Ostrakoden und Foraminiferen aus athalassischen Gewässern und deren Anwendung für die Rekonstruktion quartärer Ökosysteme

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Kurzfassung

Athalassische Gewässer sind durch erhöhte Salinität ausgezeichnete Wasserkörper des Binnenlandes, ohne Verbindung zum Meer. Die in ihnen lebenden athalassischen Faunen sind ein seltenes, aber im Diskurs der geowissenschaftlichen Literatur immer wiederkehrendes Phänomen. Diese Faunenassoziationen sind individuell verschieden und für bestimmte Salinitätsbereiche charakteristisch, ähneln aber niemals vollmarinen Faunengemeinschaften. Die vorkommenden Arten stammen aus dem marinen Intertidal, welches durch instabile ökologische Bedingungen charakterisiert ist, was eine hohe Anpassungsfähigkeit erfordert. In der vorliegenden Arbeit werden athalassische Foraminiferen- und Ostrakodenfaunen identifiziert, dokumentiert, klassifiziert und für die Rekonstruktion athalassischer Gewässer verwendet.

Die Klassifizierung athalassischer Gewässer auf Basis von Ostrakoden und Foraminiferenassoziationen erfordert eine besondere Methodik, denn gerade in diesen Gewässern ist die Diversität besonders gering und die vorkommenden Arten haben hohe ökologische Toleranzen, vor allem gegenüber der Salinität. Jedoch erlauben morphologische Besonderheiten, wie Missbildungen von Foraminiferen oder die Ausbildung von Buckeln und Variabilität von Siebporenumrissen bei eine Rekonstruktion der Salinität.

Bei niedrigen Salzgehalten kommen Brackwasserorganismen mit salztoleranten Süßwasserformen in athalassischen Gewässern vor, während bei höheren Salinitäten Brackwassertaxa überwiegen. In hypersalinen Gewässern leben nur noch wenige euryhaline Arten, die aufgrund fehlender Konkurrenz massenhaft auftreten können.

Für athalassische Gewässer sind neben der allgemein geringeren Diversität, verglichen mit randmarinen Lebensräumen ähnlicher Salinität, einige wenige Arten randmarinen Ursprungs, oft in Vergesellschaftung mit salztoleranten Süßwassertaxa typisch. Treten Foraminiferen in Binnengewässern auf, sind sie durch hohe Missbildungsraten gekennzeichnet.

Während athalassische Gewässer geogener Salinität wegen des hohen Niederschlags/Verdunstungsverhältnisses überwiegend in humiden Klimaten zu finden sind, liegen die klimatogenen athalassischen Gewässer in ariden Gebieten. Hypersaline Gewässer können eindeutig dem klimatogenen Typ zugeordnet werden und sind an dem geringen Artenspektrum ausschließlich euryhaliner Taxa erkennbar.

Basierend auf den hier vorgestellten Fallstudien konnte ein Klassifizierungsschema erarbeitet werden, das die Erkennung von randmarinen und verschiedenen athalassischen Gewässertypen anhand von fossilen Ostrakoden- und Foraminiferenfaunen erlaubt.

Abstract

Athalassic waters are characterised by elevated salinity and continental location with full separation from the sea. The fauna living in such waters has been discussed rarely but for a long time already in scientific literature. Faunal assemblages of athalassic waters are individually distinct and characteristic for specific salinity ranges. They are never, however, identical to fully marine assemblages. Athalassic taxa derive from the marginal marine, intertidal zone, where instable ecological conditions require a high adaptability of species. The present thesis identifies, documents and classifies athalassic foraminifer and ostracod associations and applies them for palaeoenvironmental reconstructions.

The classification of athalassic waters based on ostracod and foraminifer assemblages needs a specialised methodology because of generally low diversity and high ecological tolerances of typical species, especially towards salinity. Additional methods allow to compensate for this weakness; morphological features as malformations in foraminifer tests as well as noding and sieve pore variability in *Cyprideis torosa* are applicable for reconstructing salinity changes of the past.

Athalassic waters of the low salinity range are characterised by brackish water and tolerant freshwater taxa, dominance of brackish water species, however, is typical for higher salinities. Hypersaline waters are inhabited by a few euryhaline species only, often occurring in very high numbers because of lacking competing species.

Some species of marginal marine origin, often associated with salinity-tolerant freshwater species, are typical for athalassic waters, as a generally low diversity as well. If Foraminifera occur, a high proportion of their tests is malformatted.

Climatically generated athalassic waters are located in arid climate zones while those with geogenic salinity are typical for humid climate zones because of a high precipitation/evaporation ratio. Hypersaline waters are of climatogenic type and characterised by very low diversity and the exclusive occurrence of euryhaline taxa.

Based on the case studies of this thesis, a classification of athalassic waters is presented enabling discrimination of several types relying on fossil ostracod and foraminifer faunas.

Inhalt

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1 Einleitung

1.1 *Athalassische Gewässer – Definition und Bedeutung*

Athalassische Gewässer befinden sich auf allen Kontinenten, einschließlich der Antarktis (Jung 1990; Gerlach 2013). Im Gegensatz zum marinen (thalassischen) Lebensraum werden salzhaltige Binnengewässer als athalassisch bezeichnet, vorausgesetzt sie sind oder waren nicht mit dem Meer verbunden. (Perthuisot 1995). Die Gesamtsalinität und die Ionenkomposition können sowohl der marinen Salinität ähneln als auch stark von ihr abweichen. Der Wasserchemismus kann jedoch von Gewässer zu Gewässer sehr verschieden sein (Last 2002). Je niedriger der Salzgehalt im Brackwasser, desto geringer ist der thalassoide Charakter der Lebensgemeinschaften. Ebenso unterscheiden sich die Faunen und Floren bei steigenden Salzgehalten unter hypersalinen Bedingungen zunehmend von den marinen (Remane & 1958) (Abb. 1 und 2).

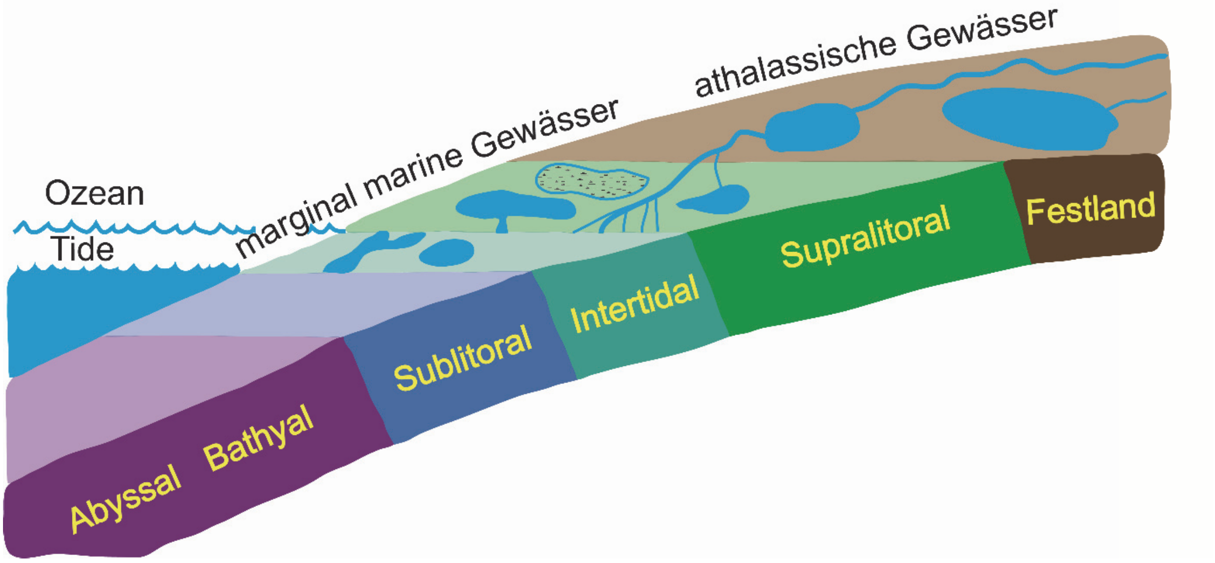

Abb. 1: Schema der Zonierung von Gewässertypen in ihrer Beziehung zur Küste

Eine etwas abweichende Definition unterscheidet thalassohaline von athalassohalinen Seen: Während erstere durch klimatisch begünstigte Evaporation ihren Salzgehalt entwickeln, welcher in der Ionenkomposition vom Meer abweichen kann, bilden sich letztere durch den Kontakt des Wassers mit salzhaltigen Gesteinen und Sedimenten und haben eine dem Meer ähnliche Ionenkomposition, da das Salz aus ehemaligen Ozeanen stammt (Bohle 1995). Bei den Sodaseen führt die hohe Konzentration von Carbonat und Bicarbonat zu einer starken Erhöhung des pH-Wertes. Diese Gewässer sind deshalb besonders lebensfeindlich.

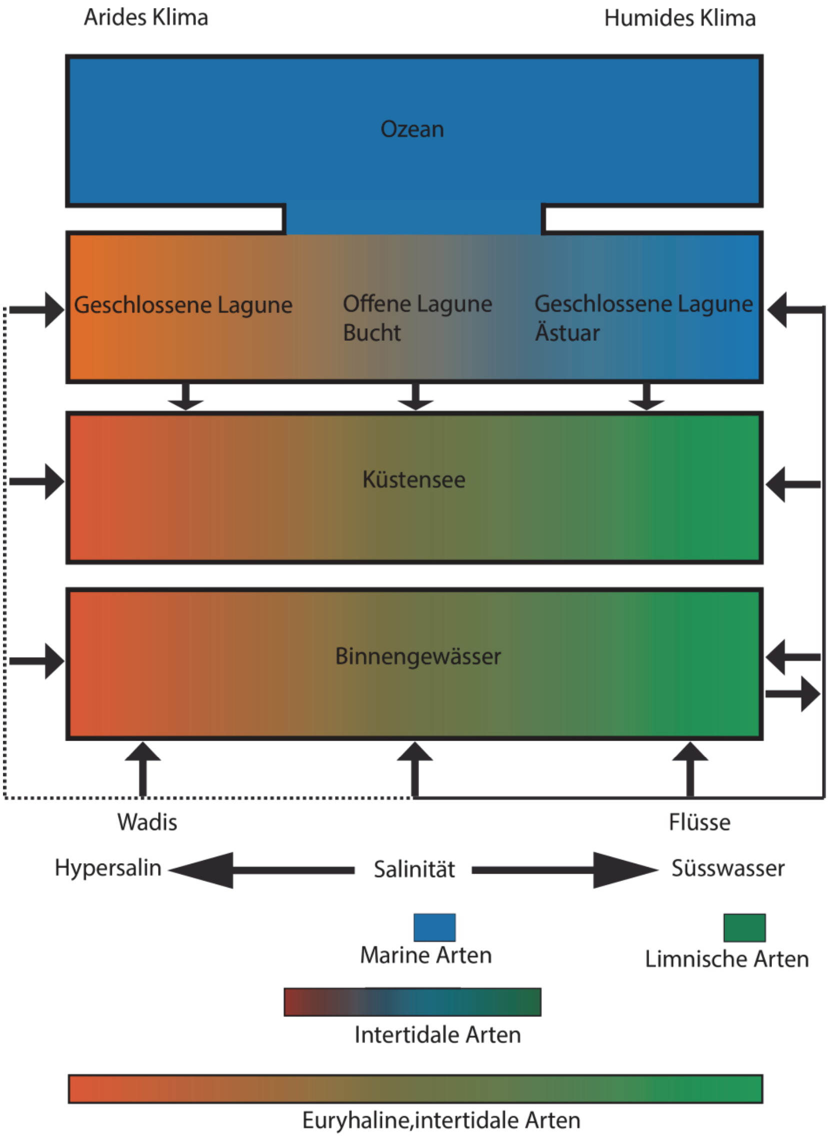

Abb. 2: Klassifikation aquatischer Ökosysteme; stark verändert nach Perthuisot (1995)

Als athalassisch klassifizierte Sedimente bilden wichtige Geoarchive zur Interpretation der Hydrographie und des Klimastatus einer bestimmten Region zu einer bestimmten Zeit. Auch in der Paläogeographie spielen sie eine bedeutende Rolle – die Entfernung zur Küste spiegelt sich über die Assoziationen und Diversität der Gemeinschaften wieder.

Die heutigen Seen sind mehrheitlich exogen entstanden vor ca. 14.000 Jahren nach der letzten größeren Landschaftsveränderung während der pleistozänen Vereisung. Küstenseen, die durch Meeresspiegelschwankungen und Küstenlängsströmungen entstehen, bildeten sich erst nach dem Meeresspiegelhochstand im Atlantikum vor 6000 Jahren. Nur Seen in tektonisch aktiven Becken haben eine vergleichsweise lange Lebensdauer, die sogar bis ins Tertiär zurückreichen kann. Als ältester Süßwassersee der Erde gilt der sibirische Baikalsee mit einem Alter von 25 Millionen Jahren, und ist mit 1642 m Wassertiefe auch der weltweit tiefste See

(Röpstorf & Reitner 1994; Wein 2002). Zwei der größten Seen des Tibetplateaus, Tangra Yumco und Nam Co existieren wahrscheinlich seit dem Mittelpleistozän, mindestens jedoch seit dem letzten glazialen Maximum (Frenzel pers. Mitt. 2015). Größere permanente Seen in ariden Gebieten können auch Restseen ehemaliger Binnenmeere sein. So sind Aralsee, Kaspisches und Schwarzes Meer Relikte der ehemaligen Parathetis (Schäfer 1997). Die Salinität dieser Gewässer entwickelte sich aber nach deren Isolation völlig eigenständig. Eine Besonderheit stellen Kraterseen dar. Sie haben häufig ein sehr kleines Einzugsgebiet und sind deshalb durch den geringen Sedimenteintrag besonders langlebig. Ephemere Seen existieren nur während regenreicher Jahreszeiten und fallen das übrige Jahr trocken. Häufig gehen permanente Seen vor der Verlandung in ein ephemeres Stadium über. Der Wasserchemismus von Seen kann sich ganz unterschiedlich entwickeln, da dieser vor allem vom Klima, der Hydrographie und dem Untergrundgestein und weniger von Alter und Größe abhängig ist.

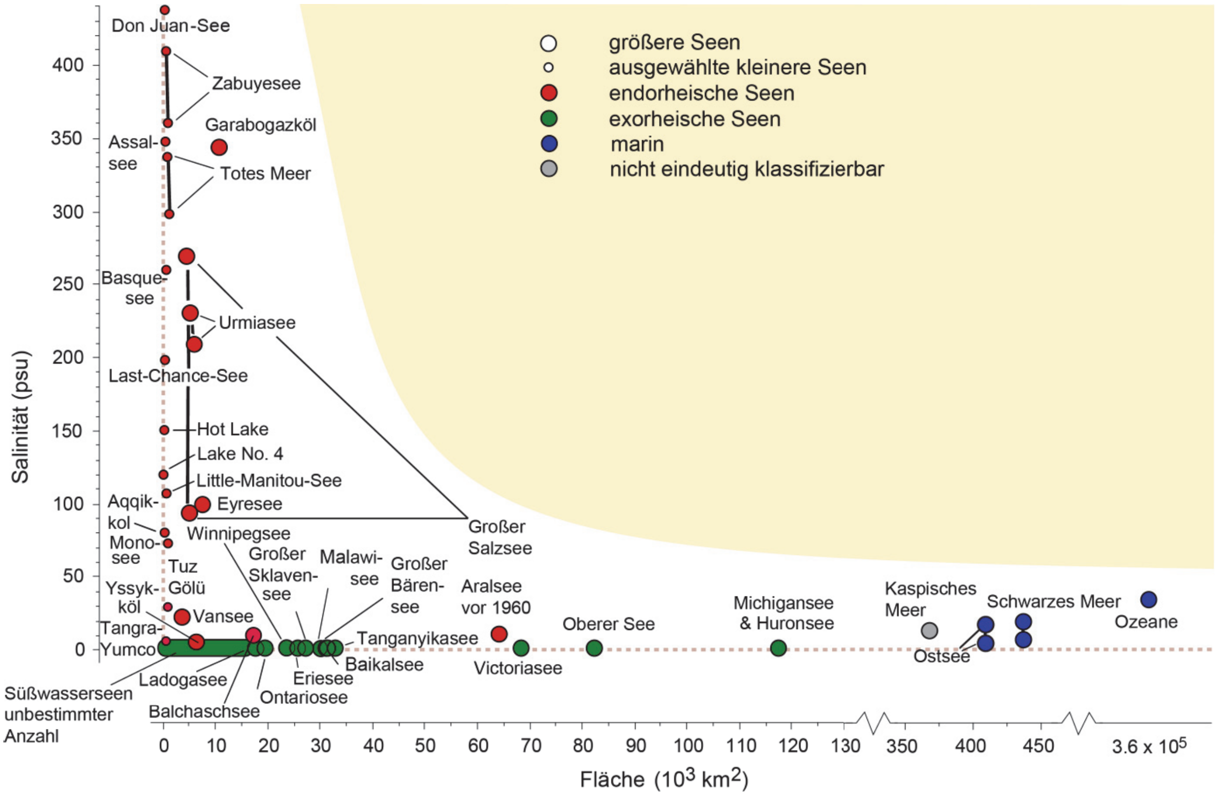

Abb. 3: Zusammenhang von Salinität und Fläche bei Seen. Verändert und ergänzt nach Railback (2006).

Die größten Seen der Erde überschreiten die marine Salinität nicht und Salzseen sind nicht größer als 20×10^3 km^2 (Railsback 2006; Abb. 3). Ursache dafür ist, dass die größeren Seen entweder in regenreichen Gebieten liegen oder von großen Flüssen aus niederschlagsreichen Gebirgen gespeist werden. So liegt der Aralsee in einem semiariden bis aridem Gebiet mit sehr wenig Niederschlag. Möglicherweise regulieren die größten Seen ihre Salinität zunehmend ähnlich wie die Ozeane durch Salzentzug während der Ablagerung von Sedimenten. Auch Austrocknen führt zum Ausfällen von Salzen, wodurch diese aus dem aquatischen System entfernt werden (Holland 2003).

1.2 Hydrographie und Ökologie

<u>Geographische und geologische Situation</u>

Endseen haben im Gegensatz zu Durchflussseen keinen Abfluss und bilden so das Ende eines hydrologischen Systems. Sie liegen häufig in endorheischen Senken. Das Verdunstungs-/Niederschlagsverhältnis ist so hoch, dass sich kein Abfluss bilden kann. Davon sind besonders Seen mit geringer Wassertiefe und großer Fläche betroffen, begünstigt noch durch Lokalisation in ariden und semiariden Klimaten oder durch ein kleines Einzugsgebiet. In vollariden Gebieten kann die Verdunstungsrate in der Regel nicht durch Frischwasserzufuhr ausgeglichen werden. Dadurch kommt es zu einer allmählichen Aufkonzentration der gelösten Salze und schließlich zu deren Ausfällung zunächst an den Ufern. Hier können sie durch Wind ausgeblasen und so dem System entzogen werden. Dadurch kann der Salinitätsanstieg verzögert, in manchen Systemen sogar verhindert werden. Im Aralsee hielt sich der Salzgehalt durch diesen Effekt bei ca. 10 psu[1], erst durch den anthropogenen Wasserentzug ab 1960 stieg die Salinität drastisch an (Letolle & Mainguet 1996; siehe Beitrag 5). Salinität begünstigt die Ausbildung von Wasserschichten mit unterschiedlicher Ionenkonzentration, vor allem in permanenten Seen, sodass Oberflächen- und Tiefenwasser nicht nur unterschiedliche Salinitäten, sondern auch unterschiedliche Ionenkompositionen aufweisen können (Last 2002).

Evaporit-beeinflusste saline Binnengewässer sind seltener als klimatisch bedingte Salzseen, da sie an salzhaltige Sedimente im Untergrund gebunden sind. Sie sind daher auch in humiden Klimaten anzutreffen. Diese Klimazonen bieten ausreichend Niederschlag, um Verdunstungsprozesse von Seen auszugleichen. Versalzungen von Gewässern sind hier auf salzhaltiges Grundwasser, das mit Evaporiten des Grundgebirges in Berührung kam, zurückzuführen. Die Salinität erreicht jedoch in der Regel nur oligohaline Brackwasserwerte. In solchen Seen ist die Ionenkomposition ähnlich der marinen Salzzusammensetzung, da die fossilen Salzlager meist aus marinen Ablagerungen stammen. In Mitteleuropa sind vor allem zwei Gebiete des Flachlandes bekannt: Das Thüringer Becken bis hin zum Harzvorland in Mitteldeutschland und das Burgenland in Österreich. In Mitteldeutschland liefern vor allem die Zechsteinabfolgen des Perms, im geringeren Maße aber auch der Zellenkalk aus der mittleren Trias Salz, welches von Grund- oder Quellwasser gelöst wird (Seidel 1995; Beiträge 1 und 2). Im Gebir-

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[1] psu = Practical Salinity Units
Heutige Salinitätsbestimmungen beruhen gewöhnlich auf Messungen der spezifischen Konduktivität, woraus die Salinität berechnet wird. Dieses Verfahren ist sehr zuverlässig für Wasser mariner Ionenzusammensetzung, jedoch weniger genau für athalassische Gewässer davon verschiedener Ionenzusammensetzung.

ge, beispielweise in der Steiermark in Österreich, führt Salzaustritt aus den Sedimenten zur Ausbildung einer thermohalinen Schichtung der meist tiefen Gebirgsseen. Die intramontane Lage der Seen und eine geringe Fläche bei großer Tiefe verhindern eine wetterverursachte Durchmischung des Wasserkörpers, sodass der Sauerstoff in der basalen salzhaltigen Schicht im tieferen See meist vollständig abgereichert ist. Gebirgseen mit thermohaliner Schichtung können auch einen oberirdischen Abfluss als Überlauf haben, bei dem nur das leichtere, salzarme Oberflächenwasser abläuft (Remane 1958). Einer der wichtigsten Steuerungsfaktoren für die Salinität ist die Größe des Einzugsgebietes. Das Verhältnis von Einzugsgebiet und Seeoberfläche bestimmt die Salinitätsentwicklung eines Sees bei verdunstungsabhängiger Ionenkonzentration.

Kommt es zu strukturellen Veränderungen des Sees oder seiner näheren Umgebung und dadurch zur Öffnung oder Schließung eines Abflusses oder zu Veränderungen der Größe des Einzugsgebietes, kann sich als direkte Folge davon der Wasserchemismus ändern und damit auch die Lebensgemeinschaften im See. Ein weiterer wichtiger Aspekt sind Änderungen des Klimas. Nicht nur Niederschläge spielen eine Rolle, sondern auch die Lufttemperatur. Beispielsweise kann einer Erwärmung zur Mobilisierung von Gletschereis durch Schmelzen führen und so einen Gletschersee zum Überlaufen bringen. Auf diese Weise kann sich ein Endsee zu einem Durchflusssee entwickeln. Umgekehrt kann eine Abkühlung Wasser in Form von Eis binden, dadurch kann es zur Isolierung eines Gletschersees kommen, da der Seespiegel unter das Niveau des Abflusses fällt.

Variable Salinitäten von Gewässern sind häufig in semiariden Gebieten mit saisonalen Regenfällen und Evaporation zu finden. Die Gewässer sind meist flach und werden in Wüsten und Halbwüsten durch Wadis mit Wasser gespeist. Der ehemalige See von Tayma (Saudi-Arabien) gehört in diese Kategorie (siehe Beiträge 6 und 7).

1.3 Ökologie

Salinität und Ionenzusammensetzung haben physiologische Effekte. Eine wichtige Anpassungsstrategie ist die Osmoregulation. Hier werden zwei Haupttypen unterschieden; Osmokonformer, die die Ionenkonzentration ihrer Körperflüssigkeiten an die Ionenkonzentration der Umgebung anpassen, und die Osmoregulierer, die die Ionenkonzentration ihrer Körperflüssigkeiten unabhängig von der Umgebung konstant halten. Bei letzteren wird weiterhin zwischen Hyper- und Hypoosmotischen Regulierern unterschieden, deren osmotischer Innendruck über bzw. unter dem des umgebenden Wassers liegt. Im Gegensatz zu stenohalinen Arten, die nur einen engen Salinitätsbereich besiedeln können, tolerieren euryhaline Arten ein sehr breites Salinitätsspektrum und sind in athalassischen Gewässern häufig in sehr hoher Individuenzahl anzutreffen. Die Artenzusammensetzung ist von der Salinität abhängig und wird durch die ökologische Salinitätsklassifikation des Venedigsystems charakterisiert (Tab. 1).

Tab. 1: Klassifikation der Salinität nach dem Venedig-System (Symposium on the Classification of Brackish Waters, 1958)

Salinität	Bezeichnung
0 – 0,5	Süßwasser
>0,5	β-oligohalin
>3	α-oligohalin
>5	β-oligohalin
>10	α-mesohalin
>18	polyhalin
>30	euhalin
>40	hyperhalin

Diversität

Im Gegensatz zum marinen Lebensraum mit sehr hoher Diversität oder dem Süßwasser mit mittlerer Artenzahl, weisen paralische Lebensräume und athalassische Gewässer eine niedrige Artenzahl mit oft hohen Abundanzen opportunistischer Arten auf (Abb. 4). Das Minimum der Artenzahl liegt bei einer Salinität von etwa 7 (Remane 1958). Auffallend ist auch, dass athalassische Gewässer, selbst wenn sie weit von der Küste entfernt liegen, Arten von Ostrakoden und Foraminiferen beherbergen, die typischerweise in paralischen Lebensräumen mit starkem Tideneinfluss vorkommen (Perthuisot 1995, Debenay et al. 2000). Der Grund liegt in der Instabilität dieser Lebensräume. Besitzt ein Gewässer z. B. eine geschlossene Lagune oder ein Ästuar mehrere Salinitätsbereiche, kommt es entlang des Salinitätsgradienten zu einer Faunenzonierung, die sich vor allem in einer Änderung der Diversität bemerkbar macht, dabei allerdings weniger in der Anzahl der Arten. In einer Sukzession können daher nicht nur der über die Ökologie der Arten beschriebene Lebensraum, sondern auch die Diversität und im Besonderen die Verteilung der Individuenzahlen über die Arten (Evenness) Aufschluss über Umweltveränderungen geben. Kurzfristige Ereignisse wie Sturmfluten oder Tsunamis können durch den Eintrag von allochthonen Individuen die Diversität einer Totengemeinschaft erhöhen, sofern die eingebrachten Arten aus anderen Habitaten stammen (Hippensteel & Martin 2000).

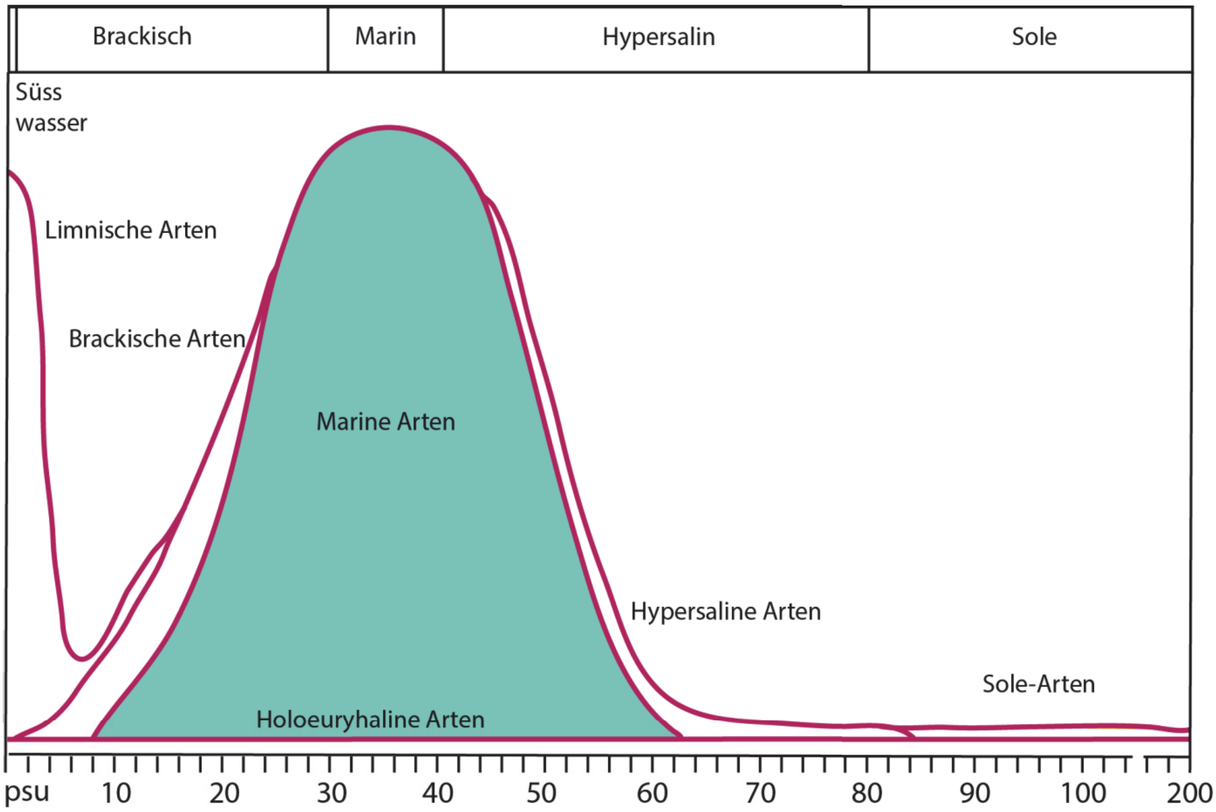

Abb. 4: Diversität aquatischer Organismen in Abhängigkeit von der Salinität (verändert nach Hedgpeth 1957)

Herkunft der Arten im Brackwasser

Remane (1958) teilte Organismen, die im Brackwasser leben, in vier Gruppen ein: Holeuryhaline Arten kommen in fast allen Salinitätsbereichen vor, bevorzugen jedoch meist einen bestimmten Bereich. Euryhalin-limnische Arten wandern vom Süsswasser ins Brackwasser ein. Euryhalin-marine Arten dringen vom Meer her ins Brackwasser vor. Spezifische Brackwasserarten kommen meist nur im Brackwasser vor. Je nach Salinität teilte Remane (1958) diese Gruppen noch weiter in Untergruppen ein.

Reproduktion

Die Reproduktion kann im Brackwasser verändert sein, sie kann sich zeitlich verkürzen, in der Zahl der Nachkommen verringern oder ganz ausbleiben. Der Bereich in dem Foraminiferen und Ostrakoden reproduzieren liegt innerhalb ihres ökologischen Optimums. So benötigt beispielsweise *Cyprideis torosa* für das Schlüpfen mindestens 15°C Wassertemperatur (Heip 1976).

Brackwasseremergenz und -submergenz

Ein besonderes Phänomen von Brackgewässern ist neben Salinitäts- und Temperaturschwankungen eine thermohaline Schichtung des Wasserkörpers, die sich im Verlauf des Jahres räumlich und zeitlich verändern kann (Frenzel 2006). Dies kann dazu führen, dass Organismen der Salinität folgend in tiefere Habitate ausweichen, was als Brackwassersubmergenz bezeichnet wird (Remane 1958). Fehlende Konkurrenz anderer Arten kann Submergenz begünstigen. Man unterscheidet die basale Submergenz, bei der die untere Vorkommensgrenze absinkt von der oberen Submergenz, bei der die obere Vorkommensgrenze tiefer liegt. Die Verschiebung beider Grenzen nennt man totale Submergenz (Remane 1958). Beim Aufsteigen von Organismen in höhere Wasserbereiche spricht man von Emergenz. Ursache hierfür kann das Ausweichen von Süßwasserarten auf die geringer saline Oberflächenschicht sein, aber auch Sauerstoffarmut des basalen Wasserkörpers kann eine Rolle spielen.

Morphologie

Brackwasserorganismen sind meist kleiner als ihre marinen Verwandten und schalentragende Organismen haben häufig dünnere Schalen, wie es schon seit langem von Mollusken der Ostsee bekannt ist (Remane 1934). Aber auch von Mikrofaunen sind salinitätsbedingte morphologische Effekte bekannt. Hypo- und Hypersalinität sowie Salinitätschwankungen, in einigen Fällen auch Schwermetallbelastungen, gelten als Ursachen für Missbildungen bei Foraminiferen (Geslin et al. 2000, 2002). Verschiedene Missbildungstypen kommen vor, die grob in drei Gruppen eingeteilt werden können: Deformationen einzelner Kammern kommen am häufigsten vor, während Richtungswechsel beim Aufwuchs der Kammern und Mehrlingsbildung deutlich seltener auftreten (siehe Kapitel 1.4.1) Der Anteil der Missbildungstypen innerhalb einer Population scheint unabhängig vom Lebensraum zu sein (Polovodova & Schönfeld 2008). Auch einige Ostrakodenarten können abhängig von der Salinität spezielle Schalenmerkmale ausbilden (siehe Kapitel 1.4.2). Änderungen von Siebporenumrissen kommen bei *Cyprideis torosa* vor (Rosenfeld & Vesper 1977). Knotenbildungen auf den Klappen wurden bei *Cyprideis*, *Cytherissa*, Limnocytheriden und *Ilyocypris* beobachtet (Meisch 2000). Nur bei *Cyprideis torosa, Leucocytherella sinensis* und *Limnocythere inopinata* wurden diese Phänomene umfassend untersucht und bei den beiden ersteren Arten mit der Salinität korreliert (z. B. Yin et al 1999, Keyser 2005, Frenzel et al. 2012, Fürstenberg et al. 2015). Bei *Cyprideis torosa* ist abhängig von der Salinität auch ein unterschiedliches Größenwachstum zu beobachten, wobei die geringsten Klappenlängen bei rund 7 psu vorkommen (Van Harten 1975, Boomer & Frenzel 2011).

1.4 Paläontologie in athalassischen Gewässern

1.4.1 Foraminiferen

Foraminiferen sind einzellige Organismen, von denen die meisten der ca. 50.000 rezenten und fossilen Arten Gehäuse aus Kalk oder agglutinierte Schalen besitzen, die von einem organischen Zement und den davon verbundenen Sand- oder Siltkörnern besteht (Ziegler 1983, Goldstein 1999). Diese mineralischen Gehäuse sind fossil leicht überlieferbar. Sicher sind Foraminiferen seit dem Kambrium nachgewiesen. Foraminiferen leben vor allem im Meer und Gewässern an der Küste. Die meisten Foraminiferenarten leben benthonisch, einige jedoch planktonisch im offenen Ozean. Nur sehr wenige Arten kommen in Binnengewässern vor, und nur sofern diese brackisch sind. Die wenigen echten Süßwasserarten tragen keine Gehäuse und sind daher paläontologisch nicht relevant (Holzmann & Pawloski. 2002). Von den mikroskopisch kleinen Foraminiferen lassen sich die Großforaminiferen abgrenzen, die in ihren bis zu 13 cm großen Gehäusen endosymbiontische Algen beherbergen. Sie leben in der photischen Zone tropischer Meere und sind daher gute Indikatoren für tropische Riffe und Küsten. Die größten von ihnen waren die Nummuliten des Eozäns mit bis zu 13 cm Durchmesser (Ziegler 1983). Sie traten auch gesteinsbildend auf und lieferten beispielsweise den Baustoff für die Pyramiden in Ägypten (Klemm & Klemm 1992). In der Erdgeschichte sind Foraminiferen besonders für die Biostratigraphie des Känozoikums wertvolle Leitfossilien.

In athalassischen Gewässern findet man die benthonische, euryhaline Art *Ammonia tepida* besonders häufig, oft als einzige Foraminiferenart. Dagegen kommt die ebenfalls euryhaline und in paralischen Gewässern oft verbreitete Art *Haynesina germanica* in athalassischen Gewässern selten vor, in den weit von den Küsten entfernten Gewässern überhaupt nicht. Mehrere Arten der Gattungen *Cribroelphidium* und *Elphidiella* sind häufiger vertreten, auch in küstenfernen Seen. Ebenso kommen einige agglutinierende Arten, ursprünglich im höheren Intertidal beheimatet, wie *Miliammina fusca* und Arten der Gattung *Haplophragmoides*, in Binnengewässern vor (Beiträge 2 und 4). Foraminiferen im Binnenland wurden schon des Öfteren in verschiedenen Studien erwähnt, meist aber nicht in Paläomilieustudien einbezogen. Bereits Bartenstein (1939) beschrieb *Haplophragmoides canariensis* aus vier Thüringer Binnensalzstellen, konnte sie aber niemals lebend nachweisen oder sie einer stratigraphischen Einheit zuordnen. Dies ist auch in weiteren Studien in Thüringen bis heute nicht gelungen (Greifeld 1966, Pint et al. 2012; Beitrag 2). Bartenstein (1939) beobachtete aber, dass *Haplophragmoides canariensis* mit salztoleranten Ostrakoden wie *Limnocythere inopinata*, *Darwinula stevensoni* und *Heterocypris salina* assoziiert war und daher eine brackische Art sein muss. Nach wie vor wird der Eintrag von marinen Organismen wie Foraminiferen in athalassische Gewässer diskutiert. Obwohl der Transport von Mikroorganismen im Gefieder von Wasservögeln als wahrscheinlich gilt (Helmdach 1979), wird andererseits das Überleben mariner Taxa in Reliktgewässern ehemaliger Meere für möglich gehalten oder eine vormalige Verbindung eines Binnengewässers mit einem Meer angenommen. So sind beispielsweise nach Gusskov et al. (2008, 2012) Foraminiferen aufgrund einer Verbindung des Aralsees mit dem Weißen Meer während des Atlantikums in den Aralsee eingewandert. Für den Eintrag durch Vögel spricht wiederum, dass vor allem große Salzseen von athalassischer Fauna besiedelt werden, weil Vögel häufiger große Wasserflächen als Rastplatz erkennen und nutzen.

Missbildungen an Foraminiferengehäusen

Missbildungen von Gehäusen von Foraminiferen kommen relativ häufig vor, vor allem im randmarinen und athalassischen Lebensraum. Während in den Ozeanen höchstens 1 % der Foraminiferengehäuse Fehlbildungen aufweisen (Polovodova & Schönfeld, 2008), steigt die Rate in Küstennähe unter ökologischem Stress auf etwa 5 % (Pint & Frenzel 2010). In hypersalinen Binnengewässern können mehr als die Hälfte der Foraminiferen missgebildet sein. Der Grund könnte die relative ökologische Stabilität der marinen Lebensräume gegenüber den Binnengewässern sein. Missbildungen von Foraminiferen sind daher vor allem von anpassungsfähigen, intertidalen Arten dieser Lebensräume bekannt. Der wichtigste Steuerungsfaktor ist hierbei die Salinität. Der Mechanismus solcher Fehlbildungen ist im Detail noch unbekannt. Möglicherweise führen Fremdionen im Kristallgitter zu einer Aufwachstörung. Das würde erklären, warum Schwermetallbelastung mancher Küstenbereiche und Häfen ebenfalls zu einer Erhöhung der Missbildungsrate führen. Warum Hypersalinität die höchsten Missbildungsraten erzeugt, kann nur vermutet werden. Auch hier könnte das normale Gehäusewachstum durch die hohe Ionenkonzentration gestört werden. Man kann grob zwischen Aufwachsstörung und Teilungsstörung unterscheiden, wobei die erstere sehr viel häufiger vorkommt. Gehäusefehlbildungen scheinen auch artspezifisch aufzutreten. Missbildungen bei rotaliiden Arten mit spiralen Gehäusen kommen häufiger vor als bei milioliden Formen. Bei Arten mit sehr variabler Gehäusemorphologie können nur Teilungsstörungen als Missbildung erkannt werden (Geslin et al. 2000). Höhere Raten als 1 % werden stets in paralischen oder kontinentalen Lebensräumen erreicht. Typische Lebensräume mit erhöhter Salinität sind Lagunen, Ästuare und Salzseen. An Küsten in der Nähe von Häfen und Stätten kann es aufgrund von Wasserverschmutzung ebenfalls zur Erhöhung der Missbildungsraten kommen, am stärksten begünstigt jedoch Hypersalinität das vermehrte Auftreten missgebildeter Gehäuse von Foraminiferen. (Almogi Labin et al. 1992, 1995). Da sie meist klimatisch bedingt im ariden oder semiariden Gebieten vorkommt, können sehr hohe Missbildungsraten ein wichtiger Klimaindex sein (Beiträge 6 und 7).

1.4.2 Ostrakoden

Ostrakoden gehören zu den Crustacea und sind charakterisiert durch einen zweiklappigen Carapax, der aus Kalzit besteht. Sie besiedeln alle aquatischen Ökosysteme und sind seit dem Kambrium nachweisbar. Etwa 65.000 Arten sind bis heute beschrieben worden (Hinz-Schallreuter 1999). Die bei vielen Arten auch anhand der Klappen morphologisch unterscheidbaren Männchen und Weibchen produzieren Eier, aus denen Larven schlüpfen, die nach etwa sieben Häutungen das Adultstadium erreichen.

Die häufigste Ostrakodenart in athalassischen Gewässern ist die wahrscheinlich weltweit verbreitete *Cyprideis torosa*. In Australien kommt die sehr ähnliche *Cyprideis australiensis* vor und auch auf den amerikanischen Kontinenten leben *Cyprideis*-Arten, die sich nur geringfügig von *Cyprideis torosa* unterscheiden. Als einzige euryhaline Ostrakodenart verträgt *Cyprideis* Salinitäten von 0,5 – 100 psu, in Einzelfällen wahrscheinlich sogar darüber hinaus (Klie 1938, Meisch 2000). Nur bei sehr hohen Salinitäten und in dysoxischem Milieu kommt sie monospezifisch, aber dann häufig in großer Individuenzahl vor (Beiträge 6 und 7). Da *Cyprideis torosa* einen breiten Salinitätsbereich besiedelt, spielt die Begleitfauna eine große Rolle bei der Rekonstruktion des Lebensraums (Beitrag 3).

Ähnlich wie *Cyprideis torosa* kommt auch die Brackwasserostrakode *Cytheromorpha fuscata* in Binnengewässern mit Salinitäten bis 20 psu vor, allerdings sehr viel seltener als *C. torosa* (Neale & Delorme 1985; Wennrich 2005; Beitrag 4). Salztolerante limnische Arten der Nordhemisphäre gehören vor allem den Gattungen *Darwinula*, *Candona*, *Ilyocypris*, *Physocypria*, *Eucypris*, *Heterocypris*, *Sarscypridopsis* und *Limnocythere* an (Meisch 2000). De Deckker (1981) beschreibt diese Arten als Taxa, die mehr als 3 psu tolerieren können. Brackische Arten marinen Ursprungs leben nur in den größten athalassischen Gewässern, wie Aralsee und Kaspisches Meer. Die häufigsten Gattungen sind *Loxoconcha*, und *Leptocythere* (Boomer 2012).

Morphologische Besonderheiten und Ökophänotypen

Viele Cytheracea bilden Siebporen aus, auf ihre ökologische Verwendbarkeit wurden jedoch bisher nur die Siebporen von *Cyprideis torosa* untersucht, seitdem Rosenfeld und Vesper 1977 den Zusammenhang von Umrissform der Siebporen von *C. torosa* und der Gewässersalinität erkannt hatten. Bis zu etwa 100 Siebporen befinden sich auf jeweils einer adulten Klappe von *C. torosa*. Größe und Umriss der Poren können stark variieren. Bei geringer Salinität überwiegen Poren mit rundem Porenumriss. Bei steigender Salinität weicht der Umriss zunehmend von der runden Form ab und wird meist länglich oder seltener ypsilonförmig. Nur in hypersalinen Gewässern ist die Ypsilonform die häufigere irreguläre Variante. Die zum

Teil deutlichen Größenunterschiede der Siebporen, die nach eigenen Beobachtungen jedoch nur von Klappe zu Klappe variieren, sind bislang in keiner Studie untersucht worden und somit ungeklärt. Innerhalb einer Probe können auch große Unterschiede bei der Siebporenverteilung verschiedener Klappen auftreten. Vermutlich führen geringe Sedimentationsraten zu einer hohen Fossilkonzentration in solch einer Probe, die eine hohe Zeitspanne und potentiell mehrere Salinitätszyklen umfasst.

Knotenbildung auf den Klappen kommt bei mehreren Ostrakodenarten vor, aber nur bei *Cyprideis torosa* (Keyser 2005, Frenzel et al. 2012) und bei *Leucocytherella sinensis* (Fürstenberg et al. 2015) sind sie umfassend untersucht. Häufiger als adulte Tiere sind Individuen des letzten Juvenilstadiums A-1 betroffen. Die Knoten bilden sich an definierten Stellen und können unterschiedlich ausgeprägt sein. Sie entstehen durch eine Osmoregulationsstörung während der Häutung, wobei sich die frische Kutikula an bestimmten Stellen aufbläht. Diese Aufwölbungen werden beim anschließenden Kalzifizieren fixiert. Diese ausgeprägte morphologische Veränderung hat dazu geführt, dass *C. torosa* in zwei Ökophänotypen untergliedert wird: *Cyprideis torosa* forma *littoralis* (ohne Knoten) und *Cyprideis torosa* forma *torosa* (mit Knoten), die noch im 19. Jahrhundert als separate Arten betrachtet wurden. Der Salintätsbereich, bei dem sich Buckel bilden, lässt sich relativ genau definieren. Zwischen 2 und 8 psu bilden bis zu 10 % der Tiere Buckel, unterhalb von 2 psu steigt der Wert rasch auf etwa 90 % an (Frenzel et al. 2012). Die Buckelbildung erfolgt unabhängig vom Gewässertyp. In Seen vollarider Klimate konnte Buckelbildung bislang nicht beobachtet werden (siehe Beiträge 5 bis 7).

1.4.3 Kalkige Makrofauna

Die Kenntnis der Makrofauna, insbesondere von Mollusken, kann beim Aufspüren limnischer Sedimente hilfreich sein, weil aus dieser Gruppe ebenfalls typische Vertreter in athalassischen Gewässern vorkommen. Die meist makroskopisch erkennbaren Gastropoden und Bivalven sind ein erster Hinweis im Gelände. Charakteristische Taxa athalassischer Gewässer sind die Gastropoden *Hydrobia* spp. *Melanoides tuberculata* und *Theodoxus* spp.sowie die Bivalven *Cerastoderma* spp.und *Dreissena polymorpha*. Auch die Seepocke *Balanus amphitrite* kann vorkommen. Dagegen weisen marine Mollusken, Korallen und Seeigelreste durch ihre stenohaline Ökologie auf offenmarine Lebensräume hin (Beiträge 6 und 7).

1.4.4 Endemismus

Die geographische Isolierung eine Ökosystems, z. B. eines Sees, führt nach einer gewissen Zeit zu der Entwicklung von nur hier vorkommenden, endemischen Arten. Dabei entsteht durch Radiation und Nischenbesetzung ein Artenschwarm („species flock“) mit phänotypischen Unterschieden. Der flock entstammt entweder einer Art (monophyletisch), oder mehreren Arten (polyphyletisch), meist aus aufeinander folgenden Einwanderungswellen. Die Entwicklung eines species flock ist taxonabhängig. So bilden unter gleichen Bedingungen die Ostrakodengattungen *Cyprideis* und *Cytherissa* (Cytherideidae) ausgeprägte flocks, Darwinulidae und Cyprididae dagegen nicht (Martens 1997). Alter und Ausprägung von flocks sind ökosystemspezifisch und können daher nicht zur Alterseinschätzung von Seen eingesetzt werden. Der *Cyprideis*- flock des Tanganyika Sees ist älter als der *Cytherissa*- flock aus dem Baikalsee obwohl dieser mehr als doppelt so alt wie der Tanganiyika See ist (Wouters & Martens2001, Schön & Martens 2012). Es kann jedoch beim Auftreten von Endemismus von einem Mindestalter und einer Mindestgröße des Gewässers ausgegangen werden. Endemismus entsteht nach durchschnittlich ein bis zwei Millionen Jahren, kann sich aber jedoch deutlich schneller oder langsamer entwickeln (Martens 1997, Schäfer 1997). So entwickeln sich Artenschwärme in der Litoralzone schneller als in den tieferen Bereichen von Gewässern (Martens 1997). Der Anteil der endemischen Arten und Gattungen kann nur bedingt zur Beurteilung der Ausprägung und Dauer der Isolation der Gewässer eingesetzt werden.

1.5 Fragestellungen der vorliegenden Arbeit

Bei der Analyse aquatischer Sedimente ergeben sich folgende Fragestellungen, insbesondere bei Verdacht auf einen athalassischen Lebensraum:

a. Wie lassen sich athalassische und thalassische Mikrofaunen unterscheiden?

b. Welche Methoden der Paläomilieuanalyse lassen sich für athalassische Gewässer anwenden?

c. Lassen sich die Mikrofaunen geogener und klimatogener athalassischer Gewässer unterscheiden?

1.6 Struktur der vorliegenden Arbeit

Nach der Einführung in das Thema im Kapitel 1 werden im Kapitel 2 die verwendeten Methoden bei Probenahme, Analysen und Dokumentation beschrieben. In Tab. 2 werden die verschiedenen Auswertungsverfahren ihren Anwendungsbereichen zugeordnet und bewertet.

Kapitel 3 behandelt Fallbeispiele aus bereits veröffentlichen Studien, eingereichten und vorbereiteten Manuskripten, sowie kürzeren Beiträgen, sortiert nach den drei Hauptaspekten (A, B C und D), wie im Folgenden beschrieben:

<u>A Geogene Salinität in Gewässern humider Klimazonen.</u>

1. Die Recherche von salinen rezenten Binnengewässern in Mitteldeutschland aufgrund von Literaturhinweisen als Beispiele von Binnensalinaren in humidem Klima (Beitrag 1, Publikation, veröffentlicht 2014, Pint et al., *Palaeogeography, Palaeoclimatology, Palaeoecology*).

2. Holozäne Historie der Siebleber Senke, eines mitteldeutschen Sees mit geogenen Salzeinfluss als Beispiel eines Binnensalinars in humidem Klima (Beitrag 2, Manuskript, nach Review wiedereingereicht am 19.11. 2015, Pint et al., *The Holocene*).

3. Die Recherche zum Salzzeiger *Cyprideis torosa* in Deutschland und zu dessen Begleitfauna (Beitrag 3, Publikation, veröffentlicht 2012, Pint et al*., International Review of Hydrobiology*).

4. Die Mikrofauna der brackischen Mansfelder Seen (Beitrag 4, Manuskriptskizze).

5. Fallbeispiel aus der Literatur: Die Mikrofauna der kanadischen Seen im ehemaligen Becken des Lake Agasiz.

B Klimatisch gesteuerte Salinität im ariden Klima

6. Die artenarme Mikrofauna des Aralsees vor 1960 (Beitrag 5, Manuskriptskizze).

7. Historie des ehemaligen Salzsees von Tayma (Saudi-Arabien) (Beitrag 6, Publikation, veröffentlicht 2011, Engel et al., *Quaternary International*.

8 Detaillierte Untersuchung der extrem artenarmen Thanatozönose des frühholozänen Salzsees bei Tayma (Beitrag 7, Manuskript in Vorbereitung).

9 Fallbeispiele aus der Literatur: Tibetische Seen als Beispiel brackischer Hochgebirgsseen; hypersaliner Pool im Riftsystem des Toten Meeres; ehemalige Seen in der nördlichen Sahara; ehemalige Seen in der Rhub-Al-Khali-Wüste in Saudi-Arabien.

C Morphologische Besonderheiten

10 Knotenbildung auf den Klappen von *Cyprideis torosa* als Resultat einer fehlgesteuerten Osmoregulation der Tiere in einem definierten Salinitätsbereich. (Beitrag 8, Publikation, veröffentlicht 2012, Frenzel et al., *International Review of Hydrobiology*).

11 Siebporen-Umrisse als salinitätsabhängiges Schalenmerkmal bei *Cyprideis torosa*. (Beitrag 9, extended Abstract, veröffentlicht 2012, Frenzel et al., *Joannea*).

D Athalassische Gewässer in Küstennähe

12 Fallbeispiele aus der Literatur: Timsah springs (Israel); Salt Lake (Hawaii).

Kapitel 4 beinhaltet eine Synthese aus den Einzelbeiträgen. Daraus wird eine Empfehlung für die Klassifizierung von kontinentalen Sedimentproben entwickelt, die in Form eines Schlüssels das Erkennen und Bewerten von athalassischen Lebensräumen erleichtern soll.

2 Methoden

Für die Paläomilieuanalyse können sowohl Proben von der Sedimentoberfläche aquatischer Gewässer, aus Aufschlüssen, als auch aus Sedimentkernen verwendet werden. Bei rezenten Proben ist die Unterscheidung von Lebend- und Totengemeinschaft sinnvoll. Hierzu wird die Probe unmittelbar nach der Entnahme mit einem Gemisch aus Alkohol und Bengalrosa versetzt (Lutze & Altenbach 1991). Zum Zeitpunkt der Probenahme noch lebende Organismen nehmen eine intensive rosa Farbe an, die auch nach dem Trocknen noch erhalten bleibt, was für die Erkennung lebender Foraminiferen eine gebräuchliche Methode ist. Vor der weiteren Verarbeitung wird die Probe eingewogen und wenn möglich das Volumen ermittelt. Danach wird sie mit H_2O_2 versetzt, um feine organische Bestandteile zu lösen und so ein Verkleben der getrockneten Probe zu verhindern. Danach kann fraktioniert mit 0,063, 0,125 und 0,25 mm Maschenweite nass gesiebt werden, häufig reicht aber auch ein 0,1 mm Sieb aus. Anschließend werden die Proben getrocknet und abgefüllt. Unter einem Stereomikroskop werden in einer Zählschale die Mikrofossilien bestimmt und gezählt. Mindestens 300 Individuen werden auf diese Weise dokumentiert. Bei wenigen Arten ist auch eine Schnellanalyse mit nur 100 Exemplaren möglich. Um eine möglichst genaue quantitative Auswertung zu erhalten, ist eine Identifizierung der Taxa mindestens auf Gattungsebene erforderlich. Dafür werden zusätzlich zur taxonomischen Standardsystematik auch vorangegangene Untersuchungen aus der Umgebung des Fundortes herangezogen. Für die Auswertung der Rohdaten aus Identifizierung und Zählung steht eine Vielzahl von Methoden zur Verfügung: Zu den empirischen Methoden zählen Identifizierung von Taxa, Zählung, qualitative und quantitative Darstellung der Verteilung, Einteilung in ökologische Gruppen und Mutual-Range Methoden. Statistische Methoden umfassen Diversitätsindizes, Cluster-Analysen, Principal Component Analysis, Modern Analog Technique und Transferfunktionen (Frenzel et al. 2010). Alle Methoden erfordern eine möglichst exakte Identifizierung der Taxa, mindestens auf Gattungsebene, und ein Minimum an Zähl-daten (Tabelle 2).

Bei der statistischen Analyse athalassischer Sedimente wird aufgrund der meist geringen Diversität vor allem die PCA eingesetzt, da hier auch Daten anderer Herkunft, z. B. aus Sedimentologie und Geochemie, mit einbezogen werden können. Dadurch lassen sich auch kontinentale mit randmarinen Sedimentationsräumen vergleichen. Verwendet wird hierfür die Programme PAST (Hammer et al. 2001) oder SPSS (Backhaus et al. 2013). Transferfunktionen lassen sich nur bei ausreichender Diversität anwenden. Bei zu geringer Artenanzahl können auch geeignete Trainingssätze kombiniert werden. Hierfür wird das Programm C2 verwendet (Juggins 2007). Problematisch ist dabei allerdings, dass athalassische Arten häufig hohe Toleranzen aufweisen. Die Begleitfauna ist daher besonders wichtig. Bei sehr geringer Diversität können meist nur noch empirische Analysen angewendet werden.

Tabelle 2: Methoden zur Analyse von Foraminiferen- und Ostrakodenassoziationen

Methode		Ziel	Vorteile	Nachteile
Empirisch	Quantitative/ Qualitative Verteilungen der Taxa	Intuitiv erfassbare, visuelle Darstellung der Verteilung	Einfaches Verfahren zur ersten Darstellung	Subtile und graduelle Faunenwechsel sind vor allem bei diversen Faunen nicht leicht zu erkennen
	Ökologische Gruppen	Klassifizierung aufgrund von ökologischen Präferenzen und Toleranzen	Schnell durchführbare Gruppierung, auf verschiedenste Umweltfaktoren anwendbar	Ökologie muss bekannt sein, keine quantitative und nur separate Rekonstruktion von Umweltparametern
	Indikatortaxa	Charakterisierung des Lebensraums durch einige wenige, sehr typische Taxa	Schnell durchführbar, bei ausreichender Individuenzahl auch bei geringer Diversität anwendbar	Indikatortaxa müssen vorkommen, und ihre charakteristischen Merkmale müssen ausreichend bekannt sein
	Gemeinsame ökologische Toleranzen (Mutual Range)	Rekonstruktion ökologischer Parameter über gemeinsamen Überschneidungsbereich der ökologischen Toleranzen	Durchführbar für verschiedenste Parameter, quantitative Ergebnisse	Toleranzbereiche aus rezenten Analysen für möglichst viele Taxa notwendig, einzelne Arten bestimmen das Ergebnis, meist hohe Artenzahl notwendig
	Morphologische Methoden	Erfassung ökophänotypischer Variationen	Weitere Differenzierung von ökologischen Parametern möglich	Nur bei wenigen Arten durchführbar
Statistisch	Diversitätsindizes	Ökosystembewertung	Erster Hinweis auf ökologischen Stress und Stabilität eines Lebensraumes	Bei geringen Diversitäten nicht sinnvoll
	Juvenil/Adult-Verhältnis und Klappen/Carapax-Verhältnis bei Ostrakoden	Taphonomie	Darstellung von Strömungs– und Turbulenzregimewechseln	Individuenreiche Ostrakodentaxa und schonende Aufbereitung nötig
	Modern Analog Technique	Paläomilieurekonstruktion durch direkten Vergleich mit rezenten Assoziationen	Kombinierte Effekte von Umweltfaktoren erfassbar	Umfangreicher Rezentdatensatz ähnlicher Rahmenbedingungen notwendig
	Hauptkomponentenanalyse (PCA)	Identifizierung und Wichtung von Steuerungsfaktoren	Veränderungen einzelner Faktoren über Profile darstellbar, Integration und Kombination verschiedenster Daten möglich	Nur Darstellung, keine quantitative Rekonstruktion
	Cluster-Analyse	Gruppierung von faunistisch ähnlichen Proben, z. B. für Zonierungen	Anschauliche Darstellung von Ähnlichkeiten mithilfe eines Dendrogramms	Ergebnis teilweise methodenabhängig, homogener und umfangreicher Datensatz nötig
	Transferfunktionen	Rekonstruktion von ökologischen Parametern	Quantitative Ergebnisse mit Irrtumsabschätzung	Umfangreicher Rezentdatensatz und spezielles Programm erforderlich

3 Fallstudien

3.1 Vorbemerkungen

Entscheidende Merkmale aller athalassischer Gewässer sind die große Distanz zum Meer und das Vorkommen von Brackwasserarten. Die hier untersuchten Gewässer können zwei unterschiedlichen Typen von salinen Binnengewässern des Flachlandes zugeordnet werden: Athalassische Gewässer geogener Salinität, meist in humidem Klima, deren Salinität durch Salzvorkommen in Sedimenten hervorgerufen wird und in der Regel niedrig ist, und athalassische Gewässer klimatogener Salinität in semiaridem bis aridem Klima, deren meist hohe Salinität durch Evaporation gesteuert wird.

