Thematic set:
Cyprideis torosa

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Ostracod fauna associated with *Cyprideis torosa* – an overview

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Abstract: The ostracod *Cyprideis torosa* (Jones) tolerates a wide range of salinity from fresh to brackish water-transition to hyperhaline values. The species often dominates ostracod assemblages in oligohaline and hyperhaline waters. For a more precise determination of controlling ecological factors, mainly the salinity, the accompanying ostracod fauna needs to be investigated. In oligohaline inland water bodies of humid climates, *C. torosa* is associated with tolerant non-marine ostracods. In coastal lagoons the mostly very low-diversity ostracod assemblages are characterized by brackish taxa accompanying *C. torosa*. In saline lakes of arid climatic zones non-marine and brackish species occur together, but brackish ostracods frequently dominate the assemblages. Monospecific occurrences of *C. torosa* are realized mainly in hypersaline environments. Examples are given that represent typical ostracod taxa that co-occur with *C. torosa*.

Keywords: athalassic waters, coastal lagoons, marginal marine, assemblages, brackish water, hyperhaline

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Cyprideis torosa (Jones) is a widespread, euryhaline species mainly living in brackish waters of coastal areas (Meisch 2000). It often dominates oligohaline lagoons but it occurs monospecifically only in hyperhaline environments. *Cyprideis torosa* also lives in saline inland water bodies in all climatic zones, often in high numbers. Due to its broad tolerance of salinity, from 0.5 to more than 100 psu (Meisch 2000), only the associated fauna allows detection of salinity variations when referring to ecological tolerances. Salinity variability reflects climate and environmental changes in ancient ecosystems. Especially in coastal regions the accompanying ostracod species may help to detect salinity changes based on the connection or disconnection of coastal waters to the sea. The most common accompanying ostracod species are typical for brackish waters (Table 1).

We present modern and fossil examples from athalassic waters, coastal lakes and lagoons, salt marshes and estuaries from northern and central Germany, UK, Portugal, Italy, Turkey, the Arabian Peninsula, the Black Sea, the Aral Sea, USA and Chile (Fig. 1). The examples presented here show different types of ostracod faunas accompanying *C. torosa* and are related to salinity (Fig. 2; Table 2).

Comparison of modern and fossil assemblages provides similarities concerning the environment independent of the geographical situation. The accompanying ostracod taxa of *C. torosa* in fossil assemblages could help to detect environmental changes especially in coastal regions. Although a taphocoenosis may reflect thanatocoenosis incompletely, a general picture of the palaeoenvironment can be revealed.

Material and methods

The material considered herein comes from both Holocene sediment cores and outcrops and modern surface samples as listed within the results section. From the cores and outcrops we selected layers with the highest relative abundance of *Cyprideis torosa* compared to other ostracod species in a more or less stable environment for the present study. After wet sieving, ostracods were picked, identified and counted. A ternary plot was applied to determine the faunal composition patterns of *C. torosa* together with brackish/marine and non-marine ostracods based on the percentages of the mean number of individuals (Fig. 2). For the modern sites we describe the specific associations and classify them according to controlling environmental factors and water types. For the fossil sites we selected a representative part of the sections where *C. torosa* is dominant for the statistical analysis. In addition we list the accompanying ostracod taxa for the complete sections. Due to the inconsistent assignment of some taxa to brackish or coastal marine environments in the literature, we classify them together as the brackish/marine group.

Results

Modern assemblages

Saline inland water bodies

The Pyramid Lake is located in a semi-arid region of Nevada (USA) and is a residual lake of the former postglacial Lake Lahontan (Fig. 1). It is an endorheic salt lake with a salinity of 6 psu. *Cyprideis torosa* is associated with five non-marine ostracod taxa, the most common of which are *Candona neglecta* and *Leucocythere* sp. (Table 2).

Lagoons at marginal seas

The Greifswalder Bodden is a large coastal lagoon only partly separated from the southern Baltic Sea (Fig. 1). The salinity is around 8 and varies between about 5 and 10 depending on prevailing wind direction. *Cyprideis torosa* is associated with nine brackish/marine and two non-marine taxa (Frenzel 1996). Foraminifers are represented by four species only, the dominating species being *Miliammina fusca* (Frenzel 1996).

