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Cretaceous inoceramid biogeography: a review

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ABSTRACT

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Cretaceous inoceramid bivalves were widely distributed. They did not thrive in very shallow or very warm seas, and are therefore rare in Tethyan shallow deposits. In the Berriasian–Barremian interval they occurred mainly in the temperate seas, and their distribution is often bipolar. In the Albian–Cenomanian interval, inoceramids were varied and numerous, especially in clays and chalks, but rare in the greensand-type strata. Most inoceramid groups were cosmopolitan during this interval. From the Turonian onwards the North Pacific Province is characterized by endemic inoceramid faunas. Following the opening of the South Atlantic Ocean in the Turonian, new inoceramid lineages in the Southern Hemisphere from Brazil to Madagascar evolved in co-occurrence with other cosmopolitan groups. Many Coniacian and Santonian species were widely distributed and short-lived, but in the Campanian and Maastrichtian a homogeneous fauna was apparently confined to eastern North America and western Eurasia. Few of the last inoceramid species in the Upper Cretaceous have stratigraphic value, and, in contrast to the Lower Cretaceous, they are common in warm-water deposits, for example, in Libya, Nigeria, and Tunisia.

Introduction

Inoceramid bivalves (as a group) are considered important for stratigraphy by most Cretaceous palaeontologists, but are left to a few 'specialists' for study because they are reputed to be difficult. Aspiring inoceramid workers very quickly discover the limitations, imperfections, and problems inherent in this fossil group. As soon as an attempt is made to define 'species' or any kind of systematic entities (Mitura, 1957) these difficulties become only too obvious. The taxonomic methodology, although generally inspired from the German school of Heinz and Seitz, still varies considerably from author to author and from continent to continent. Furthermore, most research on inoceramids until about 1970 was carried out without either intraspecific variability or deformation during fossilisation being taken into account. As a result, we are left with a systematic puzzle made up of pieces of very different sizes, which are extremely difficult to fit together.

The inoceramids originated in the Permian (Waterhouse, 1970), and reached their acme first in the Jurassic and in the middle Cretaceous (Cox, 1969; Crampton, 1988). No undoubted inoceramids have been documented from Tertiary strata. Agreement exists that many inoceramid species are useful for Cretaceous stratigraphy, and may even play a key role in those strata where ammonites and other diagnostic groups are rare. Inoceramids occur in most Cretaceous strata, but are more common in fine-grained sediments than in sands. According to Kauffman (1975) their larvae were relatively long-lived, thus allowing a rapid and wide dispersal. He also discussed the ecology of the group, and came to the conclusion that some inoceramids were byssally attached, whereas others were epipelagic. The result of the wide distribution is that inoceramids are potentially good index fossils.

Palaeobiogeography of Cretaceous bivalves has

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been dealt with by Kauffman (1973). He discussed the geographical distribution of bivalves on a global scale, and considered the two broad time units Early and Late Cretaceous.

In the last two decades, Cretaceous biostratigraphy has been studied in great detail, resulting in much better correlations than previously. The stratigraphic resolution has reached a high degree, mainly based on ammonites and microfossils.

Research on inoceramids has been done in previously poorly known areas [Antarctica: Crame (1979, 1981a,b, 1982, 1983, 1985); Crame and Howlett (1988); Argentina: Riccardi (1988); Brazil: Hessel (1988); New Zealand: Crampton (1988)].

It is the purpose of the present paper to update (where possible) the data on palaeobiogeographical distributions presented by Kauffman (1973) and the Late Cretaceous inoceramid data (restricted to the Northern Hemisphere) from Tröger (1976) and Pergament (1978).

Material and methods

In a paper of this scope a large part of the information had to be inevitably compiled from the literature, and unfortunately, some facts may have been overlooked. The data on the Early Cretaceous inoceramids have been compiled most recently by Crame (1985), and the information presented by this author is used here for most Lower Cretaceous stages discussed. I have only scattered first-hand knowledge of the faunas, and only for the Santonian–Maastrichtian interval I can claim to have an extensive knowledge.

Generally speaking, the palaeobiogeography of inoceramids does not allow easy regional distinctions similar to, for example, oyster distributions. Most inoceramid species groups have a wide geographical distribution, and the distinction between Tethyan and non-Tethyan faunas, which is obvious for most bivalves, is not present in inoceramids (see also Kauffman, 1977a). Furthermore, those areas which were previously assumed to contain endemic faunas, such as the North Pacific in the Turonian to Maastrichtian, have lately been shown to contain also some cosmopolitan elements (Matsumoto and Noda, 1983).

The systematics of the inoceramids is still not fully understood, which is underscored by the fact that there is as yet no consensus on how to define a species, and there is research on the intraspecific variability. Another complication is that complete and well-preserved inoceramids are extremely rare; for many taxa entire specimens have never been found. Owing to these limiting factors, results obtained with inoceramids often remain tentative.

Palaeobiogeographic distributions of Cretaceous inoceramids

Much work on Early Cretaceous faunas was carried out in the 1960's and onwards, especially in deposits of the Boreal Realm (Jeletzky, 1964; Pergament, 1965; Zakharov, 1966; Pokhialainen, 1969, 1972, 1974; Kapitsa, 1978; Zakharov and Turbina, 1979). Recently, existing data on inoceramids have been brought together in a paper focussing on Antarctic inoceramids (Crame, 1985).

Berriasian–Ryazanian

Crame (1981b) discussed the somewhat aberrant inoceramid genus *Anopaea* (Eichwald, 1861), and demonstrated that its distribution is bipolar, occurring in the Berriasian of Antarctica, and also widely in the Boreal Realm (also in Pokhialainen, 1974; Kapitsa, 1978). Later, Crame (1985) reconsidered the stratigraphic age of Alexander Island (Antartica) material containing *Anopaea* to be possibly Aptian (Fig. 1), and more recently possibly Hauterivian–Barremian (Crame and Kelly, pers. comm.). In addition to the occurrence of *Anopaea* in the Ryazanian of eastern England (Kelly, 1977, 1984), an *Anopaea* sp. has recently been described by Bogdanova (1988) from the Berriasian of Mangyshlak. In the same paper, Bogdanova also mentioned a middle Albian *Anopaea mandibula* (Mordvilko et al., 1949) from Mangyshlak and Kopet-Dag; this taxon is probably coeval with the Albian occurrence in Australia (Crame, 1981b), and in Antarctica (Crame, 1985). Hence, Cretaceous species of *Anopaea* probably occurred from the Ryazanian to the Albian.

