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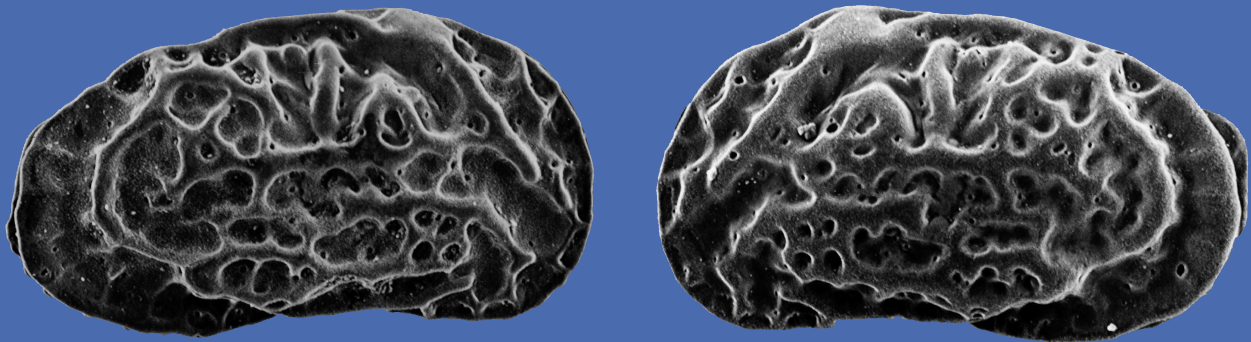of Palaeontology and Geobiology

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Cover illustration: Ostracod *Callistocythere intricatoides* (RUGGIERI, 1953) from the Thyrrenian of Altinova (Turkey). Left: Right valve, external view, BSPG 1980 X 1313 (length 0.640 mm). Right: Left valve, external view, BSPG 1980 X 1314 (length 0.646 mm). SEM Photograph: R. MATZKE-KARASZ (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

Umschlagbild: Ostrakode *Callistocythere intricatoides* (RUGGIERI, 1953) aus dem Thyrrenium von Altinova (Türkei). Links: Rechte Klappe, Außenansicht, BSPG 1980 X 1313 (Länge 0,640 mm). Rechts: Linke Klappe, Außenansicht, BSPG 1980 X 1314 (Länge 0,646 mm). REM-Foto: R. MATZKE-KARASZ (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

Mollusca in marginal marine and inland saline aquatic ecosystems – examples of Cretaceous to extant evolutionary dynamics

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Abstract

Marginal marine brackish water and intracontinental saline Mollusca were characterised by marked evolutionary processes of faunal changes and re-organisations in the course of the Cretaceous and during Cenozoic times: (1) Jurassic/Early Cretaceous oligotypic ellobiid and procerithiid dominated saltmarsh palaeocommunities exhibited an increasing diversity along with the diversification of flowering plants. Particularly cerithioidean families (Caenogastropoda: Cerithiimorpha) and corbiculids (Heterodonta: Corbiculoidea) among the bivalves occupied a broad variety of micro-habitats within the establishing coastal mangrove ecosystems, which were replacing the former type of herbaceous vegetation of the saltmarshes. (2) The greatest bio-diversity of tropical brackish water mollusc faunas coincided with the Cenozoic climatic optimum. Processes of co-evolution of mangroves and molluscs are evident from Early Eocene faunas of the South Pyrenees. First occurrences of extant mangrove plant genera are well in accordance with the first appearance data of several widespread mollusc genera, which replaced the Palaeocene/earliest Eocene faunas with highly endemic character and persisted into the Recent, still characterising extant tropical mangrove ecosystems. (3) Triggered by the climate development, the former coherent mangal with rather uniform fauna disintegrated and the characteristic molluscs migrated in the direction of their modern tropical areas of distribution. The modern bio-provinces of the Indo-Pacific (Western Indian Ocean and Indo-Polynesian Province), Westafrica and the Neotropis were forming. (4) The (Proto-)Mediterranean and Paratethyan Provinces were characterised by a special evolution of temperature tolerant faunal relic elements of the former Tethyan fauna. Again increasing temperatures led to the re-immigration of Indo-Pacific elements during the Late Oligocene/Early Miocene. Furthermore faunal elements of the temperate Atlantic Province migrated into the Mediterranean and partly into the Paratethys. These elements successively replaced the thermophile Early to mid-Miocene palaeocommunities in the course of the Middle to Late Miocene. Further climate cooling led to the diversification of the cerithiid-hydrobiid faunas of the Northern Hemisphere, whereas subtropical to temperate faunas of the Southern Hemisphere were dominated by batillariid-hydrobiid faunas. Particularly the South Australian Province apparently represented a refuge for several Tethyan relics. (5) In the course of the Late Eocene the loss of planktotrophic larval development and transition to direct development enabled primarily marginal marine-brackish taxa to colonize intracontinental saline (athalasso-saline) habitats without marine connections. The composition of the (palaeo-)communities was dependent on the salinity spectrum and the colonized micro-habitats. In Recent time anthropochory plays an important role with respect to the distribution pattern of both, marine-brackish and athalasso-saline molluscs.

Key words: Gastropoda, Bivalvia, Cretaceous, Cenozoic, euryhaline, athalasso-saline, co-evolution, biogeography.

Zusammenfassung

Marginal-marine und intrakontinentale salinare Molluskenfaunen waren während der Kreidezeit und im Känozoikum durch umfassende Faunenwandel und Reorganisationsprozesse gekennzeichnet: (1) Oligotype Salzmarschvergesellschaftungen des Jura und der frühen Kreide, welche durch Ellobiidae und Procerithiidae dominiert wurden, zeigten einhergehend mit der Diversifikation der angiospermen Blütenpflanzen zunehmende Vielfalt. Insbesondere Cerithioidea (Caenogastropoda: Cerithiimorpha) und Corbiculidae (Heterodonta: Corbiculoidea) unter den Bivalvia erschlossen ein breites Spektrum an Mikrohabitaten innerhalb der sich formierenden Mangrovenökosysteme, welche die vorausgehenden von Gräsern dominierten Salzmarschen ersetzten. (2) Die größte Biodiversität tropischer Brackwassermollusken trat zur Zeit des känozoischen Klimaoptimums während des frühen Eozäns auf. Beispiele für Prozesse der Koevolution von Mangroven und Mollusken sind aus dem frühen Eozän der Südpyrenäen belegt. Moderne Gattungen der Mangrovepflanzen traten im selben Zeitraum erstmals auf wie weit verbreitete Molluskengattungen, die Faunen aus dem Paläozän und frühesten Eozän mit überwiegend endemischem Charakter ersetzten und bis heute die tropischen Mangrovenökosysteme prägen. (3) Der

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Zerfall vormals zusammenhängender Mangroven mit nahezu einheitlicher Fauna wurde durch die Klimaentwicklung gesteuert und ging mit Migrationsprozessen der charakteristischen Mollusken in Richtung ihrer modernen Verbreitungsgebiete und mit der Bildung der Indopazifischen (Westlicher Indischer Ozean- und Indo-Polynesische Provinz), Westafrikanischen und Neotropischen Bioprovinzen einher. (4) (Proto-)Mediterran und Paratethys waren durch eine reliktäre Spezialevolution temperaturtoleranter Elemente der vorausgehenden Tethysfauna gekennzeichnet. Wieder ansteigende Temperaturen führten zu Re-Migrationen indopazifischer Elemente während des späten Oligozäns und frühen Miozäns. Weiterhin wanderten Elemente der atlantischen Faunenprovinz ins Mittelmeer und z. T. in die Paratethys ein und ersetzen sukzessive im Verlauf des mittleren und späten Miozäns die für das frühe bis mittlere Miozän charakteristischen thermophilen Vergesellschaftungen. Weitere Klimaabkühlung führte zu besonderer Artenvielfalt von Cerithiidae-Hydrobiidae-Faunen auf der Nordhalbkugel, wogegen Faunen subtropischer und gemäßigter Bereiche auf der Südhalbkugel von Batillariidae-Hydrobiidae-Faunen dominiert wurden. Insbesondere die südaustralische Provinz stellt offenbar ein Refugium für einige reliktäre Elemente der Tethysfaunen dar. (5) Im Verlauf des späten Eozäns waren vormals marginal marine brackische Taxa durch die Aufgabe des Modus der planktotrophen Larvalentwicklung und den Übergang zur Direktentwicklung in der Lage intrakontinentale salinare (athalasso-salinare) Habitate ohne marine Verbindungen zu besiedeln. Die Zusammensetzung der fossilen und modernen Vergesellschaftungen hängt vom Salinitätsspektrum und vom besiedelten Mikrohabitat ab. Rezente Verbreitungsmuster marin-brackischer und athalasso-salinarer Mollusken werden wesentlich durch Anthropochorie beeinflusst.

1. Introduction

Gastropods and bivalves frequently occur in aquatic ecosystems with varying salinities, usually forming oligotypic assemblages, sometimes monospecific populations with large population sizes. Under salinity conditions different from that of sea water molluscs are frequently the only macro-faunal elements occurring within the extreme biotopes, representing important tools with regard to the interpretation of palaeoecology, and thus concerning the reconstruction of palaeoenvironments. Furthermore the composition of the mollusc palaeocommunities provides information concerning the biostratigraphic and biogeographic context. Two general types of biotopes are colonized: 1) brackish water and (partly) hypersaline habitats with marine connections and 2) athalasso-saline, i.e. hydrologically isolated inland saline habitats. Within the tropics, highly structured mangroves are forming the predominant biotope type, colonized by marginal marine brackish mollusc assemblages. Mangroves extend into the warmer subtropics, with extant occurrences for instance in the northern Red Sea, the East coast of Florida, Japan, or northern New Zealand on

the southern hemisphere respectively. In temperate latitudes correspondingly salt marshes, lagoons and estuaries with different herbaceous vegetation are colonized.

Apart from osmo-regulation, the tolerance regarding changes of environmental factors, including extreme variations of the temperature, low oxygen content of the water, and the ability of a partly amphibious mode of life along with corresponding changes of the respiratory system, represent the main adaptations particularly of the brackish water gastropods. Colonization of extreme aquatic ecosystems is advantageous regarding the occupation of new and in many cases temporal ecological niches, and to avoid predators and nourishment competitors, which more commonly occur in normal marine and fresh water habitats.

Euryhaline gastropod assemblages are mainly composed of grazers feeding on micro-algae and of detritus feeders among the Neritimorpha (see e.g., GRÜNDEL et al. 2000; HARZHAUSER & KOWALKE 2001) and among the basal Caenogastropoda – Littorinimorpha and Cerithiimorpha (PLAZIAT 1989, 1993; PLAZIAT & GAUDANT 1984; KOWALKE 1998a, 1998b; SQUIRES 1999; HARZHAUSER & KOWALKE 2002, 2004; GRÜNDEL & KOWALKE 2002; KOWALKE & REICHENBACHER 2005). To a lesser degree amphibious Archaeopulmonata occur in landward portions (KOWALKE 2002). Primarily marine predators among the Neogastropoda managed to penetrate marginally brackish water environments (VONHOF et al. 1998; KOWALKE 2002; VERMEIJ & WESSELINGH 2002; HARZHAUSER & KOWALKE 2004). The accompanying bivalves are considerably less diverse. However representatives mainly of cardiids, corbiculids, dreissenids, and scrobiculariids could establish mass populations in various marginal marine and athalasso-saline environments associated with the typically occurring gastropods (see HARZHAUSER & MANDIC 2004; KORNIUSHIN 2004; KOWALKE & REICHENBACHER 2005).

The diversity of the fauna is generally strongly declining in coastal habitats with euryhaline character, such as estuaries and marginal marine lagoons with brackish water and – in case of (partial) disconnection from the open sea – hypersaline conditions (REMANE & SCHLIEPER 1958). A special case is represented by the colonization of intra-continental saline lakes that are hydrologically isolated and lack marine connections where not only varying salinities but also the differing water chemistry plays an important role (ANADÓN 1989). Many invertebrate taxa in these ecosystems had an origin in fresh water. Consequently the term "athalasso-saline waters" is used rather than "brackish" (see discussions in BAYLY 1967 and HAMMER 1986). From the gastropods' point of view the term brackish would be applicable, since thalassoid taxa frequently had an origin or co-occur in marginal marine environments (KOWALKE 2001a). However the term "athalasso-saline waters" is used in this paper to avoid confusion with the marginal marine classification (cf. BEADLE 1943; HAMMER 1978; HAMMER et al. 1983).

Colonization of extreme biotopes by euryhaline molluscs implies an appropriate mode of early ontogenetic development. Marginal marine taxa are mainly characterised by planktotrophic larval stages, i.e. free-swimming veliger larvae, which feed on phyto-plankton. Shortly after the deposition of the spawn, the larvae hatch from the eggs in a more or less advanced developmental stage. General descriptions of the modes of

early ontogenetic development can be found in SHUTO (1974), SCHELTEMA (1977, 1978), JABLONSKI & LUTZ (1983), JABLONSKI (1986), KOWALKE (1998a, 2001b), and HARZHAUSER & KOWALKE (2001). Planktotrophic larval development is advantageous compared to direct development with hatching of crawling young, since considerably larger numbers of descendents are released. Thus a rapid establishment of populations and the ability to colonize temporary biotopes such as flood plains and temporary or seasonally saline habitats is achieved.

On the other hand, the establishment of gastropod populations within intra-continental athalasso-saline habitats excludes a planktotrophic reproduction, because planktonic veliger larvae with strongly restricted active mode of swimming need a fair connection to the open sea where distribution is mainly triggered by currents. Thus planktotrophic development in brackish water and hypersaline gastropods, e.g., in lagoonal habitats, implies an at least partly or seasonally marine connection of the colonized habitat. On the other hand, apart from direct development with hatching of crawling young, an intermediate lecithotrophic larval development also enabled gastropods from coastal assemblages to colonize athalasso-saline habitats. In this case advanced developmental stages hatch, i.e. pediveliger stages, which are characterised by a velum as a transitional organ, but already have a functional foot. These late veliger stages are able to actively colonize the preferred adult habitat and, after metamorphosis, proceed to the benthic mode of life. However, in the pediveliger stage the larvae may relocate if the habitat is not suitable (KOWALKE, in prep.). In contrast to the early ontogenetic development in gastropods, larvae of bivalves are characterised by a stronger velar apparatus. Thus larval development in bivalves is also possible within restricted and even within athalasso-saline ecosystems without significant currents.

The aim of this paper is to contribute to the knowledge on the temporal and spatial distribution of euryhaline marginal marine and athalasso-saline molluscs within their palaeoenvironmental context since the Cretaceous. Aspects of interactions with other groups of organisms and patterns of co-evolution are discussed. Special emphasis is given to the description of changes in palaeocommunity-structures, particularly in Cenozoic times, and their possible reasons.

2. Increasing Diversity – the Late Jurassic and Cretaceous Radiations

The fossil record of pre-Mesozoic euryhaline molluscs appeared to be comparatively sparse. On the one hand problems of convergences with not closely related marine taxa regarding the teleoconch morphology preclude exact systematic assignments in case of the lack of early ontogenetic shells. Furthermore particularly several gastropod taxa are characterised by direct development, lacking larval stages and characteristic larval shells. In many of these cases the exact systematic position remains uncertain, even if the protoconch-morphology is known.

Aside from hardly determinable Carboniferous Anthracopupinae and Zaptychiinae, which probably represent ellobiids (Archaeopulmonata), confirmed brackish water gastropods are known from the Middle to Late Jurassic on, particularly from North America and Europe (YEN 1951; HUCKRIEDE 1967; GRÜNDEL et al. 2000). Among the described faunas from the French Dogger and from the Late Jurassic of North America and northern Germany, only a few neritimorph (Neritidae) and lower caenogastropod taxa (Hydrobiidae, Littorinidae, Procerithiidae) have been documented. Many of these representatives co-occurred in marine palaeoenvironments and apparently had entered brackish waters from the adjacent shallow seas within the discussed time intervals (see GRÜNDEL 1999; GRÜNDEL et al. 2000). Late Jurassic Ellobiidae among the Archaeopulmonata represent a more diverse group, which obviously already had been restricted to the landward brackish coastal swamp environments in that time interval (HUCKRIEDE 1967). A second group, which was already associated to brackish water habitats in Jurassic times, is represented by Pseudamauridae. Pseudamaurids co-occurred on marine mud-flats since the Late Jurassic. Pseudamauridae represent a family of large lower caenogastropods of uncertain systematic affinities and without closer extant relatives. This gastropod family has been differentiated from convergent but not related marine naticids (Naticoidea) and brackish archaeopulmonates by comparisons of the protoconch morphology (KOWALKE & BANDEL 1996; KOWALKE 1998a, 1998b).