The Oderhaff is a coastal lagoon at the border between Germany and Poland and strongly influenced by the large river Oder (Fig. 1). Salinity varies quite unpredictably between 0.5 and 2.5, averaging around 2 psu depending on freshwater input through the Oder and wind pushing water from the open Baltic Sea via a connecting stream, the Peenestrom, into the lagoon. One brackish/marine and five non-marine taxa occur together with *C. torosa* (Frenzel 1991). Foraminifers are lacking.

The Strelasund is a sea strait connecting two lagoon-like embayments of the southern Baltic Sea (Fig. 1). The salinity is around 7 but may rise up to 10 or drop to 5, depending on prevailing

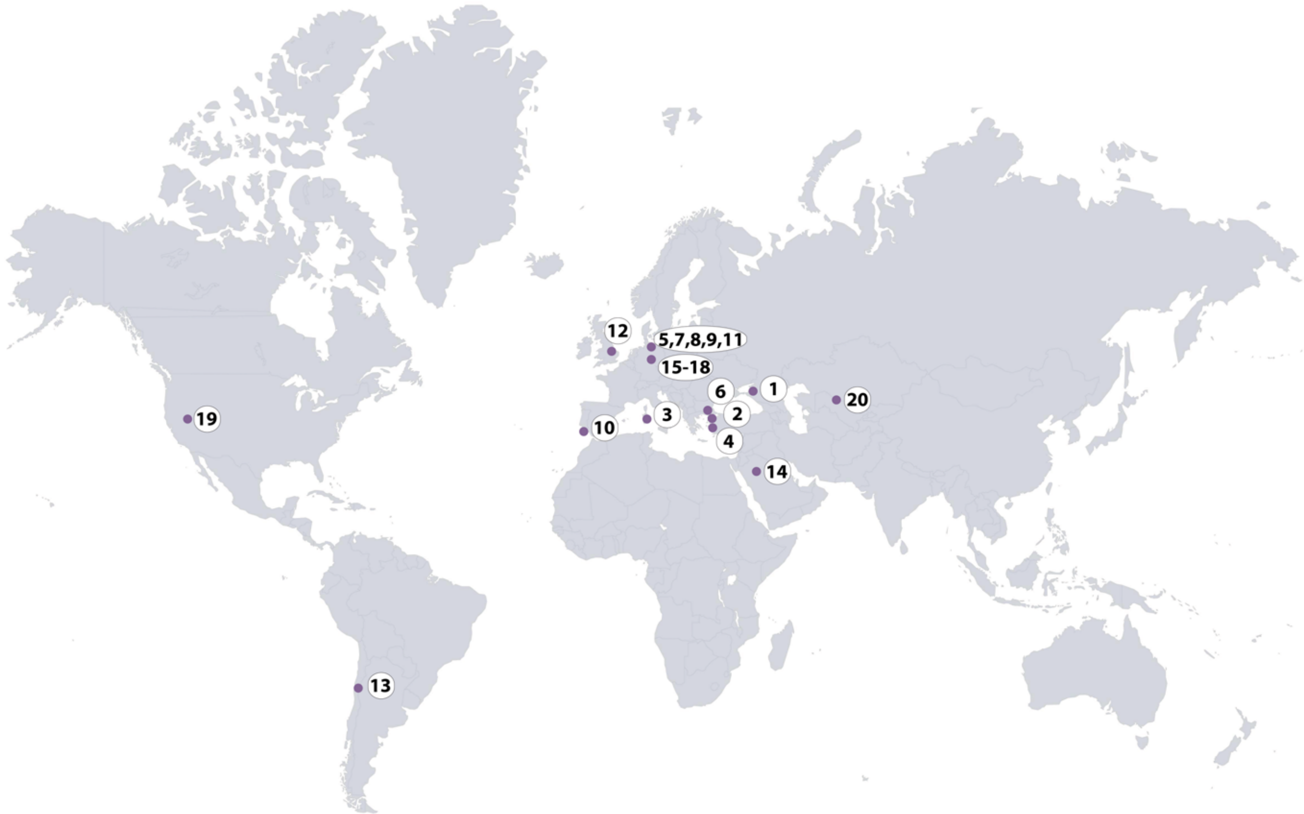

Fig. 1. Map of investigated sites. 1 – 9: lagoons; 10 – 12: estuaries; 13: coastal lake; 14 – 20: athalassic waters. See Figure 2 for location names.

winds. Eight brackish/marine and two non-marine taxa occur together with *C. torosa* (Frenzel & Oertel 2002). Foraminifers are common and represented by six species dominated by *M. fusca* (Frenzel 2005).

