, which characterizes a new *Mytiloides* species to be described in WALASZCZYK & COBBAN (*in press*).

KAUFFMAN's (1977, Pl. 10, Fig. 2) report of *I. labiatoidiformis* from the US Western Interior represents the juveniles of other *Mytiloides* species.

OCCURRENCE: Upper Upper Turonian; apparently limited to Europe and western margins of Central Asia (belonging to the North European Paleobiogeographical Province).

Comments on *Inoceramus callosus* (HEINZ, 1932), *Tethyoceramus ernsti* (HEINZ, 1928), and *Mytiloides costellatus* (WOODS, 1912)

Inoceramus callosus (HEINZ, 1932) (not illustrated)

1911. *Inoceramus lamarcki* PARKINSON; H. WOODS, p. 325 (*pars*), Text-fig. 85.
1928. *Inoceramus ernsti* n.sp.; R. HEINZ, pp. 73-74 (*pars*).
1932. *Tethyoceramus* (*Proteoceramus*) *callosus* nov. spec.; R. HEINZ, p. 11.
non 1967. *Inoceramus ernsti* HEINZ; K.-A. TRÖGER, pp. 128-130, Pl. 14, Figs 1-4, 6.
non 1979. *Inoceramus ernsti* HEINZ; A.V. IVANNIKOV, p. 51, Pl. 8, Figs 1-2.
non 1980. *Inoceramus* (*Inoceramus*) *ernsti* HEINZ; E.G. KAUFFMAN *in*: KLINGER & *al*., pp. 310-314, Figs 10G-P.
non 1985. *Inoceramus ernsti* HEINZ; L. SZASZ, p. 172, Pl. 29, Fig. 3.
non 1991. *Inoceramus ernsti* HEINZ; R. TARKOWSKI, p. 108, Pl. 14, Fig. 5.
1992. *Cremnoceramus ernsti* HEINZ; I. WALASZCZYK, pp. 55-56 (*part*), Text-fig. 18, Pl. 32, Figs 1-2 [*non* Pl. 32, Fig. 3].

TYPE SPECIMEN: By original designation of HEINZ (1932b, p. 11) the holotype, BGS GSM 21237, is the specimen illustrated by WOODS (1911, p. 325, Text-fig. 85, and reillustrated by WALASZCZYK 1992, Pl. 32, Fig. 2). The original is housed in BGS, Keyworth.

DESCRIPTION: The following description is based on a single specimen, the holotype, represented by a relatively complete and well preserved right valve of a moderately large specimen.

The valve is subquadrate in outline, orthocline, with posteriorly convex growth axis, markedly inflated. There are two distinct growth stages, the juvenile and adult (this was the reason for including the species earlier into the genus *Cremnoceramus*), with fairly distinct boundary. The juvenile part is slightly inflated, subquadrate, with the umbo not projecting above the hinge line. Posterior auricle moderately large, separated from the disc with a very shallow auricular sulcus. Anterior margin widely convex. The growth axis is straight. The surface ornament composed mainly of raised growth lines with superimposed, indistinct rugae.

The adult part is markedly larger than the juvenile part and joins it an angle of almost 90°. Markedly inflated, trapezoidal in outline. Anterior wall distinctly and widely convex, steep, or even overhanging. Ventral and ventroposterior margins widely rounded, with indistinct sulcus in the axial part of the disc. Although no posterior auricle is preserved, the general shape of the concentric rugae indicate that the specimen originally possessed a moderate- and even possibly large-sized posterior auricle, well separated from the disc. The surface is covered with marked, subrounded, *lamarcki*-type rugae. They bear conspicuous, simple growth lines, parallel to the rugae, with slightly irregular margins.

REMARKS: HEINZ referred twice to the specimen illustrated by WOODS (1911, Text-fig. 85), in both cases in a slightly unclear manner, resulting subsequently in different interpretations. HEINZ (1928a) referred the specimen to his new species *Inoceramus ernsti*. In his original description he wrote (HEINZ 1928a): "Diese neue Art ist bereits von H. WOODS (1911, p. 325, Text-fig. 85) als *I. lamarcki* abgebildet worden. Sie [i.e. *I. ernsti* as defined by WOODS' specimen – our comment] unterscheidet sich jedoch von dieser unterturonen Form [i.e. from *I. lamarcki*] durch die stärkere Wölbung, die größere Länge, den tiefen Eindruck auf der Vorderseite unter dem Wirbel sowie durch den nur wenig gebogenen Verlauf der Anwachslinien auf dem im allgemeinen sanft abfallenden kleinen Flügel". In the latter sentence he listed those characters of WOODS' specimen (i.e. Text-fig. 85) that differentiate it from *Inoceramus lamarcki*. He also noted that growth marks often developed in later ontogenetic stages. However, subsequent workers have interpreted this sentence differently, namely as a list of characters distinguishing this specimen from typical representatives of *Inoceramus ernsti* (see e.g. PERGAMENT 1971, SORNAY 1980). Such an interpretation was based partly on the fact that the same specimen was designated later by HEINZ (1932b) as the type of his new species *Tethyoceramus* (*Proteoceramus*) *callosus*. In this paper he placed his species *ernsti* in the new subgenus *Proteoceramus*, of which he designated it the type species. HEINZ' (1932b) description of the new species, *T.* (*P.*) *callosus* is actually valid, as is also the designation of WOODS' specimen as its type specimen. In this sense, both PERGAMENT and SORNAY were right. In 1928 HEINZ included WOODS' specimen into *I. ernsti*, but he did not designate it as the type. Therefore, he could subsequently exclude this specimen from the synonymy of *I. ernsti* and designate it as the type of another new species, which is what he actually did. His paper (HEINZ 1932b) contains both the required type indication and differential diagnosis of his new species *Tethyoceramus* (*P.*) *callosus*, which is thus, according to the Code, a valid taxon. What, then, is *I. ernsti* HEINZ, 1928?

In his 1928a paper, when erecting his *I. ernsti*, HEINZ indicated two specimens as typical representatives: WOODS' specimen; and the specimen of *I. brongniarti* illustrated by INOSTRANZEFF (1897) from the Upper Cretaceous of the Caucasus. The latter specimen is very similar in general outline to WOODS' specimen but differs in ornament. While the English specimen possesses *lamarcki*-type ornament, INOSTRANZEFF's specimen has ornament of *Cremnoceramus*-type (*see* Pl. 19, Fig. 6 for illustration of INOSTRANZEFF's original, housed in the University Museum in St. Petersburg). HEINZ (1932a) recognized this difference, as is shown in his differential diagnosis of *T.* (*P.*) *callosus*, since only in the case of *I. ernsti* did he mention growth-marks, which are characteristic of *Cremnoceramus*-type ornament. He consequently separated both morphotypes, designating the English specimen (*i.e.* the forms without growth marks) as the type of the new species *T.* (*P.*) *callosus*. This shows that HEINZ regarded the forms represented by INOSTRANZEFF's specimen as *I. ernsti*, and this specimen is therefore here designated as the lectotype of *I. ernsti* HEINZ, 1928. HEINZ himself later (HEINZ 1933), mentioned a specimen from Lüneburg, Germany, as the typical specimen of *I. ernsti* but this specimen is unidentifiable. *I. ernsti* HEINZ, 1928, thus belongs to the genus *Tethyoceramus* SORNAY, and is relatively well represented in the middle and upper Lower Coniacian (*see e.g.* IVANNIKOV 1979, Pl. 8, Fig. 1; WALASZCZYK 1992, Pl. 18, Fig. 3). The specimen from Madagascar (HEINZ 1933, Pl. 19, Fig. 1 – and reillustrated herein – *see* Pl. 19, Fig. 5), referred by HEINZ to *I. ernsti* is an inequivalve specimen with subquadrate juvenile part, distinct geniculation, and much less distinct rugae, which differs from the lectotype. SORNAY (1980) placed this specimen into synonymy of his *Inoceramus* (*Tethyoceramus*) *basseae*, the type species of his subgenus *Tethyoceramus* (see discussion above).

OCCURRENCE: The horizon of the type was given by WOODS as *Holaster planus* [i.e. *Sternotaxis plana*] Zone (Upper Turonian). However the specimen is preserved in a chalkstone of a type that is found in the (Lower Coniacian) *Micraster cortestudinarium* Zone chalk of southern England.

Mytiloides costellatus (WOODS, 1912)
(Pl. 19, Fig. 1)

non 1834-40. *Inoceramus undulatus* MANTELL; A. GOLDFUSS, p. 115, Pl. 112, Fig. 1.

1912. *Inoceramus costellatus* sp.n.; WOODS, p. 336 (*pars*), Pl. 54, Fig. 5-6 [non Pl. 54, Fig. 7].

non 1930. *Inoceramus costellatus* WOODS; K. FIEGE, p. 35, Pl. 5, Figs 3-7, 9.

non 1967. *Inoceramus vancouverensis vancouverensis* SHUMARD; K.-A. TRÖGER, pp. 89-92, Pl. 9, Figs 6-9.

non 1967. *Inoceramus vancouverensis parvus* n.ssp.; K.-A. TRÖGER, pp. 92-95, Pl. 9, Figs 1-5, Pl. 10, Fig. 3.

non 1982. *Inoceramus costellatus costellatus* WOODS; S. KELLER, pp. 92-94, Pl. 7, Fig. 2.

non 1992. *Inoceramus costellatus* WOODS, 1911; I. WALASZCZYK, pp. 31-32, Pl. 12, Figs 3-9.

TYPE: By original designation the holotype is B.4564 (Sedgwick Museum, Cambridge) from the Upper Turonian Chalk Rock of Cuckhamsley, illustrated by WOODS (1912, Pl. 54, Fig. 5).

REMARKS: It should be emphasized that the name *Inoceramus costellatus* is preoccupied by *I. costellatus* CONRAD, 1855-58. BÖHM (1915) introduced the name *Inoceramus woodsi* as a replacement name for *I. costellatus* WOODS, 1912 *non* CONRAD, 1855-58, but this has been largely ignored, except by Russian workers.