3.2 Athalassische Gewässer geogener Salinität

3.2.1 Thüringen und Sachsen-Anhalt

Zur Mitteldeutschen Trockenzone gehören das Thüringer Becken und der südliche Teil von Sachsen-Anhalt (Wennrich 2005). Durch seine Lage im Windschatten des Harzes regnet es hier im Durchschnitt etwas weniger als im übrigen Deutschland. Diese klimatische Anomalie reichte jedoch nicht aus, um salzhaltige Gewässer durch Verdunstungskonzentration zu erzeugen. Hier spielen Salze aus den unterlagernden Sedimentgesteinen eine bedeutende Rolle. Sie werden gelöst und gelangen so in die Gewässer. In Mitteldeutschland sind vor allem der permische Zechstein, sowie der Mittlere Muschelkalk und der Mittlere Keuper aus der Trias salzführend (Seidel 1995). Solequellen und salzhaltiges Grundwasser erhöhten die Ionenkonzentration vieler postglazialer Gewässer in Mitteldeutschland. Im Bergbauzeitalter kontaminierte zusätzlich Kalisalz aus den Rückstandshalden die Gewässer. Verlandungsflächen ehemaliger Seen sind aufgrund salzhaltiger Böden heute noch von halophilen Floren bewachsen. Ab dem Mittelalter breiteten sich die halophilen Floren aufgrund der Landnutzung zunächst aus. Diese Salzflecken sind jedoch ebenso wie salzhaltige Gewässer seit dem vorherigen Jahrhundert stark rückläufig aufgrund von Sanierungen zugunsten der Landwirtschaft (Rebele 2009). Auch für den Bergbau wurden, wie im Fall des Süßen Sees in Sachsen-Anhalt, Gewässer trockengelegt. Gewässerschutzmaßnahmen rund um den Kalibergbau trugen ebenfalls zur Verminderung des Salzeinflusses der Binnensalzstellen bei.

Beitrag 1:

Ostracoda from inland waterbodies with saline influence in Central Germany: Implications for palaeoenvironmental reconstruction

veröffentlicht 2015, Pint et al., *Palaeogeography, Palaeoclimatology, Palaeoecology*

Mehrere Gewässer des Thüringer Beckens wurden ausgewählt und untersucht. Die Auswahl erfolgte aufgrund von Literaturhinweisen auf ein Salzvorkommen, der räumlichen Nähe zu Salzflecken, Solegewässern oder Rückstandshalden des Kalibergbaus. Sowohl die Ostrakodenfauna wie auch der Wasserchemismus wurden untersucht, um Salzgehalt und typische Salzzeiger zu ermitteln.

Ergebnis: Alle Gewässer zeigten maximal leicht erhöhte Salzgehalte. Die Ionenkomposition variierte zwischen Chlorid und Sulfat als Anionen und Calcium und Natrium als Kationen. Die Gewässer enthielten individuelle Ostrakodenfaunen mit typischen Vertretern der jeweiligen Habitate, typische Salzzeiger oder Brackwassertaxa fehlten aber in der Lebendfauna und blieben auf wenige Taxa subrezenten Materials beschränkt. Dies bestätigt das Verschwinden der vormals vorhandenen Binnensalinare.

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Konzeption	**X**	X								
Geländearbeiten	**X**	X		X	X	X	X	X		X
Datengewinnung	**X**	X		X	X	X	X	X	X	X
Datenauswertung und Interpretation	**X**	X	X	X		X			X	
Schreiben	**X**	X								
Publikationsäquivalent	**1,0**	n. a.	n. a.	n. a.	n. a.	n. a.	n. a.	n. a.	n. a.	n. a.

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Ostracoda from inland waterbodies with saline influence in Central Germany: Implications for palaeoenvironmental reconstruction

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ABSTRACT

As a necessary precursor to reconstructing the palaeoenvironmental conditions likely to be temporarily influenced by salt bearing ground waters, modern sites of Central Germany, known from the literature to be continental salt water localities, were investigated for their ostracod faunas. Analysing their associations enables the test of several methods in palaeoenvironmental analysis based on ostracods. In total, 54 ostracod taxa are documented. One species, *Microdarwinula zimmeri*, is new for the area. Interesting is the historical occurrence of *Cyprideis torosa* and *Cytheromorpha fuscata*, typically regarded as indicators of brackish water. The draining of wetlands has led to the disappearance of many former inland salt sites so that only a few of the sampled water bodies still show slightly elevated salinity (oligohaline range). The most important factors for the distribution of ostracod associations are groundwater influence, turbidity and ecological stability, whereas the type of dominating ions is of lesser importance because of time-averaging using taphocoenoses from surface sediments in our study. The relative proportion of ecological groups of ostracods appears to be the best tool for reconstructing past habitat types. The newly established Ostracod Permanence Index and Ostracod Turbulence Index allow the recognition of the influx of ground and surface waters, perennial habitats and flowing waters. A test of the Mutual Ostracod Temperature Range (MOTR) method demonstrates its capability to reconstruct, with a precision of +/−2 °C, the mean July and January air temperatures for the time interval 2002–2012. Additionally, the study contributes to the poorly known Recent distribution of ostracods in Central Germany.

1. Introduction

Ostracoda, small bivalved crustaceans, are one of the microfossil groups best suited for reconstructing past continental environments. For such purposes, ecological and distribution data are needed. However, studies on Recent ostracods in the German federal states of Thuringia and Saxony-Anhalt are very rare, despite numerous investigations on Pleistocene Ostracoda by Pietrzeniuk, Diebel and Fuhrmann (e.g. Diebel and Pietrzeniuk, 1969, 1977, 1978a, 1978b, 1984; Fuhrmann, 2008, 2013). The aim of the present study is 1) to test ostracods as indicators of habitat types and 2) to establish baseline distributional data for the modern ostracod fauna from Central German localities previously reported to have salt water influence. Our analysis includes the test of 3) the Mutual Ostracod Temperature Range (MOTR) method for palaeoclimate reconstruction. The study prepares palaeoenvironmental reconstructions based on Holocene ostracod associations in Central Germany.

2. Study area

In Central Germany, alternating sequences of Triassic sandstone and limestone reflect the oscillation between shallow sea and terrestrial fluvial sedimentation in the Thuringian Basin during the Permian and Triassic. Jurassic and Cretaceous as well as Tertiary strata are rarely preserved today. The larger central part of the Thuringian Basin is covered by Triassic rocks whereas sediments of the Permian, including Zechstein evaporites, are only exposed at its margin. Numerous sinkholes formed due to the dissolution of Permian and Triassic evaporites (Seidel, 2003; Wirth, 2008). After the silting up or artificial draining of the lakes covering the depressions in historical times, large reed flats with small relict water bodies developed. Although most of these water bodies contain salinities less than 2 psu today, halophytic plants still grow on the salt bearing soil in many places (Westhus et al., 1997). The 23 sites

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investigated in this study are situated in the Thuringian Basin and its surroundings (Fig. 1).

The modern climate in Germany is generally humid, however, large parts of Central Germany are characterised by relatively dry conditions resulting from the rain shadow caused by the Harz Mountains. The annual precipitation is 450–500 mm/year (Fabig, 2007). Annual air temperature fluctuations are characterised by strong seasonality in the temperate climate zone. Mean values of −0.5 °C for January and 17.5 °C for July are published for the period 2002–2012 in Jena, south-eastern Thuringian Basin (weather station of the Max Planck Institute for Biogeochemistry, Jena).

3. Material and methods

We carried out a sampling campaign in the Thuringian Basin and adjacent areas (see Supplementary data) from summer 2006 to late spring 2007 complemented by samples from the former Süsser See and Bindersee taken in 2004. Additionally, more detailed collections were carried out around Bilzingsleben and in the area of Bad Kösen–Groß Heringen in summer 2010 as well as the Pennickental at Jena in summer 2011. Data from Altenburg (Fuhrmann, 2010) and the Plothener fish ponds sampled in spring 2012 by Gemeinhardt and Frenzel (2014) as well as older material from Erfurt and Bad Kösen probably taken in 1966/68, from Siebleben taken in 1969 and from Bilzingsleben taken in 1978/79 (material from the Diebel & Pietrzeniuk ostracod collection in the Museum für Naturkunde Berlin) complete our data set. Those older collections are stored dried in micropalaeontological slides. The valves were identified and counted by us for adding the data to our modern training set. During our sampling campaign in 2006 and 2007, conductivity, pH and temperature of the water were measured using a multiprobe WTW 340i and the habitats were characterised. The sampling was carried out exclusively in shallow waters (<1 m water depth) reflecting the small size of the majority of water bodies. Many of the 23 sites were sampled at multiple stations covering different habitat types and almost all stations were sampled only one time resulting in 77 modern samples in total (compare Fig. 1 and Supplementary data).

Water quality analyses included ion chromatography (Dionex DX-120) for anions and ICP-OES (Varian 725 ES) for cations. After transformation of ionic masses into equivalent masses, the percentages of the main ions were calculated and used for chemical classification of water bodies.

Ostracods were sampled with a hand net (ca. 0.1 mm) by scraping the uppermost 1–2 cm of the surface sediment. The 100–200 ml sample was washed through a 200 μm sieve. Ostracod carapaces and valves were picked from the dry residues using a wetted fine-tipped brush. Ostracods were counted and identified relying on Meisch (2000) and Fuhrmann (2013). Valves recognisable as reworked through abrasion or corrosion marks were excluded from analysis. For most samples, it was not possible to identify individuals that were still living during sampling due to the use of material from various collections. Therefore, we decided to use total associations instead.

The software package PAST (Hammer and Harper, 2005) served for statistical analyses. A PCA on samples containing at least 50 valves each was carried out in order to identify associations and groups of samples bound to habitat types and environmental factors respectively. This PCA is based on 62 of the 77 samples and untransformed relative abundances of 36 ostracod species after excluding species present in less than three samples or never exceeding 5% of the association of each sample. Before analysis, the matrix was tested on highly correlated (>|± 0.9|) variables using Spearmen's Rank Correlation as recommended by Backhaus et al. (2010). The MOTR method uses calibrated temperature ranges determined from a combination of species distributions and an interpolated climate model in a Geographical Information System (Horne, 2007; Horne and Mezquita, 2008). The calibrated

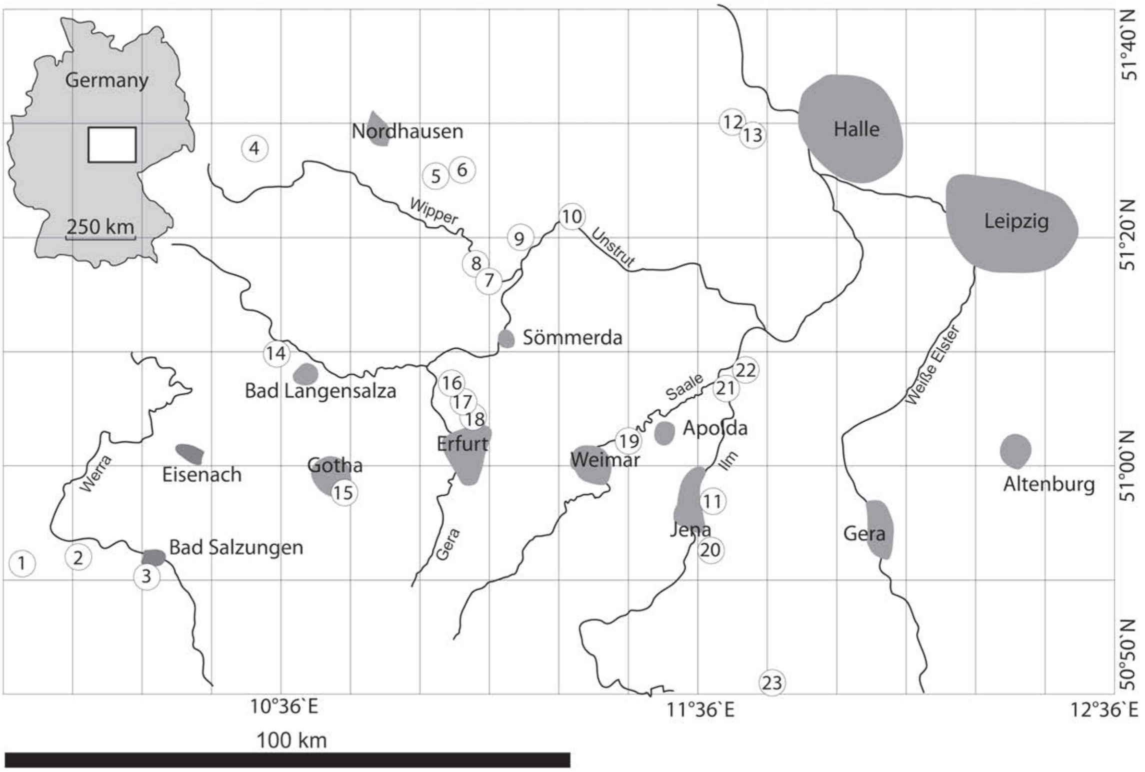

Fig. 1. Map of the investigated sites in Central Germany. The numbers indicate the studied modern localities; number of sampled stations are bracketed: 1 — Unterbreizbach (1); 2 — Merkers (1); 3 — Etmarshausen (1); 4 — Kraja (1); 5 — Numburger Quellen (1); 6 — Stausee Kelbra (1); 7 — Kindelbrück (4); 8 — Bilzingsleben (13); 9 — Esperstedt (2); 10 — Solequelle Artern (1); 11 — Fürstenquelle Jena (2); 12 — Süsser See (2); 13 — Bindersee (3); 14 — Grossengottern (2); 15 — Siebleben (2); 16 — Hasslebensee (2); 17 — Alperstedter See (1); 18 — Stotternheimer See (1); 19 — Oßmannstedt; 20 — Pennickental (7); 21 — Groß Heringen (3); 22 — Bad Kösen (9); and 23 — Plothener fish ponds (2).

ranges used herein are based on OMEGA (Ostracod Metadatabase of Environmental and Geographical Attributes; Horne et al., 2011, 2012). As a test of its performance, the MOTR method is applied to the Recent sites of the Thuringian Basin comparing its temperature estimations with measured January and July temperatures. The Ostracod Permanence Index was calculated using the percentage of species living in permanent waters divided by the sum of species living in permanent and temporary waters. The Ostracod Turbulence Index is defined as the ratio of turbulent and streaming water preferring species (mesorheophilic + polyrheophilic) and calm water preferring species (rheophobic + oligorheophilic) not counting rheoeuryplastic species. Both indices rely on ecological classifications given by Meisch (2000) and Fuhrmann (2013). The ecological classification of main species is given in Table 1.

Quantitative distribution data are to be added to the NODE (Nonmarine Ostracod Distribution in Europe) database (Horne et al., 1998) which contributes to OMEGA. The ostracod material collected in this study will be archived in the museum Mauritianum in Altenburg, Thuringia.

4. Results

4.1. Water bodies

We exclusively sampled shallow waters, because all Recent aquatic habitats affected by salt water brines in Central Germany are small water bodies. Most sampled habitat types were ponds (natural and man-made) and streams. However, there is a remarkable proportion of spring-fed waters (Table 1). Despite preferentially sampling sites reported in literature as saline influenced, only a few showed elevated salinity (oligohaline range). Salinity ranges from 0.1 to 1.8 with a median of 0.5. The majority of the studied waters is SO_4^{2-}-dominated (Table 1).

4.2. Ostracoda

37 ostracod species were identified in 65 samples from 23 sites in Thuringia and southern Saxony Anhalt (Table 1, Plate I, Appendix A). The most frequent and abundant species include *Candona candida*, *Candona neglecta* and *Ilyocypris bradyi* (Table 1). True brackish water species are *Cyprideis torosa*, which occurs in a few sites, and *Cytheromorpha fuscata* found in one site with low numbers only; however, both species are represented exclusively by empty valves. All valves of *C. torosa* are representing the smooth (not noded) form. Semiterrestrial ostracod species such as *Microdarwinula zimmeri* and *Scottia pseudobrowniana* were found in the Bilzingsleben area in high abundance.

Most ostracod species found are either present in a few samples or widely scattered over habitat types. Thus, associations indicative for selected habitats are hardly recognisable. Only the helocrenic species *Fabaeformiscandona brevicornis* and *Cryptocandona vavrai* are limited to spring-fed waters. Taxa preferring turbulent water are present in almost all samples in large numbers. Perennial forms are rare and mostly limited to temporary water bodies, the littoral zone of lakes and ponds and in ditches. Despite their indication of perennial waters, forms of permanent waters mostly co-occur with them in such samples. *Scottia pseudobrowniana*, a semi-terrestrial species (Meisch, 2000), is limited to fen and spring sites. Taxa of lakes and ponds are widely scattered over all habitats, their highest diversity (>3 species), however, is found in lake and pond samples only (Table 1).

In the present study we tested the MOTR method by applying it to combined Recent ostracod assemblage of 35 species for which a reliable calibration set exists (Horne and Mezquita, 2008). The reconstruction was obtained by integrating records from all studied 65 samples and 23 sites in the Thuringian Basin. The result indicates a mean July air temperature range of +16 to +20 °C and a mean January air temperature range of −1 to +2 °C (Fig. 2).

5. Discussion

A grouping of the studied inland water bodies was done based on its ionic composition with a focus on ionic dominances (Table 1). Two main groups of anionic composition may be distinguished: Cl^-- and SO_4^{2-}-dominated waters. To explain the origin of these ions, a groundwater contact to NaCl- or $CaSO_4$-bearing sediments underground is assumed in most cases. NaCl is typical for evaporites of Zechstein strata underground but can also occur in Triassic sediments (Seidel, 2003; Wirth, 2008). In the case of $CaSO_4$-dominated water, sediments from outcrops in addition to that from the underground are also possible sources. Gypsum-rich sediments occur frequently in Permian and Triassic formations and may lay on the surface.

The list of ostracod species found in our material comprises all taxa frequently found in Quaternary sediments of Central Germany associated with *Cyprideis torosa* (Pint et al., 2012). The only exceptions are *Limnocytherina sanctipatricii* and *Cytherissa lacustris* which are absent from our Recent material. Both species are known to prefer cold water (Meisch, 2000), hence they are more typical for glacial or transitional climatic conditions or the deep water of oligotrophic lakes and are not expected for our Holocene interglacial shallow water associations. Remarkable is the occurrence of living *Microdarwinula zimmeri* in a fen sample at Bilzingsleben, a species previously known from sites south of the Alps only (Fuhrmann, 2013).

Principle Component Analysis (PCA) on ostracod distribution over samples shows only two species and a few samples with high loadings onto the first two axes (Fig. 3). The first axis explains only 16.4%, the second one 11.0% of the variance of data. This finding points to a heterogeneous data set and a multitude of factors influencing ostracod distribution. Examining loadings of samples reveals waters dominated by $CaSO_4$ on the right side and those dominated by NaCl on the left side of the diagram. *Candona candida* shows the highest loading on axis 1, hence is typical for $CaSO_4$-rich waters in our data set. *Heterocypris salina* characterises the other side of the first axis, which fits its characterisation as preferring NaCl-rich waters (Meisch, 2000). The second axis may be explained by its being negatively impacted by flowing water. Whereas four species preferring flowing water (*Ilyocypris bradyi*, *Prionocypris zenkeri*, *H. salina*, *Candona neglecta*) are grouped at the lower end of the second axis, the highest loadings are associated with *Potamocypris zschokkei* which prefers stagnant waters (Meisch, 2000). The placing of samples within the PCA is reflecting our interpretation of the two axes as well.

Surprisingly, presence/absence distribution of species does not allow the discrimination of habitat types (Table 1). A possible explanation for this circumstance is the lack of differentiation of living and dead individuals in parts of our data set. Due to this, samples are time-averaged tentatively containing subfossil material or maybe even allochthonous specimens in rare cases. As Westhus et al. (1997) report, and we have noticed in many locations, many salt water sites known from older literature were drained and converted into areas for agriculture after the Second World War. Hence, we could find a low number of sites with elevated salinity only and many smaller water bodies have disappeared and were replaced by reed areas (Ried). Biasing effects of sampling season are assumed to be marginal because of analysis of total associations comprising assemblages of probably some years.

Taxa given in Meisch (2000) and Fuhrmann (2013) as helocrenic occur not only in springs and spring influenced water bodies, but also in streams, fens and in some of the ponds (Table 1). The presence of helocrenic ostracod species in other than spring-fed water bodies may be caused by seepage in or close to such waters not recognised by us during field work. We assume therefore more species than only *Fabaeformiscandona brevicornis* and *Cryptocandona vavrai* as documented by our study to be indicator-species for spring impact. We decided to use the proportion of helocrenic species and also the proportion of cold water species within the associations to investigate its proxy value assuming that the sampled springs have constant low water temperatures

Table 1

Distribution of modern Ostracoda in surface samples from Central Germany. Species never exceeding 2% in any sample or occurring in less than two samples are omitted. The remaining are sorted based on ecology (Meisch, 2000; Fuhrmann, 2013). Samples listed according to water type and salinity range, which are derived from the measured conductivity. The dominate anion and cation are listed if they were measured. Samples from the oligohaline range and *Cyprideis torosa* as the only true brackish water species present in numbers are shaded. The relative abundance of ostracod taxa is given by dominance values following Engelmann (1978): full circle = eudominant (≥32%), three quarter circle = dominant (≥10%), half circle = subdominant (≥3.2%), quarter circle = recedent (≥1.0%) and empty circle = (present with <1.0%).

Locality (site number)	Coordinates		Ecology	Helocrenic								Meso- to polyrheophil								Perennial					S	Permanent					Lakes and ponds										Environment				
	Nord	East	Sample	*Psychrodromus olivaceus*	*Ilycypris inermis*	*Fabaeformiscandona brevicornis*	*Cryptocandona vavrai*	*Fabaeformiscandona breuli*	*Potamocypris zschokkei*	*Eucypris pigra*	*Cavernocypris subterranea*	*Ilyocypris bradyi*	*Prionocypris zenkeri*	*Candona candida*	*Limnocythere inopinata*	*Potamocypris unicaudata*	*Ilyocypris gibba*	*Cyclocypris ovum*	*Pseudocandona rostrata*	*Pseudocandona sucki*	*Physocypria kraepelini*	*Fabaeformiscandona fabaeformis*	*Cyprois marginata*	*Potamocypris arcuata*	*Scottia pseudobrowniana*	*Candona neglecta*	*Cypridopsis vidua*	*Cyprideis torosa*	*Pseudocandona marchica*	*Herpetocypris reptans*	*Heterocypris salina*	*Cyclocypris laevis*	*Plesiocypridopsis newtoni*	*Sarscypridopsis aculeata*	*Heterocypris incongruens*	*Darwinula stevensoni*	*Cypria ophtalmica*	*Cypris pubera*	*Pseudocandona albicans*	*Notodromas monacha*	Water type			Salinity	Chemistry
8	51°17,440'	11°03,560'	DP-Bilz-8	●	●	○	○	◔				◔		◑				◑								◔											◑		◔		Spring	Discharge	Permanent	Freshwater	no data
8	51°17,440'	11°03,560'	DP-Bilz-1	●	◔	◕	◑							○								○			●				◑			○					○		◔						
8	51°16,605'	11°03,561'	DP-Bilz-2	●	◑	◔			◑			◑										◑			◑				○			◑							◔						
7	51°15,816'	11°04,600'	DP-Bilz-11			◑						○		○				◕								●											◕		◑						
11	50°54'56.98"	10°16'22.64"	Fü-1						●					◑																			◑				◔								SO_4^{2-}; Ca^{2+}
22	51°7'44.56"	11°43'9.98"	J.Berg		◑					●				◕												◕													◑				?		
21	51°6'9.13"	11°40'14.52"	ABKL7							◔	●		◑	◑	○																														
21	51°6'9.13"	11°40'14.52"	Bahnd								●		◑	◑		◔																													
22	51°7'49.10"	11°43'24.19"	ABKL4							◑		◕	◕	●	◕											◕																		Oligohaline	Cl^-; Na^+
22	51°7'49.10"	11°43'24.19"	Quelle							◑		◕	◕	●	◕											◑																			
19	51°0,999'	11°25,593'	B9						◑			◕				●	◕										◑								◕							Standing	P.?		SO_4^{2-}; Ca^{2+}
19	51°0,998'	11°25,598'	B1/2						◑			◑				●											◕				○				◕										
5	51°25'39.91"	10°57'47.05"	Nu-2									◔				○		○													●				◕						Spring influenced			Freshwater	Cl^-; Na^{2+}
3	50°48'06.68"	10°16'22.64"	Et-1						◑			◕			●												◑				◔														
9	51°19'22.63"	11°10'28.39"	Esp-3									●		◕			◔	◑					○	○			◕				◕	◔	◑		◑										Cl^-; Na^+
11	50°49'50.46"	10°07'36.38"	Fü-2									●		◔		◑	●							○		◔					○														SO_4^{2-}; Ca^{2+}
8	51°15,816'	11°04,600'	Grü-1											○				◕								◕		●									●								
8	51°17,440'	11°03,560'	DP-Bilz-9	◔								○		◕				◑								◕						○					●								no data
8	51°17,328'	11°03,608'	Bilz-1	◑	◔							◔	●												◔	◕			◔										○			Flowing			
7	51°15,816'	11°04,600'	DP-Bilz-7	◑	◑	◑		◔				◕	◕				○	◑				○			◔	◕													◔						
22	51°7'49.10"	11°43'24.19"	ABKL5		◑					◑		◑	◕	●	◕											◕											◑				Spring			Olig.	Cl^-; Na^+
22	51°7'49.10"	11°43'24.19"	Saale		◔					◑		◑	◕	●	◑	◑										◕					◔						◑								
21	51°06,279'	11°40,107'	ABKL11							◔	◑	◕	◕	●	◑											◑											◔		◑						SO_4^{2-}; Ca^{2+}
22	51°6'16.36"	11°40'6.55"	ABKL9							○	◕	◕	◕	●	◑											◔											◔		○						
22	51°7'38.86"	11°43'6.21"	ABKL6		◕					◑		◕	◕	◕												◕											◔		◑						
22	51°7'38.86"	11°43'6.21"	Kalkw.		◕					◑		◕	◕	◕		◔										◕						◔					◔		◑						
22	51°7'44.56"	11°43'9.98"	ABKL3		◑					●				◕												◕													◔						

4	51°27'03.57"	10°30'51.07"	Kra-1						◔			◑	●	◔			◑		◕							◕					◔		◔								Stream		Permanent	Freshwater	
8	51°16,965'	11°04,330'	Bilz-12				◔					◑			◕			◔								◑				◑	●														no data
8	51°17,328'	11°03,608'	DP-Bilz-4	◕	◑	○						◔	●	○					○							◑			◔			◔													
7	51°15,829'	11°04,682'	DP-Bilz-6	◕	◑							◕	◕	◔			◕									◑					●														
8	51°16,128'	11°04,083'	Bilz-10		○							●	◕	○												◑				◔	◕				◕										
1	50°48'59.00"	9°58'49.98"	Br-1									●	◔	●						◔						○																			Cl^-; Na^{2+}
20	50°54,385'	11°37,896'	P3	◕	◕	◔		◕	◑	◕				○				○											◕																SO_4^{2-}; Ca^{2+}
20	50°54,355'	11°37,630'	P5.1	◔	○				●																																Pond	Standing			
9	51°20'46.55"	11°10'50.48"	Esp-1									◔	◕	◑												◕	○				◑										Ditch				Cl^-; Na^+
16	51°06'06.97"	11°00'01.92"	Haß-4											●			◕	◑		◔																								Oligohaline	SO_4^{2-}; Ca^{2+}
16	51°06'06.97"	11°00'50.29"	Haß-5									◑		●			◑																												
14	51°08'33.29"	10°35'22.35"	Gros-7											●				◑			◕																●								no data
14	51°08'33.29"	10°35'22.35"	Gros-6											○	◔		●	◕	◔				◔			◕						◑													
13	51°29'12.29"	11°29'12.29"	1018-1												◕	◕												◕								●					Lake or pond				Cl^-; Na^+
13	51°29'12.29"	11°29'12.29"	1018-3												◑	●										◔	◔	◑			◑					◕	◕								
13	51°29'12.90"	11°43'24.20"	Rol-1									◑			◑	◑	◔		◑	◑						◑	◕	◕	◑		◑		◑				◔			◔					
17	51°04'28.86"	11°02'21.97"	Alp-1									◕	◑	◕	◑	◔		◔									◕				◕	◑		◑			◕							Freshwater	SO_4^{2-}; Ca^{2+}
6	51°25'36.54"	10°58'13.11"	Ke-1													◔								◑			◔	◑			◕	◔	●		◔			◕	○						
12	51°29'43.65"	11°40'21.41"	Sü-1									◕		◔	◑			◕	◕	◕						◑	◑	◑			○	◑	○												Cl^-; Na^+
12	51°29'55.99"	11°39'44.10"	1017-1									◔		◑	◕	◑							○			◑	◔	○			○					●									
18	51°02'56.08"	11°03'29.29"	St-1									●	◕	◔			◑	◑		◔								◔					◑	◕	◔										SO_4^{2-}; Ca^{2+}
15	50°56'07.87"	10°45'46.81"	Sieb-Grei											○	◔					◔		◔	●								◔	◕						◕		○			Perennial		SO_4^{2-}; Mg^+
16	51°05'47.33"	11°00'50.29"	Haß-3									◑		◕	◕		●			○	◑						◑					○					◑								SO_4^{2-}; Ca^{2+}
16	51°05'47.33"	11°00'50.29"	Haß-2									◕		●				◔		○							●					◑													
20	50°54,396'	11°37,950'	P2		◕				●	◕		○		●						○																									
20	50°54,388'	11°37,953'	P2.1		◑				◕	○		○		●						○																									
2	50°49'38.67"	10°07'12.49"	Me-1									○		◑						◔						●					●				◔										SO_4^{2-}; Na^+
23	50°39,310'	11°45,631'	SRT 1											●							◑						○						○				○								SO_4^{2-}; Ca^{2+}
23	50°38,927'	11°45,695'	SGT 2											●			◕				◕					○										●									
15	50°56'07.87"	10°45'46.81"	Sieb-2									◑		◔	◕	◕	◑	◔					◑	◑		◕	◔				◕	◑	○			○									SO_4^{2-}; Mg^+
20	50°54,390'	11°37,458'	P6.1	◕	●					◔		◕		◔																															SO_4^{2-}; Ca^{2+}
20	50°54,390'	11°37,458'	P6	◕	●			◔	◑					◔				○																				◔							
8	51°17,226'	11°03,668'	DP-Bilz-10									◕						◔													◔			●					◑						no data
8	51°16,124'	11°06,526'	Bilz-3									◔		◕	○	◔		◕									◕									◕	◕			◔					
7	51°15,879'	11°04,734'	Bilz-7		◔							●		◑	◑			◕								◑	◑		◔	◔	◔	◔								◕					
8	51°17,340'	11°03,661'	Bilz-2	◑		◕								◔				◑				◑			◑				●			◑						◔		Fen	Flow.			
8	51°17,340'	11°03,661'	DP-Bilz-3	◕	◔	◕	◔					◔		○				◔				◑			◕	◑			◕		◔	◑		◔					○						
20	50°54,371'	11°37,835'	P4						◑	●								●																								S.			SO_4^{2-}; Ca^{2+}

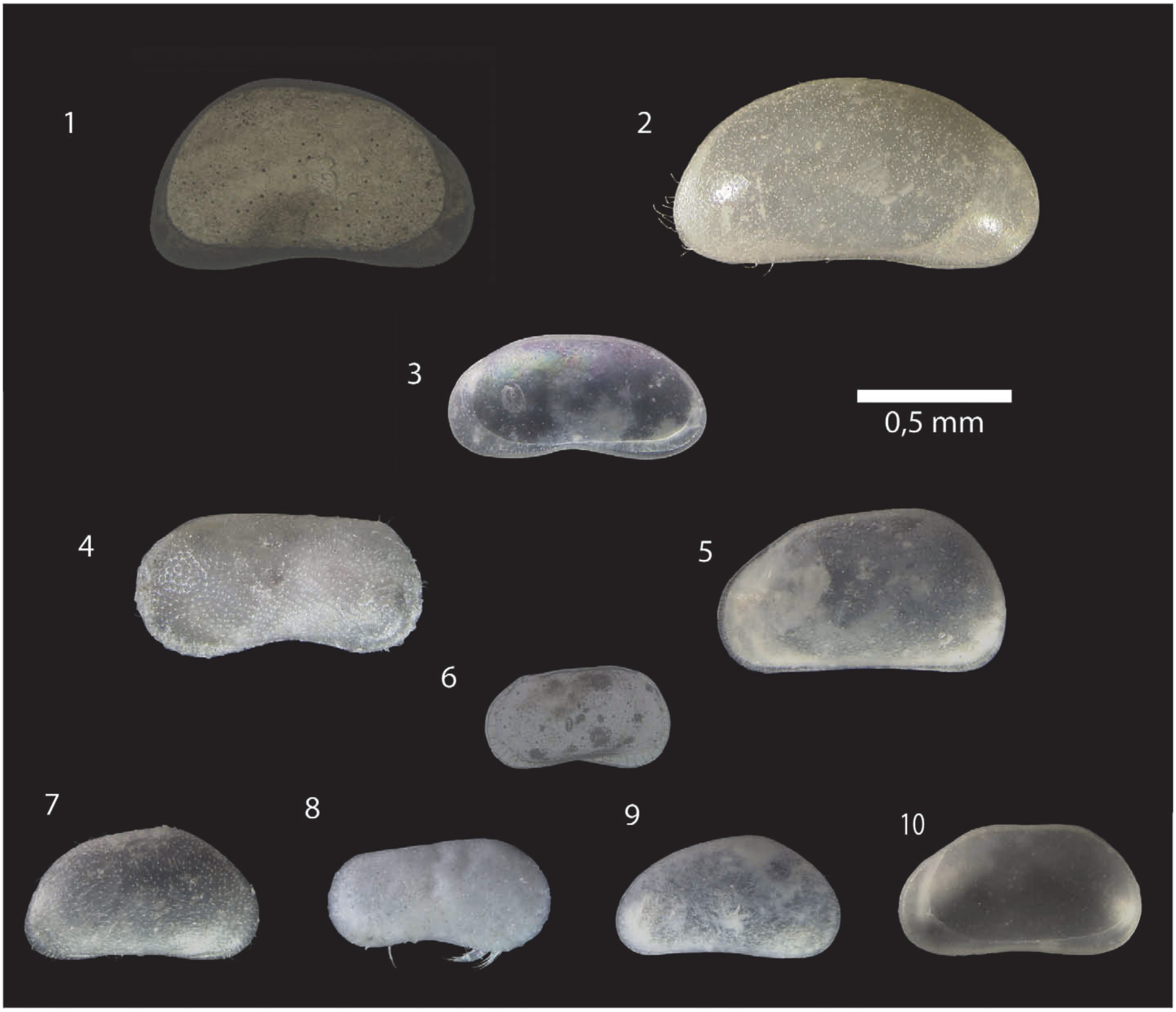

Plate I. Selected ostracods found in modern surface sediments of Central Germany: 1: *Candona candida*; 2 : *Psychrodromus olivaceus*; 3 : *Fabaeformiscandona brevicornis*; 4: *Ilyocypris inermis*; 5: *Pseudocandona marchica*; 6 : *Limnocythere inopinata*; 7 : *Potamocypris zschokkei*; 8 : *Ilyocypris bradyi*; 9 : *Potamocypris unicaudata*; 10: *Pseudocandona albicans*. All specimens are from Pennickental at Jena, except *L. inopinata* and *C. candida* from Stausee Kelbra.

thus being favoured by cold water taxa. A mutual high proportion of helocrenic and cold water taxa is indeed characteristic for clearly spring influenced habitats (Fig. 4). Furthermore, all samples without documented spring influence do not contain any helocrenic ostracod species. On the other hand, there are some spring samples without helocrenic taxa — in fossil samples like those the groundwater influence would not be detectable by ostracod analysis alone.

The general presence of ostracod species preferring turbulent waters, even in standing water bodies, is not surprising if considering the shallow water depth of all sampling sites. Waves and currents triggered by wind create turbulence in shallow waters — most of our samples come from less than 30 cm water depth. For discriminating flowing waters from other habitats by using the Ostracod Turbulence Index (OTI = relative abundance of rheophobic and oligorheophilic species within the sum of those and meso- to polyrheophilic species) and for checking the reliability of the Ostracod Permanence Index (OPI = relative abundance of species occurring in permanent waters only within the sum of those and others preferring perennial waters) we cross-plotted both indices. We expected a high OTI and OPI for rivers and other flowing waters and a high OTI and low OPI for the very shallow water of the littoral zone in standing waters. Except for one spring-fed brook, all ostracod associations from flowing waters plot above a value of 90% of the Ostracod Turbulence Index (Fig. 5) illustrating its value as current proxy. Several other associations plot into the same field of the diagram in Fig. 5, mainly springs. Ostracod associations from perennial waters and the littoral zone of stagnant permanent waters probably temporary falling dry due to lake level variability can only be found at values of the Ostracod Permanence Index <12% (Fig. 5). There are, however, ostracod associations from permanent waters that can be found as well. As our data show, flowing waters may be identified in the fossil record by an OTI of >90% and a consideration of the OPI is not necessary for this. Identifying temporary waters or the littoral zone of standing permanent waters with a fluctuating water level requires a low OPI, in our data set <12%, but a high diversity of species attributed by Meisch (2000) and Fuhrmann (2013) to lakes and ponds may help to distinguish such samples.

The brackish water indicator *Cyprideis torosa* (Pint et al., 2012) occurs in five localities, one time together with another brackish water

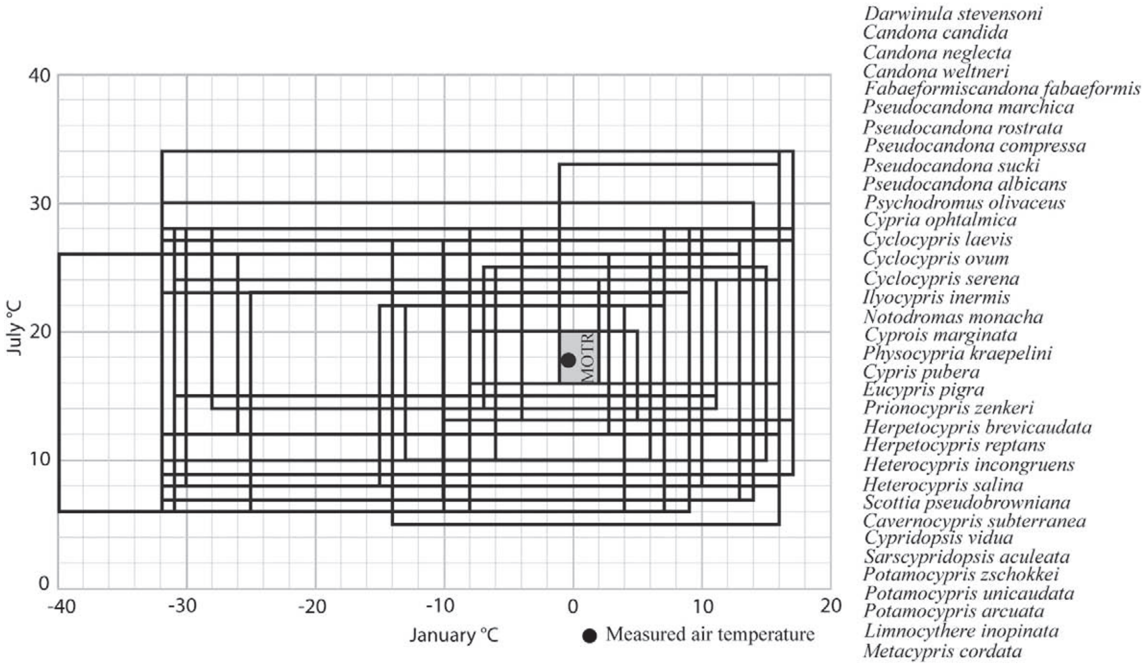

Fig. 2. Mutual Ostracod Temperature Range (MOTR) of recent sites of the Thüringer Basin with calibrations based on Horne and Mezquita (2008) and updates from OMEGA, December 2011. The black lines represent the temperature range of each species listed here. Only species for which a reliable calibration set exists (Horne and Mezquita, 2008) are used for the MOTR.

ostracod, *Cytheromorpha fuscata* (Frenzel et al., 2010). Both species are considered to represent a salinity >0.5 psu, while the single presence of the un-noded form of *C. torosa* may signify even higher salinity (Frenzel et al., 2012). *C. torosa* is known to be wide-spread in Quaternary athalassic brackish waters of Central Germany (Pint et al., 2012) and forms stable and long-living populations in larger salty inland waters as it is known for *C. fuscata* as well (Salziger See, Wennrich, 2005). Four of the seven studied localities yielding this indication were, however, freshwater sites during sampling (Table 1). We know for some of these water bodies (Süßer See, Stotternheim) that they were brackish in the recent past and assume all those *C. torosa* and *C. fuscata* valves to be subfossil. This seems to be the case for the very few freshwater literature records of *C. torosa* as well (Pint et al., 2012). Hence, they are interpreted to reflect past salinity values. *Heterocypris salina* occurs throughout the covered salinity range and does not show an indicator value for brackish water as already stressed by Meisch (2000) and Fuhrmann (2013).

Analysis of water chemistry preferences indicates *Psychrodromus olivaceus*, *Fabaeformiscandona brevicornis*, *Pseudocandona marchica*, *Ilyocypris inermis* and *Potamocypris zschokkei* as typical for Ca-dominated waters (Fig. 6). *Ilyocypris gibba* and *Potamocypris unicaudata* are characteristic species for SO_4-dominated and *Heterocypris salina*, *Limnocythere inopinata* and *Prionocypris zenkeri* for Cl-dominated water. *Heterocypris incongruens* and *Cypridopsis vidua* do not occur in Ca-dominated water in our material and their absence could support the identification of Ca-dominated water in reconstructions.

The test of the MOTR method (Horne, 2007), using an aggregated species assemblage for the region, satisfactorily reproduced the

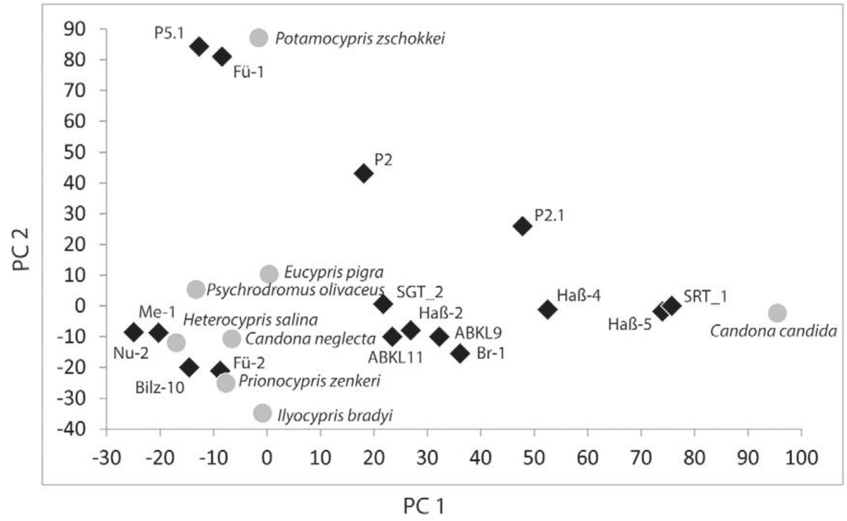

Fig. 3. Principle Component Analysis (biplot) of 62 modern samples and 36 associated ostracod species from the Thuringian Basin. The first axis, reflecting water chemistry, explains 16.4% and the second 11.0% of the variance. $CaSO_4$-dominated waters are found at high loadings and NaCl-dominated waters at low loadings on the first component. Only species with loadings higher than +20 and lower than −20 (sites); higher than +10 and −10 (species) are labelled.

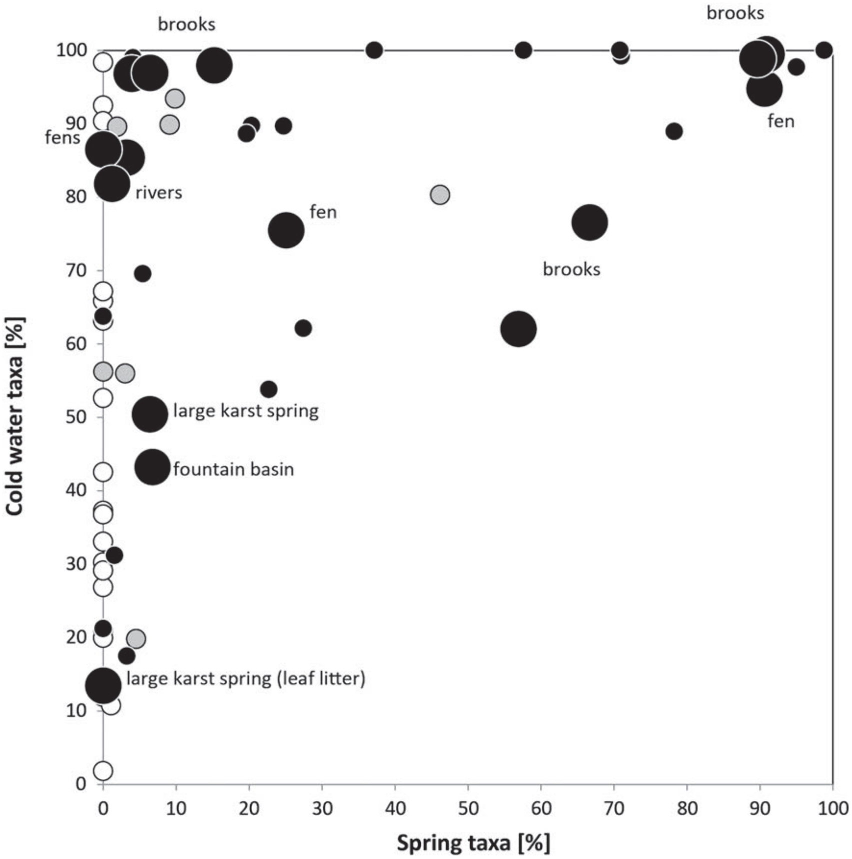

Fig. 4. Cross-plot of relative abundances of ostracod species occurring often in springs versus cold-stenothermal species based on ecological classifications by Meisch (2000) and Fuhrmann (2013). The habitat types are indicated by large black circles for sites immediately in front of a groundwater discharge, small black circles for sites close to a spring, small grey circles for sites with assumed spring influence and white circles for other sites without spring influence. Text within the diagram refers to springs (large black circles) and gives further habitat details.

present-day mean July and January air temperatures to within +/−2 °C. This is consistent with measured air temperatures for the region of these sites (July +17.5 °C, January −0.5 °C, Weather Station of the Max Planck Institute for Biogeochemistry, Jena, 2002–2012). This demonstrates very well its potential for palaeotemperature reconstructions. However, it is worth noting that no single site in the Thuringian Basin dataset contained all 35 species; MOTR analyses based on less diverse assemblages from individual sites would not yield such a precise, closely-constrained result, although even very broadly reconstructed temperature ranges would still enclose the true values. Moreover, inspection of Fig. 2 shows that obtaining a narrow-ranging reconstruction is not necessarily reliant on the presence of stenothermal taxa (i.e. with narrow calibrated ranges) but can also be obtained from the mutual overlap of the wide temperatures ranges of more or less eurythermal taxa. The MOTR method, as with all mutual climatic range methods, tends to provide greater precision with higher numbers of taxa.

6. Conclusions

The distribution analysis of living ostracods is compulsory to gain ecological data needed for palaeoenvironmental analysis. Total associations not differentiating between living and dead specimens hampers the interpretation of species autecology, however, it allows water type comparisons with fossil associations. A purely qualitative approach in analysing ostracod associations from potential inland brackish water sites is of limited use for palaeoenvironmental analysis because of its low habitat and water chemistry discrimination. Quantitative analyses relying on proportions of ecological groups show a much better discrimination performance. By using the proportion of helocrenic taxa, the Ostracod Permanence Index and the Ostracod Turbulence Index, the recognition of groundwater inflow, current of flowing waters and perennial habitats is possible in most cases. In addition, *Scottia pseudobrowniana* and *Microdarwinula zimmeri* may be used as indicators for semi-terrestrial habitats. The occurrence of subfossil *Cyprideis torosa* and *Cytheromorpha fuscata* in surface sediments indicates a historical salinity change for those water bodies caused by land amelioration. *Heterocypris salina* alone is not a reliable brackish water indicator. For the reconstruction of mean monthly air temperature, the precision and utility of the MOTR method has been demonstrated by means of a test on the modern ostracod fauna of Central Germany.

7. List of ostracod taxa

Candona angulata Müller, 1900
Candona candida (O.F. Müller, 1776)
Cando na neglecta Sars, 1887
Candona weltneri Hartwig, 1899
Candonopsis kingsleii (Brady & Robertson, 1870)
Cavernocypris subterranea (Wolf, 1920)
Cryptocandona vavrai Kaufmann, 1900
Cyclocypris laevis (O.F. Müller, 1776)
Cyclocypris ovum (Jurine, 1820)
Cypria ophtalmica (Jurine, 1820)
Cyprideis torosa (Jones, 1850)

The present specimens are all smooth shelled, i.e. without nodes, and are therefore assigned as *Cyprideis torosa* f. *littoralis* sensu Brady, 1868.

Cypridopsis vidua (O.F. Müller, 1776)
Cypris pubera O.F. Müller, 1776

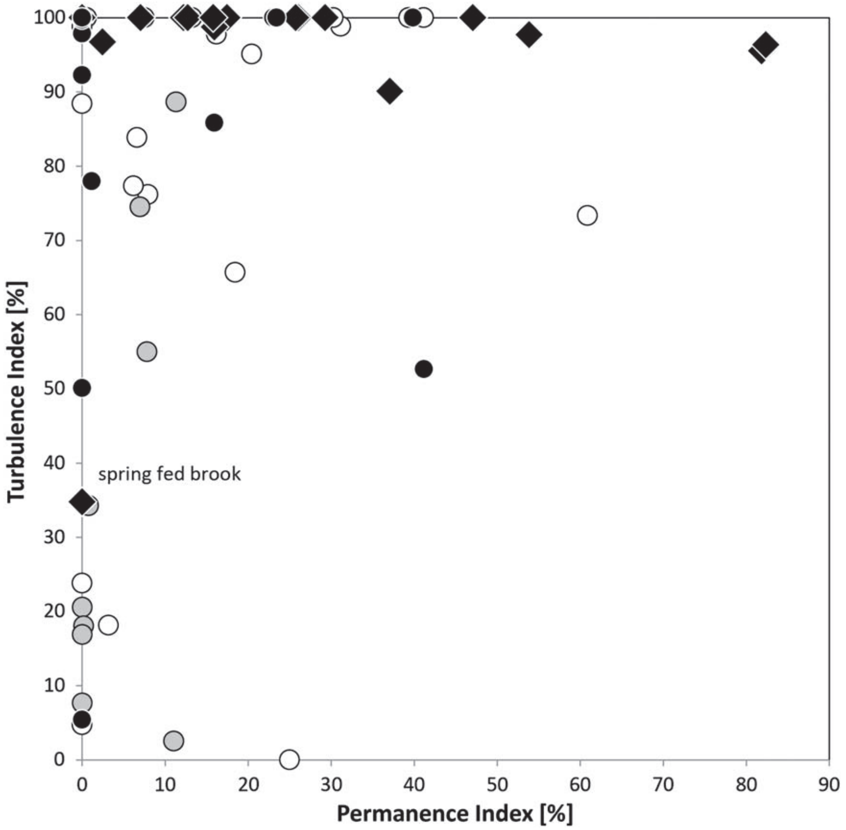

Fig. 5. Ostracod Permanence Index (relative abundance of species occurring in permanent waters only within the sum of those and others preferring perennial waters) compared to Ostracod Turbulence Index (relative abundance of rheophob and oligorheophilic species within the sum of those and meso- to polyrheophilic species). The ecological classification of species is based on Meisch (2000) and Fuhrmann (2013). The habitat types are indicated by black diamonds for flowing water, black circles for springs, small grey circles for the littoral of standing water bodies and perennial waters and white circles for other habitat types. The only flowing water site with a low Ostracod Turbulence Index is marked.

Cyprois marginata (Straus, 1821)
Cytheromorpha fuscata (Brady, 1869)
Darwinula stevensoni (Brady & Robertson, 1870)
Eucypris pigra (Fischer, 1851)
Eucypris virens (Jurine, 1820)
Fabaeformiscandona breuili (Paris, 1920)
Fabaeformiscandona brevicornis (Klie, 1925)
Fabaeformiscandona fabaeformis (Fischer, 1851)
Herpetocypris brevicaudata Kaufmann, 1900
Herpetocypris reptans (Baird, 1835)
Heterocypris incongruens (Ramdohr, 1808)
Heterocypris salina (Brady, 1868)
Ilyocypris bradyi Sars, 1890
Ilyocypris gibba (Ramdohr, 1808)
Ilyocypris inermis Kaufmann, 1900
Ilyocypris sp.

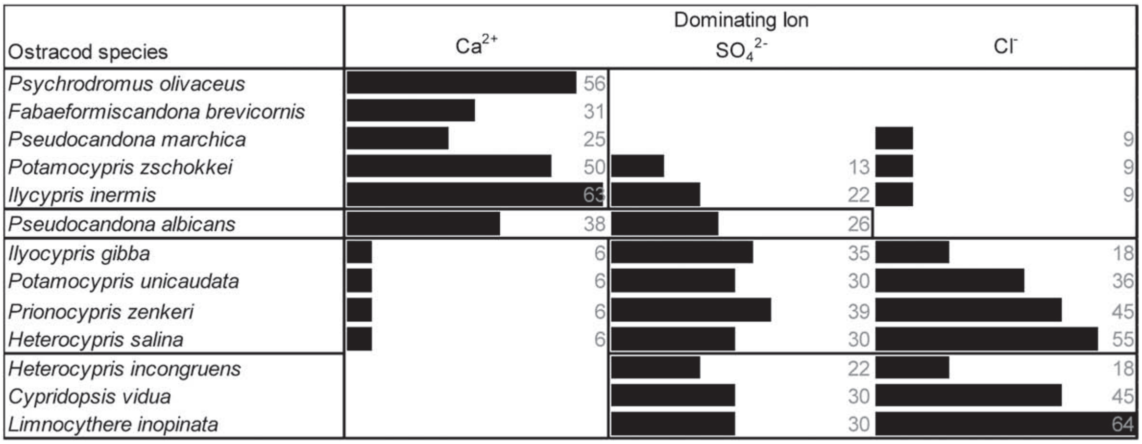

Fig. 6. Steadiness (black scales and grey numbers) of ostracod species occurrence in waters of different dominating ions. Rare and ubiquitous species are omitted. Groups with similar preferences of water chemistry are separately framed.

Ilyocypris sp. could not be assigned to a species given in Meisch (2000). The marginal zone of the left valve of this species is smooth without ripplets.

Ilyocypris species were identified using valve size, morphology (marginal spines and nodes) and the presence and degree of marginal ripplets in the posterior-ventral part of the left adult valves sensu Van Harten (1979) and Janz (1994).

Limnocythere inopinata (Baird, 1843)
Metacypris cordata Brady & Robertson, 1870
Microdarwinula zimmeri (Menzel, 1916)
Nannocandona faba Ekman, 1914
Notodromas monacha (O.F. Müller, 1776)
Physocypria kraepelini G.W. Müller, 1903
Plesiocypridopsis newtoni (Brady & Robertson, 1870)
Potamocypris arcuata (Sars, 1903)
Potamocypris fallax Fox, 1967
Potamocypris fulva (Brady, 1868)
Potamocypris smaragdina (Vávra, 1891)
Potamocypris unicaudata Schäfer, 1943
Potamocypris zschokkei (Kaufmann, 1900)

Potamocypris species were identified based on articulated valves. If separated and juvenile valves were not distinguished, they appear in our counts as *Potamocypris* spp.

Prionocypris zenkeri (Chyzer & Toth, 1858)
Pseudocandona albicans (Brady, 1864)
Pseudocandona compressa (Koch, 1838)
Pseudocandona marchica (Hartwig, 1899)
Pseudocandona rostrata (Brady & Norman, 1889)
Pseudocandona sucki (Hartwig, 1901)

The five *Pseudocandona* species, especially *P. marchica* and *P. rostrata* are hard to distinguish. For juvenile specimens it is even impossible. Therefore, we assign all specimens to *Pseudocandona* spp. for quantitative analyses and give qualitative distribution data only for the species.

Psychrodromus olivaceus (Brady & Norman, 1889)
Sarscypridopsis aculeata (Costa, 1847)
Scottia pseudobrowniana Kempf, 1971
Trajancypris clavata (Baird, 1838)

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2014.07.042.

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Beitrag 2:

Late Quaternary lake history of the Siebleber Senke (Thuringia, Central Germany) – methods of palaeoenvironmental analysis using Ostracoda and pollen

nach Review wieder eingereicht 2015, Pint et al., *The Holocene*

Südlich von Gotha bei Siebleben im Thüringer Becken entstand im obersten Pleistozän nach der letzten Vereisungsphase ein See. Dieser füllte eine Subrosionssenke aus, die sich aufgrund von Salzauslaugungsprozessen im Untergrund gebildet hatte. Heute befindet sich nur noch ein kleines Restgewässer in der Senke. Die Ostrakodenfauna und das Pollenspektrum zweier Bohrungen wurden für die Rekonstruktion der Seegeschichte untersucht. Salzeinfluss und Temperatur wurden mithilfe von Mutual-Range-Methoden, Transferfunktionen und Moderne Analogie-Techniken über das Profil herausgearbeitet.

Ergebnis: Die Seesedimente enthalten eine typische Süßwasserostrakodenfauna, die mit mindestens 18 Arten ungewöhnlich divers ist und einen größeren permanenten See vermuten lässt. Die Sequenz lässt sich mithilfe einer Pollenchronologie und ^{14}C-Datierungen ins Holozän und Obere Pleistozän stellen. Die meisten der nachgewiesenen Arten können eine leichte Erhöhung der Salinität tolerieren. Auffällig ist ein Horizont in dem *Cyprideis torosa* in sehr großer Anzahl vorkommt und Salzeinfluss anzeigt. Nahe des heutigen Restgewässers wurde in Oberflächenproben die Foraminiferenart *Haplophragmoides* sp. gefunden, die in den Bohrkernen nicht nachweisbar und daher stratigraphisch nicht einordbar ist. Diese Art wurde bereits von Bartenstein (1939) von Siebleben und auch aus anderen Gewässern innerhalb von Riedflächen in Thüringen beschrieben. Die Gattung *Haplophragmoides* ist vor allem in Küstensalzsümpfen verbreitet und scheint daher auch im Binnenland einen gewissen Salzgehalt anzuzeigen (Murray 2006). Die Rekonstruktion der Luft- und Wassertemperatur ergab, dass die über eine Transferfunktion ermittelte Wassertemperatur vorwiegend der unteren Jahresdurchschnittskurve der Lufttemperatur folgte, was möglicherweise darauf zurückzuführen ist, dass das Tiefenwasser eines Sees in der Regel auch während des Sommers kühl bleibt, im Winter hingegen nicht unter –4°C fällt. Einen ähnlichen Effekt könnten Quellaustritte in das Gewässer bewirken. Aufgrund der durch MOTR und Transferfunktion für Lufttemperatur bzw. Wassertemperatur ermittelten Werte lässt sich das Profil in drei Bereiche unterteilen: Zunächst kommt es bis zum Präboreal zu stärkeren Temperaturschwankungen, anschließend waren die Winter besonders kalt, aber die Sommer etwas wärmer im Präboreal, danach wurde das Klima ausgeglichener. Alle Methoden zur Rekonstruktion der Salinität zeigen leichte Schwankungen über das Profil und einen stärkeren Anstieg im „*Cyprideis*-Horizont“ an. Es muss demnach während des Subboreals zu einem verstärkten Salzeintrag in das Gewässer gekommen sein.

Anna Pint, Heike Schneider, Peter Frenzel, David J. Horne, Marcus Voigt, Finn Viehberg (in review). Late Quaternary lake history of the Siebleber Senke (Thuringia, Central Germany) – methods of palaeoenvironmental analysis using Ostracoda and pollen (eingereicht bei *The Holocene*)

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Late Quaternary lake history of the Siebleber Senke (Thuringia, Central Germany) – methods of palaeoenvironmental analysis using Ostracoda and pollen

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Late Quaternary lake history of the Siebleber Senke (Thuringia, Central Germany) – methods of palaeoenvironmental analysis using Ostracoda and pollen

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Abstract

We test several methods of ostracod-based palaeoenvironmental reconstruction using indicator species approach, mutual ecological/climatic range methods, transfer functions, modern analogue technique and morphological variation within *Cyprideis torosa* in reconstructing the site evolution of a late Quaternary small lake basin in Thuringia, Central Germany. Sediment sections containing a diverse ostracod fauna were studied and compared with those from modern water bodies of Thuringia. Palynological investigations were executed to reconstruct the environmental conditions in the catchment area and for a obtaining a biostratigraphical framework. The brackish water ostracod *Cyprideis torosa* as well as the foraminifer *Haplophragmoides* indicate phases of salty groundwater influence, fed by salt bearing sediments of the Triassic basement. The accompanying freshwater ostracod fauna, however, reflects only low variations of salinity and temperature. Environmental changes in salinity, temperature and ecological stability indicated by microfossils and pollen are caused by an interplay of climatic shifts and the local geological and hydrological setting.

1 Introduction

Athalassic saline waters are typical for arid regions of the world. Humid regions, however, can yield such continental brackish water bodies as well (compare Pint et al., 2012). Their existence is normally related to evaporite sediments producing brines in contact with groundwater and feeding the lake water through springs. Athalassic brackish waters of humid regions are normally geologically short living and small compared to many of those in arid regions. According to literature, a number of water bodies in Central Germany are indicated to be saline based on the occurrence of foraminifers far from the sea (Bartenstein, 1939, Wennrich, et al., 2007). Two sources of saline contamination of these modern waters are considered: evaporite bearing sediments of Zechstein or Middle Triassic rocks and mine dumps. We think, however, that the presence of continental salt water sites in Central

Germany is not solely driven by distribution of evaporites and tectonic or erosional processes giving groundwater access to those evaporites in the underground, but is also influenced by a climatic component either by shifting the groundwater levels or by a relatively low precipitation/evaporation ratio which can additionally enhance the salinisation of the surface water but may restrict the leaching in the underground by less groundwater on the other hand (compare Pint et al., 2012). A detailed study of Holocene sediment profiles from a former shallow saline lake at Siebleben near Gotha was therefore started for testing these assumptions.

We document the fossil ostracod associations of two cores from Siebleber Senke in order to reconstruct palaeoenvironmental changes. The following methods are applied: indicator species approach, mutual ecological tolerance methods (incl. MOTR sensu Horne, 2007), transfer functions for salinity and temperature, modern analogue technique and morphological variation within *Cyprideis torosa* (noding and sieve pore shape). Palynological analysis provides the independent reconstruction of climate and vegetation changes as well as chronology. The synthesis of palaeoecological results from ostracod and palynological analyses produces a model for site evolution. Relying on this model, we intend to test our hypothesis of climatically driven salinisation in a temperate humid region.

2 Setting

The Siebleber Senke (Depression of Siebleben) close to Gotha belongs to a number of natural saline inland water (athalassic) sites in the Thuringian Basin which are in contact with evaporite bearing sediments of Triassic or Permian age. In the Siebleber Senke, a fish pond (diameter about 400 m, maximum depth 1.5 m, height above sea level: 275 m) was created in 1717 (Greifeld 1966) in place of a small remnant lake of natural origin in this depression. The present day salinity of the small pond is 0.5 psu, and the water is SO_4^{2-} dominated. Its water is fed by one inflow and drained by one outflow. A wide reed belt surrounds the modern pond.

In the 1960ies the area around the pond had been declared a nature reserve – it is an important place for resting and breeding of birds.

Bartenstein (1939) reported the brackish water foraminifer *Haplophragmoides* for the first time from Siebleber Senke. However, he could not find living individuals. Empty tests of *Haplophagmoides* (Fig. 1) sampled in 2005 were given to the authors by H. Huckriede (TLUG Weimar). Their excellent preservation indicates a modern or sub-recent population in the lake. The index brackish water ostracod *Cyprideis torosa* could not be found in surface samples. Sediment cores, however, contain a typical freshwater macro- and microfauna including sections with high numbers of *C. torosa*. Their lateral spacing indicates a former brackish lake in the area as already assumed by Greifeld (1966) in her unpublished Diploma thesis.

3 Material and methods

3.1 Sampling and analysis of collection material

Three sediment cores from nearly the same position in the area of the Siebleber Senke are investigated in this study. The first of them with a length of 525 cm (core Sieb 1966) was drilled in 1965 in the framework of a Diploma thesis by Ingrid Greifeld (1966). In the lower part of this core pollen grains were analysed for chronological interpretation of the Late Glacial (Lange 1966). The complete ostracod fauna from this core (46 samples) is achieved in the Natural History Museum of Berlin within the Diebel-Pietrzeniuk ostracod collection. This material was re-analysed for the present study. In 2006 and 2010 parallel long cores in one position were drilled for investigations of both pollen and ostracods with a manual gauge (core Sieb P/06 – 385 cm; core Sieb P/10 –235 cm). Whereas core Sieb P/06 covers the Preboreal and Boreal, core Sieb P/10 includes the sequence from Boreal to modern. The correlation of the cores was possible using marker horizons and show only variations in small cm scale (Fig. 2). From core Sieb P/06, 61 samples were taken for ostracod analysis covering the whole core length and 34 samples for palynology covering the Holocene. The ostracod samples have 25 mg wet weight each; the pollen samples a volume of 1 ml each.

3.2 Sample preparation and documentation

The ostracod samples were completely sieved over a 200 µm sieve using tap water. The sieve residue was than oven-dried at 50 °C. All ostracod valves were picked from the residues, identified, counted and stored in microslides. Taxonomic identification relies on Meisch (2000) and Diebel (1965, 1968) and was done under a low-magnification stereoscopic microscope. The excellent plates by Fuhrmann (2013) supported identification additionally when using SEM and light microscope photographs. The studied material, except this from the Diebel-Pietrzeniuk collection, will be transferred to the museum Mauritianum in Altenburg (Thuringia), where the large Fuhrmann collection of Quaternary ostracods from Central Germany is housed also.

Preparation of pollen samples follows Faegri and Iversen (1975); additionally the samples were sieved through an 8 µm Nylon mesh with ultra sound to remove clastic material. For analyses, the samples were embedded in silicon oil. Pollen identification was carried out with help of Moore et al. (1991), Reille (1992) and Beug (2004) and the pollen collection of the Friedrich Schiller University Jena. Pollen counts are presented as diagram with regional and local part and with ecological summary curves.

3.3 Statistical analyses

The modern training set of ostracods from Central Germany by Pint et al. (2015) complemented by another modern training set from the Baltic Sea coast (Frenzel et al., 2010) limited to oligohaline samples allowed the setup of an ostracod-based transfer function for salinity. The modern training set comprises 73 samples, 26 from Central Germany and 47 from the southern Baltic Sea coast, and covers salinities from 0.1 to 6.1 (psu). The performance calculated by bootstrapping is R^2=0.74 and a RMSEP (Root Mean Square Error of Prediction) of 0.9 for the WAPLS model (Weighted Average Partial Least Square) of the transfer function. We inferred the water temperature throughout the cores “Sieb 1966” and “Siebleben P/06” based on the calibration dataset from NE-Germany (Viehberg 2006). A one component weighted averaging partial least squares (WA-PLS) model for calibration and regression (Viehberg & Mesquita-Joanes 2012) was used. Alternatively, we set up a WA-PLS model that included also species from the calibration dataset, which have a broader temperature tolerance and are recorded in the fossil assemblages of Siebleben (i.e., *Cyclocypris laevis*, *C. ovum*, *Cypridopsis vidua*, *Cyprideis torosa*, *Darwinula stevensoni* and *Limnocythere inopinata*). Consequently, the performance of the transfer function decreases, but the number of matching species in the sediment record is maximised (Table 2).

3.4 Zonation, correlation and chronology of cores

An ostracod-based zonation for the studied core was set up relying on ostracod distribution data, whereas the palynological zonation refers to changes in pollen composition (Moore et al. 1991). The sediment cores of 1966, 2006 and 2010 could be correlated based on lithological features, pollen and ostracod distribution (Fig. 2). Furthermore, pollen zones of the present study could be correlated based on a late glacial pollen diagram composed by Lange (1966) as stratigraphical framework for Greifeld (1966). An approximately chronological interpretation was possible using other dated pollen diagrams from this region as base for comparison (Meschner 2008, Schneider 2014). Palynological results of the oldest part are given in a simplified pollen diagram by Lange (1966). The original dataset of this diagram is not available. The basis of calculation in 1966 and today is different and thus the diagram of Lange (1966) is reconstructed here (Fig. 6a). Starting with the Holocene, a pollen diagram of the depression is presented in Fig. 6b.

For dating the profiles two samples were used for AMS-^{14}C-Mesurement (Table. 1). Measured radiocarbon ages were calibrated using Calib 7.1 and the IntCal13 calibration curve (Reimer et al. 2013) and ages are given in calibrated years Before Present (cal BP) with a 2 sigma error age range.

Table. 1 Details of radiocarbon datings in core Sieb P/06

Depth in cm	Labnumber	Material	BP	BP error	Δ C13	cal. BP (2σ) range
115-120	UBA-24821	*Gyraulus*	4473	27	-	**4977 - 5286**
350-355	UBA-25755	gyrogonites	9844	78	-	**11187 - 11605**

3.5 Palaeoenvironmental Analysis

We apply a range of methods for palaeoenvironmental reconstruction to the Siebleben profile. These are index species approach, ecological classification, Mutual Ostracod Temperature Range method (MOTR), Mutual Ostracod Salinity Range method (MOSR), modern analogue technique and ostracod-based transfer functions for temperature and salinity (compare Frenzel et al., 2010). Additional information on salinity is provided by morphological analysis of *Cyprideis torosa* valves.

The index species method relies on the occurrence of sensitive and characteristic species like *Cyprideis torosa* as true brackish water indicators in our material to figure out saline influences in the pond. It gives no detailed results, however, it is easy and fast to use. Ecological classification of ostracod groups and the mapping of their distribution is a classical and reliable method but shows mainly trends and no quantitative reconstructions for environmental parameters. We rely on ecological ostracod classifications by Meisch (2000), Fuhrmann (2006, 2013). The MOTR method combines species distributions from a modern non-marine ostracod database and GIS-derived air temperature ranges (Horne, 2007, Horne & Mezquita, 2008). The used databases are NODE and OMEGA (see Horne et al., 2012). For the Recent sites of the Thuringian Basin, MOTR is applied as a test for its performance (Pint et al. 2015) and thereafter for each ostracod zone of the core Sieb 1966 reconstructing palaeo-air-temperatures. The MOTR results are presented with 3 pt mean smoothed values (Table 3). Additionally, we applied an ostracod-based transfer function for palaeo-water-temperature by Viehberg (2006) and Viehberg & Mesquita-Joanes (2012).

Salinity estimation is based on mutual salinity tolerances of the encountered ostracod taxa in a similar way as for MOTR; the general principle of this approach is not new but we introduce it here for the first time as a systematic Mutual Ostracod Salinity Range (MOSR) method based on specified datasets. Salinity ranges of individual taxa are taken from Frenzel et al. (2010) and Meisch (2000). The data used by Frenzel et al. (2010) are collected on the southern Baltic Sea coast and cover salinities from 0.05 to c. 20 relying on 745 samples.

Additional information on palaeosalinity is provided by sieve-pore analysis sensu Rosenfeld and Vesper (1977). These authors recognized that the shapes of sieve-pores of *Cyprideis torosa* and salinity are correlated. The increase of rounded shaped sieve-pores indicates a decrease of salinity. With the aid of a transfer-function (compare Pint et al., 2012), it is possible to calculate salinity directly from the percentage of round sieve-pores:

$$S = e^{-0.06\ RS + 4.7}$$

[S – salinity, RS – percentage of round sieve-pores]

It has to be stressed, however, that this formula is based on marginal marine populations and that it is not known so far if a water chemistry different from that of marginal marine settings influences the proportion of round sieve-pores. This problem is similar for noding of *Cyprideis torosa*. In marginal marine environments, *C. torosa* develops nodes below a salinity of about 7 psu. Below 2 psu, mostly more than 50 % of valves of a population are noded (Frenzel 1991). This phenomenon is caused by osmotic problems during moulting. There are indications of an influence of different ionic composition of ambient water (Frenzel et al., 2012).

Palaeoecological interpretation of fossil pollen and spores based on uniformitarian principles (Jacomet & Kreuz 1999). Lange (1966) resigned the separation between local and regional components for the late glacial and early Holocene in core Sieb 1966. Aquatics are missed in her study. According to a difficult attribution especially of grasses to special ecological groups during that period the classification during early Holocene in core Sieb P/06 follows the interpretation of Lange (1966). During Holocene the classification of the plants into ecological groups follows Ellenberg (1992) and allows the reconstruction of vegetation pattern in the catchment. The values of Chenopodiaceae are in other studies interpreted as ruderal indicators, but in this case they document relatively high values and coincide with the changes in salinity in the depression, which is observable in actual studies from Thuringia (Schuster et al. 2010). The high values in Poaceae are also typical for this kind of archive in Thuringia, like visible in different depressions in Thuringian Basin (Meschner 2008) and the Werra valley (Schuster et al. 2010). The often used local name for such depressions in the Thuringian Basin is ‘Ried’ or ‘Rieth’, which hints at the characteristic vegetation form with different species of Cyperaceae and Poaceae. Both pollen types, Chenopodiaceae as well as Poaceae, are therefore interpreted as a local signal in the mid and late Holocene. During the early Holocene they are part of the regional vegetation.

4 Results

4.1 Lithology

To understand the development of the Siebleber Senke, the drillings of Greifeld (1966) and recent investigations are combined in the following studies. Altogether more than 250 sounding, twelve trenches and six gouge corings were made, most of them already by Greifeld (1966). According to these results the sediment thickness in the depression reaches between one and seven meters, whereas the deepest part is situated in the western area (Fig. 2). Core Sieb 1966 starts with a basal unit of clay, which contains small pieces of the Triassic bedrock (5.25 m to 5.00 m). Up to 3.80 m it is followed by grey-green clayey silt with solitaire gypsum pieces. The next bright layer up to 2.95 m has a high level of carbonate with scattered gypsum, therefore it is interpreted as lake marl. Grey-green clayey silt with gypsum characterizes the next layer up to 1.70 m. Up to 0.8 m a lake marl horizon occurs again. The last layer up to 0.2 m contains brownish silt with plant remains.

As expected, the lithology of cores Sieb P/06 and P/10 looks very similar among to each other, only the thickness of the described strata varies in low cm scale (Fig. 2). The 3.85 m long core Sieb P/06 mainly consists of greenish or greyish clayey silt with small intercalations of dark silt (2.12 m to 1.91 m and 0.78 m to 0.73 m). Horizons with a high content of calcareous material, interpreted as lake marl, are visible in a depth of 2.40 m to 2.18 m, 1.60 m to 1.47 m, 0.93 m to 0.87 m and 0.30 m to 0.15 m.

4.2 Ostracoda

The state of ostracod preservation is good in general (Fig 3). Only a few valves are broken or show traces of dissolution. A total of 21 ostracod species was identified in the sediments of Siebleber Senke. One of them *Limnocytherina santipatricii*, occur with only one valve and are therefore not included in distribution charts and ecological analysis. The most common species are *Limnocythere inopinata, Ilyocypris bradyi, Ilyocypris gibba* and *Candona candida* (Fig. 4 and 5). A complete list of taxa can be found attached as a taxonomic reference list.

Based on ostracod distribution, a differentiation of core Siebleben 1966 into five units (unit 1-5) and core Siebleben P/06 into two units (unit 4 and 5) is possible (Fig. 4 and 5). The distribution of ostracods and especially a distinct horizon with a mass occurrence of *Cyprideis torosa* allow a correlation of the zones of both cores.

Unit 1 (525 cm – 470 cm): Only a few ostracods were found in this Unit. The dominating species is *Limnocythere inopinata*; *L. blankenbergensis*, *Limnocytherina santipatricii* and *Cytherissa lacustris* occur occasionally only.

Unit 2 (470 cm – 390 cm): Ostracod diversity increases distinctively. The dominant species are *Limnocythere inopinata*, *L. blankenbergensis* and *Ilyocypris gibba*. Less abundant are

Sarscypridopsis aculeata, *Cytherissa lacustris*, *Ilyocypris bradyi*, *Leucocythere baltica* and *Candona candida*.

Unit 3 (390 cm – 285 cm): Ostracod diversity and abundance further increase. Dominating species are *Candona candida*, *Limnocythere inopinata*, *L. blankenbergensis*, *Ilyocypris gibba*, *I. bradyi* and *Cypridopsis vidua*.

Unit 4 (285 cm – 165 cm): Whereas ostracod abundance is similar to that of the Unit below, diversity decreases. *Candona candida*, *Limnocythere inopinata*, *L. blankenbergensis*, *Ilyocypris gibba* and *I. bradyi* are still dominant, in contrast to the rare occurrence of *Candona neglecta* and *Cypridopsis vidua*.

Unit 5 (165 cm – 20 cm): This uppermost part of the section contains the highest diversity and abundance of Ostracoda. *Cyprideis torosa* appears in the lower part of the Unit and reaches mass occurrence in 95 – 115 cm. 20 – 30 % of the valves are noded. Sieve-pore analysis of the valves shows a mean percentage of 74 % rounded sieve-pores. Abundant are *Candona neglecta*, *Limnocythere inopinata*, *Ilyocypris bradyi*, *Cypridopsis vidua*, *Cyclocypris laevis*, *Heterocypris salina* and *Pseudocandona sucki*. Less abundant are *Ilyocypris gibba*, *Cyclocypris ovum*, *Pseudocandona rostrata*, *P. marchica* and *Darwinula stevensoni*.

4.3 Palynology

Pollen concentration and preservation are very variable over the profiles. In core Sieb 1966 Pollen are completely absent between 300 and 280 cm, 265 and 235 cm as well as in core Sieb P/06&10 between 183 and 169 cm.

In core Sieb 1966 (Lange 1966) the first pollen section (410 – 280 cm) documents, with the exception of two samples, a distinct *Betula* dominance followed by *Pinus*. Heliophilous herbs and open land species are regularly present. The local pollen component shows very low values. After a hiatus in pollen preservation (300-280 cm), a pollen association with high values in *Pinus*, lower values in *Betula* and a high amount of heliophilous herbs as well as

Cyperaceae and Poaceae is documented between 280 and 265 cm. A second gap (275-235 cm) disrupt the in the pollen record, which is followed by an increase of *Corylus* values up to 20 % and also first thermophilous trees between 235 and 215 cm. Trees now dominate the vegetation with nearly 90% and indicators for open landscape are very low.

Core Sieb P/06 shows a complete different pollen composition in the lower part (Fig. 6b). The section between 385 and 290 cm reflects a *Pinus* dominance (40-60%), *Betula* values around 20% with relatively high values in heliophile herbs (*Plantago major* type, *Artemisia*, Cichorioideae). The local component indicates a shallow water system with *Pediastrum* in the study site. This development is continued between 290 and 207 cm core depth with an additional rise in Cyperaceae and Poaceae, but also an increase in *Pediastrum*. This second phase is comparable with the pollen association in core Sieb 1966 (Lange 1966) between 280 and 265 cm. A rise in *Corylus* combined with lower values in open land communities marks the last zone and is to correlate to the upper phase in core Sieb 1966 (Lange 1966).

In core Sieb P/10 the last pollen zone is also very clearly to correlate to core Sieb P/06 and show similar vegetation patterns until 185 cm. After this period, a phase without pollen preservation is documented until 167 cm. Then the pollen sequences show distinctly higher values in *Quercus, Ulmus, Corylus, Tilia, Betula* and *Alnus*. The local pollen component documents relatively high values of cane brake (*Dryopteris, Sparganium, Equisetum, Typha latifolia*) and wet meadow species (*Filipendula ulmaria* type, Cyperaceae, *Galium* type) as well as aquatics (*Lemna, Pediastrum*). Between 144 and 127 cm, *Pinus* is decreasing while *Quercus* and grassland communities rise in abundance. Within the local vegetation, aquatics are decreasing. The following section (127 – 87 cm) is once more characterized by higher values in *Quercus, Corylus, Picea* and grassland communities. *Pinus* and *Ulmus* show distinctly lower values. *Pediastrum* as well as wet meadow indicators are regularly found and Chenopodiaceae show increasing values. The vegetation development in the core section between 87 and 72 cm documents a rise in *Alnus, Betula* and *Pinus* as well as indicators for stronger human impact (Cerealia type, ruderal species), while *Quercus, Tilia, Ulmus* and *Corylu*s decrease. In the local vegetation, *Lemna, Potamogeton*, cane brake communities with *Equisetum, Dryopteris* and *Sparganium* as well as Cyperaceae are documented. During the next phase (72 – 55 cm), *Pinus* and *Quercus* as well as indicators for meadows and open land communities are increasing in proportion. In contrast, aquatics (*Lemna, Potamogeton*) and plants of cane brake habitats are decreasing. In the upper phase between 55 and 44 cm, most tree species decrease and cereals as well as grassland and ruderal species increase in number. The local component documents cane brake species especially with *Equisetum* and *Thelypteris* as well as wet meadow types like Poaceae, Cyperaceae and Cichorioideae.

5 Interpretation and Discussion

5.1 Biostratigraphical Interpretation

According to the regional pollen composition documented in core Sieb 1966 by Lange (1966), the phase between 410 and 285 cm is to correlate with the Late Glacial (Fig. 6a). Warmer interstadial phases and cooler stadial phases are documented by different values of open land communities and forest habitats within the analysable sequences. The permanently high values of *Betula* could document the correlation of this phase into the Bølling Interstadial (Litt & Stebich, 1999; Schneider, 2006), but the value changes in heliophilous herbs within this phase point to different stadials and interstadials. Probably *Betula* was also a part of the local vegetation and grew in the marginal areas of the depression. For solving this problem Lange (1966) discussed two different chronological models – one according to tree pollen composition and another one according to general pollen combination with open land communities. Taking into account the temperature curve based on ostracods of this paper (Fig. 7) the phase between 385 and 300 cm is correlated to the Bølling/Allerød-Complex. Between 315 and 300 cm in core Sieb 1966 the *Artemisia* values reach more than 30 %. Such high values are characteristic for steppe communities during the cold stadials (Litt & Stebich, 1999). In this case, trees as well as other open land communities document very low values, which indicate a very local signal of *Artemisia* as a result of populations at the margins of the depression. A hiatus in pollen between 300 and 280 cm is possibly correlated to the Younger Dryas period, because the following section (280- 250 cm in core Sieb 1966, 385-207 cm in core Sieb P/06) reflects pollen spectra with higher values in *Pinus*, lower values in *Betula* and a high amount of open land communities pointing to an early Preboreal vegetation phase (comp. Schneider, 2006). This is also confirmed by the temperature curves (Fig. 7). From 235 cm, the rise of *Corylus* and first proofs of thermophilous trees indicate the early Boreal, which is also visible in the pollen diagram of core Sieb P/06 and P/10 (Fig. 6b, c). An AMS radiocarbon dating presents an age of 11,187 – 11,605 cal BP. These points to a reservoir effect affecting skeletons of aquatic organisms in the lake. Due to the lack of any terrestrial datable material it was not possible to calculate the reservoir effect. After this period, a sediment accumulation without pollen conservation is documented in all cores and is typical for this landscape (Schneider 2012). In this position, Lange (1966) stopped pollen analysis and the following Holocene development bases on the investigation of core Sieb P/10 (Fig. 6b).

The core section in Sieb P/10 starting at 167 cm shows a typical mixed forest with *Tilia, Ulmus* and *Quercus* which points to the late Atlantic (Firbas, 1949; Schneider, 2006). The following zone (144 – 87 cm) reflects the biozone of the Subboreal with an increase in *Quercus, Picea* and *Fagus*. According to the changes in local scale, the zone is divided into two subzones, the early Subboreal (144 – 127 cm) and the late Subboreal (127 – 87 cm). Shells of the gastropod *Gyraulus* sp. of the horizon (Sieb P/06 115-120) with the highest abundance of *Cyprideis torosa* were AMS radiocarbon dated to 4977 - 5286 cal BP (Table 1). As for the other radiocarbon date a reservoir effect can be assumed.

The pollen composition of the next section (87 – 55 cm) documents the early Subatlantic phase with an increase in *Fagus*, *Picea* and *Abies* together with a rise in pioneer trees. It shows in its second part a further increase in *Quercus* and *Pinus* as well (compare Schneider, 2006). In the younger phase between 55 and 44 cm, most trees are decreasing and indicators for anthropogenic use (Behre, 1981) are rising distinctly in proportion. This pollen composition indicates the late Subatlantic (Firbas, 1949).

A biostratigraphical identification of sediment units from the core Sieb 1966 based on ostracods is only roughly possible. The ostracod-based stratigraphical classification for Central Germany provided by Fuhrmann (2013) allows a differentiation between Late Glacial and Holocene sediments for our section, however, no further differentiation within the Holocene: Considering the general shallow water character of the palaeohabitats at Siebleben, the ostracod faunas of Unit 1 and Unit 2 reflect Late Glacial conditions (*Leucocythere baltica*, *Cytherissa lacustris*). All the following Units are typical for warmer conditions. The occurrence of such an ostracod fauna more typical for the Holocene below 300 cm within a Late Glacial pollen association indicates interstadial conditions which could be typical for late glacial interstadials (Litt & Stebich, 1999; Schneider, 2006).

5.2 Palaeoenvironmental Reconstruction

The following palaeoenvironmental reconstruction for the core Sieb 1966 is based on ecological interpretation of ostracod associations following data given in Meisch (2000), Fuhrmann (2006) and Pint et al. (2012) applying MOTR, MOSR, ostracod-based transfer functions, palynological analysis as well as lithological observations. In general, the ostracod distribution patterns of the Units are different to those of recent sites (Pint et al., 2015). However, all sites except of Stausee Kelbra are small and mostly temporary waters. Even the ostracod assemblage of the small modern pond of the Siebleber Senke is quite different from the associations from the cores. It is dominated by *Cyprois marginata* and *Cypris pubera* typical for small temporary ponds.

Palaeotemperature reconstructions made with the MOTR method often produce wide ranges of temperatures which are difficult to interpret because the actual temperature could have been anywhere within the given range. However, it is noteworthy that the minimum MOTR value curves for mean January and mean annual air temperature show similar trends to the WAPLS-reconstructed water temperatures, and particularly suggest colder temperatures in Unit 4. Salinity analyses show that in general curves of transfer function and modern analogue lay within the MOSR. One notable exception is located in zone 5 based on the short term dominance of *Cyprideis torosa* which produced a higher peak of the TF curve.

Unit 1 (Oldest Dryas/Meiendorf/Pleniglacial; 525 – 470 cm): The ostracod record starts with a typical pioneer assemblage (*Limnocythere inopinata*, *Candona candida* and *Leucocythere baltica*) characteristic for the Late Glacial (Diebel, 1965; Griffith & Evans, 1995; Frenzel & Viehberg, 2004). More than 80 % of the valves indicate permanent and cold freshwater – these species belong to the “oligostenothermal/boreo-alpine” group of Fuhrman (2006). The MOTR method provides a mean annual air temperature range of +2 to +12 °C. This result is mainly controlled by *Leucocythere baltica*, for which values of the very similar and probably synonymous *Leucocythere mirabilis*, the most common species in Unit 1, are used here. The estimated air temperature range is very broad because of the low species number and does not facilitate precise palaeoclimatic reconstruction of the initial lake phase. We assume a permanent water body, probably a shallow lake, under cold climatic conditions. The missing pollen record could be caused by a fluctuating water level in the shallow marginal zone of the lake. A saline influence is not recognisable if looking for brackish water species. The few valves of the brackish water ostracod *Cyprideis torosa* are probably reworked from older sediments. MOSR provides a large range of salinity from 0 to 5. The ostracod-based transfer functions for salinity estimate 1.5 to 2.3 psu which indicate oligohaline conditions making a saline water discharge probable.

Unit 2 (Oldest Dryas/Meiendorf/Pleniglacial: 470 – 390 cm): The much higher ostracod diversity and abundance of this Unit point to ecologically improving and probably more stable environmental conditions likely coupled to higher productivity. The high proportion (40 %) of species living in permanent waters indicates a permanent water body. Regarding the presence of mesorheophilic and the lack of polyrheophilic taxa, a shallow lake seems most likely (Pint et al., 2015) which is also documented in the pollen results by Lange (in Greifeld, 1966) with wide wet meadow areas (*Galium, Thalictrum,* Cyperaceae) within the depression. Using the classification by Fuhrmann (2006), rheophobic species are dominant. The typical glacial species *Leucocythere baltica* indicates cold climatic conditions (Diebel, 1965) in agreement with *Cytherissa lacustris* which is regarded as a cold water species (Meisch, 2000) and some other species. On the other hand, both species perish within this Unit and polythermophilic species start to increase in abundance. This attests at least warmer summers than in the previous Unit. The MOTR analysis suggests an annual temperature range of -11 to +17 °C. The lower limit is defined by the rare species *Leucocythere baltica* and *Candona neglecta.* The upper limit is controlled by the only sporadically appearing species *Cytherissa lacustris*. The range of July is determined by *Leucocythere baltica*, the dominant species *Limnocythere inopinata* (lower boundary) and *Cyclocypris laevis,* the latter occurring very rarely (upper limit). Maybe a distinct continentality of the regional climate produced cold winters and warm summers. The ostracod-based salinity transfer function estimates oligohaline conditions (c. 2) as before. Palynological analyses of Lange (in Greifeld, 1966) show a mosaic of light birch forests and open land habitats with grasses and heliophilous herbs like Cistaceae, *Plantago* spec. and *Artemisia* during this period.

Unit 3 (Bølling/Allerød-Complex – Younger Dryas: 390 – 285 cm): Ostracod diversity and abundance further increase. This observation and the lithological change from silty clays to calcareous muds point to increased temperatures and productivity. Cold stenothermal species disappear and taxa preferring warm water such as *Limnocythere inopinata, Ilyocypris gibba* and*Cypidopsis vidua* (Meisch, 2000; Fuhrmann, 2006) show highest proportions within the entire succession. Hence, warm waters of the shallow lake in summer and cold winters as indicated by the high proportion of *Candona candida*, a winter form (Meisch, 2000), are assumed. The MOTR analysis suggests a mean annual temperature range of -1 to +15 °C, and similar variations as in Unit 1 and 2. Except the upper limit of July, which is determined by *Cyclocypris laevis*, the MOTR is mainly controlled by *Pseudocandona sucki*, which occurs frequently. The winter temperature range is not significantly different from this one of the preceding Unit, the July estimation, however, points to rising summer temperatures. The pollen record between 390 and 300 cm documents, with the exception of two samples, still a distinct *Betula* dominance followed by *Pinus*. A short peak of non-arboreal pollen (upland herbs), *Artemisia,* Chenopodiaceae and *Thalictrum* in between (Sieb 1966, Lange 1966), points to a short phase with dryer conditions possibly during the Allerød. In general, the local pollen component shows very low values, which hints at open water conditions until a depth of 300 cm. These conditions are also visible by high percentages of ostracod species living in permanent water bodies and the rheoeuryplastic to mesorheophil association indicate a shallow lake. Furthermore, because *C. torosa* has no desiccation resistant eggs (Heip, 1976), the brackish water character of the water body has to be concluded as permanent at least in parts of it. The small percentage of species from perennial waters could reflect a littoral zone with water level fluctuations. This zone seems to be relatively distant. The mesohalophilic species increase remarkable in proportion and a small but growing proportion of the brackish water ostracod *Cyprideis torosa* appears. This pattern reflects an increasing saline influence by salty brines from the underground. The ostracod-based salinity transfer function estimates slightly increased (c. 2.5) oligohaline conditions. The sieve-pore analysis on valves of *C. torosa* indicates a salinity of about 1, but 20 – 30 % of the valves of *C. torosa* are noded. According to Frenzel et al. (2012) this corresponds to a salinity of approximately 1.7.

Unit 4 (Younger Dryas, Preboreal, early Boreal and late Atlantic; 285 – 165 cm) is characterized by decreasing diversity of the ostracod associations pointing to less stable or degrading ecological conditions. The lithological change from calcareous muds to silty clays reflects also lower overall temperatures. This is underlined by lowered proportions of polythermophilic species and a more than doubled proportion of oligothermal species sensu Meisch (2000). Regarding the high percentage of species living in permanent waters and the lack of such from perennial waters, the Siebleber Senke was at least partly covered by a permanent lake. The local vegetation is characterized by fluctuating values of local pollen types and points to a shallow water system where two dryer phases lead to temporary drying disabling pollen conservation. Hence, permanent water bodies were present but did not existed over the whole time period under consideration.

Between 280 and 265 cm a wetter phase allows the reconstruction of wet meadow communities with Cyperaceae in the marginal areas of the water filled depression (Lange 1966). The regional pollen combination at the transition between Late Glacial and Holocene indicates a light pine forest with a high amount of heliophilous herbs, while birches grew in the surrounding area of the depression and in the floodplains. The section between 265 and 235cm is characterised by a pollen hiatus in core Sieb 1966 (Lange 1966), but not in core Sieb P/10. The reason for this phenomenon is unclear, but possibly a local one according to subrosion processes.

Between 235 and 215 cm in core Sieb 1966 as well as between 207 and 185 cm in core Sieb P/06 pine-birch forests with an increasing amount of hazel as understorey and also first elms, limes and oaks as indicators for warmer conditions grew in flood plain areas. At the end of the zone, a rise in charcoal pieces points to an increase in natural fire activity (Vanniere et al., 2008).

Clearly reduced numbers of poly- and mesohaline ostracod species indicate a dwindling saline influence. This is reflected by salinity estimations of less than 1 by the transfer function. The

MOTR analysis provides a mean annual temperature range of -11 to +17 °C, mean January of -32 to +9°C and mean July of +10 to +26°C. Actual temperatures could have been anywhere within these ranges, but the minimum value for mean January temperature is significantly lower than in the other Units, with a corresponding cooling trend reflected in the mean annual and mean July curves, suggesting the possibility of significantly colder winters and possibly cooler summers. The lower limit of the July range is defined by the frequently occurring *Limnocythere inopinata* and the upper limit is set by *Candona candida* and the very rare *Cytherissa lacustris*. This represents a dryer and continental climate than in the other zones. Starting with 192 cm, sediments are changing from lake marl to a very thin layer with small stones and concretions which is overlain by black brown silty clays with bad pollen preservation. In core Sieb P/10 between 185 and 165 cm the sediments show a hiatus in pollen preservation. According to the pollen combination below and above this section, the hiatus covers the period between begin of the late Boreal and end of the early Atlantic. Different investigations in several geo-archives in Thuringia document a drastic change in sedimentation during this period, indicating lower lake or groundwater levels (Schneider 2012), the decrease of sedimentation rates in bogs and fens or in some cases the loss of material (hiatus). The ostracod assemblages do not show any changes until the end of the pollen hiatus, but due to sampling strategy the differences in this short part of the section are probably not detectable.

Unit 5 (late Atlantic to late Subatlantic; 165 – 20 cm) yields the maximum ostracod species number of the studied core. A reason for this high diversity could be the higher temperature as indicated by returning calcareous sedimentation and a slightly higher proportion of meso- to polythermophilic species. The air temperature range of the MOTR analysis is only controlled by *Pseudocandona sucki* and comprises a mean annual temperature range of 0 to +14 °C. The MOTR of zone 5 reflects the highest winter and the lowest summer temperatures of the section with less variation. Up to 144 cm, a mixed forest with oak, elm, hazel and lime grew in the surrounding area, while birch and alder dominated in the wet areas. The local pollen component documents a system with large cane brake and wet meadow areas as well as very shallow open water habitats with *Lemna* and *Pediastrum*. The very high number of charcoal pieces implicates a higher intensity in natural fires as a result of dryer climate conditions. Later, pine woods decrease and mixed forests with a high amount of oak extend in the pollen zone of 144 – 127 cm. Increasing grassland communities point to stronger anthropogenic influences. Within the depression, aquatics are decreasing in number and document a fen with small open water areas. The following section (127 – 87 cm) is once more characterized by a spreading of oak, hazel, and grassland communities, which points to an anthropogenic use by coppice with standards. Wet meadow indicators like *Pediastrum* extended in the archive and represent dryer conditions. Here, the abundance maximum of the brackish water ostracod *Cyprideis torosa* is reached indicating higher salinities but also permanent waters. This increase coincides with a drastic rise in Chenopodiaceae and gives an evidence for a local interpretation and also an indicator function of this pollen type during periods with higher salinity. Local spreading of Chenopodiaceae in salt solution depressions is actual visible in Werra valley (Schuster et al. 2010). The vegetation development in the upper section (87 – 72 cm) of Unit 5 documents very disturbed forest habitats with pioneer trees (birch, pine, alder) according to human impact. Tree species of the sub montane forest like beech, spruce and fir extend and show forest regeneration in the neighbouring regions. The depression is characterized by a permanent water surface and wide margins with cane brake and wet meadows. During the next phase (72 – 55 cm), pine and oak as indicators for strong used forest are spreading again and indicators for meadows and open land communities are rising in proportion. In the depression, open water and cane brake habitats are decreasing when *Cyprideis torosa* disappears, probably because of the loss of a permanent brackish water body. Between 55 and 44 cm, the most forest habitats are cleared and indicators for arable land and meadows document an intensively used landscape (Schneider, 2006; Meschner, 2008), which enclosed a wet depression, where reed communities and wet meadows extended. A relatively high salinity of 1 – 3 between 160 and 100 cm sediment depth and the very high proportion of *C. torosa* imply permanent brackish water conditions, a strong ecological stressor for most of the freshwater species. Therefore, we assume a more and more fragmented lake broken into separated smaller basins with different habitats and varying salinity. A fluctuating water level and rain-wash could cause a mixing of different associations over longer time. The highest proportion (8 %) of species living in temporary waters within the core fits this model. A slight influence of a surface inflow is also recognisable. The lower species number in the upper half of this unit and the change to siliciclastic sedimentation reflects the terminal silting up phase of the basin development. The highest numbers of phytophilic ostracod species indicates the existence of a broad reed fringe during silting up of the lake, similar to present day conditions.

5.3 Summary of Late Glacial to Holocene Site Evolution

The documented Late Glacial period (525 – c. 260 cm in core Sieb 1966) is characterised by the existence of a water body in the Siebleber Senke. Warmer and more productive phases of the Bølling-Allerød-Complex are indicated by changes in the ostracod and pollen association. The water of the Siebleben shallow lake(s) was slightly brackish (oligohaline) and the lake level fluctuated. We assume subrosion of Keuper salt by a rising groundwater table as origin of the salinization. The slightly rising salinity points to increasing saline water discharge caused by more precipitation during the Bølling-Allerød-Complex. The landscape was dominated by birch woods and open land vegetation.

During the early Preboreal (>285 to at least 250 cm in core Sieb 1966 and 385 – 207 cm in core Sieb P/06), small groups of pine and birch surrounded the temporary waters in a slightly cooler climate. Saltwater discharge decreased due to a sinking groundwater table. Hazel and thermophilous trees appear in the pine and birch woods of the early Boreal (>235 to at least

215 cm in core Sieb 1966, 207 to 185 cm in cores Sieb P/06 & P/10) in a warmer climate. Apparently, salt water discharge does not play a role in this time. Hence, we assume small temporary rain fed ponds in the depression of Siebleben.

Between 183 and 167 cm (core Sieb P/10) a gap in pollen preservation documents a change in hydrology from late Boreal to early Atlantic.

In the late Atlantic (167 – 145 cm in core Sieb P/10), the temperature increased as indicated by higher ostracod diversity and returning calcareous sedimentation. The pollen record reflects shallow open water habitats, cane brakes and wet meadows in the depression of Siebleben. The area was surrounded by a mixed forest often affected by natural fires caused by dryer climate conditions. Subsequently, the increasing anthropogenic influence during Subboreal (145 – 85 cm in core Sieb P/10) becomes clear due to the extension of grassland communities and forest use indicating tree pollen combination (Behre, 1981). The areas of open water decreased within the depression. The high abundance of *Cyprideis torosa* and halophytic plants demonstrates brackish conditions of the still permanent water. The increasing salinity is likely caused by the inflow of saline waters deriving from leaching of salt bearing sediments of the Triassic basement. During the progressive siltation the water was likely separated into small ponds with different ecological conditions.

5.4 Discussion of Proxies and Methods

The MOTR method was applied to the five assemblages identified in the sequence (Fig. 7), using calibrations (Table 4) based on those published by Horne & Mezquita (2008) but revised by reference to the Ostracod Metadatabase of Environmental and Geographical Attributes (OMEGA; Horne et al., 2011) in a few cases of species which occur in North America as well as Europe. *Leucocythere baltica* is considered to be synonymous with *Leucocythere mirabilis* for the purpose of MOTR analysis. Several species are not calibrated and could not be used in the analyses, because they are extinct, due to taxonomic uncertainty, or because they are not adequately represented in the dataset: *Microdarwinula zimmeri, Paracandona euplectella, Nannocandona faba, Fabaeformiscandona breuili, Pseudocandona lobipes, Cyclocypris diebeli, Potamocypris fallax, Ilyocypris gibba, I. bradyi, Cyprideis torosa, Limnocythere blankenbergensis.* The MOTR results are illustrated in Fig. 7; they show disappointingly little variation, probably due to the relatively low number of calibrated species in each assemblage, although the reconstructed temperature ranges are at least consistent with other palaeoclimate proxy data for this region and interval. For example, for Unit 3 the MOTR July range is +12 to +23 ^{o}C and the January range is -10 to +7 ^{o}C; the interstadial equivalents of the late Late Glacial in Central Western Europe. Pollen-based palaeotemperature reconstructions by Davis *et al*. (2003) indicate summers around two degrees cooler and winters seven degrees cooler than today (i.e. around +15 and -8 respectively), both values falling within the MOTR estimates. Similarly, pollen-based palaeotemperatures for July and January for the past 6,000 calendar years (mid to late Holocene) have varied by less than one degree either way from modern values (Davis et al. 2003). This falls within the MOTR estimates for Unit 5 (Fig. 7), while, as already noted above, the MOTR-based reconstructions possibly indicate a significant cooling in Unit 4, which corresponds at least in part with the Younger Dryas cold interval that immediately preceded the Holocene.

For recent ostracod association in Thuringia (Pint et al., 2015) the MOTR method was applied for all species having a reference in the MOTR calibration list (cf. Horne & Mezquita 2008). The reconstructed air temperatures for the region of these sites lie (July +17.5 ^{o}C, January -0.5 ^{o}C) within +/- 2 ^{o}C of modern measured mean air temperature values. This means that the test of MOTR on Recent sites of the Thuringian Basin works very well and can be applied to the section of Siebleben. The MOTR of the fossil Units are mainly controlled by species with low relative abundance and low frequency. As expected, Units containing low species numbers produce a wide range for temperature estimation. The estimations by MOTR for the Siebleben core present no distinct variation between the Units and are usually less sensitive than index species method or ostracod-based transfer function. One reason is the exclusive application of absolute ecological tolerances and for a small number of species only. Another reason could be the direct connection of the ostracod distribution to air temperature in contrast to methods applying water temperature. *Ilyocypris gibba* and *Ilyocypris bradyi*, two of the most frequent species of the Siebleber Senke, have not yet been calibrated. The recent measured air temperature lies within the ranges of all zones; therefore it is not possible to recognise air temperature variations in the past.

Similarly, the calibration dataset of freshwater ostracods from NE Germany and its related temperature transfer-function are not covering the species assemblage of Siebleben to a satisfactory extend (Viehberg 2006, Viehberg & Mesquita-Joanes 2012). In particular, *Candona candida*, *Candona neglecta* and *Pseudocandona marchica* are the only matches in the list of stenothermal species used for the aforementioned regression models. Due to this shortcoming, only one or two species could be considered simultaneously for temperature reconstruction leading to questionable values with little variation. Maximising the number of species included in the calibration dataset (Viehberg 2006) extends the number of significant species in the Siebleben fossil record. Up to seven species are then simultaneously used for calculating past water temperature. However, the performance of the model is afflicted with the inclusion of species with broader temperature tolerance. In addition, the reconstructed values are hard to interpret, as the extended model includes a mix of winter and summer species. Given the fossil species assemblages, it is plausible that not water temperature, but salinity was the dominating environmental variable in the past that determined the composition of the species assemblages. Hence, the weak performance of the water temperature transfer function and MOTR is most likely related to the unusual fauna of Siebleben, which includes many rare taxa.

Similar to the MOTR method, the salinity range the MOSR is controlled by rare species. If very rare species are excluded, the salinity differences between the zones are very low. Using salinity tolerance ranges from Frenzel et al. (2010) the salinity estimations are 0 – 3 for Unit 1, 0.5 – 1.8 for Unit 2, 0.5 – 4 PSU for Unit 3, 0.5 – 1.8 for Unit 4 and 0.5 – 3 for Unit 5 (Fig 8).

The ostracod associations of core Sieb 1966 reflect permanent water bodies in the Siebleben basin from the base of the core to the surface. The uppermost samples point to silting up of the lake. In contrast, the pollen analyses show three periods without pollen preservation, pointing to phases with temporary drying out. Two of those phases are documented during the Late Glacial, the third one is visible from the start of the late Boreal to the end of the early Atlantic. The reason for this phenomenon is the different chronological resolution of the samples and preservation problems. While pollen grains are destroyed very fast under aerobic conditions (Moore et al. 1991), remains of ostracods and foraminifers are not sensible to this. Sedimentation hiati could have destroyed the pollen during phase of drying out.

A brackish water influence is visible during the warmest periods, in the Allerød and Atlantic to Subboreal, times which are reported to be wettest with widely traceable subrosion processes in the study area (e.g. Schneider, 2006). Hence, climatic conditions are the driving factor for subrosion or, inversely, salt water signals reflect humid phases in climate evolution of this area with evaporites not deep below the ground. Ostracods, in this case the brackish water indicator *Cyprideis torosa*, prove to be a valuable salinity proxy.

Shells of freshwater molluscs found on reed beds in Thuringia like those of the Esperstedter Ried and Grossengottern Ried point to larger postglacial lakes vanished today. Despite the occurrence of halophytic plants, the modern ostracod fauna in the recent residual ponds situated in those reed areas do not contains brackish water ostracod taxa (Pint et al., 2014). The extension of postglacial lakes in Central Germany in space, time and its climatic implication needs further investigations to figure out saline water influences as local events or probably climatic controlled effects.

5.5 Conclusions

Although the ostracod distribution of the section of Siebleben suggests strong ecological variations, not all the results of the applied methods reflect these changes. The reasons for the partly low performance of mutual ecological tolerance methods as well as transfer functions are the low species number and often the dominance of very tolerant species. The lack of studied comparable recent water bodies complicates an actualistic analysis. However, the combination of the pollen and ostracod data sets provides a consistent basis for the palaeoenvironmental reconstruction of the Siebleber Senke. A large lake existed there during the Holocene and was temporary influenced by salt brines. These probably short-term periods are likely caused by subrosion of salt bearing sediments of the Triassic underground. Wetter climate periods enhanced subrosion by a higher groundwater level producing salty brines locally.

The presented study demonstrates the need for more ecological data of several ostracod species as well as for investigation of palaeoecology of extinct species. This would enhance the performance of MOTR and transfer functions considerably. We can already state, however, that the combination of ostracod and fossil pollen analyses allows a comprehensive reconstruction of hydrological and climatic conditions as well as site evolution, also for the surrounding area. The different methods complement each other and enable conclusions, which would be impossible by using only one method.

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8 Taxonomic reference list

Candona candida (O.F. Müller, 1776) = *Cypris candida* O.F. Müller, 1776.

Candona neglecta Sars, 1887.

Cyclocypris laevis (O.F. Müller, 1776) = *Cypris laevis* O.F. Müller, 1776

Cyclocypris ovum (Jurine, 1820) = *Monoculus ovum* Jurine, 1820

Cyprideis torosa (Jones, 1850) = *Candona torosa* Jones, 1850.

The present specimens are all smooth shelled, i.e. without nodes, and are therefore assigned as *Cyprideis torosa* f. *littoralis* sensu Brady, 1870.

Cypridopsis vidua (O.F. Müller, 1776) = *Cypris vidua* O.F. Müller, 1776.

Cytherissa lacustris (Sars, 1863).

Darwinula stevensoni (Brady & Robertson, 1870) = *Polycheles stevensoni* Brady & Robertson, 1870

Heterocypris salina (Brady, 1868) = *Cypris salina* Brady, 1868.

Ilyocypris bradyi Sars, 1890.

Ilyocypris gibba (Ramdohr, 1808) = *Cypris gibba* Ramdohr, 1808.

Ilyocypris species were identified using valve size, morphology (marginal spines and nodes) and the presence and degree of marginal ripplets in the posterior-ventral part of the left adult valves sensu Van Harten (1979) and Janz (1994). The *Ilyocypris* sp. could not be assigned to a species given in Meisch (2000). The marginal zone of the left valve of this species is smooth without ripplets.

Limnocythere inopinata (Baird, 1843) = *Cythere inopinata* Baird, 1843

Limnocythere blankenbergensis Diebel, 1968.

Leucocythere baltica (Diebel, 1965) = *Limnocythere baltica* Diebel, 1965.

L. baltica from core Siebleben 1966 was checked and identified by Diebel. This species is likely synonymous with *Leucocythere mirabilis* Kaufmann, 1892.

Pseudocandona marchica (Hartwig, 1899) = *Candona marchica* Hartwig, 1899.

Pseudocandona rostrata (Brady & Norman, 1889) = *Candona rostrata* Brady & Norman, 1889.

Pseudocandona sucki (Hartwig, 1901) = *Candona sucki* Hartwig, 1901.

Sarscypridopsis aculeata (Costa, 1847) = *Cypris aculeata* Costa, 1847.

Table captions

Table 1: Details of radiocarbon datings from core Sieb P/06

Table 2: Comparison of performance of regression and calibration models – weighted averaging partial least squares apparent and cross-validated statistics. WAPLS (stenothermal species) from Viehberg & Mesquita-Joanes (2012)

Table 3: MOTR ranges in 3pt mean in °C (Celsius) of the five zones.

Table 4: MOTR calibrations based on Horne & Mezquita (2008) with updates from OMEGA, December 2011

Figure captions :

Fig 1: *Haplophragmoides* sp. from surface sediments of the modern fishpond in the Siebleber Senke. The material was provided by H. Huckriede (TLUG Weimar).

Fig. 2: Topographic map and core position and correlation of the area of investigation (map after Greifeld, 1966; redrawn); A- core Sieb 01/06, B-, Sieb 1966.

Fig. 3: Ostracods of the Siebleber Senke; black scale bar = 0.1mm. 1 – *Pseudocandona sucki* (LV), 2 – *Pseudocandona marchica* (LV), 3 – *Pseudocandona rostrata* (LV), 4 – *Candona neglecta* (LV), 5 – *Limnocythere blankenbergensis* (LV), 6 – *Candona candida* (LV), 7 – *Heterocypris salina* (RV), 8 –*Limnocythere inopinata* (RV), 9 – *Ilycypris gibba* (LV), 10 – *Cyprideis torosa* (RV), 11 – *Darwinula stevensoni* (LV), 12 – *Ilyocypris bradyi* (RV), 13 – *Cyclocypris ovum* (LV), 14 – *Cypris pubera*, 15 – *Cyclocypris laevis* (LV). Repository: A. Pint 2006.

Fig 4: Lithology and ostracod distribution of the core Sieb 1966 and the hereon based unit differentiation. The chronozones are based on the pollen diagrams by Lange 1966 (Fig 6a) below 230 cm, and on this study above 230 cm (Figs 6b and 6c).

Fig 5: Lithology and ostracod distribution of the core Sieb P/06 and the hereon based unit differentiation. The chronozones are based on the pollen diagrams of this study (Figs 6b and 6c).

Fig. 6: Palynological diagrams: 6a: Pollen diagram of core Sieb 1966 based on remarks of E. Lange 1966. 6b: Pollen diagram of core Sieb P/06. 6c: Pollen diagram of core Sieb P/10

Fig. 7: Synopsis of Mutual Ostracod Temperature Range (MOTR) and Transfer-function (TF) of the ostracod species of Siebleben based on the ostracod distribution of core Sieb 1966.

Fig 8: Synopsis of Mutual Ostracod Salinity Range (MOSR), Transfer-function (TF) and Modern Analogue (MA) based on the ostracod distribution of core Sieb 1966.