Two lagoons are situated around the city of Enez (Turkey; Fig. 1). Depending on the season, the salinity varies between 15 and 27, as measured in 2013 – 15. Black sediments and the smell of hydrogen sulphide point to dysoxic conditions. Surface sediment samples, taken from the central parts of the lagoons, show that *C. torosa* is accompanied by coastal brackish/marine taxa dominated by *Loxoconcha elliptica* and also accompanied by a few individuals of the non-marine ostracod *Limnocythere inopinata*, known to live in salinities up to 25 (Griffiths & Holmes 2000). Most common foraminifers are *Ammonia tepida* and *Haynesina germanica*.

The Tuzla lagoon close to the city of Erikli in Turkey (Fig. 1) is a coastal lagoon with a water depth of less than 2 m. The salinity varies seasonally between 37 and 40. *Cyprideis torosa* occurs together with *Leptocythere* spp. and *Eucypris inflata*. The most common foraminifer is *H. germanica*.

The lagoon of Cabras is situated on the western coast of Sardinia (Fig. 1). It is connected with the Bay of Oristano by a narrow channel. A surface sediment sample, taken in the southern littoral zone of the lagoon, was investigated. The salinity was around 5 psu during sampling in 2015; variability is unknown. The only ostracod accompanying *C. torosa* is *L. elliptica*. The most common foraminifer is *A. tepida*.

The ancient harbour of Elaia is located in the Bay of Çandarlı in western Turkey (Fig. 1). There are small residual ponds within a salt marsh area in what was the former harbour basin. It has a salinity of about 37 and is tidal-influenced.

Estuary

The Warnow estuary, located at the city of Rostock (Fig. 1), flows into the southern Baltic Sea. The salinity is around 12 and may be lowered slightly depending on freshwater inflow. Together with *C. torosa*, seven, exclusively non-marine, ostracods occur. Most common are *Darwinula stevensoni* and *Physocypria kraepelini*. Seven foraminifer species were found in the estuary, *Cribroelphidium* species dominate.

Fossil assemblages

Saline inland water bodies under humid climate

The depression of Siebleben, situated in central Germany close to the city of Gotha (Fig. 1), formed due to postglacial subrosion within the salt-bearing Triassic basement. The sediments

Table 1. *Cyprideis torosa's most common accompanying ostracod species*

Taxon	Environment	Salinity range (psu)	References
Loxoconcha elliptica	Coastal lagoons and estuaries	0.5 – 30	Theisen (1966)
Cytheromorpha fuscata	Saline inland water bodies and coastal lakes and lagoons	0.5 – 20	Neale & Delorme (1985)
Limnocythere inopinata	Saline and fresh inland water bodies, coastal lakes, estuaries	0 – 25	Ruiz *et al.* (2013)
Candona neglecta	Saline and fresh inland water bodies, coastal lakes, estuaries	0 – 15	Ruiz *et al.* (2013)
Heterocypris salina	Saline and fresh inland water bodies, coastal lakes, estuaries	0.5 – 27	Ruiz *et al.* (2013)
Sarscypridopsis aculeata	Saline and fresh inland water bodies, coastal lakes	0.5 – 17	Frenzel *et al.* (2010)
Darwinula stevensoni	Saline and fresh inland water bodies	0 – 15	Ruiz *et al.* (2013)

