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HISTORY OF MOLLUSC COMMUNITY TYPES AND FAUNAL DYNAMICS IN CONTINENTAL SALINE ECOSYSTEMS OF THE SOUTH MEDITERRANEAN QUATERNARY

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Abstract. Quaternary continental aquatic ecosystems characterised by poly/eusaline waters, and without a connection to the Mediterranean Sea, are dominated by the potamidid gastropod *Potamides conicus* (Blainville) and the cardiid bivalve *Cerastoderma glaucum* (Poiret). Metasaline environments are characterised by monotypic occurrences of *C. glaucum*. The primarily freshwater-dwelling thiarid gastropod *Melanoides tuberculata* (Müller), in contrast, colonised oligo/mesosaline habitats, similarly to its precursors from the Upper Messinian Lago-Mare ecosystems. In case of the establishment of saline conditions in former freshwater environments, characteristic taphocoenoses document the dynamic development in the context of progressive evaporation: the *Melanoides* palaeocommunity from a Holocene ecosystem at In Ecker (S Algeria) is accompanied by freshwater inhabitants, which did not reach their adult size of complete development due to the temporal character of their habitats. Oligo/mesosaline conditions are reflected in oxygen isotope signatures of the *Melanoides* shells. High variations in carbon isotope values indicate changes in the composition of the diet during ontogeny, and may support the interpretation that the ecosystem developed progressively. In comparison to Neogene and fossil Quaternary assemblages, the composition of extant eusaline communities is considerably more diversified: larger North African lakes in Libya and Egypt are characterised by neozoan elements originating from the Mediterranean fauna. The dynamic development of these faunas was predominantly supported by anthropochory in the context of fish cultures. The mode of early ontogenetic development played an important role with regard to the introduction of gastropods to continental environments, since the entire spectrum of euryhaline coastal gastropods with planktotrophic larval development is absent from these ecosystems. The preadaptational loss of planktotrophy enabled *Potamides* to establish persisting populations. Apart from its brooding mode, *Melanoides* is characterised by parthenogenesis, and thus a single individual, introduced to a continental ecosystem, can establish a population.

Riassunto. Gli ecosistemi acquatici del Quaternario continentale, caratterizzati da acque poli/stenohaline e senza connessioni dirette con il Mar Mediterraneo, sono dominati dal gasteropode *Potamides conicus* (Blainville) e dal bivalve *Cerastoderma glaucum* (Poiret). Ambenti metahalini sono caratterizzati dalla presenza monotipia di *C. glaucum*. Il gasteropode *Melanoides tuberculata* (Müller), originariamente di acque dolci, invece colonizzava ambienti oligo/mesohalini, in analogia con i precursori dell'ecosistema del Lago-Mare del Messiniano superiore. Qualora si venissero a stabilire condizioni saline in ambienti precedentemente di acque dolci, le tafocenosi caratteristiche documentano lo sviluppo dinamico in un contesto di progressiva evaporazione. La paleocomunità a *Melanoides* dell'ecosistema olocenico di In Ecker (S Algeria) è accompagnata da forme di acque dolce, che non raggiungono la dimensioni adulte con sviluppo completo, a causa del carattere temporaneo del loro habitat. Le condizioni oligo/mesohaline sono registrate dalla segnatura isotopica dell' ossigeno nelle conchiglie di *Melanoides*. Forti variazioni isotopiche del carbonio indicano cambi di dieta durante l'ontogenesi e possono corroborare l'interpretazione che l'ecosistema si sia sviluppato progressivamente. In confronto con le associazioni neogeniche e del Quaternario, le attuali comunità stenohaline sono sensibilmente più diversificate.

I grandi laghi nord-africani di Libia ed Egitto sono caratterizzati da nuovi elementi derivati dalla fauna del Mediterraneo. Lo sviluppo dinamico di queste faune è stato particolarmente sostenuto per antropocoria nel contesto di comunità di pescatori. Le modalità di sviluppo dei primi stadi ontogenetici giocò un ruolo importante nell'introduzione dei gasteropodi negli ambienti continentali, in quanto l'intero spettro dei gasteropodi costieri eurihalini con sviluppo larvale planctotrofico è assente in questi ecosistemi. La perdita pre-adattativa della planctotrofia consentì a *Potamides* di sviluppare popolazioni persistenti. *Melanoides* si può riprodurre anche per partenogenesi e quindi un singolo individuo inserito in un ecosistema continentale può dare luogo ad una popolazione.

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Introduction

Depending on the climate conditions and geological/hydrological features, athalasso-saline (= intracontinental saline) aquatic ecosystems are either isolated, groundwater fed or connected to endorheic fluviatile systems. Considerable variations in salinity, a water chemistry that may differ considerably from that of sea water, and the often ephemeral character prohibit many euryhaline marine organisms from colonising these extreme biotopes (Bayly 1967; Por 1972; Kiener 1978; Williams 1981; Hammer 1986; Ben Quezdou 1989).

Among the macro-fauna in these extreme environments gastropods and bivalves often represent the dominating elements. Apart from adaptations with regard to the osmo-regulation, the colonisation of athalasso-saline habitats necessitates an appropriate mode of early ontogenetic development since planktotrophic larval development prevents e.g. euryhaline coastal gastropods from forming stable and persisting populations. Veliger larvae disintegrate because the velar apparatus is weak and the larvae are usually distributed by water currents (Kowalke 1998). Although ubiquitous Neogene potamidids such as *Granulolabium* and *Terebralia* and neritines tolerated considerable changes in salinity, colonisation of protected coastal habitats were initiated from estuarine/fluviatile environments or lagoons that were at least temporarily connected to the marine realm (Kowalke 2001b).