Inoceramus costellatus is one of the most widely quoted inoceramid names in the Upper Turonian of Europe, with its range being broadly regarded as coextensive with the substage. On the other hand, the forms that are usually referred to WOODS' species, particularly outside United Kingdom, are not conspecific with the type. They are small, subquadrate, upright forms, with a pointed beak projecting well above the hinge line and a long, straight or even slightly concave anterior margin. The growth axis is straight. The ornament consists of regular, uniform, symmetrical or slightly asymmetrical rugae. To this morphotype belong also the forms from the basal Upper Turonian *costellatus/plana* Event (*see* ERNST & *al.* 1983). This morphotype is also represented by one of the specimens illustrated by WOODS (1912, Pl. 54, Fig. 7). This "commonly accepted type" is different, however, from the actual type which is a mytiloid form [*see* WOODS 1912, Pl. 54, Fig. 5 and reillustrated herein (and slightly enlarged) – Pl. 19, Fig. 1], characterized by a short and convex anterior margin, high obliquity and is relatively (in relation to the other form) slender.

The "commonly accepted type" of *Inoceramus costellatus* [= *Inoceramus vancouverensis* of TRÖGER (1967] is actually conspecific with *Inoceramus perplexus* WHITFIELD (WHITFIELD 1880, Pl. 8, Fig. 3; Pl. 10, Figs 4-5), described from the lower Upper Turonian of the Black Hills area, in the United States Western Interior (see full description and illustration *in* WALASZCZYK & COBBAN, *in press*), and consequently the *costellatus* Zone of the European lower Upper Turonian should be renamed the *Inoceramus perplexus* Zone. The *costellatus/plana* Event, taken in Germany as the marker for the base of the Upper Turonian Substage, (ERNST & *al.* 1983) should be likewise termed the *perplexus/plana* Event.

Also very similar to *Inoceramus perplexus* WHITFIELD is HEINZ' (1933) species *Inoceramus hoepeni* (reillustrated here – *see* Pl. 19, Figs 2-3), described by him from the Turonian of Madagascar. Small, geniculated forms from the topmost Turonian of the Vistula section, referred to *I. hoepeni* by WALASZCZYK (1992) should be referred to other species.

OCCURRENCE: *Inoceramus perplexus* WHITFIELD seems thus to be a widely distributed form, occurring in North America, Europe and Madagascar. The form is also very close to the Japanese species *Inoceramus teshioensis* NAGAO & MATSUMOTO, 1939. In the US Western Interior, *I. perplexus* appears at the base of the *Scaphites whitfieldi* Zone, which was regarded as a middle Upper Turonian, but which apparently represents an equivalent of the base of the Upper Turonian as commonly accepted in Europe.

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PLATE 1

1-2, 6, 8, 12 – *Mytiloides labiatoidiformis* (TRÖGER)
1 – FU: Sa 43.1; *scupini* Zone, Salzgitter-Salder, bed 43
2 – FU: Sa 43.2; *scupini* Zone, Salzgitter-Salder, bed 43
6 – holotype of *Inoceramus striatoconcentricus sabzakensis* SORNAY
8 – UW: Sa 39.2; *scupini* Zone, Salzgitter-Salder, bed 39
?12 – FU: Sa 39.1; *scupini* Zone, Salzgitter-Salder, bed 39

3, 5, 7 – *Mytiloides herbichi* (ATABEKIAN)
3 – FU: Sa 41.2; *scupini* Zone, Salzgitter-Salder, bed 41
5 – UW: Sa 41.1; *scupini* Zone, Salzgitter-Salder, bed 41
7 – FU: Sa 41.3; *scupini* Zone, Salzgitter-Salder, bed 41

4 – *Mytiloides* sp. (?*M. scupini* (HEINZ); FU: Sa 41.4; *scupini* Zone, Salzgitter-Salder, bed 41

10 – *Mytiloides scupini* (HEINZ); FU: Sa 41.5; *scupini* Zone, Salzgitter-Salder, bed 41

11 – *Mytiloides striatoconcentricus* (GÜMBEL); original to *I. striatoconcentricus striatoconcentricus* GÜMBEL as given by TRÖGER (1967)

9, 13 – *Inoceramus lusatiae* ANDERT;
9 – UW: Sa 39.3; *scupini* Zone, Salzgitter-Salder, bed 39
13 – UW: Sa 39.5; *scupini* Zone, Salzgitter-Salder, bed 39

All figures in natural size

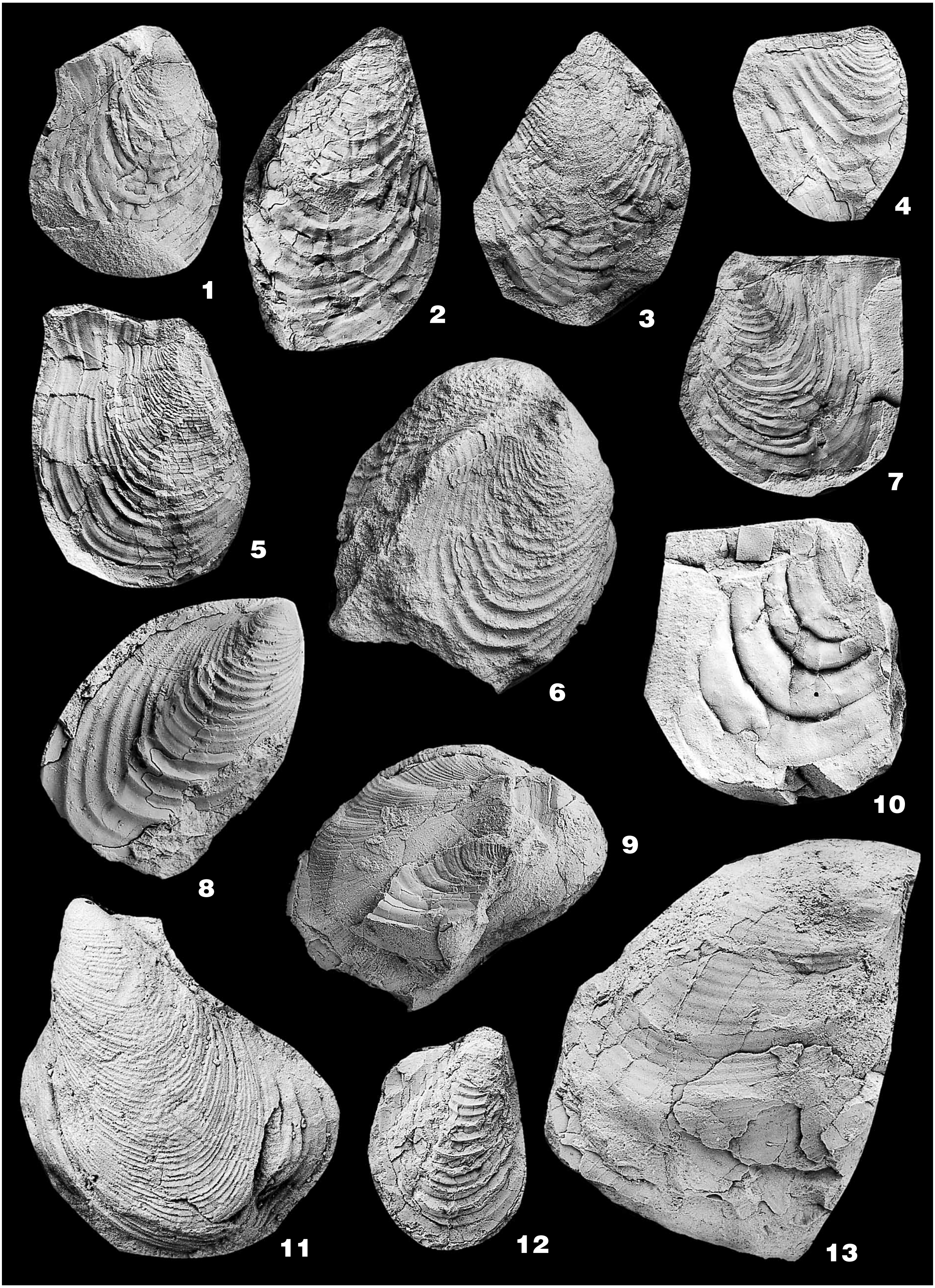
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PLATE 2

Inoceramus lusatiae (ANDERT); unregistered specimens from ANDERT's original collection from the topmost Turonian of the Sonnenberg near Waltersdorf (*see* WALASZCZYK 1996, Fig. 1 for location), Saxony, SE Germany; housed in the State Museum of Mineralogy and Geology in Dresden, Germany

4 – Lectotype, original to ANDERT (1911, Pl. 2, Fig. 1, Pl. 8, Fig. 3)

All figures in natural size

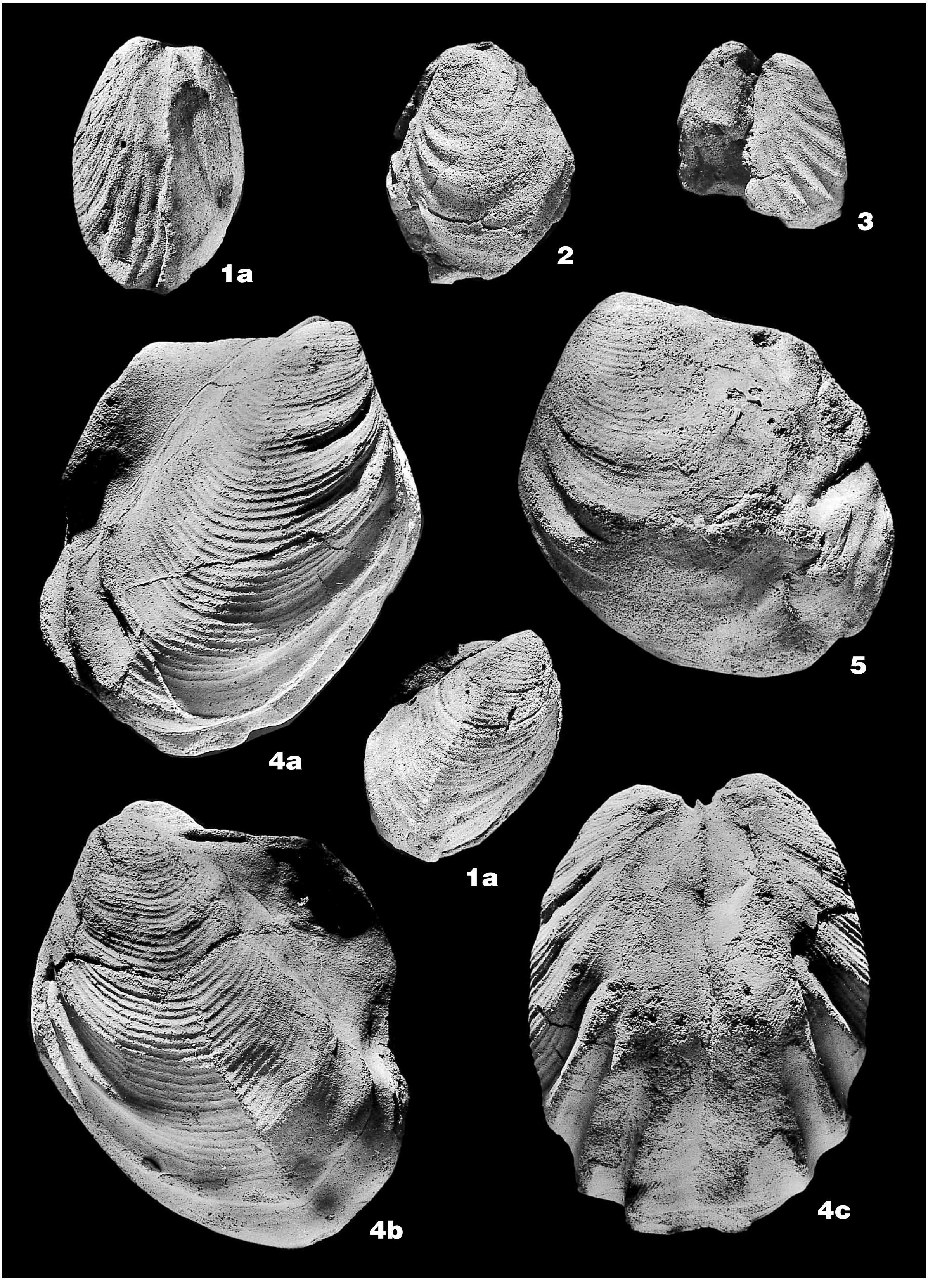
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PLATE 3

1, 3-6 – *Inoceramus lusatiae* ANDERT

1 – UW: Sa 39.4, *scupini* Zone, Salzgitter-Salder, bed 39, *scupini* Zone; 3-6 – unregistered specimens from ANDERT's original collection from the topmost Turonian of the Sonnenberg near Waltersdorf, SE Germany; housed at the State Museum of Mineralogy and Geology in Dresden, Germany; 5 – original to ANDERT (1911, Pl. 3, Fig. 3) (*see* Pl. 4, Fig. 7 for posterior and LV view)

2 – *Inoceramus annulatus* GOLDFUSS; lectotype, the photograph after the plaster cast in the collection of the Geological Survey of Lower Saxony, Germany

All figures in natural size


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PLATE 4

1-7 – *Inoceramus lusatiae* (ANDERT); unregistered specimens from ANDERT's original collection from the topmost Turonian of the Sonnenberg near Waltersdorf, Saxony, SE Germany; housed in the State Museum of Mineralogy and Geology, Dresden, Germany

7 – Original to ANDERT (1911, Pl. 3, fig. 3) (*see* Pl. 3, Fig. 5 for the RV view)

All figures in natural size


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PLATE 5

1, 3-7, 9-13, 15-18 – *Cremnoceramus waltersdorfensis waltersdorfensis* (ANDERT)

1 – UW: SW.4-5.200, *erectus* Zone, Słupia Nadbrzeżna; 3 – FU: Sa 45.3, *waltersdorfensis* Zone, Salzgitter-Salder, bed 45; 4 – FU: Sa 47.4; *erectus* Zone, Salzgitter-Salder, bed 47 (*erectus* I Event);

5 – FU: Sa 45.4, *waltersdorfensis* Zone, Salzgitter-Salder, bed 45; 6 – FU: Sa 46.2, *waltersorfensis* Zone, Salzgitter-Salder, bed 46; 7 – FU: Sa 45.1, *waltersdorfensis* Zone, Salzgitter-Salder, bed 45

9 – FU: Sa 46.1, *waltersdorfensis* Zone, Salzgitter-Salder, bed 46; 10 – FU: Sa 46.3, *waltersdorfensis* Zone, Salzgitter-Salder, bed 46; 11 – UW: SW.3.11, *waltersdorfensis* Zone, Słupia Nadbrzeżna; 12 – UW: SW.3.38, *waltersdorfensis* Zone, Słupia Nadbrzeżna; 13 – FU: Sa 45.2, *waltersdorfensis* Zone, Salzgitter-Salder, bed 45; 15 – UW: SW.4-5.2, *erectus* Zone, Słupia Nadbrzeżna; 16 – UW: SW.4-5.3, *erectus* Zone, Słupia Nadbrzeżna; 17 – UW: SW.3.37, *waltersdorfensis* Zone, Słupia Nadbrzeżna;18 – UW: SW.3.57, *waltersdorfensis* Zone, Słupia Nadbrzeżna

2, 8 – *Cremnoceramus waltersdorfensis hannovrensis* (HEINZ); *hannovrensis* Zone (*hannovrensis* Event), Salzgitter-Salder, bed 52 (earliest *hannovrensis*); 2 – FU: Sa 52.1; 8 – FU: Sa 52.2

14 – *Cremnoceramus deformis erectus* (MEEK); FU: Sa 47.3; *erectus* Zone, Salzgitter-Salder, bed 47

All figures in natural size

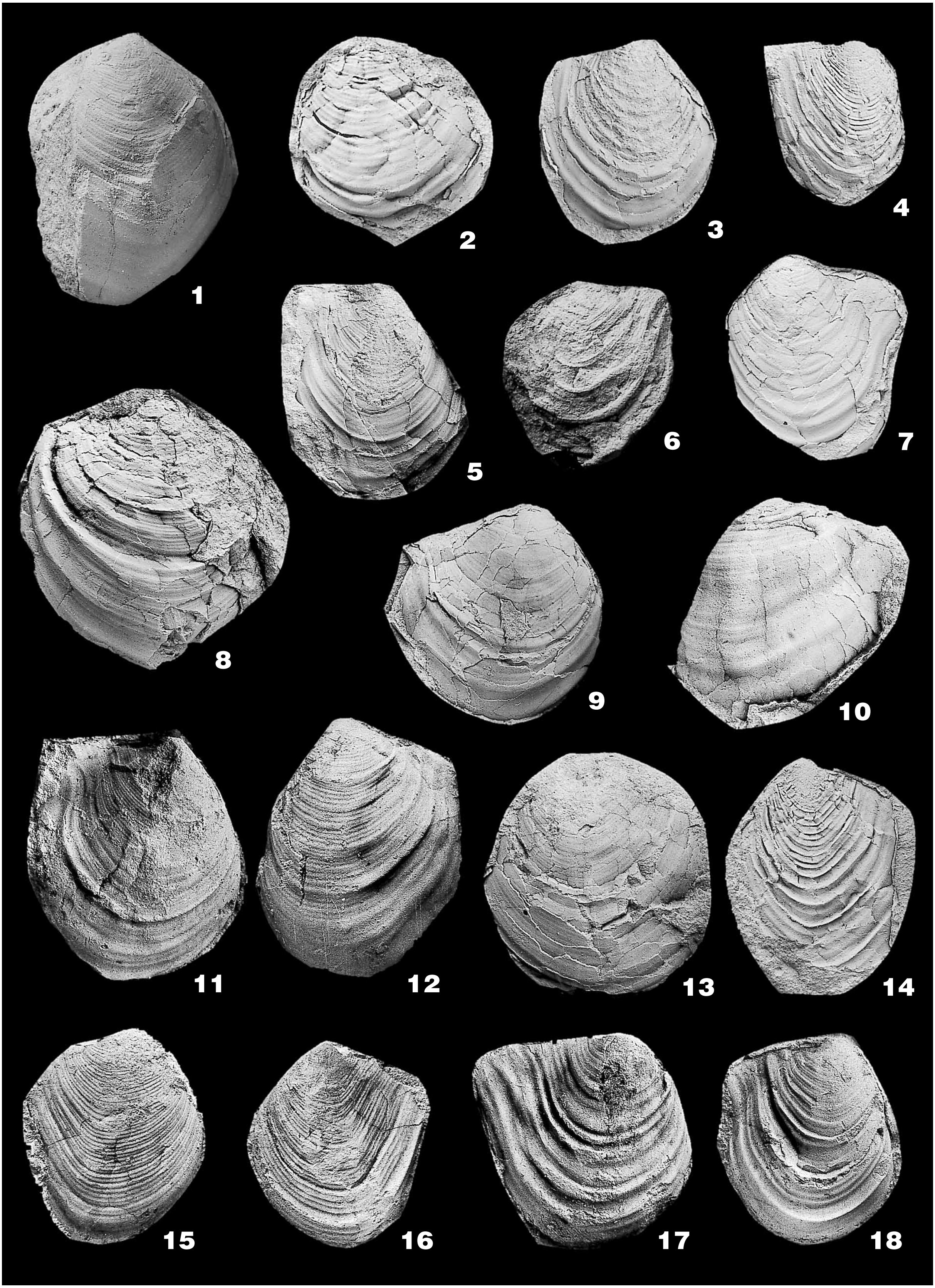
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PLATE 6

1-6, 8 – *Cremnoceramus deformis erectus* (MEEK)
1 – UW: 1.K12.0.89, *erectus* Zone, Kolonka 2 section (*see* Text-fig. 4 for location); 2 – GS: 1401.II.138, *erectus* Zone, Brzezno (*see* WALASZCZYK 1992, for location); 3 – GS: POŻARYSKI's collection, Słupia Nadbrzeżna; 4 – *Inoceramus sowerbyi* PAVLOVA; Khodzal-Mahi section, Dagestanian Caucasus, Russia; Museum of the Moscow State University, Specimen No. 17120; 5 – GS: POŻARYSKI's collection, Słupia Nadbrzeżna; 6 – UW: 1.K12.0.85, *erectus* Zone, Kolonka 2 section (*see* Text-fig. 4 for location); 6a – lateral view, 6b – anterior view; 8 – UW: 1.SW.4-5.73, *erectus* Zone, Słupia Nadbrzeżna

7 – *Cremnoceramus rotundatus* (FIEGE), lectotype; Ruhrland Museum, Essen, Germany

All figures in natural size

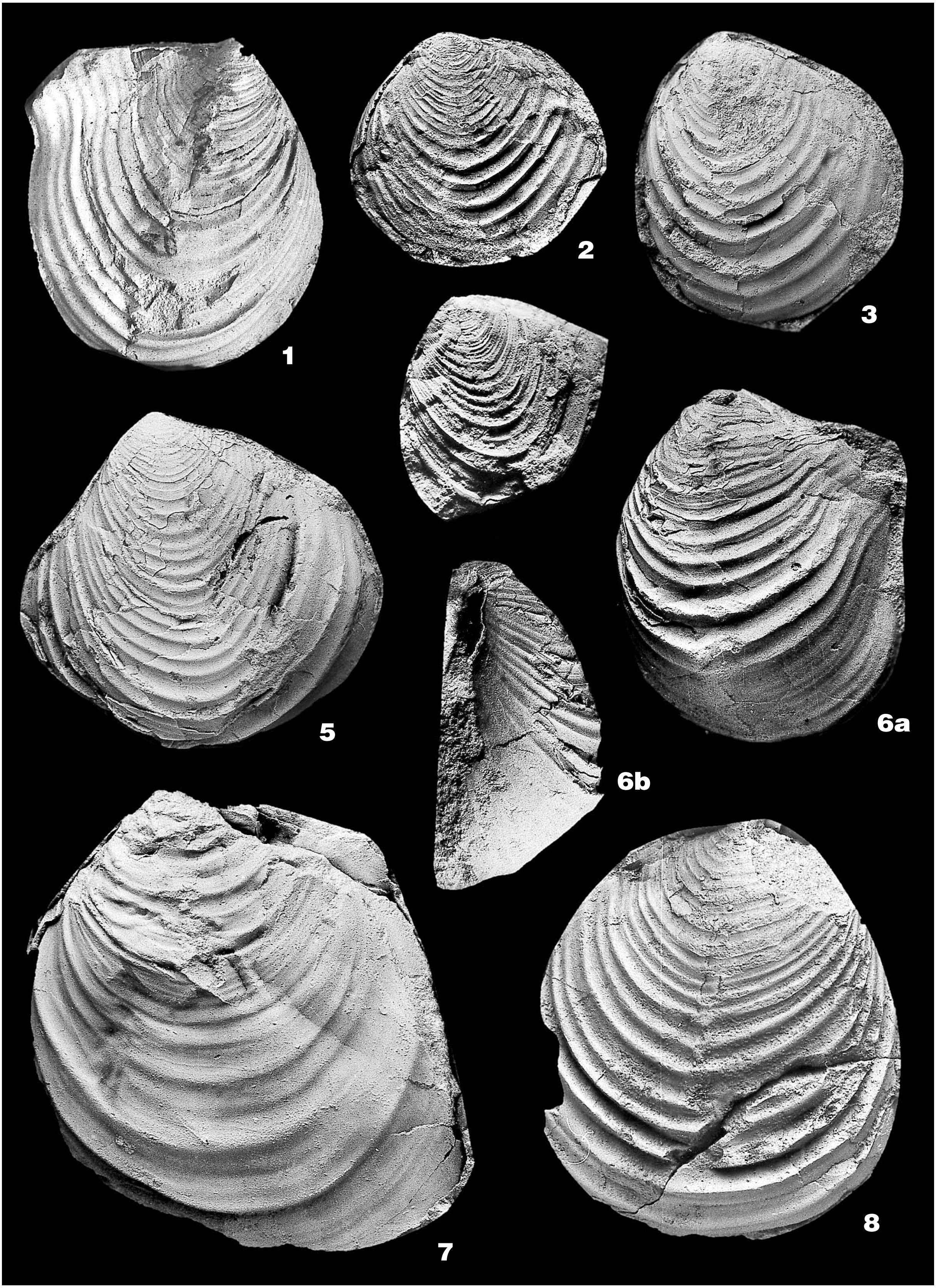
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PLATE 7

Cremnoceramus deformis erectus (MEEK)

1 – UW: Sa 47.4, *erectus* Zone, Salzgitter-Salder, bed 47
2 – UW: Sa 47.1, *erectus* Zone, Salzgitter-Salder, bed 47
3 – FU: Sa 47.2, *erectus* Zone, Salzgitter-Salder, bed 47
4 – FU: Sa 47.5, *erectus* Zone, Salzgitter-Salder, bed 47
5 – UW: Sa 47.6, *erectus* Zone, Salzgitter-Salder, bed 47
6 – FU: Sa 47.7, *erectus* Zone, Salzgitter-Salder, bed 47
7 – FU: Sa 53.1, *erectus* Zone, Salzgitter-Salder, bed 53
8 – UW: Sa 49.7, *erectus* Zone, Salzgitter-Salder, bed 49

All figures in natural size

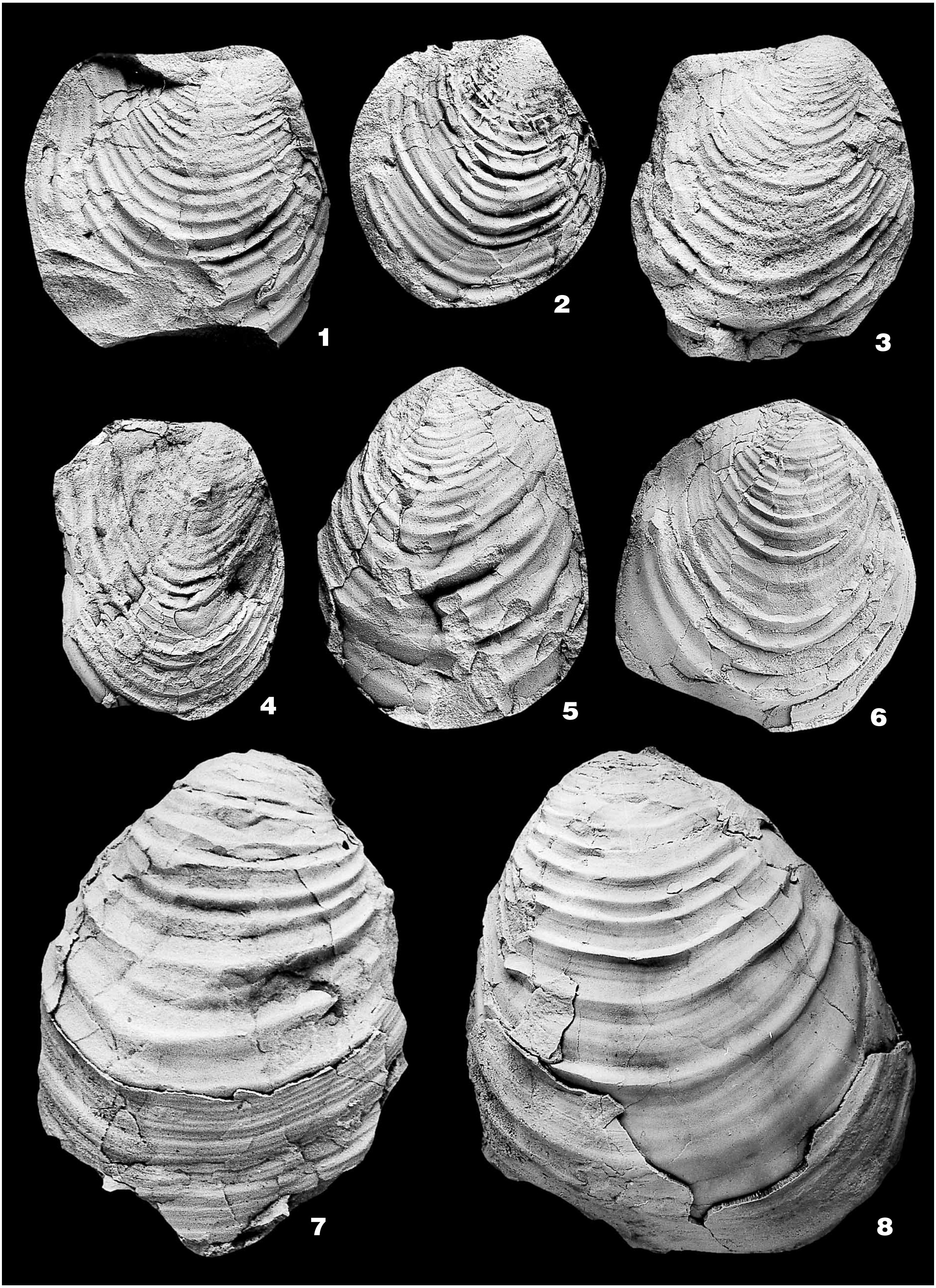

PLATE 8

Cremnoceramus deformis erectus (Meek)

1 – FU: Sa 47.8, *erectus* Zone, Salzgitter-Salder, bed 47
2 – UW: Sa 49.5, *erectus* Zone, Salzgitter-Salder, bed 49
3 – UW: Sa 49.3, *erectus* Zone, Salzgitter-Salder, bed 49
4 – UW: Sa 49.11, *erectus* Zone, Salzgitter-Salder, bed 49
5 – UW: Sa 49.9, *erectus* Zone, Salzgitter-Salder, bed 49
6 – UW: Sa 49.4, *erectus* Zone, Salzgitter-Salder, bed 49
7 – UW: SW.6.201, *erectus* Zone, Słupia Nadbrzeżna section (*erectus* II Event)
8 – UW: Sa 49.8, *erectus* Zone, Salzgitter-Salder, bed 49

All figures in natural size

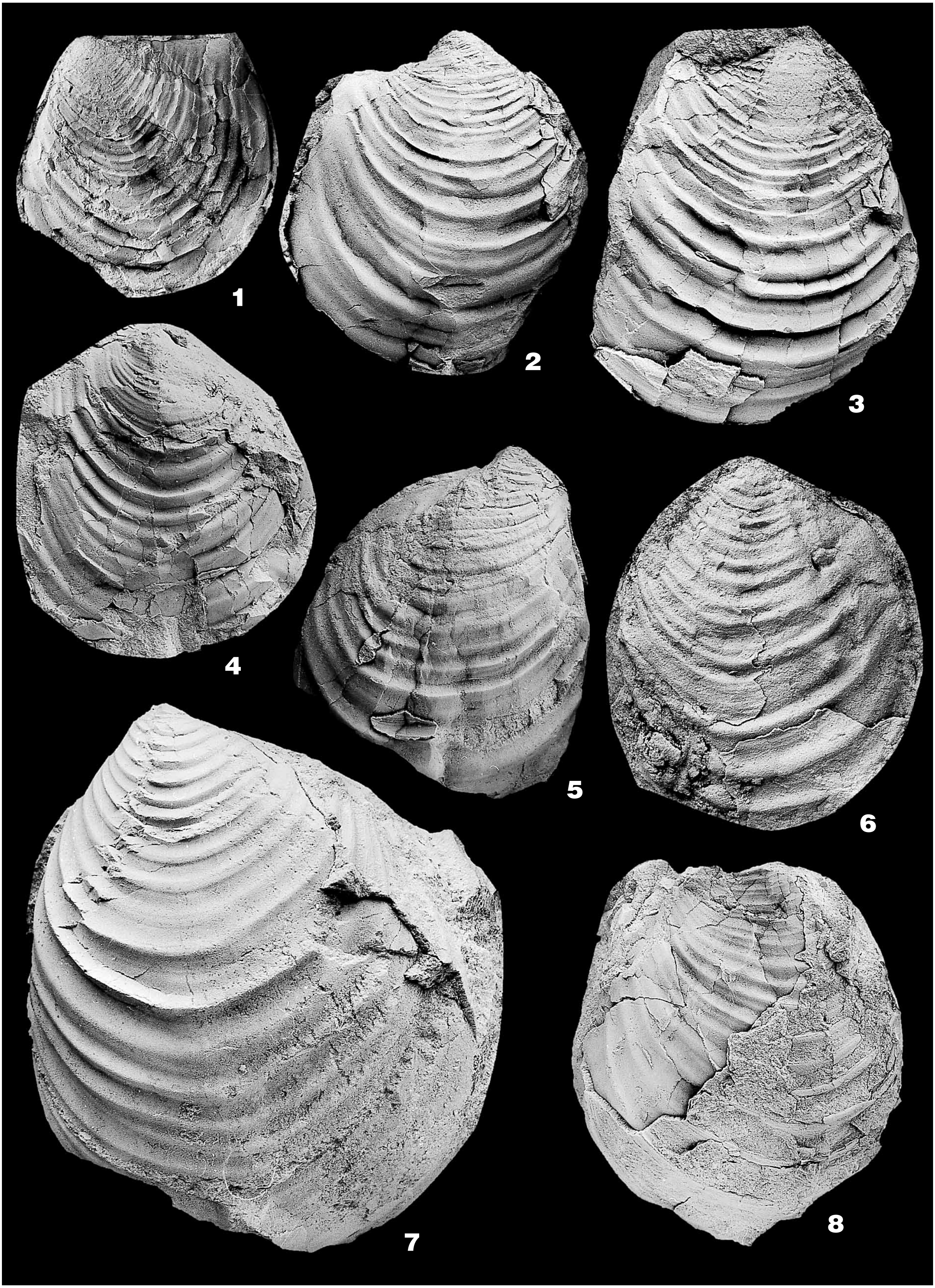
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PLATE 9

1, 3-6 – *Cremnoceramus deformis erectus* (MEEK)
- 1 – UW: Sa 49.6, *erectus* Zone, Salzgitter-Salder, bed 49
- 3 – UW: Sa 49.2, *erectus* Zone, Salzgitter-Salder, bed 49
- 4 – UW: Sa 75.1, basal *inconstans* Zone, Salzgitter-Salder, bed 75
- 5 – UW: SW.6.202, *erectus* Zone, Słupia Nadbrzeżna section (*erectus* II Event)
- 6 – UW: Sa 49.10, *erectus* Zone, Salzgitter-Salder, bed 49

2 – *Cremnoceramus waltersdorfensis hannovrensis* (HEINZ); UW: Sa 52.1, *hannovrensis* Zone, Salzgitter-Salder, bed 52

All figures in natural size

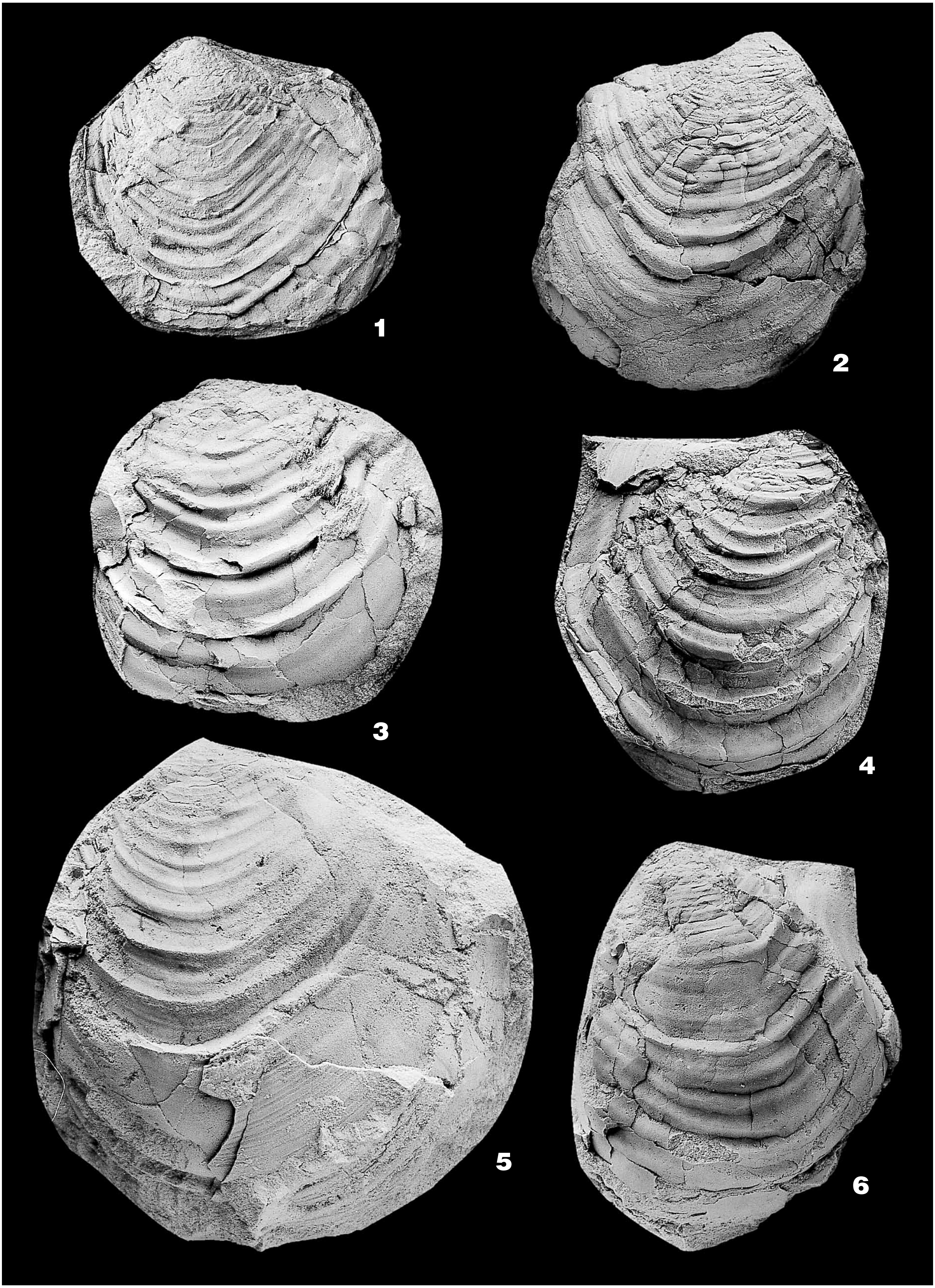
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PLATE 10

1-4, 6 – *Cremnoceramus deformis erectus* (MEEK)
1 – FU: Sa 47.9, *erectus* Zone, Salzgitter-Salder, bed 47
2 – UW: Sa 49.1, *erectus* Zone, Salzgitter-Salder, bed 49
3 – UW: Sa 49.12, *erectus* Zone, Salzgitter-Salder, bed 49
4 – UW: Sa 49.13, *erectus* Zone, Salzgitter-Salder, bed 49
6 – UW: Sa 49.14, *erectus* Zone, Salzgitter-Salder, bed 49

5 – *Inoceramus lusatiae* ANDERT/*annulatus* GOLDFUSS; UW: SW. 6.203, *hannovrensis* Zone, Słupia Nadbrzeżna (*hannovrensis* Event)

All figures in natural size

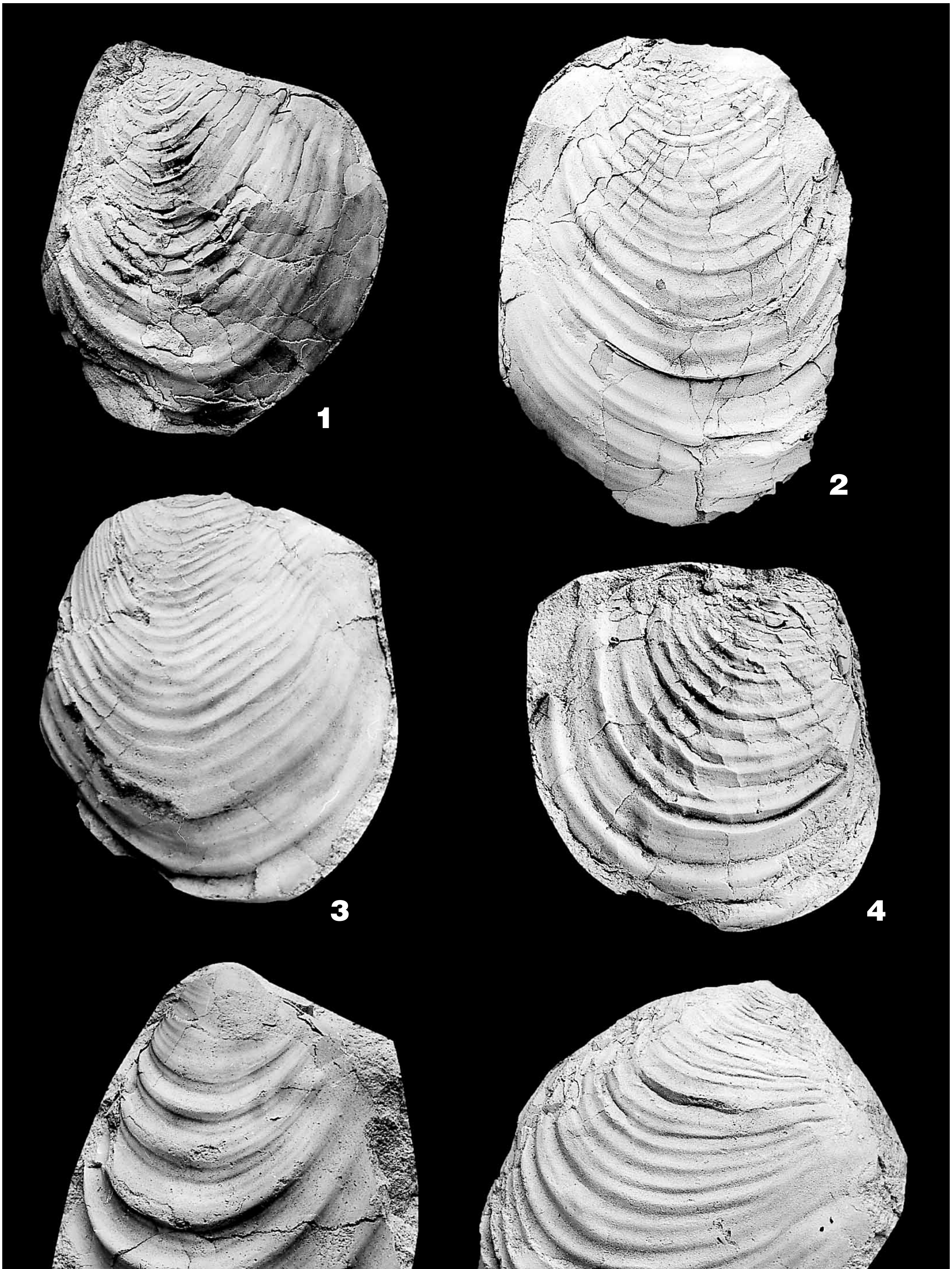

PLATE 11

1, 3, 5-7 – *Cremnoceramus deformis erectus* (MEEK); GS: POŻARYSKI's collection, *erectus* Zone, Słupia Nadbrzeżna

2 – *Cremnoceramus waltersdorfensis hannovrensis* (HEINZ); GS: POŻARYSKI's collection, *hannovrensis* Zone, Słupia Nadbrzeżna

4 – *Cremnoceramus denselamellatus* (KOTSYUBINSKY); UW: SW.7.39, *hannovrensis* Zone, Słupia Nadbrzeżna

All figures in natural size

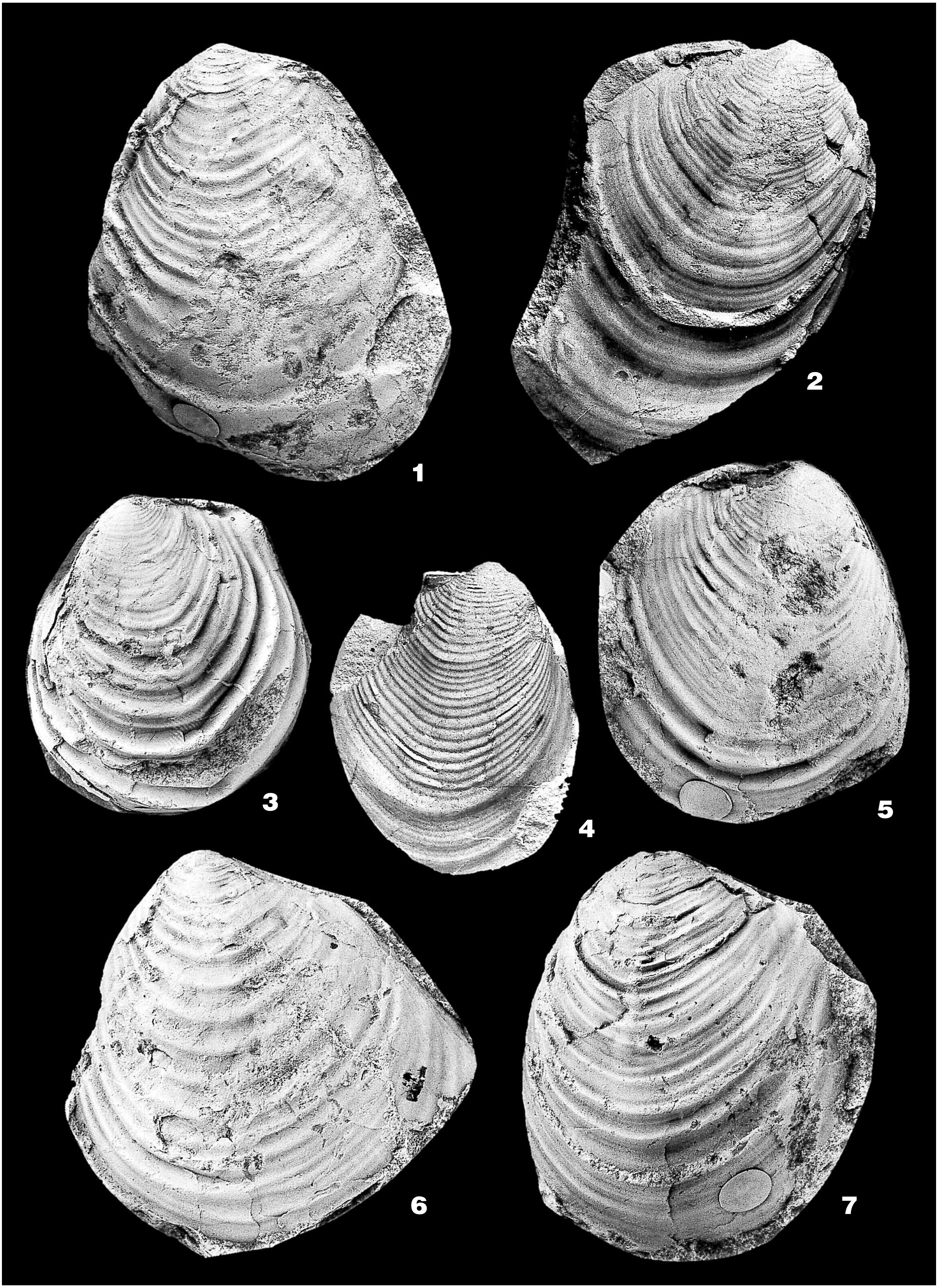
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PLATE 12

1-4 – *Cremnoceramus waltersdorfensis hannovrensis* (HEINZ);
1-3 – GS: POŻARYSKI's collection, *hannovrensis* Zone, Słupia Nadbrzeżna;
4 – UW: SW.7.1, *hannovrensis* Zone, Słupia Nadbrzeżna

5-6 – *Cremnoceramus rotundatus* (FIEGE)
5 – GS: Spławy section, *hannovrensis* Zone, northern periphery of the Holy Cross Mountains, Central Poland
6 – UW: SW.9.1, *hannovrensis* Zone, Słupia Nadbrzeżna (*erectus* III Event)

All figures in natural size

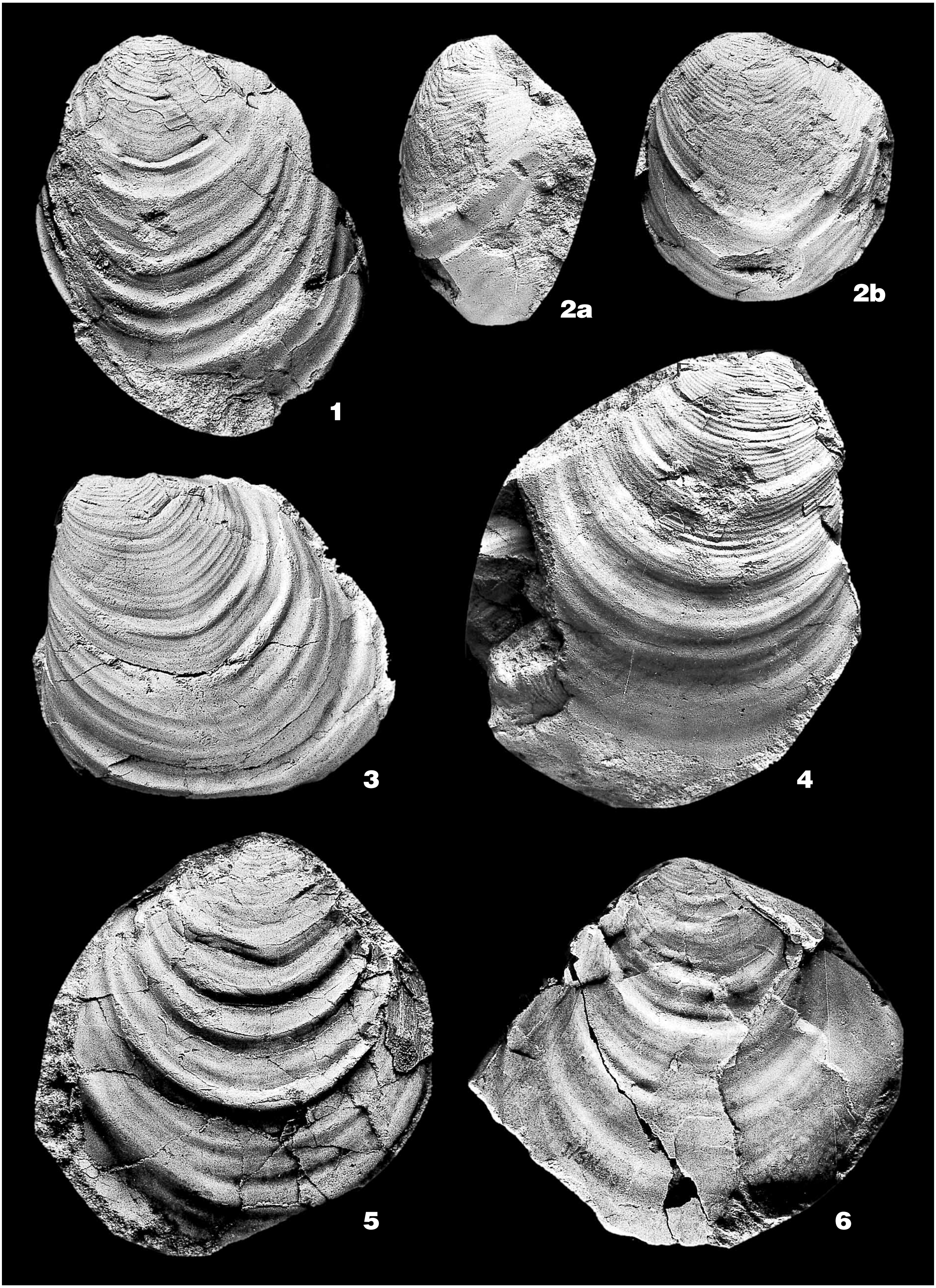
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PLATE 13

1 – *Cremnoceramus deformis erectus* (MEEK); Specimen FU: Sa 49.15, *erectus* Zone, Salzgitter-Salder, bed 49

2-7 – *Cremnoceramus waltersdorfensis hannovrensis* (HEINZ); 2 – FU: Sa 52.3, *hannovrensis* Zone, Salzgitter-Salder, bed 52; 3-6 – *hannovrensis* Zone, without precise location, Salzgitter-Salder; 7 – UW: Sa 75.2, basal *inconstans* Zone, Salzgitter-Salder, bed 75

All figures in natural size

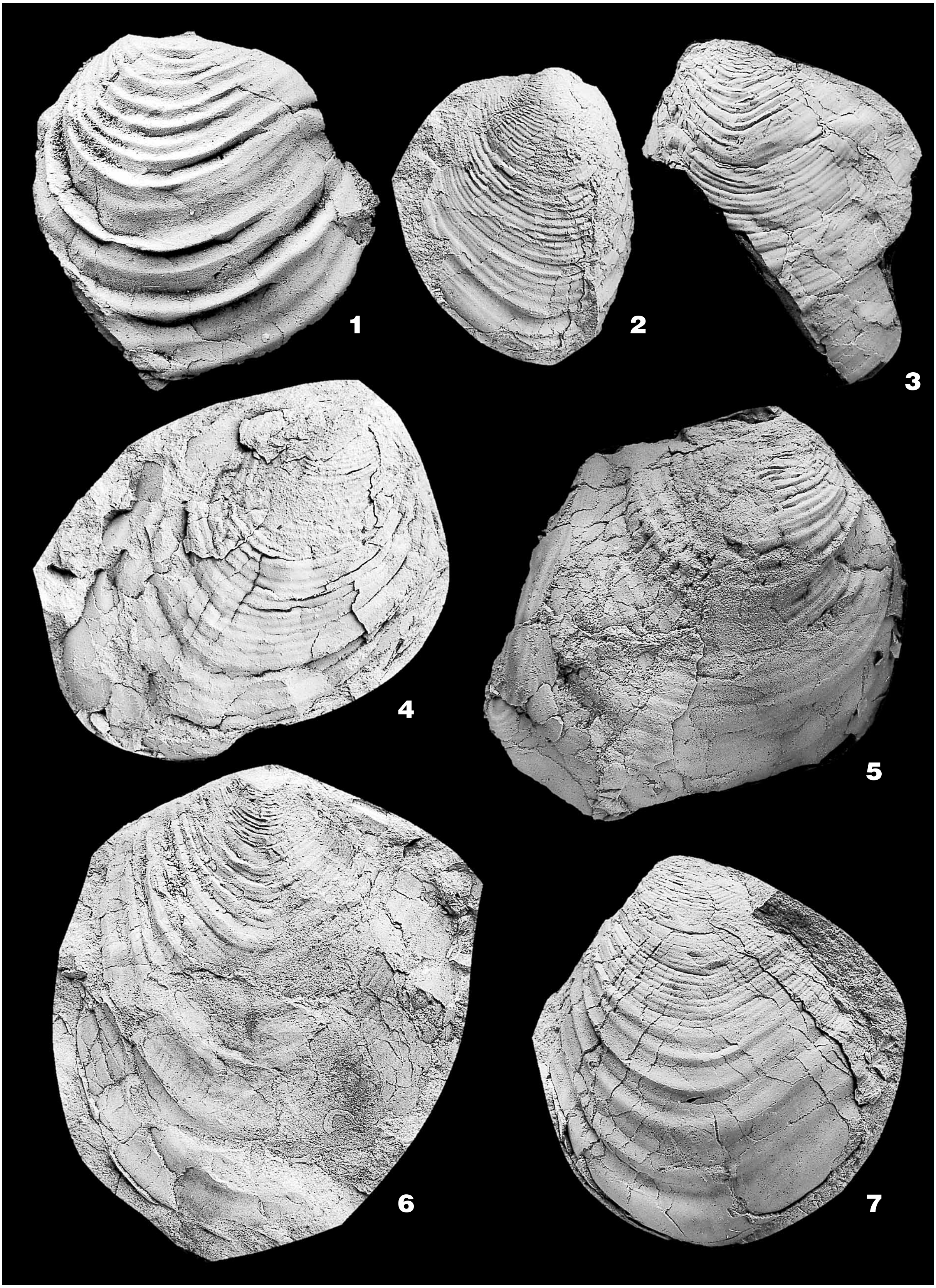
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PLATE 14

1-2 – *Inoceramus vistulensis* WALASZCZYK;
1 – UW: Sa 52.4, basal *hannovrensis* Zone, Salzgitter-Salder, bed 52
2 – UW: SW.6.14, basal *hannovrensis* Zone, Słupia Nadbrzeżna (*hannovrensis* Event)

3-7 – *Tethyoceramus* sp.
3 – FU: Sa 53.2, *hannovrensis* Zone, Salzgitter-Salder, bed 53 (*erectus* III Event)
4 – UW: Sa 53.10, *hannovrensis* Zone, Salzgitter-Salder, bed 53 (*erectus* III Event)
5 – UW: Sa 52.5, basal *hannovrensis* Zone, Salzgitter-Salder, bed 52
6 – FU: Sa 53.3, *hannovrensis* Zone, Salzgitter-Salder, bed 53 (*erectus* III Event)
7 – UW: unregistered, Wielkanoc quarry, Polish Jura Chain (*see* WALASZCZYK 1992, for locality details; *crassus*/*deformis* Zone)

All figures in natural size


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PLATE 15

1-3 – *Cremnoceramus waltersdorfensis waltersdorfensis* (ANDERT);
1 – BMNH LL. 28251, no locality or horizon data, inferred Upper Chalk, *Micraster cortestudinarium* Zone (Lower Coniacian), England
2 – BMNH LL. 28252, as above
3 – BMNH L. 81293, Upper Chalk, *Micraster cortestudinarium* Zone (Lower Coniacian), Hillsborough, near Swaffham, Norfolk, eastern England

4-5 – *Cremnoceramus denselamellatus* (KOTSYUBINSKY); GS: POŻARYSKI's collection, *hannovrensis* Zone, Słupia Nadbrzeżna

6 – *Cremnoceramus deformis erectus*; GS: POŻARYSKI's collection, *erectus* Zone, Słupia Nadbrzeżna section;

7 – *Cremnoceramus* sp. of the *deformis* lineage; FU: Sa 53.5, *hannovrensis* Zone, Salzgitter-Salder, bed 53

All figures in natural size


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PLATE 16

1-2, 5-6 – *Cremnoceramus crassus inconstans* (Woods); basal *inconstans* Zone, Salzgitter-Salder, bed 75
1 – UW: Sa 75.2
2 – UW: Sa.75.3
5 – UW: Sa 75.4
6 – UW: Sa 75.5

3-4 – *Tethyoceramus* sp.; *hannovrensis* Zone, Salzgitter-Salder, bed 53
3 – FU: Sa 53.6
4 – FU: Sa 53.7

All figures in natural size

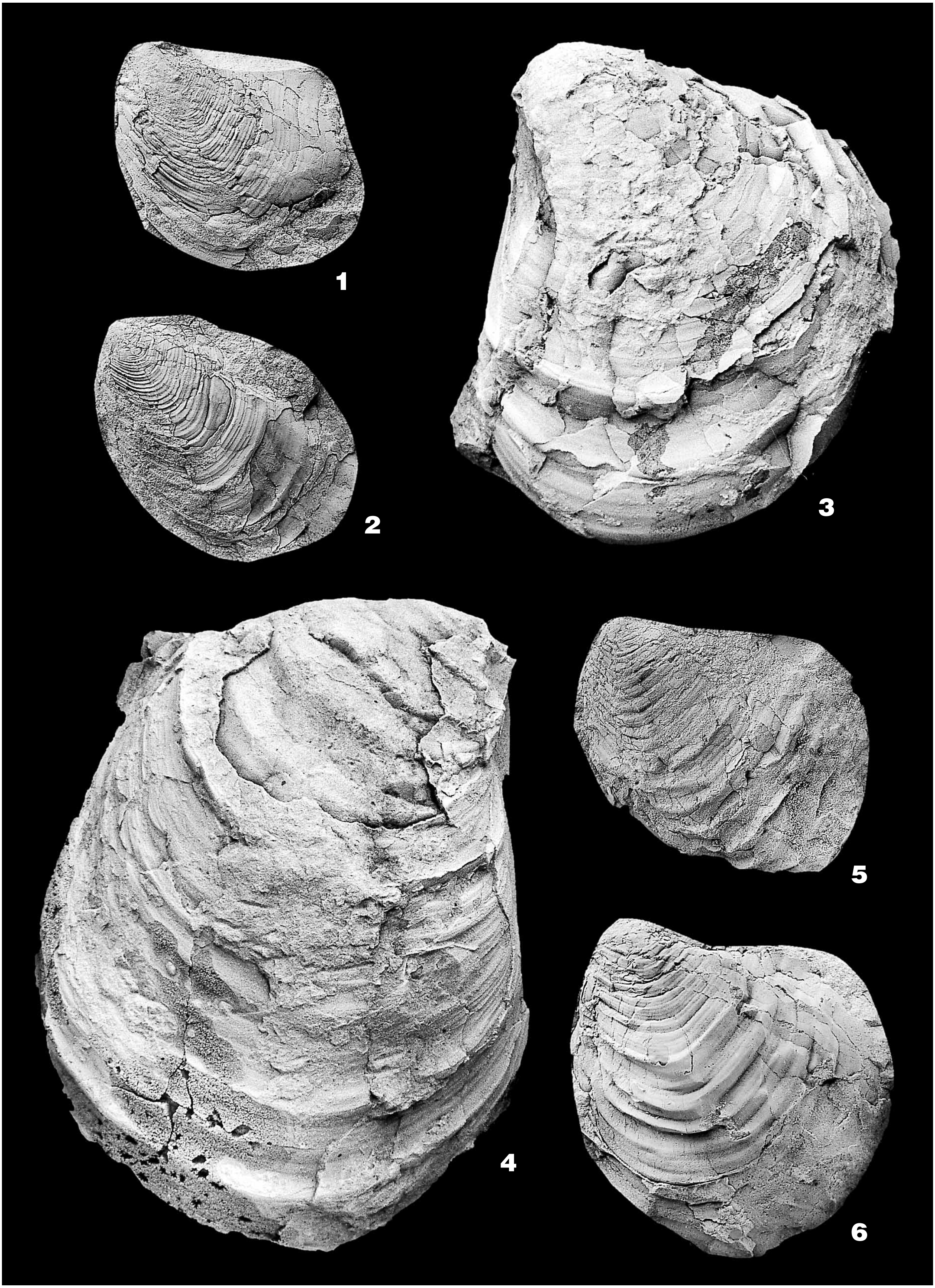
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PLATE 17

1, 4 – *Tethyoceramus* sp.; *hannovrensis* Zone, Salzgitter-Salder, bed 53
1 – FU: Sa 53.8
4 – FU: Sa 53.9

2 – *Cremnoceramus crassus crassus* (PETRASCHECK); BMNH unregistered, fibreglass replica of specimen in Geological Survey of Lower Saxony, *crassus-deformis* Zone (inferred), Lüneburg-Zeltberg, Lower Saxony, Germany (? HEINZ' collection)

3 – *Cremnoceramus waltersdorfensis waltersdorfensis* (ANDERT) (=*Inoceramus striatus* MANTELL); BMNH LL. 28253, no locality or horizon data, inferred Upper Chalk, *Micraster cortestudinarium* Zone, England

5 – *Cremnoceramus denselamellatus* (KOTSYUBINSKY); GS: POŻARYSKI's collection, *hannovrensis* Zone, Słupia Nadbrzeżna

All figures in natural size


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PLATE 18

1-2, 4 – *Tethyoceramus* sp.

1 – UW: unregistered specimen from the *crassus-deformis* Zone of Crimea

2 – UW: Kl.1.3.2, *hannovrensis* Zone, Kolonka section

4 – UW: Sa 53.10, *hannovrensis* Zone, Salzgitter-Salder, bed 53

3 – *Inoceramus annulatus* GOLDFUSS; UW: SW, unregistered, *hannovrensis* Zone, Słupia Nadbrzeżna

All figures in natural size

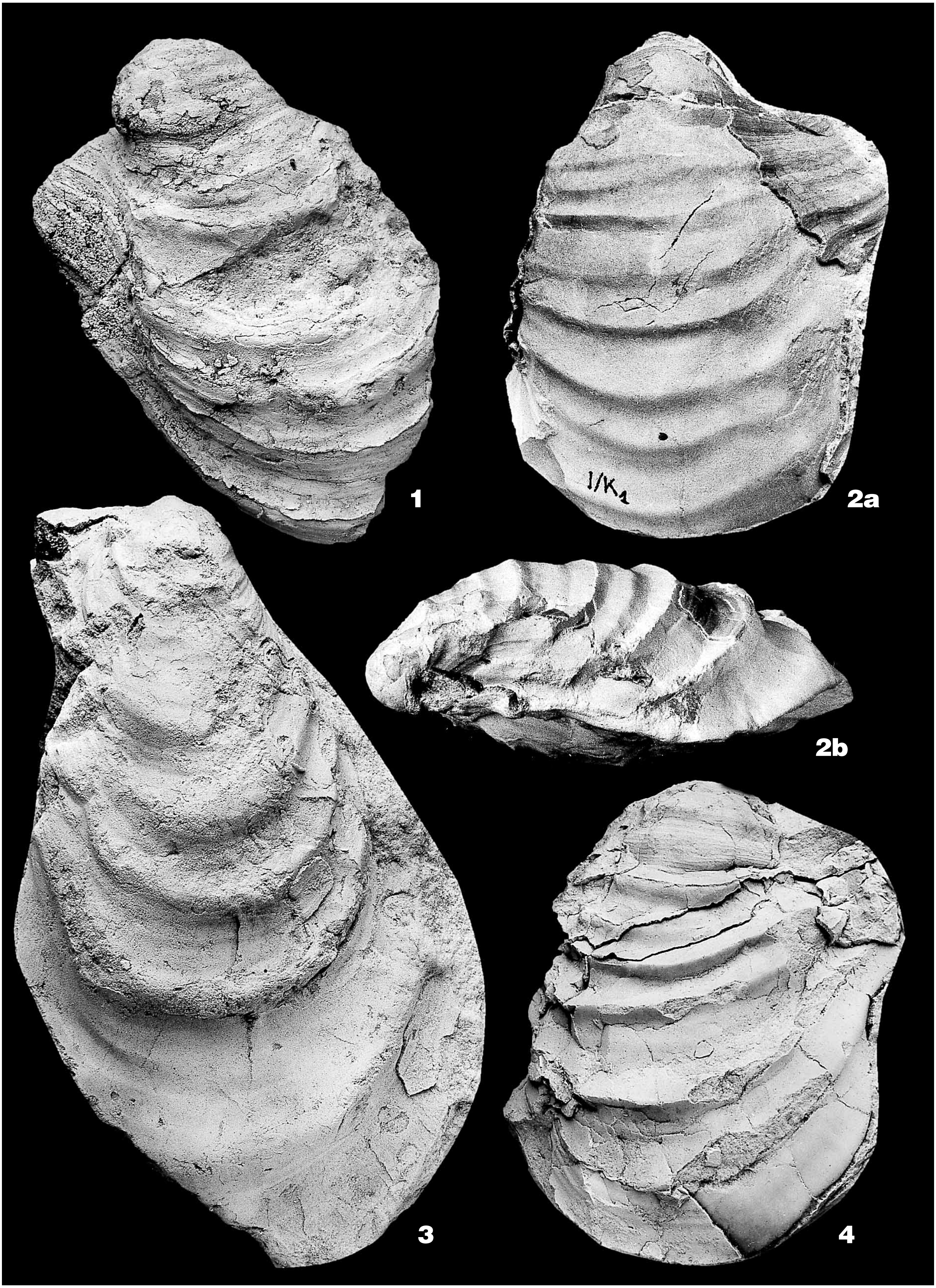

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PLATE 19

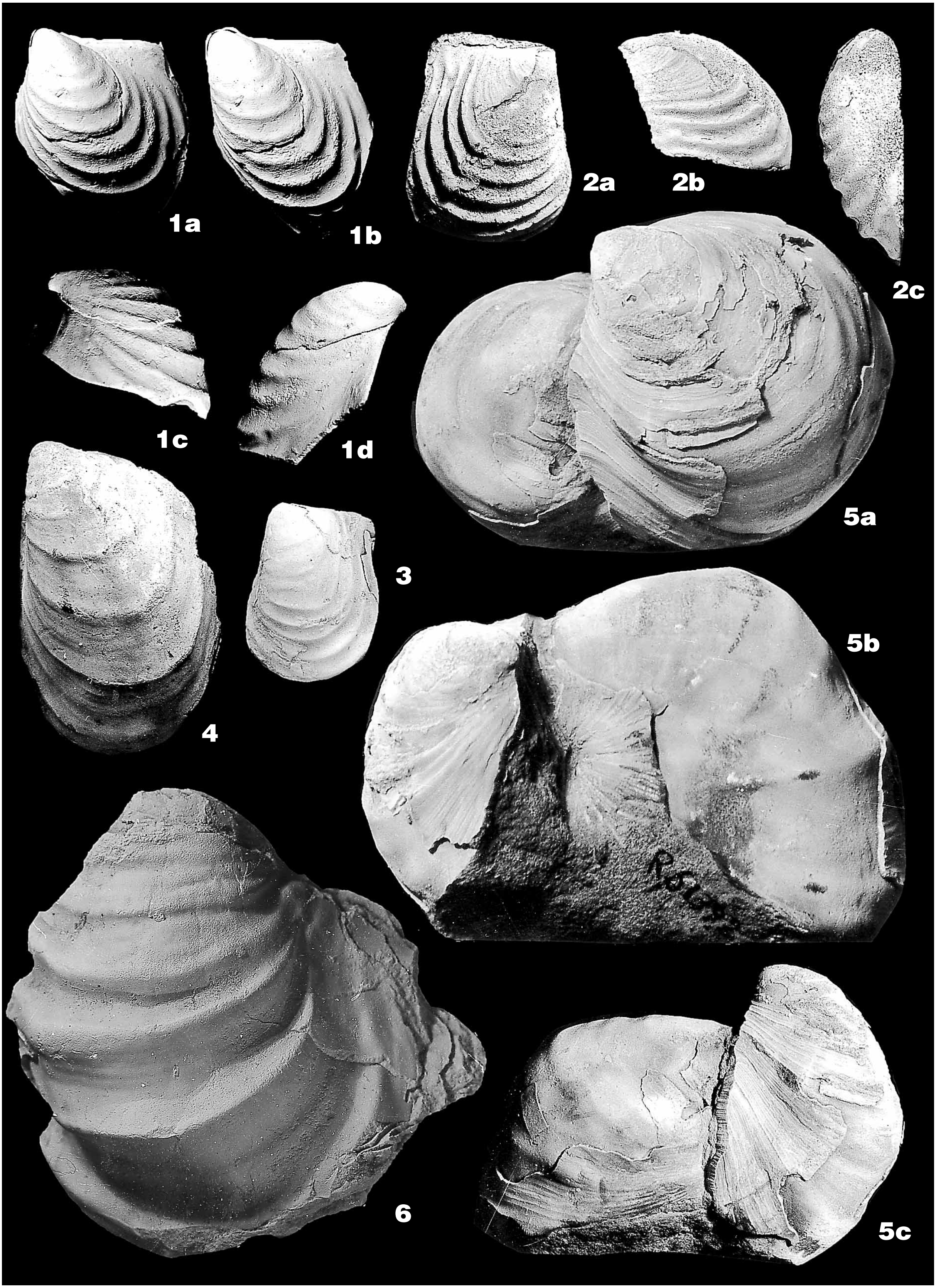
1 – *Mytiloides costellatus* (WOODS); holotype; Upper Chalk, Chalk Rock, *Sternotaxis plana* Zone (Upper Turonian); Cuckhamsley, England; SM B.4564 (original to WOODS 1912, Pl. 54, Fig. 5); × 1.3

2-3 – *Inoceramus hoepeni* HEINZ; Upper Turonian; Antsalova – Bekopaka, Madagascar; Museum of Natural History, Paris; × 1.3
2 – Holotype; original to HEINZ (1933, Pl. 18, Fig. 2)
3 – Syntype; original to HEINZ (1933, Pl. 18, Fig. 3)

4 – *Tethyoceramus madagascariensis* (HEINZ); Lower Coniacian of Manasora at Onilahy, Madagascar; Museum of Natural History, Paris; holotype; original to HEINZ (1933, Pl. 20, Fig. 2); × 1

5 – *Tethyoceramus basseae* (SORNAY); original to *Tethyoceramus ernsti* of HEINZ (1933, Pl. 19, fig. 1); Museum of Natural History, Paris; × 1

6 – *Tethyoceramus ernsti* HEINZ; original to *Inoceramus brongniarti* of INOSTRANZEFF (1896, Pl. 7, Fig. 13); Museum of the State University, Sankt-Petersburg, Russia; × 1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