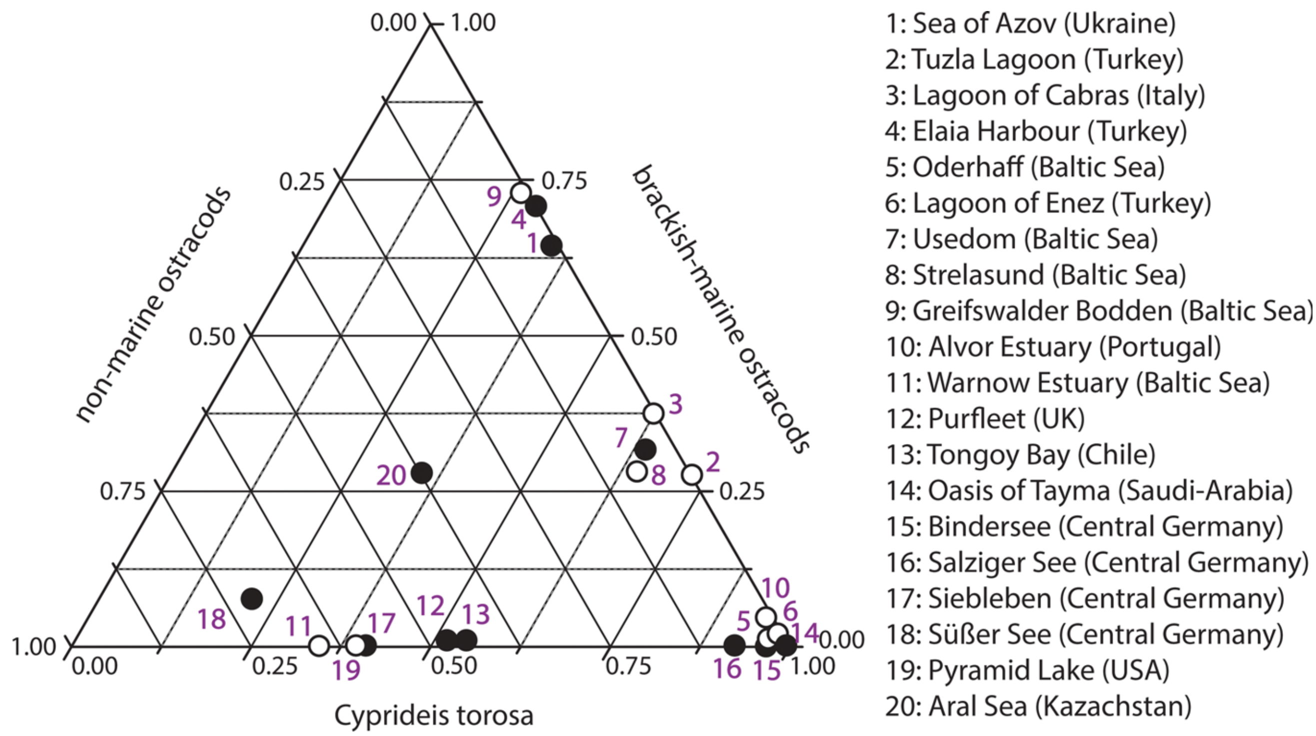

Fig. 2. Ternary percentage plot of the relative abundances of *Cyprideis torosa,* freshwater and brackish-water taxa from the studied sites. Modern sites are presented by white circles and fossil sites are presented by filled circles. 1 – 9: lagoons; 10 – 12: estuaries; 13: coastal lake; 14 – 20: athalassic waters (see Table 2).

Table 2. *The various types of ostracod faunas accompanying C. torosa in different water bodies*

	Type of water	Most common species	Example in this study	Age
Athalassic environment	Oligohaline inland water bodies	*Heterocypris salina* *Candona neglecta* *Sarscypridosis aculeata Limnocythere inopinata* *Darwinula stevensoni* *Ilyocypris bradyi*	Siebleben, Germany Süßer See, Germany	Middle Holocene
	Mesohaline inland water bodies	*Candona neglecta* *Leucocythere* sp.	Pyramid Lake, USA	Recent
		Limnocythere inopinata Cytheromorpha fuscata	Salziger See, Germany Bindersee, Germany	Middle Holocene
			Aral Sea, Kazakhstan	Holocene until AD 1960
	Hyperhaline inland water bodies	Monospecific occurrence of *Cyprideis torosa*	Tayma, Saudi Arabia	Early Holocene
Marginal marine environment	Coastal lagoons	*Loxoconcha elliptica Leptocythere* spp. *Pontocythere turbida*	Enez, Turkey Sardinia, Italy	Recent
		Leptocythere spp. *Eucypris inflata*	Erikli, Turkey	
	Lagoons at marginal seas	*Cytheromorpha fuscata* *Cytherura gibba* *Xestoleberis aurantina* *Loxoconcha elliptica*	Strelasund, Germany Greifswalder Bodden, Germany Oderhaff, Germany	Recent
			Usedom, Germany	Middle Holocene
	Coastal lakes at marginal seas	*Loxoconcha* spp. *Xestoleberis* spp.	Lake Chokrak, Ukraine	Holocene
		Sarscypridopsis aculeata *Heterocypris salina*	Coastal lake, Tongoy Bay, central Chile	Late Holocene
	Estuaries	*Darwinula stevensoni Physocypria kraepeli*	Warnow Estuary, northern Germany	Recent
		Loxoconcha elliptica Leptocythere sp. *Urocythereis distinguenda*	Alvor Estuary, Portugal	Holocene
		Ilyocypris spp. *Darwinula stevensoni* *Limnocythere inopinata* *Fabaeformiscandona caudata*	Purfleet Thames Estuary, UK	Pleistocene
	Salt marsh	Strong dominance of *Cyprideis torosa*	Bay of Çandarlı, Turkey	Recent

