# Notes on the biogeography of Campanian-Maastrichtian gastropods

Steffen KIEL

**Abstract:** A new Campanian/Maastrichtian gastropod biogeography is presented, based on an evaluation of two gastropod faunas from the Tethys, a re-evaluation of the literature, and on current developments in climate modelling and paleoceanography. The distribution of rudist facies gastropods might have been mainly controlled by the presence of slightly hypersaline, nutrient-depleted water rather than by temperature. The rudist facies alone cannot be considered synonymous with "tropical" in a zoogeographical sense. Many typically tropical gastropods occur outside the Tethys and because of the warm, equable climate of the Late Cretaceous, the 20°C isotherm must have been located considerably further north and south of the limits of rudist occurrences. A tropical Atlanto-Indian Province is postulated here for the Campanian-Maastrichtian. It included the entire North Atlantic, the central and eastern South Atlantic, the European and eastern Tethys, and the Indian Ocean. Contrary to previous reconstructions, a temperate North Atlantic Province is thought to be unlikely. The broader latitudinal extent of the Pacific Ocean enabled the development of temperate faunas in the northern and southern Pacific. The boundaries between tropical and temperate gastropods in the eastern Pacific is not yet well understood, but there are indications for broad transitional zones. The differences between the eastern Pacific and the western Atlantic gastropods support the hypothesis of a central American landbridge in the later Late Cretaceous. Based on this biogeographic reconstruction, the hypothesis of a cool-temperate origin and early radiation of the Neogastropoda is strongly doubted. Two hypothesises regarding faunal distribution are suggested: (a) In times of warmer, more equable climates, the significance of temperature for faunal distribution decreases. The extent to which other ecological factors become more important mostly depends on the needs of the individual organism. (b) A more equable climate than today facilitated the development of much broader transitional zones between faunal realms.

**Keywords**: Late Cretaceous, Gastropoda, Palecology, Palaeobiogeography

## 1. INTRODUCTION

In previous reconstructions of Late Cretaceous gastropod biogeography, much emphasis has been laid on a clear distinction between a tropical Tethys-belt and temperate or cool-temperate provinces north and south of this belt (SOHL, 1971, 1987; ZINSMEISTER, 1979, 1982). Strong similarities between the northern and the southern temperate faunas have

Geologisch-Paläontologisches Institut, Universität Hamburg, Bundesstrasse 55, 20146 Hamburg, Germany, E-mail: steffen.kiel@gmx.de

been discerned with astonishment, because respective relatives were unknown in the Tethys (Sohl, 1964). No satisfying explanation has been offered for this phenomenon.

Many extant gastropod groups appeared in the Cretaceous (Wenz, 1938–44; Taylor et al. 1980; Kollmann, 1982; Sohl 1987; Bandel, 1993). Although Allmon (1992) suggested that the climatic affinities of the Turritellinae have shifted from tropical in the Late Cretaceous to temperate in the Neogene, it can generally be assumed that habitat and temperature preferences of the extant groups are also valid for their Late Cretaceous ancestors. Thus, some of these groups can be used in biogeographic reconstructions.

The intentions of this study are to outline biogeographically usable gastropod groups, to present a new Campanian-Maastrichtian gastropod biogeography, and finally to discuss evolutionary implications and possible reasons for the outlined distribution-patterns. The study is based on (1) the current evaluation of two gastropod faunas from the Tethyan Campanian/Maastrichtian carried out by the author. The first one is from the Tremp basin in northern Spain, which was first described by Vidal (1921); new material has been collected during the last ten years by K. Bandel and colleagues, including myself. The stratigraphy and molluscs of the second locality, in Guerrero, southern Mexico, have recently been presented by Perrilliat et al. (2000). Subsequent collection by myself has revealed additional species. (2) Comparison with material from the following localities: Ammonite Hills (Egypt, Maastrichtian), Fruška Gora (Serbia, Maastrichtian), Trichinopoli (India, Santonian and Maastrichtian), Mungo River (Cameroon, Coniacian), Paita (Peru, Maastrichtian), Quiriquina (Chile, Maastrichtian), and Umzamba (South Africa, Santonian-Campanian). (3) A critical evaluation of the literature. (4) The ecological data outlined in chapter three. (5) New plate tectonic, paleoclimatic and paleoceanographic data from the literature. Yet unpublished results and my own observations on material from the localities mentioned above are cited as such.

## 2. TERMINOLOGY

Tropical, temperate and cool-temperate are used in a strictly zoogeographical sense (see Ekman, 1935). Tropical refers to faunas confined to areas approximately between the 20°C isotherms. Geographically and climatologically, this comprises the tropical and subtropical zones. Temperate describes the middle and higher latitudes north and south of the tropical belt, with pronounced seasonallity. Cool-temperate applies to the polar regions. Rudist facies refers to the carbonate platforms, reef and lagoon environments and rudist biostromes of the tropical Tethys.

## 3. BIOGEOGRAPHICALLY USABLE GASTROPOD GROUPS

Many extant gastropod groups can be traced back into the Late Cretaceous, and it is assumed that their present-day ecology also applies to their Late Cretaceous relatives. Several ecological needs of astropods can be used for biogeographic reconstructions. The most important is temperature. Numerous groups are confined to tropical waters (e.g. always warmer than 20°C), although some live exclusively in cooler temperatures.

Such groups can be employed to distinguish climate zones. Adaptations to brackish water suggests ancient shorelines. The bathymetric range of gastropods indicates sedimentary environments, such as intertidal or outer shelf. This is important where groups confined to cooler waters have a broad bathymetric range, because they might also have occurred in the tropics, but only in deeper and therefore cooler waters.

## 3.1. Archaeogastropoda

In theory, archaeogastropods make excellent paleobiogeographic indicators. They spread slowly and only along shelves, because they do not have plankton-feeding larvae; their time as free swimming veliger is restricted to the amount of yolk they carry (BANDEL, 1982). Therefore, they are more or less unable to cross large ocean basins or deep trenches. Unfortunately, there are three major drawbacks. The habitat of most archaeogastropods are rocky shores or other hard substrates (KOLLMANN, 1982; BANDEL & WEDLER, 1987; HICKMAN & MCLEAN, 1990) and consequently their potential to become fossilised is rather low. Secondly, convergence of shell shape is common among groups of different phylogenetic relation. Thirdly, rates of evolutionary changes differ greatly and are very low in some groups (see KIEL & BANDEL, 2000).

Two groups which have been presented as good biogeographic indicators by SOHL (1987) need to be discussed here. He postulated that the trochid *Chilodonta* was restricted to the rudist facies and therefore serves as a typical representative of the Tethys. This appears to be true for the Jurassic and Early to mid-Cretaceous. In the later Late Cretaceous however, *Chilodonta* also occurs in the South African Umzamba Formation (RENNIE, 1930) and in the Quiriquina Formation in central Chile (own obs.), far away from the rudist facies.

*Calliomphalus* was considered to be an indicator of sub-tropical to warm-temperate conditions (SOHL, 1971). It has now become apparent that *Calliomphalus*-like shells are also built by *Solariella* (KIEL & BANDEL, 2001a). The only distinguishing character is the sculpture of the very first teleoconch whorl, detectable exclusively on well-preserved specimens using scanning electron microscopy. Among the material investigated so far, *Calliomphalus* lived north of the 30°N paleolatitude and the *Solariella montsecana*-group south of it (KIEL & BANDEL, 2001a). If further evaluations confirm this pattern, and if well preserved material is available, *Calliomphalus* and *Solariella* may be used as paleogeographical indicators.

## 3.2. Neritimorpha

The extant neritid genera *Nerita* and *Dontostoma* belong to the tropical fauna and live in the rocky intertidal zone (ABBOTT, 1974). In the Late Cretaceous, *Dontostoma* is known from California (SQUIRES & SAUL, 2001), South Africa (WOODS, 1906) and northern Spain (VIDAL, 1921). Among the Late Cretaceous neritids *Otostoma* and *Pileolus*, the latter was mostly restricted to a narrow belt in the central and western Tethys (SOHL, 1987), while *Otostoma* reached a wide distribution and is known from California (SAUL & SQUIRES 1997), Europe (GEINITZ, 1871–75; HOLZAPFEL, 1888), Armenia (HACOBJAN, 1976), and India (STOLICZKA, 1868). Figure 1 shows occurrences of the Neritidae during the Campanian/Maastrichtian.

## 3.3. Caenogastropoda

The Vermetidae today live in shallow tropical waters (MORTON, 1965). The taxonomic position of the Late Cretaceous species of *Vermetus* and *Laxispira* within the Vermetidae has been verified by protoconch morphology (DOCKERY, 1993; BANDEL & KOWALKE, 1997; BANDEL & KIEL, 2000). The same habitat as for the extant members is assumed for the Late Cretaceous genera.

Late Cretaceous species of *Campanile* are known from tropical Tethyan waters from India to the Gulf of Mexico and thus show a distribution similar to that of *Otostoma*, except for its seeming absence from the eastern Pacific (KIEL et al., 2000). The Recent *Campanile symbolicum* lives in the shallow sub-tidal zone (HOUBRICK, 1989). The same habitat has been documented for Eocene *Campanile* and it is assumed for the Cretaceous species as well (KIEL et al., 2000).

While many gastropods are confined to the tropical realm, it is more difficult to name exclusively cool or temperate groups. Extant Aporrhaidae represent such a case; the few species are present in the North Atlantic and eastern South Atlantic but absent in between (KRONENBERG, 1991). Mesozoic aporrhaids, on the other hand, were a large and widespread group and suffered strongly during the K/T mass extinction (PIETTE, 1891; GARDNER, 1875; WENZ, 1938–44; ROY, 1994). Thus, their present day distribution does not necessarily apply to the Late Cretaceous. However, KIEL & BANDEL (2002) showed that *Drepanocheilus* preferred more temperate regions, while *Graciliala* and the *Anchura*-clade were widely distributed in the tropics. A distinct group of aporrhaids apparently evolved in the Weddellian Province and adjacent areas including *Struthiochenopus*, *Struthioptera* and *Austroaporrhais* (ZINSMEISTER & GRIFFIN, 1995). Extant aporrhaids live on sandy or muddy bottoms (BARNES & BAGENAL, 1951; PERRON, 1978).
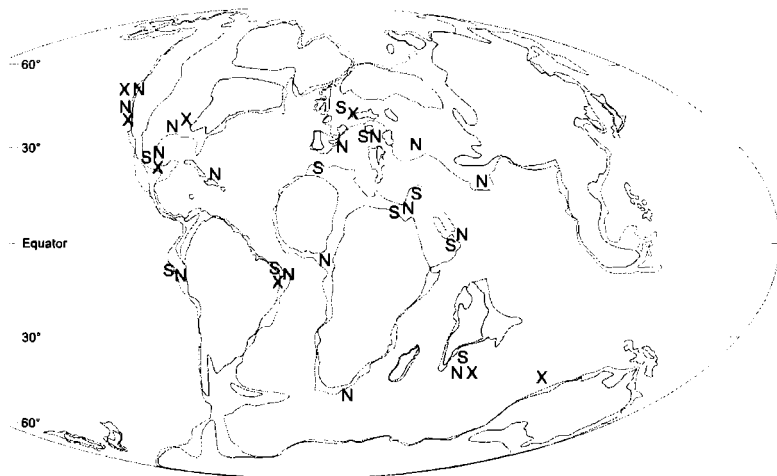


Fig. 1: Occurrences of the gastropod families Neritidae (N), Strombidae (S), and Xenophoridae (X) in the Campanian/Maastrichtian (reconstruction modified after HAY et al., 1999).

ELDER & SAUL (1996) pointed out that *Anchura* preferred middle- to outer-shelf environments. This is in contrast to most other gastropod groups discussed herein and should be considered in the interpretation of fossil gastropod assemblages.

Extant Strombidae and Xenophoridae are confined to the tropical fauna (ABBOTT, 1960, 1974; PONDER, 1983). Among the Late Cretaceous strombids, *Hippocrenes* is known only from the European Tethys and its marginal seas, where it is associated with shallow water inhabitants such as *Campanile, Otostoma* and vermetids (KAUNHOWEN, 1897; PETHÖ, 1906; KIEL & BANDEL, 2002). *Calyptraphorus* apparently reached a wider distribution with India and perhaps Peru as most easterly and most westerly occurrences respectively (PERRILLIAT & VEGA, 1997). *Rimella* has as yet only been documented from southern Mexico (KIEL & PERRILLIAT, 2001). In summary, they were confined to tropical waters like their modern relatives. Their Campanian/Maastrichtian occurrences are shown in Fig. 1.

Naticidae today are found from the tropics to the coolest polar regions (POWELL, 1951; ABBOTT, 1974) and their activities are easily recognised by drillholes in mollusc shells. Their Late Cretaceous biogeography, however, is still puzzling. Naticoid shells occur frequently, but drillholes do not. SOHL (1969) and TAYLOR (1981) presumed that earlier Naticidae had different modes of feeding. However, it has recently been revealed that one or two gastropod groups with naticoid shells – which also occurred in the Late Cretaceous – apparently do not belong to the Naticoidea. Preliminary investigations of the soft body of *Globularia fluctuata* indicated characteristics of the Architaenioglossa (KASE, 1990). *Pseudamaura* yields a protoconch different from Naticidae and is now considered a cerithioidean of uncertain affinities (KOWALKE & BANDEL, 1996). As a result, many Late Cretaceous "naticids" may in fact belong to other groups, which could partly explain the absence of drillholes at sites where those "naticids" are found. *Gyrodes* on the other hand, has a typical naticid protoconch (BANDEL, 1999), but occurs in places where drillholes are either abundant or absent.

*Calyptraea, Trochita, Hipponix* and *Thylacus* of the Calyptraeoidea are known already from the Late Cretaceous (STEWARD, 1927; OLSSON, 1944; DOCKERY, 1993; BANDEL & RIEDEL, 1994a; BANDEL & STINNESBECK, 2000). Their extant members live in the intertidal to the shallow sublittoral zones on primary or secondary hard substrates (WERNER, 1953; RIEDEL, 2000; own obs.). The same habitat has been documented for the Late Cretaceous species (DOCKERY, 1993; BANDEL & RIEDEL, 1994a).

Cypraeidae are largely tropical, although they penetrated further into the temperate regions than most other tropical groups (ABBOTT, 1974; ABBOTT & DANCE, 1982).

Neogastropoda first appeared in the Albian (TAYLOR et al., 1980; BANDEL, 1993; TRACEY et al., 1993), subsequently underwent rapid radiation, and many distinct groups developed in the Late Cretaceous ocean basins. Therefore, Late Cretaceous neogastropods are excellent biogeographical indicators.

## 3.4. Heterostropha

The only Allogastropoda of biogeographic value are the Nerineoidea. They were by and large confined to the rudist facies (SOHL, 1971, 1987; but see SAUL & SQUIRES, 1998) and tropical lagoons or shallow waters are considered to have been their preferred habitat (BARKER, 1990; KOWALKE & BANDEL, 1996).

Among the Opisthobranchia, the globular ringiculids of the *Avellana-Biplica-Eripty-chia-Oligotychia*-group are characteristic for the Late Cretaceous (POPENOE, 1957; HACOB-JAN, 1976; KASE, 1990). However, their taxonomy and biogeography is not yet settled (see KOLLMANN, 1976; KIEL & BANDEL, 2001b). *Acteonella* and *Trochactaeon* of the Acteonellidae are typical Late Cretaceous gastropods. Their habitats were fully marine lagoons but at least some species seem to have tolerated a brackish influence. Although they were most abundant in the Tethys, they are also known from South Africa, central Europe and California (KOLLMANN, 1967; SOHL & KOLLMANN, 1985; KOWALKE & BANDEL, 1996).

Among the Archaeopulmonata, *Siphonaria*, *Anisomyon*, *Auriculinella*, *Leopoldium*, and *Laemodonta* are known from Late Cretaceous deposits and lived in the intertidal zone, just like their modern counterparts (STEPHENSON, 1941; SOHL, 1964; DOCKERY, 1993; BANDEL & RIEDEL, 1994b; BANDEL & STINNESBECK, 2000; BEESLEY et al., 1998; own data).


## 4. DISTRIBUTION-PATTERNS IN THE CAMPANIAN-MAASTRICHTIAN

### 4.1. The gastropods of the rudist facies

Four groups of gastropods are considered typical representatives for the circum-equato-rial rudist facies: the Nerineoidea, *Pileolus*, *Discotectus*, and the Acteonellidae (SOHL, 1971, 1987). In previous reconstructions of Late Cretaceous gastropod biogeography, these gastropods of the rudist facies have been treated synonymously with "tropical" gastropods. This must be reconsidered.

The northern and southern boundaries of the tropical faunas today are marked by latitudes 30–35°S in the Indian Ocean and 35–40°N and 30–35°S in the western and central Pacific (EKMAN, 1935). On the other hand, the Late Cretaceous northern bound-ary of the rudist facies in the Mediterranean apparently stayed quite constant, at about 30°N (VOIGT et al., 1999). The present-day tropical fauna in the western Atlantic extends to about 35°N (EKMAN, 1935), and also the Caribbean Late Cretaceous rudists ranged up to 35°N (JOHNSON et al., 1996). Thus, the Late Cretaceous rudist facies and its affiliated gastropods apparently had an equal or even narrower latitudinal distribution than the Recent tropical fauna. The latitudinal distribution of Late Cretaceous tropical gastropods, however, should range far beyond the average recent 35°N and S, considering the warmer and more equable Cretaceous climate.

A change in the climatic regime from arid to humid at 30°N was offered as an explanation for the northern boundary of Mediterranean rudist build-ups at this latitude by VOIGT et al. (1999). According to this model, rudist build-ups (and carbonate plat-forms in general) could only have grown in environments with a negative freshwater balance which resulted in basins of slightly hypersaline, nutrient-depleted waters. Also, KAUFFMAN & JOHNSON (1988) suggested that rudists favoured warm and slightly hypersa-line waters, which they coined the term "supertethyan". Nerineans, *Pileolus*, and *Discotectus* arose in carbonate platform environments during the Jurassic (WENZ, 1938–44) and only rarely left this habitat during their almost 100 ma of evolutionary history. This may have led to such close ties with this environment – for example regarding water chemistry – that temperature played only a secondary role in controlling their distribu-tion. Their contemporaneous extinction with the rudists at the end of the Cretaceous

may further support this suggestion. Some reservations remain, because no close living relatives of the nerineans, *Discotectus* and *Pileolus* exist, so that palecologic reconstructions are more speculative than those of other groups.

The almost equal latitudinal ranges of coral reefs and tropical gastropods today may be coincidental, because the 20°C isotherm and the change from a negative to a positive freshwater balance lies at almost the same latitude. The water-chemistry controlled range of the rudist facies could well be decoupled from the temperature controlled range of the tropical gastropods in the warm, equable Cretaceous climate. HALLAM (1969) has already noticed and discussed this matter for the Jurassic.

## 4.2. The tropical Atlanto-Indian Province

In his extensive evaluation of the US Gulf coast gastropods, SOHL (1960, 1964) recognized the strong similarities of this fauna with those of the South African Umzamba Formation and the Indian Trichinopoli group. Since SOHL interpreted these faunas as "temperate", this observation was surprising because respective relatives were unknown from the tropical Tethys. A similar observation concerning bivalves was made by KAUFFMAN (1973: 358), who recognized numerous "trans-temperate forms that ranged widely on either side of Tethys but were not common within". The existence of typical "temperate" gastropods within the Tethys belt has been documented (see PETHÖ, 1906; QUAAS, 1906; ROMAN & MAZERAN, 1913; LEES, 1928; RIEDEL, 1932; DARTEVELLE & BREBION, 1956), although it seems to have been largely overlooked in biogeographic reconstruction. My own studies of the gastropods from Spain and southern Mexico confirm the presence of these "temperate" gastropods within the Tethyan realm. Thus, the classical distinction of Tethys and temperate gastropod provinces in the Late Cretaceous appears inappropriate. Instead, a broad tropical Atlanto-Indian Province is postulated here, based on the evidence discussed below.

As shown in the previous chapter, the term "tropical" cannot be applied to the gastropods of the rudist facies alone. Most gastropods today are not as sensitive to substrate, turbidity, and the nutrient-content of the water as corals are (BANDEL & WEDLER, 1987). This was most likely the case with many Cretaceous gastropods, too. Reviewing later Late Cretaceous gastropod associations of the Atlantic and Indian Ocean, numerous tropical faunal elements are found: *Otostoma*, Xenophoridae, and Vermetidae lived in the Aachen greensands of Germany (HOLZAPFEL, 1888), Strombidae, Vermetidae and Cypraeidae are known from Maastricht in the Netherlands (KAUNHOWEN, 1897). Xenophoridae, Vermetidae, Cypraeidae, and Neritidae have been reported from the Ripley Formation of the US Gulf coast (SOHL, 1960; DOCKERY, 1993), Strombidae, *Otostoma*, and *Campanile* occurred in southern India (STOLICZKA, 1868), and Cypraeidae, *Nerita*, and *Dontostoma* are even known from South Africa (WOODS, 1906; RENNIE, 1930; own data).

The most stable features of the modern oceans are the stratified tropical-subtropical gyres with warm saline surface waters. These lie between ~15° and ~45° latitude in each hemisphere. The same conditions have been inferred for the Late Cretaceous oceans (HAY, 1995). While today the 20°C isotherm lies within this zone, climate models for the Campanian-Maastrichtian predict its position at around 45°N and S, and thus on the poleward margins of the tropical-subtropical gyres (HAY & DECONTO, 1999). In plate-

tectonic reconstructions of the Late Cretaceous, the northern shores of the Atlantic lie at about 40°N in the Campanian, and no deep-water connections with the Arctic Ocean existed (SCOTESE et al., 1988; HAY et al., 1999). Therefore, the entire gastropod fauna of the Late Cretaceous North Atlantic, including the rich and diverse faunas of the American Gulf coast plains and the European Atlantic coast should be regarded as tropical. This also explains the obviously close relationships between faunas of the northern and southern hemisphere previously considered "temperate".

Comparisons with other organisms provides further evidence. Based on otolithes, NOLF & DOCKERY (1990) considered the climatic conditions of the US Gulf coast Coffee Sand Formation as tropical/subtropical. The here delineated Atlanto-Indian Province falls within the range of the "megathermal" flora of WOLFE & UPCHURCH (1987), or the "tropical-paratropical" flora of SAWARD (1992). A temperate gastropod fauna most probably did not exist in the Late Cretaceous North Atlantic, analogous to the situation in the present-day northern Indian Ocean (see EKMAN, 1935). The changes in the gastropod assemblages northward through the Western Interior Seaway of North America as noted by SOHL (1971) may be interpreted as a change to a temperate fauna. The data on Cretaceous gastropod assemblages of the Arctic Ocean are yet too sparse to allow the postulation of a "Boreal" Province (SOHL, 1971).

The proposed tropical Atlanto-Indian Province includes the entire North Atlantic from the American Gulf coast plains in the west, to the European Atlantic coast and interior basins. It ranges eastwards through the central Tethys to Oman and India, and southwards through the South Atlantic to the south-western Indian Ocean. On the southern margin of the tropical Atlanto-Indian Province, the fauna of the Umzamba Formation in South Africa not only shows tropical elements, but also affinities with the Antarctic Weddellian Province (KIEL & BANDEL, 2002). Also, from the floristic point of view, Late Cretaceous southern South Africa lay in a transitional zone (WOLFE & UPCHURCH, 1987; SAWARD, 1992), and the foraminifera show a transitional character from Tethyan to polar forms as well (HUBER, 1992). The fauna of the North American Pacific coast has a very different character (see following chapter). Common and widespread genera of the Campanian-Maastrichtian Atlanto-Indian Province include *Campanile*, *Graciliala*, *Pterocerella*, *Hippocrenes*, *Sargana*, *Liopeplum*, *Bellifusus*, *Drilluta*, *Mitridomus*, and *Mesorhytis*.

How far it extended into the western Pacific remains unclear, due to insufficient data. The fauna of the Japanese Maastrichtian described by KASE (1990) shows neither tropical elements, nor any characteristic Atlanto-Indian genera. Rather, it has close ties with Californian faunas. Eastward from the Indian Ocean, the vast Pacific Ocean might have prevented exchange between the tropical faunas on its eastern and western shores, as it does today. This suggestion is in contrast to the proposed trans-Pacific spread of tropical shallow marine benthos (SKELTON & WRIGHT, 1987).

### 4.3. The northern and eastern Pacific

Along the North American Pacific coast, distinction between tropical and temperate provinces was also carried out mainly on the basis of the presence or absence of rudists (SOHL, 1971; SAUL, 1986). SOHL (1971) regarded the Californian fauna as transitional to the North Pacific fauna and recognized warm-temperate to subtropical conditions throughout

the region. SAUL (1986) characterised the North Pacific Province as latitudinally inordinately broad, and the rather endemic aspect of that fauna has repeatedly been pointed out (POPENOE, 1957, 1983; SOHL, 1971; SAUL, 1986, 1988; KIEL & BANDEL, 1999).

Among the typically tropical gastropods, Xenophoridae and *Dontostoma* occur as far north as southern California (SQUIRES & SAUL, 2001), while Cypraeidae and *Anchura* are known even from south-western Canada (SAUL, 1986; ELDER & SAUL, 1996). On the other hand, *Nekewis, Perissitys, Pseudocymia* and *Murphitys* from the North Pacific fauna also occur several hundred kilometres south of the northernmost rudists (POPENOE & SAUL, 1987; SAUL, 1988). These data, however, bear a considerable amount of uncertainty, since many Cretaceous deposits of the American Pacific coast have been displaced northward; ~1000 km in the case of Baja California and California west of the San Andreas fault, as suggested by BECK (1991), or ~3000 km in case of the eastern Coast Belt of British Columbia (WYNNE et al. 1995). Although other authors consider these estimates too high (MONGER & PRICE, 1996; SCHAAF et al. 1995), the uncertainties concerning the reconstruction of climatic faunal zones remain.

However, the Late Cretaceous North Pacific reached about 70°N (see BARRERA & SAVIN, 1999: fig. 1), and thus facilitated the development of a temperate gastropod fauna – in contrast to the North Atlantic. SOHL's (1971) concept of a North Pacific Province from northern Japan to southern California with a broad transitional zone on the Californian coast is largely followed here. Genera with more temperate affinities include *Zinsitys, Christitys* and *Forsia* (SAUL, 1988), and *Pseudoperissitys* and *Taniella* which are endemic to Japan (KASE, 1990). There is an endemic Californian lineage within *Pyktes* (POPENOE, 1983; KIEL & BANDEL, 1999).

The most diverse gastropod faunas of the South American Pacific coast are those of the Amotape and Paita-region in northern Peru and of Quiriquina in central Chile. The Paita and Amotape faunas contain rudists and a mixture of Tethyan and endemic gastropods, and groups that show relations to the fauna of Quiriquina (OLSSON, 1934, 1944; KIEL & BANDEL, 1999; own data). The Quiriquina fauna is usually considered highly endemic (PHILIPPI, 1887; WILCKENS, 1904; BANDEL & STINNESBECK, 2000), but ZINSMEISTER (1982) emphasised relationships to the Weddellian Province (see following chapter), and it also shows relationships to the North Pacific fauna (POPENOE, 1957; POPENOE & SAUL, 1987; own data). In conclusion, it appears that temperate and tropical gastropods on the American Pacific coast are difficult to distinguish, and that many groups have extraordinarily wide latitudinal ranges.

### 4.4. The Weddellian Province

A cool-temperate fauna existed in the southern Pacific (ZINSMEISTER, 1979, 1982; STILWELL, 1997), ranging from New Zealand and the Chatham Islands along the Antarctic Pacific coast to the Pacific and Atlantic coasts of southern South America. In this Weddellian Province (ZINSMEISTER 1979) the gastropods were isolated from Early Cretaceous through Eocene times and consequently evolved quite independently from those of the outside world. ZINSMEISTER & GRIFFIN (1995) considered the Weddellian Province an important source area for many low latitude groups during the Cenozoic.

However, there is some doubt about this hypothesis. Firstly, BANDEL & STINNESBECK (2000) showed that *Seymourosphaera,* which has been considered a typical represent-

ative of the Weddellian Province in the Paleocene (OLEINIK & ZINSMEISTER, 1996), was already abundant in the Quiriquina Maastrichtian; the same genus also occurred in the Paita Maastrichtian (own data). Secondly, other typical Pacific coast gastropods also occur on Seymour Island of the Weddellian Province (e.g. *Pyropsis gracilis* WILCKENS, 1910). Thirdly, two aporrhaids characteristic for the Weddellian Province have been found in the Umzamba Formation in South Africa (KIEL & BANDEL, 2002). Fourthly, relationships of the echinoids of Seymour Island in the Weddellian Province to South America and to South Africa have been demonstrated (NÉRAUDEAU et al., 2000).

In conclusion, transitional zones between the Weddellian Province and the tropical faunas along the South American coasts appear more likely than an highly isolated Weddellian Province. Faunal exchange apparently also existed with South Africa. In the cases of *Seymourosphaera* and the aporrhaid subfamily Struthiopterinae, it appears that Late Cretaceous mid-latitude groups moved to the cool-temperate South where they survived the K/T mass extinction and subsequently radiated.

## 5. LOCAL ASPECTS AND EVOLUTIONARY TRENDS

### 5.1. The taxonomic level

The genus is usually considered the most reliable taxonomic unit in paleobiogeographic reconstructions (KAUFFMAN, 1973). As shown herein, families which are confined to climatic zones can be used to identify these zones in earth history, especially since families usually have longer geologic ranges than genera. The following example, given by EKMAN (1935), shows that the comparison of genus- and species-level relationships can become crucial in the interpretation of ancient distribution patterns. Recent Caribbean *species* show closer relationships to those of the West African coast than to those of the Indo-Pacific. Concerning the *genera*, the opposite is the case. EKMAN (1935) argued that the relationships on genus-level have *historical* reasons; faunal exchange with the Indo-Pacific was possible until only about 3.1 ma ago, when the Isthmus of Panama closed. Relationships on the species level, on the other hand, are the result of *present* migration-routes, which are open towards West Africa but closed towards the Indo-Pacific.

### 5.2. The Caribbean – seaway or landbridge?

In current reconstructions of the Caribbean, the distance between the American continents reached its maximum during the Campanian/Maastrichtian (PINDELL & BARRETT, 1990; MESCHEDE & FRISCH, 1998; HAY et al., 1999). Surprisingly, exchange of marine gastropods between the Atlantic and Pacific appears quite limited at this time. A similar observation was made by RICCARDI (1991), who considered the affinities of Campanian-Maastrichtian ammonoids of the central South Atlantic clearly Tethyan, but noted low similarities to those of north-western South America. Exchange of terrestrial vertebrates between North and South America took place in the Campanian (BENTON, 2000). This led to the postulation of some kind of landbridge between the two continents at this time.

Comparing only gastropod-*genera* between the present-day Pacific and Atlantic coasts of Central America, a landbridge would seem highly unlikely. However, an

examination on species-level reveals obvious differences between the east- and the westcoast (EKMAN, 1935).

A preliminary survey of Campanian/Maastrichtian gastropods in the eastern Pacific and western Atlantic displays a noticeable pattern of relationships. For example, affinities can be observed between mangrove-snails from Paita and those from Pernambuco in eastern Brazil (WHITE, 1887; OLSSON, 1944), and the pugnellids of Paita show relations to those of the European Tethys (KIEL & BANDEL, 1999). Interestingly, these similarities exist only on genus-level but not on species-level. Additionally, none of the typical post-Turonian East Pacific gastropods are known from the Atlantic. Thus, the distribution of gastropod species and genera supports the hypothesis of a temporary landbridge, and it suggests that it may even have been continuous rather than a chain of islands.

## 5.3. The Sierra Madre Occidental and the evolution of the north Pacific fauna

Several gastropod genera regarded here as typical for the Campanian-Maastrichtian Atlanto-Indian Province (*Sargana, Liopeplum, Gymnarus,* and the *Drilluta/Paleopsephaea/Remera*-group) also occur in the Turonian of California, but seem to have disappeared afterwards (POPOENOE, 1983; SAUL & POPOENOE, 1993; SAUL, 1996). Almost simultaneously, the development of the typical North Pacific fauna began (POPOENOE, 1983; POPOENOE & SAUL, 1987). SAUL (1986) considered the post-Turonian cooling responsible for this development. Another event which might have intensified the effect of this cooling could be the contemporaneous rise of the Sierra Madre Occidental in western Mexico. The closure of shallow marine connections across central Mexico in the Coniacian was documented by IMLAY (1944: figs. 2–6) and ALENCÁSTER (1984: figs. 4–7), and belts of plutonic rock in south-eastern Mexico have been dated as Late Cretaceous by SCHAAF et al. (1995). Together with the possible central American landbridge, this mountain chain could have effectively prevented faunal exchange between the western Atlantic and the eastern Pacific, and thereby made the development of distinct faunal realms possible.

## 5.4. Transitional zones

In the present day oceans, the broadest transitional zone from a tropical fauna to a temperate one is found along the north-eastern Atlantic coast due to the very gentle transition from tropical to temperate climate in this region (EKMAN, 1935). Thus, the more equable climate of the Late Cretaceous might have resulted in generally broader transitional zones between faunal realms than today.

Evidence of this has been documented in the Western Interior Seaway of North America, where the tropical *Anomalofusus* and *Liopeplum* are interfingered with the more northern *Serrifusus* and *Vanikoropsis* over a distance of more than 1000 km (SOHL, 1971). Along the North American Pacific coast, the transitional zone also appears to have been extremely wide (SOHL, 1971; SAUL, 1986), with cypraeids extending as far north as British Columbia and the North Pacific genera *Nekewis, Perissitys, Pseudocymia* and *Murphitys* occurring far to the south of the northernmost rudists (see discussion above). Similarly, along the South American Pacific coast, groups with extremely wide latitudinal distribution existed, as shown for *Seymourosphaera* and *Pyropsis*.

Bipolar distribution and tropical submergence today occurs most commonly along the west coast of the Americas, due to cool currents and upwelling of cooler central waters (EKMAN, 1935). Such cooler central water, which underlay the surface water, must also have existed during the Campanian/Maastrichtian, albeit with a smaller difference in temperature than today. Thus, upwelling would have been easier (HAY, 1995). Additionally, sediments of deeper waters are subject to uplift on this active continental margin. These factors must also be considered in interpretations of American Pacific coastal faunas and may account for the wide latitudinal distribution of certain taxa.

## 5.5. The early history of the Neogastropoda

The Neogastropoda are considered to be one of the rare examples of a large and successful group of animals which did not originate in the tropics, but in cooler regions (TAYLOR et al., 1980; SOHL, 1987). It has been suggested that they originated in the temperate European seas and had their maximum diversity and centres of evolution in the Late Cretaceous temperate realms north and south of the Tethys. After the K/T-boundary, they switched to their present-day distribution with a maximum of diversity in the tropics.

This implies that a large number of gastropods confined to temperate waters repeatedly travelled across the tropical realm – e.g. from northern Europe through the tropical Caribbean into the eastern Pacific, in the opposite direction into the western Pacific, and perhaps three times across the equator to the southern Pacific, Indian and Atlantic oceans – without becoming adapted to this environment.

The hypothesis of a temperate origin needs to be reassessed in the light of the new biogeographic interpretation outlined here. The earliest abundant occurrences of Neomeso- and Neogastropoda are known from the later Albian of central western Europe (MARLIÈRE, 1939; KOLLMANN, 1976; TAYLOR et al., 1983). The paleoposition of this part of the world was situated at around 35–40°N latitude (SCOTESE et al., 1988; HAY et al., 1999) and a warm, equable climate is assumed for the later Albian (see FASSELL & BRALOWER, 1999 for discussion). Consequently, a tropical habitat is a more likely model for evolutionary breeding grounds of the earliest Neomeso- and Neogastropoda.

## 5.6. Temperature and its role in faunal distributions

Today, temperature is the most important factor controlling faunal distribution (EKMAN, 1935). However, the temperature-control hypothesis fails to explain several biogeographic patterns of past periods with warm, equable climate. HALLAM (1969) discussed several objections on the temperature-control hypothesis concerning Jurassic faunal realms, and considered facies to be more important. VOIGT et al. (1999) proposed that the northern boundary of rudist-buildups in the Mediterranean was controlled by the change from a negative to a positive freshwater balance in the basins north of 30° latitude. As shown herein, distribution of Late Cretaceous tropical gastropods was most likely controlled by the 20°C isotherm. I would expect that within a latitudinally extended tropical faunal realm the significance of other factors like salinity, turbidity, nutrients, substrate, length of the day, and wave-energy increases, depending on the ecological needs of the individual taxon. Those gastropods with close ties to the rudist facies might
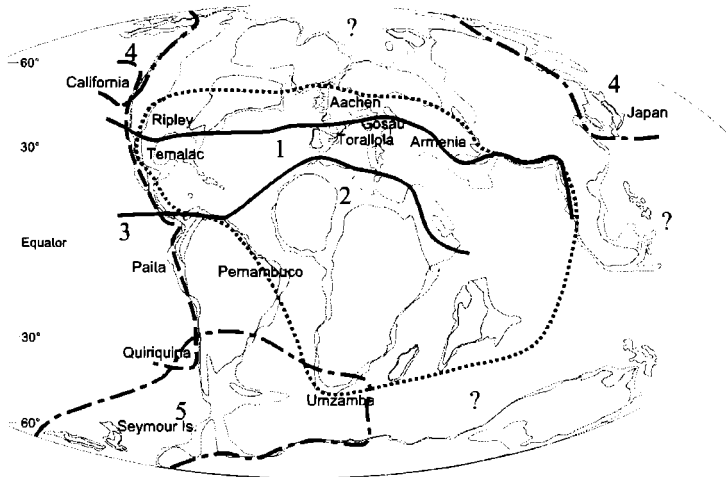
Fig. 2: Paleogeographic reconstruction for the Campanian (modified after HAY et al., 1999) with the outlined gastropod provinces. 1 (solid line), Gastropods of the rudist facies. 2 (dotted line), tropical Atlanto-Indian Province. 3 (broken line), tropical East Pacific Province. 4 (dotted and dashed line), temperate North Pacific Province. 5 (dotted and dashed line), cool-temperate Weddellian Province. The gastropods of the northern Polar Ocean, the western Pacific and the southern Indian Ocean are not yet well known.

represent such a case. Thus, the distribution patterns of different groups of organisms are likely to show a considerably higher variability in times of warm, equable climate than today.

## 6. CONCLUSIONS

The gastropod biogeography of the Campanian/Maastrichtian (see Fig. 2) was characterized by a broad tropical belt with two more or less distinct faunal provinces: the Atlanto-Indian Province and the East Pacific Province. These were probably separated by a landbridge between the American continents, and by the vast Pacific Ocean.

Within the tropical belt, zones of slightly hypersaline, nutrient depleted water facilitated the development of the rudist facies and their typical gastropods. Temperate gastropod provinces apparently existed in the northern Pacific, and in the south the Weddellian Province included the southern Pacific and parts of the South Atlantic. Where known, the transitional zones between tropical and temperate faunas are broad, as documented for the Western Interior Seaway and along the American Pacific coasts. Others, such as those along the South American eastcoast or from Southeast Asia to Japan are still too poorly documented for such conclusions.

Whether the biogeographical features outlined here for gastropods also apply to other marine groups remains to be examined. In future biogeographic reconstructions of

gastropod provinces in geological history, especially when climatic conditions were warmer than today, it should be considered that the distribution of reefs does not necessarily coincide with the "tropical realm". Tropical gastropods (and perhaps other marine groups, too) could well have had a much broader latitudinal distribution. The present day similarity between reef and tropical gastropod distribution might be coincidental and rather exceptional in earth history.

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