

# The Karpatian (Late Burdigalian) of the Korneuburg Basin A Palaeoecological and Biostratigraphical Syntheses

by

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## Abstract

An extraordinary large dataset on the distribution and composition of the Karpatian flora and fauna from the Austrian Korneuburg Basin allows a detailed reconstruction of the palaeoecology.

The small, elongated basin was divided into a southern, estuarine part and a northern, predominately marine part. In the latter, shallow marine settings of 20–30 m water depth formed where scattered corals dwelled the silty to sandy bottom. High percentages of strongly specialised, carnivorous gastropods witness a palaeoenvironment with sponges, corals, echinoderms and molluscs.

The southern basin, separated from the marine northern basin by the Obergänserndorf-Mollmansdorf swell, is characterised by estuarine settings. Along the seaward fringe the impoverished Mediterranean *Avicennia* mangrove became established. Tidal mudflats were settled by vast *Crassostrea* reefs which gave rise to an extremely specialised ecosystem. Brackish marshes, shallow lakes, oxbows and rivers developed as the typical wetland types of the southern Korneuburg Basin. A diverse mammalian fauna derives from the swamps and forests. Freshwater influx is documented by molluscs and aquatic vertebrates, such as the fishes *Esox* and *Barbus* or the turtle *Trionyx*. Slightly drier habitats of the more elevated margins are documented by plants like *Acer*, *Cericiphyllum*, or *Celtis*.

A subtropical climate with a minimum value of the mean annual temperature (MAT) of 17° C based on the requirements of crocodiles and cordylid lizards is interpreted. The winter months were frost free; the minimal cold month temperature (CMT) ranged from at least 3° C to about 8° C.

The analyses of the small mammals, ostracods and molluscs in relation to most recent paleomagnetostatigraphic results date the investigated strata into the latest Early Miocene Central Paratethyan Karpatian stage (early MN5, Chron C5Cn3n between 16,5 and 16,7 Myr.).

## Zusammenfassung

Durch die umfangreiche Bearbeitung der Flora und Fauna aus dem Korneuburger Becken wird eine detaillierte Rekonstruktion der Lebensräume ermöglicht, die sich im Karpatium vor rund 16,5 bis 16,7 Millionen Jahren am Westrand der Zentralen Paratethys bildeten. Die stratigraphische Einstufung basiert wesentlich auf Kleinsäugern, die eine Datierung in die frühe MN5 erlauben (DAXNER-HÖCK, 1998).

Nach WESSELY (1998) ist das rund 20 km lange und nur 7 km breite Korneuburger Becken deutlich in einen nördlichen und einen südlichen Teil getrennt. Diese tektonische Gliederung im Raum Obergänserndorf dürfte sich bereits im Karpatium auch auf die Entwicklung der Lebensräume des kleinen Beckens ausgewirkt haben.

Die initiale Phase der Karpatischen Transgression dürfte bei Leobendorf und Bisamberg nachweisbar sein. Vollmarine Faunen mit Bohrmuscheln, Ostracoden und Korallen dokumentieren Biotope, die sich entlang der durch die Flysch Zone geformten Felsküste entwickelten. Auffällig ist hier das Vorherrschen der Seepocke *Megabalanus tintinnabulum*, die im gesamten übrigen Korneuburger Becken durch die ästuarin-brackische *Balanus amphitrite* verdrängt wird.

Nach dieser marinen Phase begann sich im südlichen Korneuburger Becken ein Ästuar auszubreiten. Fluviatiler Einfluß ist am Teiritzberg aber besonders auch bei Obergänserndorf nachweisbar. Limnisch fluviatile Elemente sind zahlreich durch Gastropoden wie *Tinnyea escheri*, *Theodoxus crenulatus* *Lymnaea dilatata* oder *Stagnicola laurillardii*, Süßwasserfische wie *Esox*, *Barbus* (*Barbus*) und *Aphanius konradi* sowie die Sumpfschildkröte *Trionyx* vertreten. Innerhalb des Ästuars bildeten sich Marsche, Sumpfwälder und verschiedenste Stilwasserbereiche. Brackische Marsche wurden durch *Cladium* und Ruppiaaceae besiedelt. *Decodon*, *Myrica*, *Cladiocarya* und *Sparganium* zeugen von Seen und Altarmen, während *Glyptostrobos*, *Myrica* und *Calamus* den Bestand der Sumpfwälder repräsentierte. Etwas trockenere Standorte, wie sie wahrscheinlich entlang der Beckenränder auftraten, wurden von *Acer*, *Cericiphyllum*, *Celtis* und *Fagus* besiedelt – Standorte, die auch von Landschnecken wie *Helicigona planata*, *Klikia orbiculata* und *Miozonites costatus* bevorzugt wurden. Eine vergleichba-

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re topographische Erhebung dürfte sich auch im Bereich der Obergänserndorf-Mollmannsdorf Schwelle entwickelt haben. Die Zusammensetzung der Säugerfaunen und die Amphibien deuten hier auf relativ offene Lebensräume über dem Grundwasserspiegel hin.

Entlang der Küsten bildete sich eine verarmte *Avicennia* Mangrove, die lateral in ausgedehnte *Crassostrea* Bänke überging. Als sekundärer Hardground waren die riesigen Austern Basis für eine hochspezialisierte Lebensgemeinschaft aus Ätzwürmern, Balaniden, Wurmschnecken und Bohrmuscheln. Die Schlammflächen des Gezeitenbereiches wurden von großen Populationen von Hydrobien und Potamididen abgeweidet.

Generell bestätigen alle Organismengruppen den geringsten Brackwassereinfluß für die Fundpunkte aus dem nördlichen Korneuburger Becken. Innerhalb der Mollusken sind die höchsten Diversitäten von den Fundpunkten Kleinebersdorf und Karnabrunn nachweisbar; der Anteil an carnivoren Arten steigt auf bis zu 70%. Die Fischfauna läßt auf Wassertiefen zwischen 10 und 50 m schließen, während Ostracoden und Foraminiferen sogar noch seichtere Bedingungen bis maximal 30 m anzeigen. Zahlreiche Arten innerhalb der Korallen, Scaphopoden, Gastropoden, Ostracoden und Bryozoen sind ausschließlich aus dem nördlichen Becken bekannt und konnten nicht in den ästuarinen Süden vordringen. Gute faunistische Übereinstimmungen ergeben sich mit der normal marinen Bucht von Kreuzstetten.

Da im nördlichsten Korneuburger Becken im Raum Helfens durch Ostracoden und Gastropoden wieder Süßwassereinfluß nachweisbar ist, dürfte die marine Verbindung des Korneuburger Beckens zur Paratethys entlang des nordöstlichen Beckenrandes zu suchen sein. Im Gegensatz zu der somit gut geschützten Position des Korneuburger Beckens war die Bucht von Kreuzstetten direkt mit der Paratethys verbunden. Trotz ähnlicher Wassertiefen weisen die zahlreichen Sanddollar wie *Parascutella paulensis* und *Amphiope* sp., die aus dem Korneuburger Becken unbekannt sind, auf höher energetische Bedingungen hin.

Aufgrund des Auftretens von Gürtelchsen und Krokodilen dürfte die Jahresdurchschnittstemperatur nicht unter 17° C gefallen sein. Insgesamt weist die Wirbeltierfauna auf frostfreie Winter und eine Minimumtemperatur des kältesten Monats von 3° C bis 8° C hin. Die Jahresniederschläge dürften bis zu 2000 mm erreicht haben. Im marinen Bereich lassen die Gastropodenfaunen auf minimum Temperaturen von ca. 15-16° C im kältesten Monat schließen.

## Schlüsselwörter

Korneuburger Becken – Frühes Miozän – Karpatium – Paläoökologie – Paläoklima – Ästuar – Mangrove

## Key Words

Korneuburg Basin – Early Miocene – Karpatian – Palaeoecology – Palaeoclimate – Estuary – Mangrove

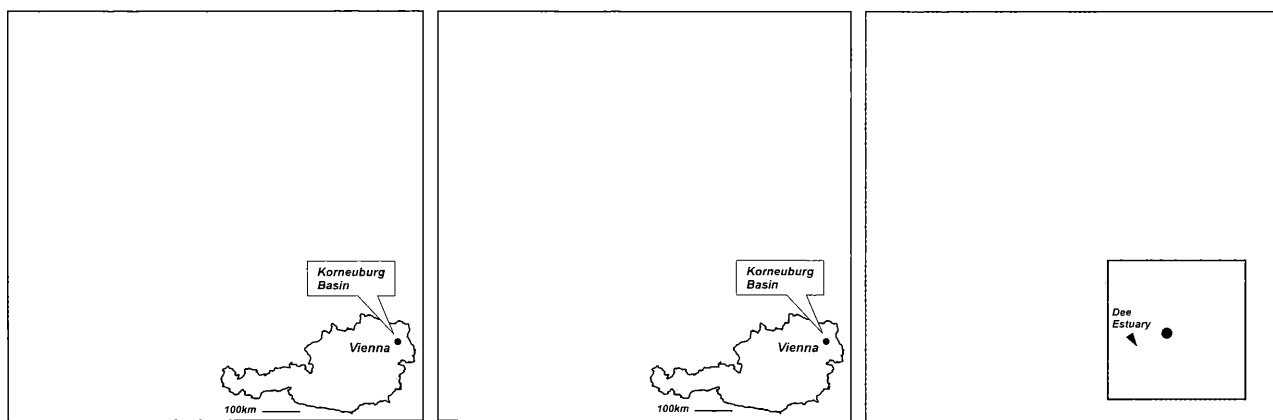
## Introduction

For the first time comprehensive data on the late Early Miocene of Austria are summarized. Recently, 36 earth scientists focussed on various zoological and botanical groups which were collected in detail from 1982 to 1995 by W. SOVIS and a large number of local collectors. Co-operations with the Institute of Palaeontology Vienna and the Museum of Natural History Vienna granted the scientific background during excavations. The efforts of W. SOVIS and B. SCHMID caused considerable synergies, which finally culminated in the edition of two volumes of the monograph "Das Karpat des Korneuburger Beckens". Aside from "standard groups" such as the foraminifers, ostracods or the smaller mammals even "freak groups" such as the charophytes, balanids, or even chemofossils (VAVRA, 1998) came into the focus of the studies. The list of documented taxa consists of 12 species of calcareous nannoplankton (C. MÜLLER, 1998), 13 diatoms (STRADNER, this volume), 5 charophytes (BERGER, 1998), 33 taxa based on fruits & seeds (MELLER, 1998), 15 taxa based on leaves (KOVAR-EDER, 1998), 22 taxa based on palynomorphs (HOFMANN & al. this volume), about 90 foraminifera (1 new) (RÖGL, 1998), 5 corals (KLEEMANN, this volume), 162 gastropods (HARZHAUSER, this volume; BINDER, this volume) (6 new taxa), 65 bivalves (CTYROKY, this volume), 1 cephalopod (SCHULTZ, this volume), 2 scaphopods (HARZHAUSER, this volume), 48 ostracod species (4 new) (ZORN, 1998), 7 decapod crustaceans (2 new) (P. MÜLLER, 1998), 1 tracefossil which can be affiliated with a thalassinidean shrimp (PERVESLER, this volume), 2 cirripedia (WÖHRER, 1998), 3 echinid taxa (KROH, this volume), 1 ophiuroid (MEYER, this volume), 11 + 1 bryozoans (SCHMID, this volume; KLEEMANN & ZAGORSEK, this volume), 30 fishes, (1 new) (SCHULTZ, 1998; BÖHME, this volume), 20 otolith taxa (3 new) (REICHENBACHER, 1998), 5 amphibians and 13 reptiles (BÖHME, this volume; GEMEL, this volume, 1 species new) and 33 mammals (DAXNER-HÖCK, 1998; RÖSSNER, 1998; RABEDER, 1998; BOON-KRISTKOIZ, 1998; HEISSIG, this volume; BARNES, this volume [1 new]). Thus, in total more than 650 taxa have been studied during these investigations. This large number of taxa and the synoptic approach reveals the Korneuburg Basin as one of the best studied basins of Europe. A synthesis of the data published in SOVIS & SCHMID (1998) and this volume allows a detailed approach in the reconstruction of the various palaeoenvironments of the Korneuburg Basin some 16 million years ago. The comprehensive and accurate dataset presented in the two volumes will necessarily represent a reference tie point for future palaeobiogeographic and palaeoecological models for the late Early Miocene of Europe.

## Geological Setting

The most recent data on the geology of the Korneuburg Basin have been summarised already by STEININGER (1991), WESSELY (1998) and SOVIS (1998). The history of investigations in the area was outlined by SOVIS (1998), WESSELY (1998) and HARZHAUSER (this volume).





**Fig. 2: Tentative reconstruction of the Korneuburg Basin in two time slices.**

Rotation of  $22^\circ$  follows the magnetostratigraphic interpretation of SCHOLGER (1998). Light shading indicates the hypothetical distribution of the wetland areas. Generally, the course of the estuary and its tributaries is speculative; however, a main flow along the western margin is likely because of the significant syndepositional subsidence along the Schlieberg Fault. Furthermore the facies-distribution at Obergänserndorf hints to a western discharge. An elevated barrier might have been developed between Obergänserndorf and the eastern basin margin following a subsurface swell. This is also indicated by the composition of the vertebrate fauna, which points to a less humid environment above groundwater (BÖHME, 1998; DAXNER-HÖCK, pers. comm.). The fauna of the northern part of the basin was little affected by the freshwater discharge and is represented mainly by normal marine, sublittoral molluscs.

The sketchmaps show two hypothetical situations of facies distribution: one during relatively low water level and one during a transgressive phase respectively. As documented from most sections in the southern Korneuburg Basin, fully marine conditions variously developed after lacustrine and estuarine phases. Note that a delta plain developed in the southern Vienna Basin at that time west of the Korneuburg Basin (WEISSENBACK, 1996; SEIFERT, 1996). Therefore, the connection to the marine Paratethys Sea was only possible in the north-eastern part of the basin.

The Dee Estuary close to Liverpool might serve as modern counterpart of a small-scale estuary similar to the Korneuburg Basin Estuary. This small estuary is cut into Palaeozoic rocks; it is protected by a small "barrier-island" which is reminiscent of the proposed swell in the vicinity of Obergänserndorf (Map of Dee Estuary is mirrored for easier comparison).

### Biostratigraphy and the Karpatian "flair"

Although more than 500 taxa are documented from the Karpatian of the Korneuburg Basin and the Kreuzstetten Bay only an astonishing small number of species can be considered to occur exclusively during the Karpatian.

The fauna of foraminifers has been studied in detail by RÖGL (1998) who concluded that the assemblage is inappropriate for biostratigraphic conclusions. Most of the fauna is also common to the older Otnangian (Middle Burdigalian), whilst *Globigerina* cf. *pseudociperoensis* and the large-sized morphs of *Elphidium fichtelianum* indicate a post-Otnangian age.

Among the diverse ostracod fauna studied by ZORN (1998) the assemblage of *Cytheridea paracuminata*, *Cyamocytheridea derii* and *Senesia* ex. gr. *vadaszi* indicates a Karpatian to Badenian age. Only the co-occurrence of *Loxoconcha vaissonna*, which is restricted to the Karpatian of the Central Paratethys, allows the dating into the Early Miocene.

Correspondingly, only few mollusc species bear some biostratigraphic potential. The terrestrial gastropods *Megalotachea turonensis* and *Tropidomphalus extinctus* are apparently restricted to Karpatian deposits in the study area (BINDER, this volume). Also a small number of aquatic gastropods is known only from the Karpatian. These are *Agapilia pachii*, *Turritella bellardii*, *Clavatula barbarae*, and *Clavatula dorotheae* (HARZHAUSER, this volume). In contrast, none of bivalve taxa documented by CTYROKÝ (this volume) is restricted to the Karpatian. Moreover ex-

cept for two first (*Arcopsis rollei* and *Thracia grundensis*) and two last occurrences (*Aequipecten scabrella hungarica* and *Tugonia ornata*) within that Central Paratethys stage, the recorded fauna has principally a persistent character occurring likely in older Late Eggenburgian-Otnangian as well as in younger Badenian deposits.

Among the vertebrates the otolith *Aphanius konradi* is restricted to the Otnangian and Karpatian and *Paraplaggusia roseni* is only known from the Late Burdigalian (REICHENBACHER, 1998), whereas the associated fish taxa described by SCHULTZ (1998) and REICHENBACHER (1998) display rather long ranges in the Early and Middle Miocene. Similar results are established by the terrestrial Lower Vertebrates (BÖHME, this volume). Especially, the coexistence of *Barbus* (*Barbus*) sp., *Latonia ragei* and *Pelobates* sp. points to Karpatian age. Generally, little biostratigraphic information can be derived from the studied flora. A much better tool for the biostratigraphic frame are the Rodentia among the small mammals. According to DAXNER-HÖCK (1998) the occurrence of *Prodryomys satus* and *Microdryomys koenigswaldi* is restricted to the mammal zone MN5 in Central Europe. Furthermore the occurrence of *Keramidomys thaleri* (the most abundant species), the absence of *Ligerimys* and the evolutionary level of *Spermophilinus besanus*, *Palaeoscirus sutteri* and *Girulus diremptus* clearly indicate an early phase of MN5. The data presented by SCHOLGER (1998) and DAXNER-HÖCK (1998) allow a magnetostratigraphic correlati-