Model type	WAPLS (stenothermal species)	WAPLS (all species)
Apparent		
R²	0.74	0.54
RMSE	3.22	4.39
Avg. bias	0.58	-0.025
Max. bias	3.44	8.586
Cross-validation bootstrapping (n=100)		
R²	0.64	0.41
RMSEP	4.01	5.19
Avg. bias	0.52	-0.164
Max. bias	4.72	9.656

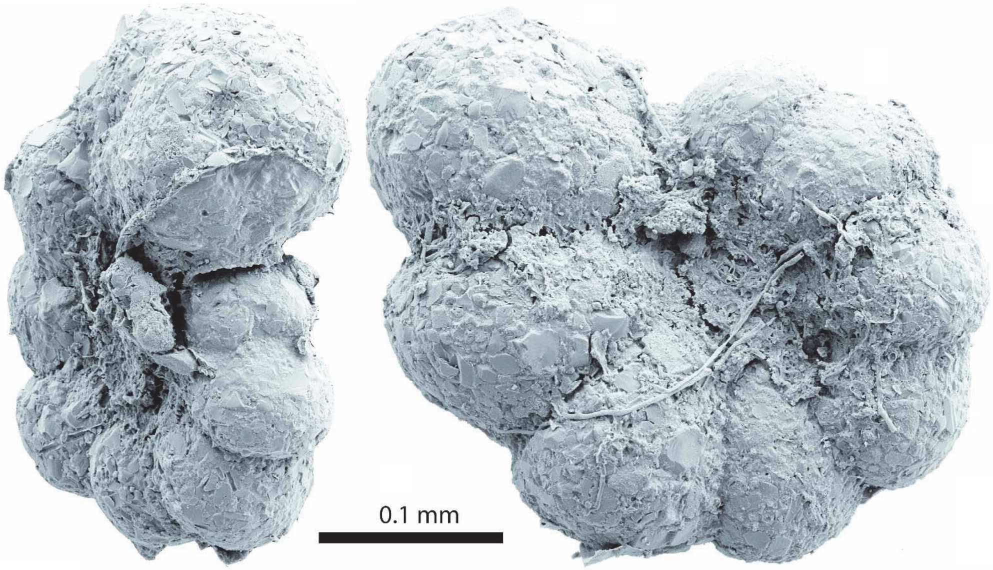
Table 2

Zone	Annual min	Annual max	July min	July max	January min	January max
5	0 to +5	+12 to +14	+14 to +16	+22 to +23.3	–15.7 to –8	+2 to +5.3
4	–11 to –2.5	+13.5 to 17.7	+10 to +12	+22.5 to +26	–32 to –12.5	+5 to +9
3	–5 to +1	+14 to +15.3	+13.3 to +16	+23 to +25	–19.5 to –8	+2 to +6.7
2	–11 to –2.5	+12 to +17	+10.7 to +12	+24 to +26.5	–24 to –10	+6 to +12.5
1	–2 to +1.7	+12 to +12.7	+11.3 to +12	+24 to +25	–17.3 to –10	+6.3 to +9.3

Table 3

Species	Annual		July		January	
	Min	Max	Min	Max	Min	Max
1. *Candona candida* (O. F. MÜLLER, 1776)	-15	+16	+6	+26	-40	+9
2. *Candona neglecta* SARS, 1887	-1	+21	+7	+27	-10	+13
3. *Cyclocypris laevis* (O. F. MÜLLER, 1776)	-9	+14	+6	+23	-32	+7
4. *Cyclocypris ovum* (JURINE, 1820)	-8	+15	+7	+27	-32	+14
5. *Cypridopsis vidua* (O. F. MÜLLER, 1776)	-5	+21	+9	+34	-32	+17
6. *Cytherissa lacustris* (SARS, 1863)	-11	+15	+4	+26	-32	+4
7. *Darwinula stevensoni* (BRADY & ROBERTSON, 1870)	-4	+21	+12	+30	-31	+14
8. *Heterocypris salina* (BRADY, 1868)	-7	+21	+8	+28	-31	+16
9. *Leucocythere mirabilis* KAUFMANN, 1892	+2	+12	+10	+25	-10	+10
10. *Limnocythere inopinata* (BAIRD, 1843)	-9	+22	+12	+34	-32	+16
11. *Pseudocandona marchica* (HARTWIG, 1899)	-4	+16	+15	+24	-31	+11
12. *Pseudocandona rostrata* (BRADY & NORMAN, 1889)	-10	+12	+8	+22	-15	+7
13. *Pseudocandona sucki* (HARTWIG, 1901)	+5	+14	+16	+24	-8	+2
14. *Sarscypridopsis aculeata* (COSTA, 1847)	-7	+21	+9	+28	-31	+17

Table 4



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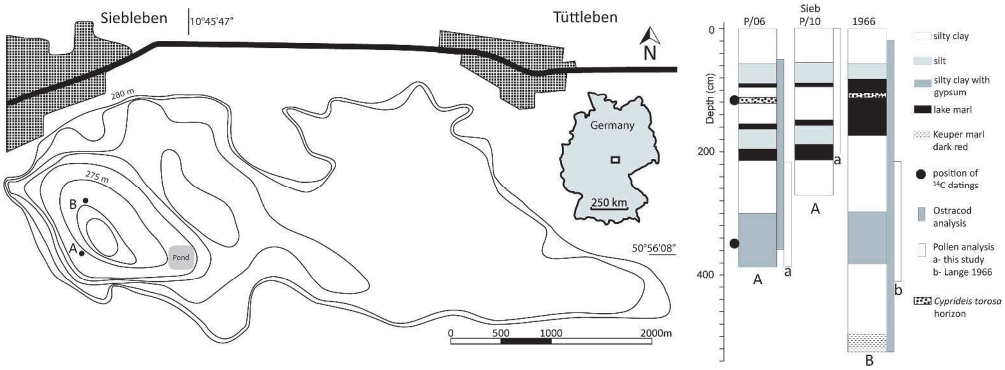

Fig. 2: Topographic map and core position and correlation of the area of investigation (map after Greifeld, 1966; redrawn); A- core Sieb 01/06, B-, Sieb 1966.
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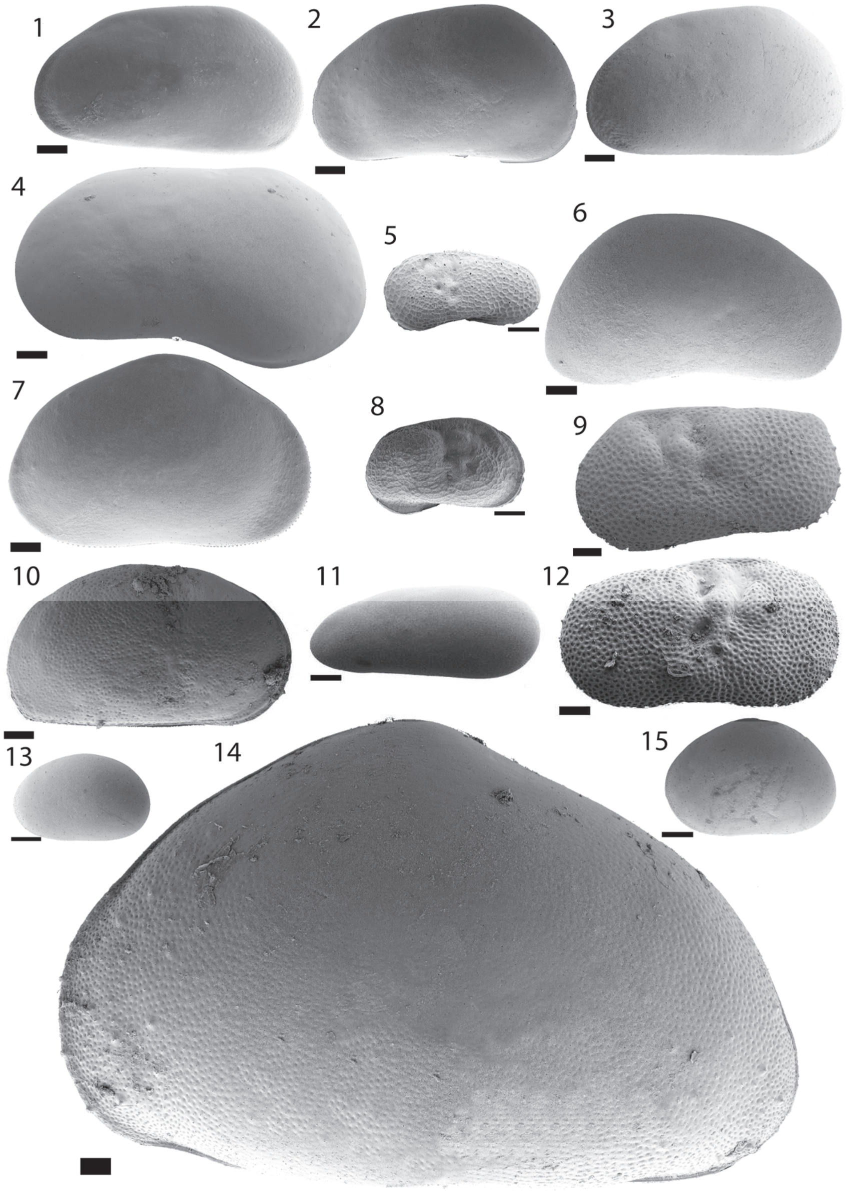

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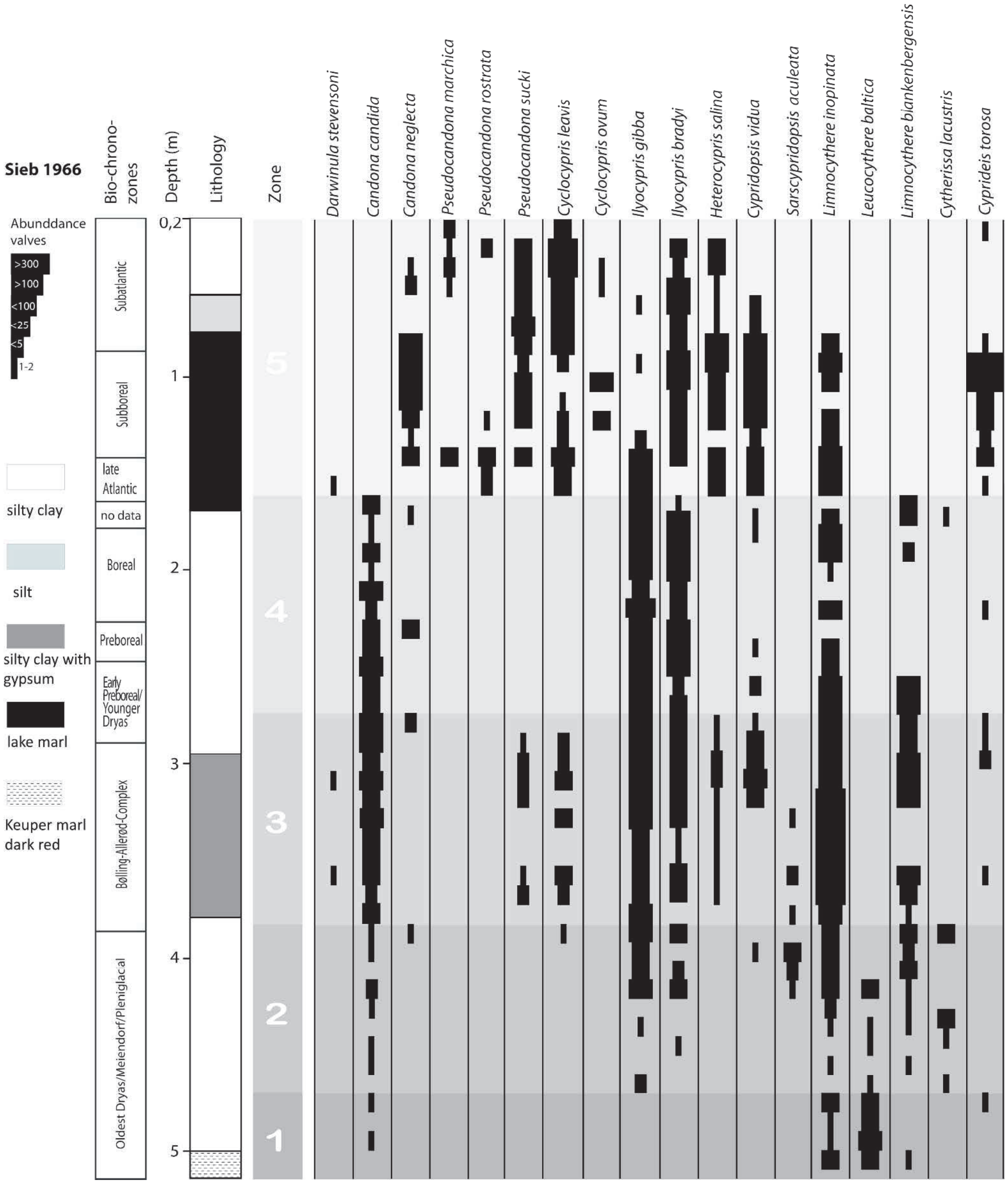

Fig 4: Lithology and ostracod distribution of the core Sieb 1966 and the hereon based unit differentiation. The chronozones are based on the pollen diagrams by Lange 1966 (Fig 6a) below 230 cm, and on this study above 230 cm (Figs 6b and 6c).
240x282mm (300 x 300 DPI)

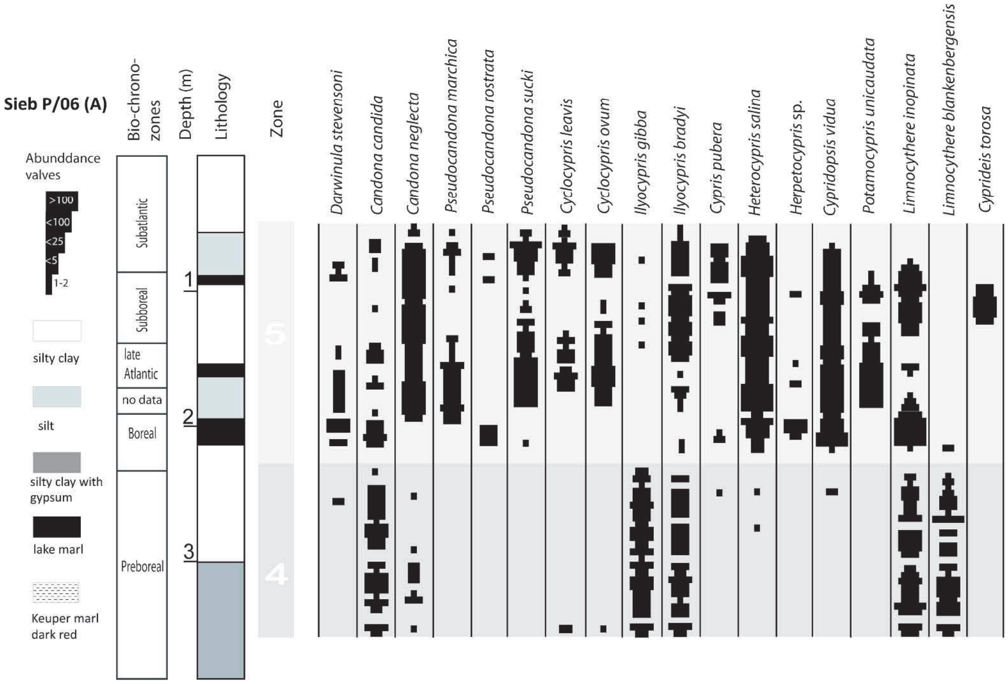

Fig 5: Lithology and ostracod distribution of the core Sieb P/06 and the hereon based unit differentiation. The chronozones are based on the pollen diagrams of this study (Figs 6b and 6c).
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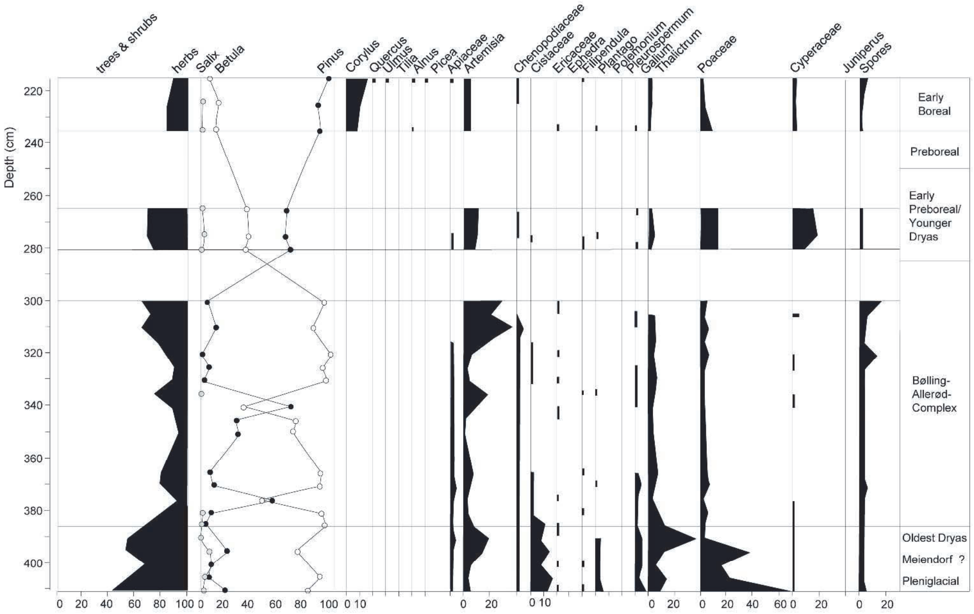

Fig. 6: Palynological diagrams: 6a: Pollen diagram of core Sieb 1966 based on remarks of E. Lange 1966. 6b: Pollen diagram of core Sieb P/06. 6c: Pollen diagram of core Sieb P/10
420x297mm (300 x 300 DPI)

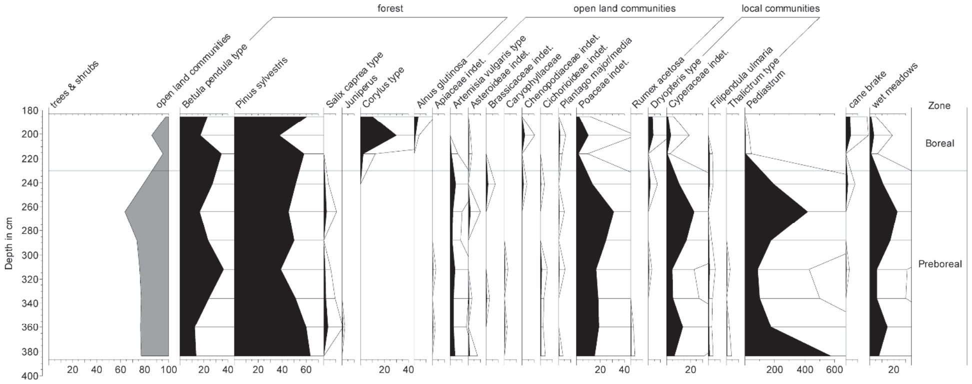

Fig. 6: Palynological diagrams: 6a: Pollen diagram of core Sieb 1966 based on remarks of E. Lange 1966.
6b: Pollen diagram of core Sieb P/06. 6c: Pollen diagram of core Sieb P/10
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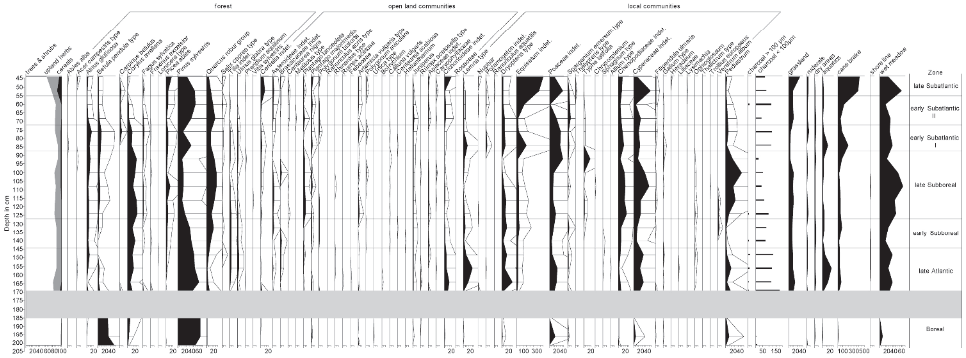

Fig. 6: Palynological diagrams: 6a: Pollen diagram of core Sieb 1966 based on remarks of E. Lange 1966. 6b: Pollen diagram of core Sieb P/06. 6c: Pollen diagram of core Sieb P/10
297x210mm (300 x 300 DPI)

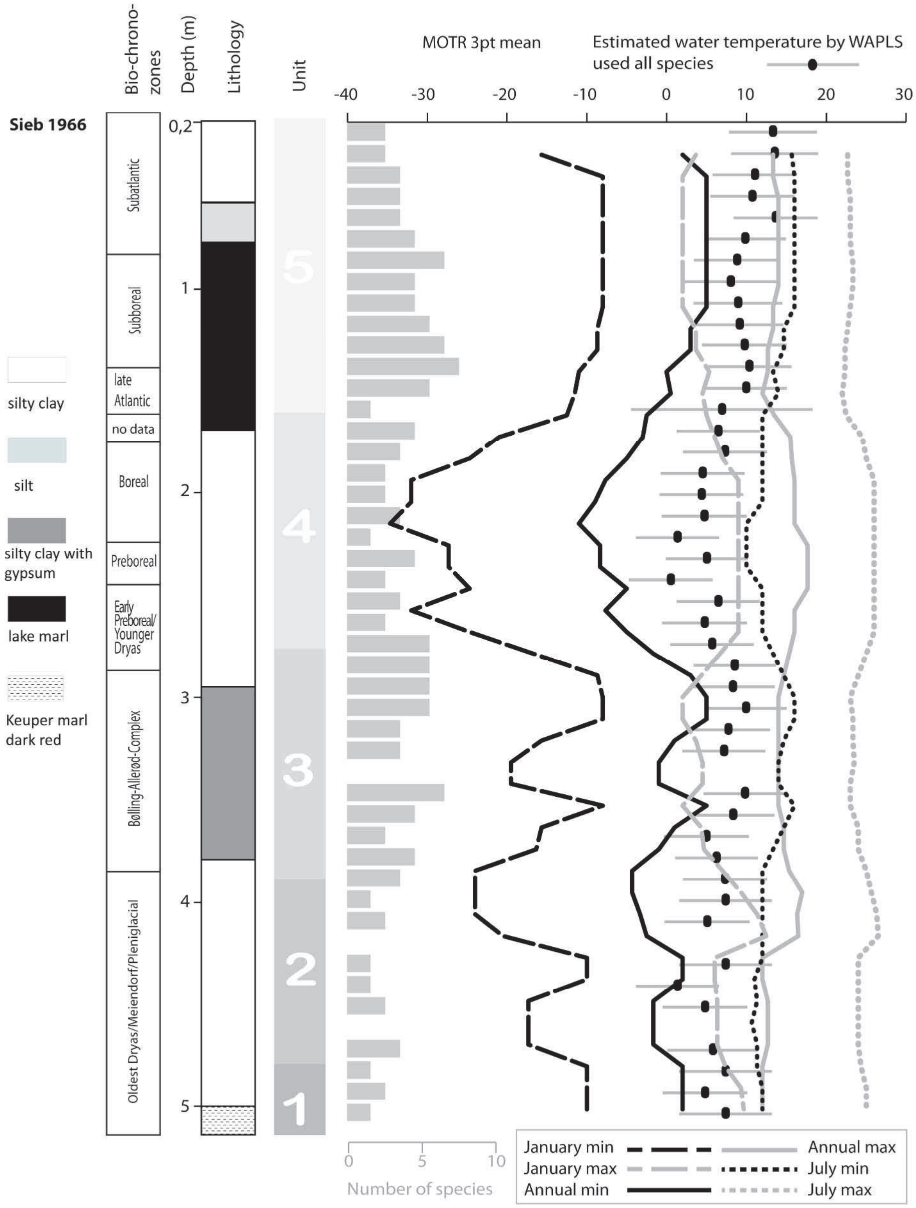

Fig. 7: Synopsis of Mutual Ostracod Temperature Range (MOTR) and Transfer-function (TF) of the ostracod species of Siebleben based on the ostracod distribution of core Sieb 1966.
223x286mm (300 x 300 DPI)

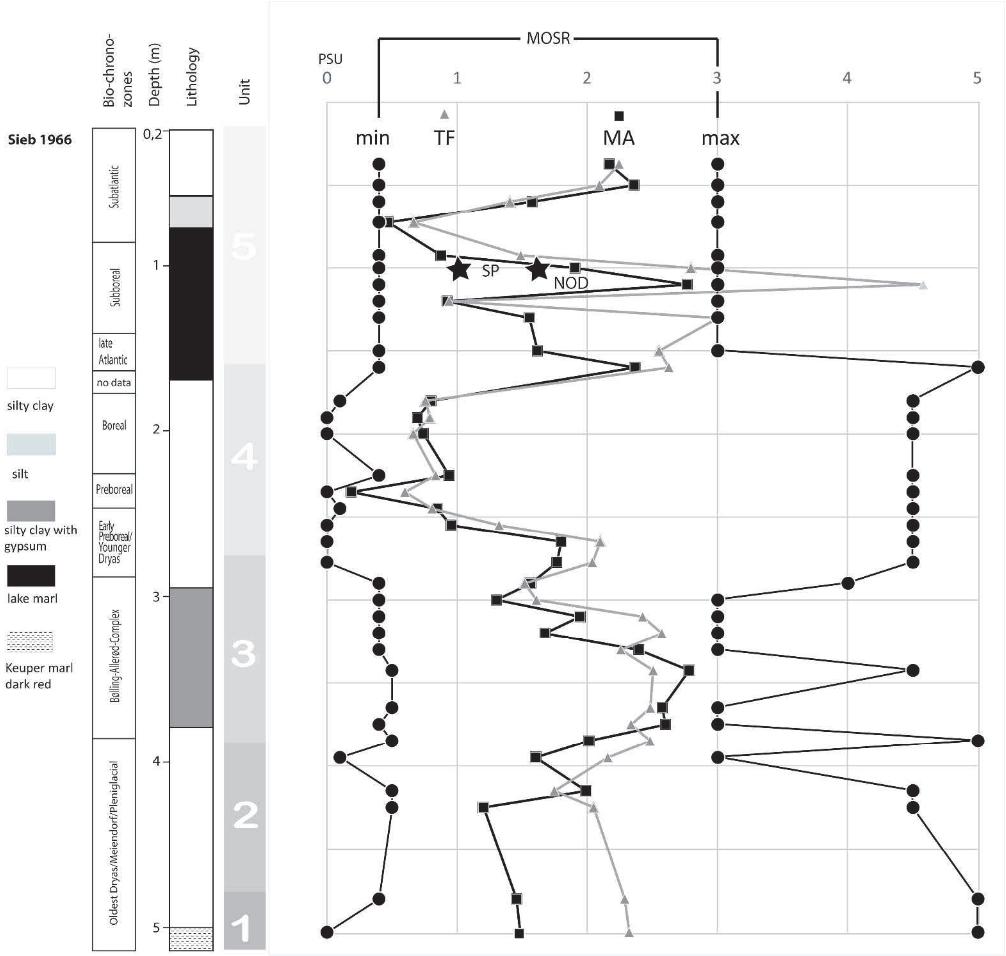

Fig 8: Synopsis of Mutual Ostracod Salinity Range (MOSR), Transfer-function (TF) and Modern Analogue (MA) based on the ostracod distribution of core Sieb 1966.
288x275mm (300 x 300 DPI)

Beitrag 3:

Distribution of *Cyprideis torosa* (Ostracoda) in Quaternary Athalassic Sediments in Germany and its Application for Palaeoecological Reconstructions

veröffentlicht 2012, Pint et al., *International Review of Hydrobiology*

Das Auftreten von *Cyprideis torosa* als markanter Salzzeiger im Quartär wurde für Gesamtdeutschland recherchiert. Neben eigenen Untersuchungen wurden auch Daten aus der Literatur verwendet. Für die indikative Bedeutung von *C. torosa* spielt die begleitende Ostrakodenfauna eine entscheidende Rolle.

Ergebnis: *Cyprideis torosa* kommt in Deutschland nur noch in thalassischen Lebensräumen, vor allen an den Küsten von Nord- und Ostsee und in Ästuaren vor. In athalassischen Binnengewässern war sie besonders im Atlantikum häufig, existierte noch in den Mansfelder Seen bis zur Trockenlegung des Salzigen Sees im 19ten Jahrhundert. *Cyprideis torosa* ist in Küstennähe mit Brackwasserostrakoden und in Binnengewässern mit Süßwasserostrakoden assoziiert. Die Mehrheit dieser begleitenden Ostrakodenarten ist salztolerant, in den Mansfelder Seen sowie in einigen Gewässern rund um Gotha konnten zudem auch subrezente Foraminiferen nachgewiesen werden, die als sicherer Salzzeiger gelten.

Anna Pint, Peter Frenzel, Roland Fuhrmann, Burkhard Scharf, Volker Wennrich (2012). Distribution of Cyprideis torosa (Ostracoda) in Quaternary athalassic sediments in Germany and its application for palaeoecological reconstructions,. International Review of Hydrobiology, 4: 330-355.

	A. Pint	**P.Frenzel**	**R. Fuhrmann**	**B. Scharf**	**V. Wennrich**
Konzeption	**X**	X			
Geländearbeiten	**X**	X	X	X	X
Datengewinnung	**X**	X	X	X	X
Datenauswertung und Interpretation	**X**	X	X		
Schreiben	**X**	X			
Publikationsäquivalent	**1,0**	n. a.	n. a.	n. a.	n. a.

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Research Paper

Distribution of *Cyprideis torosa* (Ostracoda) in Quaternary Athalassic Sediments in Germany and its Application for Palaeoecological Reconstructions

key words: Central Europe, Baltic Sea, saline inland waters, sieve-pore, noding

Abstract

Cyprideis torosa (JONES, 1850) is a very common brackish water ostracod of the German coasts, but, despite empty valves are found occasionally in surface sediments of some modern inland waters, *C. torosa* could not be found living in modern athalassic waters of Germany so far. During interglacial periods, including the Holocene, however, fossils of this species are quite common in Central Germany, at a distance of more than 300 km away from the coasts of the Baltic and North Seas. All 31 Quaternary localities with *C. torosa* known so far from Germany are documented. *C. torosa* is an indicator for brackish waters and widely used as index-fossil in palaeosalinity reconstructions relying on water chemistry bound morphological changes (nodes, sieve-pores). The comparisons imply a general underestimation of palaeosalinity in oligo- to mesohaline athalassic waters if using nodes and sieve-pores of *C. torosa* as proxy. A water chemistry (ionic composition) driven morphological response is assumed instead one by salinity only. Palaeosalinity estimations for athalassic waters, relying on morphological variability alone, should therefore be used with caution. Palaeosalinity trends, however, can be detected. Distinguishing thalassic and athalassic sediments with *C. torosa* is possible by using the associated ostracod fauna as a discriminator. Regarding the ecology and distribution of *C. torosa*, permanent, brackish, and shallow water bodies under relatively warm conditions are required for its settlement. The source of the salt are brines originating from Zechsteinian or Triassic underground evaporites. Warm and relatively dry climates could enhance the process for such water bodies of becoming salty, a situation present in Holocene Central Germany. The occurrence of *C. torosa* can therefore be used for palaeoclimatological studies. The most probable migration path of this ostracod species to athalassic waters is by avian transport.

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1. Introduction

The widespread and ecologically opportunistic ostracod species *Cyprideis torosa* (Jones, 1850) occurs both in marginal marine environments and inland water bodies with slightly brackish up to hypersaline conditions (Klie, 1938; Bronshtein, 1947; Meisch, 2000). It is an index species of the *Cyprideis litoralis-Manayunkia aestuarina* coenosis typical for soft bottoms of shallow coastal lagoons where it occurs often in high numbers (Remane, 1940). The species tolerates a wide range of salinity, temperature, and oxygen conditions (Meisch, 2000). *C. torosa* is commonly regarded as an index fossil for brackish waters (Vesper, 1972; Rosenfeld and Vesper, 1976; Gramann, 2000). In permanent inland water bodies with saline conditions, *C. torosa* can be associated with athalassic foraminifers, under oligohaline conditions with freshwater ostracod taxa (Wennrich *et al.*, 2007). A clue to successful palaeoenvironmental reconstruction is the ecologically driven morphological variability of the valves. Salinity dependant size, ornamentation, and sieve-pore changes, as well as the formation of nodes are known (Vesper, 1972; Rosenfeld and Vesper, 1976; Carbonel, 1982; Van Harten, 1996, 2000; Keyser and Aladin, 2004; Marco Barba, 2010). Whether athalassic *C. torosa*, however, shows the same morphological variation pattern as in the marine realm is not known.

There is a relatively high number of fossil occurrences of *C. torosa* in Central and Northern Germany as already stated by Gramann (2000). Whereas its general distribution along the Holocene and Pleistocene coast lines of the North and Baltic Sea is not surprising, there are many reports from inland water sediments of these time periods. Gramann (2000) reported four athalassic localities with *C. torosa* shells in surface sediments, however, no specimens with soft parts were discovered. The question arises why *C. torosa*, the most frequent ostracod species of the German coast today, could not be found living in oligo- or mesohaline inland waters. Which environmental conditions are needed for colonization of an athalassic brackish water body by *C. torosa*? Are there differences in environmental or climatic conditions between today's and fossil occurrences? Is it possible to discriminate between athalassic and thalassic associations containing *C. torosa*? Are the proportions of noded valves and round sieve pores applicable for salinity reconstructions in athalassic waters also?

To answer these questions of relevance for palaeoenvironmental reconstructions, the distribution data of *C. torosa* from Quaternary sediments of Germany are compared to recent ones. Additionally, a morphological analysis of material from selected sites contributes to an evaluation of node proportion and sieve pore shape as proxies for salinity in athalassic waters.

2. Material and Methods

The compilation of distributional data for *Cyprideis torosa* in Quaternary sediments of Germany is based on (1) an overview on published studies mentioning this species in Germany as well as the Fossil Ostracod Database for Central Germany by R. Fuhrmann (Fuhrmann, 2006), and (2) new studies of fossil material from Siebleben and Voigtstedt (Thüringen), Salziger and Süßer See (Sachsen-Anhalt), and Bad Laer (Niedersachsen) (Fig. 1). Additionally, we sampled recent inland salt water sites in Central Germany in search for *C. torosa* in the summer of 2006 and 2007. Those are mainly localities from where athalassic foraminifers were reported by Bartenstein (1939): Siebleben near Gotha, Großengottern, Alperstedt, and Stotternheim near Erfurt, as well as Esperstedt south of the Harz mountain. A database of Recent ostracod occurrences along the German Baltic Sea coast (Frenzel, 2009) was used for comparison and additional ecological data (Frenzel *et al.*, 2010).

Sampling of living ostracods was done using a hand net scraping the topmost cm of the sediment from the bottom of the selected water bodies. The sediment samples were stored in ca. 70% ethanol in order to recognize "living" individuals during picking.

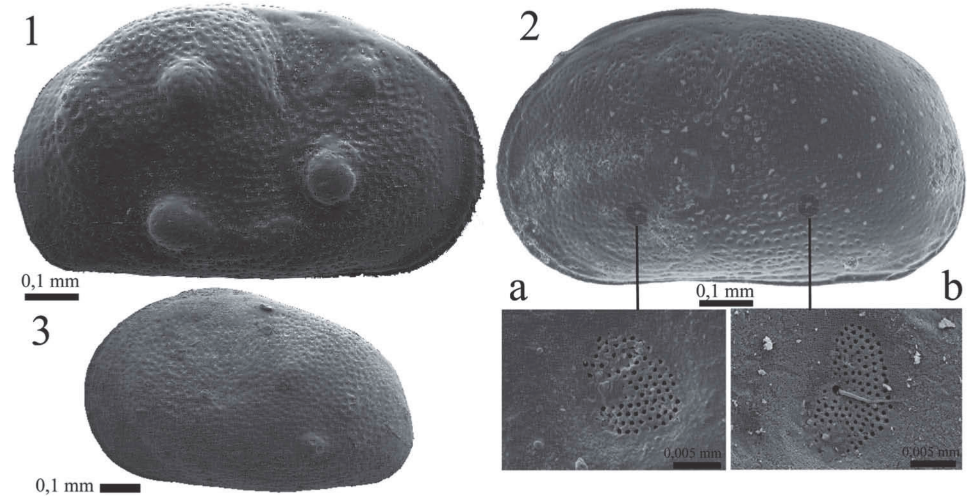

Figure 1. The two forms of valve modification of *Cyprideis torosa* (JONES, 1850). 1: Strongly noded right femal valve, 2: Smooth left female valve, 3: Slightly noded left juvenile valve. Two types of sieve-pore shape: a: Rounded shape, b: elongated shape.

A detailed study of morphological peculiarities was carried out using (1) material from the DIEBEL and PIETRZENIUK collection of Quaternary Ostracoda in the Museum of Natural History Berlin as well as a new sediment core from Siebleben near Gotha, (2) an outcrop profile from the Pleistocene Muscheltone (Mussel Clays) near Voigtstedt (THOMAS, 2010), (3) already picked ostracod valves from sediment cores of Süßer and Salziger See in Sachsen-Anhalt (WENNRICH, 2005), and (4) two archive samples from Bad Laer (HILTERMANN and LÜTTIG, 1960) (Fig. 2). Additionally, for comparison, palaeo-salinities were estimated using mutual ecological tolerances of ostracod species within the local associations.

Fossil sediments were disintegrated with H_2O_2 when necessary. All other samples were washed without preparation with tap water using a 200 µm sieve. The residues were dried on air at room temperature.

If not already isolated, microfossils were picked under a low-power binocular microscope using a fine tipped brush. After determining the accompanying fauna, the proportion of noded valves of *C. torosa* was counted. Ten valves of *C. torosa* (female or male, preferentially smooth valves) of each sample were investigated under a light microscope with a magnification of 400× to determine the shape of at least 30 sieve-pores following the method by ROSENFELD and VESPER (1976). For this analysis the state of valve preservation should be very good because even a minor recalcification can hamper the correct attribution of the sieve-pore types. The percentage of rounded shaped sieve-pores was used for calculating palaeo-salinities using a transfer function based on data by ROSENFELD and VESPER (1976) and own data from the Baltic Sea coast (FRENZEL, 2009). According to an exponential regression of field data by FRENZEL *et al.* (2011) the following formula was applied:

$$S = e^{-0.06\ \mathrm{RS} + 4.7},$$

where S = salinity [psu], RS = proportion of round sieve pores [%])

The correlation coefficient between measured and estimated salinities of this transfer function is $R^2 = 0.95$.

3. Localities and Ecology

The studied sites and most of the locations from literature are situated in Central and Northern Germany (Fig. 2). The recent climate in Central Germany lies within the European subcontinental climate zone (SCHRÖDER, 1986). The recent annual mean temperature in Cen-

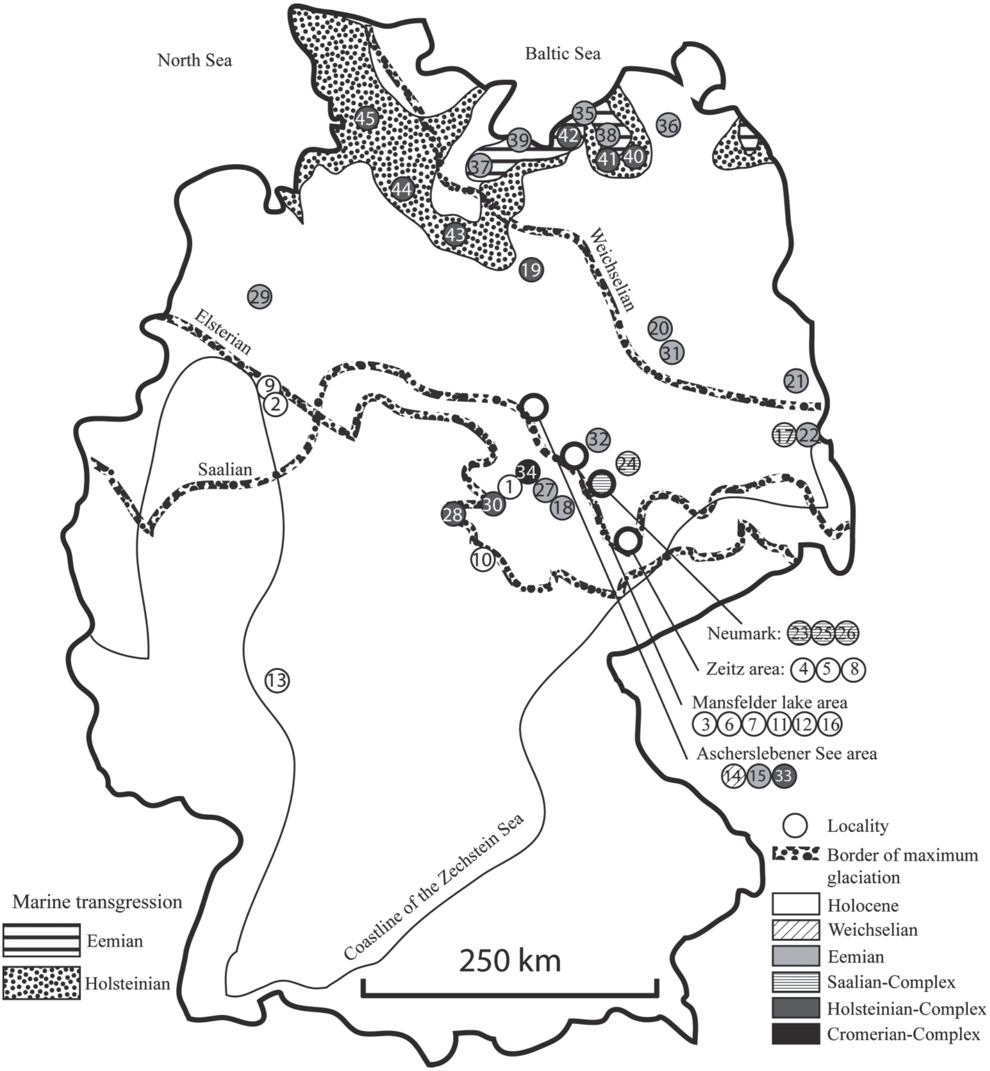

Figure 2. German Quaternary localities with fossil *Cyprideis torosa*. Holocene marine locations are omitted because of the abundant distribution along the coasts. The palaeo-coastline of the Zechsteinian Sea is plotted as a limit of evaporite distribution, potential sources for salty brines (after KIERSNOWSKI *et al.,* 1995). Ice-marginal grounds of the Weichselian, Saalian, and Elsterian glaciations are taken from LITT *et al.* (2008). Locality numbers refer to athalassic waters of Tab. 1; nr. 35 – 45 are marginal marine sites listed by FRENZEL and VIEHBERG (2004) for Mecklenburg-Vorpommern, by BENDA and MICHAEL (1966) and LORD *et al.* (1995) for Schleswig-Holstein and Niedersachsen (35 – Kühlungsborn 36 – Grimmen [glacial erratic lump], 37 – Herrnburg, 38 – Schwaan, 39 – Klein Klütz Höved, 40 – Thürkow, 41 – Güstrow, 42 – Neubukow, 43 – Lüneburg, 44 – Hamburg-Blankenese, 45 – Eggstedt).

tral Germany is 8–9 °C and the mean precipitation is 500 mm per year (Schröder, 1986). Precipitation clearly exceeds evaporation in the present climate.

The present review of athalassic occurrences of *Cyprideis torosa* in Germany is based on 31 localities in total (Table 1 and 2; Fig. 1). There are much more German sites with marine influence because of a wide distribution of this brackish water species along the coast. An overview is given in Frenzel and Viehberg (2004) and Frenzel *et al.* (2010). In Table 1 all those German athalassic localities with *C. torosa* known so far are listed. In all these localities the material consists of either empty shells from surface sediments of modern waters or fossil shells from outcrops and cores.

4. Results and Discussion

4.1. Distribution of Cyprideis torosa*-Thalassic (marginal marine) distribution*

Cyprideis torosa is the most abundant and most frequently occurring marginal marine ostracod species in the Baltic Sea (Frenzel *et al.* 2010) and of the German North Sea coast (Klie, 1938). The data set used by Frenzel *et al.* (2010) for their compilation on the ostracod fauna of the Baltic Sea enables an evaluation of modern salinity and water depth dependant distribution of *C. torosa*. The species clearly prefers shallow waters of maximum 10 m water depth (Fig. 3), less than the 30 m depth limit given by Meisch (2000). A plot of *C. torosa* abundance versus salinity shows a minimum of 0.5 psu (Fig. 4). Lower values, *i.e.,* in the freshwater range, are very rare and can be explained by short time variations in estuarine coastal waters. Maximum abundances are found around 1 psu; at 9 psu a sudden drop in numbers is recognizable. A second drop occurs at 14 psu and very low numbers are left from about 16 psu to the maximum of the studied salinity interval. The 9 and 14 psu thresholds interestingly coincide with Aladin's (1993) limits of osmoregulation. Wagner (1964) gives 2–16.5 psu as main distribution range for *C. torosa*, which is close to our general picture, despite the lower limit is a little too high. A combination of osmoregulation and competition driven abundance pattern for *C. torosa* in marginal marine environments of the Baltic Sea is assumed here.

Marine influenced fossil ostracod associations yielding *C. torosa* in northern Germany have been described several times (*e.g.*, Frenzel and Viehberg, 2004; Benda and Michael, 1966; Lord *et al,.* 1995; compare Fig. 2). They clearly trace the coasts of the Eemian and Holsteinian seas. Gramann (2000) noted *C. torosa* to be an index fossil for coast lines of the geological past.

4.2. Nodes and Sieve-Pores

It is well known that *Cyprideis torosa* forms nodes on its valves under oligohaline conditions. Keyser (2005) explains the phenomenon by pathological reactions during the moulting process; the formation of nodes is influenced by total ion concentration and Ca^{2+} availability. Different salinity limits for noded valves were proposed (Vesper, 1972; Frenzel, 1991; Keyser and Aladin, 2004; Marco Barba, 2010). It seems, however, that nodes occur mainly below the switching point of osmoregulation at about 9 psu (Aladin, 1993) and become dominant within the β-oligohaline range (<2 psu) (see Frenzel *et al.*, 2012 for details). This hypothesis applies for the marginal marine realm.

There is no stratigraphical/climatical pattern recognizable in the number of noded valves from athalassic localities (Table 2). Evaluating the proportion of node-bearing valves with palaeosalinity estimations for the material of Voigtstedt, Siebleben, Bad Laer, Salziger and Süßer See (see Sieve-pore analysis below), a high number for all sites would be expected,

Table 1. German localities with athalassic *Cyprideis torosa* and their features. The number in the second column refers to the locality numbers in Fig. 2.

Locality	Nr.	Sample Type	Water type	Age/duration of the water body	Origin of salt	Author
Sachsen-Anhalt						
Bindersee	3	Surface	Remnant lake of the former Salziger See (subrosion basin)	Since 19th century	Zechstein	This paper
Rollsdorf	6/16	Outcrop	Lake (subrosion basin)	Late Holocene and Eemian	Zechstein	Fuhrmann (unpublished)
Unterröblingen	7	Outcrop	Lake (subrosion basin)	Late Holocene	Zechstein	Fuhrmann (unpublished)
Zeitz	8	Outcrop	Alluvial clay	Middle and Late Holocene	Zechstein	Fuhrmann. 2008
Salziger See	12	Sediment core	Lake (subrosion basin)	Older Dryas-19th century (duration 13000 a)	Zechstein	Wennrich, 2005, this paper
Süßer See	11	Sediment core	Lake (subrosion basin)	Praeboreal-Recent, main stage since Atlanticum (duration 7000 a)	Zechstein	Meng *et al.*, 2004, this paper
Memleben	18	Outcrop	Fluvial gravel	Eemian	Zechstein	Wüst, 1903
Schadeleben	14	Outcrop	Lake (subrosion basin)	Early Weichselian	Zechstein	Fuhrmann (personal observation)
Königsaue	15	Outcrop	Lake (subrosion basin)	Late Eemian	Zechstein	Fuhrmann (unpublished)
Neumark-Nord	23/25	Outcrop	Lake (interglacial basin)	Saalian-Complex (Interglacial period „Grabschütz-Warmzeit“)	Zechstein? Evaporation	Fuhrmann and Pietrzeniuk, 1990b
Neumark-Süd	26	Outcrop	Lake (interglacial basin)	Holsteinian	Zechstein	Fuhrmann (unpublished)
Aschersleben	33	Outcrop	River with flood plain	Holsteinian	Zechstein	Mania, 1967
Benkendorf	32	Outcrop	Fluvial gravel	Holsteinian	Zechstein	Wüst, 1902a
Thüringen						
Esperstedt	1	Surface	Brine ditch system within a salt marsh (Esperstedter Ried) close to a brine spring	Since 14th century	Zechstein	This paper
Zipsendorf	4	Sediment core	Alluvial clay	Late Holocene	Zechstein	Fuhrmann (unpublished)

Table 1. (Continued)

Locality	Nr.	Sample Type	Water type	Age/duration of the water body	Origin of salt	Author
Rositz	5	Sediment core	Alluvial clay	Late Holocene	Zechstein	Fuhrmann (unpublished)
Siebleben	10	Sediment core	Former lake with a remaining pond (subrosion basin)	Allerød-Subatlanticum (duration 8000 a)	Zechstein	Greifeld, 1966, this paper
Bottendorf	27	Outcrop	Fluvial gravel	Holsteinian	Zechstein	Wüst, 1902b
Mühlhausen-Klippe	28	Outcrop	Tufa spring	Holsteinian	Zechstein	Fuhrmann (unpublished)
Bilzingsleben	30	Outcrop	Tufa spring and pond	Holsteinian	Zechstein	Daniel and Frenzel, 2010
Voigtstedt	34	Outcrop	Lake or large oxbow (subrosion basin)	Cromerian-Complex	Zechstein	Thomas, 2010
Brandenburg						
Cottbus	17/22	Outgrop	Lake	Late Warthian and Eemian	Zechstein	Fuhrmann (unpublished)
Derwitz	20	Outcrop	Lake	Eemian	Zechstein?	Diebel and Pietrzeniuk, 1975
Frankfurt/Oder	21	Outcrop	Interglacial basin	Eemian	Zechstein?	Hucke 1912
Bornim	31	Outcrop Sediment core	Lake	Holsteinian?	Zechstein?	Diebel and Pietrzeniuk, 1975
Niedersachsen						
Glockensee	2	Surface	Artificial pond influenced by brines through a ditch	Since 1970	Zechstein	Gramann, 2000
Bad Laer	9	Outcrop	Tufa spring	Younger Dryas-Atlanticum (duration 6000 a)	Zechstein	Hiltermann and Lüttig, 1960
Woltersdorf	29	Sediment core	Interglacial basin	Holsteinian		Gramann, 2000
Quakenbrück	19	Sediment core	Lake (interglacial basin)	Eem	Zechstein	Gramann, 2000 Hahne *et al.*,1994
Sachsen						
Grabschütz	24	Outcrop	Lake (Interglacial basin)	Saalian-Complex (Interglacial period „Grabschütz-Warmzeit“)	Evaporation	Fuhrmann and Pietrzeniuk, 1990a
Rheinland-Pfalz						
Bad Soden	13	Outcrop	Permanent Pond	Holocene	Zechstein	Triebel, 1950

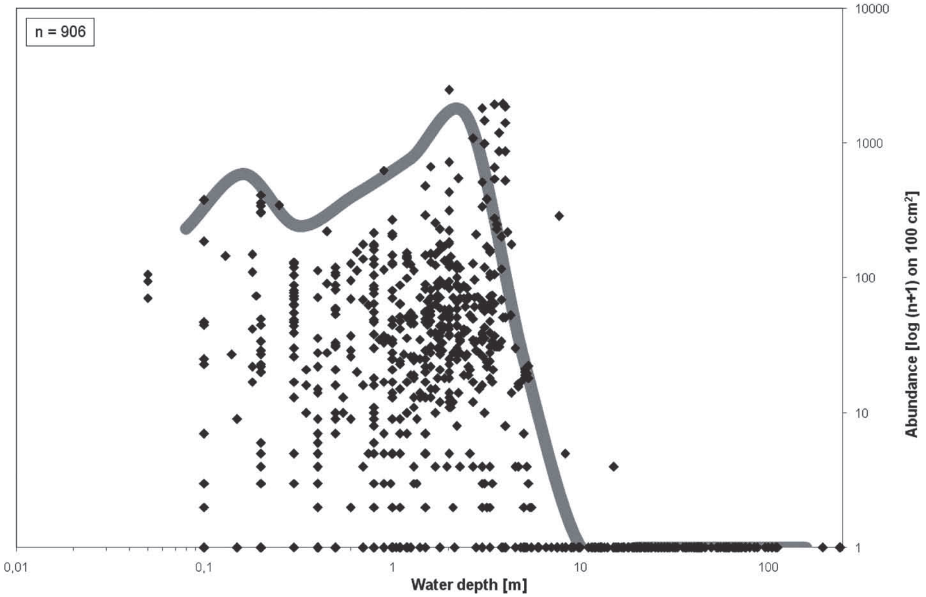

Figure 3. Water depth dependant distribution of living *Cyprideis torosa* in 906 samples from the southern Baltic Sea coast (0.1–241 m water depth) based on an unpublished data set used for compilation of FRENZEL *et al.* (2010) including data by DELLING (1981), KÖHLER (1990), ROSENFELD (1979) and USSKILAT (1975). The average graph (grey line) is smoothed.

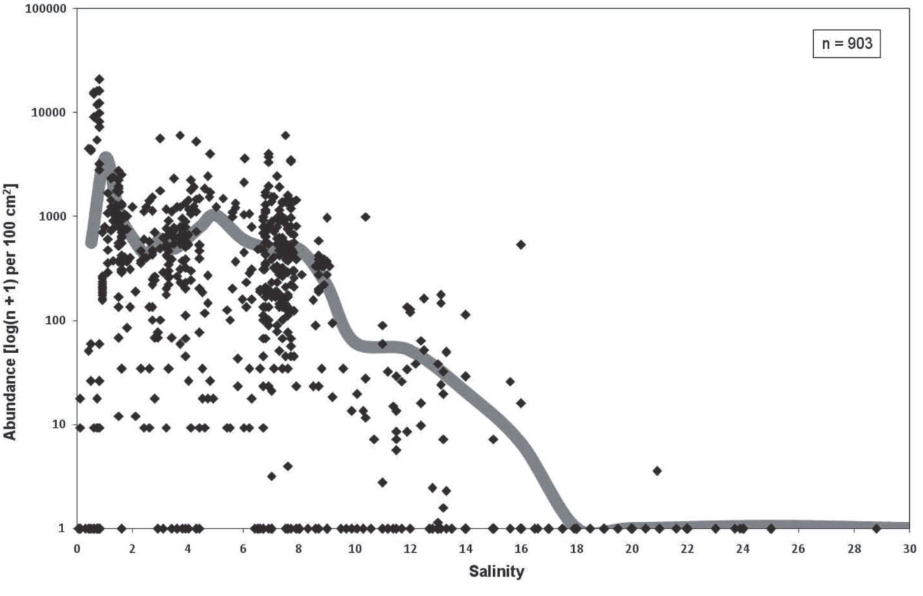

Figure 4. Salinity dependant distribution of living *Cyprideis torosa* in 903 samples from the southern Baltic Sea coast (0.1–28.8 psu) based on an unpublished data set used for compilation of FRENZEL *et al.* (2010) including data by DELLING (1981), KÖHLER (1990), ROSENFELD (1979) and USSKILAT (1975). The average graph (grey line) is smoothed.

Table 2. Relative abundance and noding in *Cyprideis torosa*. Abundance: D = dominating, d = dominating in horizons, C = common, A = accessory. Noding: N = noded form, S = smooth form, ( ) = form is less frequent than the other, * = no quantitative data.

Morphological form	Abundance	Locality		L = Late, M = Middle, E = Early	Stratigraphy	
N(S)	C	Esperstedt	1		Recent	
N(S)	D	Glockensee	2			
N(S)	C	Bindersee	3			
S	A	Zipsendorf *	4	L	Holocene	
S	A	Rositz *	5	L		
S(N)	D	Rollsdorf *	6	L		
S(N)	D	Unterröblingen	7	M-L		
S	A	Zeitz *	8	M-L		
S(N)	D	Bad Laer	9	M		
S(N)	d	Siebleben *	10	M		
S(N)*	D	Süßer See	11	E-M		
N	D	Salziger See	12	E-L		
No data	C	Bad Soden	13	?		
		No localities		M-L	Weichselian	
S(N)	d	Schadeleben *	14	E		
S(N)	D	Königsaue *	15	L	Eemian	
S(N)	D	Rollsdorf *	16	M		
N(S)	D	Cottbus *	17	E-L		
S	D	Memleben	18	?		
S(N)	D	Quakenbrück	19	?		
N(S)	A	Derwitz	20	?		
S	D	Frankfurt/Oder	21	?		
S	A	Cottbus *	22	L	Warthian	Saalian Complex
		No localities		E-M		
		No localities		L	Grabschütz Interglacial	
NS	d	Neumark-Nord *	23	E-M		
S(N)	A	Grabschütz *	24	E		
S	A	Neumark-Nord *	25	L	Saalian s. str.	
		No localities		M		
S(N)	A	Neumark-Süd *	26	E		
N(S)	D	Bottendorf	27	L	Holsteinian Complex	
S	A	Mühöhausen-Klippe*	28	L		
S(N)*	d	Woltersdorf	29	?		
S	A	Bilzingsleben**	30	?		
N(S)	A	Bornim	31	?		
N(S)		Benkendorf	32	?		
S	C	Aschersleben	33	?		
S	D	Voigtstedt	34		Cromerian	

with at least 10% of the valves being noded. This is not the case for Voigtstedt, where only smooth forms were found, and for Siebleben, where noded valves are less abundant than smooth valves. Only Salziger See shows a dominance of noded valves.

4.3. Sieve-Pore Analysis

Sieve-pores are external openings of normal pore canals trough the outer lamella provided with sieve-plates. Approximately 80 sieve-pores are located on an adult valve of *Cyprideis torosa.* Sieve-pores include a bristle that protrudes out of the pore (ROSENFELD, 1982). ROSENFELD and VESPER (1976) discovered that sieve-pore shapes on valves of *C. torosa* vary due to different salinity conditions. The proportion of rounded shaped sieve-pores proportion decreases with increasing salinity. Based on this observation, the authors provide diagrams allowing estimation of palaeosalinity from rounded sieve-pore proportion of fossil *C. torosa* valves. This type of analysis needs adult valves in a very good state of preservation.

Except the study by KEATINGS *et al.* (2007), the method has not been checked so far and the mechanism behind is not really understood. Testing the method on material from marginal marine settings of the Baltic Sea coast confirmed ROSENFELD and VESPER'S observations (FRENZEL, 2009). It remains unclear, however, if the transfer function is applicable to athalassic settings, where different water chemistry (ionic composition) could alter the results despite comparable salinity values.

The sieve-pore analysis resulted in lower salinity estimations than was expected for Voigtstedt, Siebleben, Bad Laer, and Süßer See. Reconstructed values are 0.2 to 0.4 psu in contrast to 0.5–4.5 psu estimated by mutual ecological tolerance data for Voigtstedt, 0.5–0.7 psu vs. 0.5–3.0 psu for Siebleben, c. 1 psu vs. 0.5–4.4 psu for Bad Laer, 0.3–1.0 psu vs. 0.5–5.7 psu for Süßer See, and 0.3–5.0 psu vs. 0.5–3.0 (5.0) psu for Salziger See. The only location with matching salinity estimation from sieve-pore analysis is Salziger See. This is the same result as the matching estimation by the proportion of noded valves (see above).

A systematic error from sieve-pore analyses can be assumed when applying marginal marine observations to athalassic waters with differing ionic composition, but the general trends in sieve-pore proportions should be indicative of past salinity changes. KEATINGS *et al.* (2007) found higher estimations of salinity using sieve-pore counts in comparison to salinity measurements in athalassic Lake Quarun, Egypt. The same overestimation is probable for Early Holocene sediments from an athalassic lake at Tayma, northern Saudi-Arabia (ENGEL *et al.,* 2011). Those observed overestimations under poly- to hyperhaline conditions are in contrast to our general under-estimations in oligohaline inland waters of Germany. The reason for such contradictive systematic errors is probably due to different ionic composition of the individual waters. An explanation for the matching estimation in Salziger See could be a palaeo-water chemistry close to marginal marine conditions. Unfortunately, the ionic composition of the palaeo-lakes can not be reconstructed. Each lake could have had a different ionic composition. Furthermore, it is not known how salinity influences the sieve pore shape and which ions are crucial for their deformation.

Up to date, we are not able to reconstruct the palaeo-salinities of athalassic sediments when relying on *C. torosa* alone. Systematic observations on Recent *C. torosa* populations from athalassic environments could provide a clue for solving this problem.

4.4. Associated Fauna

There is a high number of ostracod species associated with *Cyprideis torosa* (Table 3). The analysis of 31 athalassic localities in Germany shows 127 species belonging to 39 genera. The number of associated taxa along the Baltic coast is much lower (46 species and

Table 3. Ostracod species associated with *Cyprideis torosa* in athalassic water bodies in Germany. The ecological groups refer to the system of FUHRMANN (2006). *The stratigraphic position of the Grabschütz-Interglacial is discussed controversially (FUHRMANN, 2011 and STRAHL *et al.*, 2010).

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Cluster 1: Interglacial species																																						
Darwinula stevensoni (BRADY and ROBERTSON, 1870)						x	x	x		x	x	x			x	x	x	x		x	x					x	x					x			x			
Vestalenula pagliolii (PINTO and KOZIAN, 1961)																		x																				
Paracandona euplectella (ROBERTSON, 1889)																x																						
Candona vernalis FUHRMANN, 2008								x																														
Fabaeformiscandona caudata (KAUFMANN, 1900)																				x										x								
Fabaeformiscandona clivosa (FUHRMANN, 1991)																														x								
Fabaeformiscandona fabaeformis (FISCHER, 1851)						x															x					x												
Fabaeformiscandona fragilis (HARTWIG, 1898)																		x																				
Fabaeformiscandona spelaea (KLIE, 1941)				x		x		x								x		x																				
Pseudocandona insculpta (G. W. MÜLLER, 1900)																																					x	
Candonopsis kingsleii (BRADY and ROBERTSON, 1870)								x								x		x																				
Physocypria kraepelini G. W. MÜLLER, 1903						x	x	x																														

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Herpetocypris brevicaudata KAUFMANN, 1900																																x					x	
Herpetocypris chevreuxi (SARS, 1896)	x					x						x														x	x											
Herpetocypris helenae G. W. MÜLLER, 1908							x																															
Psychrodromus olivaceus (BRADY and NORMAN, 1889)						x		x																								x						
Heterocypris neumarkensis FUHRMANN and GOTH, 2011																										x												
Scottia pseudobrowniana KEMPF, 1971						x		x																														
Scottia tumida (JONES, 1850)																																			x			
Tonnacypris lutaria (KOCH, 1838)																																					x	
Cypretta eissmanni FUHRMANN and PIETRZENIUK, 1990																											x											
Cypridopsis groebernensis FUHRMANN and PIETRZENIUK, 1990																																						
Cypridopsis hartwigi G. W. MÜLLER, 1900																		x																				
Potamocypris similis G. W. MÜLLER, 1912																		x									x											
Potamocypris acuminata FUHRMANN and GOTH, 2011																										x												

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																						Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Potamocypris neumarkensis Fuhrmann and Goth, 2011																										x												
Metacypris cordata Brady and Robertson, 1870																x		x		x	x					x	x						x		x			
Cluster 2: Glacial Species																																						
Fabaeformiscandona harmsworthi (Scott, 1899)															x																							
Fabaeformiscandona rawsoni (Tressler, 1957)															x																				x			
Cyclocypris meischi Fuhrmann and Goth, 2011															x																							
Ilyocypris glabella Fuhrmann and Goth, 2011															x															x								
Juxilyocypris schwarzbachi (Kempf, 1967)															x																				x			
Eucypris dulcifons Diebel and Pietrzeniuk, 1969															x																				x			
Eucypris heinrichi Diebel and Pietrzeniuk, 1978															x																							
Tonnacypris tonnensis (Diebel and Pietrzeniuk, 1975)															x																							
Tonnacypris convexa Diebel and Pietrzeniuk, 1975															x																							
Potamocypris foveolosa Fuhrmann and Goth, 2011															x																							

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Limnocythere blankenbergensis Diebel, 1968										x																									x			
Limnocythere falcata Diebel, 1968															x																				x			
Limnocythere goersbachensis Diebel, 1968															x																							
Cluster 3: East-European/continental species																																						
Candona muelleri Hartwig, 1899																																					x	
Fabaeformiscandona balatonica (Daday, 1894)															x				x																		x	
Fabaeformiscandona holzkampfi (Hartwig, 1900)															x											x				x								
Pseudocandona sucki (Hartwig, 1901)						x	x			x						x																						
Cyclocypris detruncata Fuhrmann and Goth, 2011															x																							
Cyclocypris diebeli Absolon, 1973																																x						
Cyclocypris impressopunctata Hirschmann, 1909															x			x					x			x				x								
Cyclocypris labialis Sywula, 1981															x	x		x					x							x								
Cyclocypris luetzkendorfensis Fuhrmann and Goth, 2011															x															x								
Cyclocypris ovoides (Alm, 1914)								x							x								x															

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Cyclocypris pygmaea Croneberg, 1895						x									x	x														x								
Ilyocypris absentiva Fuhrmann, 2008				x				x																														
Ilyocypris grabschuetzi Fuhrmann and Pietrzeniuk, 1990																											x											
Ilyocypris uncinatus Fuhrmann and Pietrzeniuk, 1990															x								x			x				x								
Trajancypris laevis (G. W. Müller, 1900)								x							x	x																			x			
Trajancypris serrata (G. W. Müller, 1900)																																					x	
Heterocypris rotundata (Bronshtein, 1928)								x							x																							
Cypridopsis concolor Daday, 1900															x												x											
Cypridopsis parva G.W.Müller, 1900																x		x																				
Limnocythere suessenbornensis Diebel, 1968															x											x												
Cluster 4 : Oligostenothermal/boreo-alpine species																																						
Fabaeformiscandona tricicatricosa (Diebel and Pietrzeniuk, 1969)															x			x					x							x								

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Cyclocypris serena (Koch, 1838)				x				x							x			x									x			x								
Ilyocypris getica Masi, 1906								x							x											x												
Ilyocypris lacustris Kaufmann, 1900															x															x								
Cavernocypris subterranea (Wolf, 1920)								x																														
Leucocythere mirabilis Kaufmann, 1900															x																							
Limnocytherina sanctipatricii (Brady and Robertson, 1869)											x				x	x		x		x			x				x			x					x		x	
Cytherissa lacustris (Sars, 1863)										x					x			x		x	x		x			x	x			x	x		x				x	
Cluster 5 : species of springs																																						
Cluster 5a : Rheokrene springs																																						
Fabaeformiscandona breuili (Paris, 1920)				x				x																								x						
Potamocypris fallax Fox, 1967								x																								x						
Potamocypris zschokkei (Kaufmann, 1900)				x		x	x	x																						x								
Cluster 5b : Helo-/limnokrene																																						
Nannocandona faba Ekman, 1914					x			x												x												x						
Fabaeformiscandona brevicornis (Klie, 1925)						x		x																														
Cryptocandona vavrai Kaufmann, 1900				x	x			x																						x		x						

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Cyclocypris helocrenica Fuhrmann and Pietrzeniuk, 1990								x																						x								
Cyclocypris humilis Pietrzeniuk, 1985						x		x																						x		x						
Eucypris pigra (Fischer, 1851)				x				x							x															x		x					x	
Potamocypris fulva (Brady, 1868)				x																																		
Cluster 6 : Rhithronal species																																						
Candona lindneri Petkovski, 1969								x																						x								
Ilyocypris bradyi Sars, 1890	x	x	x	x	x	x	x	x		x			x		x	x		x	x		x	x	x			x	x			x		x	x		x		x	x
Ilyocypris inermis Kaufmann, 1900				x				x																								x						
Prionocypris zenkeri (Chyzer and Toth, 1858)	x			x				x																													x	
Cluster 7 : Oligothermophilic, rheophobic species („winter/spring“)																																						
Cluster 7a : Temporary ponds																																						
Pseudocandona lobipes (Hartwig, 1900)																x																						
Pseudocandona parallela (G. W. Müller, 1900)				x	x	x		x					x																	x		x						
Pseudocandona pratensis (Hartwig, 1901)								x																														
Pseudocandona sarsi (Hartwig, 1899)				x	x			x							x															x								
Eucypris virens Jurine, 1820											x																										x	

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Cyprois marginata (Straus, 1821)			x								x				x																						x	
Cypris pubera O. F. Müller, 1776								x		x					x	x							x			x												
Cluster 7b : Permanent ponds																																						
Candona altoides Petkovski, 1961															x																							
Candona candida (O.F.Müller, 1776)		x		x	x	x	x	x	x	x	x	x	x		x	x		x		x	x		x			x	x			x	x	x					x	
Candona neglecta Sars, 1887	x	x	x					x	x	x	x	x			x	x		x	x	x	x		x			x	x			x			x		x		x	x
Candona weltneri Hartwig, 1899															x	x			x							x				x			x		x		x	
Fabaeformiscandona hyalina (Brady and Robertson, 1870)															x	x		x			x		x			x				x							x	
Fabaeformiscandona levanderi (Hirschmann, 1912)															x			x					x							x					x			
Fabaeformiscandona protzi (Hartwig, 1898)															x			x		x			x							x								
Pseudocandona marchica (Hartwig, 1899)			x					x	x	x		x			x	x		x								x				x								
Pseudocandona rostrata (Brady and Norman, 1889)										x																												
Cyclocypris ovum (Jurine, 1820)								x	x	x	x	x			x			x		x	x		x			x	x			x					x			
Gruppe 8 : Polythermophilic, rheophobic species ("summer")																																						
Pseudocandona compressa (Koch, 1838)		x				x	x	x	x						x	x			x		x		x			x	x			x			x		x		x	
Cypria ophtalmica (Jurine, 1820)																							x			x	x			x		x						

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian		Eemian							Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Cyclocypris laevis (O. F. Müller, 1776)		x						x		x					x	x							x			x				x		x			x		x	
Cyclocypris taubachensis Diebel and Pietrzeniuk, 1984								x								x		x												x								
Ilyocypris aestivalis Fuhrmann, 2008						x	x								x	x										x				x								
Ilyocypris biplicata (Koch, 1838)						x	x	x							x	x	x													x					x			
Ilyocypris decipiens Masi, 1905															x	x										x	x								x			
Ilyocypris gibba (Ramdohr, 1808)								x		x									x				x			x	x			x					x		x	x
Notodromas monacha (O. F. Müller, 1776)								x								x		x								x												
Herpetocypris reptans (Baird, 1835)					x	x		x		x					x	x			x				x			x				x		x					x	x
Heterocypris incongruens (Ramdohr, 1808)					x		x	x				x	x																								x	x
Heterocypris salina (Brady, 1868)	x	x	x			x	x	x	x	x	x	x	x		x	x	x		x		x					x	x			x		x				x	x	
Dolerocypris fasciata (O. F. Müller, 1776)								x							x																							
Cypridopsis vidua (O. F. Müller, 1776)			x					x		x	x				x	x		x			x					x	x			x					x		x	
Plesiocypridopsis newtoni (Brady and Robertson, 1870)						x	x					x			x																							
Sarscypridopsis aculeata (Costa, 1847)						x	x				x	x			x	x																						

Table 3. (Continued)

Stratigraphy	Recent			Holocene										Weichselian	Eemian								Saalian-Complex								Holsteinian-Complex							Cromerian-Complex
																							Warthian		Interglacial (Grabschütz-Warmzeit)*			Saalian s. str.										
L = Late, M = Middle, E = Early				L	L	L	M-L	M-L	M	M	E-M	E-L	?	M-L	E	L	M	E-L	?	?	?	?	L	E-M	L	E-M	E	L	M	E	L	L	?	?	?	?	?	
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13		14	15	16	17	18	19	20	21	22			23	24	25		26	27	28	29	30	31	32	33	34
Species	Esperstedt	Glockensee	Bindersee	Zipsendorf	Rositz	Rollsdorf	Unterröblingen	Zeitz	Bad Laer	Siebleben	Süßer See	Salziger See	Bad Soden	No localities	Schadeleben	Königsaue	Rollsdorf	Cottbus	Memleben	Quakenbrück	Derwitz	Frankfurt(Oder)	Cottbus	No localities	No localities	Neumark-Nord	Grabschütz	Neumark-Nord	No localities	Neumark-Süd	Bottendorf	Mühlhausen Klippe	Woltersdorf	Bilzingsleben**	Bornim	Benkendorf	Aschersleben	Voigtstedt
Potamocypris arcuata (Sars, 1903)															x											x												
Potamocypris paludum Gauthier, 1939															x															x								
Potamocypris unicaudata Schäfer, 1943			x							x						x										x	x											
Potamocypris villosa (Jurine, 1820)						x	x								x																						x	
Limnocythere inopinata (Baird, 1843), amphigonic						x									x	x		x			x		x			x	x			x								
Limnocythere inopinata (Baird, 1843), parthenogenetic			x			x	x	x		x	x	x			x		x			x		x				x				x							x	x
Paralimnocythere bicornis Fuhrmann, 1991																														x								
Paralimnocythere psammophila Flössner, 1965															x																							
Cluster 9 : Halophilic species																																						
Candona angulata G. W. Müller, 1900															x	x	x				x					x	x										x	
Candona natronophila Petkovski, 1969						x	x																															
Eucypris inflata (Sars, 1903)						x											x																					
Cythermorpha fuscata (Brady, 1869)						x	x				x	x					x																					

Table 4. Frequent ostracod species associated with *Cyprideis torosa* in German athalassic waters and marginal marine environments of the southern Baltic coast. The compilation is based on Tab. 3 for athalassic associations and on counts of living ostracods (see Frenzel *et al.,* 2010) from samples with at least 30 specimens of *C. torosa* for the marginal marine environments. There, the covered salinity range is 0.4 to 20.9 psu. Species frequency is given as: XX – in 75–50 %, X – in 49–25%, * – in less than 25% of localities. Species occurring in no water type group in at least 25% of localities are omitted. The shading indicates associations characteristic for athalassic respectively marginal marine waters.

Species	athalassic	marginal marine, total	β-oligohaline	α-oligohaline	β-mesohaline	α-mesohaline to polyhaline
Ilyocypris bradyi	XX					
Limnocytherina sanctipatricii	X					
Pseudocandona marchica	X					
Ilyocypris gibba	X					
Cypridopsis vidua	X	*	*			
Cytherissa lacustris	X	*	*			
Heterocypris salina	XX	*	*	*		
Herpetocypris reptans	X	*	*	*		
Cyclocypris ovum	X	*	*	*		
Cyclocypris laevis	X	*	*	*	*	
Candona candida	XX	*	X	*	*	
Pseudocandona compressa	X	*	*	X	*	
Candona neglecta	XX	*	X	X	*	*
Limnocythere inopinata	XX	X	X	XX	*	
Darwinula stevensoni	X	*	XX	*		*
Cypria ophtalmica	*	X	XX	X	*	*
Cytheromorpha fuscata	*	X	*	*	X	*
Elofsonia baltica		*	*		X	X
Loxoconcha elliptica		*	*	*	*	XXX

26 genera). Because of the qualitative and semiquantitative character of the faunistic data from athalassic localities, it is not possible to calculate diversity indices. However, in general lower diversities are expected in marginal marine ostracod assemblages containing *C. torosa* than in athalassic ones.

The index species associated with athalassic *C. torosa* are *Ilyocypris bradyi, Limnocytherina sanctipatricii, Pseudocandona marchica*, and *Ilyocypris gibba* (Table 4). Other typical associated species are *Cypridopsis vidua, Cytherissa lacustris, Heterocypris salina, Herpetocypris reptans, Cyclocypris ovum, Cyclocypris laevis*, and *Candona candida*, which are all rare in marginal marine environments. The index species of thalassic brackish waters with *C. torosa* are *Elofsonia baltica* and *Loxoconcha elliptica*. Typical are *Cypria ophtalmica* and *Cytheromorpha fuscata*, both rare in saline inland waters. Regarding the species associated with *C. torosa*, a discrimination of athalassic and thalassic ostracod faunas is possible. This discrimination plays an important role in palaeogeographical studies in North Germany and other regions.

A common companion of *Cyprideis torosa* is the gastropod genus *Hydrobia,* both in athalassic and marginal marine brackish waters. Interestingly, this gastropod is absent in modern athalassic saline waters (Meng *et al.*, 2004; Meng, 2009; Strahl *et al*., 2010). Other

Table 5. Ostracod genera associated with *Cyprideis torosa* in athalassic brackish waters of Germany and in marginal marine environments of the southern Baltic coast. The compilation is based on counts of living ostracods (see Frenzel *et al.*, 2010) from 402 samples containing *C. torosa*. The covered salinity range is 0.4 to 20.9 psu. XXX – in >75%, XX – in 75–50%, X – in 49–25 %, * in <25% of localities. Species occurring in no water type group in at least 25% of localities are omitted. The shading indicates the characteristic associations of genera for athalassic respectively marginal marine waters.

Genera	athalassic	marginal marine, total	β-oligohaline	α-oligohaline	β-mesohaline	α-mesohaline to polyhaline
Eucypris	X					
Limnocytherina	X					
Cypridopsis	X	*	*			
Cytherissa	X	*	*			
Ilyocypris	XXX	*	*		*	*
Herpetocypris	XX	*	*	*		
Heterocypris	XX	*	*	*		
Potamocypris	X	*	*	*		
Cyclocypris	XX	*	X	*	*	
Pseudocandona	XX	X	X	X	*	
Limnocythere	XX	X	X	XX	*	
Candona	XXX	X	XX	XXX	X	*
Darwinula	X	*	XX	*	*	*
Fabaeformiscandona	X	*	X	*	*	*
Cypria	*	X	XX	X	*	*
Cytheromorpha	*	X	*	*	X	*
Cytherura		*	*	*	X	X
Elofsonia		*	*		X	X
Xestoleberis		*		*	*	X
Leptocythere		*			*	XXX
Loxoconcha		*	*	*	*	XXX

taxa with a marine origin co-occurring with *C. torosa*, in Central Germany are foraminifers (Wennrich *et al.*, 2007).

In order to enable a more than Central European discrimination between athalassic and thalassic ostracod faunas containing *C. torosa*, discriminating genera from the study area were identified. Those are *Eucypris* and *Limnocytherina* as index genera and *Cypridopsis, Cytherissa, Ilyocypris, Herpetocypris, Heterocypris, Potamocypris*, and *Cyclocypris* as typical for athalassic waters (Table 5). Index genera for marginal marine environments associated with *C. torosa* are *Cytherura, Elofsonia, Xestoleberis, Leptocythere*, and *Loxoconcha*; typical are *Cypria* and *Cytheromorpha*.

Considering the presence of representatives of ecological ostracod groups *sensu* Fuhrmann (2006), we found the highest number of athalassic localities (28 from 34) with species from warm standing waters (summer forms), followed by species from permanent small water bodies and winter forms (27), species of the rhithron (22), and interglacial species (20). Interestingly, halophile species other than *C. torosa* are not so frequent (11 localities). This pattern confirms the assumption of permanent, warm and shallow water bodies as typical for the athalassic occurrence of *C. torosa*.

5. Conclusions

For the colonization of an athalassic water body by *Cyprideis torosa* permanent, preferentially larger, shallow, and warm water bodies with an increased salinity are needed. Differences in environmental or climatic conditions between today's and interglacial fossil occurrences in general are not recognizable. There are many modern water bodies meeting the preferences of *C. torosa* in Central Germany. The lack of living *C. torosa* in that region, however, could be caused by drainage of many salty inland water sites during the last century. Nevertheless, empty valves of *C. torosa* are present in surface sediments of some localities. Athalassic and thalassic ostracod associations containing *C. torosa* are discriminable by their considerable differences in species composition. Whereas *Loxoconcha elliptica*, *Elofsonia baltica*, *Cypria ophtalmica*, and *Cytheromorpha fuscata* are associated ostracod species typical for the Baltic Sea coast, *Ilyocypris bradyi, I. gibba, Limnocytherina sanctipatricii*, and *Pseudocandona marchica*, are restricted to co-occurrences with *C. torosa* in German athalassic waters. On a generic level, typical coastal assemblages contain *Cytherura, Elofsonia, Leptocythere*, *Loxoconcha*, and *Xestoleberis*, whereas *Cypridopsis, Cytherissa, Eucypris*, and *Limnocytherina* indicate brackish inland waters. The proportions of noded valves and round sieve pores are applicable to reconstruct trends of salinity changes in thalassic and athalassic environments. On the other hand, it is not possible to estimate exact salinity values using athalassic *C. torosa* valves so far. Despite the depicted problems, sieve-pores analysis is a simple and important tool to support palaeosalinity reconstructions, particularly when *C. torosa* is occurring monospecifically. Experiments are needed to evaluate the different chemical composition of athalassic waters and morphological responses of *C. torosa*. Both, faunal associations and morphological valve features are important for interpreting *C. torosa* occurrences from other regions.

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3.2.2 Mansfelder Seen

Beitrag 4:

Die Mikrofauna der brackischen Mansfelder Seen

Manuskriptskizze

Einleitung

Zum Mansfelder Seengebiet in Mitteldeutschland gehören drei Seen, die postglazial subrosiv durch Auslaugung des permischen Zechsteinsalzes entstanden sind. Nur der Süße See existiert noch in seiner ursprünglichen Ausdehnung, während der Faule See bereits im 12. und 13 . Jahrhundert und der Salziger See 1895 trockengelegt wurden, um Landwirtschaft und die Ausbeutung der permischen Kupfervorkommen zu ermöglichen (Wennrich 2005). Heute sind in dem ehemaligen Seengebiet neben einigen temporären Tümpeln noch der Kernersee und der Bindersee Relikte des ehemaligen salzigen Sees. Im Westen des Gebietes befindet sich heute noch eine Solequelle im Gebiet des Igelsumpfes (Trost 2006). Durch seine Lage im Wetterschatten des Harzes gehört die Umgebung der Mansfelder Seen zu den niederschlagsärmsten Arealen Zentraleuropas mit weniger als 500 mm pro Jahr.

Detaillierte Multi-Proxi-Untersuchungen an Bohrkernen aus dem Salzigen See, dem Süßen See und dem Bindersee wurden von Wennrich 2005, Meng et al. 2004, Krichel 2009 und Rinke-Hardekopf 2012 durchgeführt. Eine für diese Studie überarbeitete Bestandsaufnahme der Ostrakoden und Foraminiferen der Mansfelder Seen zeigt, dass typische Salzzeiger häufig vorkamen. Der Salzige See entstand vor 13.000 Jahren, der Bindersee etablierte sich vor ca. 10.000 Jahren im östlich vom Salzigen See gelegenen Nachbarbecken. Eine Verbindung beider Seen bestand ab ca. 3500 Jahren vor heute. Die Seeentwicklung des Süßen Sees begann erst nach einer längeren Phase von Temporär- und Fließgewässern ca. 8000 Jahre vor heute. Eine Verbindung des Süßen Sees mit den anderen Seen des Mansfelder Gebietes konnte bisher nicht nachgewiesen werden. In der hier vorgestellten Studie werden Ostrakoden- und Foraminiferen-Assoziationen aus mehreren Sedimentkernen detailliert ausgewertet und miteinander verglichen. Das Ziel ist, über eine zeitliche und fazielle Korrelation basierend auf Ostrakoden und Foraminiferen die Gesamtentwicklung der Mansfelder Seen im klimatischen Kontext herauszuarbeiten.

Methoden

Vier Sedimentkerne aus dem Salzigen See (Lz1001-3, Süssen See (Lz1003) und Bindersee (Lz1018) (Abb. 4) wurden mithilfe der Radiokarbon-Methode datiert und kalibriert (Meng et al. 2005, Wennrich et al. 2007, Krichel 2009, Rinke-Hardekopf 2012). Nach Erstellung eines

Alters–Tiefenmodells wurden Chronozonen festgelegt. Jeweils drei cm Kernmaterial wurden gesiebt und untersucht. Ostrakoden und Foraminiferen wurden für diese Studie identifiziert, gezählt und semiquantitativ dargestellt. Bereits vorhandene Zähldaten des Kerns Lz1001-3 wurden überarbeitet. Zum Vergleich wurde ein von Meng et al. (2004) untersuchtes und ausgewertetes Kernfragment vom westlichen Rand des Süßen Sees herangezogen (Kern Becker 2, Abb. 4).

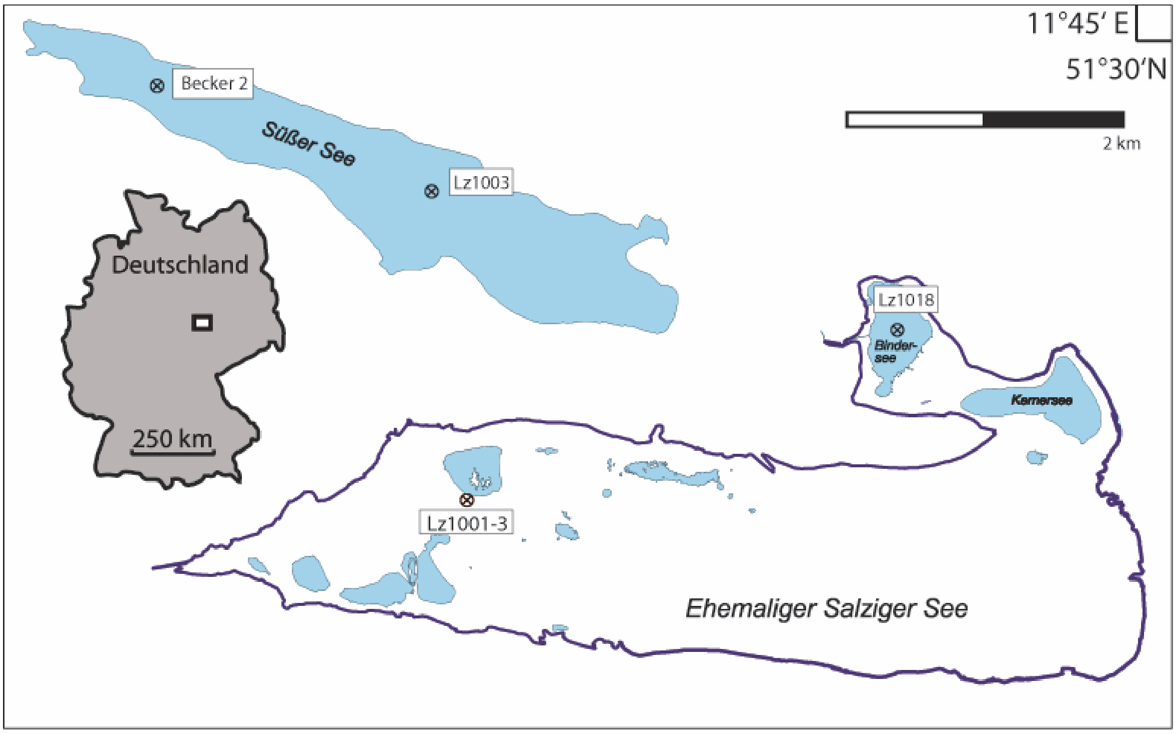

Abb. 4: Karte Mansfelder Seen mit Lage der Bohrungen, verändert nach Trost & Rauchhaus (2000) und Wennrich (2005)

Ergebnisse

Insgesamt wurden 25 Ostrakodenarten und acht Foraminiferenarten identifiziert. Von den Ostrakodenarten sind 23 Arten limnisch mit mehr oder weniger ausgeprägter Salztoleranz. *Cyprideis torosa* und *Cytheromorpha fuscata* sind dagegen als Brackwasserarten bekannt. Von den acht nachgewiesenen Foraminiferenarten kommen fünf nur sehr vereinzelt im Salzigen See vor (259-262 cm - Subboreal, 588-591 und 600-603 cm - Präboreal, 696-700 cm - Ältere Dryas, 748-750 cm - Älteste Dryas) und von diesen sind vier aufgrund ihres schlechten Erhaltungszustands und ihrer marinen Herkunft als aus tertiären marinen Sedimenten umgelagert identifizierbar (Wennrich et al. 2007). Die beiden Foraminiferenarten der Gattung *Ammonia* (Salziger See: 396-402 cm - Atlantikum; Süßer See: 514-527 und 529-531 cm - Subboreal, 554-596 und 601-624cm - Atlantikum; Bindersee: 778-780 und 808-810 cm - Atlantikum) sowie die agglutinierende Art *Miliammina fusca* sind wesentlich häufiger (Süßer See

160 und 208 cm; Subatlantikum,) kommen aber nur in wenigen Horizonten vor (Meng et al. 2004, Wennrich et al. 2007, Krichel 2009, Rinke-Hardekopf 2012) (Tab. 3).

Tabelle 3: Übersicht Kerne Mansfelder Seen

Lokalität	**Salziger See**	**Bindersee**	**Süßer See Zentral**	**Süßer See West**
Kern	Lz1001-3	Lz 1018	Lz1003	Becker 2
Teufe	0-840 cm	0-1100cm	0-766 cm	500-680cm
Alter	13.800 a cal BP	12.000 a cal BP	5159 a cal BP	Präboreal-Subboreal
Ostrakodenarten	15	21	15	7
Dominante Ostrakodenart	*Cyprideis torosa*	*Limnocythere inopinata*	*Dawinula stevensoni*	*Cyprideis torosa*
Vorkommen *Cyprideis torosa*	Mit Unterbrechungen durchgängig vom mittleren Präboreal bis subrezent	Durchgängig und sehr häufig vom Alleröd bis mittleres Atlantikum	Durchgängig und häufig im unteren Subboreal	Durchgängig und häufig im mittleren Atlantikum bis Subboreal
Vorkommen *Cythermorpha fuscata*	selten	selten	häufig	Nicht nachgewiesen
Foraminiferen	*Ammonia tepida*	*Ammonia tepida*	*Miliammina fusca* *Ammonia tepida*	*Ammonia tepida* *Ammonia aberdoveyensis*

Im Salzigen See kommt *Cyprideis torosa* deutlich dominant, und in einigen Kernabschnitten sogar ausschließlich vor. Im Bindersee und Süßen See gehört *Cyprideis torosa* zwar zu den häufigsten Arten, tritt aber hier nur zeitweilig dominant auf. *Cytheromorpha fuscata*, ebenfalls eine Brackwasserart, erscheint häufig im Süßen See, in den anderen beiden Seen dagegen selten. Sie tritt meist nicht gemeinsam mit *Cyprideis torosa* auf (Tab. 3).

Tabelle 4: Merkmale der Salinitätsbereiche von Süßwasser bis mesohalin

Salinitätsbereich	**Mesohalin**	**Oligohalin**	**Süßwasser bis ß-oligohalin**
Merkmale	Geringe Diversität, salzzeigende Ostrakoden dominant, Foraminiferen	Mittlere Diversität, salzzeigende Ostrakoden assoziiert mit salztoleranten Ostrakoden	Hohe Diversität, Limnische Ostrakoden dominant

Basierend auf diesen Merkmalen kann für die Mansfelder Seen folgende generelle Zonierung vorgenommen werden (Tab. 4): Präholozän und Präboreal waren oligohalin geprägt, anschließend kam es im Boreal und Atlantikum zu einer deutlichen Erhöhung der Salinität, ab dem Subboreal erfolgte eine zunehmenden Aussüßung der Seen. Ab dem oberen Subatlantikum entwickelte sich die Salinität der einzelnen Seen individuell.

Die Entwicklung des Salzigen Sees begann mit der Etablierung eines sehr flachen Sees mit variierender Salinität in einem durch Salzauslaugung subrodierten Beckens vor mehr als 13.000 Jahren. Typisch sind Süßwasserostrakodenarten, die leicht erhöhte Salinitäten tolerieren können, die deutlichen Salzzeiger sind jedoch noch selten. Ab der Jüngeren Dryas stiegen Salinität und Wassertiefe an. Das dominante, zum Teil monospezifische Vorkommen von *Cyprideis torosa* in dieser Phase und bis zum Ende des Atlantikums spricht für einen permanenten See. Siebporenanalysen an *Cyprideis torosa* zeigen ein Maximum der Salinität im mittleren Atlantikum. In dieser Phase kam auch die Foraminifere *Ammonia tepida* vor. Im gesamten Boreal und Atlantikum ist *Cyprideis torosa* nur mit den ebenfalls sehr salztoleranten Arten *Eucypris inflata*, *Heterocypris salina* und *Limnocythere inopinata* assoziiert. Warum es in dieser warmen und feuchten Klimaphase trotz des hohen Seespiegels zu einer Erhöhung der Salinität kam, könnte durch den verstärkten Kontakt des Sees mit dem salzhaltigen Untergrund erklärt werden. Im Subatlantikum sank die Salinität, erkennbar an der zunehmenden Diversität der limnischen Ostrakoden. Ab dem mittleren Subatlantik kam nur noch *Cyprideis torosa* vor, die Siebporenanalyse sowie das vermehrte Auftreten gebuckelter Exemplare zeigen jedoch nur eine leichte Erhöhung der Salinität an (Wennrich 2005).

Die Geschichte des Bindersees begann etwas später als die des Salzigen Sees vor mehr als 11.000 Jahren. Bis zum Präboreal dominierten jedoch, anders als im Salzigen See, salzzeigende Arten, vor allem *Cyprideis torosa*. Auch die Brackwasserart *Cytheromorpha fuscata* konnte hier ebenso wie in den anderen Mansfelder Seen nachgewiesen werden, sie kam aber meist nicht gemeinsam mit *Cyprideis torosa* vor. Ab dem Boreal verlief die Entwicklung dann ähnlich wie im Salzigen See. Im mittleren Atlantikum wurden auch hier die höchsten Salinitäten erreicht, erkennbar am Maximum der Siebporenkurve, dem Vorkommen von Foraminiferen und dem Rückgang der limnischen Arten. Ab dem Subboreal kam es zu einer Verbindung beider Seen (Wennrich 2005), die bis zur Drainage des Salzigen Sees andauerte. Die Wiederkehr limnischer Arten zeigt eine Aussüßung beider Gewässer an. Anders jedoch als im Salzigen See kam es im Bindersee zu keinem Salinitätsanstieg mehr. Als Grund kann angenommen werden, dass die Seen vor allem im oberen Subatlantikum eine partielle Separation erfuhren, da sie in unterschiedlichen Becken angelegt waren. Zwei Süßwasserzuflüsse, die in den Bindersee münden, verstärkten diesen Effekt wahrscheinlich noch.

Der Geschichte des Süßen Sees konnte mikrofaunistisch bis jetzt nur unvollständig rekonstruiert werden. Meng et al. (2004) untersuchten ein Kernsegment aus dem westlichen Teil des Süßen Sees, das eine Kerntiefe zwischen 680 cm und 500 cm umfasst und, basierend auf vier

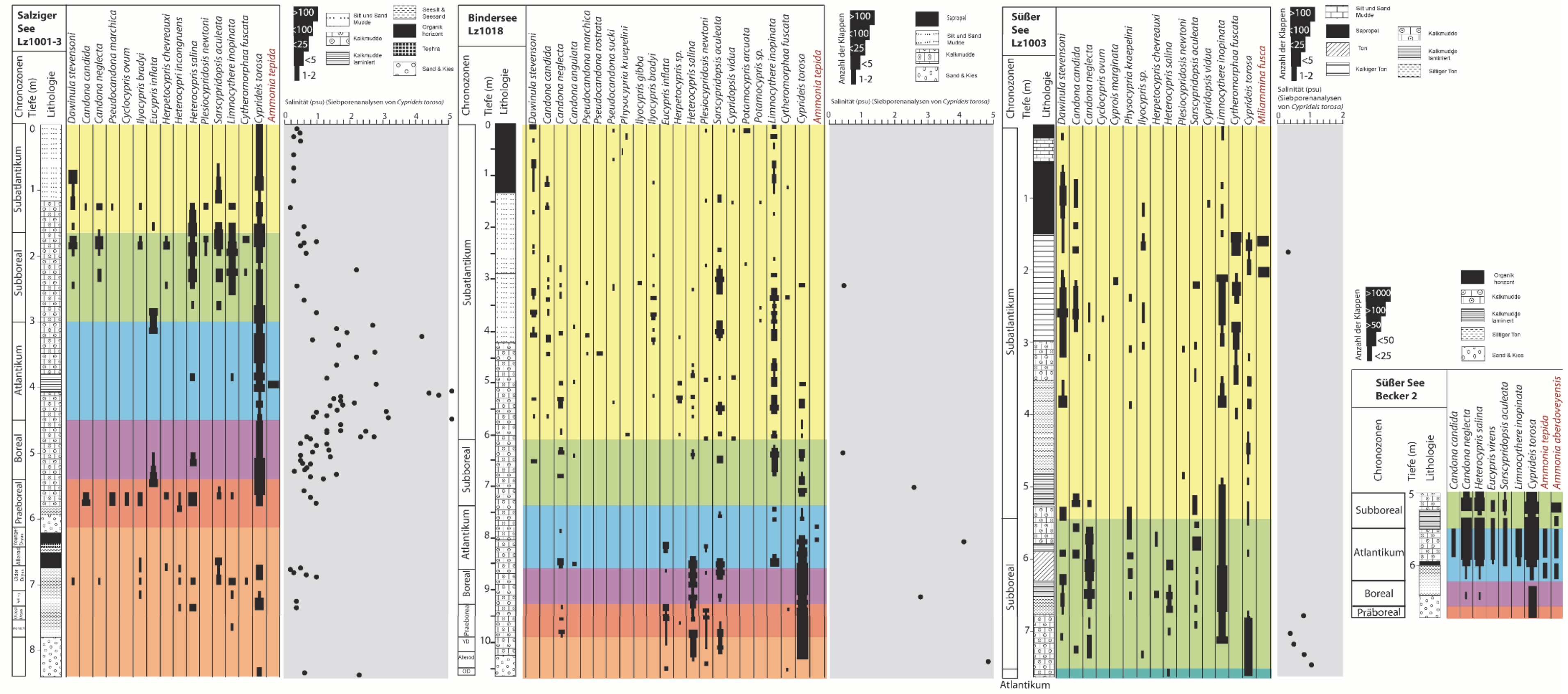

Abb. 5: Verteilung von Ostrakoden und Foraminiferen sowie Siebporenvariabilität in den Kernen der Mansfelder Seen

^{14}C-Datierungen, vom Präboreal bis ins untere Subboreal reicht. Lithologisch wurden zehn Einheiten mit unterschiedlichen Mächtigkeiten unterschieden. Sämtliche in diesen Einheiten vorkommende Ostrakoden wurden von den Autoren bestimmt und gezählt. Der im Jahre 2001 im zentralen Bereich des Sees gezogener, und für diese Studie ausgewerteter Kern Lz1003 ist ca. 2 km von dem westlichen Bohrpunkt entfernt und reicht bis ins oberste Atlantikum. Die Rekonstruktion des Sees basiert auf den Daten aus diesen beiden Kernen. Die Kernsequenz von Meng et al. (2004) im westlichsten Teil des Sees reflektiert im obersten Präboreal und untersten Boreal Brackwasserverhältnisse, da *Cyprideis torosa* als einzige Art vorkommt. Der Bathymetrie des Sees folgend muss der See zu dieser Zeit schon fast auf die heutige Größe ausgedehnt gewesen sein. Der Beginn der Seegeschichte muss demnach noch weiter zurückreichen. Ab dem Atlantikum kamen zwar einige limnische Arten dazu, *Cyprideis torosa* blieb jedoch die deutlich dominierende Art mit meist über 70%, im unteren Subboreal sogar mit über 90%. Die höchste Diversität wurde im mittleren und oberen Atlantikum erreicht. In dieser Zeit scheint der Süßwassereinfluss des insgesamt mesohalinen Milieus am höchsten gewesen zu sein. Die Ostrakodenfauna des zentralen Kerns reflektiert im obersten Atlantikum und unteren Subboreal aufgrund der Dominanz von *Cyprideis torosa* mesohaline Bedingungen. Ebenso wie in den anderen Seen kommen auch hier im Atlantikum die Foraminiferen *Ammonia tepida* und *Ammonia aberdoveyensis* vor. Ab dem mittleren Subboreal nahm die Diversität der Ostrakoden zu und die Salzzeiger traten zurück, was auf verstärkten Süßwassereinfluss zurückzuführen ist. Auch Siebporenanalysen zeigen oligohaline Bedingungen an, die bis heute bestehen blieben. Im mittleren Subboreal trat *Cytheromorpha fuscata* in hoher Anzahl auf, ebenso wie die Foraminifere *Miliammina fusca*, was möglicherweise auf eine leichte Erhöhung der Salinität zurückzuführen ist.

Insgesamt nehmen die Mansfelder Seen ab dem Präboreal eine zunächst ähnliche Entwicklung. Die hier schon mesohalinen Bedingungen steigerten sich bis zum Atlantikum, in dem die höchsten Salinitäten erreicht wurden. Ab dem Subboreal kam es dann zu einer Aussüßung der Seen mit einigen Schwankungen, und nur im Salzigen See stieg die Salinität vor etwa 2500 Jahren nochmals an. Die Ostrakodenfaunen von Salzigem See und Bindersee ähneln sich stark, was auf ihre Verbindung zurückzuführen ist, während der Süße See aufgrund seiner Separation eine etwas abweichende Fauna zeigt.

Schlussfolgerungen

Die Mansfelder Seen entwickelten sich seit ca. 13.000 Jahren. Es ist davon auszugehen, dass sich die durch Salzauslaugung subrodierten Becken zunächst mit Süßwasser füllten, welches sich jedoch bald ionisch aufkonzentrierte und bereits im oberen Alleröd im mesohalinen Bereich lag. Die Salinität stieg noch bis zum Atlantikum und ging dann graduell zurück. Die Salzionen gelangten durch Kontakt des Wassers aus See, Zuflüssen und/oder Grundwasser mit den salzführenden Sedimenten des Zechsteins in die Gewässer. Evaporitische Vorgänge hatten keinen entscheidenden Einfluss auf die Salinität, da das Klima im Holozän nicht sehr stark von der heutigen Situation abwich (Mayewski et al. 2004, Litt et al. 2009) und es ausreichend Niederschlag gegeben haben muss. Eine der wichtigsten Grundlagen für die Rekonstruktion der Geschichte der Mansfelder Seen ist die Analyse der Ostrakoden– und Foraminiferenverteilung. Der als wichtigster Faktor zu wertende Salinitätsverlauf konnte durch das Zusammenspiel von limnischer Fauna mit athalassischen, salztoleranten Arten detailliert herausgearbeitet werden.

3.2.3 Weitere Fallbeispiele aus der Literatur

Manitoba (Kanada)

Der Lake Winnipegosis in Manitoba, Kanada, einer der größten Seen der Region und gemeinsam mit dem Lake Winnipeg und Lake Manitoba Restgewässer des postglazialen Lake Agassiz, weist in seinem nördlichen Teil unterschiedliche und zum Teil sehr hohe Salinitäten auf. Das Salz stammt aus den salzführenden Prairie Evaporites – Schichten des Mittleren Devons – und aus einem Brinepool im Williston–Becken (Tudorancea et al. 1979). In diesem Teil des Sees kommen mehrere Arten von Foraminiferen vor, am häufigsten *Jadammina macrescens*, *Miliammina fusca* und *Polysaccammina ipohalina* (Patterson et al. 1997). *Cribroelphidium gunteri*, rezent in den Seen von Manitoba nicht mehr nachweisbar, war besonders vor ca. 5000 Jahren eine der häufigsten Arten (Boudreau et al. 2001). Sie repräsentiert dort das Hypsithermal, ein Wärmeoptimum des Mittleren Holozäns. Es wird angenommen, dass *C. gunteri* aus subtropischen Küstenhabitaten, die mindestens 2000 bis 3000 km entfernt liegen, durch Vögel in den See eingetragen wurde (Patterson et al. 1997). Ebenso tritt in den Seen die Brackwasserostrakode *Cytheromorpha fuscata* auf. Neben der Süßwasserostrakodengattung *Candona* mit mehreren Arten kommt sie am häufigsten vor (Tudorancea et al. 1979). Acht weitere hier sehr selten vorkommende Süsswasserostrakodengattungen sind wie *Candona* salztolerant. *Cytheromorpha fuscata* repräsentiert ebenso wie die hier vorkommenden Foraminiferenarten, die typischerweise in Salzmarschen vorkommen, zusammen mit den salztoleranten Süßwasserostrakoden, einen athalassischen Lebensraum mit regional und saisonal variierenden Salinitäten.

3.3 Athalassische Gewässer klimatogener Salinität

3.3.1 Aralsee in Kasachstan

Beitrag 5:

Die artenarme Mikrofauna des Aralsees vor 1960

Manuskriptskizze

Einleitung

Der Aralsee war bis 1960 das viertgrößte Binnengewässer der Welt mit 68.000 km^2 Fläche (Zavialov 2005, Letolle & Mainguet 1996). Danach wurde im Zuge der Baumwollbewässerung den beiden Zuflüssen des Aralsees, Syrdarja und Amudarja, Wasser entzogen, sodass der See zu verlanden begann (Abb. 6). Der Abfall des Seespiegels und die drastische Volumenverminderung hatten dramatische Folgen: In den späten 1980er Jahren teilte sich der See in zwei Hälften, die je von einem Zufluss gespeist wurden und durch einen schmalen Kanal miteinander verbunden waren. Ein Versuch 1998 den nördlichen, Kleinen Aralsee durch Abtrennung vom südlichen, Großen zu retten, scheiterte zunächst, ein zweiter Damm, gebaut 2003, hatte jedoch Bestand und führte dazu, dass sich das Becken wieder füllte, sodass sich der Fischbestand im Kleinen Aralsee wieder erholte (Mirabdullayev et al. 2004). Durch diese Maßnahme wurde allerdings der Verlandungsprozess des Großen Aralsees beschleunigt. Aufgrund der extremen Flachheit des Seebeckens wanderte die Küstenlinie schnell seewärts, sodass in sehr kurzer Zeit große Flächen trockenfielen. Schon vor 2010 zerfiel auch der Große Aralsee in zwei Teile von denen der östliche, sehr flache Teil 2014 erstmals vollständig trockenfiel, während der westliche, tiefere Seebereich noch als schmaler Restsee vorhanden ist (Breckle et al. 2011). Obwohl die Bewässerungsmaßnahmen in den 1990er Jahren eingestellt wurden, erreicht der Amudarja den Aralsee nicht mehr. Daher ist die Verlandung des Großen Aralsees nicht mehr aufzuhalten (Micklin 2014).

Die Zunahme der Salinität von 10 auf 110 psu im Großen Aralsee hatte gravierende Auswirkungen auf die Lebewelt des Sees: Fast die gesamte Seefauna musste in die geringer salinen Flussmündungen ausweichen und starb letztendlich aus (Mirabdullayev et al. 2004). Dadurch kam die Fischerei fast völlig zum Erliegen. Um den Fischbestand zu erhalten, wurden schon vor den 1960er Jahren fremde Fischarten eingeführt, die sich sehr schnell im nördlichen Aralsee etablierten. Um diese Fische ernähren zu können, war jedoch die Einfuhr von Futterorganismen nötig, die wiederum die restliche endemische Fauna verdrängten (Letolle & Mainguet 1996). Durch den Dammbau von 2003 hatte sich jedoch die Salinität im Kleinen Aralsee wieder unter 15 psu abgesenkt, sodass sich die Fauna erholen konnte. Auch vor 1960 war der See offenbar mehrmals starken Seespiegelschwankungen ausgesetzt, die Salinitätsveränderungen zur Folge hatten (Boomer et al 1996, 2000). Von diesen Ereignissen erholte sich der See jedoch stets wieder. Wann der See seinen höchsten Seespiegel hatte, konnte noch nicht nachgewiesen werden (Boomer et al. 2009). Tiefstände wurden jedoch sehr detailliert durch Analysen mit Dinoflagellatenzysten und Pollen dargestellt rekonstruiert, da sie mit deutlichen Salinitätsanstiegen einhergingen (Sorrel 2006). Diese Untersuchungen umfassen aber nur die letzten 2000 Jahre. Erst 2012 wurde von Boomer et al. ein 18.000 Jahre zurück reichender Kern aus dem Süd-West-Becken des Sees präsentiert. Die Ostrakodenfauna weicht vom bisher nachgewiesenen Artenspektrum nicht ab. Sie repräsentiert drei markante Faunenwechsel um 18.000, 10.000 und 4000 BP, ausgelöst durch veränderte Zuflussmenge und -richtung des südlich im Aralsee einmündenden Amudarja. Dadurch kam es zu einem kurzfristigen Abfall der Salinität, repräsentiert durch einen Rückgang von *Cyprideis torosa*.

Abb. 6: Satellitenbild des Aralsees im Jahre 2002 mit der Position der Bohrung „Aral 16“

Material und Methoden

Der 3 m lange Kern Aral 16 aus der Tschebasbucht im nördlichen Aralsee (Abb. 6) wurde zentimeterweise beprobt und nass gesiebt. Foraminferen und Ostrakoden wurden unter dem Binokular vollständig ausgelesen, identifiziert und gezählt. Die Missbildungen der Foraminiferengehäuse wurden den drei Missbildungstypen „Kammermissbildung“, „Windungswechsel“ und „Mehrling“ zugeordnet und quantifiziert.

Ergebnisse

Die schluffigen bis tonigen, gut sortierten Sedimente sind graugrün bis grau und fein laminiert. Zur Altersbestimmung wurden an Algenresten und Mollusken ^{14}C-Datierungen durchgeführt. Für den Kern Aral 16 ergaben sich Alter für folgende Tiefen: 163-167 cm: 982-1035 cal. BP, 185-187 cm: 3700 cal. BP und 200-201 cm: 1010-1053 cal. BP (Sorrel 2006) Aufgrund der Altersinversion konnte kein Alters/Tiefenmodell erstellt werden.

Die kalkschaligen Organismen werden von drei Gruppen vertreten: Ostrakoden mit sechs Gattungen und sieben Arten kommen am häufigsten vor und sind relativ gleichmäßig über das ganze Profil verteilt. Mollusken mit vier Gattungen (drei Bivalvia und ein Gastropode) sind besonders im obersten und mittleren Profilmeter sehr häufig. Drei schon aus den Kernen Aral 16 und 17 bekannte Foraminiferenarten kommen auch im mittleren Teil von dem von Boomer et al. (2012) bearbeiteten Kern vor, sowie eine weitere bereits bei Riedel et al. (2011) beschriebene Art.

Bei der Zonierung des Kerns, basierend auf der Verteilung von Ostrakoden und Foraminiferen, kann grob eine Dreiteilung vorgenommen werden (Abb. 7).

Zone 1: In einer Teufe von 275 – 200 cm dominiert *Tyrrhenocythere amnicola*, auch *Limnocythere inopinata*, *Loxoconcha immodulata* und Amnicythere *cymbula* treten häufig auf. In 205 - 200 cm Teufe tritt *Candona* häufiger auf, eine Süßwassergattung die insgesamt sehr selten im Kern vorkommt. Insgesamt ist dieser Abschnitt als mesohalin zu klassifizieren. Ein kurzfristiger Süßwassereinstrom könnte die durch *Candona* sp. angezeigte Aussüßung zwischen 205 und 200 cm bewirkt haben.

Zone 2: Ab 200 cm Teufe tritt *Cyprideis torosa* in dieser Sequenz erstmalig häufiger auf und wird ab 170 cm dominant. Bei 163 und 149 cm kommt es sogar zu einem Massenvorkommen, wodurch *C. torosa* auch insgesamt die häufigste Art darstellt. *Cyprideis torosa* ist hier meist assoziiert mit Foraminiferen, die nur zwischen 200 cm und 110 cm im Kern vorkommen. Etwa 20 – 30 % der Foraminiferengehäuse sind missgebildet. In dieser Zone ist ein deutlicher Salinitätsanstieg erkennbar, der vor rund 1000 Jahren eingesetzt haben muss und möglicher

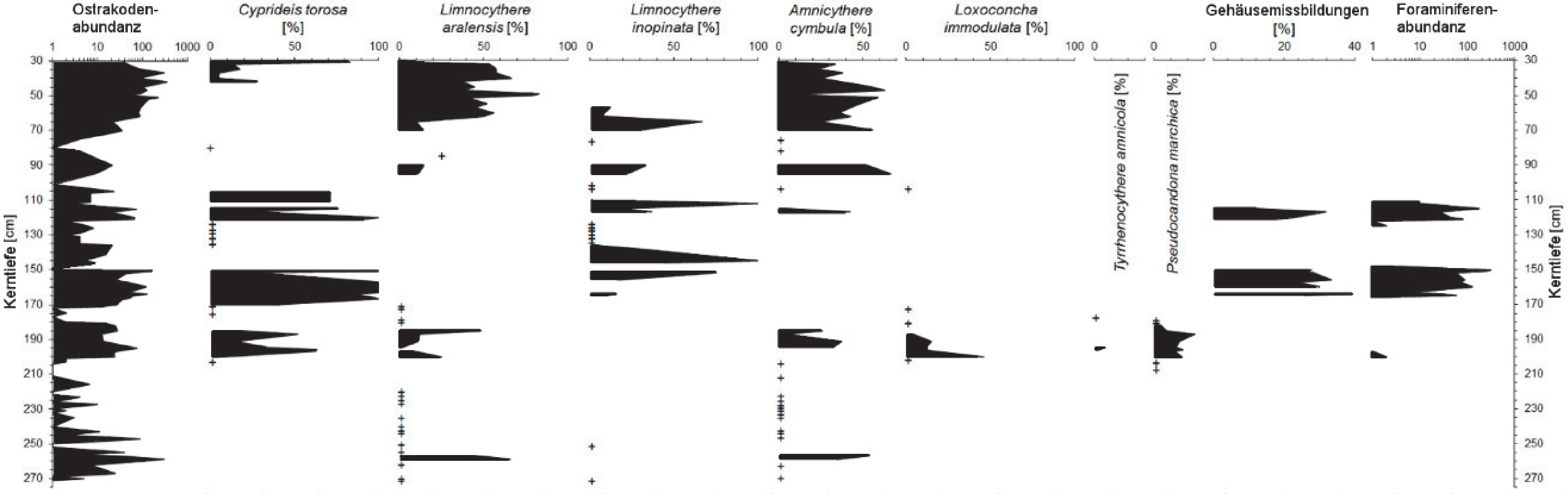

Abb 7: Verteilung von Ostrakodenarten und Foraminiferen im Kern „Aral 16“ aus der Tschebasbucht im nördlichen Großen Aralsee. Kreuze zeigen das Vorkommen der Taxa in Proben mit für die Berechnung von Dominanzwerten zu geringen Individuenzahlen an.

weise auf einen Abfall des Seespiegels zurückzuführen ist. Auch Dinoflagellatenzysten zeichnen diesen Trend des Salinitätsanstiegs nach (Sorrel 2006).

Zone 3: Ab 100 – 30 cm geht *C. torosa* deutlich zurück und kommt nur noch vereinzelt vor, dagegen dominiert wieder *T. amnicola*, die wiederum mit *L. inopinata, L. immodulata* und A. *cymbula* assoziiert ist. In den obersten 10 cm tritt *C. torosa* wieder häufiger auf. Die Salinität der Zone geht insgesamt wieder zurück, erreicht aber wahrscheinlich nicht ganz die niedrigen Werte von Zone 1. Als Ursache wird ein erneuter Seespiegelanstieg angenommen.

Schlussfolgerungen

Die Salinitätswechsel, hervorgerufen durch Seespiegelschwankungen des Aralsees der letzten 2000 Jahre, lassen sich durch die deutlichen Wechsel der Ostrakodenassoziationen sehr gut nachzeichnen. Bei Salinitätsanstieg dominiert *Cyprideis torosa* gemeinsam mit Foraminiferen. Die anderen Ostrakodenarten, von denen die Brackwasserostrakode *Tyrrhenocythere amnicola* am häufigsten auftritt, charakterisieren niedrigere Salinitäten bei höherem Seespiegelstand. In diesen Phasen geht *C. torosa* stark zurück und es treten keine Foraminiferen auf.

3.3.2 Tayma in Saudi-Arabien

Beitrag 6:

The early Holocene humid period in NW Saudi Arabia e Sediments, microfossils and palaeo-hydrological modelling

veröffentlicht 2011, Engel et al., *Quaternary International*

In der Oase von Tayma im ariden Norden von Saudi-Arabien dokumentieren Sapkhasedimente einen frühholozänen See der mindestens 3000 Jahre bestanden haben muss. Obwohl die Sedimente eine brackische Mikrofauna und Makrofauna enthalten, belegt das Vorhandensein eines ausgedehnten permanenten Sees eine feuchtere Klimaphase zu Beginn des Holozäns. Danach kam es zu einer allmählichen Verlandung des Sees, begünstigt durch eine zunehmende Aridisierung der Arabischen Halbinsel.

Ergebnisse: Die ältesten Sedimente wurden auf 10.000 Jahre vor heute datiert. Der See muss sich relativ rasch entwickelt haben, das genaue Ende der Seephase bleibt jedoch bisher ungewiss. Das monospezifische Vorkommen von *Cyprideis torosa*, assoziiert mit wenigen anpassungsfähigen Foraminiferenarten spricht für einen extremen Lebensraum. Siebporenanalysen bei *C. torosa* zeigen wechselnde Salinitäten des Wassers und zeitweise Werte im hypersalinen Bereich.

Max Engel, Helmut Brückner, Anna Pint, Kai Wellbrock, Andreas Ginau, Peter Voss, Matthias Grottker, Nicole Klasen, Peter Frenzel (2012). The early Holocene humid period in NW Saudi Arabia e Sediments, microfossils and palaeo-hydrological modelling, Quaternary International, 266: 131-141

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Konzeption	X	X	**X**						
Geländearbeiten	X	X		X	X	X	X	X	
Datengewinnung	X		**X**	X	X	X	X	X	
Datenauswertung und Interpretation	X		**X**	X	X	X	X	X	X
Schreiben	X	X	**X**						X
Publikationsäquivalent	1,0	n. a.	**0,5**	n. a.	n. a.	n. a.	n. a.	n. a.	n. a.

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The early Holocene humid period in NW Saudi Arabia – Sediments, microfossils and palaeo-hydrological modelling

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ABSTRACT

An early to mid-Holocene humid period has been inferred from a variety of geo-bio-archives of the Sahara and the Arabian Peninsula including sabkhas, palaeo-lakes, sand dunes, wadis, speleothems or marine sediments. On the Arabian Peninsula, most of these records are located in the southern and southeastern part. Studies from the northern part are rare. This paper presents the first results from palaeo-environmental and hydrological investigations on the sabkha basin of the Tayma oasis, northwestern Saudi Arabia. Sedimentary characteristics, micro- and macrofauna, a digital elevation model based on DGPS measurements, and ^{14}C-AMS data indicate the presence of a perennial lake with a minimum depth of 13 m, a stored water volume of 1.16×10^7 m^3 and a surface of 18.45 km^2 between 10,000–9000 cal BP. Foraminiferal test malformations and the shape of sieve pores on ostracod valves were used to detect trends in palaeo-salinity and ecological stress conditions. The reconstructed gradual contraction of the lake at least after 8500 cal BP reflects the long-term aridisation trend on the Arabian Peninsula after the early Holocene. Based on the hydrological water balance equation, quantitative data on minimum palaeo-rainfall during the early Holocene humid period were calculated. Input parameters for the equation are the minimum lake level, lake surface, and lake volume during the peak of the early Holocene humid period as well as palaeo-evapotranspiration, groundwater infiltration, and surface runoff. Accordingly, a perennial lake in the endorheic basin of the modern sabkha with a lake level at the same elevation as the uppermost shoreline deposit would have required a minimum annual precipitation of 150 ± 25 mm. This value amounts to c. 300% of recent precipitation rates.

1. Introduction

Holocene climate fluctuations have been inferred from different geo-archives of the Arabian Peninsula, such as palaeo-lakes, wadis, sand dunes, speleothems or marine basins. Most of them are located in its southern (e.g. McCorriston et al., 2002; Fleitmann et al., 2003; Davies, 2006; Lézine et al., 2007) and southeastern parts (e.g. Wood and Imes, 1995; Neff et al., 2001; Bray and Stokes, 2003; Radies et al., 2005; Parker et al., 2006; Fuchs and Buerkert, 2008). The central and northern parts – including most of the Saudi Arabian Kingdom – are relatively unexplored.

Information on the Holocene palaeo-climate from the northern section of the Arabian Peninsula is restricted to interdunal sediment records from the northwestern branch of the An-Nafud erg which, according to investigations by Whitney et al. (1983) and Schulz and Whitney (1986), provide evidence for the presence of shallow lakes and swamps around 8400–5400 radiocarbon years ago (c. 9500–5800 cal BP). Signs of early to mid-Holocene pedogenesis implying wetter conditions were found nearby at Jubbah (Garrard et al., 1981). A northward shift of the intertropical convergence zone (ITCZ) and associated monsoonal precipitation during the early Holocene is generally accepted for the southern and southeastern Arabian Peninsula (e.g. Fleitmann et al., 2003; Radies et al., 2005). Based on absent Holocene speleothem growth in northern Saudi Arabia, Fleitmann et al. (2004) assume that the ITCZ might not have migrated farther than c. 23–24°N.

This paper compiles first results on a series of geoarchaeological and palaeo-hydrological investigations in and around the oasis of Tayma (Fig. 1), northwestern Saudi Arabia (27°38′N, 38°33′E). Its focus is set on the implications of the sedimentary infill and microfossil record of a sabkha for regional palaeoclimatic changes

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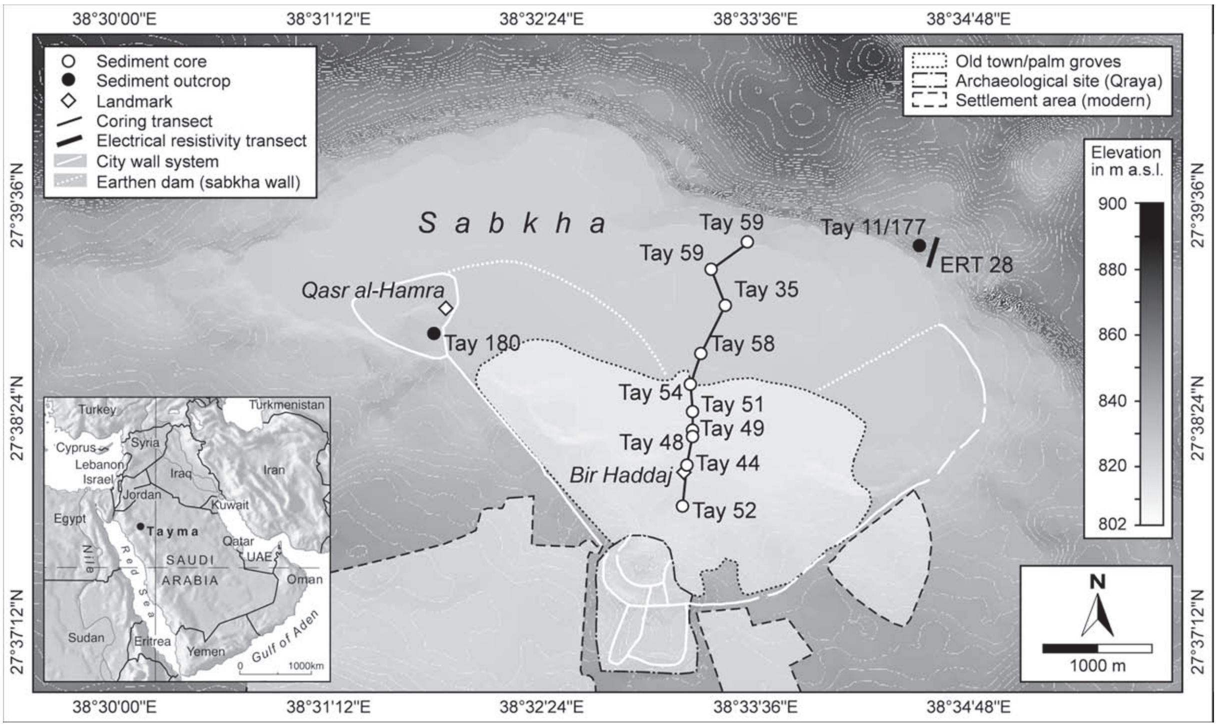

Fig. 1. Digital elevation model (DEM) of the Tayma oasis showing sampling sites as well as the location of the electrical resistivity tomography profile. The reconstruction of the ancient city wall system is according to Schneider (2010). The location of the oasis on the Arabian Peninsula is indicated on the overview map (lower left).

throughout the Holocene. Major changes of the local environment are reconstructed, considering the impact of a more humid phase during the early Holocene as inferred from several geo-archives of the southern/southeastern Arabian Peninsula. Based on sedimentary and geomorphologic evidence, radiometric dating, as well as a detailed geodetic dataset and palaeo-hydrological modelling, the aim is to present the timing of wet conditions, various aspects of local environmental change and quantitative data on palaeo-rainfall.

2. Background

2.1. The oasis of Tayma

Tayma, situated at the northwestern branch of the An-Nafud sand sea, is located in an area of rich archaeological heritage, and can itself look back on a long settlement history. Almost full-size human and cattle petroglyphs from the Tayma area show significant parallels to the Neolithic early Jubbah style rock art (Khan, 1988) and relate to a settlement pattern of “partially settled communities based on small-to-medium-sized mammal herding” (Masry, 1977, p. 11) at that time. Flint tools widely distributed in the Tayma oasis were used to produce circular carnelian beads and are ascribed to the first phase of permanent settlement during the late Chalcolithic to the early Bronze Age (4th-3rd millennium BC) (pers. comm. C. Purschwitz). These industrial activities heralded the period of permanent occupation from the mid-3rd millennium BC until the advent of Islam (Eichmann et al., 2006a,b). Tayma’s importance as a caravan city in the past is based on the high abundance of artesian groundwater in attainable near-surface layers and its position within a ramified trading network linking Arabia to the major political and economic urban centres of Near Eastern antiquity (Bawden et al., 1980). Remnants of an extensive and sophisticated water management system (Hamann et al., 2008) indicate a high level of socio-technical organisation. At its largest extent, the ancient settlement exceeded the size of the modern town (Fig. 1). The related city wall structures embrace an area of c. 8 km^2 (Bawden et al., 1980) with a length of more than 18 km in total (pers. comm. A. Hausleiter).