Table 3. *Complete ostracod associations from studied sites*

Alvor Estuary (Portugal)	**Baltic Sea (Germany)**	**Central Germany**	**Aral Sea**	**Sea of Azov**
Aurila convexa (Baird) *Callistocythere littoralis* (G.W. Müller) *Cyprideis torosa* (Jones) *Cytherois fischeri* (Sars) *Elofsonia pusilla* (Brady & Robertson) *Falunia* cf. *sphaerulolineata* (Jones) *Heterocythereis albomaculata* (Baird) *Leptocythere fabaeformis* (G.W. Müller) *Leptocythere macallana* (Brady & Robertson) *Leptocythere* sp. *Loxoconcha elliptica* Brady *Loxoconcha malcomsoni* Horne & Robinson *Loxoconcha rhomboidea* (Fischer) *Neocytherideis subulata* (Brady) *Paracytheridea* aff. *Triquetratriquetra* (Reuss) *Paradoxostoma trieri* Horne & Whittaker *Pontocythere elongata* (Brady) *Sagmatocythere variesculpta* (Ruggieri) *Semicytherura acuticostata ventricosa* (G.W. Müller) *Semicytherura robertsi* Horne & Whittaker *Semicytherura* sp. *Semicytherura sulcata* G.W. Müller *Thaerocythere hoptonensis* (Brady, Crosskey & Robertson) *Urocythereis distinguenda* Athersuch *Xestoleberis aurantia* (Baird) *Xestoleberis communis* G.W. Müller	*Candona* spp. *Cypria ophtalmica* (Jurine) *Cypria subsalsa* Redeke *Cyprideis torosa* (Jones) *Cytheromorpha fuscata* Hirschmann *Cytherura gibba* (O.F. Müller) *Darwinula stevensoni* (Brady & Robertson) *Fabaeformiscandona protzi* (Hartwig) *Hirschmannia viridis* (O.F. Müller) *Ilyocypris decipiens* Masi *Leptocythere lacertosa* (Hirschmann) *Leptocythere porcellanea* (Brady) *Leptocythere psammophila* Guillaume *Leucocythere baltica* Diebel *Limnocythere inopinata* (Baird) *Loxoconcha elliptica* Brady *Semicytherura nigrescens* (Baird) *Xestoleberis aurantia* (Baird)	*Candona angulata* G.W. Müller *Candona candida* (O.F. Müller) *Candona neglecta* G.O. Sars *Cyclocypris laevis* O.F. Müller *Cyclocypris ovum* (Jurine) *Cyprideis torosa* (Jones) *Cypridopsis* sp. *Cypridopsis vidua* (O.F. Müller) *Cypris pubera* O.F. Müller *Cyprois marginata* (Straus) *Cytherissa lacustris* (G.O. Sars) *Cytheromorpha fuscata* Hirschmann *Darwinula stevensoni* (Brady & Robertson) *Eucypris inflata* (Sars) *Herpetocypris* sp. *Herpetocypris chevreuxi* (Sars) *Heterocypris incongruens* (Ramdohr) *Heterocypris salina* (Brady) *Ilyocypris bradyi* Sars *Ilyocypris gibba* (Ramdohr) *Ilyocypris* sp. *Leucocythere baltica* Diebel *Limnocythere blankenbergensis* Diebel *Limnocythere inopinata* (Baird) *Physocypria kraepelini* G.W. Müller *Plesiocypridopsis newtoni* (Brady & Robertson) *Potamocypris arcuata* (Sars) *Potamocypris* sp. *Pseudocandona marchica* (Hartwig) *Pseudocandona rostrata* (Brady & Norman) *Pseudocandona* sp. *Pseudocandona sucki* (Hartwig) *Sarscypridopsis aculeata* (Costa)	*Candona sp.* *Cyprideis torosa* (Jones) *Leptocythere cymbula* (Livental) *Limnocythere aralensis* Schornikov *Limnocythere inopinata* (Baird) *Loxoconchissa immodulata* Stepanaitys *Tyrrhenocythere amnicola* (Dubowsky) **Cabras (Sardinia)** *Cyprideis torosa* (Jones) *Loxoconcha elliptica* Brady	*Callistocythere* sp. *Cyprideis torosa* (Jones) *Heterocypris salina* (Brady) *Leptocythere histriana* Caraion *Loxoconcha pontica* Klie *Palmoconcha* sp. *Pontocythere* sp. *Xestoleberis* sp. **Enez (Turkey)** *Cyprideis torosa* (Jones) *Limnocythere inopinata* (Baird) *Loxoconcha elliptica* Brady
Tuzla Lagoon	**Warnow Estuary**	**Harbour of Ellaia, Candarli Bay (Turkey)**	**Pyramid Lake (USA)**	**Tongoy Bay (Chile)**
Cyprideis torosa (Jones) *Eucypris inflata* (Sars) *Leptocythere bacesoi* (Rome)	*Candona neglecta* G.O. Sars *Candona* spp. *Cypria ophtalmica* (Baird) *Cyprideis torosa* (Jones) *Fabaeformiscandona fabaeformis* (Fischer) *Ilyocypris decipiens* Masi *Physocypria kraepelini* G.W. Müller	*Cyprideis torosa* (Jones) *Leptocythere bacesoi* (Rome) Purfleet estuary (UK) *Cyprideis torosa* (Jones) *Fabaeformiscandona caudata* (Kaufmann) *Herpetocypris* sp. *Ilyocypris decipiens* Masi *Ilyocypris inermis* Kaufmann *Ilyocypris lacustris* Kaufmann *Ilyocypris salebrosa* Stepanaitys *Limnocythere inopinata* (Baird) *Scottia tumida* (Jones)	*Candona candida* (O.F. Müller) *Candona neglecta* G. O. Sars *Cyprideis torosa* (Jones) *Heterocypris salina* (Brady) *Leucocythere* sp. *Limnocythere inopinata* (Baird) *Sarscypridopsis aculeata* (Costa)	*Cyprideis torosa* (Jones) *Cypridopsis* sp. *Darwinula stevensoni* (Brady & Robertson) *Herpetocypris* sp. *Heterocypris salina* (Brady) *Ilyocypris* sp. *Limnocythere inopinata* (Baird) *Potamocypris unicaudata* Schäfer *Sarscypridopsis aculeata* (Costa)