In the course of the Early Cretaceous brackish palaeocommunities were still dominated by Procerithiidae, and especially by Cassiopidae, a ceritioidean family that was characterised by a particular Early Cretaceous radiation (KOLLMANN 1979; CLEEVELY & MORRIS 1988). Like the Procerithiidae, the Cassiopidae co-occurred in, or probably even preferred, normal marine environments, but managed also to enter extreme coastal habitats. A second marked radiation occurred during the Late Cretaceous. New taxa appeared, coinciding with the increasing diversity of structured marginal marine habitats, and with the continuing development of mangrove vegetation. Mangroves were successively replacing the preceding herbaceous vegetation of coastal swamps and salt marshes. The cassiopid radiations were characterised a by rather word-wide extension, with particular diversity in Britain (CLEEVELY & MORRIS 1988), France and Spain (MENNESSIER 1984), in the Gosau-Formation of the Northern Calcareous Alps (KOLLMANN 1979; KOWALKE & BANDEL 1996), in Russia (PCHELINTSEV 1953; AKOPYAN 1976) and in North- and South America (STEPHENSON 1952; CLEEVELY & MORRIS 1988).

Further cerithioidean radiations coincided with the rise of the mangrove vegetation in the wet coastal ecosystems, with the first confirmed occurrence of *Pyrgulifera* and Potamididae, which most probably derived from procerithiid-like ancestors during the late Early Cretaceous. *Pyrgulifera* represents a cerithioidean genus with unclear family affiliation. Representatives known with regard to the protoconch morphology are characterised by a lecithotrophic larval development with a corresponding larval shell, which lacks characteristic features shared with any known cerithioidean genus (KOWALKE 1998a). *Pyrgulifera* represented a frequent faunal element that characterised the oligohaline lagoonal and coastal swamp facies, usually forming large monospecific populations. A late representative of the genus occurred in the Middle Eocene

of Hungary (STRAUSZ 1966; KECKSKEMÉTI-KÖRMENDI 1972). Investigated potamidid species with preserved protoconchs from the Coniacian of the northern Alpine Gosau-Formation are characterised by an indirect development that includes a planktotrophic veliger stage. These representatives can be distinguished from convergent Procerithiidae by comparisons of the protoconch morphology (KOWALKE 1998a). Potamididae were already confined to brackish environments during the Late Cretaceous time interval.

The oldest Melanopsidae were documented from the Maastrichtian of the South Pyrenees (KOWALKE & BANDEL 1996). In contrast to the European Cenozoic representatives of the family, Late Cretaceous melanopsids of the South Pyrenees are characterised by planktotrophic veliger larvae (KOWALKE 1998a). Comparative investigations of the protoconch morphology confirmed a close relation of Melanopsidae and Procerithiidae. In contrast to the early ontogenetic development in procerithiids and potamidids planktotrophy rarely occurred in melanopsids. However no general loss of planktotrophy in the course of the Cenozoic could be documented in melanopsid genera. This mode of early ontogenetic development is still present in one genus of the modern euryhaline melanopsids, i.e. the extant estuarine genus *Zemelanopsis* from New Zealand.

The euryhaline cerithioidean families exhibited a greater tolerance regarding strong fresh water influx within the coastal swamps of the Tethys and apparently superseded the Procerithiidae in the landward brackish habitats. Procerithiidae persisted until the Cretaceous/Tertiary-boundary, inhabiting shallow to deeper marine environments. Coastal habitats with varying salinities on the contrary were avoided by the procerithiids. The rise of Potamididae and Melanopsidae led to a strong decline of Cassiopidae during the Late Cretaceous. At the end of this period the more euryhaline families apparently completely occupied the landward ecological niches of Cassiopidae, i.e. habitats reflecting the lagoonal and coastal swamp facies. The normal marine habitats were continuously colonized by procerithiids and, to a lesser degree, cassiopids; however the diversifying cerithiids began to replace the precursors from the Latest Cretaceous on (KOWALKE 1998a).

Typically intertidal Neritidae (subfamily Neritinae), which exhibited significant radiations in Cenozoic brackish communities, still represented rare elements of the accompanying fauna characterising brackish assemblages of the Late Cretaceous marginal marine Tethys. Investigated sections of the North Alpine Gosau-Formation (Late Coniacian/Early Santonian) and the South Pyrenees (Maastrichtian) are characterised by a single species of the genus *Neritoplica* (KOWALKE & BANDEL 1996). *Neritoplica* most probably represents a precursor of the Cenozoic neritine *Agapilia*/*Neritina*- and *Theodoxus*-radiations (HARZHAUSER & KOWALKE 2001; KOWALKE 2002; LOZOUET 2003).

The salinity preference of many Late Cretaceous Allogastropoda remains largely unclear. Small shelled anomalorbids frequently occur in the brackish layers of the North Alpine Gosau and South Pyrenees, and have also been documented from the British Palaeogene (see PAUL 1991). This author described anomalorbids that occur in marine to brackish environments. Owing to the small size (1-2 mm) of these organisms the autochthonous palaeo-habitat was difficult to verify, since the light

shells could easily have been washed in from adjacent shallow marine biotopes, e.g., from the sea grass facies. On the other hand autochthonous co-occurrences of anomalorbids with typically brackish water *Tympanotonos*-palaeocommunities have been observed in Rupelian deposits of the Thrakian Basin (HARZHAUSER & ISLAMOĞLU, pers. commun.). The interpretation concerning the brackish water tolerance of *Trochactaeon* (Actaeonellidae), a frequent faunal element characterising Gosau deposits, was based on the accompanying fauna consisting of Cassiopidae (KOLLMANN 1965). However, Cassiopidae co-occurred in the fully marine shallow sea (CLEEVELY & MORRIS 1988). Furthermore associations of *Trochactaeon* with *Radiolites*, which occurred in the Late Coniacian/Early Santonian of the Gosau Formation at Brandenberg/Tyrol, more likely indicate marine conditions. Small nerineids of the genus *Parvonerinea* from lagoonal habitats of the same site lived under normal marine to polyhaline/pleimesohaline conditions, indicated by the accompanying fauna that consists predominantly of cassiopids and potamidids.

The accompanying bivalves still appeared to display low diversity during the Cretaceous. However, Corbiculidae, typical brackish water elements of Cenozoic ecosystems, were already confined to the coastal habitats. Corbiculids represent ubiquitous elements within the Late Cretaceous of the Gosau Formation and the Pyrenees, forming mass populations within coastal swamps and lagoons associated with Cerithioidea and being part of the characteristic palaeocommunities.

3. The Tropical Tethys – Co-evolution of Molluscs and Mangroves

Along with the rise of angiosperm vegetation, which replaced the former herbaceous vegetation in shallow wet coastal ecosystems during the Late Cretaceous, new types of structured habitats characterised the intertidal zone between the marine and terrestrial littoral ecosystems: the mangroves were establishing. For a detailed characterisation of the ecosystem see CHAPMAN (1977) and TOMLINSON (1986), among others. The mangroves usually form a sharp boundary to the shallow marine sea-grass facies or to adjacent reefs, respectively, but the landward portion is frequently highly structured including several gradual plant assemblages. The mangrove vegetation colonized various types of coastal swamps and lagoons as well as estuaries of large rivers and smaller creeks which are typically bordered. The composition mainly depends on the water energy and salt content. Usually a sharp vegetation boundary is present where the influence of brackish water ends and fresh water plant assemblages of the fluviatile and fresh water swamp facies thrive. Within the mangrove ecosystem diverse habitats such as mud flats, estuaries and structured landward coastal swamps are colonized by particular euryhaline mollusc assemblages. The composition of these associations depends on several abiotic factors, such as substrate, water energy, mean annual temperatures and precipitation. In addition micro-habitats such as roots and stems of mangrove trees could be colonized by the molluscs. To a lesser degree the mangrove plants serve as a resource for food, e.g., when specialised gastropods feed on the
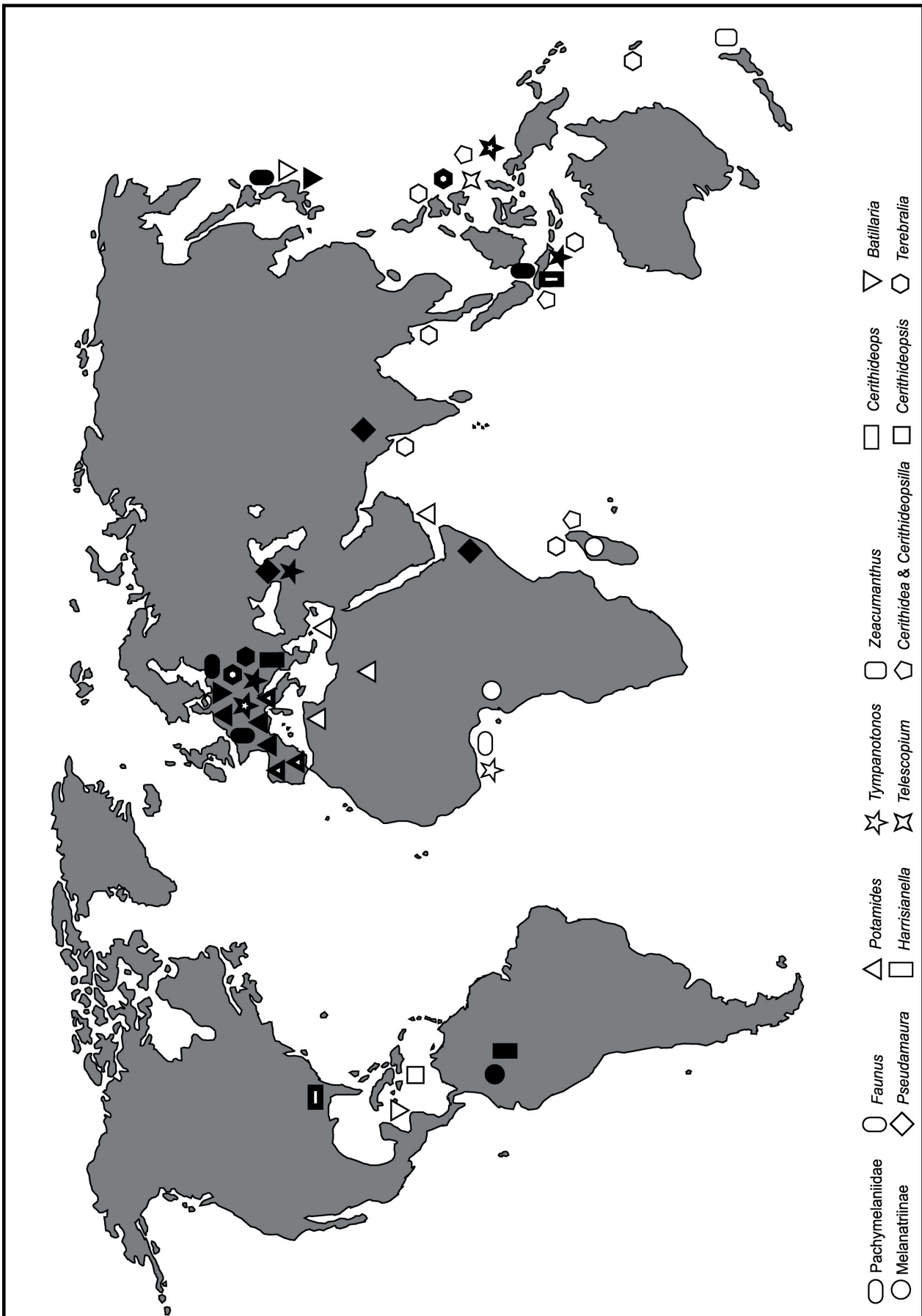
Figure 1: Occurrences of tropical Paleogene (filled symbols), Neogene (half filled symbols) and extant (white symbols) brackish water taxa.

leaves of mangroves (Houbrick 1991). Furthermore mangroves serve as (temporary) habitats that are marginally penetrated by marine and also, to a lesser degree, by fresh water forms. The mangroves are exploited by primarily marine molluscs in the context of reproduction since in many cases the shallow marine environments lack protected microhabitats for the early ontogenetic development of the molluscs. Avoiding epistism of the stenohaline spectrum represents another important advantage for marine elements that exhibit a certain tolerance with regard to polyhaline and pleiomesohaline conditions, and thus could colonize the outer regions of the mangroves. On the other hand, to a lesser degree, predators of marine origin managed to enter the mangrove ecosystems. Neogastropods, particularly thaidids and fasciolariids, represent rare molluscan episites within the mangal (Bandel & Kowalke 1999).

References of first occurrences of mangrove vegetation are based on the pollen *Spinizonocolpites* (see Tralau 1964; Gee 1990). However corresponding fruits of mangrove palms similar to the extant genus *Nypa* are first documented from Lower Palaeocene deposits of Egypt and Brazil (Chandler 1954; Dolianiti 1955; Gregor & Hagn 1982). Diverse Early to Middle Eocene findings of *Nypa*-fruits come from Britain (Tralau 1964; Chandler 1978) and Southern France (Plaziat 1984). *Nypa* co-occurred in various Middle Eocene coastal swamp deposits of the northern Tethys margin. Occurrences are for example known from the Lutetian of Hungary (Kowalke 2001b). In addition to the genus *Nypa*, which predominantly colonized the landward portions of the mangal, Sonneratiaceae and Rhizophoraceae occurred in the latest Palaeocene/earliest Eocene of Western Europe. These taxa gave rise to the development of a modern, highly structured mangrove-ecosystem. The highest biodiversity of the mangal was reached during the Early and Middle Eocene. Associations of modern taxa, such as *Avicennia* and *Acrostichum*, with *Nypa* were for example described from tropical northern Spain (Plaziat et al. 2001; Dominici & Kowalke, in prep.).

The direct and exclusive connection of mangrove vegetation and molluscs is difficult to document in case of fossil assemblages. However *Ellobium* (Ellobiidae, Ellobioidea) and Pachymelaniidae (Cerithioidea) are confined to the mangroves (Janssen 1984; Bandel & Kowalke 1999). Several genera of Potamididae among the Cerithioidea either live on the vegetation (*Cerithidea*, subgenus *Cerithidea*), as well as e.g., *Littoraria* among the Littorinidae (cf. Reid 1985, 1986). Some taxa (e.g., representatives of the genus *Terebralia*, cf. Houbrick 1991a) feed on the leaves of mangrove plants.

Many of the extant gastropods occurring in the brackish-intertidal tropical zone prefer the mangroves but are not exclusively restricted to the mangal biotopes. However the marked increase of diversity, especially of the Cerithioidea, with rise of the *Nypa*-mangroves since the Late Cretaceous points to a strong preference of this habitat, and to an occupation of differentiated ecological niches/micro-habitats. Apart from the striking Late Cretaceous radiation of the Potamididae, especially during the Palaeocene, several new potamidid taxa are recognised. These are characterised by a partly endemic distribution, as described from the Dano-Montian of Mons/Belgium (Kowalke 2002). The brackish assemblage of Mons furthermore had a diverse cerithiid, pseudamaurid, and ellobiid

fauna, and several neogastropods represent carnivore elements, which marginally managed to enter the mangrove ecosystem in that time interval (buccinids, melonginids, fasciolariids). Rissooidea represented comparatively rare, predominantly shallow to deeper marine elements in Cretaceous times, but exhibited an increasing diversity in brackish habitats during the Palaeocene (Kowalke 2002).

With the rise of modern mangrove vegetation, including the genera *Avicennia*, *Rhizophora*, and *Bruguiera* that form the structured seaward successions of the mangroves, also the habitat-differentiation has been increasing – new additional niches for the associated molluscs formed. Especially the Early Eocene represents a time interval with occurrences of modern mangrove taxa among the Potamididae (*Cerithidea, Tympanotonos*) and Batillariidae (*Batillaria*) (Fig. 1). A marked radiation of endemic genera had been succeeding the striking extinction event of the Late Ilerdian. This scenario is well evident from the Early Eocene of the southern Pyrenees (Dominici & Kowalke, in prep.). The increasing diversity coincided with the Early Eocene sea-level maximum and Early Eocene climatic optimum, EECO, which also enabled an optimal distribution of the mangroves. The presence of a diverse mollusc fauna suggests that the investigated species occupied narrow ecological niches. The high degree of endemism may be explained by direct or lecithotrophic larval development of many taxa, or short planktotrophic larval stages respectively: compared to extant faunas, the Early Eocene mangrove molluscs were characterised by low dispersal capabilities. Another possible reason for endemism is perhaps the lack of coherent mangrove coasts, which are necessary for the "step by step" distribution particularly of the gastropods. The mangrove ecosystem in a modern composition was still establishing. The degree of endemism was reduced during the Lutetian, when the modern mangroves had formed and a coherent structured mangrove-ecosystem characterised the landward portion of the intertidal environments. The mangroves were well separated from the adjacent seaward fully marine facies dominated by sea-grass and coral reefs. A well preserved autochthonous fauna with mollusc assemblages, including all ontogenetic stages, has been described from the Lutetian of Gánt/W Hungary (Kowalke 2001b). The dominating gastropod group, the cerithiimorph superfamily Cerithioidea, is characterised by the predominant mode of reproduction by planktotrophic veliger larvae, enabling a wide distribution of species. The potamidid genera *Tympanotonos*, *Terebralia*, and *Cerithidea* first appeared in the Middle Eocene and occurred in morphologically similar morphotypes/eco-phenotypes as their extant equivalents. In case of *Cerithidea* a co-occurrence of the subgenus *Harrisianella* could be documented for the European Lutetian and for the Late Eocene of the Saman-Formation of Caleto Sal/Peru (Kowalke 2001b; Olsson 1929). Similarly to the situation during the Early Eocene time interval, associated Pachymelaniidae and Pachychilidae were present by earliest sympatric co-occurrences within the European mid-Eocene assemblages (Kowalke 2001b, 2004). Pseudamauridae obviously exhibited an optimum in diversity compared to the occurrences in Palaeocene and Early Eocene times, with co-occurrences on species level in Lutetian deposits of Hungary, Italy, and the Paris Basin (Kowalke 1998b). In that time interval Rissooidea were

characterised by an increasing diversity in brackish habitats of the Tethyan coasts.