In the European Middle and Late Eocene typical athalasso-saline palaeoenvironments and their mollusc faunas have been reconstructed, while this type of ecosystem appears to be unknown from the Palaeocene to the Early Eocene time interval (Guelorget & Perthuisot 1983). Athalasso-saline assemblages are well-known from the Upper Eocene of S France and W France, dominated by potamidids and saline Foraminifera (see Rey 1965; Plaziat & Gaudant 1984). The oldest known playa-lake and sabkha deposits of the Iberian Peninsula are described from the Middle to Late Eocene of the Ebro Basin (Anadón 1978; Riba et al. 1983). According to Anadón, these deposits contain a rich micro-fauna composed of saline foraminifera. Geochemical isotope analyses on the Palaeogene sulphates indicate that reworked Triassic evaporites are the source for the salinity (Utrilla et al. 1992). In spite of general suitability for colonisation by saline molluscs, no malaco-fauna has been reported from the Eocene athalasso-saline deposits of the Iberian Peninsula. Athalasso-saline mollusc faunas of the Iberian Peninsula have been reported from the Lower Oligocene and Middle Miocene of the Ebro Basin (Bataller 1929; Royo-Gómez 1925, 1926), the Middle and Upper Miocene of the Duero Basin (Larrazet 1897; Anadón 1989) and the Pleistocene of the Guadix-Baza Basin (Anadón et al. 1986, 1987; Robles 1989). Moreover, continental saline mollusc assemblages are well-known from Neogene deposits of the Italian Peninsula (Esu & Girotti 1974; Esu 1980).

The aim of this paper is to define mollusc community types that characterise athalasso-saline habitats of the South Mediterranean Quaternary. The origin and the Cenozoic history of the community types are discussed in order to document faunal changes through time. A comparison to marginal marine faunas of the Mediterranean and Red Sea area is presented. The ecology of the continental communities is discussed with reference to the dynamic development of their habitats. In the framework of this study the variations within the basic community types and their possible reasons are assessed in view of the heterogeneity of extant North African continental aquatic ecosystems.

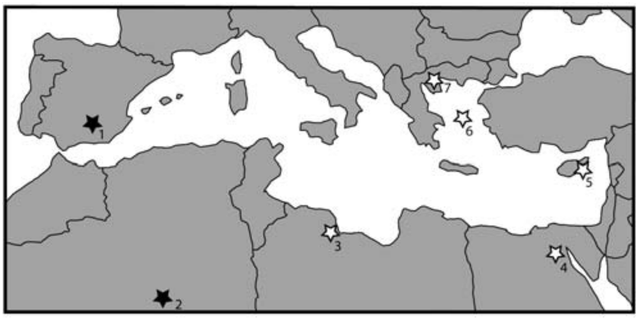

Fig. 1 - Asterisks indicate locations of the studied fossil (black asterisks) and extant (white asterisks) materials. 1 = Orce/Spain (GPS: N 37°43’07”; W 02°28’45”), 2 = In Ecker/Algeria (GPS: N 27°26’28”; E 6°25’71”), 3 = Bucrat/Libya (GPS: N 31°24’03”; E 15°44’21”), 4 = Birket Quarun, Fayoum/Egypt (GPS: N 29°18’40”; E 30°50’37”), 5 = Cape Greco/SE Cyprus (GPS: N 34°50’27”; E 34°05’04”), 6 = Delos/Greece (GPS: N 37°23’33”; E 25°16’01”), 7 = Thessaloniki/Greece (GPS: N 40°37’30”; E 22°58’21”).

Material and methods

Several hundreds mollusc shells of all ontogenetic stages from Quaternary fossil to extant athalasso-saline deposits of Algeria, Libya, Egypt and South Spain have been studied (Fig. 1). Comparisons to contemporaneous estuarine, lagoonal, coastal swamp and anchialin populations from the Mediterranean and the Red Sea area were carried out (material from the collection of the author, the Zoologische Staatssammlung Munich, ZSM, and the Bayerische Staatsammlung für Paläontologie und Geologie, BSPG). Laterally connected or stratigraphically succeeding fresh-water faunas of the particular locations are briefly characterised.

Macrofossils were cleaned from sediment remains and prepared for macroscopic photography. For analysis of juvenile shells, samples of marl and silt sediments containing molluscs were processed with 10% H_2O_2 and fractionated by sieves in fractions of < 0.3 mm, < 0.6 mm, < 1 mm and > 1 mm. Micromorph shells have been selected from the samples. Dimensions and sculpture of the early ontogenetic shells have been analysed by using a Scanning Electron Microscope (SEM, Leitz AMR 1200) in order to confirm the systematic affinities, describe the mode of early ontogenetic development, and document the sculptural development during the ontogeny. For the general classifications of early ontogenetic shells and modes of early ontogenetic development see Kowalke (1998).

For indications of relative palaeosalinities and the significance of vital effects, oxygen and carbon isotope contents of biogenic carbonate of shells of selected specimens were analysed. Geochemical analyses served as an additional tool to test results inferred from sedimentological and palaeontological interpretations and the actualistic approach. The analyses were executed in the isotope laboratory of the GeoBioCenter at the Department of Geo- and Environmental Sciences of the Ludwig-Maximilians-University Munich (LMU). Shells were cleaned from sediment in an ultrasonic bath and matrix material removed. Prior to analysis, the material was screened by SEM to confirm that the original biogenic shell structure of the aragonite shells is preserved. Shells were crushed and processed by a linked technique: THERMO/Finnigan Gasbench II sample preparation unit and THERMO/Finnigan MAT Delta *plus* isotope ratio mass spectrometer. In the course of the analyses samples reacted with Ortho-phosphorus-acid at a constant temperature of 72°C. The rising CO_2, in helium as a medium gas, was transferred into an isotope mass-spectrometer. Lab standards were calibrated against the IAEA standards, and the isotope relations were plotted relatively against PDB in the conventional delta-notation ($\delta^{18}O/\delta^{13}C$) in ppt.

Figured specimens are deposited in the collection of the Zoologische Staatssammlung, Munich (ZSM), and in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (BSPG), Germany.

Mollusc community types

The composition of the basic types of athalasso-saline mollusc communities is primarily triggered by the salinity. In addition, water depth and ephemeral or persisting character of the continental aquatic ecosystems play significant roles in the colonisation by macro-animals. Rapid changes in the water chemistry/salinity of modern athalasso-saline ecosystems have led to mixed taphocoenoses that are composed of elements from both freshwater and saline communities. However, each of the characteristic communities defined in the following sections is confined to a suite of distinct environmental conditions, and hence clear assignment to the corresponding developmental stages of the fossil and extant aquatic ecosystems is possible.

Melanoides communities

Composition. The thiarid *Melanoides tuberculata* (Müller) and the hydrobiid *Hydrobia aponensis peraudieri* (Bourguignat) form a community that typically characterises oligo- to mesosaline Quaternary continental lakes in North Africa (Brown 1980, van Damme 1984; Gasse et al. 1987). An example has been studied from a Holocene fossil saline lake NE In Ecker, west of the Tassili der Adjer Mountains in South Algeria. *Melanoides tuberculata* (Fig. 2A-B) is an abundant element of the assemblage and represented by all ontogenetic stages; it represents 80 % of the malaco-fauna. *Hydrobia aponensis peraudieri* (Fig. 2C) appears to be a comparatively rare element, with abundances less than 20 % of the assemblage. Rare freshwater athalassic elements such as *Bulinus truncatus* Audoin (Fig. 2D) and *Corbicula fluminalis* (Müller) are exclusively represented by juveniles and not fully grown specimens. Common oligosaline ostracods such as *Candona* and *Limnocythere* co-occur with rare ostracods of the *Darwinula* type, which usually inhabits freshwaters ecosystems. The presence of freshwater species, which do not reach their adult size of complete development, reflects suboptimal conditions for the fresh-water inhabitants. Similar "mixed" assemblages have been reported from other closed depressions of the Great Western Erg/Algeria (Gasse et al. 1987).

Ecology. The thiarid *M. tuberculata* represents a semi-infaunal detritus feeder, usually active by night, whereas the hydrobiid *H. aponensis peraudieri* prefers micro-algae on the surface of the sediment. While hydrobiids may represent opportunistic elements in temporary aquatic environments (Kowalke 1998), the presence of mature individuals of *M. tuberculata* is indicative of an aquatic ecosystem with permanent water cover that persisted for at least a few years (van Damme 1984).

Melanoides tuberculata represents the only thiarid that colonises athlasso-saline habitats. In contrast to the marginal marine thiarids of the tropics, *M. tuberculata* is a direct developer. Early ontogenetic development takes place within a brood pouch where the embryos undergo a histotrophic development, and juveniles comprising several whorls remain within the brood pouch until they reach a size of >1mm (Kowalke 1998). This mode of early ontogenetic development without a free-swimming veliger stage implies that the species possesses the ability to build stable populations in athalasso-saline habitats that lack marine connections. Moreover, *M. tuberculata* is characterised by parthenogenesis, and thus a single individual introduced to an intra-continental aquatic ecosystem can establish a population.

Oxygen isotope contents of *Melanoides tuberculata* from the continental fauna at In Ecker have been determined (Tab. 1). The oxygen isotope signatures for *M. tuberculata* indicate progressive increase of the evaporation and the establishment of low saline conditions, based on a comparison with the extant precipitation values of In Ecker ($\delta^{18}O$ = -2.41 ‰). The data are in accordance with results of Gasse et al. (1987), who described Early Holocene assemblages containing *Melanoides* and *Hydrobia* from oligosaline intervals of aquatic ecosystems of the Great Western Erg. Oxygen isotope values are considerably less negative than the data for pure freshwater diatom assemblages, which are similar to $\delta^{18}O$ contents of extant fresh waters of the aquifer of the Great Western Erg ($\delta^{18}O$ ~ 5 ‰); for details see Conrad & Fontes (1970) and Gonfiantini et al.

(1974). The oxygen isotope data of *Melanoides* from In Ecker are slightly more positive than the data obtained from conspecific Early Holocene material of the Ethiopian Rift Valley (Leng et al. 1999). However, the values for pure fresh waters are less negative than the extant data for the Great Western Erg (Leng et al. 1999). The presence of a dynamic development of the In Ecker ecosystem is supported by the corresponding carbon isotope values of the *M. tuberculata* shells. The high variation could well reflect changes in the diet during the ontogeny. The "mixed assemblages" containing *Melanoides*, and juvenile freshwater elements result from a considerably more rapid evaporation and increase of salinity.

Beadle (1943) indicated a salinity range of 1-5 ‰ TDS for *M. tuberculata* and 0.5-8 ‰ TDS for *Hydrobia aponensis peraudieri* in Algeria. The extant *M. tuberculata* usually prefers freshwater to oligosaline conditions. For example, populations from the Fayoum oasis in Egypt (material from the ZSM), occur in pure fresh water pools adjacent to, but well separated from, the saline lake with a salinity level close to that of sea water. Within the saline lake the ecological niche of *Melanoides* is occupied by *Potamides* (see below). In these fresh water pools *M. tuberculata* (Fig. 2E) is typically accompanied by *Corbicula fluminalis* (Fig. 2F), which is represented by all ontogenetic stages. However, *M. tuberculata* is known to tolerate a great spectrum of salinity levels, occurring in saline waters with up to 28 ‰ TDS. Examples for this remarkable salinity tolerance have been reported from saline waters in Senegal (Rosso 1983). According to Glaubrecht (1996, and literature cited therein), extant *M. tuberculata* from warm oligosaline athalassic saline waters in Asia Minor and North Africa is characterised by larger size and coarser sculpture, whereas very large individuals rarely occur in colder pure fresh water environments, and individuals from brackish coastal habitats exhibit diminutive growth. Coastal brackish populations are unknown from northern Africa (van Damme 1984). My analyses corroborate the presence of coarser sculpture in saline environments: particularly juvenile individuals (Fig. 2B) display a strongly reticulate sculpture with the formation of nodes in the points of intersection of the spiral and axial elements, whereas juvenile individuals from pure freshwaters are characterised by weakly developed sculptures (Kowalke 1998).

Hydrobia aponensis peraudieri represents an athalasso-saline element that primarily inhabits freshwaters. In contrast to the Neogene hydrobiids of marine origin, which managed to colonise low salinity-waters, *H. aponensis peraudieri* in the low salinity spectrum lacks the characteristic feature of an open coiling of the teleoconch whorls. A corresponding ontogenetic development was observed in oligo- to mesosaline hydrobiids of the Middle Miocene Duero Basin/Spain (own observations; Kowalke, in prep.) and the Pannonian of the Lake Pannon/Central Paratethys (Harzhauser et al. 2002).

Species	n	δ^{18}O min.	δ^{18}O max.	δ^{18}O mean (SD)	δ^{13}C min.	δ^{13}C max.	δ^{13}C mean (SD)
Melanoides tuberculata	10	-1.28	-0.32	-0.76 (±0.44)	-1.71	0.76	-0.9 (±1.14)

Tab.1 - Isotope contents of *Melanoides tuberculata* shells from a Holocene lake palaeoenvironment NE In Ecker/Algeria.

History. Eocene occurrences of the closely related thiarid *Melanotarebia* from W Hungary (Kowalke 2001a) and *Melanoides* from France (Plaziat 1984) exclusively refer to lacustrine fresh water ecosystems, but are missing from the adjacent oligo- to mesohaline coastal swamp facies. Early Oligocene lacustrine freshwater faunas of the Ebro Basin in northern Spain are dominated by *Melanoides albigensis* (Noulet) (Anadón 1989), a species that is morphologically very similar to the modern type species *M. tuberculata*. Late Miocene faunas from lacustrine habitats in SE Spain are composed of associations of *Melanoides* with *Melanopsis*. Mein et al. (1978) described lacustrine freshwater deposits from the Turolian of Tolosa which are dominated by "*Melania*" (= *Melanoides*).

In the course of the Late Tortonian/Early Messinian time interval, *Melanoides* occupied the ecological niches within oligo-/mesosaline environments that were formerly colonised by mid- to early Late Miocene *Potamides*. Oligosaline continental *Melanoides*-faunas have been described from the Early Messinian of Tuscany (Ghetti et al. 2002) and, in greater diversity, from the Upper Messinian Lago-Mare facies of Italy and the Pliocene of Spain (Esu & Girotti 1974; Esu 1980). *Melanoides curvicosta* v. Martens, 1897 extended back to the Messinian (Esu & Girotti 1974; Esu 1980). According to Esu (1980), the Miocene species co-occurred in a palaeocommunity with euryhaline elements such as neritids, dreissenids, and lymnocardiines, which indicate oligo-to mesosaline conditions. A probably oligohaline palaeocommunity has also been described from the Pliocene of Barcelona where *M. tournoueri* (= *M. curvicosta*) occurred associated with *Neritina*, *Valvata*, *Melanopsis* and *Hydrobia* (Almera et al. 1892; Esu 1980).

During the Pliocene to Early Pleistocene times, the thermophilous element *Melanoides* was characterised by a considerably more northern geographic distribution, e.g. in northern Spain and in Italy. Non-African occurrences of the extant species *M. tuberculata* have been reported from the Lower Pleistocene of the Guadix-Baza Basin (Anadón et al. 1987; Robles 1989), the Balearic Islands, and the Upper Pleistocene of Apulia/Italy (Esu 1980). According to Robles (1989), *M. tuberculata* from southern Spain may also have lived under oligosaline conditions, associated with *Theodoxus* and *Melanopsis*.

Melanoides species obviously colonised saline waters in Late Neogene to Quaternary ecosystems, wherever oligo- to mesosaline conditions were established, and in case of the lack of *Potamides* tolerating this salinity spectrum. Associations of *Melanoides* and freshwater/oligosaline elements with *Potamides*, co-occurring in the same layers, do not represent communities, but rather successive associations. These successive developments reflect a sudden increase in salinity. An example has been described from Holocene deposits of Dahlak Kebir (Eritrea, Red Sea) by Belluomini et al. (1980) where clionid borings in the molluscan shells indicate a temporary connection of a freshwater/oligosaline coastal ecosystem to the sea.

With regard to these Oligo-Miocene occurrences, the accompanying fauna consists of fresh water inhabitants. Contemporaneous oligo- to eusaline marginal marine and athalasso-saline habitats were avoided, and were instead colonised by *Potamides*-corbiculid (Oligocene), *Potamides-Hydrobia* (Middle Miocene), and *Potamides-Cerastoderma* palaeocommunities (Middle-Upper Miocene).

Potamides-communities

Composition. Different types of extant communities dominated by the potamidid *Potamides conicus* (Fig. 3A, D-E, G-H) are known from athalasso-saline ecosystems of the South Mediterranean. For example, in North African continental saline habitats, characterised by a salinity level close to that of marine water of the Mediterranean Sea, *P. conicus* is abundant and associated with mass populations of the cardiid *Cerastoderma glaucum* (Poiret) (Fig. 3B-C).

The Birket Quarun (Fayoum) in North Egypt represents a typical intra-continental aquatic ecosystem, characterised by progressive increase in salinity. The "step by step" colonisation by primarily marginal marine and marine-brackish faunal elements had been demonstrated in various studies of the mollusc fauna in the course of the 20th century. *Cerastoderma glaucum* has been introduced to the lake between 1908 and 1927 (Smith 1908; Gardner 1932). The typically accompanying *P. conicus* was absent, and first colonised the lake

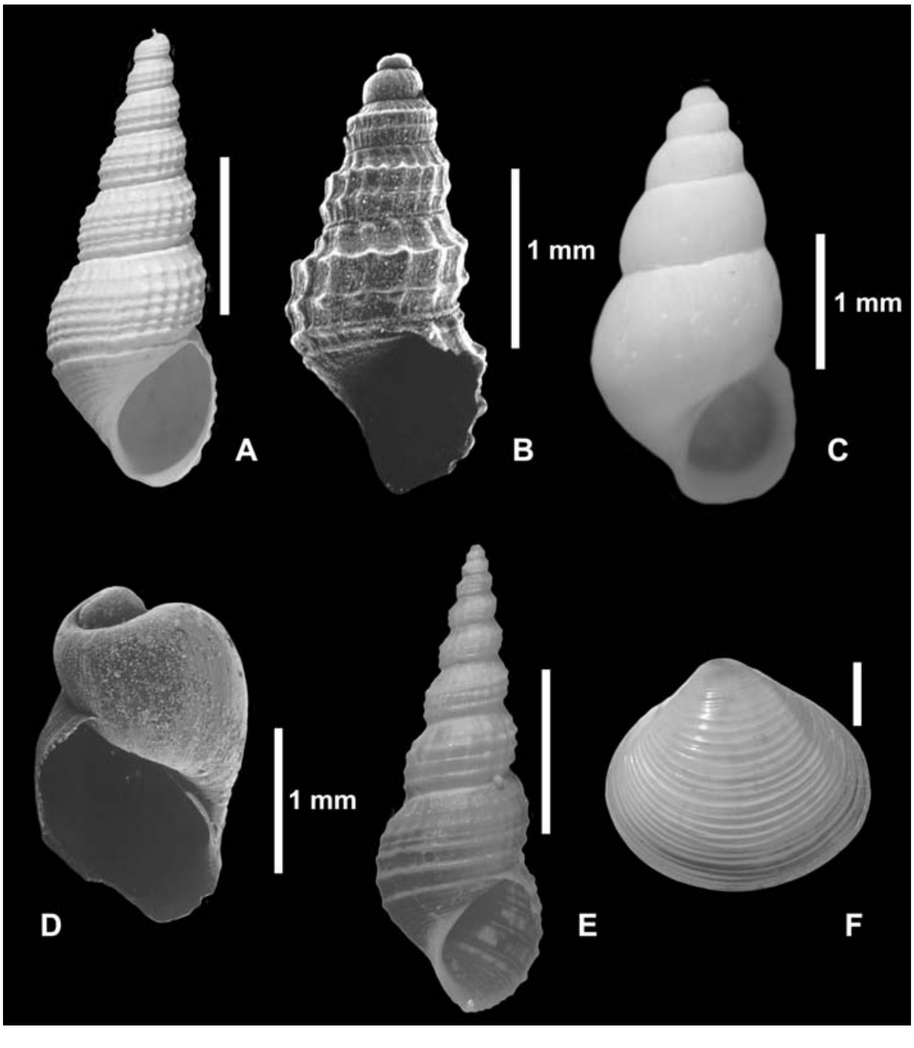

Fig. 2 - *Melanoides* communities. A-C: characteristic athalasso-saline representatives of a *Melanoides-Hydrobia* community from a Holocene lake palaeoenvironment NE In Ecker/Algeria. A: *Melanoides tuberculata*, BSPG, grown specimen. B: juvenile specimen, BSPG. C: *Hydrobia peraudieri*, BSPG. D: *Bulinus truncatus*, juvenile specimen, BSPG, from In Ecker, reflecting a fresh water episode of the ecosystem. E-F: athalassic *Melanoides*-community, from a fresh water pool separated from Lake Quarun, Fayoum/Egypt. E: *Melanoides tuberculata*, ZSM. F: *Corbicula fluminalis*, ZSM. Scale bars = 5 mm (except B, C and D).

when polysaline conditions became established due to the increase in salinity within a time interval between 1927 and 1968 (Rose 1972). Further thalassic elements such as marine hydrobiids of the *H. acuta* relation, *Nassarius*, *Haminoea*, the scrobiculariid *Abra*, mytilids and balanids with planktonic larvae occurred during the last 30-40 years, when salinity levels reached close to that of normal sea water of the Mediterranean Sea.

A second *Potamides* community type is dominated by *P. conicus* (Fig. 3E). This type is found in a salty lake of the Sinak-Oasis, an athalasso-saline ecosystem in the Libyan Desert (material from the ZSM). The accompanying fauna consists of *Cerithium rupestre* Risso (Fig. 3F). This species is characterised by direct development, and thus is capable of reproducing in athalasso-saline ecosystems, if eusaline conditions close to that of sea water prevailed.

A special case is displayed in extant very shallow coastal pools of the South-east coast of Cyprus at the rocky shore of Cape Greco (Kowalke 2001b). During the summer months, monotypic occurrences of *P. conicus* (Fig. 3H) occur in these pools, only occasionally affected by high tides. Water seepage is strongly restricted due to the predominant hard substrates. *Cerithium vulgatum* Bruguière (Fig. 3J) usually occurs well-separated in adjacent lagoons, which are permanently connected to the Mediterranean Sea, or affected by each tide respectively. During autumn and winter *C. vulgatum* migrates into the restricted lagoonal habitats. *Cerithium vulgatum* usually avoids environments with changing salinity levels, but tolerates enriched salinities and brackish waters to a certain degree. As a result, the influx of fresh water during winter and spring permitted the establishment of temporary assemblages of *Potamides* and *Cerithium*.

Potamides-Cerithium communities appear to be restricted to extant athalasso-saline ecosystems of the eastern Mediterranean, and especially North Africa. Late Pliocene/Early Pleistocene co-occurrences of *Potamides* with *Cerithium* (determinated as *C. vulgatum*), which were described from Umbria/Central Italy (Mancini et al. 2003-2004), do not represent athalasso-saline, but rather marginal marine faunas, since the Tiberino basin in that time interval was connected to the Mediterranean Sea.

The often temporary character of the *Potamides-Cerithium* community type is also evident in the population density of *Potamides* and *Cerithium*. In coastal pools of the southern Cyprian coast, the proportional abundance of *C. vulgatum* is maximal 20 % of the assemblage. Any accompanying macro-fauna is absent. In contrast to *Cerithium vulgatum*, *C. rupestre* is able to reproduce in athalasso-saline environments since it displays a direct mode of early ontogenetic development: crawling young are directly hatching from the eggs, without developing into an additional larval stage. *Cerithium vulgatum*, in contrast, develops into a planktotrophic veliger stage (Kowalke 1998), and hence requires at least temporary connections to the open sea.

Anthropochory played an important role in the artificial establishment of the "marine" faunas in the larger North African athalasso-saline lakes since these elements were normally introduced together with fish cultures (Al Kholy & Abdel Malek 1972; Badawi 2001). The accompanying athalasso-saline micro-fauna usually consists of foraminifers (*Ammonia*, *Trichohyalus*) and ostracods (*Cyprideis*). The striking macro-faunal diversity of the culture-influenced ecosystems contrasts the oligotypic composition of aquatic North African ecosystems not under cultivation.

Ecology. Potamides-Cerastoderma communities commonly occur in Quaternary fossil to extant athalasso-saline ecosystems of the Great Western Erg/Algeria (Gasse et al. 1987), oases in Libya and Egypt and in sabkhas of Tunisia and the Red Sea area (see e.g. Gavish 1979; Purser 1985; Plaziat 1989, 1991, 1993). Although *P. conicus* occurs within a salinity ranging from 5 to150 ‰ TDS, and *Cerastoderma glaucum* tolerates salinity levels between 3 and 90 ‰ TDS (Rosso and Gaillard 1982; Gerdes et al. 1985; Plaziat 1993), *Potamides-Cerastoderma* assemblages typically characterise saline ecosystems with salinity levels close to that of sea water. The establishment of stable, persisting populations appears to be possible within a salinity range that enables sufficient reproduction, e.g. in case of *Potamides* in waters with salinity levels between 20 and 40 ‰ TDS at least during the reproductive period (Gasse et al. 1987; own observations in coastal lagoons of Cyprus).

The extant *P. conicus* from normal marine to metahaline Mediterranean habitats is characterised by variation in sculptural development that depend on the salinity level (see also Plaziat 1993; Kowalke 2001b, 2003): coarsely sculptured individuals occur in normal marine waters, whereas weakly sculptured to rather smooth morpho-types develop in temporary metahaline waters. In comparison to extant individuals of *P. conicus* from normal marine waters in coastal lagoons at Thessaloniki and Delos/Greece (Fig. 3G) that are sculptured by regular rows of nodes, individuals colonising habitats with (seasonally) enriched salinities are characterised by reduced sculpture. An example is present from Bucrat, Libya (Fig. 3D). With regard to the sculptural development that depends on the salinity, *P. conicus* shows similarities to *Potamides gaudryi* (Larrazet, 1894) (= *P. munieri*) from the late Middle Miocene of the Duero Basin/NW Spain (Calzada et al. 2001). *Potamides gaudryi* occurred in the context of oligo- to mesosaline waters and has been characterised by a considerably more developed sculpture than *P. conicus* morphs from euhaline waters.

The potamidid *Potamides conicus* represents the dominant eurytopic macro-faunal element that characterises Quaternary athalasso-saline aquatic ecosystems in the South Mediterranean. Where sandy sediments convenient for infaunal bivalves are missing, *Potamides* is accompanied by hydrobiids of marine origin that colonise soft bottoms rich in plant detritus, indicating muddy, partly dysoxic conditions, and by *Cerithium*, grazing algae on hard-substrates. Contrasting the accompanying fauna, *Potamides* represents a comparatively eurytopic element, predominantly feeding on micro-algae that grow on the surface of various substrates.

History. The oldest known *Potamides* assemblages have been described from Lower Ludian (Upper Eocene) deposits of Fons in South France. They consist of *Potamides*, associated with freshwater dwellers, but salinity-tolerant elements such as lymnaeids, and rare oligo/mesosaline foraminifers may also be present. The succeeding "Calcaires à cyrénes" are characterised by more divers palaeocommunities, composed of "*Corbicula*" (= *Polymesoda*, Corbiculidae), *Potamides*, and saline Foraminifera (see Plaziat & Gaudant 1984). Changes in the composition of the athalasso-saline elements and occurrences of fresh water molluscs associated with *Melanoides* indicate fluctuations in the palaeocommunities, that are due to seasonally (intra-annually?) changing salinity levels. However, these changes in the lake level are difficult to verify, since no continuous sedimentary sections exist. Contemporaneous deposits of the "Calcaires Lacustres de Mans" in W France contain a characteristic *Potamides-Hydrobia* fauna (Rey 1965).

Marked changes in community types are evident from the European Oligocene and Miocene. Associations of *Potamides* with *Polymesoda* and hydrobiids have been described from athalasso-saline ecosystems from the Lower Oligocene of the Ebro Basin in NE Spain (Vidal & Deperet 1906; Bataller 1929; Anadón 1989). Athalasso-saline deposits from France and the Iberian Peninsula appear to be unique in the fossil record because they indicate inland saline occurrences of corbiculids. Mollusc assemblages described from Oligo-Miocene deposits of Otranto (Southern Apulia/Italy) are characterised by occurrences of *Potamides*, *Polymesoda*, hydrobiids, and *Melanoides* in some layers (Esu & Girotti 2002; Esu et al. 2005). However, this succession does most probably not represent an athalasso-saline facies because it was deposited in a lagoonal/coastal swamp palaeoenvironment: the succession represents a non-marine to marine transition with alternating freshwater/brackish facies and marine conditions, in which typical marine molluscs and foraminifers probably indicate the existence of a connection with the sea (Esu & Girotti 2002, Esu et al. 2005).

In the course of the Early Miocene corbiculids were superseded by cardiids (Harzhauser & Kowalke 2001), which occupied the ecological niche by tolerating higher salinity levels, especially with regard to the salinity range in which reproduction was possible. Corbiculids are generally absent from Quaternary athalasso-saline assemblages. In spite of the fact that corbiculids exhibit a broad salinity tolerance, Mediterranean populations of *Corbicula fluminalis* (Fig. 2F) prefer fresh water conditions. The presence of planktotrophic larvae represents an advantage to *Cerastoderma*, since larger numbers of descendents can be released in comparison to the forms that exhibit the predominating mode of brooding in modern corbiculids (see Korniushin 2004). Although Pleistocene corbiculids invaded brackish habitats in estuarine portions or adjacent lagoons (Meijer and Preece 2000), in North Africa the extant *C. fluminalis* did not readapt to colonise inland saline habitats.

During the Middle Miocene relatively stable assemblages characterised the athalasso-saline habitats: associations of *Potamides* and hydrobiids (Robles 1989) occurred in oligo- to mesosaline lake environments and "*Cardium*" (= *Cerastoderma*) accompanied by *Potamides* typically characterised poly- to metasaline continental palaeoenvironments (Anadón 1989; Anadón et al. 2003).

Athalasso-saline ecosystems have to date not been reported from continental palaeoenvironments of the Paratethys. However, the recently studied potamidid-dominated fauna of the Sarmatian Eisenstadt-Sopron Basin (Austria/W Hungary) was characterised by palaeocommunities that reflect changing environmental conditions (Harzhauser & Kowalke 2002; Latal et al. 2004). Stable isotope compositions of the potamidid shells yielded enriched δ^{18}O-values in case of *Potamides disjunctus* (Sowerby), a close relative to the extant *P. conicus*, which, according to Latal et al. (2004) could have lived in evaporated stagnant and protected coastal environments. Probably *P. disjunctus*, which represents a direct developer (Harzhauser & Kowalke 2002), has also colonised continental saline aquatic ecosystems in some distance to the Sarmatian Sea.

Monotypic *Cerastoderma*-communities

Composition. In contrast to the typical *Potamides-Cerastoderma* assemblages, monotypic occurrences of *Cerastoderma* characterise shallow lakes with strongly restricted marine and fresh water influx. An additional mollusc fauna is absent. Typical intra-continental faunas with mass-occurrences of *C. glaucum* come from the Lower Pleistocene of Orce (Guadix-Baza Basin/S Spain) and Pleistocene to extant ecosystems of Algeria, Tunisia, and Libya. Additionally saline micro-fossils, e.g. foraminifers (*Ammonia*, *Elphidium*,

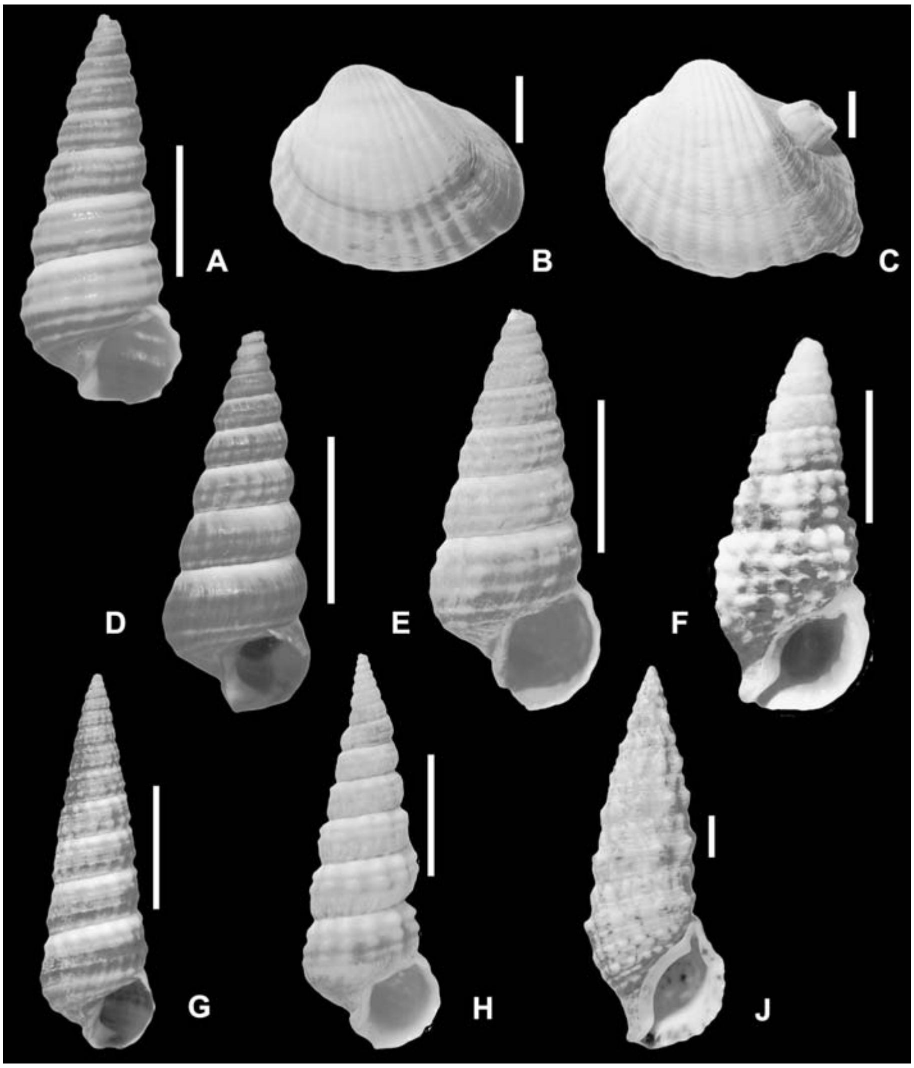

Fig. 3 - *Potamides* communities. A-C: characteristic representatives of the athalasso-saline *Potamides-Cerastoderma* community of the Birket Quarun, Fayoum/Egypt. A: *Potamides conicus*, ZSM. B: *Cerastoderma glaucum*, ZSM. C: *Cerastoderma glaucum*, ZSM, with epizoic balanid. D: *Potamides conicus*, ZSM, from a saline lake at Bucrat, Libya. E-F: characteristic representatives of the *Potamides-Cerithium* community of the Sinak oasis/Libya. E: *Potamides conicus*, ZSM. F: *Cerithium rupestre* Risso, ZSM. G: *Potamides conicus*, BSPG, from normal marine waters at Delos/Greece. H-J: characteristic representatives of the temporal *Potamides-Cerithium* community from saline lagoons at Cape Greko/SE Cyprus. H: *Potamides conicus*, BSP. J: *Cerithium vulgatum*, BSP. Scale bars = 5 mm.

Quinqueloculina) and ostracods (*Cyprideis*), are usually forming part of the oligotypic assemblages (see Gasse et al. 1987, tab. 3).

Ecology. The infaunal filter-feeding species *C. glaucum* is characterised by veliger larvae that possess a strong velar apparatus. These larvae are able to actively swim in restricted environments, contrasting gastropod's larvae, which are predominantly distributed passively by marine currents (Kowalke 1998). In *C. glaucum* reproduction is possible in restricted metasaline environments, in the context of higher salinity levels than in case of *P. conicus*, which requires at least seasonal fresh water influx by precipitation, temporary riverine connections or ground water seepage.

The remarkable absence of "transitions" from oligo-/mesosaline *Melanoides*-communities to *Potamides*-communities and *Cerastoderma*-assemblages whenever higher salinity levels are reached may be explained by a rapid increase of the salinity. In these cases, conditions – particularly for reproduction – are more convenient for associations of *Cerastoderma* and saline Foraminifera. Thus, the monospecific occurrences of *Cerastoderma* are best described as corresponding to late developmental stages of saline lakes in the context of progressive evaporation. An additional reason for the lack of *Potamides* may exist in the greater tolerance of *Melanoides* (within the oligo- to mesohaline spectrum) and *Cerastoderma* (within the eusaline to meta/hypersaline spectrum) with regard to aberrant water chemistry, since evaporated intra-continental saline waters often considerably differ from normal sea water with regard to the ionic composition (Bayly 1967; Por 1972; Kiener 1978; Williams 1981; Hammer 1986; Ben Quezdou 1989).

History. Monospecific occurrences of *Cerastoderma* are absent from Mediterranean Neogene deposits. Although *Cerastoderma* is well-known from athalasso-saline deposits of the Ebro Basin (late Middle Miocene) (Anadón 1989), the genus always occurs in the typical *Potamides-Cerastoderma* palaeocommunities. Apart from associations of *Potamides* and *Cerastoderma*, examples of monospecific occurrences of *Cerastoderma* come from the Lower Pleistocene of the Guadix-Baza Basin in South Spain (Anadón et al. 1986; Anadón et al.

1987; Anadón 1989; own observations in Orce/Guadix-Baza Basin). Corresponding occurrences in N Africa have been reported from the Upper Pleistocene of Ahnet/Algeria (Conrad 1969) and the Chott el Jerid/Tunisia (Lévy 1985, 1989), among other localities.

Conclusions

Three types of athalasso-saline mollusc communities occur in aquatic ecosystems of the South Mediterranean Quaternary: (1) *Potamides* communities of marginal marine origin colonised ecosystems with at least temporary establishment of salinity conditions close to that of the Mediterranean Sea. (2) *Cerastoderma glaucum* assemblages in very shallow metasaline aquatic ecosystems. (3) *Melanoides* communities of freshwater origin that colonised oligo- to mesosaline continental habitats – a generally eurysaline community type, but it does neither occur in athalasso-saline ecosystems with salinity levels close to that of sea water nor in marginal marine brackish habitats connected to the Mediterranean Sea.

Dynamic processes with changes in the faunal compositions could be observed in Neogene Mediterranean and Quaternary southern Spanish and North African ecosystems:

in the course of the late Early Miocene, corbiculids, which were forming part of the Mediterranean *Potamides* communities, were replaced by *Cerastoderma*. The cardiid had the advantage of an indirect larval development over the predominant brooding mode of early ontogenetic development in corbiculids. During the late Miocene oligo/mesosaline continental ecosystems were colonised by *Melanoides* communities, which primarily characterised freshwater ecosystems. In the course of the Early Pleistocene shallow eu/metasaline ecosystems were colonised by monotypic *Cerastoderma* assemblages. The Late Neogene and Pleistocene diversification of athalasso-saline community types were triggered by the decrease of *Potamides*.

The characteristic Holocene *Melanoides* community of In Ecker/Algeria occurred in oligosaline environments accompanied by juvenile fresh water molluscs. The faunal composition documents a rapid evaporation and corresponding increase of the salinity, disadvantageous for freshwater dwellers. This interpretation is supported by oxygen isotope signals. High standard deviations in corresponding carbon isotopes may confirm salinity-triggered changes in the diet in the course of the life cycles of the gastropods.

Potamides communities today inhabit the larger North African lakes that are under intensive cultivation. These communities are characterised by a great biodiversity, compared to the Quaternary fossil assemblages: a broader variety of primarily marine taxa are introduced together with fish cultures. Anthropochory plays an important role in recent times since the predominant mode of distribution by sea birds in pre-human times appears to be restricted to few taxa. The comparatively high diversity of faunas in modern continental eusaline ecosystems contrasts the composition of extant oligotypic *Melanoides* faunas in oligosaline environments.

Apart from the low number of individuals introduced into intra-continental habitats, and the resulting problems for the establishment of persisting populations, the mode of early ontogenetic development prohibits the entire spectrum of gastropods with planktotrophic larval development from colonising. Thus, the establishment of permanent athalasso-saline populations is only possible by pre-adaptational loss of planktotrophy.

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