investigated come from a core documenting the complete Holocene history of a lake (Pint *et al.* in press). Variations in ostracod assemblages point to salinity changes caused by the influence of salty groundwater. *Cyprideis torosa* occurs in high numbers during an oligohaline phase of the ancient lake in the Middle Holocene and is associated with 17 non-marine species. *Heterocypris salina*, *Sarscypridopsis aculeata*, *D. stevensoni*, *Limnocythere inopinata* and *Candona neglecta* occur frequently. The foraminifer *Haplophragmoides* sp. occurs in the surface sediments of the depression of Siebleben; however, it was not detected in the core.

The Mansfeld Lakes in central Germany comprised two lakes during the Holocene but only Süßer See still exists in its original form and extent (Fig. 1). The formerly large lake Salziger See was divided into two residual lakes: Bindersee and Kernersee. Similarly to Siebleben, the lake evolution followed subrosion processes about 13 ka ago (Wennrich, V. 2005. Die spätweichselglaziale und holozäne Klima- und Umweltgeschichte des Mansfelder Landes/Sachsen-Anhalt, abgeleitet aus Seesedimenten des ehemaligen Salzigen Sees. Unpublished PhD thesis, University of Leipzig). Salt from Zechstein (Permian) evaporitic rocks caused the brackish character of the lake water. Sediment from a core contains *C. torosa* together with 21 non-marine species and *Cytheromorpha fuscata*, another brackish species, which could tolerate salinity values up to 20 (Neale & Delorme 1985). The salinity here is estimated to be oligohaline to beta-mesohaline, with values up to 8. *Limnocythere inopinata*, *H. salina*, *S. aculeata* and *D. stevensoni* occur most frequently. In some distinct horizons of the lake sediments of Middle Holocene age, the foraminifers *A. tepida* and *Milliammina fusca* occur.