2.2. Physical setting

Tayma is built on Ordovician sandstone (Qasim Formation) which is part of a Palaeozoic-Cenozoic sedimentary sequence overlying the crystalline basement of the Arabian Shield. Today, erosion induced by Mesozoic and Cenozoic uplift is dominant, resulting in the denudation of the Arabian Shield in the westernmost part (Vincent, 2008). In the northern part of the oasis of Tayma, an endorheic depression of about 20 km^2 separates the settlement and the palm groves from a retreating escarpment (Fig. 1). It collects surface runoff and sediment in the course of each rainfall event when wadi systems are activated. Its catchment area comprises c. 660 km^2. This type of intra-plateau basin with a flat and shallow sedimentary cover characterised by syndepositional intrasediment evaporation of capillary brines may be defined as an inland sabkha. Morphodynamic processes such as aeolian erosion as well as aeolian and alluvial accumulation are partly controlled by fluctuations of the groundwater level (Barth, 1998; Warren, 2006). South-southwesterly winds prevail at Tayma. Today, the area receives an average of 45 mm annual rainfall which mostly occurs between November and April. Daytime temperatures fluctuate around 10 °C in winter and may rise above 40 °C in summer. Vegetation is very sparse including perennial shrubs and annual grasses (Vaslet et al., 1994).

3. Methods

Field work at Tayma comprised vibracoring inside the sabkha geo-archive using an Atlas Copco, type Cobra mk1 fitted with open steel auger heads (diameter: 5 and 6 cm). The stratigraphy was described in the field in terms of colour according to the Munsell Soil Color Chart, grain size and rounding, as well as texture and carbonate content (qualitatively by HCl [10%]) as recommended by AG Boden (2005). Macroscopic faunal and floral remains as well as evaporite minerals were also recorded. The grain size distribution of selected cores was analysed by means of laser diffraction spectroscopy (Malvern Mastersizer 2000). Mean grain size distribution was calculated by Gradistat software (Blott and Pye, 2001). Carbonate content of the entire coring series was measured using a Scheibler apparatus following the method outlined in Beck et al. (1993). Further sedimentary analyses are in progress. For quantitative analyses of the microfossils in the sediment cores, the sediment fraction 200–1000 μm was investigated using a binocular microscope. Age estimates are based on ^{14}C-AMS data (Table 1) and diagnostic pottery (Fig. 3). ^{14}C-AMS data based on shells, ostracods and seeds were calibrated by means of Calib 6.0.1 software (Reimer et al., 2009). No conflicting radiocarbon ages or age inversions were observed in this study. Even though ^{14}C analysis on terrestrial shells may lead to age overestimation due to the hard water effect (Garcia et al., 1992), several sites similar to the environment of Tayma showed that these errors are rather insignificant (Davies, 2006; Lézine et al., 2007).

Along the margins of the sabkha, two massive sediment bodies of bioclastic material were discovered. They were sampled for microfaunal analyses. Foraminifera and Ostracoda were identified under a binocular microscope up to a total number of 300 specimens for each group. At the same time, the rate of test malformations was recorded. The shape of 30 sieve pores of ten ostracod carapaces (*Cyprideis torosa*) per sample was recorded (round, elongate or irregular) using a light microscope (400x) following the approach of Rosenfeld and Vesper (1977).

Positions of all sampling sites as well as the topography were measured by DGPS (rover: Trimble R8 GNSS-Receiver; controller: Trimble TSC2; radio unit: Trimble PDL 450) in UTM zone 37N projected on the common WGS84 reference ellipsoid.

In order to calculate early Holocene rainfall and potential evaporation, a high-resolution digital elevation model (DEM) was established based on DGPS and tachymeter measurements (Fig. 1). Inside the palm groves, DGPS measurements provided only very few data points. For this area, SRTM elevation data was calibrated by the sparse DGPS data.

Electrical resistivity tomographies (ERT) have been performed along 2D-profiles with equidistant spacing (1–4 m) of 80 ActEle electrodes using a multi-electrodes-apparatus 4Punkt Light High Power of LGM Comp. Data handling and tomographic inversion was achieved by Geo-Test software applying Wenner Configuration. Several profiles were extended using the roll-on technique.

4. Results and discussion

4.1. Sabkha stratigraphy

The core transect indicates that the sabkha of Tayma developed in an endorheic bedrock depression while the old town and the palm groves of the settlement are situated at an elevated level on the subterraneously inclining bedrock (Figs. 1–3). Overlying the Ordovician sandstone bedrock is a unit dominated by clay and silt which contains several indicators for slightly saline lacustrine deposition. At site Tay 52, cored in a private garden in the centre of the historical part of Tayma, the deposit contains high concentrations of (par-)autochthonous ostracod valves (*C. torosa*) and foraminifer tests (*Ammonia tepida*) (Fig. 4). Both species are outstanding opportunists tolerating wide ranges of salinities (Vesper, 1972; Almogi-Labin et al., 1992; Handl et al., 1999; see also section 4.2). Towards the sabkha, the lacustrine deposit shows fine lamination (Tay 51, Tay 54) and is severely altered due to the precipitation of capillary evaporites, mainly gypsum, carbonates and halite. Input of sediment into a palaeo-lake during periodic activation of wadis resulted in the formation of millimetre-scaled, quartz-dominated, fining-up sequences. The basal sandy part may have provided an aquifer for the circulation of pore water out of which aragonite precipitated (Ginau, 2010). However, syndepositional formation of the carbonates as pelagic rain due to brine concentration at the water surface as described by Heim et al. (1997) is more likely. Based on similar "laminated marls", Parker et al. (2006, p. 472) infer deposition in a relatively deep permanent water body during early Holocene times at Awafi, UAE. Gasse et al. (1987) associate laminated carbonates with the highest Holocene water levels of a lake (Daiet al Melah) at the northwestern Saharan margin.

Evaporites within the sediments (capillary evaporites) precipitate due to a high evaporation efficiency in recent times as their concentration increases within interstitial pore water. Diffusional forces drive lateral and vertical inflow of groundwater into the sabkha basin. Idiomorphic evaporite minerals reach diameters of up to 5 cm and their abundance increases towards the lowest parts of the sabkha (Tay 35, Tay 41). Less soluble salts such as bassanite and anhydrite dominate the marginal cores (e.g. Tay 58), while halite is dominant in the central cores (e.g. Tay 43), in particular at the surface. On a vertical scale inside the sabkha, sulphates and to a lesser extent carbonates are present within the fluctuation zone of the ground water level (from the bottom up to approx. 1 m below surface [b.s.]) (Ginau, 2010).

Towards the margins where the original accumulation pattern is still preserved, wood, plant fibres, and seeds of *Ruppia maritima* (Tay 58) – a therophytic hydrohalophyte usually found in coastal waters (Khan and Qaiser, 2006) – clearly indicate a perennial saline lacustrine environment (Fig. 2). The uppermost part of this lithofacies unit related to the Holocene maximum lake expansion was radiocarbon dated to 9435–9136 cal BP (Tay 58/14), 8752–8457 cal BP (Tay 58/13H), and 8702–8451 cal BP (Tay 54/14).

Gastropod shells and barnacle fragments are abundant within the overlying unit inside the sabkha basin. *C. torosa* and *A. tepida* occur less frequently (Fig. 2). However, according to the fine-grained primary texture, this layer is also assumed to reflect a lacustrine environment, even though it is most likely associated with a contraction of the water body. Lacking microfossils in the upper part were initially thought to indicate temporary desiccation. Even

Table 1
Details on radiocarbon data used in this study. Calibration was carried out using Calib 6.0.1 software (Reimer et al., 2009). KIA = Leibniz-Laboratory for Radiometric Dating and Isotope Research, Christian-Albrechts-University of Kiel, Germany. UGAMS = Center for Applied Isotope Studies, University of Athens, Georgia, USA.

Sample	Depth (cm b. s.)	Lab ID	Material	δ^{13}C (‰)	^{14}C age	Age cal BP (2σ)
Tay 54/14	310–305	KIA34034	plant remains	−26.5 ± 0.3	7805 ± 45	8702–8451
Tay 58/13H	350	KIA34033	wood	−27.6 ± 0.2	7820 ± 45	8752–8457
Tay 58/14	358–353	KIA35465	seeds	−14.0 ± 0.4	8300 ± 45	9435–9136
Tay 11/6	10–5	KIA34032	gastropod shells	5.78 ± 0.1	8125 ± 45	9251–8992
Tay 11/2	210–205	KIA34027	gastropod shells	0.53 ± 0.2	8980 ± 45	10,235–9923
Tay 177/21	5	UGAMS7583	ostracods	−4.2	8250 ± 35	9401–9091
Tay 177/10	120	UGAMS7582	ostracods	−3.8	8530 ± 30	9542–9486
Tay 177/1	205	UGAMS7581	ostracods	−4.1	8740 ± 30	9887–9562

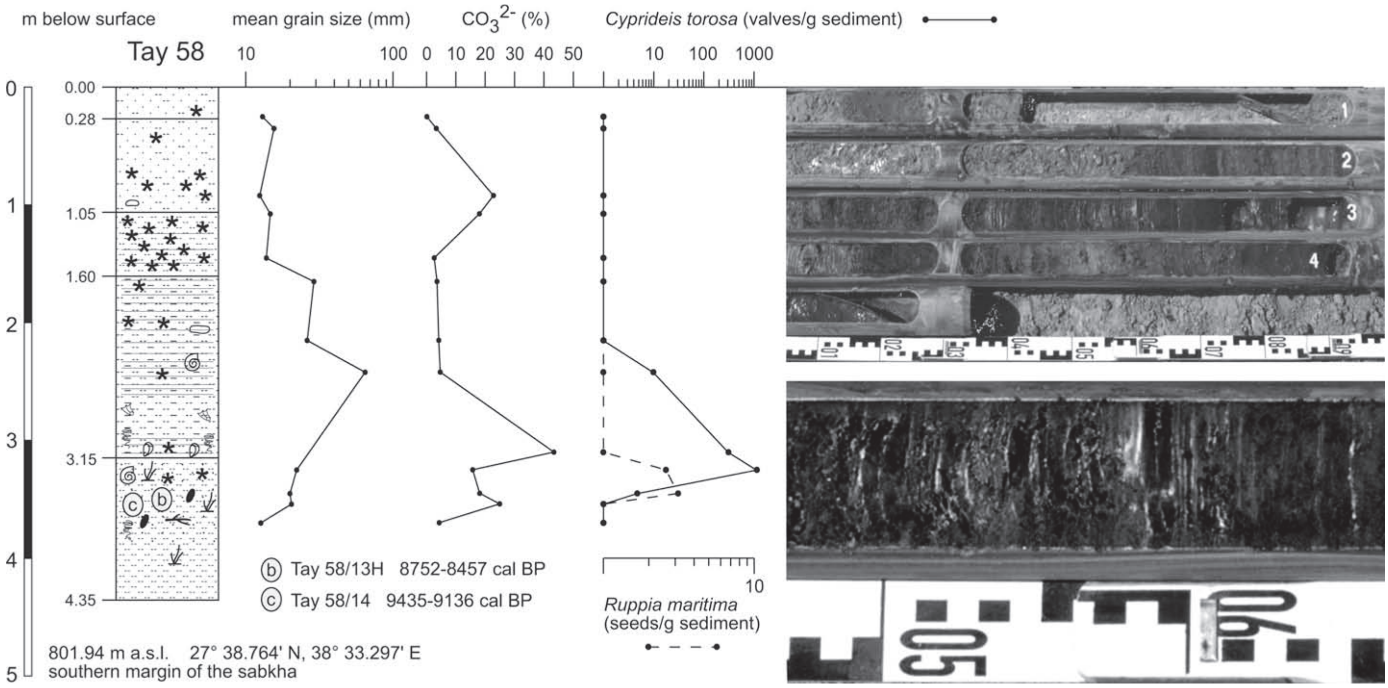

Fig. 2. Sediment core Tay 58 showing data on mean grain size, carbonate content and the occurrence of *Cyprideis torosa* as well as seeds of *Ruppia maritima*. A legend and preliminary lithofacies interpretation are provided in Fig. 3. For the location of the core see Fig. 1. Upper right: photo of core Tay 58. Lower right: (sub-)millimetre-scaled lamination of carbonate layers and clastic silt at 2.66-2.47 m b.s. (below surface).

though *C. torosa* is adapted to strongly fluctuating ecological conditions (Handl et al., 1999) with salinities of up to 90‰, these populations cannot reproduce without permanent water cover (Anadón et al., 1986; Gasse et al., 1987). However, desiccation events in this early stage can probably be excluded due to the presence of aragonitic laminae precipitated from the water column (open water evaporites) up to 1.20 m b.s., for instance at Tay 58 (Fig. 2). Increased occurrence of shells and barnacle remains may be attributed to reworking from the massive bioclastic deposits (Tay 11/177; Fig. 5) along the sabkha margins representing former lake shorelines.

A hiatus was determined in the area of the old town of Tayma (Tay 52) and the palm groves (Tay 44, Tay 48, Tay 49) between the lacustrine lithofacies and the overlying anthropogenically disturbed deposits. While the lacustrine layer corresponds to the early Holocene ^{14}C-AMS data from the sabkha basin (Tay 54, Tay 58; Table 1), the following unit of poorly sorted sand and silt could not

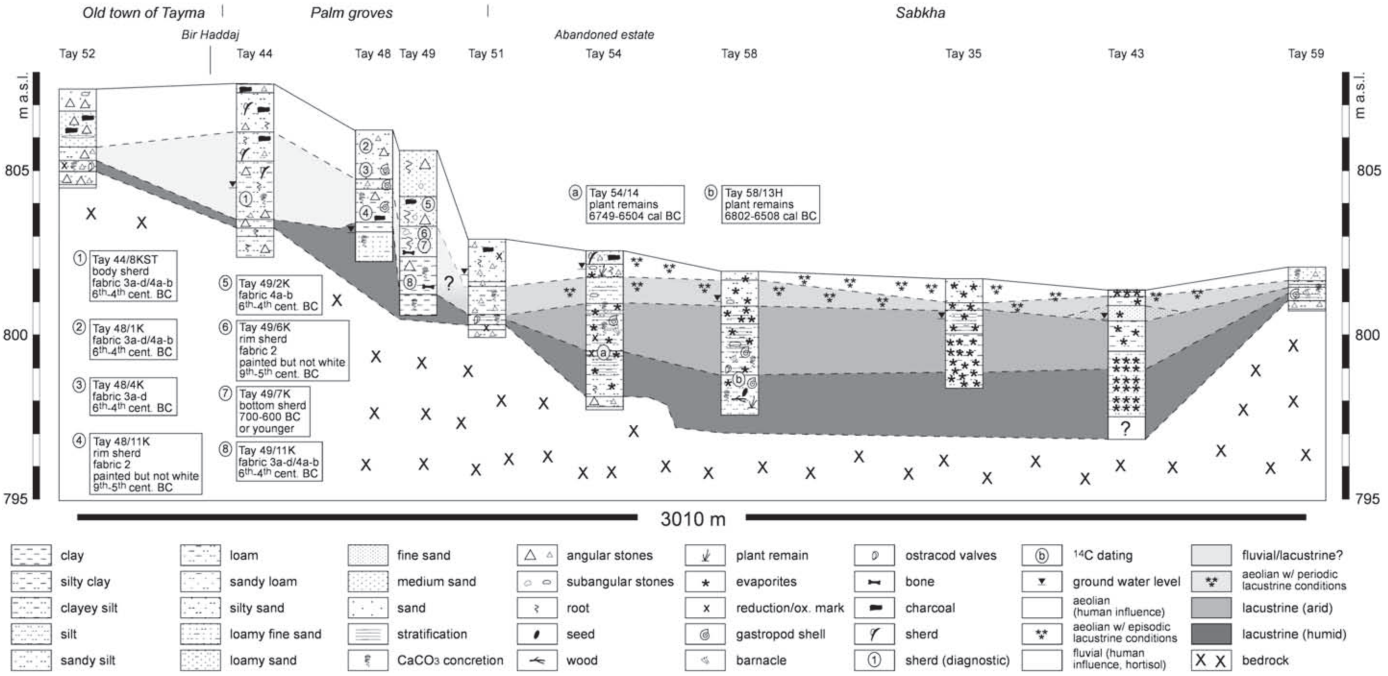

Fig. 3. Stratigraphic transect from the old town across the sabkha with preliminary lithofacies interpretation. For the location of the transect see Fig. 1. Ceramic sherds were first determined by M. Möhle. The current chronological interpretation is based on pers. comm. A. Hausleiter and F. Tourtet.

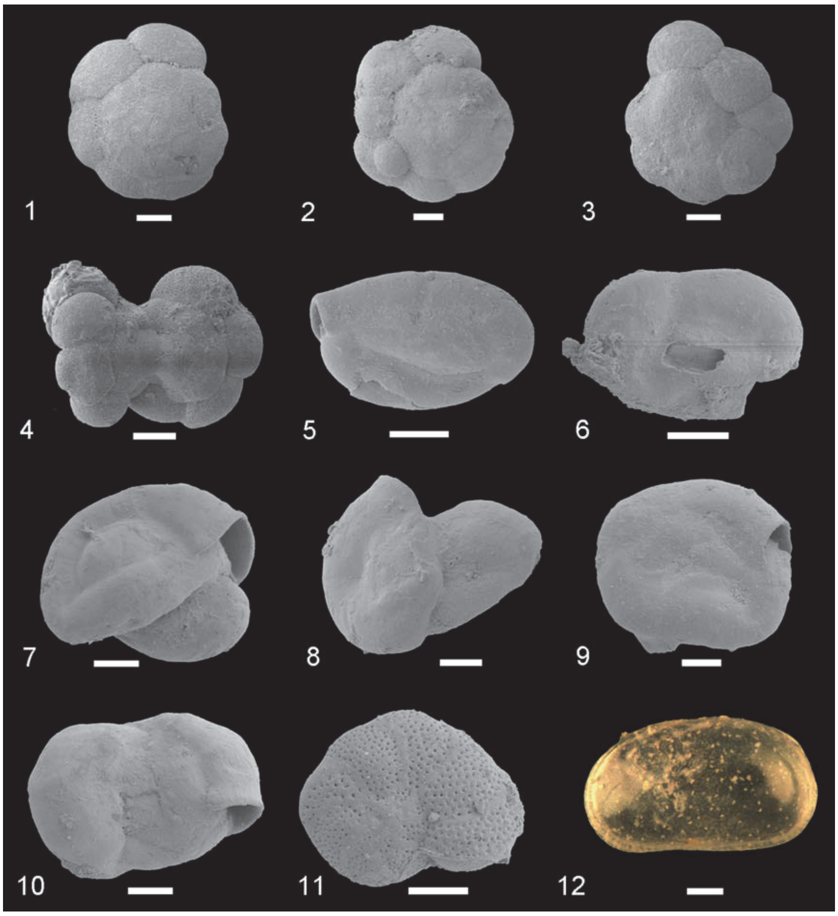

Fig. 4. Microfossils from Tayma, white scale: 0.1 mm. 1: *Ammonia tepida* (Cushman, 1926), normal test, spiral view. 2: *A. tepida* (Cushman, 1926), chamber deformation, spiral view. 3: *A. tepida* (Cushman, 1926), changes of growth direction, spiral view. 4: *A. tepida* (Cushman, 1926), multiple test. 5: *Quinqueloculina* sp., normal test. 6: *Quinqueloculina* sp., chamber deformation. 7: *Quinqueloculina* sp., changes of growth direction. 8: *Quinqueloculina* sp., multiple test. 9: *Miliolinella* sp., normal test. 10: *Miliolinella* sp., changes of growth direction. 11: *Rosalina* sp., normal test, spiral view. 12: *Cyprideis torosa* (Jones, 1850), female left valve.

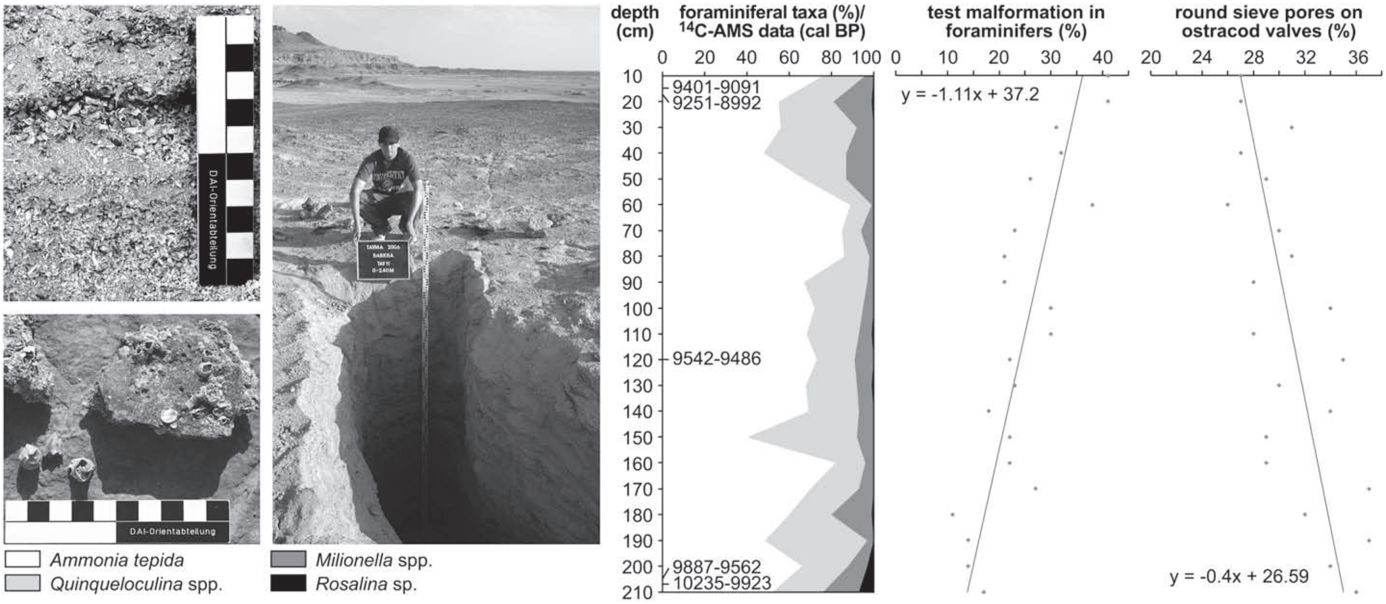

Fig. 5. Bioclastic deposit Tay 11/177 preserved in an incised section of the lowermost escarpment at the northeastern sabkha margin (cf. Fig. 1). Its surface is located at an elevation of 811.5 m a.s.l. and it has a vertical extension of up to 240 cm. Percentages of foraminiferal taxa, test malformations as well as round sieve pores on ostracod valves are presented. The right photo shows the trench which was dug for sampling. Upper left: close-up of the deposit indicating the dominance of gastropod shells and fragments of *Balanus* sp. over quartz grains (scale: 10 cm). Lower left: *Balanus* sp. in living position directly attached to the bedrock indicates in-situ sedimentation at Tay 11/177.

have accumulated before the 1st millennium BC according to the presence of ceramic fragments (Tay 44, Tay 48, Tay 49). Diagnostic sherds of local fabric 3a-d/4a-b ([1] and [8] in Fig. 3) and fabric 2 ([4] in Fig. 3) were found in the basal part close to the lower facies boundary. Further anthropogenic signatures include bone fragments and charcoal.

Inside the sabkha, the amount of quartz sand increases at the top of the sequence, indicating contraction of the lake, further aeolian influence and, finally, a shift to a decreasing frequency and duration of standing water conditions. The environment may be interpreted as a salt marsh similar to descriptions in al-Bakri's "*Mu'jam*", a descriptive geographic compendium from the 11th century AD, where the area north of the oasis of Tayma is named "*al-'Aqirah*" which may be translated as "to hinder or to obstruct marching forward" (Al-Najem, 2000, p. 192). The southern part of the sabkha at the transition to the palm grove is separated by a low earthen wall (Fig. 1) which connects the two massively built branches of the outer city wall (Schneider, 2010). This section must be younger than the oldest parts of the wall system (mid-3rd mill. BC according to Engel et al., 2009; Klasen et al., 2011). The low dam indicates that the sabkha area itself still provided an obstacle to invaders (impenetrable salt marsh) most likely due to a shallow remnant of the former lake. However, the dam was sufficient to protect the agricultural compounds within the city wall system from the intrusion of salty water in case the sabkha was flooded or the shallow lake level rose in the course of rainfall events (Hamann et al., 2008).

4.2. Palaeoecology of the lake based on microfaunal evidence

At the northeastern sabkha margin (Tay 11/177), a bioclastic deposit is preserved where the lowermost escarpment is incised (Figs. 1 and 5). It consists of gastropod shells of *Melanoides tuberculata*, Hydrobiidae and *Cerithium* sp., barnacle fragments, valves of *C. torosa*, a low-diversity foraminiferal thanatocoenosis as well as minor proportions of siliciclastic sand. At Tay 11/177, the sediment body has a thickness of 240 cm. Its upper limit is located at 811.5 m a.s.l. (above mean sea level), i.e. approx. 11 m above the bottom of the present-day sabkha. A consistent age model was established ranging from c. 10,000 to 9000 cal BP (Fig. 3, Table 1). It is the uppermost local occurrence of any Holocene lacustrine traces. Thus, it is inferred that the deposit coincides with the youngest humid period on the Arabian Peninsula. Reworking of the deposit can be ruled out since barnacles in living position were found (Fig. 5) and neither the ostracod valves nor the foraminifer tests show any signs of transport (Fig. 4). A former lake shoreline at an elevation of around 811.5 m a.s.l. is also supported by ERT 28 (Fig. 6). Very low resistivity values (less than 30 Ωm) on top of the lowermost escarpment at the northern sabkha margin near Tay 11/177 indicate high concentrations of salt likely deriving from salt water intrusion during the peak of the lake period.

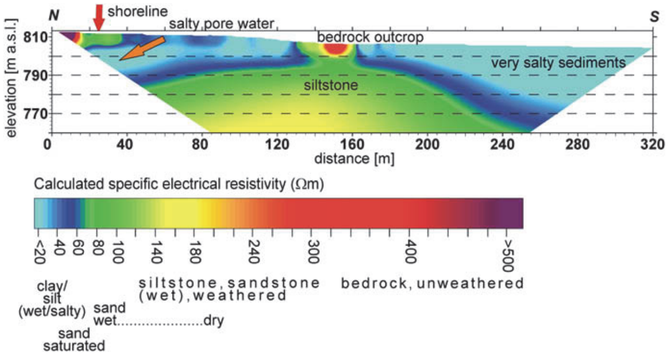

Fig. 6. Electrical resistivity tomography profile 28 (ERT 28) situated in the vicinity of Tay 11/177 (for location cf. Fig. 1) indicating a shoreline of a palaeo-lake at c. 811 m a.s.l. Low resistivity values indicate salt concentrations in joints of the bedrock.

Monotonous ostracod populations dominated by *C. torosa* and the dominance of the gastropod *M. tuberculata* among the species-poor gastropod population indicate ecological stress, thereby implying strong fluctuations in salinity and nutrient supply. *M. tuberculata* was found to withstand salinities of up to 23‰. The species dwells in littoral habitats of freshwater lake bodies in a water depth of around 2 m and feeds on aquatic and subaquatic plant detritus. The shells typically accumulate along the shores of lakes (Leng et al., 1999; Plaziat and Younis, 2005). The highly concentrated occurrence of barnacles in non-marine environments is rare (Foster, 1987). Birket Gessabia in the Siwa Oasis, Western Desert of Egypt, is one of the few sites where large inland populations have been reported. It is assumed that specimens of *Balanus amphitrite* were introduced by birds (Omer-Cooper, 1937). Marginal or non-marine environments with large populations of *B. amphitrite* are characterised by warm waters and salinities up to 40–45‰ (Por, 1972; Plaziat, 1991; Shalla et al., 1995).

The foraminiferal assemblage is dominated by *A. tepida* throughout the profile. Its dominance slightly increases from the bottom to approx. 50 cm below surface (b.s.). *A. tepida* is representing a group of small ubiquitous euryhaline foraminifera occurring frequently in shallow and saline inland lakes (Wennrich et al., 2007). They are well adapted to temporary fluctuations in salinity but require permanent water cover. In the marginal shallow water environments of the Dead Sea, *A. tepida* develops dense monospecific populations within microbial mats (Almogi-Labin et al., 1992). Outstanding opportunism of *A. tepida* and the large distance to the nearest marine environment (Red Sea: >250 km) give reasons for the low foraminiferal diversity (cf. Wennrich et al., 2007). The remaining taxa *Quinqueloculina* spp., *Milionella*, spp. and rare tests of *Rosalina* sp. (Fig. 4) also indicate high concentrations of dissolved solids. At Lake Qarum, Egypt, occurrences of *Quinqueloculina* were found to positively correlate with salinity (Abu-Zied et al., 2007).

Following own observations of several foraminiferal assemblages (Aral Sea, central Germany, Patagonia, Baltic Sea, Black Sea), the rate of malformation seems to be extraordinarily high in athalassic environments (Pint and Frenzel, unpubl. data). It positively correlates with ecological stress and instability of ecological conditions, such as strong variations in salinity and temperature, hypo- and hypersalinity, oxygen deficiency, critical trophic conditions and mechanical stress (Almogi-Labin et al., 1992; Geslin et al., 2000; Wennrich et al., 2007 and references therein). At Tay 11/177, the rate of test malformation fluctuates though it follows a positive trend towards the top of the profile.

Sieve pores of ostracods (Fig. 7) provide access for sensory bristles (*sensilla*) allowing the individual to generate information about the environment (Athersuch et al., 1989). Their shape was studied since it correlates to the level of salinity (Rosenfeld and Vesper, 1977; Frenzel and Boomer, 2005; Keating et al., 2007). Even though the percentage of rounded sieve pores is fluctuating throughout the profile and shows high standard deviations even within the same sample, a general trend towards an upward decrease was observed. Both the upward decrease in round sieve pores and the increase in foraminiferal test malformation indicate increasing salinity and ecological stress from 10,000 to 9000 BP.

At the southwestern margin of the sabkha, another disjunct bioclastic deposit of similar composition was found (Tay 180; Fig. 8). Both Tay 11/177 and Tay 180 belong to the same endorheic depression, i.e. the same palaeo-lake basin. Tay 180 is attached to an outcropping sandstone ridge on which the archaeological site of

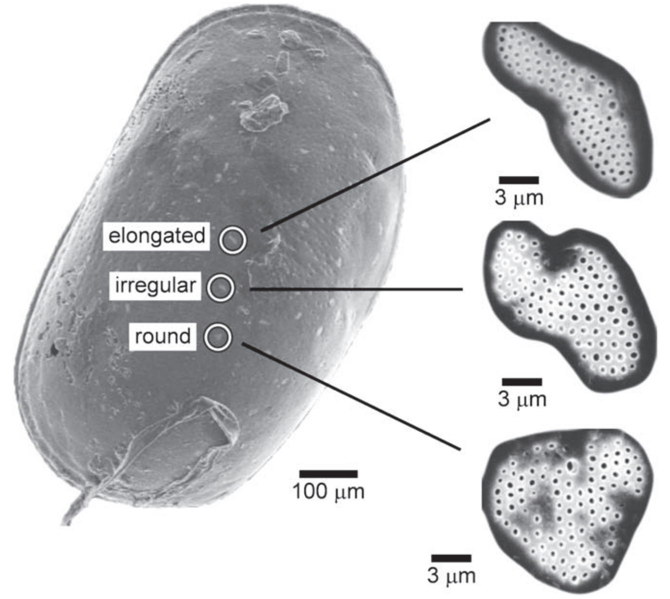

Fig. 7. Shapes of sieve pores according to Rosenfeld and Vesper (1977). The scanning electron microscope (SEM) picture shows a female specimen of *Cyprideis torosa* taken from Tay 59 (cf. Figs. 1 and 3) (Ginau, 2010).

Qasr al-Hamra was founded. Due to its lower elevation (806 m a.s.l.) it is assumed to have accumulated after the onset of long-term lake contraction and associated lowered lake levels. Thus, it is likely younger than Tay 11/177 (10,000–9000 cal BP) and significantly older than 3000 BP according to the low position of the anthropogenic layers containing diagnostic pottery from the 1st mill. BC in sediment cores Tay 49 (c. 801.5 m a.s.l.), Tay 48, and Tay 44.

A. tepida is the only foraminiferal species present in the lowermost samples of Tay 11/177. Towards the upper part of the profile, *Quinqueloculina* spp., *Milionella* spp. and even several tests of *Rosalina* sp. were found. Test malformations show an upward decrease while the percentage of round sieve pores in *C. torosa* increases. Both parameters indicate a general decrease in salinity. Even though the profile may indicate a relative shift to more stable ecological conditions providing niches for other taxa than *A. tepida*, absolute values of salinity exceeded the ones of Tay 11/177. It may be inferred that the bioclastic deposit is the result of a second wet phase interrupting the long-term mid- to late Holocene aridisation.

4.3. Palaeo-hydrological modelling

Saline inland lakes are precise recorders of hydrological and climatic changes since their water volume is primarily controlled by effective precipitation (Keating et al., 2007). Based on the findings of palaeo-lake sediments within the sabkha basin of Tayma (Chapter 4.1) and spatially limited bioclastic sediment bodies as indicators of former shorelines of a perennial lake (Chapter 4.2), a hydrological water balance equation was established implying a stable water level from year to year (Wellbrock and Grottker, 2010). It enables quantitative estimates for palaeo-hydrological parameters such as rainfall. Several simplifying assumptions were made in order to solve the equation.

The water balance equation for a closed drainage basin in a certain time span is defined as

$$Q_{in} + GW_{in} + N = Q_{eff} + GW_{eff} + E \tag{1}$$

where Q is the annual surface runoff volume (influx and efflux), GW is the amount of annual groundwater volume (influx and efflux), N is the annual volume of rainfall which directly precipitates into the sabkha and E is the annual evaporation volume. Since the endorheic depression has no outlet ($Q_{eff} = 0$) and the amount of groundwater influx was assumed to be insignificant ($GW_{in} = 0$) during the presence of a lake body (cf. Tyler et al., 2006), solving equation (1) is straightforward.

The infiltration volume (GW_{eff}) is determined by the permeability of the palaeo-lake bottom. The permeability coefficient was estimated to be $k_f = 10^{-10}$ m s^{-1} which is in line with mean rates from other desert sandstone environments (Heilweil et al., 2006). It also matches empirical values for permeability of silt or clay. Both of them are predominant sediment fractions within the sabkha. Finally, the annual infiltration volume GW_{eff} was calculated by

$$\mathrm{GW}_{\mathrm{eff}} = \sum_{i=1}^{12} \mathrm{GW}_{\mathrm{eff},i} = \sum_{i=1}^{12} A_{\mathrm{lake},i-1} \times k_f \tag{2}$$

where i indicates the months of a year. The lake surface is represented by A_{lake}. However, GW_{eff} was found to be less than 2% of annual surface runoff volume (Q_{in}).

Early Holocene insolation was only slightly higher during the early Holocene due to orbital forcing (less than + 5% according to Claussen et al., 1999; peak levels of + 8% according to deMenocal et al., 2000) and thus, influenced evaporation rates only marginally. An annual palaeo-evaporation rate of $h_e = 1500 \pm 100$ mm a^{-1} was assumed,

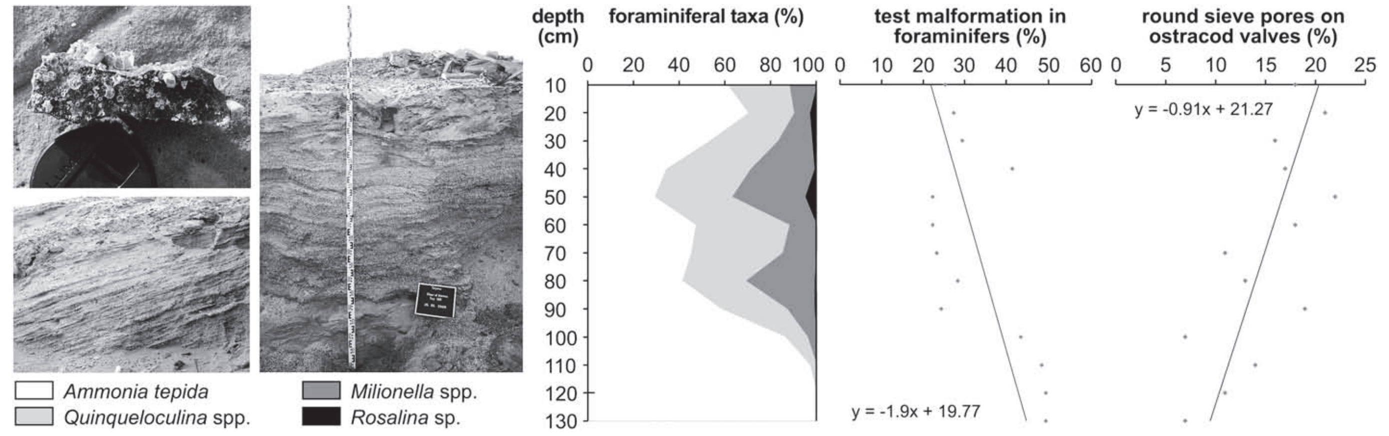

Fig. 8. Bioclastic sediment deposit Tay 180 attached to the sandstone ridge of Qasr al-Hamra (cf. Fig. 1). Its surface is located at an elevation of 806 m a.s.l. and it has a vertical extension of 160 cm. Percentages of forminiferal taxa, test malformations as well as round sieve pores on ostracod valves are presented. The right photo shows the investigated outcrop. Upper left: *Balanus* sp. in living position directly attached to the bedrock indicating in-situ accumulation of the deposit. Lower left: inclining bioclastic strata towards the sabkha centre (270° perspective from the photo on the right).

which is similar to recent values ($h_e = 1700$ mm a^{-1} according to Trabucco and Zomer, 2009) but reduced due to a likely denser cloud cover at that time. The denser cloud cover is related to the higher amount of rainfall. Annual evaporation volume E was calculated as

$$E = \sum_{i=1}^{12} E_i = \sum_{i=1}^{12} A_{\mathrm{lake},i-1} \cdot h_{e,i} \tag{3}$$

depending on monthly evaporation ($h_{e,i}$) and the lake surface of the previous month ($A_{\mathrm{lake},i\text{-}1}$).

Annual surface runoff volume Q_{in} was determined by

$$Q_{in} = \sum_{i=1}^{12} Q_{in,i} = \sum_{i=1}^{12} A_{cat} \cdot h_{n,i} \cdot r \tag{4}$$

where A_{cat} represents the catchment area and $h_{n,i}$ the monthly precipitation. The runoff coefficient r indicates the amount of rainfall which effectively becomes surface runoff. It was estimated according to the empirical equation for arid environments of Şen (2007):

$$r = 1 - e^{-k_s} \tag{5}$$

The runoff exponent k_s represents the surface texture (k_s [Quaternary sand] = 0.3; k_s [sedimentary rocks] = 0.5). Thus, for the Tayma area, characterised by Quaternary sand deposits (c. 70%) and sedimentary rocks (c. 30%), r is considered to be at a range of 0.3 ± 0.05. Other potential determinants of r such as mean surface slope, vegetation, size of the catchment area and temporal distribution of precipitation events only play a minor role in arid environments (Şen, 2007). The empirical verification of these runoff coefficients is in progress.

In order to evaluate evaporation rates (E) and infiltration rates (GW_{eff}), the lake's surface A_{lake} has to be determined. Therefore, the capacity curve, i.e. the relationship between water level h, stored water volume V and the lake's surface [$A_{lake} = f(V, h)$], was derived by high-resolution surveying using DGPS. According to the upper limit of the shoreline deposit of 811.5 m a.s.l. (Tay 11/177), a minimum lake surface of 18.45 km^2 and a stored water volume of 1.16×10^7 m^3 were calculated for the peak of the early Holocene wet period. Sediment accumulation within the sabkha since the early Holocene has been neglected. Though sediment infill influences the capacity curve of the model, it does not change the modelled lake surface which calculations of evaporation and infiltration depend on.

For solving the hydrological water balance equation (1), at first a hypothetical annual precipitation rate h_n was chosen. Afterwards, the monthly distributions of annual rainfall and reference evapotranspiration rates ($h_e = 1500 \pm 100$ mm a^{-1}) fitting today's climate pattern were assumed (Fig. 9), i.e. rainfall during wintertime and high evaporation rates during the summer, as it is typical for non-monsoon affected climates. Monthly rainfall $h_{n,i}$ has been assumed as singular rainfall events in order to neglect transmission losses of small rainfall events since they are already considered by the runoff exponent k_s (5). The monthly runoff volume $Q_{in,i}$ depending on monthly precipitation $h_{n,i}$ was calculated. Using the capacity curve, the lake surface A_{lake} relying on stored water volume for each month was determined and hence the monthly infiltration $GW_{eff,i}$ as well as the monthly evaporation volume E_i were calculated. For the calculation of the following month, another initial water volume taking the changes of the previous month into account was applied, and so on. Finally, after the calculation of each month for a whole year, the hydrological water balance has to be fulfilled. The annual precipitation rate h_n had to be changed iteratively until the initially stored water volume equated to the final water volume.

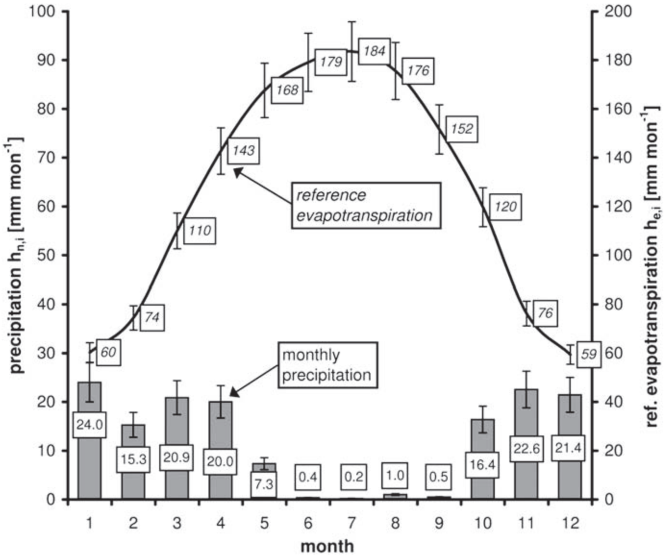

Fig. 9. Reconstructed seasonal distribution of precipitation and reference evaporation for the peak of the early Holocene lake period (c. 10,000–9000 BP) taking into account the recent annual climate pattern, annual reference evapotranspiration of 1500 ± 100 m a^{-1} and annual precipitation of 150 ± 25 mm a^{-1} (after Wellbrock and Grottker, 2010).

Thus, the annual precipitation rate for the peak of the early Holocene lake period (c. 10,000–8500 BP according to ^{14}C-AMS data of Tay 11/177, Tay 54 and Tay 58) was estimated to have been $h_n = 150 \pm 25$ mm a^{-1} considering an annual reference evapotranspiration rate of $h_e = 1500 \pm 100$ mm a^{-1} (Fig. 10).

By calculating palaeo-rainfall the same way but considering a monsoon-type climate pattern (rain periods during summer, lower reference evapotranspiration of approx. $h_e = 1400$ mm/a), h_n yields 136 ± 23 mm a^{-1}. This is within the range of the results

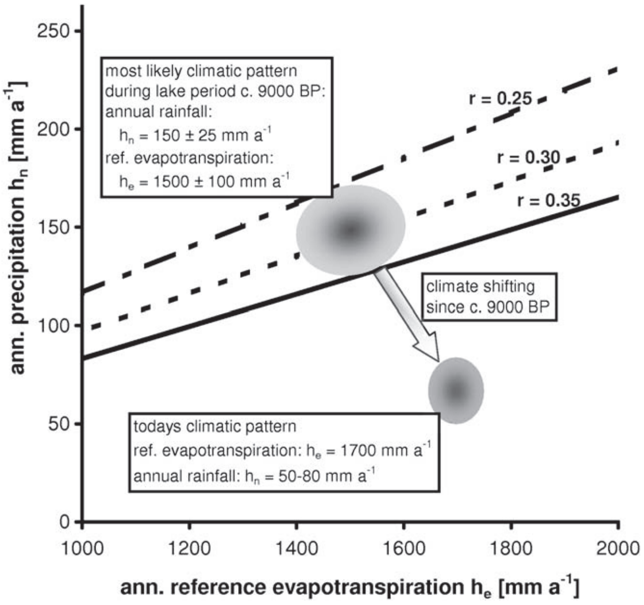

Fig. 10. Reconstructed annual precipitation h_n and reference evapotranspiration h_e rates for different mean runoff coefficients r and an equal water balance at a water level of 811.5 m a.s.l. (after Wellbrock and Grottker, 2010). As shown in this figure, a climate shifting from cooler and wetter conditions during the second lake period (around 9000 BP) to the recent hyperarid climate should be assumed.

regarding the recent climate pattern and, thus, does not entirely exclude monsoonal influence for the early Holocene of northern Arabia.

4.4. Synthesis – climate and environment

So far, a humid period around 9500–5800 cal BP was reconstructed based on calibrated ^{14}C data of palaeo-lake beds in interdunal depressions of the An-Nafud desert (Whitney et al., 1983; Schulz and Whitney, 1986). Further regional sedimentary records are scarce and a pilot study on speleothems in northern Saudi Arabia even failed to provide any evidence for increased humidity during the early Holocene (Fleitmann et al., 2004). However, in the central and southern Arabian Peninsula and the Sahara the establishment of lakes during this wet period was investigated in more detail (e.g. McClure, 1976; Gasse et al., 1987; Plaziat, 1991; Baumhauer et al., 2004; Radies et al., 2005; Parker et al., 2006; Lézine et al., 2007, 2010; Fuchs and Buerkert, 2008; Schütt and Krause, 2009). These records indicate that after a dry post-LGM phase culminating in the Younger Dryas (Fuchs and Buerkert, 2008), precipitation increased abruptly at the onset of the Holocene. In the southern Arabian Peninsula this is due to a temporary northward shift of the ITCZ which triggered a strengthening of the Indian Ocean monsoonal rainfall during summer. ITCZ migration is controlled by orbital forcing determining solar radiation on earth. After 8000 BP, monsoonal influence gradually decreased due to a slow southward shift of the ITCZ (Fleitmann et al., 2003). According to Arz et al. (2003, p. 121), it is unlikely that the ITCZ migration reached northern Saudi Arabia during the early Holocene. Instead, stronger inflow of cool continental air masses in wintertime (Arctic oscillation) and a “monsoon-type circulation pattern” due to increased land-sea temperature discrepancies – both originating from the southeastern Mediterranean – may have resulted in positive precipitation anomalies on the northwestern Arabian Peninsula. However, neither based on the sediment archive nor the water balance equation from this study, the source or season of moisture can be determined.

At Tayma, the increase in rainfall created a permanent lake environment at least since 10,000 BP according to the age model of Tay 11/177. Pre-8500 cal BP sediments in core Tay 58 indicate that the lake was at least 13 m deep. Based on the DEM, it had a minimum surface of 18.45 km^2 and water volume of 1.16×10^7 m^3. Its southern extent reached far into the recent settlement of Tayma. The aquatic fauna – most likely introduced by birds (cf. Omer-Cooper, 1937; Wennrich et al., 2007) – reveals low-diversity but high population densities. Low-diversity foraminiferal assemblages indicate ecological stress. The abundant marine taxa, shapes of the sieve pores of the ostracod *C. torosa*, and foraminiferal test malformation rates point to saline conditions and may already reflect an aridisation trend between 10,000 and 9000 BP. These findings are supported by sediment cores Tay 54 and Tay 58 which indicate lake shrinking after 8500 BP at the latest (Ginau, 2010). This is roughly in line with estimations by Schulz and Whitney (1986) for the nearby An-Nafud and also matches the timing deduced at Sedd adh Drah, Yemen (Davies, 2006), the Maqta oasis, northern Oman (Fuchs and Buerkert, 2008) or the eastern Sahara (Kuper and Kröpelin, 2006). Subsequent gradual aridisation, salinisation and contraction of the lake were interrupted by a temporary decrease of salinity inferred from a stable shoreline at Tay 180. This second wet phase may correspond with mid-Holocene ages obtained from lake deposits from the An-Nafud (Schulz and Whitney, 1986) and other locations on the Arabian Peninsula (McClure, 1976; Davies, 2006; Parker et al., 2006). The exact time of the shift from a permanent to a periodic lacustrine regime could not yet be determined, although the presence of a lake with only a fraction of its early Holocene size surrounded by salt marsh conditions during the 5th–4th millennium BP when the city wall system of Tayma was erected (Engel et al., 2009; Schneider, 2010; Klasen et al., 2011) is assumed. Agricultural sites north of the settlement were protected from flooding by only low earthen dams.

For a late Pleistocene, probably more humid period (34,000–24,000 BP according to ^{14}C data of Whitney et al., 1983; Schulz and Whitney, 1986; MIS 5 according to U/Th-dated cave deposits and speleothems, cf. Immenhauser et al., 2007; Fleitmann and Matter, 2009), an annual precipitation of 200 ± 50 mm a^{-1} was assumed by Wood and Imes (1995) based on models of groundwater recharge for the southern part of the Arabian Peninsula. These results are supported by the estimation of annual precipitation from this study (150 ± 25 mm a^{-1}), because the Holocene lake period is supposed to have been less pronounced (Whitney et al., 1983; Schulz and Whitney, 1986). Palaeo-rainfall seems to have been at least c. 300% of recent precipitation rates. However, it should be considered that the results provide approximate values of early Holocene annual rainfall and that simplifying assumptions were made in order to solve the water balance equation.

A maximum palaeo-shoreline at 811.5 m a.s.l. is a conservative assumption and so is the estimation of palaeo-rainfall rates. Higher lake deposits may have been eroded. A lake level of 818 m a.s.l., for instance, would have increased the lake surface by 22% (cf. Chapter 4.3). Due to a higher evapotranspiration and infiltration volume, the annual precipitation rates would have been in the range of 180 ± 30 mm a^{-1}.

By means of the seasonal distribution of runoff (calculated from monthly precipitation) and reference evapotranspiration it was possible to estimate the water level hydrograph for the early Holocene palaeo-lake. Taking monthly surface runoff volumes and losses due to evaporation and infiltration into account, water levels were determined by means of the capacity curve indicating maximum interannual fluctuations of c. 80 cm. It is expected that precipitation occurred mostly as rainfall events. Wadis were activated only intermittently albeit the sabkha itself had a perennial regime. After individual rainfall events, the water level may have risen by more than 20 cm. Activated wadis then transported up to 4% of the already stored water volume into the sabkha and thus caused a highly fluctuating environment regarding water level, salinity and nutrients (Wellbrock and Grottker, 2010). This fits well with the impoverished faunal assemblages found in the sedimentary record.

5. Conclusion

The oasis of Tayma in northwestern Saudi Arabia was affected by the early Holocene humid period which was likely controlled by the increased inflow of cold northern continental air masses in winter and monsoon-like circulation due to enhanced differences between land and sea surface temperatures. Nevertheless, a monsoon-related rainfall surplus in summer cannot be excluded based on these findings. A permanent lake filled the endorheic depression north of the oasis at least since 10,000 BP according to lacustrine deposits inside the sabkha and palaeo-shoreline deposits at its margins. The palaeoecology of the lake is characterised by saline waters and low-diversity faunal assemblages including the phenomenon of marine taxa in an athalassic environment. Gradual aridisation processes initiated not later than 8500 BP, but were interrupted by at least one wetter phase of temporarily decreased salinity and moderate diversification of the foraminferal assemblage (Tay 180). Inversely correlating trends of rates of foraminiferal test malformation and percentages of round sieve pores on ostracod valves are present at both bioclastic shoreline deposits (Tay 11/177 and Tay 180). Both proxies showed their high potential in the reconstruction of salinity and ecological stress. Lake contraction and lake level fall were most likely driven by a long-term aridisation process interrupted by at least one short period of increased humidity. The history of lake shrinking between 8000–4000 BP is not yet resolved. Around 4000 BP, when the eastern and western branches of the city wall system had already been erected, only shallow remnants of the lake existed, gradually turning into a salt marsh. A low earthen dam was enough to protect the oasis from flooding at that time. Salt marsh conditions were still described in the 11th century AD.

Tayma is the first site on the northwestern Arabian Peninsula for which quantitative data on minimum palaeo-rainfall during the early Holocene humid period were calculated. Input parameters for the simplified hydrological water balance equation are the minimum lake level, lake surface, and lake volume during the peak of the humid period as well as palaeo-evapotranspiration, groundwater infiltration, and the rate of surface runoff. Accordingly, a perennial lake in the endorheic basin of the modern sabkha with a lake level of at least 811.5 m a.s.l. would have required a minimum annual precipitation of 150 ± 25 mm. This value amounts c. 300% of recent precipitation rates, but is smaller than what has been calculated for the preceding humid phase (MIS 5) in the southern Arabian Peninsula.

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Author contributions

Field work was carried out by MG, ME, HB, NK, KW and AG. ME, AG and HB analysed and interpreted the sediment cores. PV and KW established the DEM. KW and MG implemented the palaeohydrological model. AP and PF conducted microfossil analyses. ME and KW wrote the manuscript.

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Beitrag 7:

How to discriminate athalassic and marginal marine microfaunas? Foraminifera and other fossils from an Early Holocene Continental lake in Northern Saudi Arabia.

Manuskript in Vorbereitung, Pint et al., *Journal of Foraminiferal Research*

Die Mikrofauna zweier Uferaufschlüsse und eines Bohrkerns wurde detailliert untersucht. Nicht nur die Verteilung der Arten wurde erfasst, sondern auch ihre Morphologie. Missbildungen der Foraminiferengehäuse sowie die Umrissformen der Siebporen auf den Klappen von *Cyprideis torosa* zeigen ökologischen Stress, vor allem Salinitätswechsel und Hypersalinität, an. Die Zunahme der Missbildungsrate wird mit einem Anstieg der Salinität infolge der klimatisch bedingten Evaporation des Sees in Verbindung gebracht.

Ergebnisse: Die fossile Mikrofauna des frühholozänen Sees in der Sapkha von Tayma setzt sich aus einer Ostrakodenart und vier Foraminiferenarten zusammen. Die Ostrakodenart *C. torosa* und die in Tayma dominant auftretende Foraminiferenart *Ammonia tepida* gelten als euryhalin mit einem Toleranzbereich von 0,5 bzw. 3 psu bis 100 psu. Sie kommen vor allem in hypersalinen Gewässern gemeinsam und häufig ausschließlich vor (De Deckker 1981). Die durchschnittlich sehr hohe Missbildungsrate bei den Foraminiferen des ehemaligen Sees ist typisch für ein salines Binnengewässer und steigt mit dem Salzgehalt. Dies konnte z. B. auch für die hypersalinen Pools rund um das Tote Meer in Israel gezeigt werden. Hier kamen ähnlich wie in Tayma Missbildungsraten von mehr als 50 % vor (Almogi Labin 1992). Missbildungen von Foraminiferengehäusen können daher in athalassischen Gewässern als relativer Salinitätszeiger genutzt werden.

Anna Pint, Max Engel, Sandra Melzer, Peter Frenzel, Birgit Plessen, Helmut Brückner (in Vorbereitung). How to discriminate athalassic and marginal marine microfaunas? Foraminifera and other fossils from an Early Holocene Continental lake in Northern Saudi Arabia (Manuskript in Vorbereitung).

	A. Pint	M. Engel	S. Melzer	P.Frenzel	B.Plessen	H. Brückner
Konzeption	**X**	X		X		
Geländearbeiten	**X**	X				X
Datengewinnung	**X**	X	X	X	X	X
Datenauswertung und Interpretation	**X**	X	X	X	X	
Schreiben	**X**	X		X	X	
Publikationsäquivalent	**1,0**	n. a.	n. a.	n. a.	n. a.	n. a.

HOW TO DISCRIMINATE ATHALASSIC AND MARGINAL MARINE MICROFAUNAS? FORAMINIFERA AND OTHER FOSSILS FROM AN EARLY HOLOCENE CONTINENTAL LAKE IN NORTHERN SAUDI ARABIA

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ABSTRACT

Athalassic foraminifers, the brackish water ostracod *Cyprideis torosa*, the barnacle *Balanus amphitrite* and brackish water gastropods prove the existence of a saline lake at Tayma, northern Saudi Arabia, during the early to mid-Holocene. Four foraminifer species were identified: *Ammonia tepida* is dominating, *Quinqueloculina seminula* is common, *Flintinoides labiosa* and *Trichohyalus aguayoi* are rare. Sieve-pore analysis and shell chemistry of *C. torosa* as well as varying but increasing proportions of test malformations in foraminifers reaching up to 50% indicate fluctuating, mostly hypersaline lacustrine conditions. Based on these results and on a literature overview on the worldwide distribution of Quaternary athalassic foraminifer taxa, we suggest that a combination of low diversity, exclusively marginal marine taxa, and, significantly, test malformation of >10 % when compared to natural marginal marine sites, or >30 % in the case of heavily polluted sites may be used for the identification of athalassic saline waters in the fossil record.

I INTRODUCTION

Foraminifera are a widely distributed and abundant microfossil group of marine origin and a classical tool of micropalaeontology. Reports on athalassic (i.e. saline water bodies without connection to the sea) Foraminifera are relatively rare. They have mainly been described from Recent, landlocked environments of elevated (brackish to hyperhaline) salinities (Almogi-Labin and others, 1992, 1995; Abu-Zied and others, 2007) and their occurrence in such environments is often regarded as a curiosity. At a number of sites they indicate environmental changes bound to salinity oscillations during the late Quaternary (Keatings and others, 2007; Wennrich and others, 2007; Gennari and others, 2011). If Foraminifera are found in athalassic sediments, connections of these locations to marginal marine habitats, reworking of older sediments, or transport by migrating birds are frequently discussed (Cann and De Deckker, 1981; Perthuisot, 1995; Wennrich and others, 2007). Hence, the question arises how to discriminate between marginal marine and athalassic foraminifer associations in fossil record.

Geoarchaeological investigations in a sabkha at Tayma, about 300 km away from the coast and 800 m a.s.l. (above mean sea level), provide evidence for foraminifers dwelling in an early Holocene salt lake; an athalassic setting never connected to the sea during the Neogene (Engel and others, 2012). Here, we intend to find generally applicable features proving an athalassic habitat by site analysis and comparison with literature from other localities. A further goal of this paper is to document the foraminifer and ostracod inventory of palaeolake sediments inside and along the margin of the continental sabkha near Tayma, as references from comparable palaeo-environments are rare. We examine if athalassic Foraminifera associations may be used for inferring salinity changes. In addition, sieve-pore investigation and the shell chemistry of *Cyprideis torosa*, a brackish water ostracod, are used for a salinity reconstruction of the lake. The results from this study are essential for ongoing high-resolution palaeoecological and palaeoclimatological of the studied palaeolake and other sites in northern Arabia.

II ATHALASSIC FORAMINIFERA

In contrast to their marine relatives, foraminifers of athalassic sites occur in a very low diversity (Table 1). The species encountered are usually found in the intertidal zone of marine coasts and are therefore well adapted to strong environmental changes (salinity, temperature). Unlike in a marine environment, athalassic foraminifers seem to develop a much higher percentage of test malformation directly correlated with increasing salinity (Almogi-Labin and others, 1992, 1995). Some faunal associations can indicate both hypo- and hypersaline waters but are different from normal marine associations.

Endemism of athalassic foraminifers has not been observed so far. This is probably due to the ephemeral nature of those habitats and the strongly oscillating salinity on geological time scales, disallowing evolutionary processes to produce new species. A frequent input of microorganisms in lakes by avian transport based on their function as resting places is probable (Perthuisot, 1995; Pint and others, 2012).

Table 1: Frequent Foraminifera species from selected athalassic sites.;**X** = living specimens; x = only preserved as fossils; ni = not indicated.

Region	North America		Australia	Northern Africa			Near East		Arabian Peninsula		Ponto Caspian			Central Europe	
Site	Salt Lake, Hawai (Resig, 1974)	Lake Winnipegosis, Canada (Boudreau and others, 2001)	Saline lakes, South Australia (Cann and De Deckker, 1981)	Great Western Erg, Algeria (Fontes and others, 1985)	Lake Quarun, Egypt (Abu-Zied and others, 2007)	Great Western Erg, Algeria) Gasse and others, 1987)	Dead Sea area, Israel (Almogi-Labin and others, 1992, 1995), Dead Sea	Timsah springs, Israel (Flako-Zaritzky and others, 2011)	Tayma, Saudi-Arabia (Engel and others, 2012)	Mundafan, Southern Saudi-Arabia (Rosenberg and others, 2011)	Aral Sea (Riedel and others, 2011)	Lake Chokrak, Sea of Azov (Boudreau and others, 2001)	Caspian Sea (Yanko and others, 1990)	Central Germany (Bartenstein, 1938)	Salziger See and Süsser See, Saxony-Anhalt (Wennrich and others, 2007)
Salinity (psu)	3,8	brackish	24	brackish to hypersaline	22	30 - 40	40-56	3	brackish to hypersaline	fresh to brackish	10	13	11 - 13	1	5
Rate of malformations [%]	3	ni	ni	ni	ni	ni	44	14	50	ni	40	ni	ni	ni	ni
Ammonia aberdoveyensis															x
*Ammonia beccarii**			**X**										**X**		
*Ammonia caspica**													**X**		
Ammonia tepida	**X**		**X**	x	**X**	x	**X**	**X**	x		x	x			**X**
Cribroelphidium gunteri		**X**													
*Elphidiella brotzkajae***											x				
Flintinoides labiosa									x						
Haplophragmoides wilberti	**X**														
Haplophragmoides sp.														x	
Helenina anderseni										x					
Mayarella brotzkajae													**X**		
Quinqueloculina seminula					**x**				x			x			
Trichohyalus aguayoi	**X**			x		x			x	x					
Trochammina inflata	**X**							**X**				x			

*Probably synonymous with *Ammonia tepida.* **Probably synonymous with *Mayarella brotzkajae.*

III THE PHYSICAL SETTING

One sediment core from the central basin as well as several outcrop sections along the margin of the continental sabkha of Tayma were investigated. Continental sabkhas – saline flats developed in endorheic intramontane basins – are common geomorphological features of Arabia's interior and to some extent correspond to playas of the North American southwest. Unlike the better studied coastal sabkhas, which are fed by sea water, continental sabkhas are characterized by evaporite minerals precipitating in the capillary zone above the shallow groundwater table (Briere, 2000; Ginau and others, 2012). Predecessor studies provided evidence for the existence of an early to mid-Holocene palaeolake inside the present sabkha basin (Wellbrock and others, 2011; Engel and others, 2012; Dinies and others, 2015).

The sabkha has formed in Palaeozoic sedimentary rocks overlying the Precambrian Arabian shield (Vaslet and others, 1994). The area's depositional history is dominated by tectonic stability, though interrupted by epirogenetic movements of the underlying craton resulting in several major unconformities. Erosion is the dominating factor in the study area, driven by Mesozoic and Cenozoic uplift (Vincent, 2008).

Tayma is hyperarid and receives an average of 45 mm annual rainfall, which mostly occurs between November and April. Daytime temperatures fluctuate around 10 °C in winter and may rise above 40 °C during summer. The vegetation, including perennial shrubs and annual grasses, is generally very sparse. The hydrographic pattern of the area south of Tayma comprises wadis directed towards the sabkha (Vaslet and others, 1994).

IV MATERIAL AND METHODS

IV.1 SAMPLING

Shoreline deposits of the early Holocene palaeolake are presented from two sites along the north-eastern (Tay 11/177; thickness: 2.40 m) and the south-western (Tay 180; thickness: 1.30 m) margin of the sabkha, respectively. Both were accessed by trenching. Furthermore, a percussion core (Tay 75) of 6.55 m length was extracted in the north-eastern part of the sabkha using an Atlas Copco, type Cobra mk1 fitted with closed PVC tubes (diameter: 5 cm) (Fig. 1). The two profiles and the coring site were levelled by DGPS. The sampling resolution for the entire study is 10 cm.

IV.2 RADIOCARBON DATING

Ostracods and gastropod shells were used for ^{14}C-AMS dating at the Leibniz-Laboratory for Radiometric Dating and Isotope Research, Christian-Albrechts-University of Kiel, Germany (KIA), 14CHRONO Centre for Climate, the Environment, and Chronology, Queen's University of Belfast, Northern Ireland (UBA), and the Center for Applied Isotope Studies, University of Athens, Georgia, USA (UGAMS). Samples were pre-treated with diluted HCl to eliminate surficial contaminants and with H_3PO_4 in a vacuum to recover CO_2, which subsequently was cryogenically purified and catalytically converted to graphite, before $^{14}C/^{13}C$ ratios were measured by AMS. ^{14}C ages were calibrated using Calib 6.0.1 software (Reimer and others, 2009).

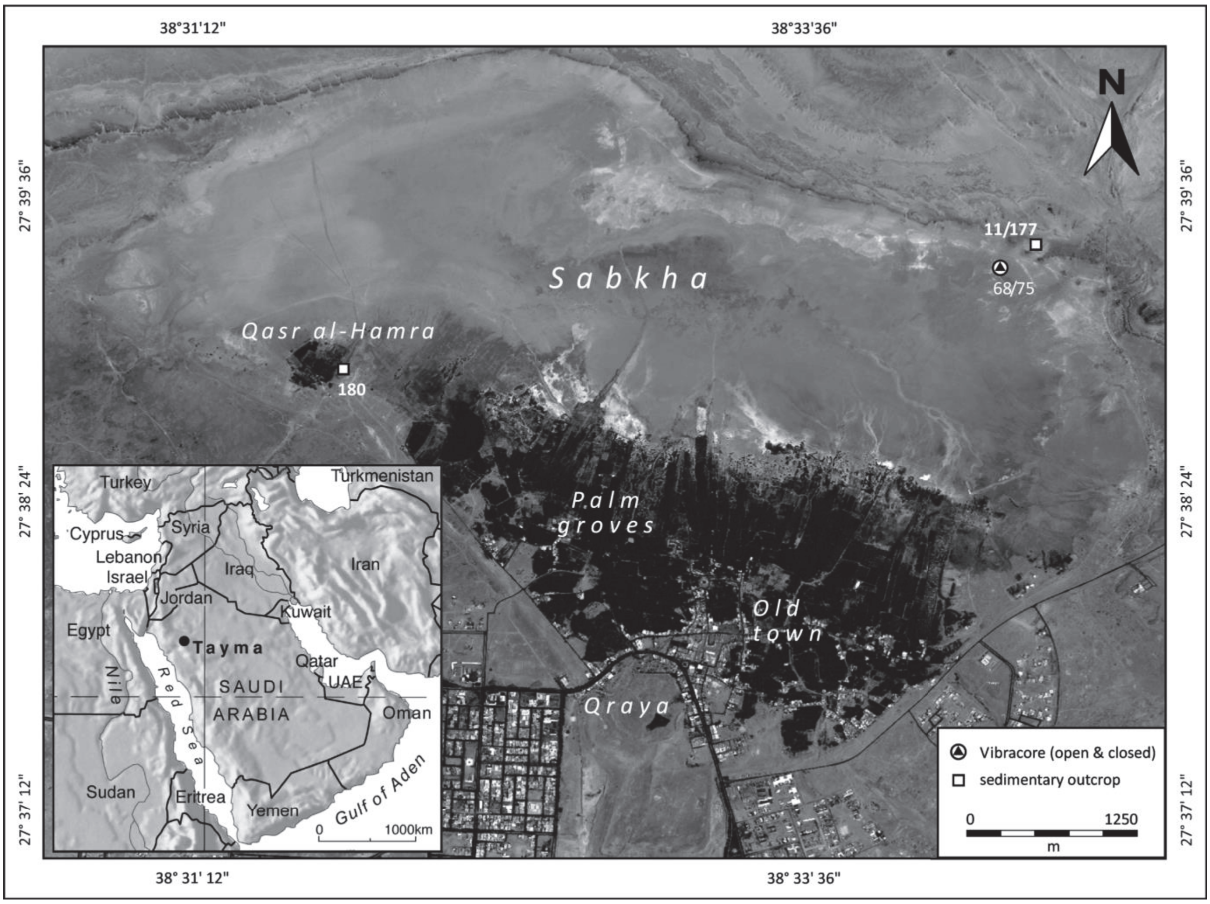

Fig. 1: The Tayma oasis based on Google Earth imagery displaying the sites sampled for this study as well as the location of previously taken mastercore Tay 34 (Engel and others, 2012). The location of Tayma on the Arabian Peninsula is shown in the overview map (Mountain High Maps ®, Digital Wisdom Inc., 1993).

IV.2 MICROFOSSIL SAMPLE PREPARATION

Fractions >0.063 mm and >0.100 mm were isolated through wet-sieving and micro- and macrofossils were picked and documented at the Physical Geography Laboratory, University of Cologne. Up to 300 individuals of foraminifers were counted in the outcrop samples (average dry weight: 25 g), and up to 30 individuals of the dominating ostracod *Cyprideis torosa* were analysed for sieve-pore shapes. Samples of the core Tay 75 (average wet weight 23 g) were completely checked for microfossils.

IV.3 MALFORMATION OF FORAMINIFER TESTS

After species identification, malformation of all foraminifer tests was quantitatively recorded. In this study, three types of test malformation are distinguished for a total of 65 samples:

1. Deformation of a single chamber, e.g. dwarf chamber or over-sized chambers.

2. Irregular whorl growth.

3. Multiple test development, e.g. twins.

IV.4 SIEVE-PORE ANALYSIS OF VALVES OF *CYPRIDEIS TOROSA*

Following the method described by Rosenfeld and Vesper (1977), the percentage of rounded sieve-pores per valve was identified for *Cyprideis torosa* in order to reconstruct salinity changes. Sieve pores of 10–15 valves per sample were investigated under a light microscope at 400x magnification. Shapes of at least 30 rounded and non-rounded sieve-pores were distinguished per valve.

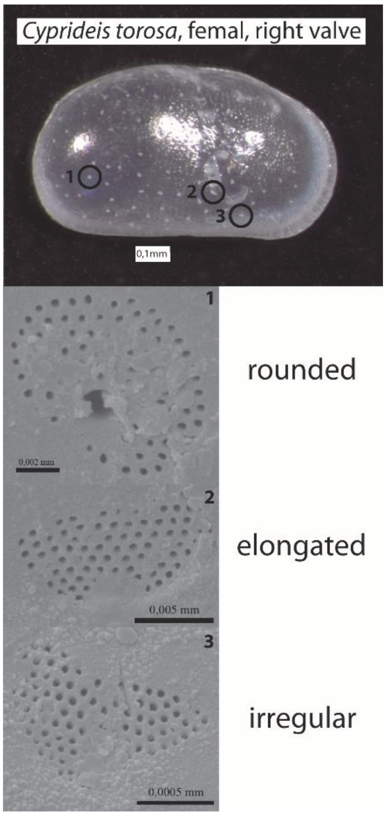

Fig. 2: Three types of sieve-pore shape: 1: rounded, 2: elongated and 3: irregular. Only the percentage of the rounded sieve-pores is used to estimate the salinity.

IV.5 SHELL CHEMISTRY

Isotopic and trace element analyses were carried out on ostracod valves from each sample of Tay 177 and 180 as well as from 23 samples of core Tay 75. The ostracod valves were analysed for $\delta^{13}C$ and $\delta^{18}O$ using a Finnigan MAT253 mass spectrometer connected to an automated carbonate-reaction device (KIEL IV) in the laboratory of Section 5.2 at the GeoForschungsZentrum Potsdam (GFZ). Samples of around 10 to 80 µg (2–5 valves) were automatically dissolved with 103% H_3PO_4 at 72°C and the isotopic composition was measured on the released and cryogenically purified CO_2. The isotopic composition is given in the delta notation relative to VPDB (Vienna Peedee Belemnite). Replicate analysis of reference material (NBS19) reported relative to VPDB yielded standard errors of 0.04‰ for $\delta^{13}C$ and 0.06 ‰ $\delta^{18}O$. Isotopes $\delta^{18}O$, $\delta^{13}C$ as well as trace elements were derived from ostracods of the same samples. For trace elements analysis an ICP-OES Varian 725ES was used after the samples had been prepared through microwave digestion.

V RESULTS

V.1 CHRONOLOGY

Calibrated ^{14}C ages from the lake-shore deposits (Tay 11/177, Tay 180) lie between 10,200 and 9000 cal BP and show no inversions. At Tay 11/177, the lowermost and uppermost sections were each dated twice: in the lower part differences are marginal (10235–9923 and 9887–9562 cal BP), whereas at the top of the profile, the error bars of both samples overlap (9401–9091 and 9251–8992 cal BP) (Engel and others, 2012). ^{14}C data from Tay 11/177 point to an accumulation rate of shell material along the palaeolake margins of at least 0.25–0.5 cm a^{-1} during the early Holocene. The top of profile Tay 180 is located c. 5 m below the one of Tay 11/177. A slightly lower sedimentation rate (0.1–0.3 cm a^{-1}) has been inferred, and the age estimates range from 10,158–9739 to 9452–9141 cal BP. The two ^{14}C ages from core Tay 75 range from 9265–9032 cal BP at a depth of 130 cm and 9477–9306 cal BP at a depth of 380–374 cm and either point to a high sedimentation rate in this part of the section or that the upper sample contains older, reworked material. The data derived from calcareous skeletons (Table 2) imply systematic age overestimation of c. 1500 years due to the hard-water effect when compared to recently presented isostratigraphic, pollen-derived data of Dinies and others (2015).

V.2 STRATIGRAPHIC DESCRIPTION

Tay 11/177 represents a laminated deposit almost entirely consisting of bioclastic remains accumulated along the shores of a large palaeolake (Fig. 3). It is preserved in the incised part of the lowermost escarpment of Ordovician shale framing the sabkha in the north. The upper limit of trench Tay 177 is situated c. 11 m above the present sabkha floor (811.5 m a.s.l. [above present sea level]). Further north on the bedrock terrace, the uppermost appearance of the deposit is at 813.8 m a.s.l. The main components are gastropod (*Melanoides tuberculata*, *Hydrobia* sp.) and *Balanus amphitrite* shells, as well as microfossils. Quartz sand is present only as a minor component. *In-situ* formation of the deposit is indicated by *Balanus amphitrite* skeletons in living position directly attached to the Ordovician bedrock (Fig. 4) (Engel and others, 2012).

Table 2: Details of the radiocarbon data used in this study. Calibration was carried out using Calib 6.0.1 software (Reimer and others, 2009). A systematic hard water effect of c. 1500 years (cf. Dinies and others, 2015) must be considered. KIA = Leibniz-Laboratory for Radiometric Dating and Isotope Research, Christian-Albrechts-University of Kiel, Germany; UBA = 14CHRONO Centre for Climate, the Environment, and Chronology, Queen's University of Belfast, Northern Ireland; UGAMS = Center for Applied Isotope Studies, University of Athens, Georgia, USA; *previously published in Engel and others (2012).

Sample	Lab ID	Depth (cm b.s.)	Material	δ^{13} (‰)	^{14}C age years BP	Age (cal BP, 2σ)
Tay 11/6*	KIA34032	10–5	Gastropod shells	5.78±0.1	8125 ± 45	9251–8992
Tay 11/2*	KIA34027	210–205	Gastropod shells	0.53±0.2	8980 ± 45	10235–9923
Tay 177/21*	UGAMS7583	5	Ostracods	-4.2	8250 ± 35	9401–9091
Tay 177/10*	UGAMS7582	120	Ostracods	-3.8	8530 ± 30	9542–9486
Tay 177/1*	UGAMS7581	205	Ostracods	-4.1	8470 ± 30	9887–9562
Tay 180/2	UBA-23785	20	Ostracods	No data	8248 ± 37	7425–7141
Tay 180/13	UBA-23786	130	Ostracods	No data	8813 ± 37	8187–7739
Tay 75/	UGAMS11620	130	Ostracods	-14.5	8200 ± 25	9265–9032
Tay 75	UGAMS11621	380–374	Ostracods	-15.8	8380 ± 25	9477–9306

Deposit Tay 180 (Fig. 5) at the south-western margin of the sabkha is very similar to Tay 11/177. It is attached to the sandstone ridge extending into the sabkha basin. The deposit has a thickness of c. 1.3 m and the layers dip towards the centre of the sabkha. Its upper limit was measured to be c. 806 m a.s.l. (Engel and others, 2012).

Sediment core Tay 75 (Fig. 6) was drilled on the north-eastern margin of the sabkha. The 6.55 m-long core is characterized by alternating strata of greenish and greyish sand and silt and brown clay layers. First fossils occur at a depth of 4.60–4.30 m b.s. (below surface). Above 4.00 m b.s. fossils occur continuously.

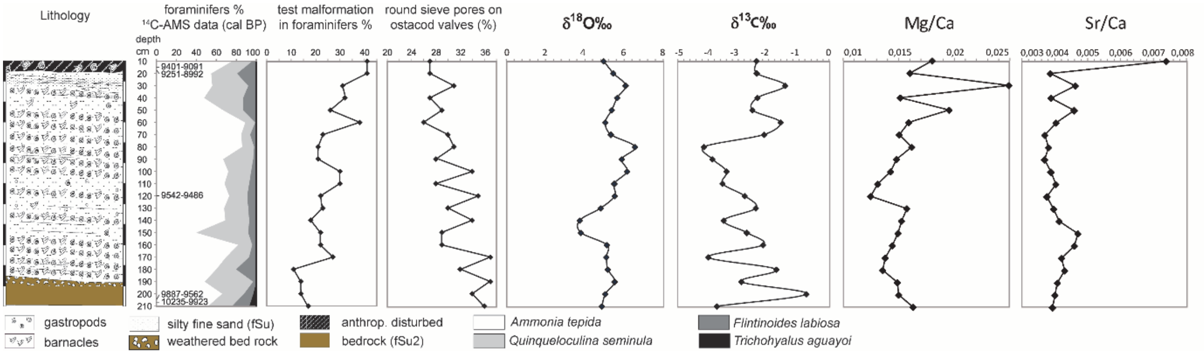

Fig. 3: Bioclastic deposit at Tay 11/177 preserved in an incised section of the lowermost escarpment at the northeastern sabkha margin (compare Fig. 1). Its surface is located at an elevation of 811.5 m a.s.l. and it has a vertical extension of up to 240 cm. Percentages of foraminiferal taxa, test malformations as well as round sieve pores on ostracod valves are shown, besides stable isotopes and ratios of trace elements.

Fig. 4: *Balanus amphitrite* in living position directly attached to the bedrock indicates autochthonous deposition at Tay 11/177 in a lakeshore environment.

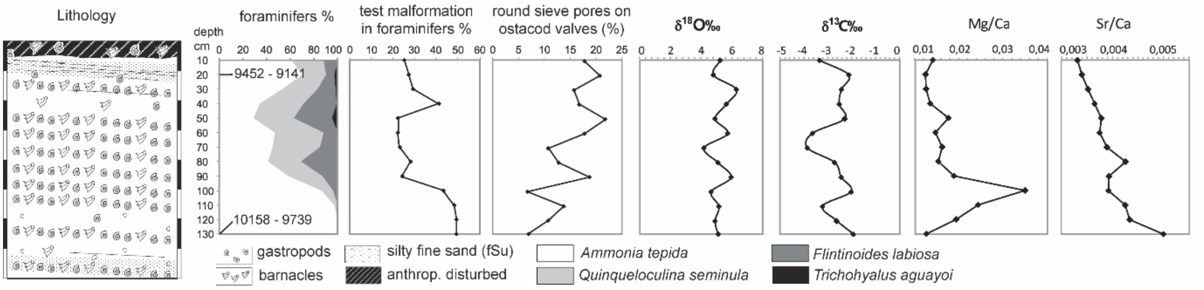

Fig. 5: Bioclastic sediment deposit at Tay 180 attached to the sandstone ridge of Qasr al-Hamra (compare Fig. 1). Its surface is located at an elevation of 806 m a.s.l. and it has a thickness of 130 cm. Percentages of foraminiferal taxa, test malformations as well as round sieve pores on ostracod valves are presented, besides stable isotopes and ratios of trace elements.

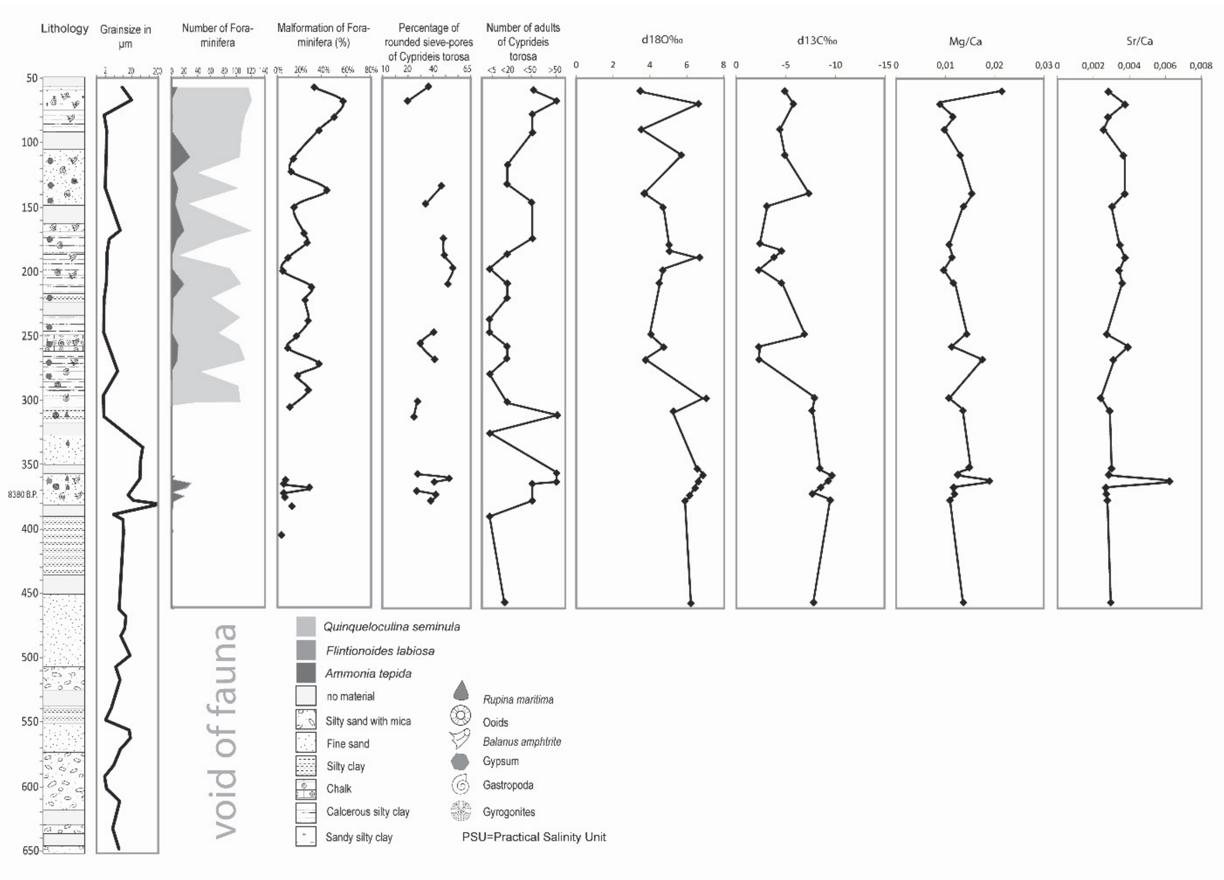

Fig 6: Core Tay 75 taken in the north-eastern part of the sabkha. Distribution of micro- and macrofossils, test malformations and sieve-pore analysis of ostracod valves are shown. Stable isotopes as well as ratios of trace elements are plotted as well.

V.3 MICROFAUNA AT TAYMA

V.3.1 Foraminifera

Four species of foraminifers were identified in the samples from Tayma. The most common species is *Ammonia tepida* with a total percentage of 75%. *Quinqueloculina seminula* is also common with a percentage of 18%. *Flintinoides labiosa* occurs with 6%, whereas *Trichohyalus aguayoi* is the rarest species (0.5%) (Fig. 7). The percentage distributions for the core and the outcrops are presented in Figs. 3, 5 and 6. In Tay 11/177 the distribution of foraminifers varies moderately across the section. Remarkable is a very strong dominance of *Ammonia tepida* at 0.80–0.60 m b.s.. The highest percentage of *Quinqueloculina seminula* with about 50% is at 1.50 m b.s.. *Trichohyalus aguayoi* mainly occurs in the lowermost part of the section, up to 1.95 m b.s.

In Tay 180 the associations of the lowermost 10 cm are completely composed of *Ammonia tepida*. The other species increase continuously up to 0.80 m b.s.. The highest percentage of *Quinqueloculina seminula* (about 40%) is at 0.60 cm b.s.. *Trichohyalus aguayoi* occurs exclusively between 0.50–0.20 m b.s.

With the exception of a minor occurrence of at 4.30–4.60 m b.s., only the four uppermost metres of Tay 75 contain foraminifers. The number of individuals and the species distribution vary strongly, whereas *Trichohyalus aguayoi* is completely absent.

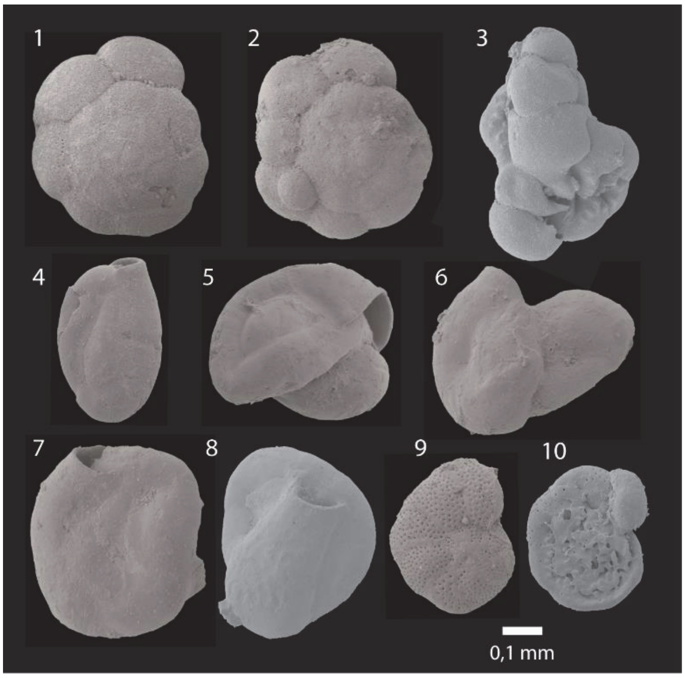

Fig. 7: Foraminifera from Tayma, white scale: 0.1 mm. 1: *Ammonia tepida*, normal test, spiral view. 2*: A. tepida*, chamber deformation, spiral view. 3: *A. tepida*, multiple test. 4: *Quinqueloculina seminula*, normal test. 5: *Q. seminula*, changes of growth direction. 6: *Q. seminula*, multiple test. 7: *Flintinoides labiosa*, normal test. 8: *F. labiosa*, changes of growth direction. 9: *Trichohyalus aguayoy*, normal test, spiral view. 10: *T. aguayoy*, normal test, umbilical view.

Taxonomy

Quinqueloculina seminula (Linné, 1758) = *Serpula seminulum* Linné, 1758 (listed as *Quinqueloculina* spp. in Engel and others, 2012)

Appearance at sites: Tay 177: 25%, Tay 180: 23% and Tay 75: 9%.

Flintinoides labiosa (d´Orbigny, 1839) = *Triloculina labiosa* d'Orbigny, 1839 (listed as *Milionella* spp. in Engel and others, 2012)

Appearance at sites: Tay 177: 8%, Tay 180: 13% and Tay 75: 0.4%.

Trichohyalus aguayoi (Bermudez, 1935) = *Discorbis aguayoi* Bermudez, 1935 (listed as *Rosalina* sp. in Engel and others, 2012)

Appearance at sites: Tay 177: 1%, Tay 180: 1% and Tay 75: missing.

Ammonia tepida (Cushman, 1926) = *Rotalia beccarii* var. *tepida* Cushman, 1926

Appearance at sites: Tay 177: 67%, Tay 180: 63% and Tay 75: 91%.

Test malformation

The total percentage of foraminiferal malformations of all sites is 28% on average. In the outcrops Tay 11/177 and 180, deformed chambers make up the major part of malformations, followed by irregular whorl growth and multiple tests, whereas the highest proportion of malformation of core Tay 75 is represented by irregular whorl growth, followed by deformed chambers and multiple tests (Table 3).

Table 3: Percentages of the minimum and maximum malformation proportions, averages and types of malformation, and the trends throughout the sections from base to top.

Site	Min/max malformation	Average malformation	Deformed Chamber	Irregular whorl growth	Multiple Test	Percentage of *Ammonia tepida* malformations	Malformation trend to the top
Tay 11/177	11–41%	25%	17.9%	7.8%	0.3%	67%	increasing
Tay 180	22–49%	33%	24.8%	8%	0.2%	78%	decreasing
Tay 75	0–57%	27%	6%	17%	4%	98%	slightly increasing

V.3.2 Ostracoda

The only identified ostracod species in both the outcrops and the core is *Cyprideis torosa* (Jones, 1850). Of the two varieties of *C. torosa*, a smooth and a noded form, the Tayma material yields only the smooth form *Cyprideis torosa* f. *littoralis*. In the outcrops, abundances of *C. torosa* are very high, whereas it is much lower in the core. The preservation of the valves is very good in the outcrops except for the uppermost 20 cm where the valves are mostly re-calcified. In the core, preservation is moderate to poor; most of the valves are re-calcified. Due to the good preservation in the outcrops, sieve-pore analysis of the valves was carried out without problems. In the core, sieve pore analysis was much more difficult.

Sieve-pore analysis

The percentages of round sieve-pores of *Cyprideis torosa* in Tay 177 show a relatively low standard deviation and range from 26–37%, with a decreasing trend towards the top (Fig.3). Values are generally lower at Tay 180 (7–22%) with stronger variation and also a decreasing trend towards the top (Fig 5), whereas the highest values and variation are reached in sediment core Tay 75 (18–60%). In the core values increase slightly towards the mid of the section and then decrease towards the top (Fig 6).

V.4 Macrofauna at Tayma

The deposits of Tay 177 and Tay 180 are mainly composed of shells of the gastropods *Melanoides tuberculata* and *Hydrobia* sp. and fragments of the barnacle *Balanus amphitrite* (Crustacea) (Fig. 7). All taxa are highly abundant throughout the profiles, therefore no quantification was performed. However, in the cores, macrofaunal remains are very rare; large fragments of *B. amphitrite* are entirely absent.

V.5 Isotope data

Isotope ratios of *Cyprideis torosa* valves in both outcrops range between -10 and 0‰ for δ^{13}C and +4 and +7‰ for δ^{18}O. While the valves from the outcrops are well preserved, except for the upper 20 cm, those from the cores are mostly re-calcified, what, however, does not affect the stable isotope composition. The ostracod valves of core Tay 75 show a similar range in δ^{18}O values from +4.5 to about +7‰, but significantly lower δ^{13}C values down to -10‰ (Fig. 8).

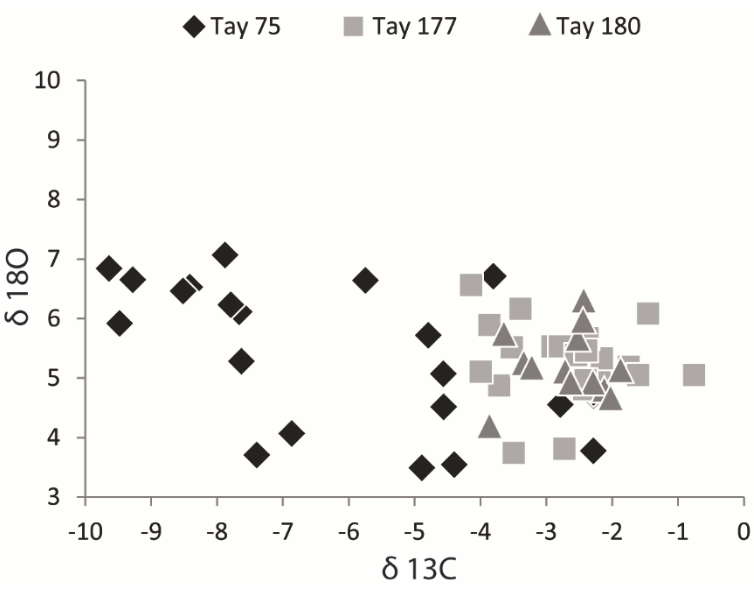

Fig. 8: Cross-plot of δ^{18}O and δ^{13}C of all samples

VI DISCUSSION

VI.1 ECOLOGY AND DISTRIBUTION OF SPECIES FOUND AT TAYMA

We discuss ecological preferences of foraminifer species found at Tayma and their occurrence in other athalassic waters in the following.

When found inland, foraminifers live exclusively in permanent water bodies, but prefer different salinities. (Resig, 1974; Almogi-Labin and others, 1992, 1995; Wennrich and others, 2007; Riedel and others, 2011).

Ammonia tepida occurs in both hypersaline environments like the Dead Sea (Israel) and waters connected to it (Almogi-Labin others, 1992, 1995) and hyposaline water bodies like the Timsah spring (Israel) (Flako-Zaritsky, 2006). According to Bradshaw (1957, 1961), the ideal salinities for reproduction of *A. tepida* range from 13–40 psu. The monospecific, recent assemblage of *A. tepida* in the Dead Sea produces an average malformation rate of 17% linked to hypersaline conditions of 39.7 to 54.5 psu (Almogi-Labin and others, 1992).

Quinqueloculina seminula: So far, the occurrence of *Q. seminula* in inland water bodies is very rare and poorly reported. In Lake Quarun (Fayum depression, Egypt), it is the most frequent species and its abundance seems to be positively correlated with salinity (Abu-Zied and others, 2007).

Flintinoides labiosa: *F. labiosa* is here described from an athalassic site for the first time. The genus, however, has already been described from Lake Quarun (*Miliolinella* in Abu-Zied and others, 2007).

Trichohyalus aguayoi: The species tolerates a broad range of salinities. However, occurrences in hypersaline marginal marine lagoons are rare. It has mainly been described from intertidal habitats such as the brackish to freshwater estuaries or mangrove swamps of the Bermudas (Javaux and Scott, 2003) or coastal waters of the Caspian Sea (Yanko-Hombach, 2007). Greater numbers were found in Holocene lake sediments near Al-Mundafan in the Rub' al Khali (Gennari and others, 2011). In early to mid-Holocene lakes of the Sahara, *T. aguayoi* occurred together with *Ammonia tepida* (Gasse and others, 1987)

VI.2 TEST MALFORMATION

Foraminifers in inland water bodies indicate both a perennial lake regime and elevated salinity. Desiccation would wipe out a foraminifer population. The exclusively intertidal origin of documented athalassic foraminifer associations is a differentiating feature when compared to marginal marine habitats where moderate amounts of open marine taxa are normally included as well. Variable salinity and a high concentration of sulphates presumably play a significant role for the composition of assemblages (De Deckker, 1981). In general, foraminiferal diversity is very low in athalassic settings (table 1). But there are exceptions: Resig (1974) found 41 species of foraminifers in an oligohaline brackish lake on Hawai'i. In the Timsah Ponds (Israel), 18 species were detected in an oligohaline (3–4 psu) environment (Flako-Zaritzky, 2006). Both water bodies are situated close to the coast enabling an easy colonisation of the athalassic waters from marginal marine habitats through animals or even with propagules coming in with sea spray. Considering the extremely low numbers of just four species at Tayma in this study, or two at Al-Mundafan (Gennari and others, 2011), it is underlined that diversity is not only a function of ecologic fluctuations or extreme conditions within a habitat, but also of distance to marine environments and ways of transport species can be introduced. For the case of bird-mediated transport, the main migratory routes may play an important role as well. Lake Quarun inside the Faiyum Depression (Egypt) is exceptional in this regard, hosting the remarkable number of nineteen species despite a distance of 350 km to the Mediterranean coast. The lake turned from freshwater to saline conditions after 2300 yr BP and is clearly dominated by *Ammonia tepida* and *Quinqueloculina seminula*. The reason for the high diversity is unclear (Abu-Zied and others, 2007), but could be explained by its relatively large size and therefore more stable water conditions and a regular introduction of Foraminifera through migratory birds due to its location close to the river Nile.

Table 4: Examples of malformation rates in athalassic and marginal marine environments

	Site	**Number of species**	**Maximal percentage of test malformations**	**Discussed reasons**	**Author**
Athalassic sites	Saudi-Arabia, Tayma	4	50	Hypersalinity	This study
	Israel, Dead Sea area, Inland pool	1	44	Hypersalinity	Almogi-Labin et al., 1992
	Central Asia, Aral Sea	5	40	Variation of salinity	Pint et al., 2012
	Central Germany, Siebleber Senke	1	36		
	Central Germany, Süßer See, Salziger See	2	16	Variation of salinity	Wennrich et al., 2007
Marginal marine	southern Baltic Sea, Kiel Fjord	9	25	Heavy metal pollution and variation of salinity	Polovodova and Schönfeld, 2008
	southern Baltic Sea, Flensburg Fjord	8	19		
	Brasilia, Rio Guarau	74	10	Variation of salinity	Geslin et al., 2002
	Norway, Sørfjord	15	3	Heavy metal pollution	Alve, 1991

Another important indicator to identify athalassic foraminifer associations seems to be the proportion of malformed tests, which is much higher than in marine sites, particularly in hypersaline settings. Test malformations in foraminifers have been recognised for quite a long time. Reasons include naturally induced and anthropogenic environmental changes or infections. While under optimised laboratory conditions or in stable marine habitats usually less than 1% of foraminifer tests are malformed (Stouff and others, 1999; Geslin and others, 2000; Polovodova and Schönfeld, 2008), the rate of malformations may reach about 10% in coastal environments, 25% in estuaries (Polovodova and Schönfeld, 2008), and up to 50% in other less favourable natural habitats (Table 4). Some of the most important natural factors causing test malformation are strongly fluctuating salinity values or those that are close to the tolerance limits of a species (Pint and others, 2012), even though heavy metal pollution may play a significant role as well (Polovodova and Schönfeld, 2008).

Remarkably, inland water bodies show the highest rates of malformation (Almogi-Labin and others, 1992; Pint and others, 2012), supposedly due to a lack of competition with other marginal marine foraminifers providing an opportunity for not well adapted and deformed individuals to survive (Table 4). Therefore, in the case of Tayma, we assume high salinity as a main controlling factor for test deformations. Strong seasonal fluctuations of salinity have to be assumed as well, which is also indicated by seasonal lamination of stellar aragonite (excess evaporation and concentration of solutes during dry season) and siliciclastic graded layers (sediment input after wadi activation and deposition out of suspension during the wet season) (Ginau and others, 2012). Furthermore, salinity reconstruction from the sections at Tayma suggests correlation of test malformation and salinity under hypersaline conditions. At Tayma, the most frequent types of test malformation are single chamber deformations followed by irregular whorl growth and multiple tests. Similar percentages were also observed at other sites, e.g. the Aral Sea (Kazakhstan; Pint and others, 2012) and the fjords of Kiel and Flensburg (Northern Germany; Polovodova and Schönfeld, 2008). However, in the core sequence of Tay 75, irregular whorl growth represents the most frequent type of malformation. This difference may be explained by lower selection pressure for regular formed tests in the calm deeper water than in the turbulent water close to the shore or, alternatively, by higher salinities in deeper water through thermohaline stratification of the water body causing oxygen depletion and increased salinity values.

VI.3 THE OSTRACOD SPECIES *CYPRIDEIS TOROSA*

The widespread and ecologically opportunistic taxon of *Cyprideis torosa* occurs in both marginal marine environments and inland water bodies with slightly brackish up to hypersaline conditions. It tolerates a wide range of salinity, temperature, and oxygen conditions. As in Tayma, it often occurs monospecifically, mainly in salt lakes with hypersaline conditions or in coastal lagoons after they became separated from the sea (Frenzel, 1991; Gasse and others 1987; Keatings and others, 2007; Marco-Barba and others, 2013). It provides further evidence for a saline inland water body. In continental waters *C. torosa* often occurs together with foraminifers of intertidal origin (Pint and others, 2012). Whereas macro- and microfossils appear in a very high abundance in the shoreline outcrops of Tayma, the concentration of microfossils in the core within the central sabkha area is very low. This may be due to a high sedimentation rate and oxygen deficiency in deeper water caused by thermohaline stratification of the water body, which had a maximum depth of >13 m during its early to mid-Holocene highstand (Engel and others, 2012). Additionally, growth of gypsum may have destroyed microfossils in these sediments. *Cyprideis torosa* also prefers very shallow water and, therefore, is mostly living close to the shoreline (Meisch, 2000; Pint and others, 2012).

Based on the broad ecological tolerances and the often monospecific occurrence of *C. torosa* in fossil associations, it is difficult to reconstruct palaeoenvironmental changes from this taxon alone. To overcome this problem, the method of sieve-pore analysis has been developed by Rosenfeld and Vesper (1977). They recognized that sieve-pore shapes on valves of adult *C. torosa* vary due to different salinity conditions. The percentage of sieve-pores with a circular shape decreases with increasing salinity. However, the calculated salinity (transfer function: $S = e–^{0.06 \text{ RS} + 4.7}$; Pint and others 2012) must be critically reviewed. Sieve-pore analyses such as those on Recent assemblages from Lake Quarun showed significantly higher values than the measured salinity of the lake water (Keatings and others, 2007). A reason for those differences may be the water chemistry of athalassic water bodies being different from marginal marine brackish waters.

At Tayma, a strong variation of sieve-pore ratios is noticeable within the samples. This variability might be the result of significant short-term, probably seasonal, salinity changes due to periodical wadi activity and is enhanced by samples comprising approximately 5–10 or even more years each. Variability may be lower in the deeper waters of the central basin, especially during phases of thermohaline stratification with low circulation of the lake water.

VI.4 MACROFAUNA

The widespread and common gastropod genus *Hydrobia* is typically found in brackish waters. It tolerates changing salinities and even hypersaline conditions and, therefore, is a common companion of the brackish ostracod *Cyprideis torosa* and of athalassic foraminifers. As an opportunistic genus, *Hydrobia* also may tolerate ephemeral aquatic environments and wetlands (Kowalke, 1998).

Melanoides tuberculata is a cosmopolitan freshwater species widely distributed in fresh and brackish water bodies of the Middle East (Ismail and Arif, 1993). It is documented from the

Quaternary Mediterranean saline lakes of Orce/Spain, Ecker/Algeria, Lybia/Bucrat, Quarun/Egypt, Cape Greco/Cyprus Delos and Thessaloniki/Greece (Kowalke, 2006; Hassan and others, 2012), as well as the early to mid-Holocene lakes of the Sahara desert (Gasse and others, 1987). *Melanoides tuberculata* is often associated with the brackish water gastropod *Hydrobia*. However, in contrast to *Hydrobia*, it dwells only in permanent water bodies (Brown, 1980; van Damme, 1984).

The barnacle *Balanus amphitrite* is a very common marine crustacean species mostly preserved in fragments at Tayma, and inhabited the rocky shores of the palaeolake in the north and around Qasr al-Hamra. *Balanus amphitrite* lives in the intertidal zone of marine coasts; therefore it is well adapted to strong environmental changes. Introduced by birds, it is also able to survive in continental salt lakes like the Salton Sea in California (Detwiler and others, 2002) or Birket Gessabia in the Siwa Oasis (Por, 1972). It tolerates a wide range of salinity, as well as polluted and eutrophic environments (Detwiler et al 2002). Large populations of *B. amphitrite* in marginal or non-marine environments are characterised by warm water temperatures and salinities up to 40–45‰ (Por, 1972; Shalla and others, 1995).

VI.5 GEOCHEMISTRY

In Tay 177 the malformation in foraminifers and the percentage of round sieve pores of ostracod valves both reflect increasing salinity (Engel and others 2012). The change towards heavier $\delta^{13}C$ values and higher Mg/Ca and Sr/Ca ratios of ostracod valves in the upper part suggest higher evaporation and less freshwater input, thereby supporting the assumption of increasing salinity. The $\delta^{18}O$ values of ostracod valves, however, show fairly stable conditions with values around +5 ‰. This pattern may be explained by a relatively constant water level maintained predominantly by precipitation, ground water inflow and local water recycling during the highest lake level period (Fig. 3). From 3.00 to 0.50 m depth in core Tay 75, malformations in foraminifers as well as the $\delta^{18}O$ and Sr/Ca values of ostracod valves suggest increasing salinities to the top pointing to the shrinking trend of the lake in a more arid climate (Fig. 6)

In Tay 180, the malformation in foraminifers, the round sieve pore proportion and the Sr/Ca of ostracod valves reflect decreasing salinity (Engel and others 2012). The stable isotope values show relatively stable conditions with values around +5 ‰ for $\delta^{18}O$ and -3 ‰ for $\delta^{13}C$. This may indicate an increased freshwater input under high evaporation conditions having led to a rising lake level. Except the lowermost part of the section, Mg/Ca ratios decrease, thereby pointing to lower salinities as well (Fig. 5).

In general, the calcite of ostracods has been found growing in equilibrium with sea or lake water (e.g. von Grafenstein and others, 1999; Decrouy and Vennemann, 2013; Marco-Barba and others, 2013). However, especially for *Cyprideis torosa*, Marco-Barba and others (2013) observed that the chemical composition shows various disequilibrium effects at higher salinities or stressfull hydrochemical conditions. Calcitic shells of *C. torosa* from Valencia, Spain, for example, show increasing δ^{18}O-depletion relative to the thermodynamic isotopic equilibrium when the water temperature increases from about 10 to 30°C (Bodergat and others, 2014).

The ostracod valves from the outcrops (Tay 11/177) probably represent the onset of the lake stage. The salinity inferred from foraminiferal test malformations and rounded sieve pores on ostracod valves co-varies with the carbonate δ^{18}O values; higher salinity is reflected in high δ^{18}O values of up to +7‰. Higher δ^{18}O values (up to +10‰) found in an aragonite layer in the equivalent lake sediments of the deeper part can be explained by different seasonal conditions during formation. While ostracod valves grow during a prolonged period with probably higher freshwater input, the inorganic carbonate precipitates after CO_2 release due to biological activity or evaporative release during evaporation maxima. The much lower δ^{13}C values of the core compared to the outcrops can be explained by microbial activity in oxygen deficient deeper water during periods of thermohaline stratification of the Tayma palaeolake.

VI.6 RECONSTRUCTION OF THE LAKE HISTORY OF THE OASIS OF TAYMA

Due to the lack of evidence of an initial freshwater lake phase like a pond, a saline lake seems to have established in just a short time interval since c. 9200 BP (cf. age model in Dinies and others, 2015). For at least 1000 years a permanent lake existed with an average depth of at least 15 m, characterized by strongly varying salinity values driven by seasonal precipitation and wadi activities. The hypothesis of Enzel and others (2015) that the deposits presented here only refer to wetland conditions and that an ephemeral lake never established during the Holocene can therefore be refuted by multiple lines of evidence (Dinies and others 2015, Engel et al.2012). However, a further division into several lake phases is impossible due to very limited time constraints of the sediment core and stratigraphical outcrop investigated here. The final stage of the main permanent lake phase remains unclear, a shifting to more ephemeral conditions, however, is anticipated at around cal 4000 BP (Engel et al., 2012). Further detailed work on this topic is pending.

VII CONCLUSIONS

Four foraminiferal taxa (*Ammonia tepida, Quinqueloculina seminula, Flintinoides labiosa, Trichohyalus aguayoi*) and the ostracod *Cyprideis torosa* were identified in the palaeolake deposits filling the basin of the sabkha of Tayma, where they are poorly preserved, as well as in the isolated, bioclastic palaeo-shoreline deposits, where they occur massively and preservation is much better. The ecologically opportunistic lake fauna, including crustaceans (*Balanus* *amphitrite*) and gastropods (*Melanoides tuberculata*, *Hydrobia* sp.), exclusively originates from marine intertidal environments, and indicates variable salinity conditions and a perennial regime in the early Holocene lake. Salinity reconstructions based on ostracod sieve-pore shape distribution show extreme variations within a sample probably caused by strongly seasonal hydrological changes. Foraminiferal test malformations are higher than in any published marginal marine environments. In the early Holocene, a rapid establishment of the lake is inferred, while sediments of the pre-lake phase are lacking in the central part of the sabkha, probably due to deflation and extreme aridity.

In order to identify athalassic associations, we conclude that they exclusively consist of marginal marine taxa. Low species diversity and an exceptionally high percentage of foraminiferal test malformations are diagnostic features. Proportions of test malformations correlate with salinity in hypersaline waters and can be used as salinity proxy in this context as values from Tayma co-vary with those of round sieve-pores on ostracod valves. In general, the results of the isotopic and trace element analyses follow the trends of the palaeontological salinity proxies, although less accentuated.

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3.3.3 Weitere Fallbeispiele aus der Literatur

Tibetische Seen

Auf dem durchschnittlich 4500 m hoch gelegenen Tibetplateau herrscht arides Klima. Die Niederschlagsmenge nimmt von Südosten nach Nordwesten deutlich ab, was auf den unterschiedlichen Monsuneinfluss an den Rändern des Plateaus zurückzuführen ist (Bookhagen 2010). Der von Süden kommende Indische Monsun und der von Nordosten kommende Ostasiatische Monsun haben einen viel stärkeren Einfluss als der wesentlich schwächere Wintermonsun aus dem Westen. Endseen und einige der Durchflussseen haben eine Salinität im oligohalinen bis unteren mesohalinen Bereich, können aber auch deutlich darüber liegen (Yu et al. 2001, Yao et al. 2007). Starke Seespiegelschwankungen führten dazu, dass sich offene und geschlossene Systeme mehrfach abwechselten und Salinitätsschwankungen auslösten. In den Seen oberhalb von 4500 m kommen nur Ostrakoden in geringer Diversität vor, in den 3000 m hoch gelegenen Salzseen im Qinghai-Becken am Nordostrand des Plateaus ist die Diversität wesentlich höher und es kamen im Quartär auch Foraminiferen vor (Sun 1997, Mischke 2012). Der Endemismus ist in den hoch gelegenen Seen stark ausgeprägt, in geringerer Höhe geht er zurück. Die häufigste endemische Ostrakodenart des Tibetplateaus ist *Leucocytherella sinensis*, auch *Leucocythere dorsotuberosa*, *Fabaeformiscandona gyirongensis* und *Candona xizangensis* kommen nur hier vor. Die einzigen nicht endemischen Arten lakustriner Habitate sind *Limnocythere inopinata*, die in den Salzseen ausschließlich auftreten kann, und *Cytherissa lacustris*, die aber nur im Profundal von Süßwasserseen lebt (Frenzel 2015, persönl. Mitt.). In den Salzseen unter 4000 m Höhe kommt die salzzeigende Art *Eucypris mareotica* (=*Eucypris inflata*) häufig vor. Der Grund für den ausgeprägten Endemismus der tibetischen Ostrakodenarten ist in der räumlichen und klimatischen Isolation im jüngeren Känozoikum zu suchen. Athalassische Faunen in Hochgebirgsseen unterscheiden sich deutlich von Faunen athalassischer Flachlandgewässer. Dies ist auf die Hochgebirgslage, die nur von wenigen Ostrakodenarten toleriert wird, zurückzuführen. Für monospezifische Populationen ist im Flachland vor allem *Cyprideis torosa* typisch, im Hochland wird diese häufig von der temperaturtoleranten *Limnocythere inopinata* abgelöst.

Hypersaliner Pool im Riftsystem des Toten Meeres

Die Salinität des Pools beträgt 39,7 – 54,5 psu (Almogi-Labin et al. 1992, 1995). Nur eine Ostrakodenart (*Cyprideis torosa*) und eine Foraminiferenart (*Ammonia tepida*) kommen vor. Die Missbildungsrate von *A. tepida* beträgt bis zu 65 % und ist auf die erhöhte Salinität zurückzuführen. Das Vorkommen von sehr wenigen euryhalinen Ostrakoden- und Foraminiferarten ist typisch für hypersaline athalassische Gewässer.

Ehemalige Seen in der nördlichen Sahara

In der heutigen Sandwüste von Algerien zeugen Sedimente ehemaliger Seen von einem humiden Klima während der ersten Hälfte des Holozäns. Die vorkommenden Ostrakoden *Cyprideis torosa, Darwinula stevensoni, Candona neglecta*, *Cypridopsis* sp. *Limnocythere* sp. *Loxoconcha elliptica*, und *Fabaeformiscandona fabaeformis* zeigen brackische Bedingungen zu Beginn des Holozäns an (Fontes et al 1985). Bis ca. 6000 BP süßten die Gewässer deutlich aus, ein deutlicher Hinweis auf zunehmend humideres Klima. Bis zur Verlandung der Gewässer um 3000 BP nahm die Salinität wieder deutlich zu und reflektiert die Aridisierung der Sahara. Repräsentiert wird dies von *Cyprideis torosa,* die zeitweise monospezifisch vorkommt, oder assoziiert ist mit den Mollusken *Hydrobia* sp. und *Cerastoderma glaucum*, sowie den Foraminiferen *Ammonia tepida* und *Trichohyalus aguayoi*. (Fontes et al 1985, (Gasse et al. 1990, Lamb et al. 1994). Die Assoziation von *C. torosa* mit wenigen euryhalinen Foraminiferenarten ist typisch für den zunehmend athalassischen Charakter eines Gewässers bei einsetzender Aridisierung und kann deshalb als Klimasignal genutzt werden (siehe Beiträge 6 und 7).

Ehemalige Seen in der Rhub-Al-Khali Wüste in Saudi-Arabien

Im Gebiet der bei Mundafan im Süden von Saudi-Arabien repräsentieren pleistozäne und holozäne ostrakodenführende Seesedimente mehrere humide Phasen während des Quartärs (Rosenberg et al 2013). Während die ersten drei pleistozänen Seephasen auf Süßwasserbedingungen hinweisen, ist in der letzten, im frühen Holozän angesiedelten Phase die Salinität erhöht, welches auch das Vorkommen von *Cyprideis torosa* und zweier Foraminiferenarten erklären könnte. (Genari et al. 2011). Interessanterweise sind diese Arten (*Helenina anderseni* und *Trichohyalus aguayoi*) in Mangrovenwäldern der südlichen Hemisphäre besonders häufig (Gupta 2003). Dies spricht für starke Schwankungen der Salinität der athalassischen Gewässer von Mundafan. *Trichohyalus aguayoi* kommt außerdem in den holozänen Sedimenten im nördlicher gelegenen Tayma vor, allerdings viel seltener. Ähnlich wie im etwa zeitgleichen Tayma (Pint et al. eingereicht) zeugt auch hier eine Erhöhung der Salinität von der zunehmenden Aridisierung der Arabischen Halbinsel. Im Gegensatz zu Tayma entwickelten sich die Salzseen von Mundafan nach einer Süßwasserphase, die in Tayma nicht dokumentiert werden konnte. Daraus lässt sich schließen, dass das humide Klima im Süden der Arabische Halbinsel wesentlich ausgeprägter als in deren Norden war (siehe Beiträge 6 und 7).

3.4 Morphologische Besonderheiten

Intraspezifische morphologische Variabilität von Arten im untersuchten Material kann durch bestimmte ökologische Faktoren ausgelöst werden. Dazu gehören vor allem Salinitätsänderungen. So können neben den bereits erwähnten Missbildungen bei Foraminiferen (Pint et al. submitted) vor allem athalassischer Gewässer, auch Siebporenumrisse (Frenzel et al. 2011) und Buckelbildung (Frenzel et al. 2012) bei *Cyprideis torosa* als Salzzeiger eingesetzt werden.

Beitrag 8:

Noding of *Cyprideis torosa* valves (Ostracoda) – a proxy for salinity? New data from field observations and a long-term microcosm experiment

veröffentlicht 2012, Frenzel et al., *International Review of Hydrobiology*

Eines der auffälligsten Schalenmerkmale von *Cyprideis torosa* ist die Knotenbildung auf den Klappen. Aufgrund dieser markanten buckelförmigen Ausbuchtungen wurde die Art ursprünglich in zwei Arten unterteilt*:* *C. littoralis* (Glattschaler) und *C. torosa* (Knotenschaler). Da sich aber herausstellte, dass es sich hierbei nur um Ökophänotypen handelt, wird inzwischen die Nomenklatur *C. torosa* forma *littoralis* bzw. forma *torosa* verwendet. Die Knotenbildung tritt in einem bestimmten, gut definierten Salinitätsbereich auf, und lässt sich daher besonders für Paläomilieuanalysen von Brackgewässern bis ca. 14 psu einsetzen.

Peter Frenzel, Isabel Schulze, Anna Pint (2012), Noding of Cyprideis torosa valves (Ostracoda) – a proxy for salinity? New data from field observations and a long-term microcosm experiment International Review of Hydrobiology, 97 (4): 314-329.

	P. Frenzel	I. Schulze	A. Pint
Konzeption	X		
Geländearbeiten	X	X	
Datengewinnung	X	X	**X**
Datenauswertung und Interpretation	X	X	**X**
Schreiben	X		**X**
Publikationsäquivalent	n. a.	n. a.	**0,5**

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Research Paper

Noding of *Cyprideis torosa* valves (Ostracoda) – a proxy for salinity? New data from field observations and a long-term microcosm experiment

key words: morphological variation, nodes, water chemistry, brackish water, Baltic Sea

Abstract

Cyprideis torosa (JONES, 1850) (Ostracoda, Crustacea) is one of the most common marginal marine ostracod species in the Northern hemisphere. We investigate the relationship between variable noding of its valves and salinity as well as Ca^{2+} concentration in the ambient water, analysing populations from an in vitro experiment and field data from the southern Baltic Sea coast. There is a clear negative linear correlation between the proportion of noded individuals from our microcosms and salinity. Deficiency of Ca^{2+} causes heavier noding in laboratory cultures. The same effect can be seen in the field, however, the increase of noded individuals with falling salinity appears to be stepped, not linear. This pattern probably reflects the ability of the animals to wait some time until better salinity conditions occur within the highly variable conditions of estuaries and lagoons.

At the southern Baltic Sea coast, proportions of more than 20% noded valves within a *C. torosa* population indicates salinities of up to 2 psu, up to 10% noded valves indicate salinities between 2 and 7 psu, and the lack of noded valves salinities >7 psu. Stable salinity conditions as in the studied microcosms cause a shift of these salinity limits to 5 and 14 psu approximately but in a linear relationship between salinity and proportion of noded individuals. Hence, athalassic populations from more stable water bodies should be used for continuous and more detailed salinity trend reconstructions. Deficiency of Ca^{2+} (approximately <120 mg/l) effects up to about 20% more noded individuals than in water with same salinity but with higher Ca^{2+} concentrations. The reproduction rates within the microcosms indicate a salinity optimum of *C. torosa* eggs of 8 psu whereas the optimum of the adults seems to be at least 14 psu.

1. Introduction

A typical phenomenon in brackish water is the prevalence of low diversity associations within most taxonomic groups. The reason is the stress impact on these organisms by salinity variation and an osmotic value of the surrounding water that is physiologically problematic for both, marine and freshwater forms intruding into brackish waters. Those low diversity

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associations are not easy to interpret in palaeoenvironmental reconstructions relying on quantitative association data.

Cyprideis torosa (Jones, 1850) is the most abundant and widely distributed ostracod species in shallow brackish waters of Europe, North and Eastern Africa, and Asia (Athersuch *et al.*, 1989; Meisch, 2000; Wouters, 2002). It is typical of the coastal and athalassic brackish waters and also occurs in Holocene and Pleistocene interglacial sediments of Europe in large numbers (Griffith, 1995; Gramann, 2000; Pint *et al.*, 2012). As a fossil, it is often bound to transgressive sequences and interglacial periods. Frequently, *Cyprideis torosa* is the dominating or even lone ostracod species in oligohaline waters of coastal lagoons (Frenzel, 1991). Ecologically driven phenotypic variability may be a clue for the interpretation of such associations.

Noding of valves is a phenomenon known from several ostracod taxa within the Cytheracea (Sandberg, 1964). The noding of *Cyprideis torosa* valves is related to water chemistry and therefore may help in interpreting the palaeoenvironment (Keyser and Aladin, 2004). The present paper tries to shed light on conditions and patterns of noding by analysing results of laboratory experiments with cultures and field data from the southern Baltic Sea coast.

2. On Salinity

The comparison of salinity-related noding published by several authors is hampered by different methods of measuring salinity. Salinity can be expressed as proportion of total dissolved solids (TDS; g/l), as conductivity (mS/cm), or chlorinity (g/l). The measurements of the present study were carried out using a hand-held conductivity probe (WTW multi 350i) converting conductivity measurement mathematically into salinity values given in practical salinity units (psu). These values correspond to TDS values given in ‰ relying on a strong correlation between salt concentration and conductivity and assuming water of marine origin but diluted with freshwater of very low concentrations of salts (Unesco, 1981). Hence, it is assumed that the measured diluted water has the same proportions of ions as oceanic water but with lower overall concentrations. The conductivity-salinity conversion method (Fofonoff and Millard, 1983) is reliable in brackish water close to normal marine conditions, however, it is problematical in oligohaline water where different proportions of salts from freshwater input influence the conductivity measurements and can cause deviations between TDS-based and conductivity-based salinity values. For instance, inner-coastal waters of the southern Baltic Sea yield relatively high concentrations of Ca^{2+} ions because of carbonate rich glacial sediments dominating the coast (see discussion below). Chlorinity measurements, which are easier to do than direct TDS measurements because of volatile substances, rely on constant ion proportions in marine water and give Cl^{-} concentrations only. They allow salinity calculation relying on constant proportion changes of ions like for conductivity measurements.

3. The Noding Phenomenon of *Cyprideis torosa*

Cyprideis torosa has two morphological forms which are not genetically fixed: forma *littoralis* with smooth valves and forma *torosa* with noded valves. Both forms have been known for about 150 years and were first described as different species (Jones, 1850; Brady, 1868). It is proven now that they belong to one species. Individuals with one noded and one smooth valve exist and nodes can appear or disappear during ontogeny in the same individual (Hartmann, 1964; Vesper, 1972a; Van Harten, 2000). The formation of nodes is driven by environmental factors but the position on the valve is anatomically determined

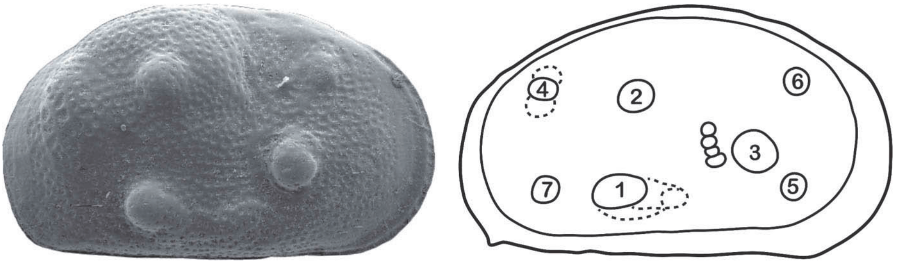


Figure 1. Noding patterns in *Cyprideis torosa*. Left: SEM picture of a noded female right valve from Michaelisdorf, Saaler Bodden, southern Baltic Sea coast. Nodes 1–4 and 6 are developed, nodes 1 and 4 sport prolongations as visible on the drawing. Length of valve approximately 1 mm. Right: Patterns of node distribution on valves of *C torosa* from the German Baltic Sea coast (redrawn from Frenzel, 1991). The designation of nodes follows its order of frequency, which is not consistent with the designation by Sandberg (1964) and Van den Bold (1976).

(Kilenyi, 1972; Vesper, 1972a, 1972b, 1975; Van den Bold, 1976; Frenzel, 1991; Van Harten, 1975, 1996, 2000; Keyser, 2005). Figure 1 shows the typical position of nodes on the valve of *Cyprideis torosa* of noded and unnoded specimens.

A connection between node formation and salinity was noted early, but the reported salinity limits are partly contradictory (Tab. 1). For instance, Vesper (1972b), Frenzel (1991), and Marco Barba (2010) observed higher percentages of noded valves within the populations under lower salinity, but there was no linear correlation detected. So, additional factors other than salinity were assumed. For the first time, Van Harten (1996) explains this phenomenon with differences in internal osmotic pressure during moulting. As a second factor Van Harten (2000) supposes the pH value or dissolved CO_2 (connected with $CaCO_3$ concentration in the water) controlling noding, because there is no 'linear' relationship between salinity and the frequency or node development of the noded valves. Other authors

Table 1. Field occurrence of noded and smooth specimens of *Cyprideis torosa* under different salinities at the southern Baltic Sea coast.

reference	Hirschmann 1912	Seifert 1938	Schäfer 1953	Hartmann 1963	Vesper 1972b	Frenzel 1991	Marco Barba 2010
smooth valves only	6 psu	6.5 psu	open Baltic Sea			>5 psu	≥20
dominance of smooth valves					<14.5 psu		>5
noded and smooth valves co-occur	1.25 and 4 psu			<5 psu			
dominance of noded valves	<1.25 psu	2 to 5 psu	0.97, 4.69 and 4.73 psu		1.8 to 5 psu	0.5 psu	≤5

assume the Ca concentration (KEYSER, 2001), a metal complex (PEYPOUQUET, 1977) or Si complex and high C_{org} concentrations (TÖLDERER-FARMER, 1985, CARBONEL *et al.*, 1988) as second factor. BODERGAT (1983) reports a correlation between high Ba and Mg concentrations and node formation.

VESPER (1972b) and FRENZEL (1991) describe that the most and strongest noding within a population is found in the juvenile A-1 stage, the nodes on the right valve are never smaller or less frequent than those on the left valve and females are normally more noded than males.

Histological studies by KEYSER and ALADIN (2004) and KEYSER (2005) explain node formation by Ca shortage under low salinity conditions. This shortage causes rupture of cell-to-cell connections during moulting if an excess of water penetrates the tissue. The penetrating water "blows up" the flexible cuticule to form nodes which are then stabilized by biomineralization. This model excellently explains the fixed position but different grade of node formation under different water chemistry conditions. KEYSER (2005) states about 5‰ as critical salinity, however, does not provide data for this statement.

MARCO BARBA (2010) studied *Cyprideis torosa* from the Spanish Mediterranean coast in detail. He states that noding of *C. torosa* as one of the best proxies for salinity reconstruction and suggests using it together with shell chemistry. MARCO BARBA (2010) explains the noding as a combined effect of low salinity and Ca shortage thus expanding KEYSER's (2005) hypothesis. For the first time, he presents a transfer function linking noded shell proportion to salinity:

$$\log_{10} \text{Salinity} = 1.22 - 0.833 * \arcsin \sqrt{\text{Pn}},$$

where Pn =: proportion of noded valves in % within a *Cyprideis torosa* population.

4. Material and Methods

Four superficial sediment samples were taken in about 50 cm water depth from the Breitling, a brackish water lagoon at Rostock, Northeastern Germany, between 11 March and 10 April 2002. The salinity fluctuated from sampling to sampling between 6.8 and 12.5 psu, the water temperature between 5.0 and 6.5 °C. Salinity fluctuation in this lagoon occurs in a rather unpredictable way because of wind and precipitation driven changing inflows of more saline water from the open Baltic or freshwater from Warnow River. The sediment was fine to coarse sand with some organic detritus. We extracted 840 living adult *Cyprideis torosa* with tweezers from this sediment using a binocular microscope. A part of the sediment, from which the ostracods had been picked before, was heated on 60 °C for 16 h. It was put into glass jars as a substrate in about 5 mm thickness. The jars had a diameter of 4.5 to 7.5 cm and a height of 3 to 4 cm and were closed by glass lids, lying loosely on the jars (Fig. 2). Water was taken from the Salzhaff lagoon (southern Baltic Sea coast near Wismar) and from the Hohensprenzer See (a lake in Mecklenburg near Güstrow). Table 2 lists the concentrations of the major cations except Na. After having mixed the water for the microcosms along salinity gradients as described below, it was filled into the jars up to a 1 to 2 cm level. All jars were stored in the laboratory at room conditions (18.3–26.8 °C, average 23.2 °C) and sheltered from direct sun light except one series, which was transferred to lower temperature in a cold room (13.3 – 14.0 °C, average 13.5 °C) with artificial light under normal day/night periods from 89 days after populating the microcosms. The setting of the experiment is summarized in Table 3.

The brackish water of the Salzhaff lagoon was diluted with distilled (distilled water, cooled, and chalk series) or freshwater (freshwater series) to get water of different chemistry along a salinity gradient (Table 2). A small amount of chalk (ca. 2 g each) was given into the jars of the chalk series to get a higher $CaCO_3$ concentration. Every two to four weeks we measured salinity and temperature for all microcosms with a conductivity probe. Normally, the salinity increased slowly with time by evaporation. This was corrected by adding distilled water until the original conductivity value was re-established. Five adult males and ten adult females of smooth *Cyprideis torosa* were included in each of the micro-

Figure 2. Microcosms of the *Cyprideis torosa* culture.

cosms. About the half of females had already born eggs in their breading cavities within the carapace during their transfer to the microcosms. Diatoms (*Nitzschia* spec.) from a laboratory culture were added two times and one time a 1 cm piece of sea grass to each of the jars as food during the experiment. Bacteria films on the culture water surface appeared in some jars and were removed during conductivity measuring. The experiment lasted 526 days in total.

After observing the first juveniles in culture, all adult ostracods were picked from the microcosms and dried in order to have only specimens that grew in the microcosms. The cooled series was placed into a cool room after the first extraction of adults. The first harvesting of adults grown completely in the cultures started after observing new juveniles in most microcosms 113 days after populating the first jars and ended 211 days later. The adult individuals were picked directly from the jars using tweezers. A second harvest was carried out 287 to 380 days after the first one. All sediment samples with adult ostracods not picked when finishing the cultures were fixed and conserved in 70% ethanol until picking.

Picked adult *Cyprideis torosa* were counted separately for males and females. Additionally, we counted the number of living juveniles during the first extraction of adults from distilled water and freshwater series. Sexes of adults and juveniles were distinguished using the outline and size of carapaces. *C. torosa* shows a strong sexual dimorphism. Females are slightly shorter than males, have a more rectangular lateral shape than the slightly sloping posterior-dorsal margin of the males, and are posteriorly broader in dorsal view. The last two features are caused by brood care within the carapace of the females (cf. Heip 1976). Juveniles tend to have a more triangular outline in lateral view and are slimmer in dorsal view. Because of the discontinuous growth of ostracods by moulting, juveniles are distinctively smaller than adults.

Table. 2. Selected cation concentrations of the water used for culturing *Cyprideis torosa*. All concentrations are given in mg/l.

Sample	Salinity	Ca	Mg	Sr
Freshwater (Hohensprenzer See)	0.1	27	10	0.2
Brackish water (Salzhaff)	13.0	220	560	3.9

Table 3. Setting of the laboratory cultures in the experiment.

	Conditions	Salinity range	Number of replicates	Total number of jars
Distilled water series	Brackish water diluted with distilled water	13 to 0.5 psu (8 classes)	4	32
Freshwater series	Brackish water diluted with freshwater	8 to 0.5 psu (6 classes)	4	24
Cooled series	Brackish water diluted with distilled water, cooled on 13 °C	8 to 1 psu (3 classes)	3	9
Chalk series	Brackish water diluted with distilled water, enriched with $CaCO_3$	8 to 1 psu (3 classes)	3	9
Total		13 to 0.5 psu	3 to 4	74

We counted all individuals with at least one slight node on at least one valve as noded individuals. Often, the nodes are poorly visible and can be recognized by turning the carapace in the light of the microscope lamp.

5. Results

5.1. General Observations

The living ostracods were observed digging in the uppermost millimetre of the sediment or more rarely crawling on the surface. When observed they seemed to avoid direct light by instantly digging. Their movement was very slow compared to many other brackish water ostracods as for instance *Loxoconcha elliptica* (Borck and Frenzel, 2005). The digging produced a complete homogenization of the sediment within days, observable after adding the chalk to the microcosms of the chalk series.

Moulting adult individuals during calcification of the new valves were recognizable during picking because of their very soft valves deforming between the tweezers. This happened during all picking only three times. Hence, we assume a short time only for biomineralization of the shell.

Many microcosms showed green algae development in the second year of culturing. This did not occur within the chalk series. No other metazoans than *Cyprideis torosa* were discovered within the microcosms as it was intended in the experiment set up.

5.2. Reproduction

In general, all ostracod populations except those of one microcosm reproduced. The second harvesting of the cooled series, however, yielded a very few individuals only, three of the nine microcosms yielded none. The first juveniles were found in almost all microcosms about 70 days after inoculion.

When picking the adults for isolation less than four months after start of the experiment, first adults of the second generation had already appeared. Between 58 and 259 living juve-

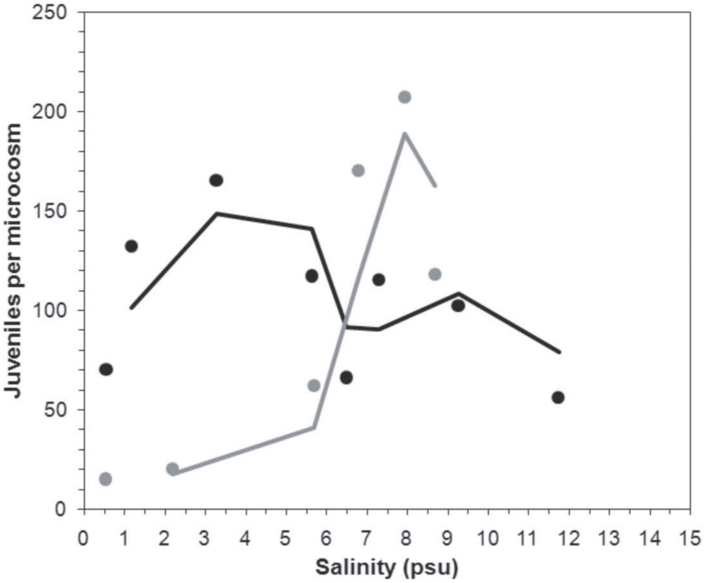


Figure 3. Number of juveniles in different salinity classes in the distilled water (black circles) and freshwater series (grey circles). The trend lines are moving averages. Data were collected when picking the first adult generation about four months after starting the experiment.

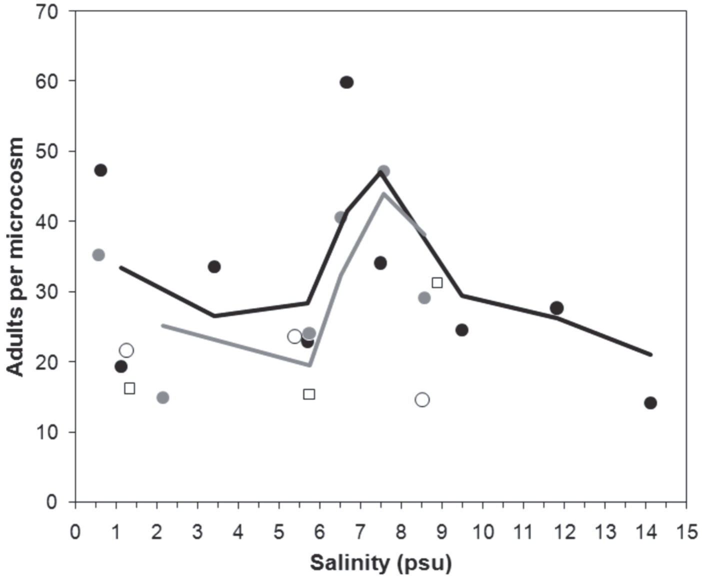


Figure 4. Number of adult individuals per microcosm for all series. The trend lines (distilled water and freshwater series) are moving averages. Distilled water series: black circles; freshwater series: grey circles; cooled series: white circles; chalk series: white squares.

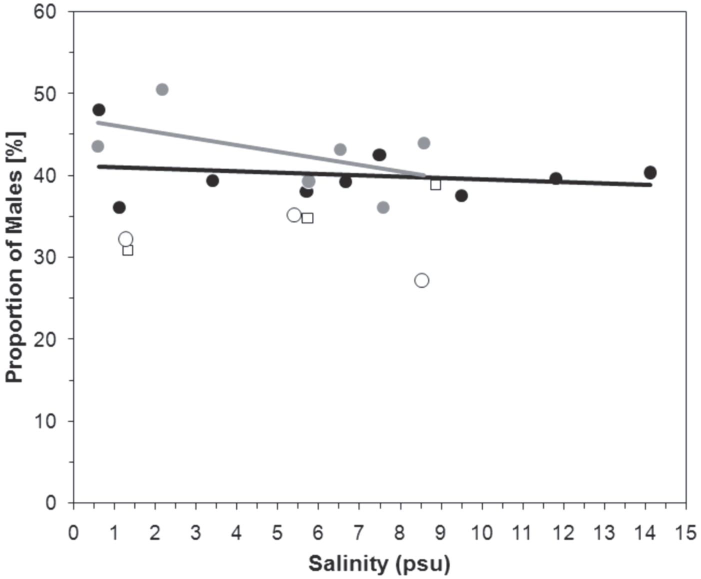


Figure 5. Percentage of males for salinity classes of all series. The salinity of each data point is given as average of each salinity range class. The trend lines (distilled water and freshwater series) are linear correlations. Distilled water series: black circles; freshwater series: grey circles; cooled series: white circles; chalk series: white squares.

niles were counted per jar. Salinity classes at 3 and 8 psu show the highest rate of reproduction (Fig. 3). The adults of both harvests are generally most numerous between 6 and 8 psu (Fig. 4). The cooled series is an exception with a little bit lower and weak frequency maximum. It has to be taken in account, however, that the number of microcosms here is with three instead of six or eight per salinity class much lower than for the other series and therefore less significant.

5.3. Sex Ratio

Because of the relatively low number of individuals per microcosm, we decided to group the counts in salinity classes thus gaining more significant calculations. In general, there is an average proportion of approximately 40% males; most data points lie between 35 and 45% (Fig. 5). This proportion remains about the same along the salinity gradient. The freshwater series, however, shows a weak tendency to higher proportions of males in lower salinities. The cooled and chalk series are less significant because of lower number of specimens and three classes each only.

5.4. Noding

5.4.1. Microcosms

Juveniles with nodes were observed in all reproducing salinity ranges. Adult noded females occurred in some jars below 9.5 psu and in all jars of each series below 6 psu. Nodes on adult

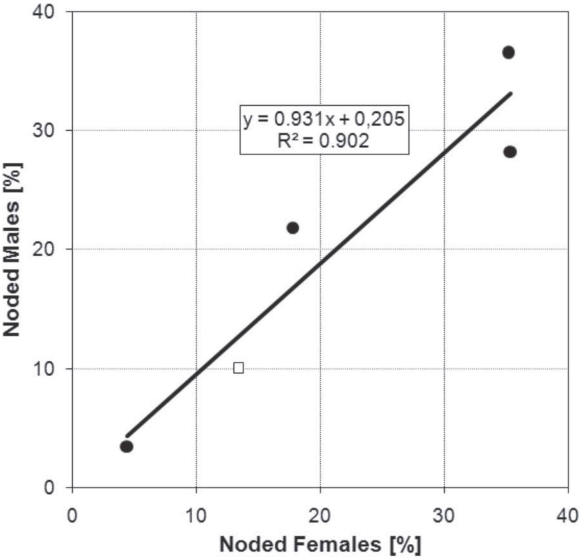


Figure 6. Correlation between percentages of noded females vs. males of salinity classes from a given series. Only classes with at least 50 adults of each sex were considered. Black circles indicate the distilled water series, the white square the only class of the chalk series with sufficient material.

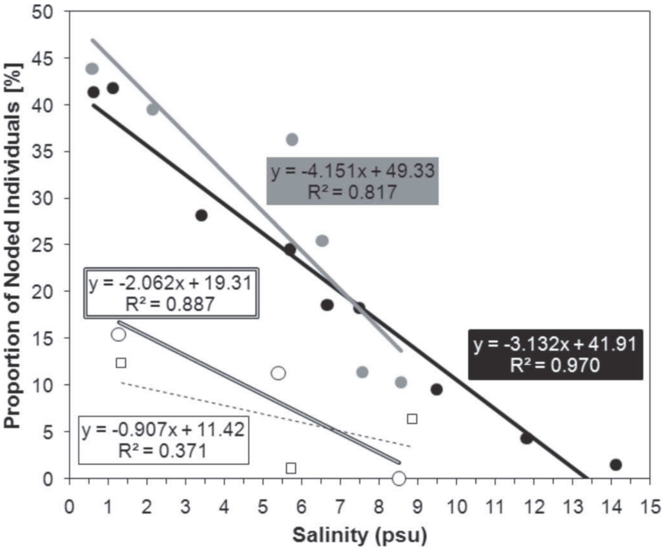


Figure 7. Percentage of noded individuals of all adults and measured mean salinity within the microcosms of each salinity class in all series. All classes of all series contain much more than 50 adults each except the highest class of the cooled series with only 44 individuals. Trend lines are linear correlations. Distilled water series: black circles; freshwater series: grey circles; cooled series: white circles; chalk series: white squares.

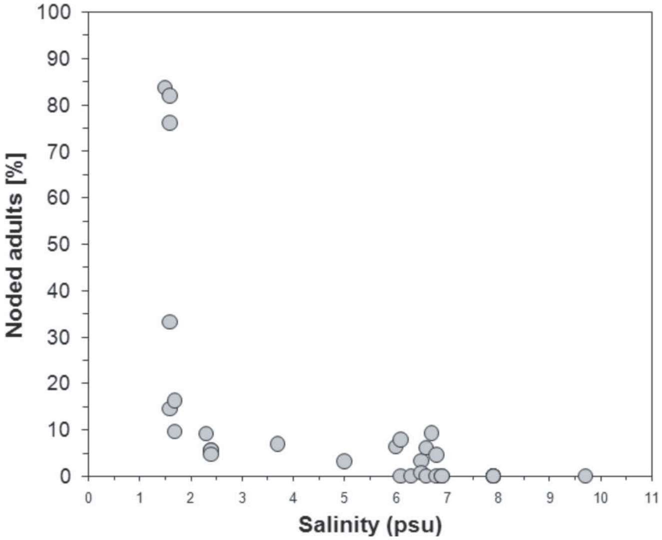


Figure 8. Percentage of noded *Cyprideis torosa* within living populations (live carapaces) in stations of the coast of Mecklenburg-Vorpommern (southern Baltic Sea) under different salinity conditions. Only samples with at least 25 individuals are figured.

males disappeared above 5 psu. A comparison of proportions of noded specimens in female and male *Cyprideis torosa* from populations with higher numbers of individuals (Fig. 6) suggests a very similar pattern. There is a slight trend to more noding in males. The nodes are more distinct and more numerous at lower salinity, whereas they are shallow and less numerous at higher salinity levels. Some specimens bear one or two shallow nodes on the right valve but not on the left one.

There is a distinct negative linear correlation between the proportion of noded adult individuals within the population and the mean salinity value (Fig. 7). The distilled water and the freshwater series display a very similar correlation line, whereas cooled and chalk series show a much lower proportion of noded valves. It has to be stressed, however, that the salinity classes of the cooled series contain a low number of individuals only.

5.4.2. Field Data

The diagram of field data (Fig. 8) shows a completely different graph than those of the in vitro experiments. The calculation is based on a minimum of 50 adult *Cyprideis torosa*. Noded valves dominate below 2 psu in most samples and occur up to 7 psu. Samples without noded specimens lie between 6 and 7 psu together with samples with noded and smooth individuals in coexistence. Above a limit of 7 psu only smooth valves occur.

6. Discussion

6.1. Microhabitat, Reproduction and Sex Ratio

The microhabitat of *Cyprideis torosa* in the microcosms is the same shallow infaunal as observed by BORCK and FRENZEL (2005), who also reported a very slow crawling and digging for this species. We assume homogenous physico-chemical conditions within the upper sediment layer of the microcosms by bioturbation by the ostracods.

The time period of about six months from inoculating the microcosms with egg-bearing females to the first adults of the new generation corresponds well to the six months reported in another in vitro study by WEYGOLDT (1960). MEZQUITA *et al.* (2000) report five to more than six months ontogenetic development for *Cyprideis torosa* from a saline environment of the Spanish Mediterranean coast. The shorter periods are explained by higher water temperature during summer. The very few adults of the second harvest in our cooled series are probably left over juveniles from the first harvest. The low temperature conditions started three months after populating the microcosms. Then, the larvae were hatched already and developed despite the low temperature until reaching the adult stage. The next generation, however, did not hatch because of a water temperature less than 14 °C. HEIP (1976) documented 15 °C as a minimum temperature for hatching *C. torosa*, very close to the conditions of our cooled series.

Based on the number of juveniles and adults of all series along the salinity gradient, we recognize a tendency of highest numbers of individuals at salinities of around 8 psu. ALADIN (1993) reported 8 psu as the tipping point between hyperosmotic and isoosmotic regulation in *Cyprideis torosa* from the Aral Sea. The organism is forced to pump inflowing water out of the body and to pick up salt under lower salinity conditions, to excrete salt and to take water under higher salinity conditions, as well as to compensate for poorer enzymatic reactions adapted to other salinity conditions than in the ambient water (REMMERT, 1980; ALADIN, 1993). All those reactions need energy which could have been utilised for growth, reproduction, and ecological tolerance to other environmental factors. Hence, the ecological stress increases with salinity distance from the isoosmotic range as it is known from other taxonomic groups living in brackish waters (REMANE, 1958). This pattern explains well the lower reproduction rate below 8 psu, but not the lower number of specimens above this salinity where ALADIN (1993) reports isoosmotic regulation. Up to now, we cannot explain this phenomenon. The more or less constant proportion of 40% males suggests a salinity independent sex ratio.

6.2. Noding

The cultures show a clearly salinity-bound formation of nodes (Fig. 7). There is a tendency of water inflow along the osmotic gradient from the less concentrated ambient water to the more concentrated haemolymph. Following the hypothesis by KEYSER (2001, 2005), inflowing water increases the pressure of the body fluid during hypoosmotic regulation under low salinity conditions and deficiencies of osmoregulation due to lack of Ca^{2+} ions cause the disruption and blowing up of tissue during the critical stage of moulting. A higher number and more distinct nodes with decreasing salinity can be explained by this hypothesis. The nodes are a pathological phenomenon without functional importance.

ALADIN (1993) places *Cyprideis torosa* into the groups of confohyperosmotic II and amphiosmotic forms. Both groups regulate hyperosmotically below 8 psu and change to isoosmotic regulation above, the former up to 30 psu where a second tipping point indicates the switch to hypoosmotic regulation, the latter group up to 100 psu (ALADIN 1993). If fixing the lower isoosmotic limit at 8 psu, there should not be any nodes above this salinity value. This seems to be true for the field data from the southern Baltic Sea coast (Fig. 8), but there are some noded adult individuals under higher salinities in our cultures (Fig. 7) and in the field data documented by MARCO BARBA (2010) from the Spanish Mediterranean coast (Fig. 9). Furthermore, noded juveniles could be found under all salinity conditions of our cultures. A higher isoosmotic point of at least parts of the *C. torosa* population used for the study would explain noded valves above 8 psu. More than 8 psu for the osmotic optimum of the Baltic

Sea form would, however, contradict our findings in reproduction*, i.e.,* an optimum at 8 psu. The maximum salinity encountered for noded valves lies at about 14 psu (the maximum of our salinity gradient; Fig. 7), approximately the maximum of 15 psu documented by MARCO BARBA (2010) for the Spanish populations. WAGNER (1957) and VESPER (1975) found noded *C. torosa* at a maximum salinity of 14.5 psu, NEALE (1988) up to 17 psu. It may be that the osmotic optimum (and osmotic pressure of the body fluid) varies between 8 and at least 14 psu for the studied *C. torosa* populations. The eggs have other mechanisms of osmoregulation than the hatched animals (ALADIN, 1993) and maybe have other salinity limits. If this assumption is applicable, it would suggest that the osmotic optimum of *C. torosa* eggs would be 8 psu, the optimum for the adults, however, at least 14 psu.

The stronger noding of juveniles could be caused by a higher surface to volume ratio, enabling a relatively higher water inflow, or by their non-mature osmoregulation capacities. We cannot explain why right valves are preferentially noded. KEYSER and ALADIN (2004) suggest a less prominent node development on this side of the animal where it is laying on the sediment during moulting, however, we assume this explanation to be not probable because of the exclusively lesser noded left side.

Looking on the chalk series graph compared to the freshwater series (Fig. 9), we see a negative shift along the y-axis and a less steep decrease of noded proportion with increasing salinity. This coincides well with KEYSER's (2001) assumption that low Ca^{2+} concentrations cause a greater risk of disrupting stabilizing structures within the cavities by spasm-like reaction. Referring to this mechanism, we are able to explain the lower percentage of noded specimens within the chalk series. The negative inclination of the chalk series trend line rules out an explanation of noding caused by Ca^{2+} concentrations alone, because plenty of carbonate was available by feeding and water input by the animals of all salinity classes.

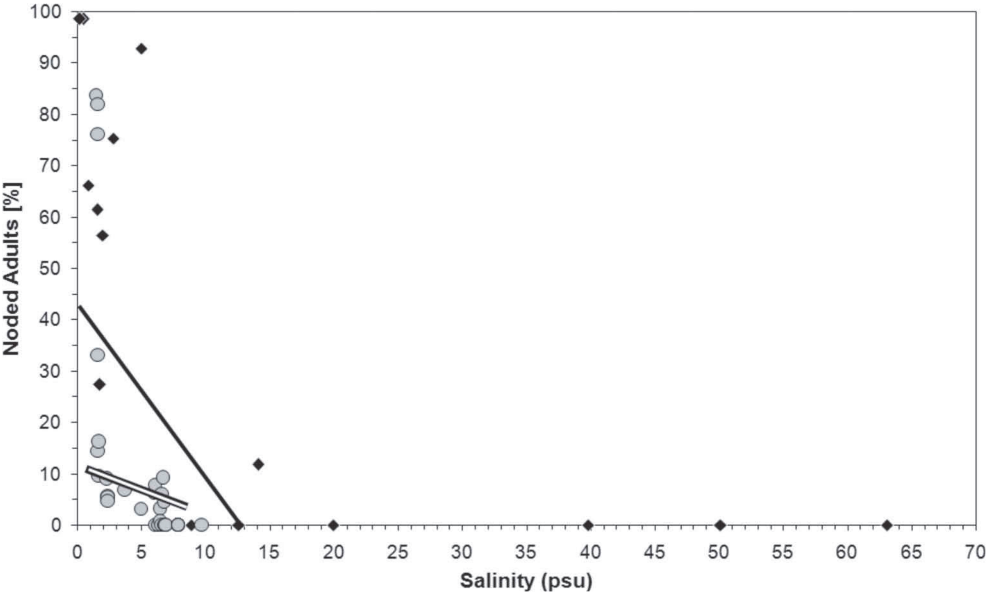


Figure 9. Percentage of noded individuals of all adults and the measured mean salinities within the microcosms of the distilled water and freshwater series (black trend line) and the chalk series (white-black trend line) given as trend lines and data points for noding vs. salinity from our field study along the southern Baltic Sea coast (grey circles) and data points from a field study at the Spanish Mediterranean coast (MARCO BARBA 2010; black diamonds).

The chalk particles are mostly fragmented Cretaceous coccoliths of a few micrometres size only which have a high dissolution potential. We conclude that salinity and Ca^{2+} availability together drive node formation. The coincidence of noding patterns from the chalk microcosm series and field data from the southern Baltic Sea coast reflects the high Ca^{2+} concentrations in rivers and lagoons within Pleistocene sediments. Those sediments (tills, sands) contain large amounts of reworked Upper Cretaceous chalk. On the other hand, the distilled water series seems to be closer to the pattern found by MARCO BARBA (2010) at the Spanish coast. The dilution is caused here by rainwater or freshwater with very low Ca^{2+} concentrations, similar to the dilution of our distilled water series.

In general the field data of Fig. 8 correspond to the literature data of Table 1. An interesting difference is, following different authors, the salinity value of dominance of noded valves which suggests a dominance between 2 and 5 psu, where we found only up to 10% noded specimens. Such samples were registered during our investigations at the southern Baltic Sea coast several times, but that were empty shells at the inflows of rivers where a temporary salinity lower than 2 psu or transport from the estuaries cannot be excluded.

The pattern in the field seems to be very different from those of the microcosm experiment at the first look (Fig. 9). Whereas the field data from the southern Baltic coast and the Spanish coast (MARCO BARBA, 2010) display a staircase pattern, the cultures show linear relationships. To explain this difference, we have to take into account the often highly variable salinity and water chemistry of the lagoons and estuaries. Within time periods, the individuals may choose the best time for moulting under these circumstances. Additionally, the Ca^{2+} concentration of the water only indirectly influences the osmoregulation because the concentration of the haemolymph is crucial and can be higher as temporarily falling concentrations of the ambient water. Therefore, the percentage of noded specimens is relatively stable between 7 and 2 psu. As indicated by a much higher proportion of noded valves below 2 psu, this regulation pattern collapses because the variation of salinity does not reaches values close to 7 psu.

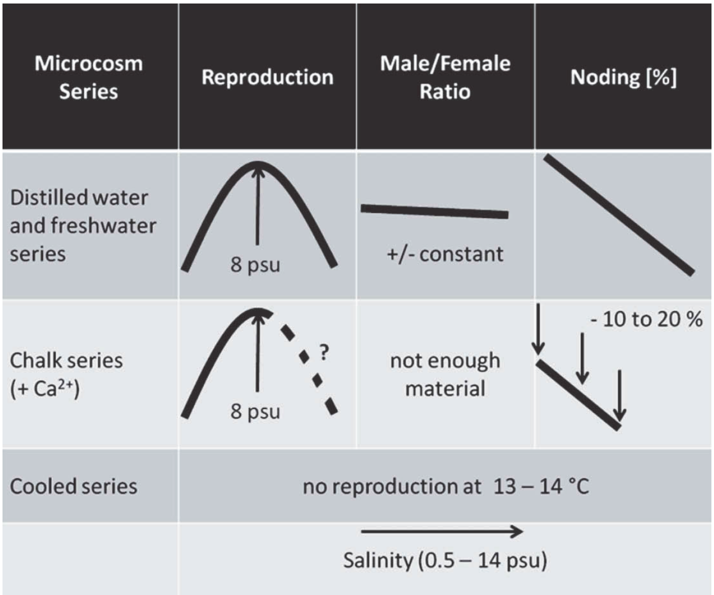
7. Conclusions

The comparison of microcosm experiments and field data from *Cyprideis torosa* under salinity gradients shows the noding as a pathological effect caused by osmotic problems in low salinity environments during moulting. The concentration of ions influencing the osmotic regulation capacity of membranes seems to effect the noding as well. A lack of Ca^{2+} clearly increases the risk of noding during moulting (Tab. 4).

Percentages of noded specimens in subfossil and fossil associations of *Cyprideis torosa* have the potential for reconstructing salinity levels and water chemistry in combination with other proxies for palaeosalinity. We expect a similar applicability of other cytheroidean ostracod species with variable noding but there is no evidence so far. In *C. torosa*, noding in marginal marine associations reflects salinities below 14 psu. More than 20% noded or even dominating noded valves indicate a salinity below 5 psu. Up to 10% noded individuals are typical for the salinity interval 2 to 7 psu. Ca^{2+} deficiency may produce higher proportions of noded valves within this range and noding above 7 psu, where normally only smooth valves occur. Analysing noding proportions alone allows the rough estimation of salinity within ranges for marginal marine settings. The transfer function by MARCO BARBA (2010) is applicable depending on ionic composition of the water. Athalassic populations of *C. torosa* live in more stable water bodies concerning the salinity. Here, the proportion of noded valves can be used for continuous and detailed salinity trend analysis, however, absolute estimates are hard to calculate because of a lack of knowledge on water ionic composition.

Detailed information on water chemistry and noding effects from the field and the laboratory are needed to develop noding analysis as a proxy for ancient water chemistry conditions.

Table 4. Schematic presentation of experimental results from microcosms.



Microcosm Series	Reproduction	Male/Female Ratio	Noding [%]
Distilled water and freshwater series	8 psu	+/- constant	
Chalk series (+ Ca^{2+})	8 psu ?	not enough material	- 10 to 20 %
Cooled series	no reproduction at 13 – 14 °C		
	Salinity (0.5 – 14 psu)		

The next step is to analyse *Cyprideis torosa* populations from athalassic brackish waters with a range of ionic compositions different from marginal marine waters.

8. Acknowledgements

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Beitrag 9:

Salinity dependant morphological variation in *Cyprideis torosa*

veröffentlicht 2011, Frenzel et al., *Joannea Geologie und Paläontologie*

Schalenmerkmale bei *Cyprideis torosa* verschiedener Fundorte werden mit Daten aus einem Züchtungsexperiment verglichen. Es konnte gezeigt werden, dass die Größenvariabilität der Klappen im Versuch sehr ähnlich zu der im Feld war, obwohl die Tiere kleiner waren. Die Korrelation zwischen Salinität und Knotenbildung auf den Klappen verläuft beim Experiment jedoch linear und nicht stufenförmig wie bei der Feldbeobachtung. Auch die Umrisse von Siebporen auf den Klappen von *Cyprideis torosa* zeigen eine salinitätsabhängige Varabilität, wie bereits von Rosenfeld & Vesper (1975) erkannt wurde.

Peter Frenzel, Isabel Schulze, Anna Pint, Ian Boomer, Martin Feike (2011). Salinity dependent morphological variation of *Cyprideis torosa,* Joannea 11, 59-61

	P. Frenzel	**I. Schulze**	**A. Pint**	**I. Boomer**	**M. Feike**
Konzeption	**X**				
Geländearbeiten	**X**	X	X	X	X
Datengewinnung	**X**	X	X	X	X
Datenauswertung und Interpretation	**X**	X	X		
Schreiben	**X**				
Publikationsäquivalent	**1,0**	n. a.	0,5	n. a.	n. a.

Joannea Geol. Paläont. 11: 59-61 (2011)

Salinity dependant morphological variation in *Cyprideis torosa*

Peter FRENZEL, Isabel SCHULZE, Anna PINT, Ian BOOMER & Martin FEIKE

Cyprideis torosa (JONES, 1850) is one of the most widespread brackish water ostracod species in the Northern hemisphere. It occurs in high frequencies in brackish marginal seas as the Baltic Sea, in lagoons, estuaries, as well as brackish athalassic waters. Often, ostracod associations with *C. torosa* are dominated by this species or even monospecific. Such low diversity associations are hard to interpret using ecological tolerance data of species alone. Intraspecific morphological variations may give a key to the reconstruction of low diversity brackish water palaeoenvironments.

We give an overview on salinity dependant morphological variation in *C. torosa* based on literature data and our own observations covering several sites along the coasts of the North Sea, Baltic Sea, Mediterranean Sea, and Aral Sea, as well as smaller saline inland waters in Central Germany and Saudi Arabia. These observations show (1) a salinity dependant size variation with a maximum around the switching point between hyper-osmotic and hypo-osmotic regulation at 8–9 psu sensu ALADIN (1993), (2) noded valves in the oligohaline range (<7–8 psu) of thalassic habitats, dominating in beta-oligohaline waters (<2 psu), (3) a correlation of the proportion of round sieve pores to salinity of ambient water according to ROSENFELD & VESPER (1975), allowing a reconstruction for marginal marine habitats following the formula:

$$S = e^{-0.06\,RS + 4.7}$$

(S = salinity [psu], RS = proportion of round sieve pores [%]; $R^2 = 0.95$),

and (4) no salinity dependant shape variation of valves. There seem to be the same tendencies to morphological changes in athalassic waters but the thresholds are different.

A culture experiment complimented the field observations. We took *C. torosa* from a site on the southern Baltic Sea coast and kept it for 550 days in the lab covering a salinity range of between 0.5 and 13 psu in several series of microcosms. The specimens hatched and developed in our microcosms and were studied for size variation, noding, sieve pores, and shape variation. The size variation along the salinity gradient shows the same pattern as in the field but are clearly dwarfed specimens. In contrast to the staircase pattern of field data a clear linear correlation of noded valve proportion to salinity is visible in our cultures:

$$S = -0.24\ NV + 12$$

(NV = proportion of noded valves [%]; $R^2 = 0.77$) for sea water diluted by freshwater, and

$$S = e^{-0.04\ NV + 2.2}$$

($R^2 = 0.72$) for sea water diluted by distilled water.

We explain the difference between field and lab data by highly variable salinity in the field allowing waiting of individuals for better salinity conditions during molting. Probably because of the same reason, the sieve pore proportion correlates linearly and not logarithmically to salinity in cultures:

$$S = -0.51\ RS + 35 \quad \text{for } S < 7.5\ (R^2 = 0.78)$$
$$S = -0.07\ RS + 12 \quad \text{for } S > 7.5\ (R^2 = 0.85)$$

The limit between both trend lines lies at 7.5 psu pointing to the osmoregulation threshold as identified by ALADIN (1993). A salinity dependant shape variability of valves is not recognizable.

Different correlations in water with different ionic composition but same conductivity values point to a prominent water chemistry influence beside total dissolved salt concentration. Our next research step is to study cultures and field samples from athalassic waters with different solute compositions.

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3.5 Athalassische Gewässer in Küstennähe

Die beiden hier vorgestellten Lokalitäten sind Beispiele aus der Literatur.

Timsah springs

Die Quellen von Timsah in Israel sind 2,5 km von der Mittelmeerküste entfernt und haben eine Salinität von 3 bis 4 psu. Fünfzehn Foraminiferenarten kommen hier vor. Dominant sind die drei agglutinierende Arten *Haplophragmoides manilaensis, H. wilberti* und *Trochammina inflata,* vor allem aus Salzsümpfen bekannt und typische Anzeiger für niedrige Salinitäten im oligohalinen Bereich. Die Timsah-Quellen liegen direkt an der Vogelzugroute zwischen Europa und Afrika. Dies und die Nähe zur Küste erklären die relativ hohe Diversität der Foraminiferenfauna (Flako-Zaritzky et al. 2010).

Salt Lake Hawaii

Der Salt Lake auf Hawaii ist ein Kratersee und liegt ca. 3 km von der Küste entfernt. Eine Verbindung mit dem Meer kann aufgrund der Höhenlage ausgeschlossen werden. Die Salinität schwankt von Süßwasser bis mesohalin. Insgesamt 41 Foraminiferenarten kommen vor, dominiert von *Trochammina inflata, Elphidium hyalocostatum, Ammonia tepida*, *Haplophragmoides wilberti*, *Quinqueloculina laevigata* und *Rosalina floridana*, alles Arten die typischerweise in Salzmarschen und dem Intertidal vorkommen. Die häufigste Ostrakodenart des Salt Lake ist *Cyprideis beaconenesis*, die ebenso wie *Cyprideis torosa* als euryhalin gilt. Die hohe Diversität wird durch die Nähe zur Küste und den regelmäßigen Eintrag durch Vögel erklärt (Resig 1974).

4 Schlussfolgerungen

4.1 Entstehung und Nutzung von Mikrofaunen athalassischer Gewässer

Die Fallbeispiele zeigen, dass besonders zwei Faktoren zur Ausbildung athalassischer Faunenmerkmale führen: Die Höhe und Stabilität der Salinität und die Entfernung zur Küste. Der Wasserchemismus ist jedoch stets individuell (Last 2002). Besonders häufig treten holeuryhaline Arten wie *Cyprideis torosa* auf. Ein wichtiges Charakteristikum athalassischer Gewässer ist das Vorkommen von brackischer Fauna, daneben können aber auch randmarine und salztolerante limnische Arten auftreten. Entscheidend ist, dass diese Arten tolerant gegenüber Salinitätsschwankungen sind. Je ausgeprägter die Salinitätswechsel sind, desto weniger divers ist die Fauna. Salinität scheint in den meisten Gewässern der Hauptsteuerungsfaktor zu sein. Nur so ist zu erklären, dass Arten, die typischerweise in Lebensräumen der Küsten vorkommen, auch saline Binnengewässer besiedeln können. Existieren isolierte Gewässer lange genug, kann sich ein Endemismus mit angepassten ökologischen Toleranzen entwickeln. Wann Endemismus auftritt, ist individuell verschieden und scheint von einer Vielzahl weiterer Faktoren abhängig zu sein, vor allem aber von Art und Dauer der Isolation (Jung 1990). Auch bei sehr anpassungsfähigen Taxa kann Endemismus auftreten, wie zum Beispiel bei der Gattung *Cyprideis* im Tanganyika-See (Wouters & Martens 2001).

Makroskopisch und sedimentologisch sind athalassische Sedimente nicht von anderen aquatischen Sedimenten zu unterscheiden. Erst die Analyse der im Sediment enthaltenden Mikrofauna macht eine weitere Differenzierung möglich. Bei der Untersuchung aquatischer Sedimente stellt sich als erstes die Frage nach dem Gewässertyp. Allein durch seine Lage in einem gewissen Abstand zur Küste kann aquatisches Sediment potentiell ein ehemaliges athalassisches Gewässer anzeigen. In Küstennähe ist dies schwieriger. Hier gilt es zu klären, ob und wann ein Gewässer mit dem Meer verbunden war. Dazu wird die ehemalige Salinität mithilfe von Mikrofossilien abgeschätzt. Werden die Kriterien einer athalassischen Faunenassoziation erfüllt, kann ein Gewässer mit einer gewissen Salinität ohne Verbindung zum Meer angenommen werden. Um die Klassifikation solcher athalassischer Phasen schnell und sicher vornehmen und differenzierter betrachten zu können, wurde ein speziell für athalassische Gewässer konzipierter Bestimmungsschlüssel entwickelt (siehe Kapitel 4.5). Umfangreiche aktualistische Analysen bilden hierfür die Basis. Ebenfalls können bei ausreichender Individuenzahl der Mikrofauna Entwicklung, Struktur, Salinitätsgradienten, Salzquellen und Klimaeinfluss in Zeit und Raum detailliert herausgearbeitet werden. Die Voraussetzungen sind optimal, wenn die Sedimente möglichst jung, möglichst im Quartär abgelagert wurden, die enthaltenen Mikrofossilien einen guten bis sehr guten Erhaltungszustand aufweisen und in ausreichender Individuenzahl vorhanden sind.

Die zunächst wichtigsten Fragen sind: Um welchen Gewässertyp handelt es sich? Wie hat sich die Salinität entwickelt? Gibt es strukturbedingte Salinitätsgradienten? Aus der mikropaläontologischen Analyse lassen sich indirekt Aussagen über Änderungen von Struktur, Fläche und Volumen des Gewässers, Zuflüsse und Abflüsse, den Einfluss anderer Gewässer und das Klima bezüglich Niederschlag, Verdunstung und Lufttemperatur ableiten. Aber auch extreme Ereignisse wie Unwetter, Erdbeben, Vulkanausbrüche und Überschwemmungen rufen unter Umständen durch die Änderung der Salinität Faunenwechsel hervor. Hochenergetische Ereignisse wie Stürme und Tsunamis können allerdings auch die Diversität von Taphozönosen durch den direkten Eintrag von allochthonen Taxa in Sedimentfallen erhöhen.

Der Rekonstruktion sind jedoch auch Grenzen zu setzen: Die Wassertiefe lässt sich nur grob abschätzen, da die athalassische Fauna zum überwiegenden Teil aus dem küstennahen Flachwasser stammt. Unter den meist extremen ökologischen Bedingungen ist die Diversität von Foraminiferen und Ostrakoden gering bis sehr gering. Diversitätsindizes und viele statistische Analysen sind bei solchen Faunen nicht oder nur bedingt anwendbar. Salinitätsgradienten lassen sich bei monospezifischen Faunen meist durch Gehäusespezifikationen herausarbeiten. Bei hoher Standardabweichung sind hierbei aber nur ungenaue Aussagen möglich.

4.2 Typische Mikrofaunenassoziationen athalassischer Gewässer

Vor allem in Gewässern nahe der Küste kommen Faunenassoziationen randmarinen Ursprungs mit höherer Diversität vor. Neben hauptsächlich marinen Foraminiferen und Ostrakodenarten können auch wenige limnische Ostrakodenarten mit hoher Salztoleranz auftreten. Die erhöhte Diversität kann unter anderem auch durch die räumliche Nähe zum Meer und die dadurch bedingten kurzen Transportwege erklärt werden. Die Salinität rangiert in der Regel leicht unterhalb der Meeresalinität. Im Gegensatz dazu findet man wenig diverse Fauna intertidalen Ursprungs vorwiegend in hypersalinen Gewässern arider und semiarider Gebiete. Hier ist häufig ein Massenvorkommen einiger weniger intertidaler Arten zu beobachten. Die geringe Diversität ist auch durch die große Entfernung zum Meer erklärbar. Mischfaunen beinhalten Arten unterschiedlichen Ursprungs. Vor allem im mesohalinen Bereich rund um 10 psu können limnische Arten neben brackischen Taxa auftreten.

4.3 Vergleich von Faunen athalassischer, Süß- und randmariner Gewässer

Athalassische Gewässer sind strukturell gesehen Binnengewässer der Kontinente. Die Salinität kann sehr unterschiedlich sein und ebenso die Zusammensetzung der gelösten Salze. In den humiden Gebieten der gemäßigten Klimazone bleibt die Salinität in der Regel unterhalb der marinen, in ariden oder polaren Gebieten kann diese bis zu zehnmal höher sein. Foraminiferen- und Ostrakodenfaunen athalassischer Gewässer ähneln je nach Salzgehalt denen der

Süßgewässer oder des Intertidals der Küsten. Sie können auch, vor allem im mesohalinen Bereich, Organismen aus beiden Faunengruppen enthalten. Die Diversität ist meist gering, vor allem im hypersalinen Bereich. Vollmarine Organismen wandern in diese Gewässer nicht ein, selbst bei ähnlicher Salinität. Daraus ist zu schließen, dass für marine Organismen noch weitere Umweltfaktoren als die Salinität eine entscheidende Rolle spielen. Vor allem eine Stabilität von Faktoren wie Temperatur, Wassertiefe aber auch Salinität fördert eine hochdiverse Fauna. In Binnengewässern sind langfristige stabile Bedingungen nicht gegeben. Dies könnte auch die deutlich erhöhte Missbildungsrate von Foraminiferengehäusen in athalassischen Gewässern gegenüber den Ozeanen erklären. Eine andere Erklärung ist die fehlende Konkurrenz in athalassischen Lebensräumen, die eine weniger ausgeprägte Selektion nicht optimal angepasster Individuen zur Folge hat.

4.4 Fazit

Athalassische Ostrakoden und Foraminiferen entstammen immer dem marinen Intertidal, im oligohalinen bis mesohalinen Brackwasserbereich können salztolerante Süßwasserostrakoden dazu kommen (Beitrag 3). Extreme Bedingungen wie starke Salinitätswechsel und Hypersalinität werden nur von euryhalinen Arten wie *Cyprideis torosa* und *Ammonia tepida* toleriert (Beitrag 5 bis 7). Wenn kein Endemismus erkennbar ist, erfolgte entweder ein regelmäßiger Eintrag durch Vögel oder das Gewässer war zeitweilig mit anderen Gewässern verbunden. Über die Fauna lassen sich Salinitätswechsel belegen, diese werden einerseits durch lokale, strukturelle Veränderungen hevorgerufen, vor allem durch das Vorhandensein oder Fehlen eines Abflusses des Gewässers, andererseits aber auch durch Änderungen des Klimas (Beiträge 2 und 4) . Der individuellen Wasserchemismus athalassischer Binnengewässer lässt sich nicht, oder höchstens grob rekonstruieren.

Ehemalige athalassische Gewässer lassen sich durch zwei Hauptmerkmale identifizieren: Die in den Sedimenten enthaltenen Fossilien stammen von intertidalen, salztoleranten oder sogar euryhalinen Organismen und der Lebensraum hatte eine klar erkennbare Abgrenzung zum Meer (Beiträge 6 und 7). Athalassische Gewässer klimatogener Salinität erreichen meist höhere Salinitäten als solche mit geogener Salinität. Die Diversität von Ostrakoden und Foraminiferen ist in klimatogenen athalassischen Gewässern geringer, da nur euryhaline Organismen hypersaline Verhältnisse tolerieren. Typischerweise sind dies die Ostrakodenart *Cyprideis torosa* und Foraminiferen wie *Ammonia tepida* und *Quinqueloculina seminula* (z. B. Beiträge 6 und 7). Diese Assoziationen können daher eine beginnende Aridisierung anzeigen. Die geringe Artenzahl mariner Gruppen in athalassischen Gewässern erklärt sich nicht nur aus der meist vom Meer verschiedenen Salinität und Ionenzusammensetzung sondern auch durch den eingeschränkten Transport von Individuen des marinen Intertidals in das Binnenland, wahrscheinlich durch Vögel.

Die Nutzung der salinitätsabhängigen morphologischen Variabilität bei *Cyprideis torosa* (Knoten und Siebporenumrisse) und der Missbildungsrate von Foraminiferen konnte über eine Quantifizierung des Zusammenhangs optimiert werden, wodurch eine weitere Differenzierung der Salinität auch bei artenarmen und euryhalinen Assoziationen möglich ist (Beiträge 7 bis 9). Fossile Foraminiferen und Ostrakoden athalassischer Gewässer erlauben vor allem über die Rekonstruktion der Salinität, aber auch über Temperaturrekonstruktionen durch Mutual Ecological Range-Methoden und Transferfunktionen, paläoklimatische Analysen.

In Mitteldeutschland, unter humiden Klimabedingungen, zeigte sich, dass Phasen höherer Niederschläge zu erhöhter Salinität durch verstärkte Mobilisierung von Salzen im Untergrund führten, nicht jedoch aridere Klimaphasen (Beitrag 2).

Nicht in allen aquatischen Sedimenten kommen Mikrofossilien vor. Für den Fall, dass sich keine Foraminiferen und Ostrakoden in den Sedimenten befinden, sind folgende Gründe denkbar: Starke Turbulenz oder Strömung, welche entweder keine Besiedlung zulassen oder Gehäuse und Klappen umlagern. Hohe Sedimentationsraten können Taphozönosen „verdünnen“, sodass Mikrofossilien nur vereinzelt vorkommen. Lebensfeindliches Milieu, z. B. hohe oder niedrige pH-Werte, können eine Besiedlung verhindern (siehe auch Kapitel 1.1). Aber auch in dicht besiedelten Habitaten können karbonatische Mikrofossilien synsedimentär oder später diagenetisch gelöst werden. Zur Beurteilung fossilführender Sedimente kann für die erste Schnellanalyse das Schema der Abb. 8 verwendet werden.

Assoziation	limnische Ostrakoden	limnische und salztolerante Ostrakoden	limnische und brackische Ostrakoden wenige intertidale Foraminiferen	limnische, brackische und marine Ostrakoden brackische und marine Foraminiferen	ausschließlich marine Ostrakoden und Foraminiferen	Cyprideis torosa und wenige intertidale Foraminiferen	ausschließlich Cyprideis torosa
Diversität	mittel	mittel	mittel	mittel	hoch	niedrig	monospezifisch
Lebensraum	Binnengewässer Süßwasser	Binnengewässer oligohalin	Binnengewässer mesohalin	Küstensee, Lagune, Salzmarsch, Mangroven, große mesohaline Seen, Randmeere	Marin	Binnengewässer mesohalin-hyperhalin	Binnengewässer hyperhalin
Beispiel	Stausee Kelbra (Thüringen)	Siebleben (Thüringen)	Mansfelder Seen (Sachsen-Anhalt)	Ostsee Große Seen (USA)	Ozeane	Tayma (Saudi-Arabien)	Aralsee nach 2000 (Kasachstan)

Abb. 8: Übersicht über Merkmale von Gewässern.

Schlüssel für die Klassifizierung von Sedimenten zur Rekonstruktion des Ablagerungsraums

1) Nur Ostrakoden (treten auch Foraminiferen auf, weiter zu 2):

1a) Nur limnische Ostrakoden: Limnisch, Süßwasser (Beispiel: Stausee Kelbra, Thüringen; Beitrag 1).

1b) Limnische und Brackwasserostrakoden: Limnisch, Süßwasser bis oligohalin (Beispiel: Siebleben, Thüringen; Beitrag 2).

1c) Monospezifische Ostrakodenfauna mit *Cyprideis torosa*: Limnisch, hyperhalin, oft eutroph (Beispiel: Aralsee nach 2000; Beitrag 5).

2) Ostrakoden und Foraminiferen

2a) Limnische und Brackwasserostrakoden und sehr wenige euryhaline Foraminiferen: Limnisch, oligohalin bis mesohalin (Beispiel: Salziger See, Sachsen-Anhalt; Beitrag 4).

2b) *Cyprideis torosa* und sehr wenige Foraminiferenarten aus dem Intertidal mit hoher Missbildungsrate: Salzseen in ariden Klimaten, polyhalin oder hyperhalin (Beispiel: Tayma, Saudi-Arabien; Beiträge 6 und 7).

2c) Süßwasserostrakoden sowie Brackwasser- und marine Ostrakoden und Foraminiferen, mittlere bis geringe Diversität: geschlossene Lagunen, Küstenseen, Ästuare, Randmeere (Beispiel: Ostsee), aber auch sehr große und langlebige Binnengewässer (Beispiel: Kaspisches Meer).

2d) Marine Ostrakoden und Foraminiferen, hohe Diversität: Ozeane und Epikontinentalmeere

4.5 Ausblick

Athalassische Gewässer lassen sich mit Hilfe von Mikrofossilien in der Regel gut erkennen und charakterisieren. Die Faunenassoziationen von Foraminiferen und Ostrakoden reflektieren Salinität, Struktur und geographische Lage der Gewässer sowie das regionale Klima. Jedoch muss vor allem der Einfluss des individuellen Wasserchemismus athalassischer Gewässer auf Foraminiferen und Ostrakoden noch weiter untersucht werden, um mehr Informationen über diesen speziellen Gewässertyp zu erhalten. Übertragungswege der Faunen sollten überprüft werden. Bis jetzt scheinen als Überträger in weiter entfernte Gewässer, vor allem in ariden Gebieten, nur Vögel in Frage zu kommen. Athalassische Faunen älterer geologischer Systeme sind schwieriger zu erkennen, da hier keine rezenten Arten zum Vergleich zur Verfügung stehen. Jedoch können höhere taxonomische Einheiten verwendet werden, wenn auch mit geringerer Aussagekraft. Ein erstes Indiz für die Erkennung erdgeschichtlich älterer athalassischer Sedimente kann die sehr niedrige Diversität sein. Auch Foraminiferen, die gemeinsam mit Brack- oder Süßwasserostrakoden vorkommen, können auf ein athalassisches Gewässer hinweisen. Missbildungen bei Foraminiferen, sowie Buckelbildung bei cytheriden Ostrakoden sind ebenfalls zu erwarten und können zur Diagnose beitragen.

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Jena, 17. Februar 2016

Anna Pint