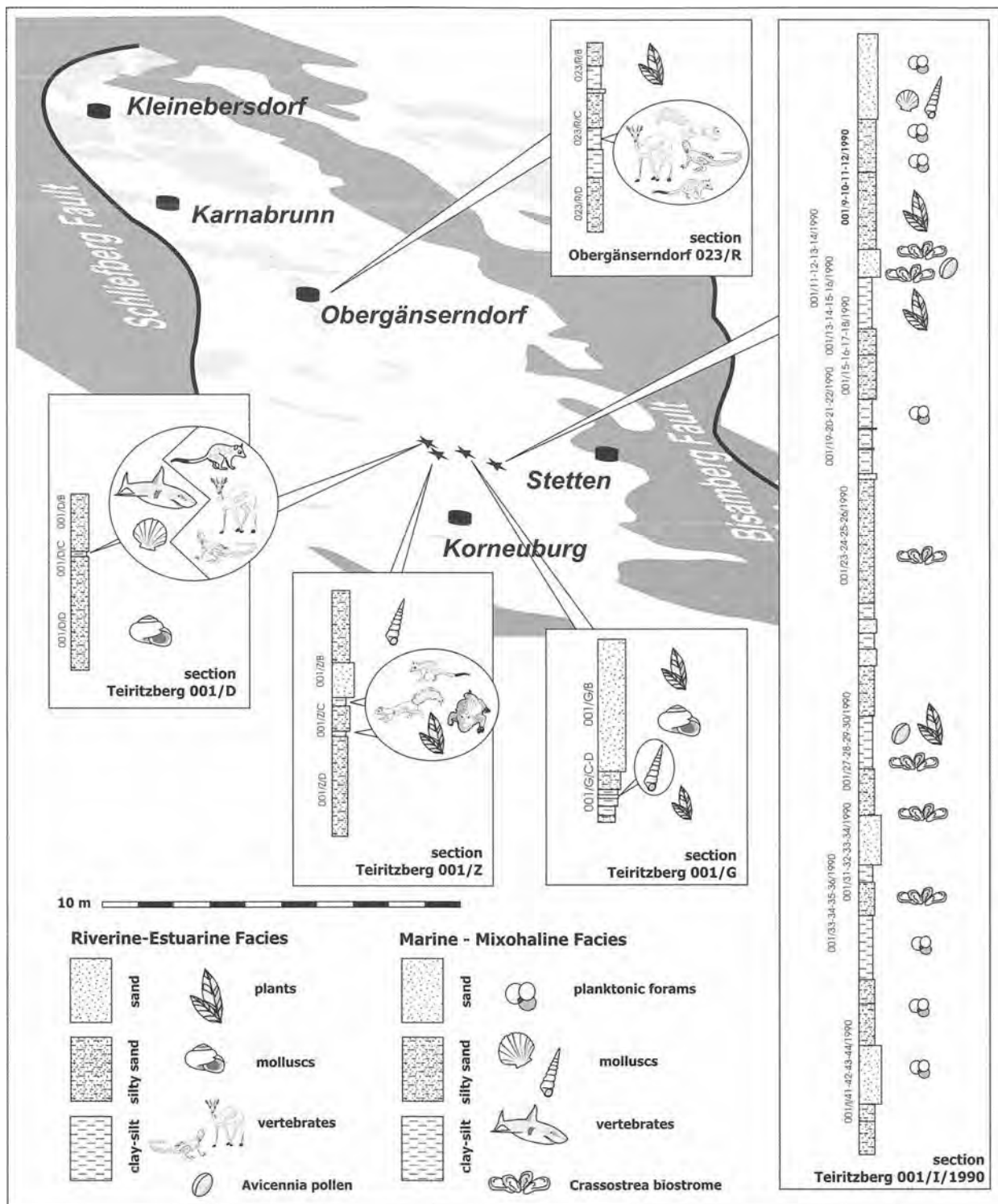


Fig. 3. Sketchmap of the Korneuburg Basin.

Dark areas represent the basin margins, whereas light shadings indicate Karpatian deposits on the surface (modified from WESSELY, 1998). The logs mediate the facies distribution and the occurrence of ecologically significant organisms in selected sections of the southern part of the basin (lithology modified from SOVIS, 1998 and DAXNER-HÖCK, 1998).

on with the chrons C5Cn2n or C5Cn3n of the latest Early Miocene. Since the chron C5Cn2n is correlated with the beginning of the Badenian (BERGGREN et al., 1995), only the earlier normal interval C5Cn3n is plausible which corresponds to an age between 16.5 and 16.7 million years (DAXNER-HÖCK, 2001).

### Palaeoecology

Generally, the protected position of the Korneuburg Basin, which was strongly cut off from the open Paratethys Sea in the south but variously connected in the north, caused a complex interplay of marine and coastal-terrestrial conditions. Rapid shifts in facies were triggered by short-

termed sea-level oscillations, local synsedimentary tectonics along the western margin of the basin and the changing courses of rivers and rivulets.

As a generalisation, the log Korneuburg 1 presented by WESSELY (1998) reveals a threefold story of the Karpatian in the Korneuburg Basin. The Karpatian deposits of the log attain about 656 m thickness. The lower part of about 70 m consists predominately of sand with various euryhaline, shallow marine molluscs. This unit represents the initial transgressive phase in a very shallow but mainly marine setting but can hardly be expected to be accessible in surface outcrops. Only the sections Leobendorf and Bismberg might be equivalent to this initial marine transgression. Due to their marginal position, the deposits might have escaped from subsidence. The following unit of about 200 m sand, silt and marl bears plenty of terrestrial and freshwater molluscs along with plant debris. It represents an estuarine phase when marshes and swamps spread in the southern Korneuburg Basin. The topunit of about 80 m sand reflects a re-newed marine influence in a generally estuarine environment. Most of the investigated sections introduced by SOVIS (1998) are part of this third and last preserved sequence of the Korneuburg Basin.

The huge amount of data, which derive from detailed palaeontological studies in the Korneuburg Basin, draw an elaborated picture of various environments during the late Early Miocene of Austria. However, the extremely difficult amalgamation of factors, influencing the depositional environments and the rather short logs of the surface outcrops, exclude a palaeoenvironmental reconstruction of single time slices. Instead, in the following several clearly differentiated palaeoenvironments will be described.

## 1. Rocky shore

In the southern part of the Korneuburg Basin the western margin was formed by the Flysch Zone. There the Schlieberg fault caused rather an abrupt and steep coast line which gave shelter to hardground dwellers. The site Leobendorf reveals an outstanding assemblage, which is unique for the Korneuburg Basin. The small section consists of about 1,5 m of gravel and boulders deriving from the nearby Flysch Zone. The slightly rounded sandstone boulders display heavy bioerosion by boring bivalves like *Petricola* which settled fully marine habitats adjoining the palaeoshore line. Correspondingly, the occurrence of *Megabalanus tintinnabulum* indicates a position in the supralittoral zone. At Leobendorf this balanid replaces the otherwise ubiquitous, euryhaline *Balanus amphitrite*, but it is absent from all other sections in the Korneuburg Basin which points to fully marine conditions. This is also proofed by the diverse ostracod fauna, since genera such as *Bairdoppilata*, *Cnestocythere*, *Callistocythere* or *Dorukella* document normal marine conditions (ZORN, 1998). According to ZORN (1998), about 50% of the ostracod fauna of the Korneuburg Basin are only known from Leobendorf. The overlying 1,5 m sand bears numerous *Turritella bicarinata* and rare fragments of the coral *Siderastrea* sp. (KLEEMANN, this volume) excluding brackish waters during the deposition at that south-western-most section.

Both, palaeoecology and lithology, differ considerably from those of all other sites in the Korneuburg Basin. In respect to the close position of the section Leobendorf to the brackish environments of the section Teiritzberg (2,5 km distance), a synchronous deposition seems unlikely. Furthermore, from the palaeogeographic point of view Leobendorf would have been even closer to the estuary than the section Teiritzberg. Thus, on the one hand the section might represent an initial phase of the marine transgression being slightly older than the documented mangrove and estuarine environments. On the other hand it may be correlated with one of the short-lived marine incursions, which are also documented from the section Teiritzberg.

## 2. Shallow marine environments

**The northern Korneuburg Basin:** Aside from its very northern tip, the northern part of the Korneuburg Basin displays a marine development. The sections Karnabrunn, Kleinebersdorf, Weinsteig, Gebmanns, Großrußbach are all situated in the north of the Obergänserndorf-Mollmannsdorf Swell. The gastropods, ostracods and otolithes of these sections display a strongly marine flair. According to REICHENBACHER (1998) the otolithes *Brachydeuterus latior*, *Pomadasyus arcuatus* and *Lesueurigobius vicinalis* from Gebmannsberg, Karnabrunn and Kleinebersdorf derive from fully marine fishes. Their modern counterparts live in shallow water between 10 and 50 m depth. Correspondingly, the ostracods of these localities described by ZORN (1998) point to normal marine conditions between 10-30 m depth. Only few remains of large land mammals such as the giraffid-like *Palaeomeryx kaupi* (RÖSSNER, 1998) and the rhino *Lartetotherium sansaniense* (HEISSIG, this volume) are transported into this marine environment.

Corals such as *Porites* and *Balanophyllia* and the lichenoporiid bryozoan *Grammascosoecia* (KLEEMANN, this volume and KLEEMANN & ZAGORSEK, this volume) are only recorded from Kleinebersdorf. Similarly, the rare scaphopod *Antalis crux* appears exclusively in samples from Karnabrunn and Kleinebersdorf (HARZHAUSER, this volume). The gastropod fauna is strongly predominated by sublittoral, carnivorous and infaunal species whereas littoral taxa such as the algae scraping potamidids are scarce. A complex marine ecosystem with sponges, corals, and various echinoderms can be predicted from the predators *Triphora perversa*, *Architectonica simplex*, *Zonaria dertamygdaloides*, *Ficopsis burdigalensis*, *Ficus cingulata* and *Phalium (Semicassis) miolaevigata*. No distinct influence from the southern estuary affecting these ecosystems is recognizable.

The bivalve assemblage of the northern Korneuburg Basin (CTYROKY, this volume), too, hints at the predominance of fully marine, shallow water environments, although occasional salinity fluctuations might have affected the littoral zone. Apparently, a more diversified epibenthic assemblage – in particular that of the stenohaline pectinids – developed only sporadically within the estuarine system of the southern Korneuburg Basin. In contrast, the "northern" fossil assemblage from the Wohlmut pit

at Kleinebersdorf is thoroughly dominated by species reclining consolidated and unconsolidated substrates. The bed E with masses of byssally attached, euryhaline *Crenomytilus? aquitanicus* represents the soft substrate facies within the lower intertidal zone. Upsection (bed D) sublittoral settings became installed. Cementing *Chama gryphina*, byssally attached *Manupecten fasciculata* and *Crassadoma multistriata* and free, bottom reclining, thick-shelled *Macrochlamis tournali* clearly indicate a well-agitated, fully marine, shallow water environment.

**The southern Korneuburg Basin:** Although the section Teiritzberg yielded mainly taxa of estuarine environments, several layers document short-termed marine incursions, allowing marine ostracods, molluscs and echinoids to settle the southern part of the Korneuburg Basin. Despite the abundance of plant remains in sample 001/X/C, KROH (this volume) documented spatangoids, which prefer fine-grained sediment and low agitation but avoid reduced salinity. Similarly, the stellaroid *Amphioplus kuehni* from sample (001/10.1991) or the common scaphopod *Antalis* are also exclusively marine taxa.

A marine incursion into the estuary is documented at section Teiritzberg 001/D. The basal layer 001/D/D is characterized by abundant freshwater genera such as *Melanopsis*, *Stagnicola* and *Theodoxus* as well as by a large number of terrestrial gastropods (BINDER, this volume; HARZHAUSER, this volume). Sedimentary structures, too, support the interpretation of a riverine setting. The following layer 001/D/C yielded a high number of terrestrial vertebrates and the fresh water fishes *Aphanius* and *Carassius* (REICHENBACHER, 1998; SCHULTZ, 1998) indicating considerable freshwater influx. However, rays and sharks as described by SCHULTZ (1998) from this thin layer exclude brackish water. The establishment of marine conditions during the progradation of the shore line is also reflected by a typical littoral gastropod fauna (HARZHAUSER, this volume). The bivalves (CTYROKY, this volume) characterized by burrowing species point out the prevailing normal marine conditions at the sea bottom within the sublittoral zone.

This contradicting evidence might point to a rather poor mixing of freshwater and normal marine water as observed in modern estuaries of the salt-wedge type. These form where a large river inputs fresh water in an area with low or moderate tidal range. Because fresh water is less dense than salt water, the river water remains near the top and flows seaward whereas a wedge of intruding seawater resists at the bottom (GARRISON, 1995).

**The Kreuzstetten Bay:** The northern Korneuburg Basin, though marine, was well protected from the open sea by an island chain along its eastern margin. In contrast, the Kreuzstetten Bay was opened wide towards the Molasse Basin. The sandy bottoms of this agitated, shallow marine environment were inhabited by large populations of sand dollars, such as *Parascutella paulensis* and *Amphiope* sp. (KROH, this volume). Both taxa are apparently missing in the Korneuburg Basin. HARZHAUSER (this volume) em-

phasized the marine character of the gastropod fauna, which points to a mixing from littoral and shallow sublittoral settings (0-30 m). Several species such as *Sassia parvula*, *Narona (Sveltia) inermis*, *Trigonostoma (Ventrilia) obsoleta*, *Conus berghausi*, *Retusa truncatula* and *Scaphander lignarius* are absent from the Korneuburg Basin. Generally, the shells in the Korneuburg Basin are often smaller than the representatives from the Kreuzstetten Bay, pointing to a less stressed environment in the bay.

### 3. Estuarine bay: *Avicennia* mangrove, tidal mudflat and *Crassostrea* reefs

Mangrove forests or swamps can be found on low, muddy, sheltered shores. Mangroves are woody plants growing between the level of high water of spring tides and a level close to, but above mean sea-level. They are characterised by their ability to tolerate regular inundation by salt water. They are found throughout the oceans of the tropics and may penetrate into the estuaries (MACNAE, 1968). Up to 20 genera of woody plants sharing these adaptations are termed mangroves although not closely related (PLAZIAT & al., 2001); from the Korneuburg Basin, however, only the Avicenniaceae are documented by pollen of *Avicennia* sp. (HOFMANN & al., this volume). Within the mangrove plants, this genus is considered to be a rather opportunistic taxon which is observed to take over as a pioneer in recent low diversity mangroves of East Africa (DENNY, 1993). This tendency correlates well with the occurrence of solely *Avicennia* in the considerable low diversity mangrove of the Karpatian Korneuburg Basin. As documented by MACNAE (1968) and FINLAYSON & OERTZEN (1993) *Avicennia* is commonly found on the outer seaward fringe.

The impoverished mangrove of the European Miocene was recently termed by PLAZIAT & al. (2001) the Mediterranean *Avicennia* mangrove.

Among the molluscs, the gastropods display several taxa, which have modern counterparts in mangroves and the adjacent environments, although none of the genera is fully restricted to mangroves (see also PLAZIAT & al., 2001). These taxa are especially the abundant *Terebralia bidentata*, and *Nerita plutonis*, and probably also *Ptychopotamides papveraceus* and some of the exceptional diverse elobiids represented by *Ovatella* cf. *pisolina*, *Melampus turonensis*, *Melampus pilula*, *Auriculastra biplicata*, and *Laemodonta* sp. (BINDER, this volume, HARZHAUSER, this volume).

According to BERRY (1963) most potamidid, neritid, and elobiid gastropods dwell between the mean tide level and the mean high water level of neap tides, whereas the barnacles are restricted to the seaward fringe. Correspondingly to the Korneuburg Basin, the balanids are also represented by *Balanus amphitrite* in BERRY'S case study of the mangrove along the coast of Singapore.

An important ecosystem of the southern Korneuburg Basin has been established in the mixohaline shallow subtidal zone of the estuarine bay through extensive *Crassostrea*



*gryphoides* biostromes. The giant euryhaline oyster formed extensive reefs adjoining offshore the lower intertidal zone and giving shelter to numerous species, which depended directly or indirectly on this ecosystem. Hardground dwelling species such as *Balanus amphitrite*, *Polydora* and clionid sponges are commonly found associated with the giant bivalves. Among the gastropods, *Thais* and *Ocenebra* preyed on the juvenile oysters and the ubiquitous balanids. *Ptychopotamides papaveraceus* is also typically associated with the *Crassostrea* biostrome whereas other potamidids such as *Terebralia bidentata* and *Granulolabium plicatum* apparently avoided this environment.

In contrast, both latter genera formed large populations on wide intertidal mudflats extending between mangroves and the subtidal zone, where they were associated with masses of hydrobiid gastropods. Subsequently, vast *Crenomytilus? aquitanicus* (= *Mytilus haidingeri*) colonies characterized the lower zone of those flats extending possibly into the shallow subtidal zone. Apparently, *Polymesoda*, a bivalve which normally characterizes those settings and which is still richly represented in estuarine bays, sloughs and tidal influenced riverine environments of the Recent tropical and subtropical North America, is missing. Closely related *Polymesoda sowerby* (= *P. convexa*) was indeed frequent within extremely calm and oligohaline to nearly freshwater lagoonal settings during Egerian, Eggenburgian and Ottnangian times, when it was associated with *Melanopsis* and rare *Granulolabium*. Obviously, this bivalve group became extinct in the Central Paratethys before the Karpatian, as it is suggested by its absence from the corresponding ecological niche of the Korneuburg Basin estuary.

#### 4. The estuary: a small-scale pattern of fluvial, slough and terrestrial environments

**The southern system:** The riverine system affecting the fauna and flora of the Korneuburg Basin during the Karpatian is well documented at the section Teiritzberg, but also at Obergänserndorf. The fluvial influx is supported by the occurrence of the gastropods described by BINDER (this volume). *Tinnyea escheri* and *Theodoxus crenulatus* which probably preferred swift estuarine-riverine environments (see also HARZHAUSER & al., 2002 for *Tinnyea*) as well as taxa of less agitated fresh water settings as *Lymnaea dilatata*, *Stagnicola laurillardii* and *Planorbarius mantelli* are frequently found. Among the aquatic vertebrates, *Esox*, *Barbus* (*Barbus*), *Aphanius konradi* and *Trionyx* witness fresh water influx (REICHENBACHER, 1998; BÖHME, this volume; GEMEL, this volume). Most of the terrestrial vertebrate remains, particularly the small mammals, the amphibians and a part of the reptiles are allochthonous and originated probably from washed out owl pellets (BÖHME, this volume).

Aside from Obergänserndorf, terrestrial, lacustrine environments and strong fresh water influence is best documented at the western sections of Teiritzberg. In particular, the sections 001/H, 001/Z and 001/G bear witness to terrestrial swampy areas. MELLER (1998) and HOFMANN

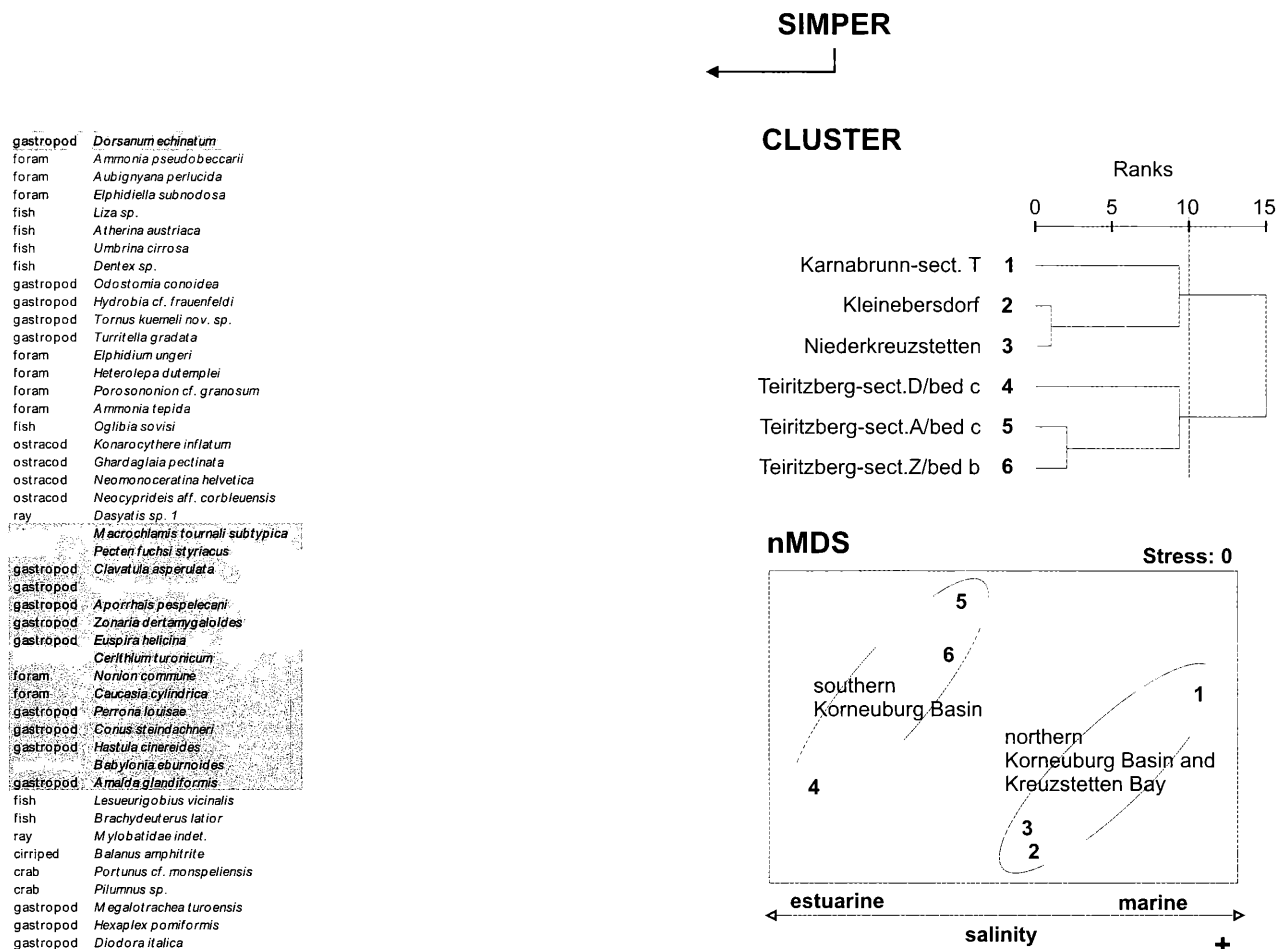
& al. (this volume) discuss brackish marshes, shallow lakes, oxbows and rivers as typical wetland types of the Korneuburg Basin. *Cladium* and Ruppiceae are characteristic of the brackish marshes. Samples with predominating *Decodon*, *Myrica*, *Cladiocarya* and *Sparganium* reflect lakesides or oxbows. The swamp forest association is characterized by *Glyptostrobos* and *Myrica* with scattered *Calamus*. Higher groundwater levels and a fluvial environment are also indicated by non-mammalian vertebrates (BÖHME, this volume), where the co-occurrence of the barb *Barbus* (*Barbus*), the frogs *Rana*, *Latonina*, *Pelobates*, the crocodile *Diplocynodon* and the soft-shell turtle *Trionyx* are common in fluvial assemblages. A diverse mammalian fauna derives from swamps. Aside from the diverse glirids and cricetids, bats and flying squirrels such as *Miopetaurista* are documented by RABEDER (1998) and DAXNER-HÖCK (1998). This humid, swampy environment gave also shelter to the tragulid *Dorcatherium* (RÖSSNER, 1998).

*Acer*, *Cericiphyllum*, *Celtis* or *Fagus* probably grew in slightly drier habitats of the more elevated margins of the basin (HOFMANN & al., this volume). From these woodlands gastropods – such as *Helicigona planata*, *Klikia orbiculata* and *Miozonites costatus* – were transported into the basin. Due to the Obergänserndorf-Mollmannsdorf Swell in the middle of the basin slightly drier habitats might have developed along the elevation. Correspondingly, BÖHME (this volume) interprets the palaeoenvironment close to Obergänserndorf as a rather open, probably abandoned floodplain environment above the groundwater level. The predominance of Cricetidae and the low percentage of Gliridae at Obergänserndorf compared to the reverse relation at Teiritzberg may also support the interpretation of a less swampy palaeoenvironment in the area of Obergänserndorf (DAXNER-HÖCK, pers. comm.).

This wetland system of the southern Korneuburg Basin may best be interpreted as a small, narrow estuary, which was bordered by rather abrupt tectonic margins. Typically, in estuaries the fresh water discharge is blocked from streaming into the open sea by either surrounding mainland, peninsulas, barrier islands or fringing salt marshes. In the Korneuburg Basin the eastern ridge of the Flysch Zone might have acted as such a barrier.

**The northern tip:** Coastal flats, marshes and swamp forests characterized the southern part of the Korneuburg Basin as far north as the Obergänserndorf-Mollmannsdorf Swell, whereas its northern part was a marine embayment. However, a second, much smaller area with fresh water influx developed in the very north of the basin at Helfens. Gastropods such as *Agapilia pachii*, *Terebralia bidentata* and ostracods such as *Ghardagliaia pectinata* and *Neocyprideis* (*Miocyprideis*) aff. *corbleuensis* (ZORN, 1998) stand in contrast to the otherwise principally marine fauna of the northern Korneuburg Basin and point to brackish water conditions. The interpretation fits well with the palaeogeographic position in the narrow northern tip of the basin where shallow lagoonal environments might have developed under the influence of the runoff by a northern rivulet.





**Fig. 4: Analyses of the six most diverse (91 to 47 taxa) marine assemblages found in the Karpatian of the Korneuburg Basin and the Kreuzstetten Bay.**

Complete linkage mode Hierarchical Cluster Analysis (CLUSTER), non-metric Multidimensional Scaling (MDS) and Similarity percentages / taxon distribution analysis (SIMPER) from the PRIMER 5 package by CLARKE & WARWICK (1994) were applied. The similarity measure was based on the Euclidean distance.

**Statistics**

The multivariate statistical treatment was applied to presence/absence data of marine assemblages described from the Korneuburg Basin using the Software PRIMER 5 (CLARKE & WARWICK, 1994). Hierarchical Cluster Analysis (CLUSTER) and non-metric Multi-Dimensional Scaling (MDS) have been carried out in order to investigate their similarities. Analyses gave best interpretable results when based on the triangular similarity/distance matrix using measure of Euclidean distances. CLUSTER in the complete linkage mode and using data ranks came out to be at best applicable to our presence/absence data. The high confidence of the MDS was indicated by the stress value remaining 0 throughout presented analyses. Low stress in MDS indicates small distortion involved in compressing the data into a small number of dimensions. Subsequently the Similarity Percentages - Species Contribution Analysis (SIMPER) was carried out to identify taxa primarily providing the discrimination between inferred clusters by designating their content. The aim of the analysis was to provide an objective investigation of similarities between fossil samples described from the Korneuburg Basin and the Kreuzstetten Bay, to

designate sample groups of similar taxonomic content and to detect taxa common to that groups in order to provide a basis for palaeoecological and palaeobiogeographical inferences. Faunal lists for 75 sites representing differently scaled entities, from bed to the site area, including 365 different species-group taxa of marine vertebrates and invertebrates became available through works published within the frame of the Korneuburg Basin monographs. These include representants of gastropods (162), scaphopods (2), cephalopods (1), bivalves (62), cirripeds (2), crabs (7), ostracods (43), sharks (10), rays (5), fishes (29) and forams (42). Except for gastropods (71), the number of described samples is, however, rather low and does not exceed 28. Moreover, most of the samples include only several taxa described. Because in consequence an important number of samples was inappropriate for statistical treatment, only some of the most diverse samples became included into the analysis. These were samples including at least the half number of taxa of the most diverse Karnabrunn-section 108/T sample with 91 taxa.

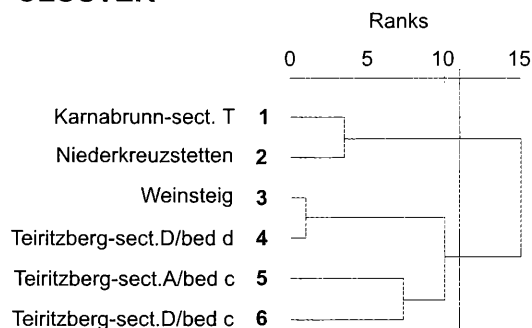
The analysis (Fig. 4) shows clearly the presence of two distinct groups. The first cluster includes samples from

## SIMPER

**gastropods**  
*Hastula cinereoides*  
*Perrona louisae*  
*Amalthea glandiformis*  
*Conus steindachneri*  
*Babylonia eburnoides*  
*Clavatula dorothaeae*  
*Pyrene polonica*  
*Granulolabium bincinctum*  
*Tudicla rusticula*  
*Subula plicaria*  
*Polinices redemptus*  
*Polinices pseudoredemptus*  
*Turritella gradata*  
*Dorsanum echinatum*  
*Diodora Italica*  
*Triptychia suturalis gracilis*

*Klikia orbiculata*  
*Agapilia pachii*  
*Retusa truncatula*  
*Cyllichna cylindracea subc.*  
*Scaphander lignarius*  
*Narona inermis*  
*Trigonostoma absoletum*  
*Conus betulinoides*  
*Conus berghausi*  
*Ocenebra credneri*  
*Jousseaumea diluviana*  
*Sassia parvula*  
*Strombus bonellii*

## CLUSTER



## nMDS

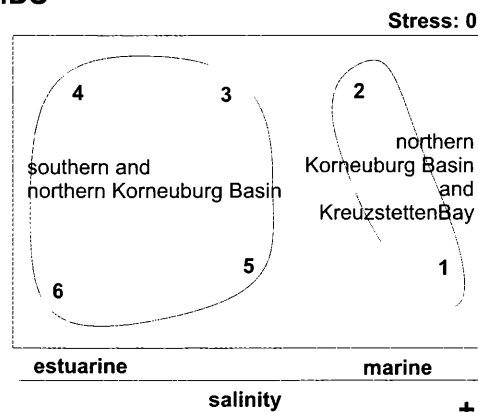


Fig. 5: The same analyses as in figure 4 applied on 6 gastropod assemblages with diversities ranging between 17 and 41 taxa.

three Teiritzberg sites in marine-estuarine beds characterized by *Crassostrea gryphoides/Crenomytilus aquitanicus* accumulations, coal lenses and occurrence of terrestrial snails. The second group includes fully marine sites from the northern Korneuburg Basin (Kleinebersdorf and Karnabrunn) and Kreuzstetten Bay. Typical stenohaline organisms like *Macrochlamis*, *Pecten* or *Aporrhais* are all absent in the first, southern Korneuburg Basin group. Therefore we correlate the horizontal axis of the MDS plot with the water salinity gradient.

The same pattern has been inferred on the basis of gastropods (Fig. 5). Estuarine influenced southern Korneuburg Basin's Teiritzberg sites grouped clearly together, based on elements absent in other groups like *Triptychia*, *Palaeoglandulina* and *Klikia*. Presence of similar habitats within the northern Korneuburg Basin is suggested through position of the Weinsteig sample, bearing the same terrestrial gastropods. In contrast the second cluster is based in on fully marine elements like *Clavatula*, *Perrona* and *Tudicla* and includes localities from the northern Korneuburg Basin and Kreuzstetten Bay. The horizontal axis of the MDS plot corresponds to the one inferred in the first analysis.

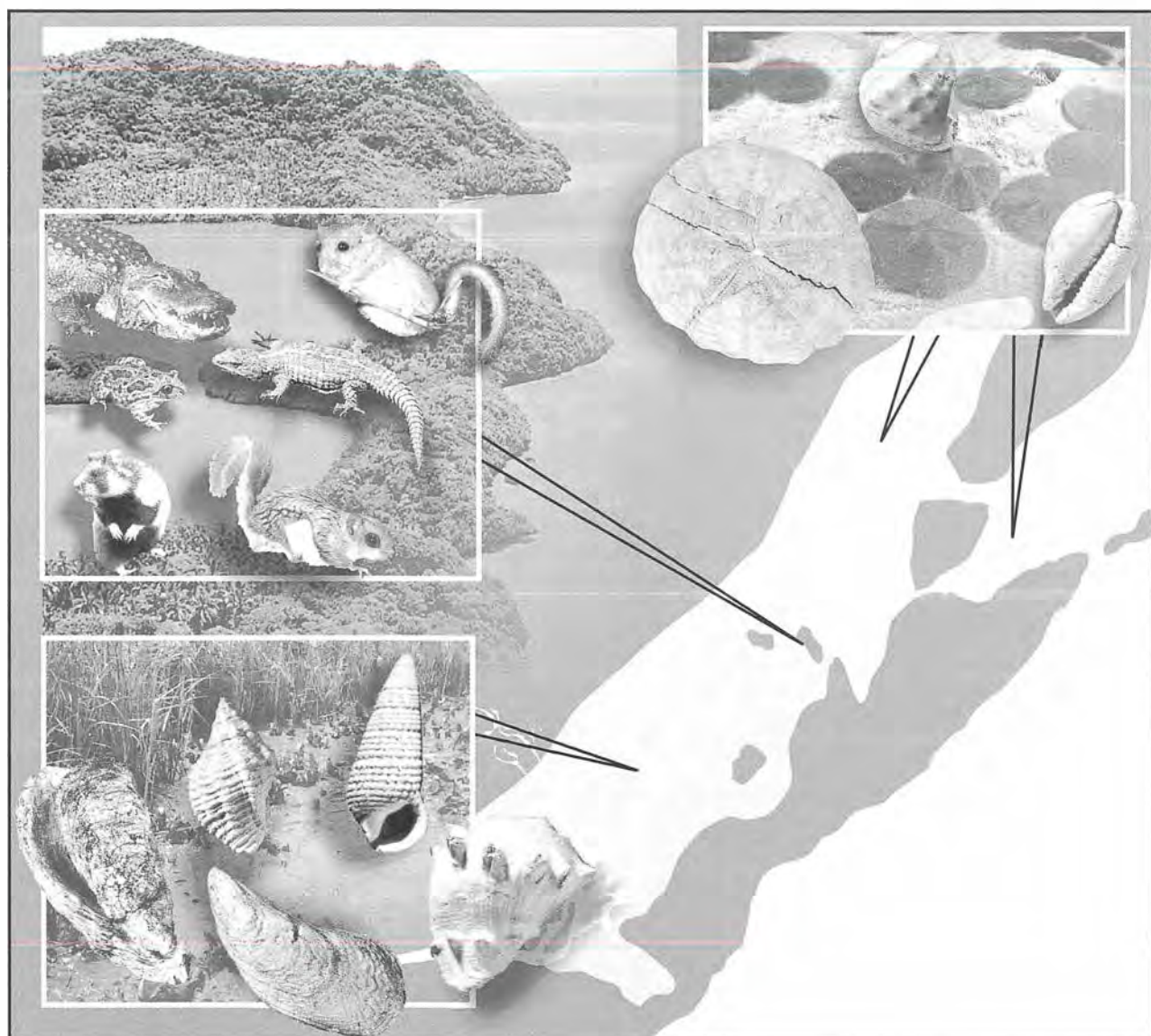
## Palaeogeography

The palaeogeography of the small-sized, elongated basin was mainly a result of synsedimentary tectonics. Thus, it is hardly possible to distinguish major fluctuations of the

depositional environment triggered e.g. by global oscillations of the sea level from local triggers such as tectonics or changing courses of tributaries. A rough idea of the swift changes is expressed by the about 40 m thick section 001/I at Teiritzberg. There, a shallow marine setting, expressed by several findings of globigerinids is indicated in its basal part (samples 001/I/41-42-43-44/1990 – 001/I/35-36-37-38/1990 in RÖGL, 1998). The first *Crassostrea* biostrome in 001/I/33-34-35-36/1990 reflects the establishment of littoral conditions. Laterally, in few metres water depth silty, calm bottoms were colonized by infaunal bivalves, such as *Solen marginatus*, *Peronea planate*, and *Cordiopsis islandicoides*. In the following sequence (001/I/27-28-29-30/1990 - 001/I/11-12-13-14/1990) coastal swamps and scattered mangroves became established. HOFMANN & al. (this volume) described pollen of *Avicennia* and a probably halophytic *Chenopodiaceae* from this unit. Extensive *Crassostrea* biostromes developed along the shore, being accompanied particularly by the gastropod *Ptychoptamides papaveraceus*. The adjacent lagoonal environments were inhabited by infaunal bivalves, such as *Lutraria jeffreysi* and *Solecurtus vindobonensis*. The increasing abundance of planktonic foraminifera and the occurrence of marine molluscs, such as *Panopea menardi*, *Aequipecten macrotis* or *Turritella gradata*, witness a further marine phase in the top of the section (001/I/9-10-11-12/1990 - 001/I/3-4-5-6/1990). At that time, the Obergänsersdorf-Mollmannsdorf Swell already seems to have divided this estuarine southern part from a predominant marine northern part. In the vicinity

**Tab. 1: List of samples with faunas considered in the present cluster analyses.**

localities	samples	groups occurring	taxa occurring	gastropod	cephalopod	scaptopod	bivalve	cirriped	crab	ostracod	shark	ray	fish	foram
Karnabrunn	108/T/B	8	91	41		2	21			7	4	1	3	12
Teiritzberg	001/A/C	11	85	30	1	1	10	1	2	12	3	3	12	10
Teiritzberg	001/D/C	9	77	34			2	1	3		6	5	21	4
Niederkreuzstetten	Niederkreuzstetten	6	51	34			1				3	2	2	9
Teiritzberg	001/Z/B-C	7	49	10			1		1	14		2	8	13
Teiritzberg	001 NHMW	2	48	34			14							
Kleinebersdorf	010 NHMW	2	47	39			8							
Teiritzberg	001/A/B	5	35	13		1	17	1		3				
Leobendorf	072/S/C	4	33				1	1		23				8
Karnabrunn	108/H/A	6	30	12		1	5				1		2	9
Teiritzberg	001/I/9	8	25	14		1	4	1	1		1	2	1	
Teiritzberg	001/D/D	4	22	19		1		1						1
Obergänserndorf	023/U/C	6	22	9		1			2	2			4	4
Teiritzberg	001/Y	4	20	7					2	2				9
Gebmannsberg	022/G/B	6	20			1	4	1		4	1			9
Weinsteig	107 NHMW	2	18	17							1			
Kleinebersdorf	010/R/B	6	16	10		1	1	1	2				1	
Teiritzberg	001/I/5-6-7-8/1990	3	15	6			2			7				
Teiritzberg	001/C/B	4	15	7		1				2				5
Teiritzberg	001/I/9-10-11-12/1990	2	14	2						12				
Teiritzberg	001/I/8	2	14	9			5							
Großrußbach	099/N/G	3	14	2			1							11
Teiritzberg	001/I/28.9.1991	3	13	1					1	11				
Teiritzberg	001/I/21-22-23-24/1989	4	12	8			2	1			1			
Teiritzberg	001/Z/D	3	11	2								1	8	
Teiritzberg	001/I/29-30-31-32/1990	4	11	5			4				1		1	
Teiritzberg	001/I/27-28-29-30/1990	2	10	1						9				
Obergänserndorf	023/R/C	3	10	2						2				6
Kleinebersdorf	010/Z/A	2	9	8				1						
Kleinebersdorf	010/W/A	4	9	6	1	1		1						
Teiritzberg	001/X/D	3	8	6		1								1
Teiritzberg	001/I/31-32-33-34/1990	2	8	2						6				
Teiritzberg	001/I/19-20-21-22/1990	3	8	1			3			4				
Teiritzberg	001/G/A	2	8	7							1			
Rückersdorf	124/S/A	1	8	8										
Kleinebersdorf	010/G/B	3	8	6			1	1						
Helfens	103/F/A	1	8	8										
Teiritzberg	001/I/19-20-21-22/1989	3	7	5				1				1		
Obergänserndorf	023 NHMW	1	7	7										
Weinsteig	107/F/A	2	7	6			1							
Kleinebersdorf	010/S/B	2	7	6			1							
Kleinebersdorf	010/L/A	2	7	2										5
Wetzleinsdorf	106/H/A	1	6	6										
Wetzleinsdorf	106/H	2	6	5			1							
Kleinebersdorf	010/G/D	1	6				6							
Teiritzberg	001/I/35-36-37-38/1990	2	5	1						4				
Gebmannsberg	022/W/B	2	5	4				1						
Gebmannsberg	022/F/A	1	5	5										
Teiritzberg	001/I/27-28-29-30/1989	2	4	2						2				
Teiritzberg	001/I/23-24-25-26/1990	2	4	1						3				
Teiritzberg	001/G/C	2	4	3									1	
Teiritzberg	001/I/15-16-17-18/1989	1	3						3					
Teiritzberg	001/I/11-12-13-14/1989	1	3	3										
Karnabrunn	108/F/A	2	3	2									1	
Karnabrunn	108 NHMW	1	3	3										
Großrußbach	099/S	1	3	3										
Kleinebersdorf	010/B/A	1	3	3										
Teiritzberg	001/I/1-2-3-4/1989	2	2	1			1							
Kleinebersdorf	108/W/A	1	2	2										
Wetzleinsdorf	106 NHMW	1	2	2										
Kleinebersdorf	010/S/A	1	2	2										
Kleinebersdorf	010/G/E	2	2	1			1							
Kleinebersdorf	010/G/C	1	2	2										
Kleinebersdorf	010/F	2	2	1			1							
Teiritzberg	001/I/17-18-19-20/1990	1	1	1										
Teiritzberg	001/I/10	1	1	1										
Teiritzberg	001/H/4	1	1	1										
Teiritzberg	001/H/B	1	1	1										
Obergänserndorf	023/W/A	1	1	1										
Obergänserndorf	023/U/D	1	1	1										
Obergänserndorf	023/K/B	1	1	1										
Hetzmannsdorf	152/B/B	1	1	1										
Kleinebersdorf	010/S	1	1	1										
Kleinebersdorf	010/R/A	1	1	1										
Kleinebersdorf	010/B	1	1	1										
	<b>TAXA IN SITES</b>			<b>509</b>	<b>2</b>	<b>14</b>	<b>121</b>	<b>15</b>	<b>17</b>	<b>129</b>	<b>23</b>	<b>17</b>	<b>65</b>	<b>116</b>
	<b>TAXA IN GROUPS</b>			<b>162</b>	<b>1</b>	<b>2</b>	<b>62</b>	<b>2</b>	<b>7</b>	<b>43</b>	<b>10</b>	<b>5</b>	<b>29</b>	<b>42</b>
	<b>SITES WITH GROUP RECORD</b>			<b>71</b>	<b>2</b>	<b>13</b>	<b>28</b>	<b>15</b>	<b>9</b>	<b>19</b>	<b>11</b>	<b>8</b>	<b>13</b>	<b>16</b>



**Fig. 6: Strongly simplified illustration of the most important palaeoenvironments of the Karpatian Korneuburg Basin.**

The northern part of the basin and the Kreuzstetten Bay are interpreted as shallow marine embayments of 10-30 m water depth. Abundant scutellid echinoids dwelled in the sandy bottom of the Kreuzstetten Bay pointing out strongly agitated water in the less protected bay. The ecosystem of the northern Korneuburg Basin was much more diversified and complex than that of the impoverished southern basin. There, the marine fauna is mainly represented by the highly adapted littoral assemblages, which depended on the *Crassostrea* reefs and the adjoining mudflats. Only few taxa such as the potamidids, oysters, mytilids and balanids constitute to most of the biomass.

The manifold documented terrestrial environments ranging from coastal marshes to a slightly elevated hinterland gave shelter to a diverse vertebrate fauna. Aside from the smaller vertebrates such as the glirids, cricetids or sciurids, which serve as biostratigraphic markers, the occurrence of the alligator *Diplocynodon* and a cordilyd lizard is most important for the palaeoclimatic reconstruction.

of Obergänserndorf a small peninsula or a chain of barrier islands formed which was connected to the eastern margin of the basin. This interpretation is fed by the observation of BÖHME (this volume) and DAXNER-HÖCK (pers comm.) that the vertebrate fauna of the section points to a less swampy, dryer habitat as at the section Teiritzberg. As documented from several small sand pits close to the section Obergänserndorf (023), marine conditions prevailed in the basal parts of the logs (e.g. 023/U). Crossbedding and channel structures and scarce cardiids indicate strongly agitated, marine conditions.

Upsection all logs around Obergänserndorf bear fluvial sands with scattered gravel layers overlain by limnic clay and silt (023/K, 023/R), which furnish evidence that terrestrial habitats already flourished along the swell.

In the north a normal marine embayment formed, which hardly exceeded 20-30 m water depth (RÖGL, 1998b). In respect to the diverse, normal marine fauna of the northern basin, to the brackish influence in its northernmost tip, and to the estuarine facies in the southern basin, a marine connection was most likely established along the northeast coast.



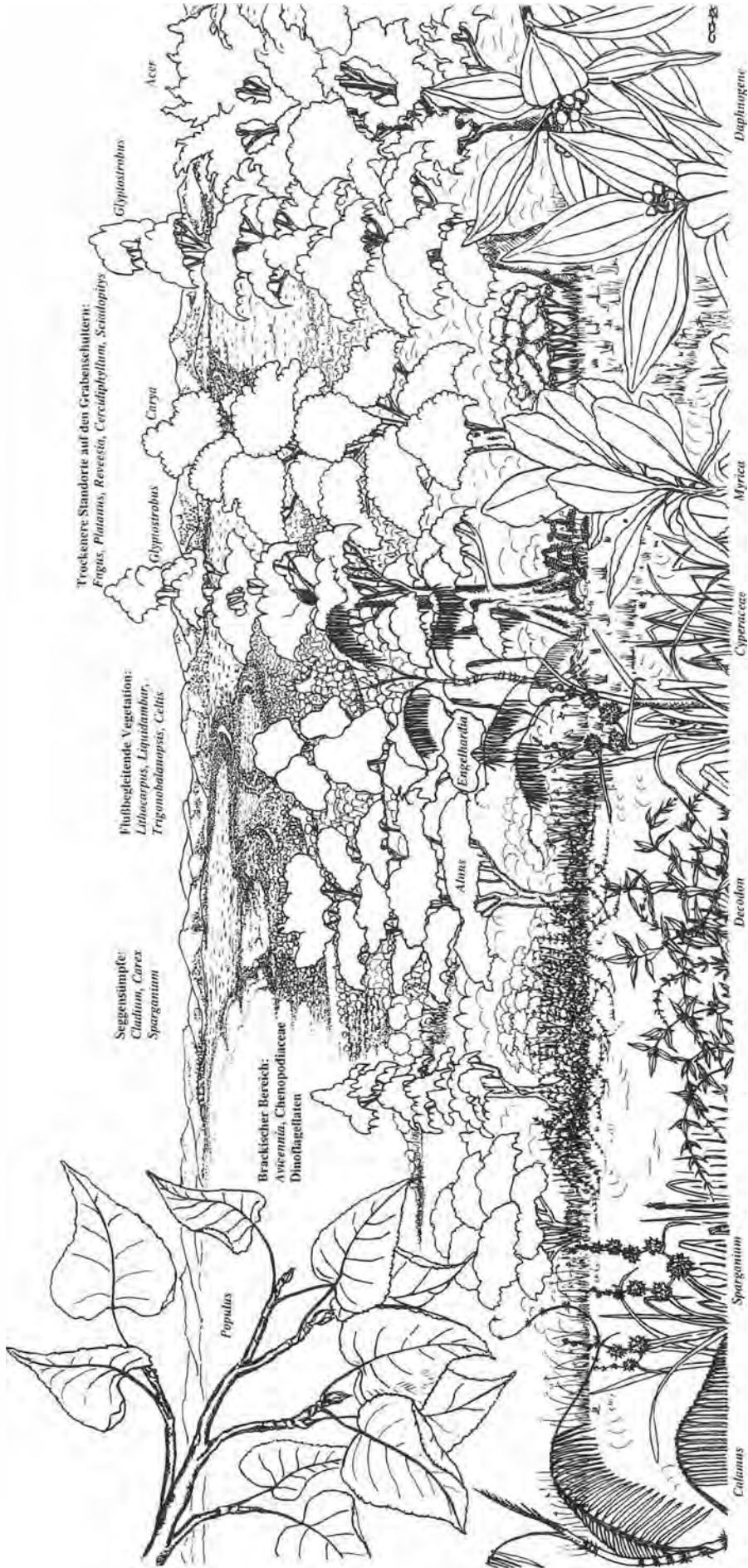


Fig. 7: The Karpatian of the Korneuburg Basin – hypothetical reconstruction of the vegetation (by Christa-Ch. Hofmann, based on data in Hofmann & al., this volume)

The proposed palaeogeographic interpretation differs significantly from the one presented by SEIFERT in SAUER & al. (1992) and SEIFERT (1996). According to his maps the Karpatian Korneuburg Basin would have been part of a delta plain system which covered the southern Vienna Basin up to the Spannberg Swell in the north. However, the depositional environment of the Aderklaa Formation, representing this cycle in the southern Vienna Basin, differs slightly from that of the Korneuburg Basin. It was summarized by WEISSENBÄCK (1996) as a delta plain with a widely ramified, meandering river but lacks any evidence for estuarine or marine environments as indicated by the mollusc fauna described by PAPP (1967). Fully marine shores as deduced from the fauna of Leobendorf and Bisamberg would have been excluded in respect to their position within the delta plain. Therefore we suggest that the Fylsch Zone has acted as barrier along the eastern margin of the Korneuburg Basin towards the delta plain environments of the Vienna Basin.

### Palaeoclimate

The dataset serves as excellent basis for a tentative reconstruction of the palaeoclimate in the late Early Miocene of Central Europe along the shores of the Paratethys Sea. The information from the terrestrial environments derives mainly from the lower vertebrates (BÖHME, this volume) and from the palynomorphs, fruits and seeds studied by HOFMANN & al. (this volume) and MELLER (1998). The latter authors predict a subtropical climate with a minimum value of the mean annual temperature (MAT) of 14° C based on the requirements of modern representatives of *Toddalia*, *Calamus* and *Glyptostrobus*. Even warmer MAT values of at least 17° C can be deduced from the occurrence of the crocodile *Diplocynodon* and cordylid lizards (BÖHME, this volume). The winter months were frost free; the minimal cold month temperature (CMT) is interpreted by BÖHME (this volume; 2002 submitted) to range from at least 3° C to about 8° C. Furthermore, an annual precipitation of approximately 2000 mm was demanded by MELLER (1998). This corresponds well with the Central European palaeoclimatic data for the climax of the Miocene climatic optimum during the Eggenburgian and Karpatian (MAT ≥ 22° C, CMT ≥ 8° C, high humidity; BÖHME, 2002, submitted).

Another climate proxy can be based on the occurrence of *Avicennia*. Modern mangroves are typically developed in the equatorial regions, but may extend as far south as 28° N (DENNY, 1993); *Avicennia* is even known to occur as far south as southern Victoria in 39° S latitude (PLAZIAT & al., 2001). The occurrence of impoverished mangroves mainly consisting of *Avicennia* aff. *marina* along the northern coast of the Mediterranean and the Central Paratethys was already recognized by PLAZIAT & al. (2001) to correlate with the Late Burdigalian to Langhian warming. The same optimum allowed the development of Miocene mangrove environments settled by a characteristic mollusc fauna along the coasts of the Japanese Honshu Island (YAMANOI & al., 1980).

A less thermophilic element is *Crassostrea* which may even thrive along coasts where the minimum sea-surface temperature may drop below 10°C. Thus, modern *Crassostrea* biostromes occur as far north as 48° along the western coast of North America. Along the Eastern Coast *Crassostrea virginica* forms dense colonies in 38° northern latitude in the Chesapeake Bay in Maryland. Correspondingly *Crassostrea* biostromes spread in the Indo-West Pacific Region up to 45° N latitude along Hokkaido in Japan. Stenotherm elements are represented in particular among the gastropods. The modern descendant of the gastropod *Strombus* (*Lentigo*) *bonelli* is *Strombus* (*Lentigo*) *latus* which is found today along the tropical western African shore as far north as the Cape Verde Islands. There, its distribution is restricted to the 15/16° C minimum SST isotherm (data from MECO, 1977). A quite similar minimum SST proxy may be derived from the giant specimens of *Melongena coronata* (HARZHAUSER, this volume). Today the genus is restricted to tropical seas. It is distributed along the coasts of the Gulf of Mexico and the Caribbean Sea. Its northernmost distribution along the western American coast is recorded in the northern part of the Gulf of California (KEEN, 1971) in about 31° latitude where minimum SST values range about 14-16° C (all SST data from the National Environmental Satellite, Data and Information Service [NESDIS] and the Atmospheric Model Intercomparison Project [AMIP II]). Climatic requirements of the fish fauna published by SCHULTZ (1998) and REICHENBACHER (1998) agree well with this interpretation and point to a transitional area between the warm temperate and tropical belt but do not support the interpretation of a fully tropical sea.

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