Euryhaline bivalves were comparatively diverse, showing similar faunal compositions and population densities as their relatives in modern mangal communities. Patterns of co-evolution are difficult to demonstrate. However special microhabitat adaptations, e.g., ostreid settlement on roots of mangrove plants, were already established. The accompanying bivalve fauna was not exclusively confined to the mangroves, but was generally euryhaline and colonized a wide variety of habitats, and formed large populations within the mangal. Euryhaline taxa such as dreissenids (*Mytilopsis*), mytilids (*Brachydontes*), corbiculids (*Corbicula*), and scrobiculariids (*Abra*) were morphologically very similar to modern congeneric representatives (see Szöts 1953).

During the latest Eocene/Early Oligocene the climate cooling led to a decline of the mangrove vegetation in Europe and to a successive migration of the mangroves to the tropical and warmer subtropical provinces. Several brackish water molluscan taxa formerly associated with the mangroves, obviously exhibited a certain tolerance with regard to decreasing temperatures and managed to enter the wet coastal ecosystems that succeeded the mangal. A re-immigration of *Avicennia*-dominated mangroves coincided with the warming period of the Late Oligocene to Early/early Middle Miocene, and, apart from occurrences in Spain and southern France, a far northward extension of the mangroves to Hungary (Nagy & Kókay 1991) and probably to the Bavarian Molasse Sea (Barthelt 1989; Reichenbacher et al. 2004) has been enabled. *Avicennia*-dominated mangroves are evident from the Karpatian of the Korneuburg Basin (central Paratethys) where also typically associated mangrove dwellers among the potamidids (*Tympanotonos* and *Terebralia*) and diverse ellobiids (*Auriculastra*, *Melampus*, *Laemodonta*, and *Ovatella*) co-occurred (cf. Binder 2002; Harzhauser et al. 2002). The climatic optimum coincided with the maximum sea-level during the Early/Middle Miocene. Late Miocene/Early Pliocene occurrences of *Avicennia*-mangroves refer to pollen data from pre- and post-Messinian strata from Sicily and Algeria, and probably represent reworked material from older Miocene deposits (Plaziat et al. 2001 and references therein). No marked co-evolution of molluscs and mangroves, similar to that present in the Paleogene, is feasible for the relic mangal of the European Neogene. Relic species of typical mangrove colonizing genera, e.g., of the potamidid genera *Terebralia* and *Tympanotonos*, independently colonized coastal swamps and estuaries – in case of *Terebralia* with far northwards extension (e.g., occurrences in Belgium), clearly exceeding the distribution of the *Avicennia*-mangroves. The dominant Neogene brackish water taxa *Granulolabium* and *Potamides* obviously originated in Palaeogene marginal marine environments of the European Atlantic coasts. Neither the Palaeogene nor the Neogene fossil record exhibits indications regarding an affinity to mangrove vegetation of these genera (Kowalke 2003).

Colonizing the mangrove palaeoenvironments was advantageous compared to colonization of corresponding wet ecosystems without coastal forests based on the fact that mangroves provide a considerably higher diversity in micro-habitats. The diversity of habitats enabled the molluscs to occupy narrow ecological niches. Apart from mangrove plants, which were colonized by several gastropod groups (predominantly Potamididae and Littorinidae) during the high tides, aerial roots and several portions with different water energy and different substrates formed additional habitats for the euryhaline molluscs. The reduced water energy in several portions of the mangroves furthermore improved the conditions for reproduction. Spawn could more easily be deposited in the finer substrates. Roots of the mangrove plants served as additional hard substrate for the attachment of sessile molluscs (e.g., ostreids) and for the deposition of spawn, e.g., in case of neritids. Veliger larvae in late developmental stages find better conditions for metamorphosis and for proceeding to the benthic mode of life within the calmer portions of the mangroves than in the strong currents of the adjacent shallow sea. Problems of low oxygen content and of the oligotrophic character of the mangroves were obviously compensated for by most taxa. Extant *Tympanotonos* of the West African mangroves, for example, managed to burrow in the uppermost 0.5 cm of the substrate, whereas syntopic *Pachymelania* spp. are feeding exclusively on the microalgae on the surface of the sediment (Bandel & Kowalke 1999).

Cerithiidae generally represent rare elements of the mangal fauna. However a few genera, e.g., the European Eocene to extant tropical genus *Clypeomorus* (Houbrick 1985; Kowalke 2001b) and the Eurasian Eocene to Oligocene genus *Bellatara* (Harzhauser 2004) occurred always in association with a typical mangrove facies. Extant *Clypeomorus* predominantly colonizes the roots of mangrove vegetation. *Bellatara* may well have thrived in a similar environment.

Although mollusc assemblages in mangroves, as well as in any other eco-systems with salinities different from euhaline conditions, represent oligotypic assemblages, the biodiversity of the mangroves is generally higher than that seen on the mud flats or estuarine portions without vegetation. Even landward portions of the mangal are characterised by a considerably diverse fauna. In West Africa, for example, additional dreissenids, neritids, and archaeopulmonates are present in landward *Nypa*-mangroves, but are absent from the outer estuarine portions and from the mud flats. One reason for this may be the considerably reduced number of predators among the crabs and neogastropods. The predators marginally penetrate the mangroves, but are usually restricted to those outer portions that are strongly affected by high tides. The protected calm parts of the inner mangal are often characterised by the formation of tidal ponds with high fresh water content and high water temperatures, usually avoided by polyhaline predators. The less diverse assemblages of the outer mangals require adaptations with regard to the teleoconch morphology. The gastropods are frequently characterised by heavy shells, in many cases bearing additional strong sculpture, including spines. The formation of these sculptural elements represents an adaptation to predation and also to the considerably higher water energy. Thin shelled and small species are predominantly part of the inner mangal associations.
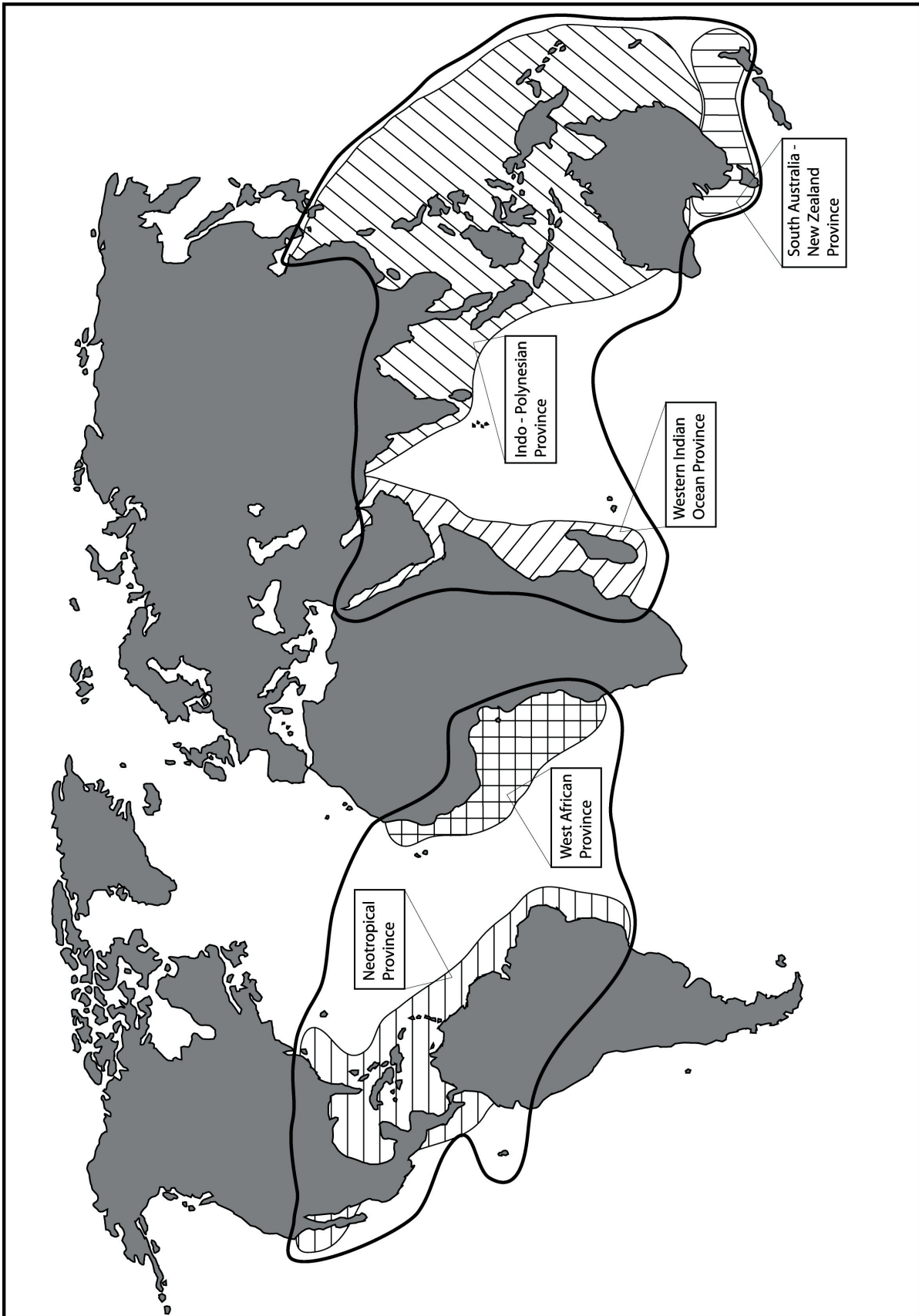
Figure 2: Extant mangroves and associated mollusc bio-provinces (explanations in the text).

4. Disintegration of the Tethys – Formation of Modern Bio-provinces

The Late Eocene/Early Oligocene cooling period led to corresponding migrations of the mangroves and associated mollusc faunas towards the tropical and warmer subtropical latitudes. In the course of the migrations the formerly coherent mangroves of the Tethys margin with their uniform and diverse fauna and flora disintegrated. The characteristic elements migrated in the direction of their modern tropical areas of distribution (Fig. 2). During Oligocene times *Nypa*-mangroves were characterised by wide Indo-Pacific distribution ranging from Pakistan to New Zealand. The *Rhizophora* dominated mangroves were distributed from West Africa to the Neotropis (PLAZIAT et al. 2001 and references therein). In the Indo-West Pacific Region associated mollusc assemblages mainly comprised potamidids associated with thiarids and neritids, and rare cerithiids and melanopsids. Among the bivalves corbiculids appeared to be the dominating elements.

The fossil history of the genus *Telescopium* is confusing to some extend, nonetheless this taxon represents an important faunal element of Neogene and extant Southeast Asian mangroves. The genus *Telescopium* has been described from several Miocene to Holocene localities throughout the Indonesian Archipelago (HOUBRICK 1991a). Two fossil species are recognised that are morphologically very similar and, according to HOUBRICK, probably conspecific with the extant type species *Telescopium telescopium* (LINNAEUS, 1758), which is widely distributed in the Indo-Pacific. *Telescopium* has to date not been documented from the European Cenozoic. Morphs from the Paleogene and Early Miocene of the Paris Basin and South France with superficial resemblance proved to belong to the genus *Campanile* (Campaniloidea, Campanilidae) (KOWALKE 1998b, 2003; LOZOUET et al. 2001).

The potamidids *Terebralia* and *Cerithidea* (subgenera *Cerithidea* and *Cerithideopsilla*) represent further cerithioidean genera that characterise the modern Indo-West Pacific Region. These genera obviously originated in the Eocene Tethys realm (KOWALKE 2001a) where their oldest known fossil representatives occur. The fossil record of forms assignable to the modern type-species *Terebralia palustris* (LINNAEUS, 1758) ranges from the Miocene to Quaternary of the Indonesian Archipelago, and from the Pliocene to Quaternary of East Africa (HOUBRICK, 1991a). AZZAROLI (1958) described *Cerithium sindiense* (?) VREDENBURG and *Cerithium kachhense* VREDENBURG from Oliocene to Lower Miocene deposits of Somalia. The two species may well be representatives of the genus *Cerithidea*, subgenus *Harrisianella*. This subgenus is known from the European Lutetian (KOWALKE 2001b) and from the Late Eocene of Peru (OLSSON 1929). The modern subgenus *Cerithidea* could be traced back to the Miocene of Saipan (LADD 1972). It co-occurred in the Pliocene of Java (REGTEREN ALTENA 1942) and in the Pleistocene of Okinava (MACNEIL 1960). The subgenus *Cerithideopsilla* is known from the Miocene of India, Japan, and from the Indonesian Archipelago (REGTEREN ALTENA 1942). *Tympanotonos* occurred in Early Miocene deposits of Pakistan (HARZHAUSER et al. 2002). This genus was apparently absent from Southeast Asia and from the West Pacific during the Middle and Late Miocene. A species described as *Tympanotonos berberkirianus* (MARTIN) by LADD (1972) actually belongs to the genus *Vicarya*, a shallow marine and euhaline representative of the family Cerithiidae, occurring well separated from mangrove ecosystems.

Cerithiids generally represent rare elements of euryhaline habitats. Only few cerithiid genera exhibited a certain tolerance with respect to the colonization of euryhaline biotops, but once adapted to the mangals could establish large population sizes. The Early Eocene to Late Oligocene genus *Benoistia*, for instance, represents an ubiquitous element of European Paleogene mangrove environments (GITTON et al. 1986; KOWALKE 2003; DOMINICI & KOWALKE, in prep.). While *Benoistia* became extinct in the course of the Late Oligocene, the morphologically similar cerithiid genus *Clypeomorus*, with the oldest known fossil representatives occurring in the Lutetian of SW France and Hungary (ROUAULT 1848; KOWALKE 2001b), persisted until present times. *Clypeomorus* represents an intertidal cerithiid that typically occurs associated with mangroves and predominantly colonizes the roots of mangrove vegetation where it feeds on microalgae from the surface of this hard substrate (HOUBRICK 1985, 1992).

Indo-Pacific thiarids entered the fresh water portions of rivers from estuarine habitats. They colonized these habitats as juveniles after metamorphosis, subsequent to planktotrophic marine larval development, and hence, in the course of their life cycles, represent anadromely migrating elements. Thiarids most probably originated from the northern Tethys margin. Species morphologically very similar to the modern fresh and brackish water dweller *Melanoides* occurred in various localities of the European Eocene and Early Oligocene (KOWALKE 2001b). Aside from these rather monospecific assemblages in fresh water deposits, brackish water thiarids are rarely documented in the fossil record. The brackish water genus *Bayania* most probably represents a thiarid, characterised by the typical protoconch morphology, reflecting a histotrophic embryogenesis within a brood pouch. For a detailed description of the protoconch and mode of early ontogenetic development see KOWALKE (2001b). Apart from the occurrences in the European Lutetian, *Bayania* has been described from the Early to Middle Oligocene of France (GITTON et al. 1986) and from contemporaneous deposits of the Mainz Basin (KOWALKE 2003), Romania (MOISESCU 1972), and Iran (HARZHAUSER 2004). Fossil thiarids with indirect development with an intercalation of a planktotrophic larval stage are unknown to date. However the presence of modern thiarids with corresponding protoconch morphology indicates that this mode of early ontogenetic development must have existed throughout the Cenozoic. On the other hand the presence of thiarids with direct development in the Middle Eocene indicates that the family must have originated from ancestors with indirect development at least during the Early Eocene. Earliest Eocene representatives with very similar teleoconchs are known from the South Pyrenees (KOWALKE & DOMINICI, in prep.). Unfortunately early ontogenetic shells are not preserved and the protoconch morphology as a tool for the systematic assignment is unknown. Thus the exact systematic position of these fossils remains elusive based on possible convergences with regard to teleoconch morphology, e.g., with shallow marine representatives of the related but fully marine

cerithioidean family Diastomidae (KOWALKE 1998a).

In addition the mangroves of the Indo-Polynesian province are characterised by the melanopsid genus *Faunus* with the single extant species *F. ater*, settling coastal swamps and predominantly landward portions of the mangroves of the Indonesian Archipelago (HOUBRICK 1991b). According to HOUBRICK the fossil record of *Faunus* probably extends back to the Middle Eocene of the Paris Basin. Similar shells are known from the Early Eocene of North Spain (DOMINICI & KOWALKE, in prep.), but due to potential convergences and fragmentarily preserved shells that lack detailed information concerning the apertural and protoconch morphology, species assigned to *Faunus* need further investigation. However the oldest known fossil Melanopsidae come from the Maastrichtian of the South Pyrenees and may well be ancestor to the Cenozoic melanopsid radiations (KOWALKE 1998a).

The conspicuous absence of any pachychilids from post-Eocene brackish water sediments documents an early complete adaptation to fresh water habitats of this cerithioidean family. Mid-Eocene representatives of the pachychilids inhabited the interior portions of well structured coastal swamps, which bordered the Tethys Ocean and were characterised by low water energy and low salinity. The representatives of the genus *Gantmelanatria* were characterised by lecithotrophic larvae, reflecting a short free swimming pediveliger stage (KOWALKE 2001b). Planktotrophic development was already absent during that time interval. After disintegration of the Tethys pachychilids still inhabited the modern subtropical and tropical provinces, but were exclusively adapted to pure fresh water habitats of rivers and lakes, with well separated occurrences of the modern genera *Pachychilus* characterising the Neotropis, *Melanatria* from Madagascar and Nossi Bé, *Potadoma* from West and Central Africa (KOWALKE 2004), and the SE Asian genera *Brotia* and *Jagora* (KÖHLER & GLAUBRECHT 2001, 2002, 2003). The ubiquitous large fresh water pachychilid *Tinnyea* is characterised by a tropical/subtropical relic evolution, with several allopatric species occurring within the fluviatile palaeoenvironments of the (Proto-)Mediterranean and Paratethys, covering a time span from the Late Oligocene to the Late Miocene (HARZHAUSER et al. 2002; KOWALKE 2004).

The South Australia/New Zealand province is characterised by oligotypic estuarine *Zemelanopsis*/hydrobiid assemblages, and by *Zeacumanthus*/hydrobiid assemblages that colonize the mud-flats. *Zemelanopsis* represents an euryhaline melanopsid that is characterised by a planktotrophic larval development. LADD (1972) described the batillariid *Zeacumanthus rickardi* from the Early Miocene of Viti Levu, Fiji. The genus migrated southwards to the temperate province during the Miocene, most probably as a result of the occurrence of competitors among the potamidids. According to LOZOUET (1986) a single extant relic species of the genus *Granulolabium* is present in marginal marine lagoons of South Australia. Turritellids are not directly confined to the mangroves, but frequently occur in the high-nutrient catchment areas of large river estuaries within the Australian province, tolerating considerably reduced poly- to pleiomesohaline salinities (WU & RICHARDS 1981; CLARKE et al. 2001).

The West African coast represents a different bio-province. The *Rhizophora* dominated mangrove is characterised by a uniform mollusc fauna that mainly consists of the extant relic type species of *Tympanotonos*, *T. fuscatus*, and three extant relic species of *Pachymelania*. *Pachymelania* forms a separate family, the Pachymelaniidae, in the Cerithioidea as recently introduced by BANDEL & KOWALKE (1999). Pachymelaniidae are well separated from the Thiaridae and Potamididae based on their anatomy and protoconch morphology. A diverse neritine fauna and archaeopulmonates occur in the landward portion of the well structured mangroves and in estuarine portions of the rivers, whereas *Tympanotonos* and two pachymelaniid species considerably decrease (BANDEL & KOWALKE 1999). On the other hand *Pachymelania fusca* invaded the inner estuarine/riverine portions tolerating very low salinities below 0.02 ppt TDS. Bivalves are absent from the outer estuarine and mud-flat portions as well as from the outer mangals. The interior calm portions of the mangroves, where *Nypa-Acrostichum* associations are bordering small creeks affected by strong fresh water influx, display a more diverse fauna that is dominated by the dreissenid bivalve *Mytilopsis* and a diverse neritine fauna. Thiaridae, which represent frequent elements of the Southeast Asian mangroves, are absent. Similar to the faunal compositions of the Australian province, turritellids characterise the high-nutrient catchment areas of large rivers, shallow subtidal but generally euryhaline habitats (ALLMON 1988).

The Neotropis displays *Rhizophora*-mangroves similar to the assemblages from the West African coast, but distinguished on species level. The gastropod fauna is completely different: The extant *Cerithidea*, subgenus *Cerithideopsis*, is restricted to the southern North and Middle America, and represents the sole potamidid characterising the mud-sand habitats of the intra- to supratidal zone (HOUBRICK 1984). The modern Neotropical subgenus *Cerithideopsis* has been described from the Late Miocene of Florida (OLSSON & HARBISON 1953). The probable precursor *Cerithideops*, which may have evolved from the Tethyan *Harrisianella*, is only known from the Miocene of New Jersey (PILSBRY & HARBISON 1933). Regarding the distribution pattern, *Cerithideopsis* partly overlaps with *Batillaria*. The latter is absent from the Mexican Pacific coast. It is characterised by a considerably more southwards distribution to southern Brasil (PLAZIAT 1989). The batillariid genus *Pyrazisinus* is known from the Early Oligocene of Italy and Greece (HARZHAUSER 2004) and persisted in Europe until the Aquitanian (LESPORT & CAHUZAC 2002). The genus obviously migrated to the Neotropis where it has been described from the Early Miocene of Florida (HEILPRIN 1887). *Pyrazisinus* could well have been ancestral to the modern *Batillaria*. *Batillaria* is ecologically well separated from *Cerithidea* in that it colonizes mud-flats of the lower intertidal to shallow subtidal portions.

An exchange of faunal elements between the three tropical to warmer sub-tropical bio-provinces is prevented by barriers with climate cooling and upwelling, e.g., at the northern and southern West African coasts (north of Senegal and south of Angola), and at the northern coasts of the Red Sea and the southern coast of South Africa. Larvae of mangrove gastropods did obviously not manage to cross neither the South Atlantic nor the South Pacific to enable an exchange of faunal elements from West Africa and from the Indo-pacific with the Neotropis. An exception may be the (extant?) introduction of

Batillaria from Japan to the western coast of North America (PLAZIAT 1989).

In geographical areas of the temperate latitudes that were not colonized by mangrove vegetation, euryhaline faunas are characterised by diversifying cerithiid and mainly by risooid elements. Apart from from fully marine elements such as *Alvania* and *Manzonia*, which tolerate reduced salinities towards polyhaline conditions to a certain degree, the genus *Rissoa* and closely related genera among the Rissoinae are characterised by a wide distribution with north European radiations. *Rissoa* and *Pusillina*, for example, occurred within the shallow Baltic Sea, colonizing brackish waters partly under mesohaline conditions (WARÉN 1996). These dominant elements of the modern temperate brackish water faunas were already present in Palaeogene times. However risooids appeared to be of subordinate importance and preferred shallow to slightly deeper normal marine habitats in order to avoid strong competition of potamidid dominated subtropical to tropical brackish mollusc faunas, which were characterised by rather worldwide distributions. Among the cerithiids mainly the genus *Bittium* GRAY diversified in lagoonal environments and occupied the ecological niches of *Granulolabium* and *Potamides* north of the 40th degree of latitude (HARZHAUSER & KOWALKE 2001). In the course of the diversification of small brackish water gastropods among the Rissooidea, particularly the Rissoinae successively replaced the palaeorissoinids, which formerly represented subordinated elements of the outer mangrove environments (GRÜNDEL & KOWALKE 2002). Mediterranean and Paratethyan subtropical faunas established with particular radiations of the potamidid genera *Granulolabium* and *Potamides*, well separated from the Atlantic temperate *Bittium*/Rissoinae faunas. Subtropical as well as temperate intertidal brackish water gastropod faunas were associated with diversifying bivalves of the cardiid relations. Cardiids successively replaced the corbiculids, which formerly had dominated the outer estuarine and lagoonal sections of the tropical and warmer subtropical mangals. The further faunal development and provincial differentiation in the European region is described in detail in the frame of the subsequent section.

5. Relic Evolution and the European Faunal "Turn Over"

Marked changes in the composition of marginal marine palaeocommunities formerly characterised by rather coherent mangrove associations are evident from the European latest Eocene/earliest Oligocene. Apart from the uncertain pollen-based record of *Avicennia* and *Rhizophora* from the Early Oligocene of Aix-en-Provence/Southern France (PLAZIAT et al. 2001) no fossil evidence points to a mangrove-vegetation during the colder time interval until the early Late Oligocene. Thus remainders of the former characteristic mangal fauna among the gastropods and bivalves had to manage comprehensive changes of the biotic and abiotic factors that affected the colonized habitats. Thermophile elements such as *Batillaria* and *Pachymelania* were restricted to the tropics. Only few typically tropical to warmer subtropical elements

tolerated the decrease of temperatures (Fig. 3). Several species of *Tympanotonos* are described from the Early Oligocene of the Transsylvanian Basin (MOISESCU 1969), France (LOZOUET 1986), and Italy (SACCO 1895; COSSMANN 1906a). These elements were restricted to the earliest Oligocene. *Terebralia* persisted during the Mediterranean Oligocene, represented by few species, whereas *Tympanotonos* probably remigrated from the Indian Ocean during the late Early/early Late Oligocene time interval. The re-migration process could have been triggered by palaeoclimate, i.e. by the again increasing temperatures. Early Rupelian faunas from Iran are turritellid-diastomid dominated, whereas overlying Late Rupelian/Early Chattian deposits and contemporaneous deposits of Pakistan (VREDENBURG 1928) are characterised by *Tympanotonos*, which also again occurred in the earliest Chattian of Doutsiko/Greece, accompanied by *Campanile* (HARZHAUSER 2004). Last occurrences of *Tympanotonos* prior to the possible re-migration with higher diversity are documented, e.g., by the presence of numerous species from the Early Oligocene of the Paris Basin (COSSMANN 1906b; GITTON et al. 1986). The Early Oligocene fauna of the Paris Basin represents a relic of the tropical Eocene Tethyan assemblages and contained neritids, last representatives of the pseudamaurids and muricids close to the Eocene precursors. These predominantly tropical elements were absent from Late Oligocene deposits. Also thiarids appeared, e.g., the genus *Bayania*, a tropical faunal element that characterised the European Lutetian mangal (KOWALKE 2001a). Late Oligocene deposits of the Proto-Mediterranean, Austria, and the Mainz-Basin are characterised by a less diverse fauna: A single widespread species of *Tympanotonos*, *T. margaritaceus* (BROCCHI), and a few species of *Terebralia* were present (KADOLSKY 1995; HARZHAUSER & KOWALKE 2001). *Tympanotonos margaritaceus* migrated into the Mainz-Basin during the latest Chattian/Aquitanian, while earlier deposits of the Rupelian and Early Chattian deposits lack this taxon (KOWALKE 2003). *Terebralia* exhibited a greater tolerance regarding changes of environmental factors such as habitat composition and climate. In the course of the Oligocene *Terebralia* adapted to the colonization of alternative habitats, particularly hypersaline lagoonal environments under semiarid climate conditions.

Potamides and *Granulolabium* tolerated lower temperatures and were characterised by a remarkably increasing diversity in the course of the Oligocene (LOZOUET 1986; GRIMM et al. 2000). *Potamides* and *Granulolabium* originated from the Paleogene Atlantic faunal province (KOWALKE 2003) and obviously successively occupied the ecological niches of the decreasing genera *Tympanotonos* and *Terebralia*. First co-occurrences of *Granulolabium* and *Tympanotonos* are documented from the Lower Stampian sections at Falun des Jeurs and Falun de Moringny within the Paris Basin (GITTON et al. 1986). During the late Early Stampian the brackish water fauna of the Paris Basin reached an increasing diversity on genus level, as documented for palaeocommunities characterising the sections of Etampes and Moulinvaux (GITTON et al. 1986): Rare thermophile elements (*Bayania*, pseudamaurids, *Tympanotonos*) occurred associated with the less termophile element *Granulolabium* and associated temperate Rissooidea. *Granulolabium* and Rissooidea had appeared in latest Cretaceous/Early Palaeocene assemblages but represented elements of subordinate impor-

Paleogene								Neogene								Quaternary			
Paleocene			Eocene				Oligocene		Miocene						Pliocene		Pleistocene		Holocene
Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Lower / Middle / Upper	
65.5		55.8					33.9	23.03						5.332			1.806		0.0115

Pachymelaniidae

Greveniella

Cerithidea

Granulolabium

Potamides

Terebralia

Tympanotonos

Melanatriinae

Batillaria

Benoistia

Pseudamaura

Corbicula
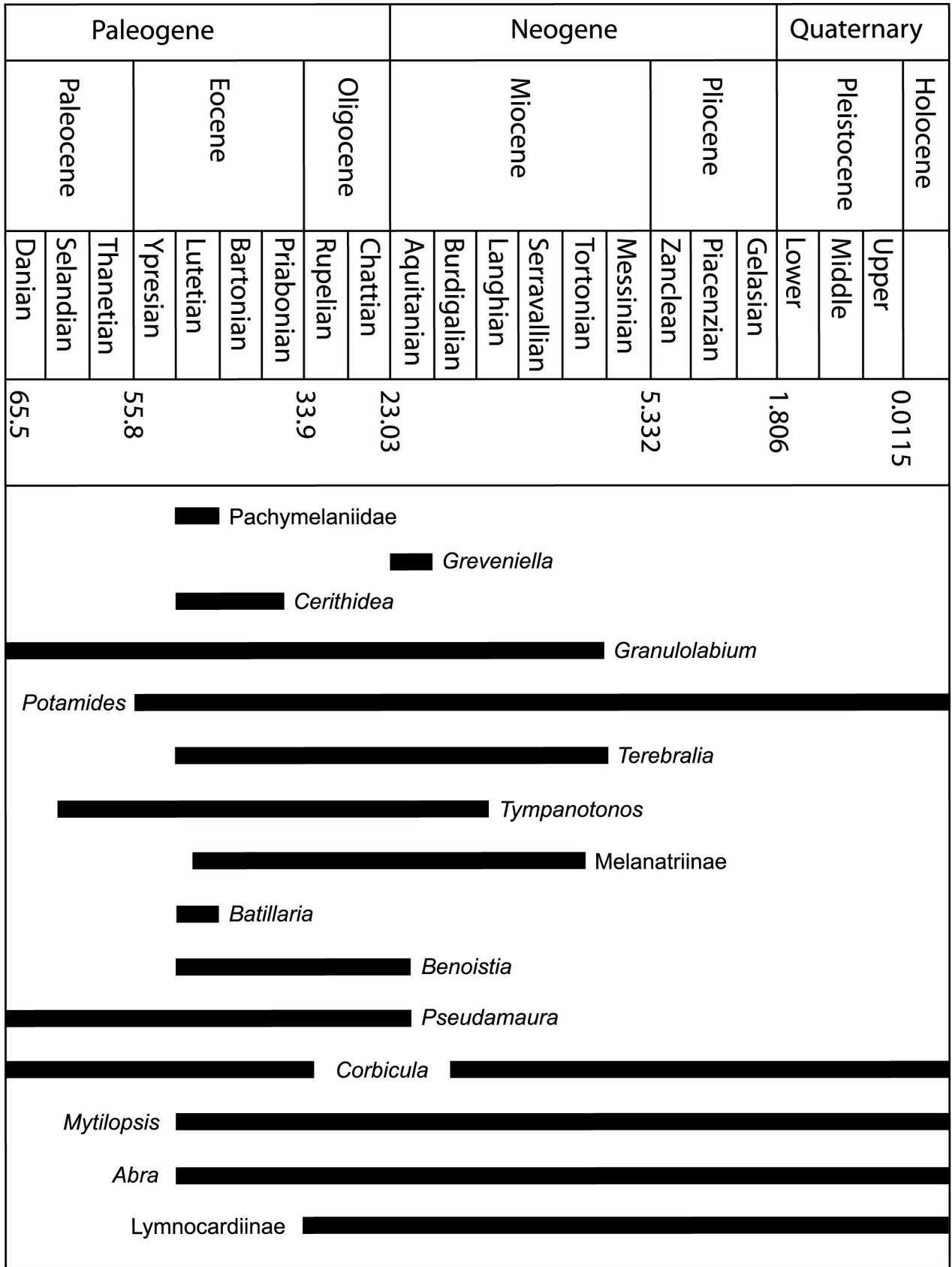
Mytilopsis

Abra

Lymnocardiinae

Figure 3: Stratigraphic distribution of characteristic brackish water molluscs in the European Cenozoic. Note the decrease of several thermophile elements in the course of the Late Eocene/Oligocene.

tance until the late Early Oligocene. In the course of the late Early Oligocene time interval *Potamides* entered the landward brackish habitats formerly dominated by *Tympanotonos* spp. *Potamides/Hydrobia*-assemblages characterised the latest Stampian sections of Ormoy (Paris Basin), a typical fauna lacking *Tympanotonos* and thiarids. In addition *Granulolabium*, cerithiids (*Benoistia*, *Bittium*), and neogastropod predators, mainly muricids (*Ocenebra*, *Ocinebrina*) and nassariids (*Keepingia*), occurred, predominantly colonizing the seaward coastal habitats. The late Stampian correlates with the early Chattian of the Mainz Basin and Lower Hesse. Corresponding deposits and the characteristic palaeocommunities have a very similar faunal composition on genus level (HUCKRIEDE & JANSSEN 1973; KOWALKE 2003).

A marked faunal "turn over" is evident from the European Oligocene. Particularly tropical elements, including archaeopulmonates, pachymelaniids, *Cerithidea* among the potamidids, and fasciolariids, associated with the mangroves migrated into the tropical bio-provinces in the course of the latest Eocene. In contrast several thermophile taxa managed to pass the Late Eocene/Early Oligocene climate cooling and had occurred in low diversity during the Early Oligocene: Thiarids (*Bayania*), potamidids (*Tympanotonos*), pseudamaurids (*Ampullinopsis*), and corbiculid bivalves occurred in brackish environments. Faunal elements tolerating lower (subtropical) temperatures, such as *Granulolabium* and *Potamides*, co-occurred associated with the less diverse stenotherm elements and successively entered their ecological niches. The faunal succession to *Granulolabium/Potamides*/Rissooidea-palaeocommunities is well evident in Stampian sections of the Paris Basin. The latest Stampian faunas lack exclusively tropical elements. Similarly contemporaneous earliest Chattian sections of the Mainz Basin and Lower Hesse show a corresponding faunal composition, dominated by *Granulolabium* and *Potamides*, and associated with neritids and neogastropods (muricids, *Keepingia*). Neritids assigned to *Vitta* and "*Clithon*" (= *Agapilia*) were already widespread in the European Late Oligocene (LOZOUET 2003). The faunal change was mainly triggered by decreasing temperatures, with obviously subordinated importance of synecological features of the dominating potamidids: In the course of the Chattian *Tympanotonos* re-migrated from the Indic into the Mediterranean, into the Parathethys and adjacent depositional basins, reflecting the again increasing temperatures. A single species established large population, but did not supersede the syntopic genera *Granulolabium*, *Potamides*, and *Terebralia*. Not only potamidid but also neogastropod migration pattern document the re-immigration from the Indo-Pacific realm, e.g., thaidids and melongenids reached the Mediterranean during the latest Chattian (HARZHAUSER & KOWALKE 2001).

Communities dominated by the potamidid *Tympanotonos margaritaceus* and the corbiculid *Polymesoda subarata sowerbii* (BASTEROT) characterised marginal marine environments of the Mediterranean Late Oligocene to Early Miocene. An example for a characteristic palaeocommunity of the Eastern Mediterranean has been described from the Mesohellenic Trough (North Greece) by HARZHAUSER & KOWALKE (2001). The accompanying fauna consists of neritines and more rarely of palaeorissoinids (GRÜNDEL & KOWALKE 2002), *Granulolabium* and predatory neogastropods, which marginally penetrated

these habitats. Within the seaward portion of the coastal ecosystem the influence of these primarily marine but to a certain degree euryhaline elements increased. *Tympanotonos-Polymesoda* communities gradually graded into associations of *Granulolabium* with rare *Tympanotonos*, which colonized intertidal mud-flat to shallow subtidal polyhaline portions, and in *Mytilus* communities, which mainly characterised the subtidal soft bottom facies. The landward mesohaline portions of the ecosystem were dominated by *Granulolabium*, subgenus *Tiaracerithium*, neritines of the genus *Agapilia*, which was widespread within Upper Oligocene to Lower Miocene of the Mediterranean and Parathethys.

Coastal euryhaline *Tympanotonos-Polymesoda* communities in their typical Mediterranean composition were recognised as far east as the Qom Basin/Iran (HARZHAUSER & KOWALKE 2001). Contemporaneous Indo-Pacific faunas had a more diverse composition. Apart from *Tympanotonos* particularly tropical euryhaline faunal elements such as *Cerithidea*, *Batillaria*, and *Pyrazus*, which are absent from the Mediterranean province, are forming part of the assemblage. While *Tympanotonos* became extinct in the Indo-Pacific in the course of the Miocene, *Cerithidea* was already established in its extant area of distribution. Batillariids migrated southwards in the direction of their modern Australian/South Pacific area of distribution. With the extinction of *Tympanotonos margaritaceus* and *Polymesoda subarata* in the Mediterranean Middle to Upper Burdigalian, the ecological niche of *Tympanotonos* in its landward estuarine and coastal swamp habitats was entered by *Terebralia*-communities, which tolerated hypersaline conditions, but also colonized portions that were considerably influenced by fresh waters. An example is present from the Latest Burdigalian of Dragasia (Mesohellenic Trough/North Greece) where a low-diversity fauna was dominated by *Terebralia bidentata* (DEFRANCE in GRATELOUP) (HARZHAUSER & KOWALKE 2001). Within the Central Parathethys *Tympanotonos cinctus* (BRUGUIÈRE), a late representative of the genus *Tympanotonos* existed and persisted until the Badenian (= Early Langhian) and which was absent from the Mediterranean province in that time interval (LOZOUET et al. 2001; HARZHAUSER et al. 2003).

While *Terebralia* dominated the euryhaline coastal assemblages of the Mediterranean, *Granulolabium* and *Potamides* reached a higher diversity in contemporaneous assemblages of the Parathethys. Especially during the Badenian and in the course of the Sarmatian a marked eco-zonation occurred. Diverse *Potamides-Granulolabium* communities characterised the structured coastal ecosystems and formed characteristic assemblages of the oliogohaline, meso-polyhaline and euhaline spectrum (HARZHAUSER & KOWALKE 2002).

6. The Neogene of the Mediterranean and Parathethys, and Relations to the Atlantic Province

The transition from the Late Oligocene to the Early Miocene is rarely documented from the Mediterranean. Marginal marine uppermost Oligocene to Aquitanian deposits have been investigated from the eastern Mediterranean Grevena Basin in

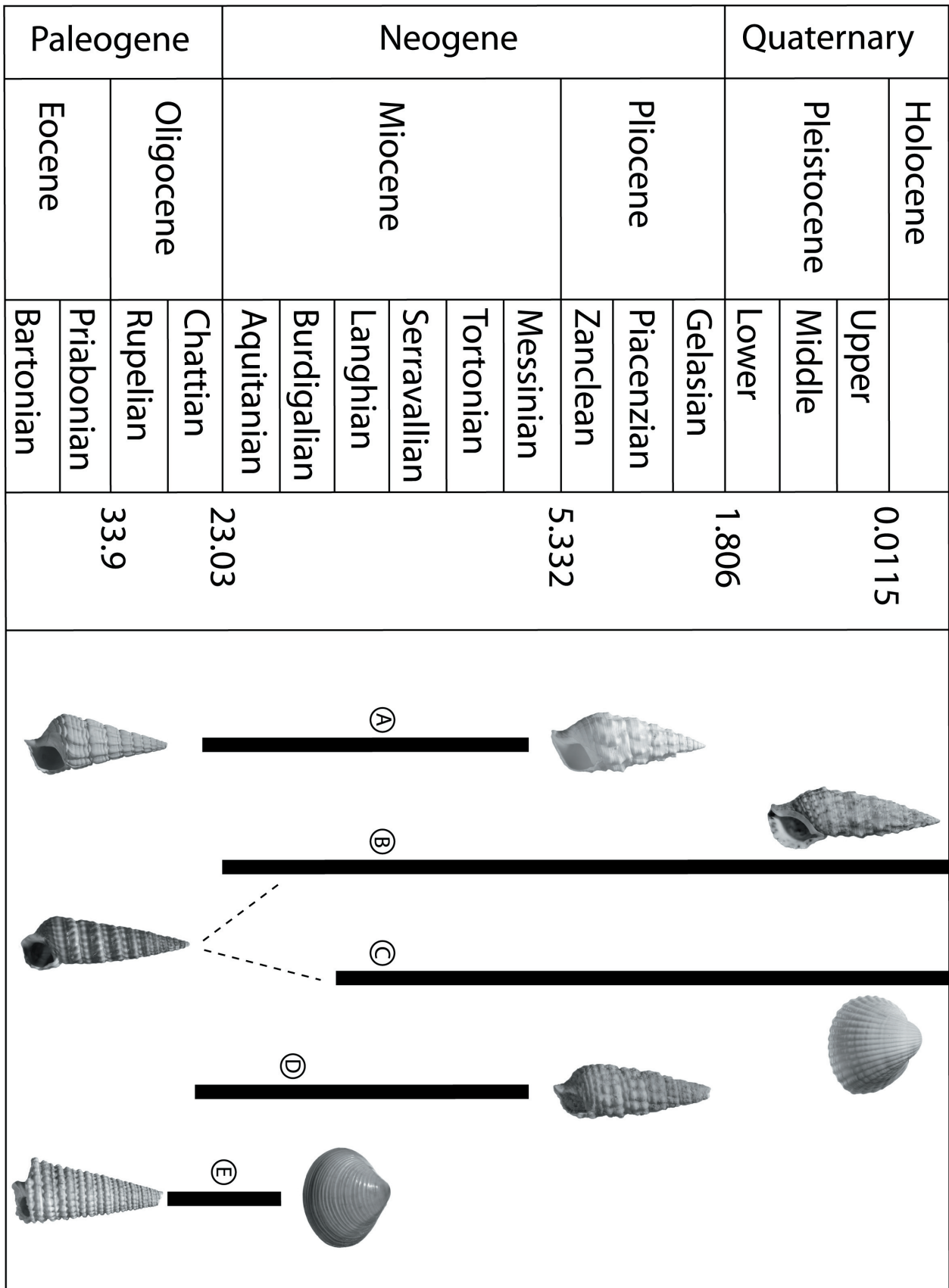| Paleogene				Neogene						Pliocene			Quaternary			
Eocene		Oligocene		Miocene						Pliocene			Pleistocene			Holocene
Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Lower	Middle	Upper	
		33.9	23.03						5.332			1.806			0.0115	

Figure 4: Stratigraphic distribution of Mediterranean marginal marine mollusc communities. A = *Terebralia-Cerithium;* B = *Potamides-Cerithium;* C = *Potamides-Cerastoderma;* D = *Granulolabium;* E = *Tympanotonos-Corbicula.*

North Greece (Harzhauser & Kowalke 2001). Euryhaline coastal assemblages were characterised by a successive faunal change during the Early Miocene (Fig. 4). *Tympanotonos* and *Granulolabium*, dominating elements during the Late Oligocene, persisted although *Tympanotonos* decreased in the course of the Burdigalian. *Terebralia*, a subordinate less diverse and less abundant element during the Late Oligocene, is characterised by a marked increase in abundance. Only two species, *T. bidentata* and *T. lignitarum*, are present and form large populations in the littoral assemblages of the eastern Mediterranean. During the Eggenburgian *Terebralia bidentata* obviously migrated northwards into the central Paratethys, but, in contrast to the development within the Mediterranean, it represented a rare element of the euryhaline assemblages. In the course of the Karpatian the situation changed and *Terebralia* established mass population in the coastal palaeocommunities. Apart from the dominant occurrence of the Oligocene relic *Granulolabium (Granulolabium) plicatum* in the eastern Mediterranean assemblages, the thermophile subgenus *Granulolabium (Tiaraceritium)* spread into the eastern Mediterranean during the Aquitanian and characterised the calm landward portions of coastal swamps until the Late Burdigalian. *Granulolabium (Tiaraceritium)* was thus ecologically well separated from *G. (Granulolabium)*. The Atlantic faunal elements *G. (Tiaracerithium) pseudotiarella* had migrated into the Mediterranean comparatively late during the Aquitanian, and co-occurred in the western Mediterranean (Aquitaine, N Italy), but did not invade the Paratethys. The lack of *G. (Thiaracerithium)* probably resulted from slightly lower water temperatures in the Paratethys during the Early Miocene, since, according to Lozouet (1986), the distribution of the stenotherm element correlates with that of colonial corals. In the eastern Mediterranean *Tympanotonos margaritaceus* as well as *Granulolabium plicatum* became extinct in the course of the Burdigalian of the Mediterranean, and in the course of the Eggenburgian of the Paratethys. *Granulolabium plicatum* was replaced by *G. bicinctum*. In contrast to the development in the Mediterranean, *Tympanotonos* was still present with one species, i.e. *T. cinctus*, during the Karpatian of the central Paratethys.

The Burdigalian faunal change is well evident from several eastern Mediterranean basins. The upper Burdigalian brackish water deposits of the Mut Basin (Turkey) are characterised by mass populations of *Terebralia bidentata* accompanied by the frequent carnivore neogastropod *Melongena lainei*. *Tympanotonos*, *Granulolabium (Tiaracerithium)*, and also the typical Early Miocene euryhaline cerithiid *Cerithium calculosum* are absent. A similar situation occurs in the latest Burdigalian of Dragasia/Mesohellenic Trough (Greece) and contemporaneous deposits of the Qom Basin (Iran) where coastal mud-flats were dominated by *Terebralia bidentata*. The neritid *Agapilia*, and the potamidids *Tympanotonos* and *Granulolabium (Tiaracerithium)*, ubiquitous elements of the Aquitanian sections, are absent (Harzhauser & Kowalke 2001). Contemporaneous deposits of the Gaj Formation (Pakistan) differ considerably (Vredenburg 1928): *Cerithidea* and *Tympanotonos* are present along with the batillariids *Batillaria* and *Pyrazus*. *Terebralia* apparently represents the only euryhaline faunal element which co-occurred in Mediterranean and Indo-Pacific deposits during the Late Burdigalian.

The Burdigalian/Late Karpatian faunal change was probably not triggered by decreasing temperatures. *Granulolabium (Tiaracerithium)* represented an exclusively thermophile element, whereas *Tympanotonos margariticeus*, *T. cinctus*, and *Agapilia picta* tolerated subtropical temperatures. The distribution of these species was never restrictively connected to the distribution of colonial corals. *Tympanotonos* disappeared from the European coasts when the Late Karpatian/Early Langhian warming period, and hence the mid-Miocene climatic optimum, was reached. The faunal shift could perhaps be explained by synecological reasons: *Terebralia* and *G. (Granulolabium)* became the dominant elements predominantly colonizing the mud-flats and the seaward portions of coastal swamps, whereas *G. (Tiaracerithium)* associated with *Tympanotonos* preferred the more restricted landward portions. Repeated ingressions are documented for the late Early Miocene of the central Paratethys and could have led to the decline of suitable habitats. The generally more euryhaline genera *Terebralia* and *Granulolabium* superseded their competitors and managed to establish large populations in short time. *Tympanotonos* co-occurred with *Terebralia* in Early to mid-Miocene deposits of Pakistan and Indonesia, but became extinct during the Late Miocene. Apparently the Indo-pacific extinction of *Tympanotonos* was not connected to climatic changes. *Terebralia* superseded the syntopic *Tympanotonos* due to the ability to settle a larger variety of habitats in the well structured tropical mangroves and also in the adjacent estuarine and lagoonal palaeoenvironments.

Synecological features may also have caused the marked changes in the brackish bivalve fauna: ubiquitous corbiculids, which had formed mass populations in the euryhaline coastal assemblages during the time interval from the Late Eocene to the Late Miocene, decreased in the course of the late Early Miocene. During this time interval cardiids were successively increasing in diversity. Cardiids appeared to be more euryhaline, regarding the colonization of the entire spectrum of habitats under more stagnant water conditions (Kowalke, in prep.).

With the extinction of *Tympanotonos* in Europe, the formerly associated but subordinate element *Terebralia* formed mass populations in coastal euryhaline palaeoenvironments. *Granulolabium* and *Potamides* reached higher diversities in estuarine environments and coastal lagoons with salinities close to that of normal sea water or with reduced salinities, respectively. *Terebralia* was characterised by further adaptations and preferred, at least partly/seasonally, hypersaline lagoonal environments. Characteristic oligotypic assemblages are evident from Upper Miocene deposits of SE Spain, particularly from the Late Tortonian/Messinian of Elche and Crevillente. The palaeocommunity was dominated by mass occurrences of the potamidid *Terebralia crevillentensis*. *Terebralia* comprises about 80% of the mollusc fauna of the palaeocommunity. The accompanying fauna consists of *Cerithium peyroti* (Dollfus) and rare *Granulolabium bicinctum* Brocchi. Juvenile individuals of *Cerastoderma* sp. and *Abra* sp. represent the accompanying bivalves. The micro-fauna consists of foraminifers of the *Elphidium* type. Isotope signals indicate enriched salinities ($\delta^{18}O = 1.17$, standard deviation = 0.29, n = 5) (Kowalke, in prep.).

Very fine clays alternating with gypsum layers indicate

calm, hypersaline palaeoenvironments. The lagoons were most probably only occasionally connected to the Mediterranean Sea. Analyses of oxygen and carbon isotopes indicate that Late Miocene *Terebralia* tolerated or preferred hypersaline conditions, whereas *Cerithium* (δ^{18}O = 0.61, standard deviation = 0.64, n = 4) rarely occurred and probably seasonally migrated, preferring salinities close to that of normal sea water. High standard deviations of the carbon isotope values (δ^{13}C = -0.21, standard deviation = 0.77) support migration activities in the life cycles of *Cerithium. Granulolabium* represents a rare element, which usually preferred normal marine to marine-brackish conditions. Exclusively juvenile individuals of *Cerastoderma* sp. and *Abra* sp. indicate suboptimal conditions for the bivalves that prevent the establishment of stable populations. *Cerastoderma* and *Abra* tolerated brackish-marine and also mesohaline waters, but avoided the hypersaline lagoons with strongly reduced currents and partly low oxygen contents. On the other hand *Terebralia* was enabled to a partly amphibious mode of live.

The presence of all ontogenetic stages of *Terebralia* indicates an autochthonous colonization of the lagoons. Early ontogenetic shells of the investigated molluscs indicate at least temporary connections of the lagoons with the open sea: All the molluscs occurring in this community type are characterised by indirect development including free planktotrophic larval stages. Owing to the mode of early ontogenetic development, the genera *Granulolabium, Terebralia*, and the Miocene representatives of the genus *Cerithium* were unable to settle athalasso-saline environments. Although extant *Terebralia* spp. represent generally euryhaline marginal marine elements of the tropics with far distribution in the Indo-Pacific, *Terebralia* has neither been described from extant nor fossil athalasso-saline environments.

Potamides-Cerastoderma communities occurred in continental and marginal marine habitats at least since the Middle Miocene. Assemblages of *Potamides theodiscus* ROLLE and *Cerastoderma* sp. characterised marginal marine-brackish habitats of the Badenian Central Paratethys (KOWALKE 2001b). The euryhaline community is not documented from athalasso-saline ecosystems. In contrast to oligotypic athalasso-saline *Potamides-Cerastoderma* communities, the accompanying fauna was considerably more diverse, consisting of typically euryhaline elements of the marginal marine ecosystem, such as *Terebralia bidentata* GRATELOUP, *Agapilia* sp., and *Littoraria scabra albertⅠ*(DUJARDIN). Diverse nassariids marginally penetrated the coastal habitats (HARZHAUSER & KOWALKE 2004).

With the decline of thermophile faunal elements, particularly in the temperate Atlantic but also in the Northwest Mediterranean, rissooids became the most important gastropods and characterised euryhaline coastal habitats – persisting mariginal marine lagoons and estuaries as well as temporary biotopes. In the latter case hydrobiids established mass populations in temporary biotopes. The Late Neogene of the northern Atlantic and of the West Mediterranean was characterised by three morphostatic hydrobiid radiations of the genera *Hydrobia, Peringia*, and *Ventrosia* (KOWALKE 1998a; WILKE et al. 2000). The hydrobiids usually occurred ecologically well separated, with, for instance, *Hydrobia* representing a brackish-marine/polyhaline taxon tolerating higher salinities, whereas *Ventrosia*

predominantly occurred in brackish waters with lower salinities (WILKE & DAVIS 2000). The primarily poly- to euhaline rissoids exhibited marked sympatric radiations in the shallow to deeper marine Mediterranean, and also in marine time intervals of the Paratethys (KOWALKE & HARZHAUSER 2004). On the other hand hydrobiids showed no evidence for long term sympatric occurrences. Closely related species appeared to be strictly allopatric, whereas the distribution pattern of distantly related clades overlapped geographically (WILKE & PFENNINGER 2002; WILKE et al. 2002).

A special endemic evolution is evident from the Ottnangian and Early Karpatian (= Middle to Late Burdigalian) of the western Paratethys. The disintegration of the former coherent aquatic ecosystem led to the formation of more or less isolated larger basins with partly endemic occurrences of several taxa, being strongly influenced by considerable amounts of fresh water. Among the bivalve fauna particularly cardiids (*Cerastoderma, Limnopagetia, Limnopappia*), which migrated into the ecosystems from the Swiss Marine Molasse, and dreissenids (*Mytilopsis*) of central Parathethyan origin were characterised by sympatric radiations with the establishment of several congeneric species. Similarly among the gastropod fauna hydrobiids exhibited endemic radiations with occurrences of diverse *Nematurella-* and *Ctyrokia*-palaeocommunities (SCHLICKUM 1971; SCHLICKUM & STRAUCH 1967, 1968; KOWALKE & REICHENBACHER 2005).

In the Central and Eastern Paratethys coherent brackish water bodies persisted for a more extended time interval. The formation of endemisms coincided with isolation events that resulted in aberrant salinities, when hydrobiid radiations established, forming up to 75% of the mollusc fauna. The genus *Mohrensternia*, for example, was characterised by a marked radiation in the Early Sarmatian (= late Middle Miocene) of the Central and Eastern Paratethys (KOWALKE & HARZHAUSER 2004).

In the course of the Late Miocene a particularly endemic evolution is evident from the Pannonian of Lake Pannon, the residual lake of the former Central Paratethys, where several salinity tolerant taxa exhibited sympatric radiations (HARZHAUSER et al. 2002). Salinities were low within the oligosaline to meio-mesosaline spectrum. Thus former dominating elements such as potamidids and cardiids were absent. Apart from neritids, endemic hydrobiids and a diverse basommatophoran fauna, primarily fresh water elements such as melanopsids diversified (HARZHAUSER et al. 2002).

7. The Ability to Colonize Athalasso-saline Ecosystems

The mollusc fauna of athalasso-saline habitats, i.e. of inland saline aquatic ecosystems without marine connections, is rarely documented in the fossil record. Colonization of such habitats require adaptations to extreme environmental conditions and often considerable seasonal changes of abiotic and biotic factors. Especially changes of the water table, salinity, and water chemistry, which usually considerably differs from that of normal sea water with regard to the ionic composition, re-
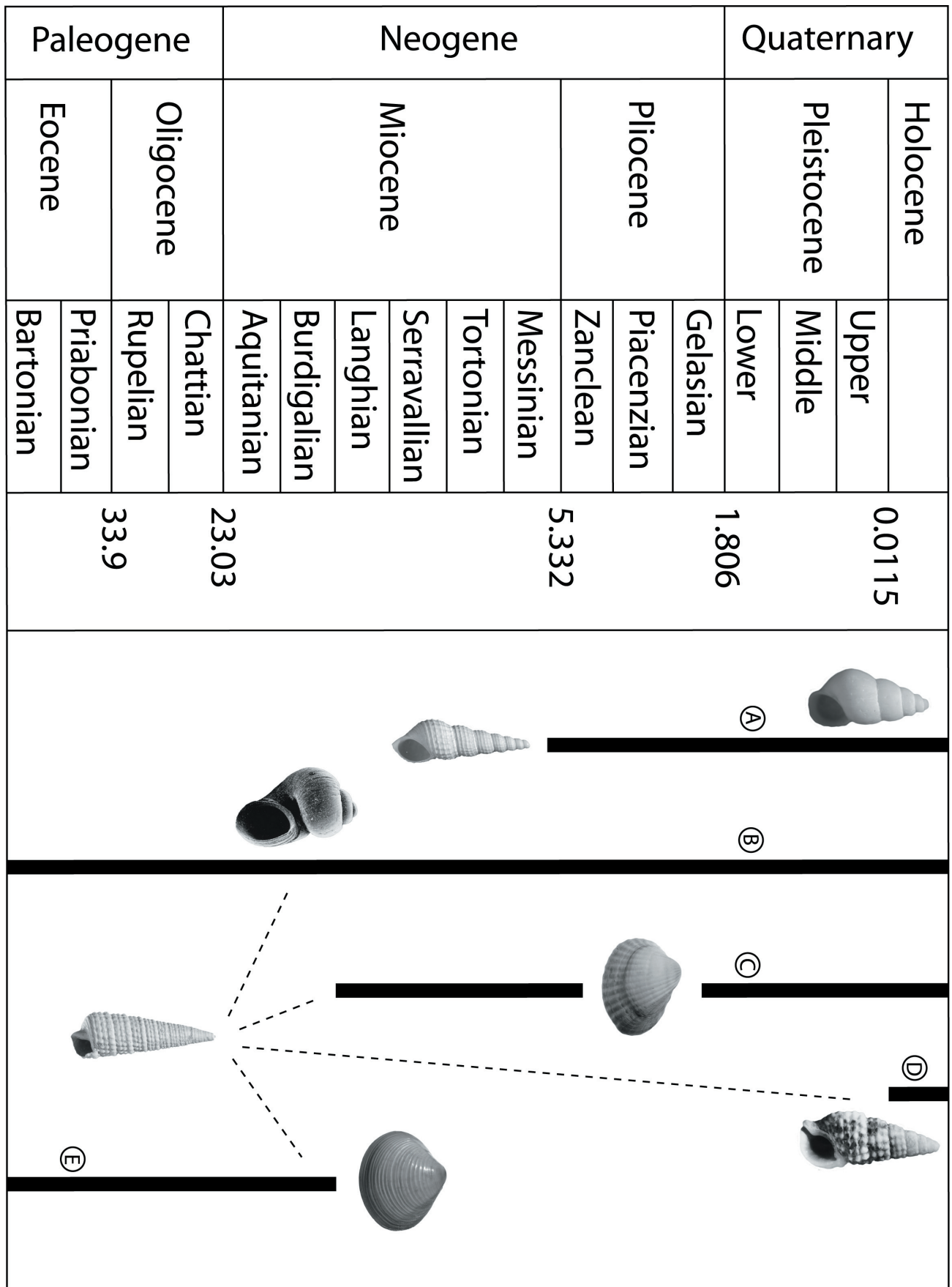
Paleogene				Neogene								Quaternary			
Eocene		Oligocene		Miocene						Pliocene		Pleistocene			Holocene
Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Lower	Middle	Upper

33.9   23.03   5.332   1.806   0.0115

Figure 5: Stratigraphic distribution of Mediterranean athalasso-saline mollusc communities. A = *Melanoides-Hydrobia;* B = *Potamides-Hydrobia;* C = *Potamides-Cerastoderma;* D = *Potamides-Cerithium;* E = *Potamides-Corbicula.*

quired adaptations with regard to osmo-regulation and a partly amphibious mode of life. Additionally early ontogenetic development plays an important role in the life of these gastropods, since the predominant indirect development with inclusion of a free planktotrophic larval stage hampers many generally euryhaline marginal marine taxa from colonizing intra-continental sites. The mechanisms of introduction of the molluscs to the athalasso-saline ecosystems limit the spectrum of taxa that are generally able to colonize athalasso-saline ecosystems. The mechanism of transport by sea birds, for example, enables only a few mollusc taxa and a comparatively low number of individuals to reach these habitats, particularly in times when anthropochory had no influence on the distribution pattern of the molluscs, or was of subordinate importance. Nevertheless several athalasso-saline palaeocommunity types of the Mediterranean and North African Cenozoic can be defined, being characteristic for stratigraphic time intervals and for certain ecological niches (Fig. 5).

The athalasso-saline *Potamides*-Corbiculidae palaeocommunity type is exclusively known from the European Paleogene. Typical associations are evident from the Late Eocene of France and from the Early Oligocene of the Iberian Peninsula. The Late Eocene species *Potamides lapidum* (LAMARCK) occurred associated with "*Corbicula*". The Oligocene type species of the genus *Potamides*, *P. lamarkii* (BRONGNIART) (frequently described as *P. rhodanicus,* which actually represents a synonym) occurred associated with the corbiculid *Polymesoda convexa* (BRONGNIART). *Polymesoda convexa* is characterised by a wide distribution in the European Eocene and particularly during Oligocene times, however almost all occurrences refer to marginal marine brackish-lagoonal and estuarine palaeoenvironments. Athalasso-saline occurrences are rarely documented. Examples are present from the Lower Ludian, i.e. Upper Eocene Calcaire de Fons in South France. In addition a rich microfauna consisting of various saline Foraminifera has been described (PLAZIAT & GAUDANT 1984). *Potamides-Polymesoda* communities have also been reported from Early Oligocene athalasso-saline ecosystems of Calaf, Río Gaià, Pontils and Santa Coloma de Queralt within the Ebro Basin in Northeast Spain (VIDAL & DEPERET 1906; BATALLER 1929; ANADÓN 1989).

The corbiculid *Polymesoda* usually represented an ubiquitous element that is part of the *Tympanotonos-Polymesoda* palaeocommunity in coastal brackish water habitats. This palaeocommunity type dominated the Mediterranean euryhaline ecosystems with connections to the open sea during the entire Oligocene and Early Miocene until the Late Burdigalian. *Polymesoda* managed to colonize intra-continental sites from the adjacent marginal marine, euryhaline habitats such as estuaries and lagoons. This corbiculid genus represents the only faunal element of the (Proto-)Mediterranean coastal euryhaline palaeocommunities that entered intra-continental ecosystems. The accompanying potamidids *Tympanotonos* and, in lower numbers, the primarily marin-brackish *Granulolabium*, which occurred in the mud-flat habitats and characterised the outer estuarine sections, were absent from continental habitats without marine connections. The absence of the marginal marine gastropods may have been a result of the mode of early ontogenetic development, since all the known

species of *Tympanotonos* as well as *Granulolabium* spp. are characterised by an indirect mode of early ontogenetic development that includes a free planktotrophic larval stage. Thus representatives of these genera required a fair connection of the adult habitats with the open sea for reproduction. On the other hand veliger larvae of the bivalves are able to sufficiently develop in lacustrine environments. Thus *Polymesoda convexa*, although characterised by a planktotrophic larval development (HARZHAUSER & KOWALKE 2001), could establish stable populations in athalasso-saline habitats after it had been introduced into the continental ecosystems. The accompanying potamidid genus *Potamides* represents a faunal element that originated from the East Atlantic province and was introduced to the Mediterranean in the course of the Late Oligocene. *Potamides* was already adapted to colonization of athalasso-saline habitats since the Late Eocene (Fig. 6), most probably supported by the prevailing mode of direct development with hatching of crawling young. Direct early ontogenetic development is, for example, documented for the type-species *P. lamarkii* (BRONGNIART) from the European Oligocene (KOWALKE 2003) as well as for the extant species *P. conicus* (BLAINVILLE) from the southern Mediterranean (KOWALKE 2001a). Thus reproduction within athalasso-saline habitats was generally possible and *Potamides* could occupy the ecological niches in the corresponding continental ecosystems, which formerly were probably dominated by stenotherm pachymelaniids and pachychilids (see discussion in KOWALKE 2001b, 2004). However, the fossil evidence for athalasso-saline colonizations of the latter families remains negative. Nevertheless, representatives of the genera *Gantmelania* (Pachymelaniidae) and *Gantmelanatria* (Pachychilidae) occurred in the most landward calm portions of coastal ecosystems and dominated the oligohaline portions of coastal swamps bordering the Eocene Tethys Ocean (KOWALKE 2001b).

In the course of the Early Miocene *Polymesoda* migrated towards the Indo-Pacific and the vacant ecological niche within the athalasso-saline ecosystems was occupied by the modern cardiid bivalve *Cerastoderma*. *Potamides-Cerastoderma* communities were common in the Middle Miocene of the Ebro Basin in northern Spain, particularly in the plane of Zaragoza (Muniesa, Belchite, Fuendetodos) (ANADÓN 1989 and references therein). Due to the meagre preservation, faunal elements are hardly determinable on species level, and thus comparisons to species that frequently occur in contemporaneous deposits of the East Mediterranean are difficult execute.

A second continental palaeocommunity type, the *Potamides-Hydrobia* communities, is known from the Ludian, i.e. from the Late Eocene on. Typical athalasso-saline palaeocommunities consisting of *Potamides* typically associated with the hydrobiid *Nystia* have been described from Mans and Mormoiron (France) (REY 1965; PLAZIAT & GAUDANT 1984). A similar palaeocommunity characterised upper Middle to lower Upper Miocene athalasso-saline deposits of the Duero Basin in Northwest Spain (KOWALKE, in prep.) – for detailed descriptions and a model for the reconstruction of the ecosystem see SÁNCHEZ-BENAVIDES et al. (1988) and SÁNCHEZ-BENAVIDES et al. (1989). The oligotypic fauna consists of the hydrobiids *H.* cf. *deydieri* DEPÉRET & SAYN and *H. calderoni* ROYO GOMEZ, which occur in association with the potamidid *Potamides*

gaudryi LARRAZET. The hydrobiids dominate the palaeocommunity; they represent the most common faunal elements of the composition and form large populations. Within the investigated layers both hydrobiid species comprise some 60% of the fauna of this palaeocommunity type, with *Hydrobia* cf. *deydieri* occurring slightly more common than *H. calderoni*, whereas *Potamides gaudryi* forms only some 25% of the total number of individuals. Primarily freshwater but salinity-tolerant elements, such as *Lymnaea* and *Theodoxus*, represent the accompanying mollusc fauna. These accompanying faunal elements typically occurred in larger numbers in connected fluviatile/deltaic portions and obviously migrated into the saline lake. The micro-fauna consisted of saline Foraminifera such as *Quinqueloculina*, *Nonion*, and *Ammonia*, and ostracods such as *Cyprideis* and *Cyprinotus* (GÓNZALES DELGADO et al. 1986; ANADÓN 1989). The composition of the accompanying fauna and stable isotope data indicate meso- to oligosaline conditions (KOWALKE, in prep). The euryhaline gastropods, which form part of this palaeocommunity-type, established permanent populations in the athalasso-saline ecosystem, which persisted for several years. The comparison of the size and number of whorls of *Potamides gaudryi* individuals with that of the extant species *P. conicus* from the Mediterranean Sea, which lives several years, indicates that the life spans of the fossils most probably exceeded annual cycles (KOWALKE 2001b). Hydrobiids in contrast are characterised by shorter life spans, and thus could also form temporal populations, for example in ephemeral habitats such as flood plains.

This type of ecosystem could generally also be settled by *Potamides-Cerastoderma* palaeocommunities. The absence of saline bivalves in this case most probably resulted from the preference of higher salinities of the genus *Cerastoderma* at least for reproduction, similarly like in case of the extant species *C. glaucum* (KOWALKE, in prep.). Apart from isotope data, shell morphology and sculptural pattern of the typical molluscs indicate moderate salinities. The potamidid *Potamides gaudryi*, for example, displays a characteristic sculptural pattern: Teleoconch whorls are characterised by the formation of coarse nodes, which may extend to short spines sculpturing the teleoconch whorls. The extant species *P. conicus* from normal marine to hypersaline Mediterranean ecosystems is characterised by different sculptural developments depending on the salinities (PLAZIAT 1993; KOWALKE 2001b): Coarsely sculptured individuals derive from normal marine waters, whereas weakly sculptured to smooth morphotypes develop in the context of meta- to hypersaline waters. In comparison to extant individuals of *P. conicus* from normal marine waters in coastal lagoons at Thessaloniki and of Delos/Greece, sculptured by regular nodes, *P. gaudryi* from athalasso-saline deposits of the Duero-Basin shows a stronger development of the nodes to short spines sculpturing the teleoconch whorls. The syntopic hydrobiids are characterised by openly coiled shells – a characteristic feature that is also known to occur in oligosaline hydrobiids of the Pannonian Lake Pannon (HARZHAUSER et al. 2002), but is unknown from meta- to hypersaline palaeoenvironments.

Another athalasso-saline community type occurred in Quaternary saline lakes of North Africa. An example is present from oligosaline lake deposits North-east In Ecker,

West of the Tassili der Adjer Mountains in South Algeria. The community is composed of the thiarid *Melanoides tuberculata* (MÜLLER) and the hydrobiid *Hydrobia* cf. *peraudieri* BOURGUIGNAT. *Melanoides tuberculata* is forming up to 80% of the malaco-fauna of the community, whereas *H.* cf. *peraudieri* is comparatively rare, comprising about 10% of the total number of individuals, contrasting the faunal composition of marginal marine communities where hydrobiids are among the dominating faunal elements. The accompanying fauna consists of oligosaline ostracods, such as *Candona* and *Limnocythere*. These forms co-occur with rare ostracods of the *Darwinula* type, which usually inhabit fresh waters. Athalassic elements, such as *Bulinus truncatus* AUDOIN, *Biomphalaria* cf. *pfeifferi* KRAUSS, and *Corbicula fluminalis* (MÜLLER) are exclusively present by rare juveniles and not fully grown specimens. The presence of fresh water species, which did not yet reach their size of complete development, indicates suboptimal conditions or ephemeral conditions for the fresh water inhabitants. Similar compositions with characteristic "mixed" assemblages have been reported from athalasso-saline deposits exposed from closed depressions of the Great Western Erg in Algeria (GASSE at al. 1987). Oxygene isotope contents ($\delta^{18}O$ = -0.76, standard deviation = 0.44, n = 4) indicate moderately saline conditions (KOWALKE, in prep.). BEADLE (1943) gave a salinity range of 0.5-8‰ for *Hydrobia aponensis* (= *peraudieri*) from oligo- to metasaline waters, and a range of 1-5‰ for *Melanoides tuberculata* in Algeria. Extant *M. tuberculata* usually prefers fresh to oligosaline waters, but is known also to tolerate a great spectrum of salinities. The considerable eurysalinity of this species, which may occur in saline waters with up to 28‰ TDS, has been documented from saline waters of Senegal (ROSSO 1983).

Melanoides tuberculata is the only representative of the family Thiaridae that is known to colonize athlasso-saline habitats. Thiarids usually occur in brackish and fresh water ecosystems of the tropics and to a lesser degree of the warmer subtropics (KOWALKE 1998a). In contrast to the marginal marine thiarids of the tropics, which are characterised by indirect development including a free swimming marine planktonic veliger stage, *M. tuberculata* represents a direct developer. The mode of direct early ontogenetic development enables this species to colonize continental saline sites. Early ontogenetic development takes place within the confines of a brood pouch where the embryos undergo a histotrophic development, and juveniles rest until they have gained a size of >1 mm. *Melanoides tuberculata* is furthermore characterised by parthenogenesis, and hence a single individual introduced to an intra-continental aquatic ecosystem may give rise to the establishment of a population. This mode of early ontogenetic development implies the ability to build stable populations in saline ecosystems that lack marine connections.

Eocene populations of the genus *Melanoides* from West Hungary (KOWALKE 2001a) as well as Oliocene to Miocene faunas of lacustrine habitats of the Iberian Peninsula (MEIN et al. 1978) and from France (PLAZIAT 1984) were confined to pure fresh water ecosystems. The accompanying fauna consisted of stenotopic fresh water inhabitants. Saline marginal marine and athalasso-saline habitats were avoided during these time intervals. The corresponding ecological niches were occupied

by characteristic palaeocommunities composed of *Potamides*-Corbiculidae (Oligocene), *Potamides-Hydrobia* (Middle Miocene), and *Potamides-Cerastoderma* associations (Middle-Upper Miocene). During Pliocene-Early Pleistocene times *Melanoides* was characterised by a considerably more northern geographic distribution described from Spain (ROBLES 1989; ESU 1980) and from Italy (ESU & GIROTTI 1974; ESU 1980).

Melanoides obviously readapted to brackish/saline conditions and developed a tolerance with regard to saline waters during the Pleistocene. Probably due to the competition of diversifying potamidids, the genus *Melanoides*, or its precursor, entered fresh water habitats during the Early Eocene. Extant Southeast Asian thiarids are characterised by planktotrophic larval stages and colonize estuaries after metamorphosis and migrate into fresh water higher portions of the rivers towards their adult habitat (KOWALKE 1998a). Oligocene and Middle Miocene continental saline habitats with considerable changes of salinities and reduced salinities/oligohaline conditions were colonized by *Potamides*-palaeocommunities. *Potamides* represented a strong competitor of the morphologically similar *Melanoides*. During the Late Pliocene-Early Pleistocene the modern *Potamides* relation developed. The extant species *P. conicus* tolerates a wide range of salinities (see below), but reproduces and forms stable population in a salinity range of 20-40‰ (GASSE et al. 1987). In comparison to its Neogene precursors *Potamides conicus* exhibits a lesser degree of salinity tolerance regarding the salinity range in which reproduction is possible. Modern *Melanoides* obviously filled the vacant ecological niches in oligosaline intra-continental ecosystems – a process of re-adaptation that explains the comparatively young history of *Melanoides*-communities in athalasso-saline ecosystems of the European Cenozoic.

8. Extant Distribution Pattern and the Significance of Anthropochory

Extant brackish water communities of the Mediterranean occur in two well separated biogeographical groups that are spread (climatically induced) to the south and to the north of the 40th degree of latitude. Modern athalasso-saline communities of the South Mediterranean region are restricted to the North African coastal zone. Oligotypic communities are composed of relics of the more diverse Neogene relation (see above). In extant North African lagoonal and anchialin as well as in continental athalasso-saline habitats with connections to fluviatile systems or water seepage two different types of *Cerastoderma* communities are recognised: The cardiid *Cerastoderma glaucum* (POIRET) along with the potamidid *Potamides conicus* represent the dominant elements of the communities. Larger perennial North African lakes are frequently characterised by a successive increase in salinity. The Birket Qarun (Fayoum) represents an example of a typical intra-continental ecosystem in North Egypt. In the course of the 20th century, this originally fresh water lake experienced increasing salinity, with present day salinity levels close to those of normal sea water. Consequently the ecosystem is characterised by a successive settlement of a primarily marginal marine fauna.

Cerastoderma glaucum, for example, has been introduced to the lake between 1908 and 1927 (SMITH 1908; GARDNER 1932). When polysaline conditions prevailed the typically accompanying species *Potamides conicus* was introduced to the lake – according to ROSE (1972) between 1927 and 1968. With the establishment of salinity conditions close to those of normal sea water of the Mediterranean Sea during the last 20-30 years shallow marine, but generally euryhaline, elements such as *Nassarius*, *Abra,* and mytilids, had also been introduced. Although *Potamides conicus* tolerates a salinity range of between 5-150‰ TDS, and *Cerastoderma glaucum* occures in waters of 3-90‰ TDS salinity (ROSSO & GAILLARD 1982; GERDES et al. 1985; PLAZIAT 1989, 1993), associations of both species typically characterise saline ecosystems with a salinity level close to that of normal sea water. Examples of corresponding Pleistocene to extant assemblages are well known from intra-continental aquatic ecosystems of the Great Western Erg/Algeria (GASSE et al. 1987), from oases of Libya and Egypt, and from sabkhas of Tunisia and of the Red Sea area (GAVISH 1979; PURSER 1985; PLAZIAT 1989, 1993).

Monotypic occurrences of *Cerastoderma glaucum*, in contrast, occur in shallow continental lakes with strongly restricted fresh water influence. *Cerastoderma* is obviously able to reproduce in restricted meta- to hypersaline environments, possibly within a slightly higher salinity range than *Potamides*, which requires seasonal fresh water influx or ground water seepage. Apart from the extant occurrences in North Africa corresponding palaeocommunities are known from the Early Pleistocene of the Guadix-Baza Basin in South Spain, in which also saline micro-fossils such as Foraminifera (*Ammonia*, *Elphidium*, *Quinqueloculina*) and Ostracoda (*Cyprideis*, *Cyrinotus*) are forming part of the oligotypic assemblages (ANADÓN et al. 1987). Corresponding extant communities are unknown from the Iberian Peninsula.

Another athalasso-saline community type is present in an extant ecosystem in the Libyan Desert: *Potamides conicus* colonizes salt swamps of the Sinali-Oasis. In addition, the oligotypic community is composed of rare *Cerithium rupestre* RISSO. *Cerithium rupestre* may have colonized the ecosystem when the salinity successively increased and eusaline conditions close to that of normal sea water of the Mediterranean Sea prevailed. Neogene examples of the athalasso-saline *Potamides-Cerithium* community type younger than Holocene age are unknown. *Potamides-Cerithium* communities occur well separated from *Potamides-Cerastoderma* communities, since the preferred hard substrates exclude colonizations by infaunal bivalves.

South Mediterranean marine-brackish and coastal habitats with slightly enriched salinities are frequently colonized by *Potamides conicus-Cerastoderma glaucum* associations, which are similar in composition to the athalasso-saline communities. A different community type occurs in hypersaline, very shallow coastal pools at the rocky shore of Cap Greco/South-east Cypris (KOWALKE 2001a). Monotypic occurrences of *Potamides conicus* are present in very shallow pools. Water seepage is strongly restricted due to prevailing hard grounds. During the summer hypersaline conditions are established when the coastal pools are only sporadically affected by high tides. The accompanying fauna is only present during the winter season,
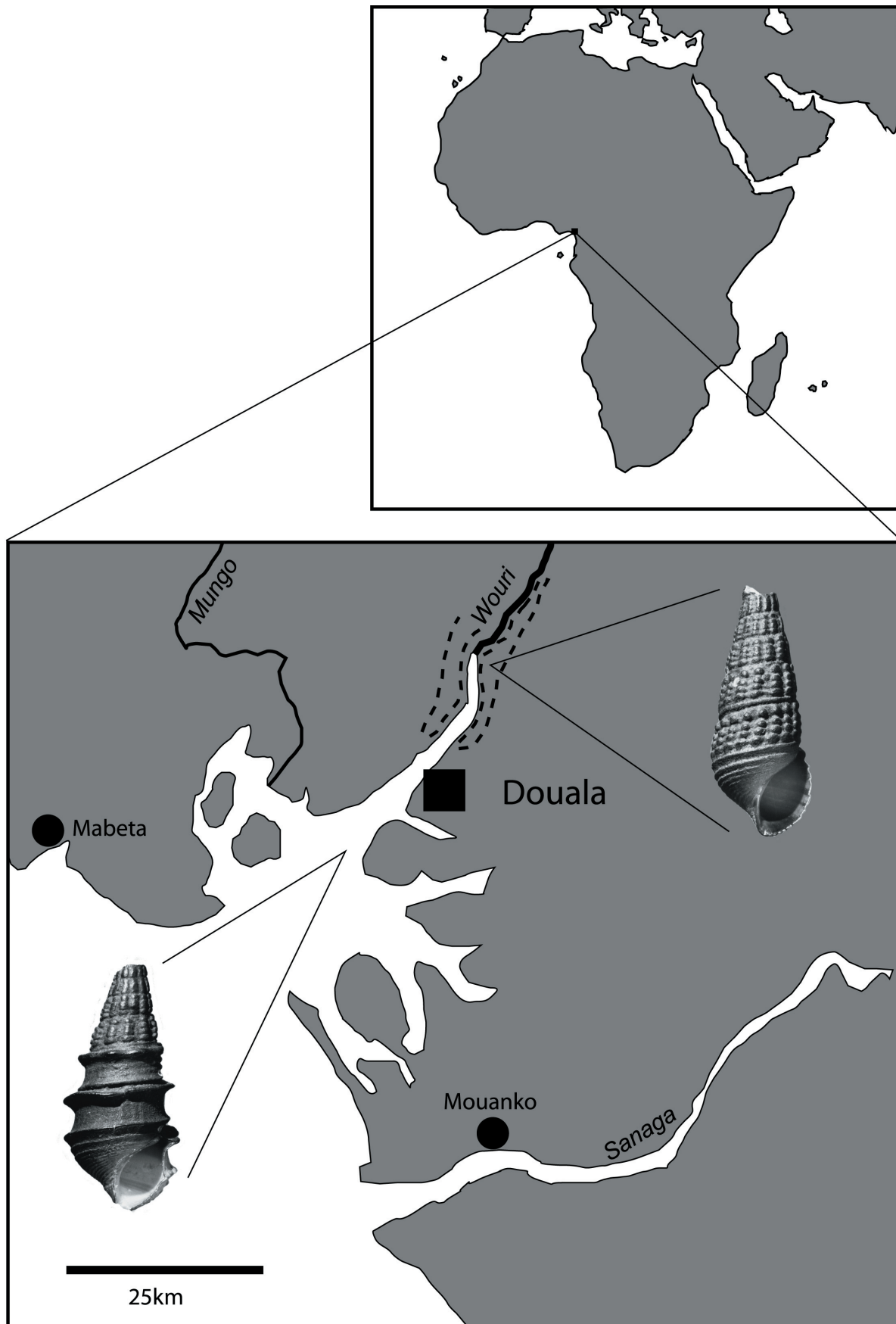
Figure 7: The pachymelaniid *Pachymelania fusca* (tuberculate morph) colonizes stagnant coastal waters adjacent to the Wouri estuary in Cameroon, which are only affected by extreme high tides. The keeled morph lives within the intertidal outer estuarine portions under considerably higher salinities.

Figure 8: The *Pachymelania* habitat is typically bordered by *Pandanus* (Pandanaceae).

when fresh water influx increases. The cerithiid *Cerithium vulgatum* BRUGUIÈRE, which usually inhabits shallow lagoonal environments with connections to the sea, migrates into the restricted *Potamides* habitats. *Cerithium vulgatum* appears to be salinity-tolerant regarding slightly enriched salinities and polyhaline conditions, but avoids the hypersaline environment. This may explain the temporal character of the coastal *Potamides-Cerithium* community. The seasonal character of this community is also evident from the population density of *Potamides* and *Cerithium*, since *C. vulgatum* individuals are usually forming about 20% of the malacofauna. *Cerithium vulgatum* is characterised by a planktotrophic veliger stage, and thus unable to reproduce in restricted continental environments. *Cerithium rupestre*, in contrast, is capable of forming permanent populations in athalasso-saline environments based on the direct mode of early ontogenetic development, i.e. crawling young are hatching while an additional larval stage is absent (KOWALKE 1998a).

Extant muddy soft bottom habitats of the southern Mediterranean with connections to the open sea are characterised by euryhaline *Potamides-Hydrobia* communities. Corresponding NW Mediterranean ecosystems lack the thermophilous element *Potamides*. The ecological niche was filled by the cerithiid *Bittium*, which exhibits euryhalinity to a certain degree. *Bittium* spp. are, for example, forming part of the "Etang-fauna" from South France where they are accompanied by a diverse hydrobiid fauna (own observations).

The modern temperate lagoons and swamps of the Atlantic coast are frequently characterised by monospecific occurrences of hydrobiids, which are ecologically well separated from each other (WILKE et al. 2000). The outer estuarine portions of large rivers, for example, are settled by *Peringia*, whereas the interior stagnant swampy environments are preferred by the morphologically similar *Ventrosia* relation. Similar to the situation in the cerithioidean communities, the distribution patterns of the taxa are connected to the mode of early ontogenetic development. *Peringia* spp. undergo indirect development and need a fair connection of the adult habitat with the open sea, whereas *Ventrosia* spp. predominantly represent direct developers that are capable of colonizing also internal habitats.

A special case of colonization of stagnant continental waters is present from extant swamps and brackish ponds bordering the Wouri River in SW Cameroon (West Africa) some 2-5 km inland from the river mouth of the estuary at Douala (Fig. 7). This portion of the river is characterised by very low salinities amounting 0.1-0.02‰ (see PLAZIAT 1977). Smaller creeks are usually bordered by mangrove vegetation predominantly consisting of the palm *Nypa*, accompanied by landward occurrences of the saline fern *Acrostichum*. The larger river mouth of the Wouri is bordered by *Rhizophora/Avicennia* mangroves, alternating with large mud-flats. The gastropod fauna of the brackish portions, affected by each tide, consists of associations of the large potamidid *Tympanotonos fuscatus* (LINNÉ), accompanied by the pachymelaniids *Pachymelania byronensis* (WOOD), *P. aurita* (MÜLLER), and keeled morphs of *P. fusca* (GMELIN) (BANDEL & KOWALKE 1999). Smaller creeks are predominantly colonized by juvenile specimens of *Tympanotonos* and *Pachymelania fusca*, associated with archaeopulmonates. In addition, a rich neritine fauna is present.

The investigated swamps and ponds, which are characterised by stagnant waters and occasional saline influx during extreme high tides, are colonized by different faunas and floras. *Tympanotonos* and *Pachymelania aurita* predominantly occur within a salinity range of 0.2-15‰ (PLAZIAT 1977) and settle
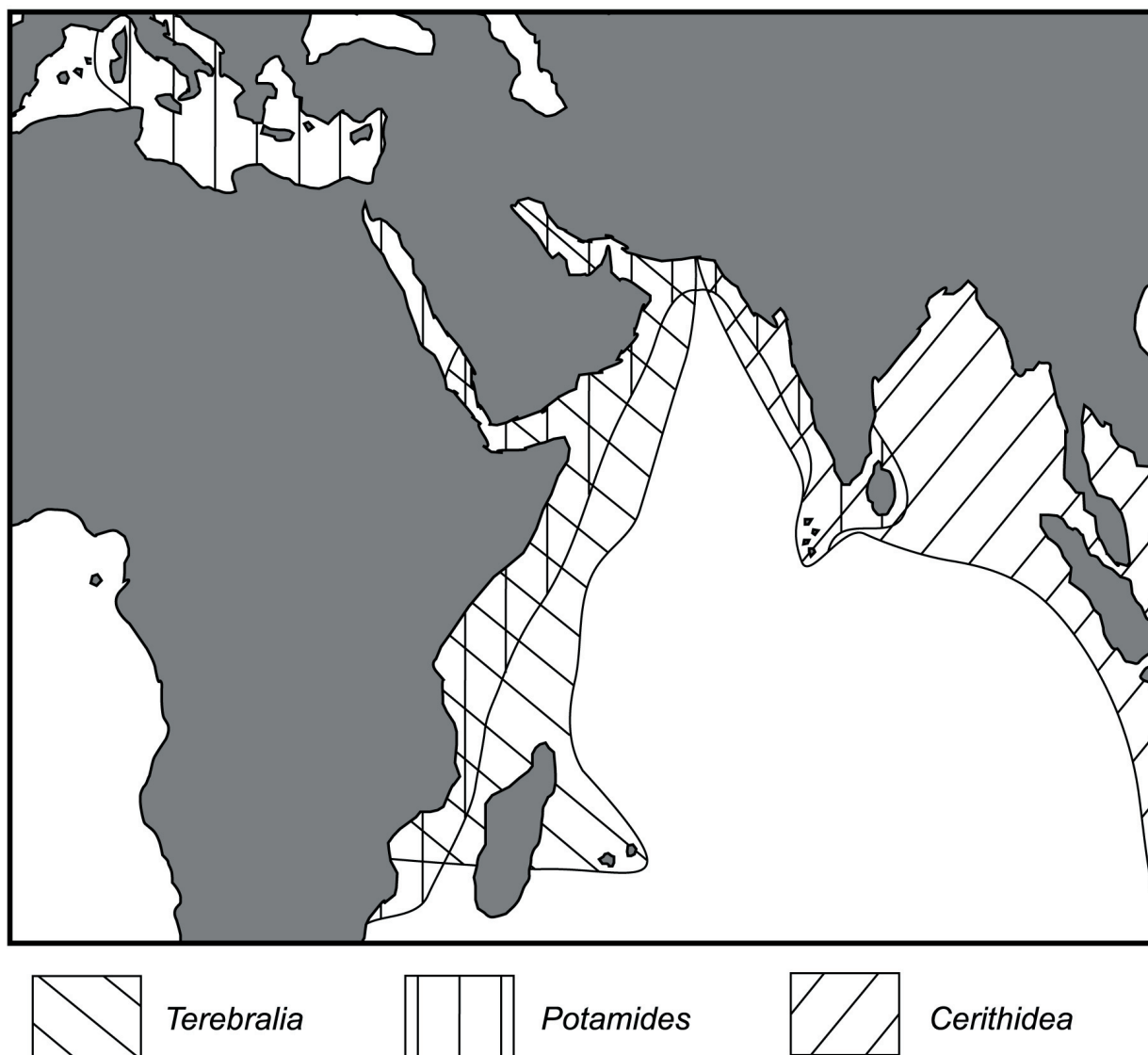
Figure 9: *Potamides conicus* has been introduced to the Indic Ocean in the context of anthropochory. The area of distribution partly overlaps with those of *Terebralia* and *Cerithidea*.

in the fluviatile portions affected by each tide. *Tympanotonos* is absent in the fluviatile portions with salinities ranging between 0.1 and 0.02‰. These parts of the river are characterised by associations of *Pachymelania byronensis* and *P. fusca*. The adjacent swamps and ponds, which are not affected by each tide, are colonized by monotypic occurrences of tuberculate morphs of *Pachymelania fusca*. A marked floral change is evident: *Rhizophora* mangroves are absent. Instead, the ecological niche is occupied by dense aggregations of the genus *Pandanus* (Pandanaceae) (Fig. 8). The internal portions of the swamps with predominantly fresh water influx have floating and submerse aquatic vegetation. The margin is bordered by semi-aquatic palms.

Pachymelania-communities are absent from Mediterranean marginal marine and athalasso-saline fossil and extant ecosystems. Pachymelaniidae were forming part of the euryhaline ecosystems of the marginal Tethys Ocean, characterising the

landward portions of coastal swamps. During the Lutetian (Middle Eocene) pachymelaniids were thus already adapted to habitats predominantly under fresh water influx (KOWALKE 2001b). With the formation of the Proto-Mediterranean the stenotherm tropical elements successively migrated southwards in the direction of their extant area of distribution, comprising the West African coast from Senegal in the North to Angola in the South.

The colonized extant habitats, a series of ponds and swamps adjacent to the fluviatile system, differ considerably from the main river estuary affected by each tide. Although the salinity of the river is low, brackish/intertidal pachymelaniids along with neritines and neritiliines establish large populations. Within the adjacent swamps and ponds, however, *Pachymelania fusca* represents the only malaco-faunal element. Very low salinities excluded colonization by of *Tympanotonos fuscatus*, *Pachymelania aurita,* and *P. byronensis*, but also prevented

fresh water gastropods, which usually characterise pure fresh water environments, to invade this part of the ecosystem. Fresh water gastropods such as *Potadoma*, *Cleopatra*, and *Lanistes*, which are documented from the West Cameroonian Mungo and Sanaga Rivers and from their tributaries (KOWALKE 2004), appeared to be absent from the swamps and ponds, which are occasionally affected by brackish water influx. The absence of the freshwater elements is not triggered by water energy because *Potadoma*, for example, forms large populations in shallow fresh water ponds adjacent to the Sanaga River at Edéa (KOWALKE 2004). Salinity seems to play an important role that prohibits the immigration of fresh water faunal elements into the slightly saline habitats. On the other hand *Pachymelania fusca* is absent from pure fresh water habitats. The most important factor preventing the permanent colonization of inland fresh water habitats appears to be the mode of early ontogenetic development, since *P. fusca* is characterised by a free plank-totrophic veliger stage. This mode of early ontogenetic development implies a fair connection of the adult habitat with the open sea. Additionally syn-ecological factors seem affect the distribution of *P. fusca*: Since pure fresh water upper sections of the rivers are settled by competitors (see above), individuals of *Pachymelania fusca* do not invade the fresh water portions during their life cycles – a feature that, in contrast, occurs in the related family Thiaridae (KOWALKE 1998a). *Pachymelania fusca* does apparently not form permanent populations in the brackish ponds and only a few specimens per square metre occur. However specimens measuring some 5 cm high indicate that they obviously can thrive there for several years. Specimens that were kept alive in tanks survived under pure fresh water conditions for more than one year (own observations).

Extant distribution pattern of brackish and inland saline molluscs are strongly influenced by man. Marginal marine faunal elements frequently show some ecological tolerance with regard to fluctuations of the salinity and water chemistry. The restricted number of individuals that are, for example, distributed by sea birds however hampers most of the coastal species from colonizing continental saline habitats, and from forming stable populations. When athalasso-saline lakes in North Africa reach salinities close to that of the Mediterranean Sea, human activities, especially in the context of fish cultures, support the introduction of species. The fauna of the Birket Quarun, for example, reached a higher diversity when fish cultures were initiated during the last 50 years. Even stenohaline elements such as balanids occurred in the most recent time. Anthropochory also plays an important role in the distribution of brackish-marine taxa. Extant *Potamides conicus* was formerly distributed in the South Mediterranean. With completion of the Suez Canal this species became the dominant faunal element of the brackish and hypersaline environments of the entire Red Sea, and was spread into the Indian Ocean with a distribution from Mozambique in the Southwest to Ceylon in the Southeast where its area of distribution partly overlaps with that of Indic Ocean potamidids, including *Terebralia* and *Cerithidea* (Fig. 9).

9. Conclusions

The earliest confined brackish water faunas of the Late Jurassic were already characterised by the larger systematic groups of molluscs (on superfamily and partly on family level) that also form part of the Cenozoic assemblages, including the extant brackish communities. Especially Corbiculoidea, Neritioidea, Ellobioidea, and dominant Littorinoidea and Cerithioidea among the Caenogastropoda were forming large populations in coastal ecosystems that were strongly influenced by fresh water. Preceding Triassic or even Late Palaeozoic faunas are difficult to characterise, since data regarding the characteristic protoconch-morphology are missing and frequent convergences with fully marine faunas obstruct an exact systematic assignment.

The increasing diversity of brackish water molluscs since the Late Jurassic/Early Cretaceous is connected to the diversification of flowering plants, particularly in the course of the late Early and Late Cretaceous. Along with the formation of mangrove vegetation, several new micro-habitats were established. Archaeopulmonates and cerithioidean families were already confined to the mangroves in that time interval. In the course of the Early Paleogene the diversification maximum with the formation of the modern mangrove taxa coincided with the Early Eocene climatic optimum. Particular brackish euryhaline families such as the cerithioidean family Potamididae exhibited marked radiations. On the other hand primarily marine taxa, which tolerated brackish water influence to a certain degree, considerably decreased. Cassiopidae and Pseudamauridae, for example, were still present, but characterised the more seaward portions of the eco-systems predominantly under polyhaline to normal marine conditions. Only representatives of the primarily marine Cerithiidae and Ostreidae persisted as subordinated elements, settling specialized micro-habitats, predominantly the roots of mangrove plants. The diversifying Paleogene Neogastropoda represent an exception, since several groups of the predators of marine origin entered the mangroves in order to tap new prey among the mass populations of the molluscan fauna of the mangroves.

In the course of the Late Eocene/Early Oligocene, coinciding with climate cooling, the former uniform tropical brackish coastal swamp and mangrove fauna of the Tethys disintegrated and thermophile elements migrated towards their extant areas of distribution. Similarly to the formation of the modern mangrove provinces, tropical molluscan bioprovinces of the associated, partly co-evolved taxa established: The modern Indo-pacific Province appeared well separated from the West-African and Neotropis-Province. Faunal exchanges of the generally euryhaline taxa between these tropical bioprovinces were hampered by climatical reasons, by upwelling and distance barriers, e.g., the South Atlantic, which apparently could not be crossed by the short time veliger larvae of the brackish molluscs. More temperate bioprovinces appeared in the North Atlantic Region, with particular diversification of hydrobiid and cerithiid gastropods, and in South Australia/New Zealand where relics of the Palaeogene Tethys/Atlantic faunas persisted. Euryhaline elements such as *Granulolabium*, *Zemelanopsis*, and battillariids, exhibited a certain tolerance with regard to the colder climate conditions.

Special relic evolutions are documented from the (Proto-) Mediterranean and Paratethys where several genera of the former Paleogene Tethyan fauna persisted independently from the mangroves, or re-migrated from the Indo-pacific Province and colonized coastal swamps of the palaeoecological succession. Late Oligocene to Early Miocene palaeoenvironments were dominated by *Tympanotonos-Polymesoda* palaeocommunities. This predominant community type was superseded by *Terebralia-Cerithium* communities, which preferred (partly/ seasonally) hypersaline coastal habitats. Furthermore the Atlantic faunal elements *Granulolabium* and *Potamides* migrated into the Paratethys and occupied the ecological niches of the former *Tympanotonos* dominated habitats. *Granulolabium* represented an outer estuarine and mud-flat dweller, which preferred polyhaline and euhaline salinities close to that of normal sea water. *Potamides,* associated with cardiids, which superseded the corbiculids, predominantly colonized the inner coastal swamp and estuarine portions under considerable fresh water influence.

While the Mediterranean was characterised by a uniform brackish water fauna during the warmer time intervals of the Miocene, the Paratethyan faunas exhibited endemic radiations, which were encouraged by the successive disintegration of the former coherent water body towards more or less connected or isolated basins. Particular endemic radiations are recognised in late Early Miocene basins of the Ottnangian Western Par.thys (particularly Lymnocardiinae, and hydrobiids such as *Nematurella* and *Ctyrokia*), and in the Middle and Late Miocene of the Central and Eastern Paratethys (Lymnocardiinae and the hydrobiid *Mohrensternia*). A special development is evident from the Pannonian (Late Miocene) of Lake Pannon, a large marine-like water body under very low salinity conditions of the oligosaline to meio-mesosaline spectrum, where brackish water (neritids) and salinity tolerant fresh water elements such as melanopsids and Basommatophora co-existed.

Athalasso-saline mollusc faunas are known from the Late Eocene on. The oldest known corresponding eco-systems are reported from West and South France. The restricted intracontinental communities partly contrast the marginal-marine brackish communities regarding faunal composition. The entire spectrum of gastropods with planktotrophic larval development, for example, was excluded from the settlement of inland saline ecosystems, since this mode of early ontogenetic development implies a fair connection of the adult habitats with the open sea. Marked changes in the compositions of athalasso-saline palaeocommunities are evident from the late Early Miocene, when intra-continental corbiculid dominated faunas were superseded by cardiid faunas, and in the course of the Early Pleistocene, when *Melanoides*-dominated faunas colonized athalasso-saline ecosystems of the oligosaline spectrum and replaced the Neogene *Potamides* faunas.

Modern distribution pattern of marginal marine and athalasso-saline faunas were mainly triggered by two factors: climate development and anthropochory. The climate cooling led to well separated spatial distribution pattern especially in case of thermophile euryhaline gastropods of the Mediterranean. Extant *Potamides*-faunas are for example restricted to an area of distribution south of the 40th degree of latitude. On the other hand humane influence caused a far distribution throughout the Red Sea into the Indic Ocean. The influence of anthropochory also played an important role regarding the introduction of primarily marginal marine elements into athalasso-saline ecosystems, since the former prevailing mode of distribution and introduction by sea birds enabled only a few taxa to establish permanent populations in the continental ecosystems. Striking examples have been described from larger North African lakes with successive increase of the biodiversity, since the progressive increase of the salinities led to salinity conditions close to that of normal sea water. During this time interval the aquatic ecosystems were economically used mainly in the context of fish cultures, and several marine taxa were introduced to the continental saline habitats.

Acknowledgements

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