Crame (1985) divided the inoceramids in 'informal' groups, two of which (the *Inoceramus ovatus* group and the *I. proconcentricus* group) were pre-

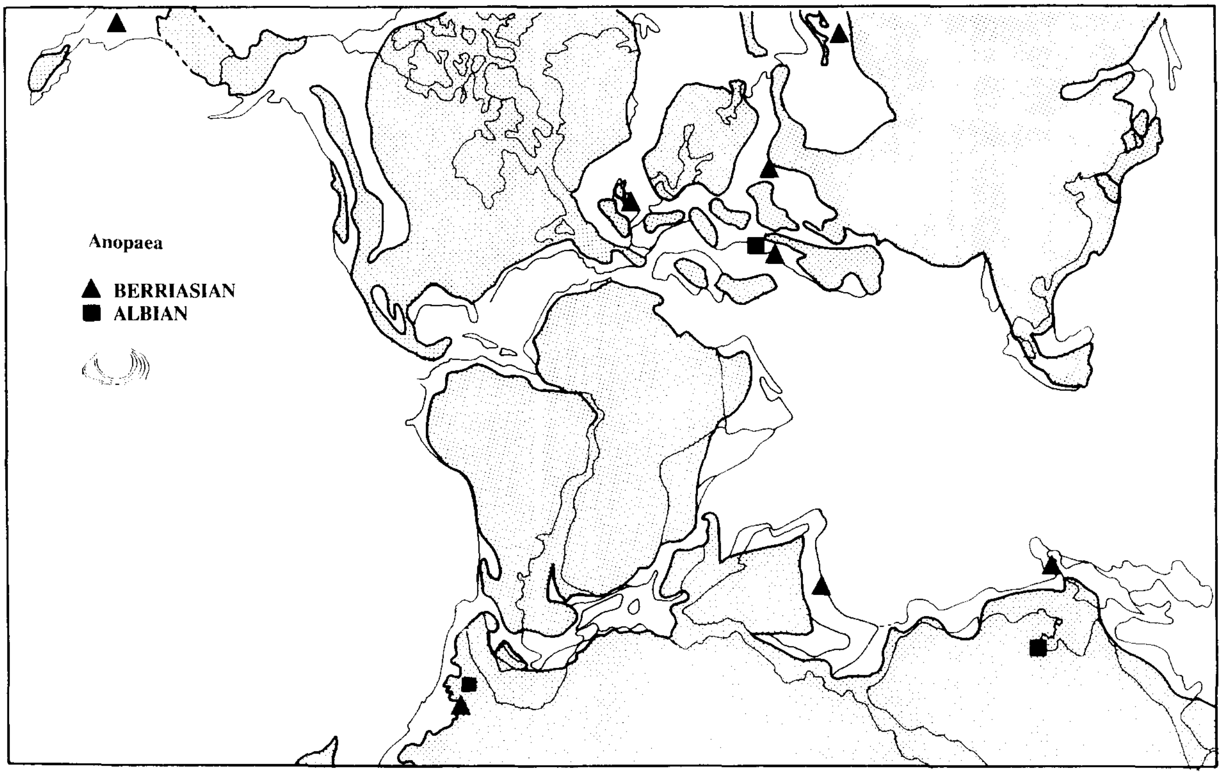

Fig. 1. Distribution of *Anopaea* in the Berriasian to Albian interval. Data are from Pokhialainen (1974), Crame (1981b, 1985), and Bogdanova (1988). Map shows the continental configurations at 140 Ma (Barron et al., 1981).

sent in the Berriasian. The first of these groups has a bipolar distribution.

According to Riccardi (1988), *I. anomiaeformis* Feruglio, 1936 occurs in the Berriasian of Patagonia. This species was mentioned by Crame (1985) as "*Inoceramus* of uncertain group affinity" and was given a somewhat younger age.

Valanginian–Barremian

Inoceramids from the Valanginian–Barremian interval are relatively less well known because: (1) in the Tethyan-warm Temperate regions most outcrops represent shallow or very shallow environments, and they contain very few inoceramids [Sornay (1965) stated *Inoceramus neocomiensis* d'Orbigny, 1847 and closely related species]. Inoceramids seem to be absent from Tethyan rudist facies, which accompany the spreading of the carbonate platform from the Barremian onwards. (2) buchiids rather than inoceramids are the bivalves used for stratigraphy in the Boreal Realm; hence inoceramids have been less well studied. Nevertheless, Soviet authors have worked on northern and northeastern Siberian faunas in particular (for example, Zakharov, 1966; Pokhialainen, 1969, 1974; Kapitsa, 1978).

In his study of the Antartic inoceramids, Crame (1985) discussed the species known to occur globally in the Lower Cretaceous and subdivided them into six informal groups, occurring in the Valanginian–Barremian or parts thereof. Only one of these groups (the *I. neocomiensis* group) is found in the Boreal Realm, warm Temperate Province, and in the Antarctic (Crame, 1985; Dhondt and Dieni, 1988). The *I. ovatus* and *I. heteropterus* groups have a bipolar distribution, occurring both in Boreal and Antarctic regions with extensions into Temperate provinces (Crame, 1985). The *I. aucella* group occurs in Boreal and Temperate strata of the Northern Hemisphere; the *I. proconcentricus* and *I. colonicus* groups are restricted to Boreal regions (Fig. 2).

Aptian

Inoceramid species of Aptian age are rare. This is probably due to a combination of factors: (a) the difficult distinction between beds of Barremian and of Aptian age in Urgonian and related facies; (b). the regressional phases found over wide areas; (c) the scarcity of cold Temperate Aptian outcrops; and (d) the relative rarity of inoceramids in shallow deposits, which represent Aptian strata in warm Temperate and Tethyan regions. Crame (1985) only mentioned the last representatives of the *I. neocomiensis* and the *I. liwerowskyae* groups of Upper Aptian to Albian age. Sornay (1965) considered that no confirmed Aptian species have been described in France.

Albian

The Albian transgressions brought about a radiation of the marine invertebrate fauna. In the inoceramids this resulted in the appearance of the Albian (–Cenomanian) genus *Birostrina* (Sowerby, 1821) and the *Inoceramus anglicus* group. According to Crame (1985), the *I. carsoni* group from Australia and Antarctica evolved at the same time. The distribution of the species of *Birostrina* and the *I. anglicus* group in large parts of the USSR has been shown by Saveliev (1962) and by Saveliev and Vasilenko (1963).