Lagoons situated at marginal seas

The material from the peninsula of Usedom derives from a sediment core taken from a coastal barrier situated in the central part of the island at the southern Baltic Sea coast in northeastern Germany (Viehberg *et al.* 2008; Fig. 1). Here, we present only that part of the sequence when limnic and fluvial environmental conditions turned to brackish/marine conditions during the Littorina Transgression (Middle Holocene, with an estimated salinity of 5 – 10; Viehberg *et al.* 2008). Eight brackish/marine and three non-marine taxa are associated with *C. torosa*. Foraminifers are rare and dominated by *A. tepida*.

The Black Sea material comes from a sediment core taken from a sand barrier separating Lake Chokrak on the Kerch Peninsula from the Sea of Azov (Fig. 1). A former marine embayment turned into a restricted lagoon due to sand spit development about 5 ka ago. Around AD 500, the water was completely disconnected from the sea (Kelterbaum *et al.* 2012). The most common species are *Loxoconcha pontica* and *Xestoleberis* sp.. The non-marine ostracod *H. salina* occurs only in small numbers. One limnic and six brackish/marine taxa are associated with *C. torosa*. Foraminifers also occur – mainly *Ammonia* spp. and *H. germanica*.

Coastal lake

A sediment core of a coastal lake in the Tongoy Bay in central Chile (Fig. 1) close to the coast covers the last 1000 years. Present-day salinity is controlled mainly by splash water events. Slightly alternating lower and higher brackish-water conditions are reflected by the ostracod and foraminifer assemblages. *Cyprideis torosa* is associated with *S. aculeata*, *H. salina* and seven other non-marine ostracods. Also the foraminifer *A. tepida* occurs in small numbers (May *et al.* 2013).

Estuaries

The Alvor estuary is located on the southern Portuguese Atlantic coast (Fig. 1). The outer part of the estuary forms a coastal lagoon. Trog *et al.* (2013) investigated the last 7.5 ka of its evolution relying on sediment cores containing brackish/marine ostracods and *C. torosa* in some parts. Beside *C. torosa* there are 25 brackish/marine taxa; non-marine taxa are missing. The most common species are *L. elliptica, Leptocythere* sp. and *Urocythereis distinguenda*. Foraminifers occur as well, mainly *H. germanica* and *A. tepida*.

The Pleistocene estuary of the Thames at Purfleet is situated east of London. Eleven ostracod taxa are described from this site (Schreve *et al.* 2002; Bridgland *et al.* 2013). We found 10 ostracod taxa as well as foraminifers, although they are not mentioned in the previous studies, in the investigated sample from the middle part of bed 5, dated to MIS 9 (see Schreve *et al.* 2002). They belong to the genera *Ammonia*, *Elphidium*, *Cibicides* and *Bulimina*. The most abundant ostracod species is *C. torosa*. Most of the valves are noded. Following Frenzel *et al.* (2012) this points to a salinity below 2. Also common are *Ilyocypris* spp. and *D. stevensoni*. *Limnocythere inopinata* (both sexes), *Scottia tumida* and *Fabaeformiscandona caudate* are rare.

Saline lakes in arid areas

Until 1960 the Aral Sea in Central Asia was the largest endorheic lake in the world (Fig. 1). The salinity was stable at around 11 (Boomer *et al.* 1996). Seven brackish and non-marine ostracod species, one of those endemic, were established more than 18 ka ago, as Boomer (2012) presented based on a sediment core taken from the southern part of the lake. The ostracod fauna of the Aral Sea was unique in the world. Within two Holocene cores investigated *C. torosa* is associated with three brackish species (*Loxoconcha immodulata*, *Thyrrhenocythere amnicola*, *Leptocythere cymbula*), one brackish species and three non-marine species (*L. inopinata*, *Limnocythere aralensis*, *Candona* sp.). This assemblage existed in a salinity of around 10 before drainage of the lake started in 1960. After the rapid increase in salinity since 1980, *C. torosa* was the only surviving ostracod (Aladin & Plotnikov 2003). