

Marine Palaeobiogeography of the Central European Late Cretaceous

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Late Cretaceous shallow marine mollusc assemblages show a distinct vertical differentiation into those of the inner and the outer shelf. The realms Theia (pro Tethys) and Kalais (pro Boreal, Temperate) can only be distinguished by means of inner shelf assemblages. Outer shelf assemblages are uniform across realm boundaries. The boundary between the inner and the outer shelf is biologically significant. It is interpreted to reflect the lower boundary of the tropical/subtropical surface mixed layer and extended as far north as southern Sweden in the Late Cretaceous.

Key words: Palaeobiogeography, marine, Late Cretaceous, Europe.

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Marine surface water organisms are most sensitive to the thermic regime. Recent biogeographical provinces, realms or biomes are therefore defined based on the distribution of surface water biota (Masse 1992; Longhurst 1998). During late Cretaceous times, three marine realms are distinguished on the northern hemisphere (Kauffman 1967): the Tethys or Mesogean, the 'North temperate' or 'Boreal', and the 'Circumpolar'. They are defined by the horizontal distribution of shallow-water benthic organisms (Masse 1992).

For formal and objective reasons I have introduced the new names Theia and Kalais for the Cretaceous realms called Tethys and 'Boreal' (Kollmann 2002). The horizontal distribution of Lower Cretaceous benthic organisms in these two realms has been discussed in detail by Masse (1992) and is generally valid also for the Upper Cretaceous. The present paper deals with the bathymetric distribution of gastropod assemblages and other selected groups on the shelf and interprets them within a palaeoecological framework. The main goal is to discriminate marine layers by their assemblages, which is essential for a better understanding of Cretaceous palaeobiogeography.

Inner and outer shelf

Sedimentological and palaeobiological parameters provide simple qualitative criteria for the distinction

of inner and outer shelf environments. Particle size and sorting depend on physical conditions and source (Reineck & Singh 1973; Gray 1997). The inner shelf is characterized by a reworking of sediments and accumulations of hard parts of organic origin due to water turbulence. The diversity is high. Bivalves are generally disarticulated. Hard parts are not in life position and commonly fractured.

The outer shelf is characterized by fine-grained sediments deposited under physically stable conditions. Fossil assemblages are of moderate to low diversity. In the proximal outer shelf *Turritella* is common (Hertweck 1971; Reineck & Singh 1973; Allmon 1988). Inoceramids have proved to be valuable for indicating water energy (Kauffman 1967). Byssate taxa were restricted to high-energy environments (inner shelf) while non-byssate, cup-shaped forms lived on the substrates of the outer shelf. Coral assemblages are valuable for determining the position of sedimentary environments in relation of the limits of the photic depth.

Kalaisian gastropod assemblages

Rocky shore, Marsh, Foreshore and inner shelf

Surlyk & Christensen (1974) have described the early Campanian rocky coast ecosystem of Ivö Klack

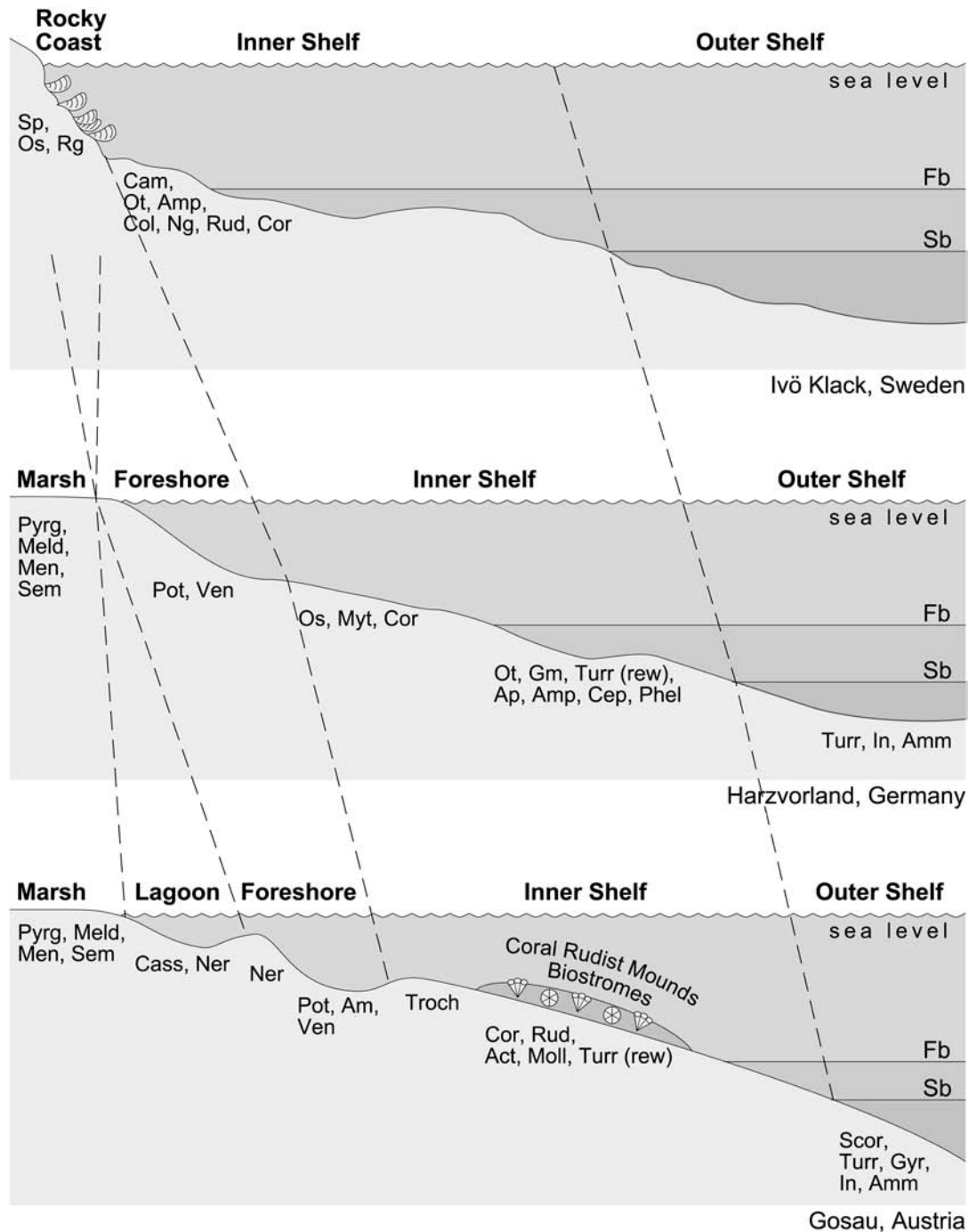


Fig. 1. Environmental correlation between two Kalaisian sections (Ivö Klack, Harzvorland) and a Theian section (Gosau).

Symbols: Fb Fair weather wave base. Sb Storm wave base.

Taxa: Act Acteonella, Am Amauropsis, Amm Ammonites, Amp Ampullinidae, Cam Campanilidae, Cass Cassiope, Col Colombellinae, Cor Hermatypic corals, Gm Gymnentome, Gyr Gyrodes, In Inoceramidae, Mel Melanopsis, Meld Malanoides, Moll Molluscs s.l., Myt Mytilidae, Ner Nerineidae, Ng Neogastropoda?, Os Ostreidae, Ot Otostoma, Pt Potamididae, Pyrg Pyrgulifera, Rg rock-clinging archaeogastropods, Rud Rudists, Sem Seminerita, Scor Single and pseudocolonial corals, Sp Spondylidae, Troch Trochactaeon, Turr Turritellidae, Turr (rew) reworked Turritellidae, Ven Veneridae. After Surlyk (1997, top); Martin (1939, mid) and Sanders *et al.* (1997, bottom).

(Scania, south Sweden; Fig. 1). Along the shoreline, a high-diversity oyster bank community with abundant spondylids flourished (Surlyk 1997). The gastropod fauna includes rock-clinging archaeogastropods of the littoral (patelliform groups and others). Inner shelf soft substrate mollusc assemblages of Ivö Klack consist of gastropod taxa such as Neritopsidae (genus *Otostoma*), Cerithiidae, Ampullinidae (?*Ampullina*), Colombellinae, large Campanilidae, and canaliculate taxa, possibly neogastropods (own observations on material of the Geologisk Museum, Copenhagen). From the same locality, a fauna of colonial corals of low diversity has been recorded (Voigt 1929; Surlyk & Christensen 1974).

Mertin (1939) was the first to develop a model of relative water depth and fossil ecology for near-shore late Cretaceous Kalaisian siliciclastic environments (Fig. 1). A gastropod fauna comprising *Pyrgulifera*, *Melania* and *Melanopsis* indicates marsh environments. The foreshore assemblage (Mertin's 'Cyrena-Cerithium assemblage') is characterized by bivalves (Veneridae) and gastropods of the family Potamididae. The *Ostrea-Arca-Mytilus* assemblage (Mertin 1939) in which a single taxon of colonial corals has been recorded marks the proximal inner shelf. The distal inner shelf is characterized by *Gymnentome*, Aporrhaidae, cephalaspideans, coccinas of reworked Turritellidae, as well as the byssate bivalve genus *Phelopteria*. The assemblage is representative of an environment below the fair weather wave base. Temporary storm waves have accumulated turritellids.

The inner shelf assemblage described by Kaunhowen (1898) from the 'upper beds' of Maastricht, Netherlands (= uppermost portion of the lower and parts of the upper 'series' of Maastricht by Voigt 1929) shows diverse Fissurellidae, Patellidae, Cerithioidea, Ampullinidae (*Gyrodes*), Aporrhaidae, Ampullinidae, and Cephalaspidea. Taxa considered as Nerinoidea in the earlier literature (van den Binkhorst 1861; Kaunhowen 1898) belong in fact to the Campaniloidea. The occurrence of both algal-feeding Fissurellidae and Patellidae along with predominantly filter feeders like Turritellidae indicates an environmental range between the rocky shore and the inner shelf/proximal outer shelf. Umbgrove (1925) recorded 36 taxa of scleractinian corals from Maastricht, both solitary and colonial.

Outer shelf

Most Late Cretaceous gastropod assemblages known from central and north Europe originate from the outer shelf (Favre 1869; Abdel-Gawad 1986; Holzap-

fel 1887–88, 1988–89; Fric 1893; Müller 1898; Ravn 1921; Cleevely & Morris 1987). Assemblages from Braunschweig and Ilsede (Müller 1898) and from Bavnodde on the island of Bornholm, Denmark (Ravn 1921, and own observations on material of the Geologisk Museum, Copenhagen) have yielded Pleurotomarioidea, Trochoidea, Amberleyidae (*Trochacanthus* and *Helicacanthus*), Turritellidae, Epitoniidae, Ampullinidae (*Gyrodes*) Cerithioidea, diverse Aporrhaidae, Volutoderminae, Cephalaspidea and the cup-shaped *Brunonia*. The cephalopod fauna of Braunschweig and Ilsede is diverse and contains both ammonites and Belemnites (Müller & Wolleermann 1906). In the basal Maastricht beds (Kaunhowen 1898), which have been deposited under outer shelf conditions, hexactinellid sponges and sponge spicules are abundant (Voigt 1929). Belemnites have been recorded from this part of the section. More distal outer shelf assemblages are of low diversity. Dominant elements are large, flat inoceramids (Sanders *et al.* 1997). These assemblages are not discussed in detail here.

Kalaisian versus Theian faunal elements

To a high extent, marsh and foreshore assemblages are similar in Kalais and Theia. Marsh assemblages are dominated by low-diversity *Pyrgulifera* assemblages (Mertin 1939; Herm 1977; Kowalke & Bandel 1996; Sanders *et al.* 1997). In both realms, the foreshore is characterized by Potamididae and bivalves like *Phelopteria* which Kauffman (1973) has considered as typically Kalaisian and the fast-burrowing Veneridae. In the Gosau group of the Eastern Alps (Austria), Nerinoidea and *Amauropsis* are common (Herm 1977; Sanders *et al.* 1997; Fig. 1). Nerinoidea have further been recorded, locally in mass occurrences, from shallow subtidal, protected environments ('lagoonal' in a broad sense, see Herm 1977). They may be associated with *Phelopteria* (Herm *et al.* 1979; Sanders & Baron-Szabo 1997; Sanders 1998), rare byssate inoceramids and radiolitid rudists which latter definitely preferred protected settings (Sanders 1996, 1998; Sanders & Pons 1999).

Differences between the realms are largest among inner shelf assemblages. Theian inner shelf assemblages are dominated by rudist mounds and biostromes (Masse 1982; Sanders *et al.* 1997; Sanders & Pons 1999). Only solitary rudists and small rudist clusters extend into Kalais. They occur as far north as Ivö Klack in south Sweden (Kühn 1949; Surlyk &

Christensen 1974). Among gastropods, *Trochactaeon* (Family Acteonellidae) and Nerineoidea assemblages characterize the proximal inner shelf of Theia (Fig. 1). Abundant winnowing of sediments has led to densely packed, sometimes unispecific mass occurrences of these taxa. *Trochactaeon* does not extend into Kalais where the *Ostrea-Arca-Mytilus* assemblage (Mertin 1939) represents the proximal inner shelf.

Theian distal inner shelf gastropod assemblages are characterized by the infaunal taxon *Acteonella* (Sanders *et al.* 1997). In Kalais, its niches probably were inhabited by Cephalaspidea. Equally, the Trochidae taxon *Discotectus* did not spread into Kalais (Sohl 1971, 1987). At environmentally stable intervals, *Turritella* spread into the distal inner shelf. The diversity of molluscs and corals decreases northwards into Kalais (Masse 1982).

The outer shelf, with its low-energy regime, is characterized in both Kalais and Theia by assemblages of Pleurotomariidae, Turritellidae and the Ampullinidae genus *Gyrodes*. Besides the increase of gastropod taxa with well-developed siphonal canals ('negastropods') towards the K/T boundary, the composition of assemblages is similar throughout the late Cretaceous. Inoceramids are represented, also in both realms, by low-energy morphotypes ('cup-shaped') (Kauffman 1967). In contrast to the inner shelf, ammonites are diverse in outer shelf lithologies.

A distinct outer shelf assemblage is that of the nodular limestones facies at the margin of Theian carbonate platforms (Wilson 1975). Its faunal assemblage differs from that of siliciclastic environments by the dominance of *Tylostoma* and Aporrhaidae taxa, by the abundance of internal moulds of articulated bivalves and the occurrence of ammonites (Kollmann *et al.* 2003).

Discussion

In the European Upper Cretaceous, the distribution of foreshore and inner shelf assemblages shows a lateral change from Theia to Kalais, while outer shelf assemblages are remarkably uniform in both realms. Kauffman (1973) has pointed out that the difference between Theian and Kalaisian assemblages is mainly due to the polewards thinning out of Theian elements. This was largely caused by the increasing seasonal variation towards north. From fossil assemblages of Ivö Klack in South Sweden, Surlyk & Christensen (1974) have deduced minimum surface water temperatures of 18°C close to the northern margin of Kalais. This is supported by the occurrence of

spondylids, which are restricted to tropical and subtropical environments in modern seas.

In contrast to the gradual lateral change, the vertical change of assemblages at the limit between the inner and outer shelf was abrupt. In the Upper Cretaceous of the Bohemian/Saxonian Basin, inner shelf Theian assemblages inhabited submarine highs (Tröger 1969; Voigt *et al.* 1994; Voigt & Tröger 1996; Kollmann *et al.* 1998; Tröger 2003). Outer shelf deposits have yielded a low-diversity assemblage with turritellids, Cerithioidea, Pleurotomarioidea. Sections by Tröger (1969) suggest a difference of water depth between the highs and the basin of approximately 15 m (Kollmann *et al.* 1998). Comparable conditions have been observed in the Upper Turonian of Uchaux, France (Mennessier 1952) and from the Upper Santonian of Gosau, Austria (Sanders *et al.* 1997). In the Charente Basin, France, inner and outer shelf environments and assemblages alternated with eustatic changes (Kollmann 1985).

Besides its mollusc fauna, Theian inner shelves assemblages like those of Uchaux and the Gosau Group have yielded diverse coral and mollusc faunas. In the Basin of Gosau, an increase of water depth beginning in the late Upper Santonian (Sanders *et al.* 1997) has led to a total replacement of the fossil assemblages. In contrast to stratigraphically earlier deposits, the coral assemblage consist exclusively of solitary and pseudocolonial taxa which according to Coates & Jackson (1987) are dominantly azooxanthellate. This suggests a change of water depth below the photic zone which is positioned in modern oceans at 10 to 15 m below the water surface (Achituv & Subinsky 1990). The accompanying rich mollusc assemblages have been interpreted as dominantly Kalaisian (Dhondt 1987; Kollmann 1980; Summesberger 1879). It is therefore evident that the 'Kalaisian influence' was in fact an effect of the increasing water depth.

This is evident from the gastropod family Pleurotomariidae which has been considered as a Kalaisian faunal element (Sohl 1971, 1987; Kollmann 1992). In fact, recordings of Upper Cretaceous pleurotomariids of south France (d'Archiac 1854; Leymerie 1881; Astre 1935; Kollmann 1985; Kollmann & Odin 2001), Spain (Astre 1935; Bataller 1949), and the Near East (Delpey 1940) which are located within Theia oppose this interpretation. Recent Pleurotomariidae represent a conservative gastropod group. Remains of Hexactinellidae in digestive ducts and observed feeding of the pleurotomariid *Perotrochus midas* Bayer suggest a diet of sponge tissue for this group (Hara-sevych *et al.* 1988). This points to a link between Pleurotomariidae and Hexactinellidae. In Recent seas, this group inhabits primarily abyssal and bathyal depths

(Reid 1868), but it has lived also in more shallow environments in the Late Cretaceous (Wiese & Wood 2001). This was probably due to more stable conditions in higher water strata during this time interval than in present-day Boreal. It may be concluded that a palaeobiogeographical interpretation of Cretaceous assemblages is impossible without knowing their palaeoecological distribution. This concerns especially outer shelf assemblages. Most mollusc taxa have first been described from outer shelf environments of Kalais. They have frequently been interpreted as representing Kalaisian influence when they were recorded from equivalent Theian ecologies (Sohl 1971; Kauffman 1973; Dhondt 1992; Kollmann 1992 and others). In fact, there is no evidence for climate-induced differences between outer shelf assemblages of both realms.

Palaeobiogeographical interpretations of ammonites need to be treated with special scepticism. This mollusc group is absent or rare in inner shelf deposits but common and diverse in those of the outer shelf (see Masse 1992). This distinct limit of distribution suggests that the thanatocoenosis reflects the original environment (see Lewy 2002) and agrees with the interpretation of ammonites as epibenthonic predators (Wiedmann 1988; Hoedemaeker 1995). The availability of specific nutrients on different parts of the shelf was certainly one factor controlling the ammonite distribution. Another one was the restriction of taxa to certain parts of the water column. Allen (1983) has shown the sophisticated nerve-muscle physiology and the high degree of sensory function in Cephalopods which adapts each taxon to a specific range of pressure. The ammonite distribution in the Upper Cenomanian to Lower Turonian of Spain and Portugal provides a good example for this mechanism demonstrated by (Wiedmann 1988).

Belemnites have been interpreted as 'stenothermal neritic shelf dwellers' common in Kalais (Christensen 1996). According to the model of Surlyk (1997) the environment was part of the outer shelf. Theian recordings are rare but do exist, as in the Late Santonian 'Marnes bleues' of Sougraigne, south France (Christensen *et al.* 1990; Christensen *et al.* 1993). According to the associated fauna (d'Archiac 1854) they were deposited below the zone of zooxanthellate corals.

The fossil fauna of Ivö Klack shows that warm surface water extended as far north as southern Sweden. This water mass is interpreted as the near-shore equivalent of the Tropical-Subtropical surface mixed layer. In modern oceans, surface waters are generally permanently stratified at latitudes lower than 40° (Angel 1997). The loss of heat is insufficient at any season to produce a convective deepening of the trop-

ical-subtropical surface waters mixed by the wind between 10 and 100 m. A Tropical-Subtropical surface mixed layer is therefore maintained continuously.

The northern boundary of warm surface waters coincides with the northern limit of Tethys of Neumayer and Suess in its original palaeogeographical sense (see Kollmann 2002). It is limited towards the Boreal by the Subtropical front was an effective, although not impermeable palaeobiogeographical boundary (Hay 1995). In fact, the Maastrichtian gastropod faunas of West Greenland kept in the Geologisk Museum Copenhagen which are of outer shelf origin do not have equivalents in Europe. They contain taxa like *Serrifusus* and *Atrina* which hitherto have only been known from North America (Sohl 1967).

Conclusions

Late Cretaceous foreshore and inner shelf benthic assemblages are laterally differentiated and have been used to define the realms Theia and Kalais.

Vertically, the lower limit of inner shelf assemblages is biologically significant. The inner shelf of both realms represents the shallow water equivalent of the Tropical-Subtropical mixed layer. It extended as far north as Scania.

Kalaisian inner shelf gastropod assemblages are 'thinned out' Theian assemblages. Belemnitellids are common in Kalaisian outer shelf deposits but might have been restricted to certain niches in Theia.

Outer shelf assemblages are highly uniform in Theia and Kalais. They represent the upper limit of the permanent thermocline.

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