Birostrina contains some of the better known Cretaceous inoceramid species from Eurasia, such

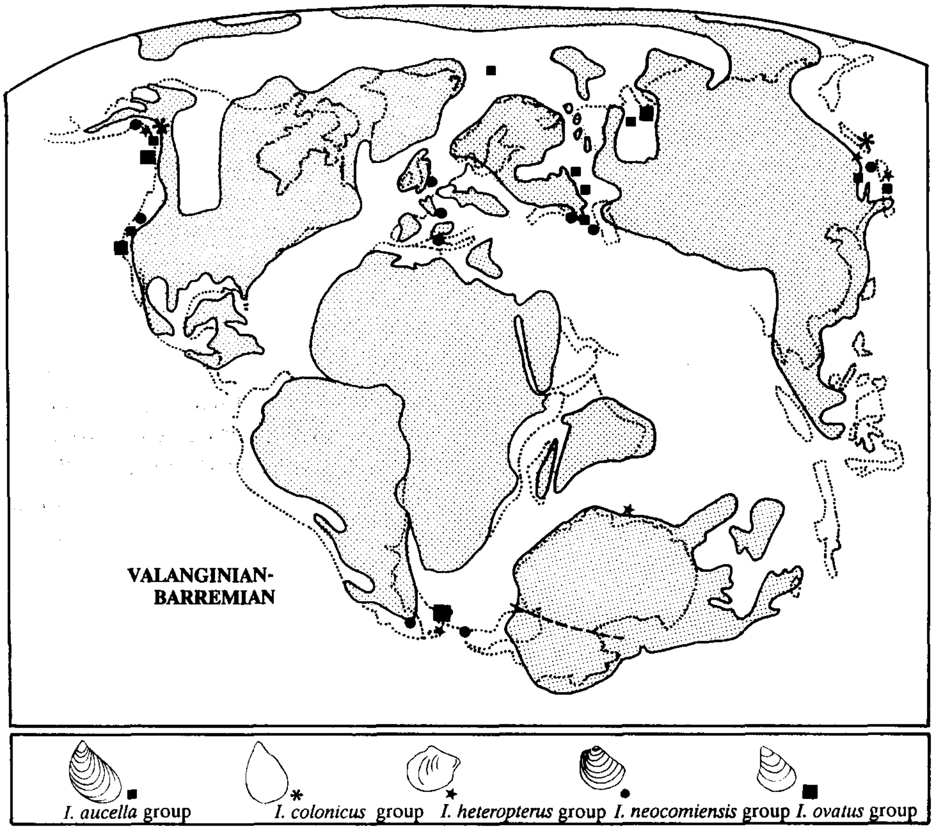

Fig. 2. Distribution of the *Inoceramus aucella* group, *I. colonicus* group, *I. heteropterus* group, *I. neocomiensis* group, and *I. ovatus* group in the Valanginian–Barremian interval. Data are from Zakharov (1966), Pokhialainen (1974), and Crame (1981b, 1985). Map shows the continental configurations for the Hauterivian at 125 Ma (Howarth, 1981).

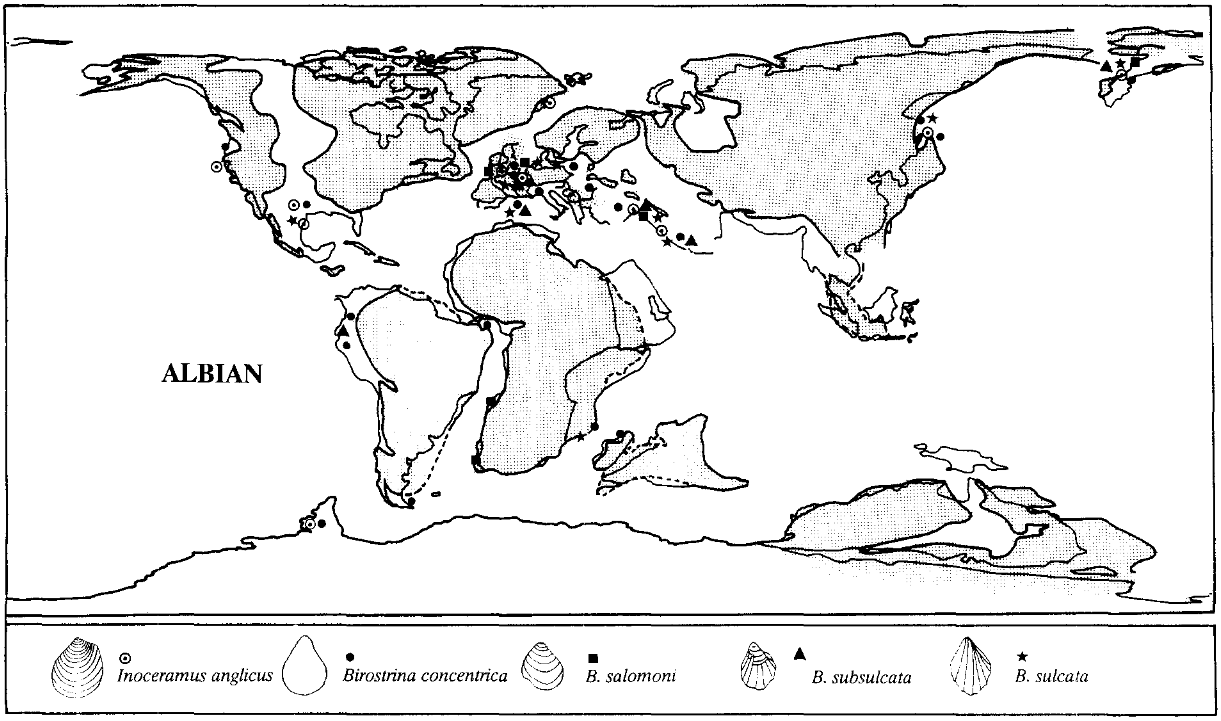

Fig. 3. Distribution of *Inoceramus anglicus*, *Birostrina concentrica*, *B. salomoni* s.l., *B. subsulcata*, and *B. sulcata* in the Albian. Data are from Reeside (1927), Richards (1947), Saveliev (1962), Pergament (1966), Crame (1985), and Dhondt and Dieni (1988). Map shows the continental configurations for the late Albian from Barron (1987).

as *B. salomoni* (d'Orbigny, 1847) (Lower –? middle Albian), *B. concentrica* (Parkinson, 1819) (middle-Upper Albian, ?Cenomanian), *B. sulcata* (Parkinson, 1819) (?middle-Upper Albian); and all the three are widely distributed (Fig. 3).

Crame (1985) discussed the distribution of the *Birostrina concentrica* group. I have had the opportunity to study the specimens from Peru figured by Richards (1947), and those from Ecuador figured by Reeside (1927) They seem to fall completely within the range of variation of *B. concentrica*. After studying the type specimens of *B. concentrica nipponica* (Nagao and Matsumoto, 1939) from the Cenomanian of Japan, I agree with the interpretation of Pergament (1966) that *B. nipponica* is a distinct species. The genus *Birostrina* continued to exist into the Cenomanian (Matsumoto and Noda, 1986) in the North Pacific region, but in agreement with Pergament (1966, 1978) I consider the species *B. concentrica* to be restricted to the Albian.

Birostrina has a truly cosmopolitan distribution and does not allow palaeobiogeographic subdivisions based on presence–absence patterns only. This genus is only found in facies representing fine sediments, and possibly relatively deep seas.

The *Inoceramus anglicus* group also shows a wide distribution (Fig. 3). It contains taxa first described from the Albian of England (*I. anglicus* Woods, 1910) from the Upper Albian of Texas (*I. comancheanus* Cragin, 1895). Both these forms are similar and may represent a single species. Crame (1985) listed other taxa possibly belonging to this group (distributions are shown in Fig. 3). The last Albian group distinguished by Crame (1985) is the *I. carsoni* group, which is restricted to Australia and Antarctica.

Cenomanian

The transgressive phase, which began in the Albian, continued into the Cenomanian, and the sea level was high throughout most of this age (Hancock and Kauffman, 1979). The transgressions resulted in extensive epicontinental seas and in a variety of marine facies, among which especially the chalk sediments were favourable for inoceramids. The inoceramids are stratigraphically useful in the Cenomanian, and this zonation is applicable to large parts of Europe (Tröger, 1966, 1967, 1968; Kauffman, 1977a, 1978a,b; Pergament, 1978; Wiedmann and Kauffman, 1978; Sornay, 1978b, 1980; Keller, 1982), North and Central America (Cobban, 1977; Kauffman, 1978d; Kauffman et al., 1977a,b, 1978; Young and Powell, 1978) and South Africa (Kauffman, 1978c). The summary and discussion of the stratigraphic schemes given by Pergament (1978) show that in the Far Eastern USSR and Japan a different scale is used. However, from the North American Western Interior, Cobban (1977) reported a species, which was originally described from the Far Eastern USSR (Kamchatka and Sakhalin). Also, in a recent paper by Matsumoto et al. (1987), the occurrence of *I. tenuis* Mantell, 1822 and *I. virgatus* Schlüter, 1877 was reported from Japan. This demonstrates that some of the species used for zonation in Europe also occurred in Japan. Thus the European inoceramid zonation could perhaps in the future be used for correlations with East Asian deposits. According to Matsumoto et al. (1988), the beginning of the isolation of the North Pacific faunas can already be seen in the Cenomanian of Japan and the Far Eastern USSR.

On the other hand, it is likely that the Cenomanian faunas described from North America (mainly Texas and the Western Interior, for example Cobban, 1977; Kauffman, 1977b; Kauffman et al., 1977; Stephenson, 1953, 1955) are closer to the European faunas than what is actually stated in the North American literature. After studying the type specimens of *I. prefragilis* Stephenson, 1953 from the middle Cenomanian of Texas, I consider this taxon close to or even conspecific with *I. pictus* Sowerby, 1829 as figured by Woods (1911, plate 49, 5 and 6). Other taxa probably also occurred on both sides of the Atlantic Ocean in Cenomanian times: this is apparent from the tables of stratigraphic ranges of taxa, given by Kauffman (1978a) for the English chalk. This is also indicated by the fact that several European Cenomanian taxa occur in Oklahoma, USA (Kauffman et al., 1977b). A definite conclusion concerning the similarities between European and North American taxa cannot be given at the present time because a taxonomic revision of Cenomanian inoceramids from England and France is not available. Only for Saxony (Germany) and Bohemia (Czechoslowakia) do we have detailed systematic data (Tröger, 1967; Fig. 4).

Turonian

According to the geologic time scales currently available, the Turonian was a relatively brief age, ranging from 1 to 3 Ma, e.g., Odin (1982) and Harland et al. (1990). It was an extremely prosperous time as far as inoceramids are concerned. The Cenomanian–Turonian transition has traditionally been recognised by the appearance of a group of flattened, elongate inoceramids, previously known as the *Inoceramus labiatus* group (after *I. labiatus* Schlotheim, 1813), and currently as the *Mytiloides* group s. l. In the Upper Turonian chalks, entire beds seem to contain little else than inoceramids of the *Mytiloides* group. Several species, such as *Mytiloides labiatus* (Schlotheim, 1813), *M. mytiloides* (Mantell, 1822), *M. submytiloides* (Seitz, 1934), *M. goppelnensis* (Badillet and Sornay, 1980), *M. hercynicus* (Petrascheck, 1903), *M. transiens* (Seitz, 1934), have a world wide or nearly world wide distribution in the Lower Turonian (Keller, 1982). Some less abundant late Turonian *Mytiloides* species, such as *M. incertus* (Jimbo, 1894) (=*Inoceramus fiegei fiegei* Tröger, 1967), had an equally wide palaeogeographic distribution as shown by Keller (1982), Matsumoto and Noda (1983), and Tröger (1986). Tröger (1987) studied the Strehlener Kalkstein of Saxony, including also other inoceramid species (Fig. 5).

Apart from the world wide *Mytiloides* faunas, other inoceramid groups seem to have developed more endemic species. Good examples are the genera *Sergipia* Maury and *Rhyssomytiloides* Hessel, 1988), which are (as yet) known primarily from the Turonian of Sergipe, Brazil. Once the South Atlantic rift was wide enough to let fully marine waters reach Sergipe, inoceramid faunas developed there, containing world wide species of the *Mytiloides* group and geographically restricted

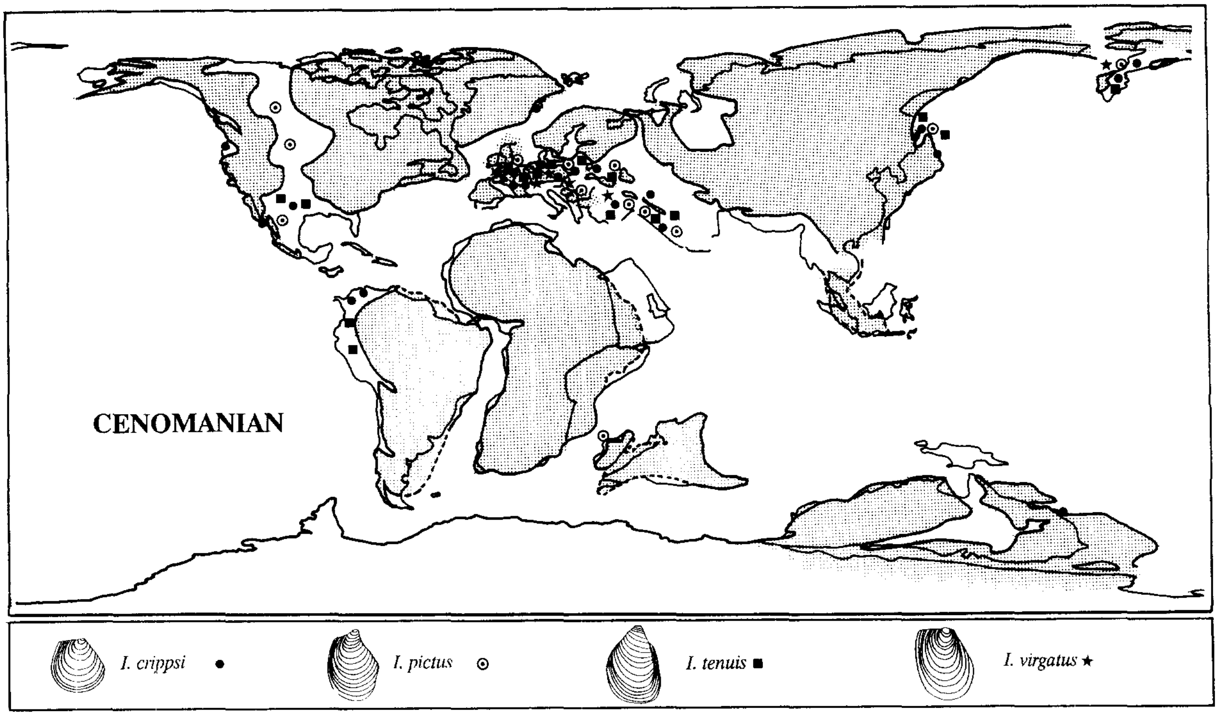

Fig. 4. Distribution of *Inoceramus crippsi*, *I. pictus*, *I. tenuis*, and *I. virgatus* in the Cenomanian. Data are from Tröger (1967, 1968), Cobban (1977), Kauffman (1978a,b), Pergament (1978), Sornay (1978b), Keller (1982), Naidin and Krassilov, 1981, and Matsumoto et al. (1987). Map from Barron (1987) is for the late Albian.

genera such as *Sergipia* and *Rhyssomytiloides* (Fig. 5).

In the Upper Turonian the earliest representatives of inoceramids are referable to the *I. lamarcki* group, which, according to Pergament (1978), was distributed almost world wide during the late Turonian (Fig. 5).

Coniacian–Maastrichtian

From the Turonian–Coniacian onwards the North Pacific region was characterised by faunas different from those of the rest of the world. Thanks to intensive work by Soviet, Japanese, Canadian and U.S. scientists, these North Pacific faunas are among the best known (more details are found in Nagao and Matsumoto, 1940; Jones and Gryc, 1960; Pergament, 1961, 1965, 1966, 1971, 1974, 1977, 1978; Jones, 1963; Jeletzky, 1977; Kauffman, 1977a; Ward, 1978; Ward and Haggart, 1981; Matsumoto and Noda, 1983; and Noda, 1984). These regions contain endemic inoceramids; the specific character of the Coniacian–Maastrichtian fauna was discussed by Jeletzky (1971, 1977).

In central and eastern North America and in western Eurasia the lower Coniacian is characterised by taxa of the *I. deformis–I. inconstans* group. In Europe, another group, the *I. wandereri* Andert, 1911 group is found, which occurs from northern England to the Caucasus; it has not yet been found in European White Chalks (Fig. 6). This group may have evolved from the late Turonian *I. lamarcki* group.

In North America and western Eurasia the upper Coniacian contains species of *Volviceramus*, such as *V. involutus* (Sowerby, 1828), *V. koeneni* (Mueller, 1888), *V. exogyroides* (Meek, 1876). According to Pergament (1978), the genus is also found in Kamchatka. The first representative of the genus *Cordiceramus*, *C. cordiformis* (Sowerby, 1823) had its earliest appearance in the Coniacian, but it is not restricted to that stage. The genus had a wide geographic distribution, particularly in the Santonian–Campanian interval (Fig. 7).

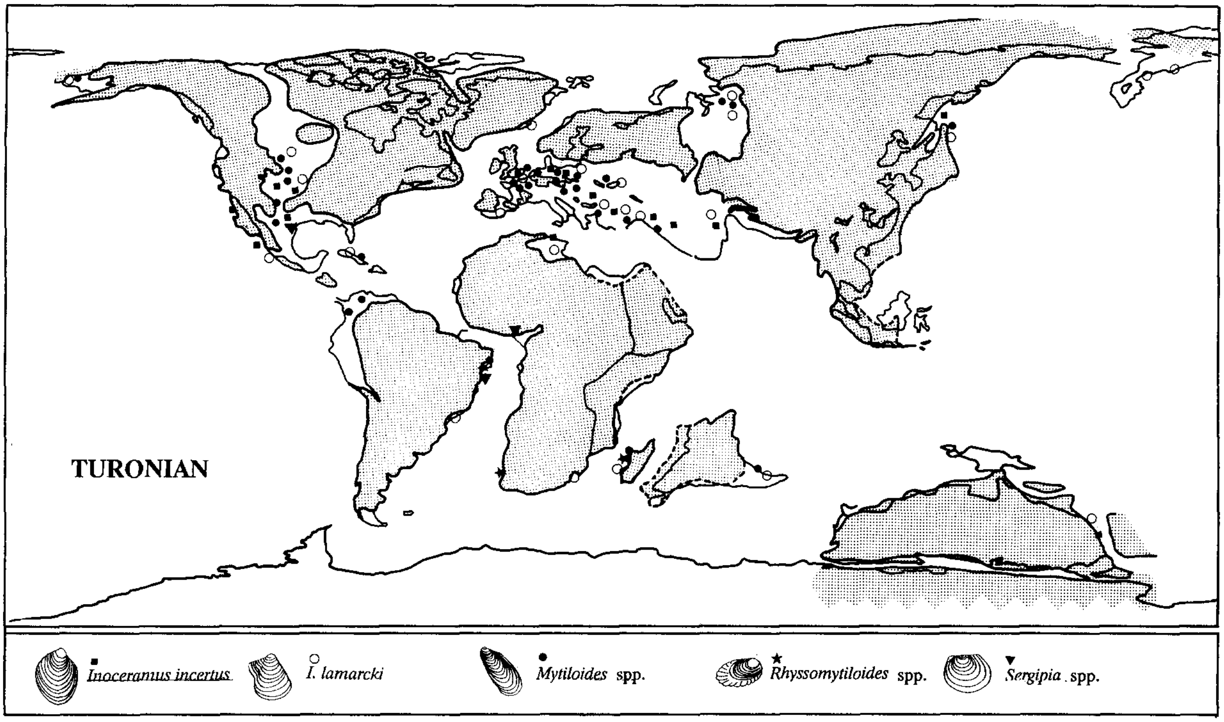

Fig. 5. Distribution of *Inoceramus incertus*, *I. lamarcki*, *Mytiloides* spp., *Rhyssomytiloides* spp., and *Sergipia* spp. in the Turonian. Data are from Pergament (1978), Keller (1982), Matsumoto and Noda (1983), Tröger (1986), and Hessel (1988). Map from Barron (1987) is for the late Turonian.

The Coniacian–Santonian transition is characterised by (a) the occurrence of *Magadiceramus subquadratus* (Schlueter, 1887) and related species in the uppermost Coniacian; (b) the occurrence of *Cladoceramus undulatoplicatus* (Roemer, 1852) in the lowermost Santonian; and (c) the first appearance of the genus *Sphenoceramus* in the lowermost Santonian. *Magadiceramus subquadratus* occurs widely in the Northern Hemisphere (Seitz, 1970; Pergament, 1978; Fig. 6), but is not found in the North Pacific Subprovince. *Cladoceramus undulatoplicatus* is found world wide (Fig. 7), and in most facies types. Species of *Sphenoceramus* occur in the Santonian and Campanian; they are used for stratigraphic subdivision in the northern European White Chalks (Seitz, 1965). The genus had a world wide distribution (Pergament, 1978; Fig. 7), but has only rarely been found in Tethyan or Temperate–Tethyan border regions (such as the Charente, South West France).

The genus *Platyceramus* had its first occurrence in the Coniacian–Santonian (Seitz 1961, 1967) and continued until the Maastrichtian. *Platyceramus* species have been found in Santonian to lower Maastrichtian strata from the Western Interior of North America and eastern USA, western Eurasia and in North Africa. My recent research has shown that the distribution extends beyond what was indicated in Dhondt (1983b): thus *Platyceramus* species occur frequently in the Campanian of Tunisia and North America. From the Santonian through Maastrichtian, they are found especially in the Gulf and Atlantic Coastal deposits (Fig. 7). At the species level *Platyceramus* is difficult to study, because whole tests of large specimens are extremely difficult to collect.

Unlike *Sphenoceramus*, *Platyceramus* and *Cordiceramus* occur also in the Tethyan Realm and in the Temperate–Tethyan border area (Fig. 7). Other genera which are mainly recognized in German literature, originated in the Santonian: *Selenoceramus* and *Endocostea* (? = *Cataceramus*). Since the work of Tröger and Röhlich (1981), the range of *Selenoceramus* has been extended into the

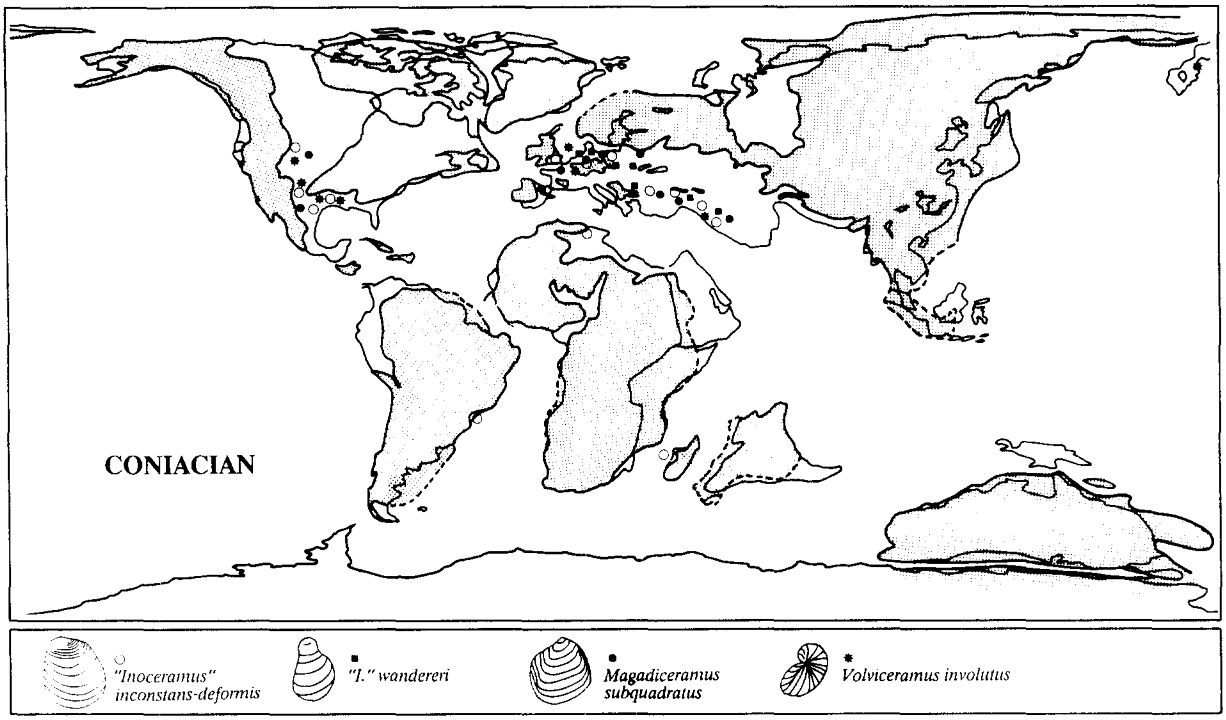

Fig. 6. Distribution of *Inoceramus deformis-inconstans*, *I. wandereri*, *Magadiceramus subquadratus*, and the *Volviceramus involutus* group in the Coniacian. Data are from Seitz (1970), Pergament (1978), and own research. Map from Barron (1987) for the Coniacian.

Maastrichtian. *Endocostea baltica* (Boehm, 1909) s.l. is generally considered as to reach into the Maastrichtian (Fig. 8).

The Santonian–Campanian transition can be defined by the occurrence in the boundary layers of *Cordiceramus muelleri* (Petrascheck, 1906), This species is found mainly in Tethyan regions, but occurs also in western Eurasia (Dhondt, 1987; Fig. 8). At the generic level no changes are documented between the late Santonian and early Campanian. This is probably due to a fairly continuous sedimentation pattern from the Santonian to the Maastrichtian in most regions.

During the Campanian the genus *Trochoceramus* appeared. Although the concept of this genus, as can be understood from Seitz (1970), Sornay (1973), Tröger and Röhlich (1980), is unfortunately not fully consistent, but it is a representative of the Euro-African–South American Tethyan Realm and warm Temperate Subprovince of the Temperate Realm (Fig. 9). Until now, *Trochoceramus* has not been found in North America; Etayo-Serna (1985) has demonstrated its occurrence in Colombia.

Maastrichtian inoceramids are more numerous than was previously assumed (Dhondt, 1983b); the restudy of the ammonites of the Craie à Baculites (Kennedy, 1986) and the Maastrichtian stratotype ammonites (Kennedy, 1987) has resulted in better correlations and in the recognition of mid- or late Maastrichtian ages for some inoceramids, which I had previously (Dhondt, 1983b) considered early Maastrichtian. The specific Maastrichtian inoceramids *Spyridoceramus tegulatus* (von Hagenow, 1842) and *Tenuipteria argentea* (Conrad, 1858), which are used for stratigraphic purposes, were discussed in Dhondt (1979, 1983a). I must add a rectification to previous conclusions regarding the taxonomic affinity of *Inoceramus kusiroensis* Nagao and Matsumoto, 1940. I have now had the opportunity to study topotypes of this species, and these specimens definitely do not belong to *Tenuipteria* as I previously suggested (Dhondt, 1983a). Also, T.D. Zonova (Leningrad; oral commun.,

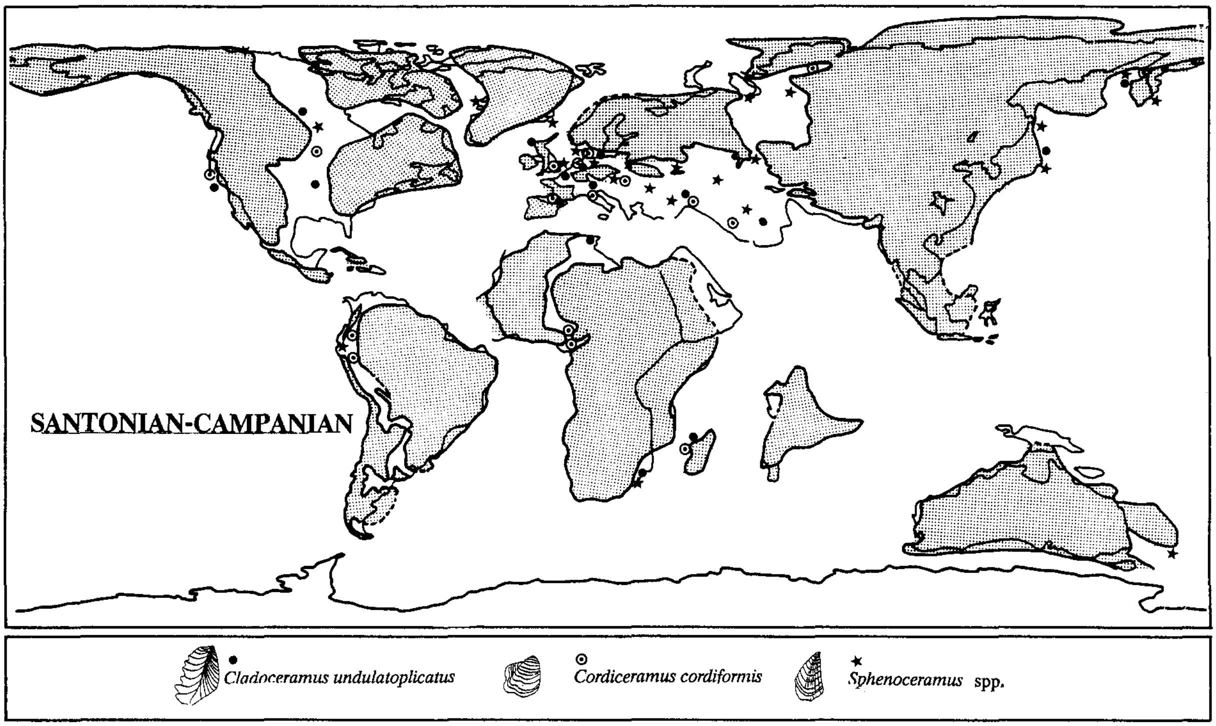

Fig. 7. Distribution of *Cladoceramus undulatoplicatus*, *Cordiceramus cordiformis* group, *Sphenoceramus* spp. in the Santonian and Campanian. Data are from Seitz (1961, 1965, 1967), Pergament (1978), López (1986), and own research. Map from Barron (1987) is for the early Maastrichtian, which does not fit entirely for the Santonian, but is better than the Coniacian map for the Santonian–Campanian interval.

1982) informed me that she does not consider "*Inoceramus* ex gr. *tegulatus*" in Pergament (1974) as belonging to *Spyridoceramus*. Therefore, the distribution shown in Fig. 9 for *Spyridoceramus* and *Tenuipteria* is more restricted than that published in Dhondt (1983a,b). The late Campanian and Maastrichtian inoceramid faunas known from Japan (Nagao and Matsumoto, 1939–1940), Far Eastern Siberia (Pergament, 1978; Poyarkova, 1987) and Pacific Coast of North America (Ward and Haggart, 1981) seem to have few elements [possibly some taxa related to *Endocostea baltica* (Böhm, 1909)] in common either with the other faunas from the Euroamerican region from the North Temperate Realm or with those of the Tethyan Realm.

Conclusions

At the beginning of the Cretaceous the inoceramid fauna was characterized by *Anopaea* and other inoceramids. Many groups had a wide (possibly bipolar) distribution, but only a few are known from Tethyan outcrops.

The distribution of the inoceramids in the Valanginian–Barremian interval is comparable to that of most bivalves (Dhondt and Dieni, 1989). Although inoceramids are rare in the Tethyan Realm, different Tethyan and non-Tethyan faunas may be recognised.

Aptian inoceramids represent a typical transitional fauna. A few taxa from the Hauterivian–Barremian period have their last occurrences in the Aptian, and new groups which later become important in the Albian have their first occurrences in the upper Aptian strata.

Numerous, mostly cold-water Albian outcrops contain a rich fauna of inoceramids: several taxa of *Birostrina* and representatives of the *Inoceramus anglicus* group. This allows a fine stratigraphic subdivision, but, palaeobiogeographically, this fauna is generally cosmopolitan.

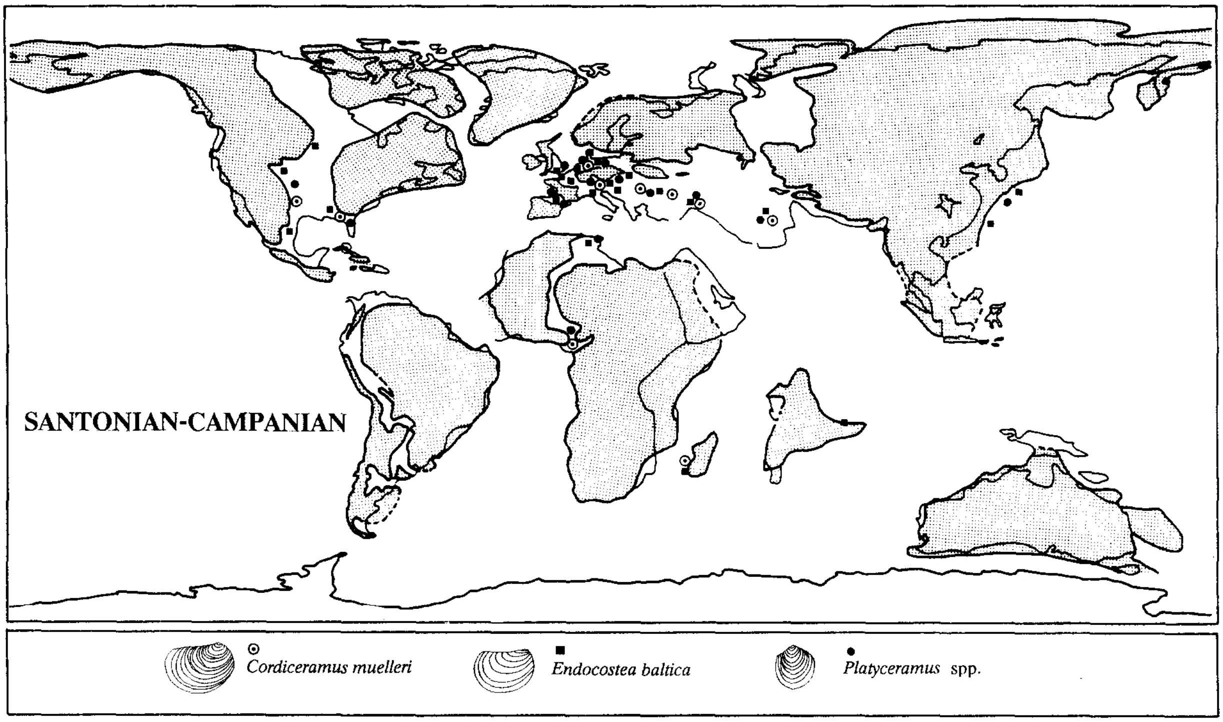

Fig. 8. Distribution of *Cordiceramus muelleri*, *Endocostea baltica* group, and *Platyceramus* spp. in the Santonian and Campanian. Data are from Seitz (1961, 1967), Gambashidze (1963), Tsagarelli (1963), Kociubynskij (1968, 1974), Sornay (1976), Pergament (1978), Sornay and Bilotte (1978), Ivannikov (1979), Tzankov (1981), López (1986), Scott et al. (1986), and own research. Map from Barron (1987) is for the early Maastrichtian.

In the widely distributed Cenomanian chalks, several consecutive (in time) species are recognized, such as *Inoceramus crippsi* Mantell, 1822, *I. virgatus* Schlüter, 1877, *I. tenuis* Mantell, 1822, and *I. pictus* Sowerby, 1829. Some of the typical species from the chalks are also found in North America, and a few species have recently been shown to occur also in Japan.

Species of *Mytiloides* characterise the lower Turonian; species of the *Mytiloides* group s. l. occur also in the upper Turonian, but they are less common there. The upper Turonian contains taxa of the *I. lamarcki* group in most areas. In Brazil, Nigeria, and Madagascar there occurred two genera with a restricted distribution, namely *Sergipia* and *Rhyssomytiloides*.

The Coniacian–Maastrichtian inoceramid faunas are morphologically less diverse than those of the Albian–Turonian interval. The relatively homogeneous sedimentary conditions towards the end of the Cretaceous probably helped to slow down the evolutionary changes. Towards the end of the Mesozoic era the influence of the North Atlantic Ocean can be seen; it is especially pronounced in warm Temperate and Tethyan outcrops as can be demonstrated by the distribution of *Trochoceramus*. The North Pacific faunas evolved independently during this period of time, and only occasionally share elements with the central and western parts of North America and western Eurasia.

Summary

On account of their planktonic larvae, inoceramids attained wide biogeographic distributions. Judging by the faunas known, for most of the Late Cretaceous and during the Cenomanian–Turonian distribution was dominantly worldwide. However, in the Berriasian–Albian interval Tethyan inoceramids are very rare, and inoceramid distributions

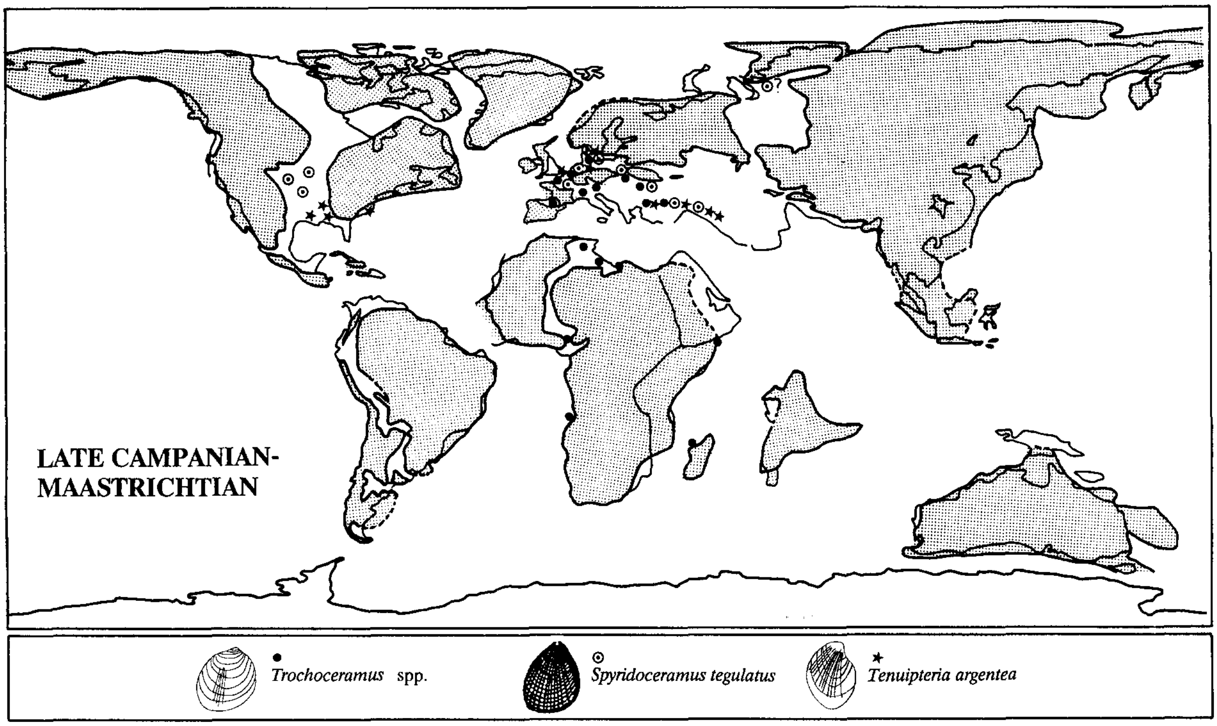

Fig. 9. Distribution of *Trochoceramus* spp., in the late Campanian and Maastrichtian, and *Spyridoceramus tegulatus*, and *Tenuipteria argentea* in the Maastrichtian. Data are from Kociubynskij (1958, 1968), Seitz (1970), Sornay (1973), Kociubynskij and Savczinskaja (1974), Dhondt (1979, 1983a), and more recent own research. Map from Barron (1987) is for the early Maastrichtian.

are often bipolar and presumably limited to colder seas.

From the Turonian–Coniacian onwards the inoceramid fauna (and other faunas) of the Northern Pacific seem to have been isolated as shown by a certain amount of endemism.

The Coniacian–Maastrichtian inoceramid faunas of North America and Eurasia are notably similar. However, the genus *Trochoceramus* has so far not been found in North America and although relatively rare in Maastrichtian white chalks in northern Europe, species of this genus are common in marls and warm water Temperate and Tethyan strata.

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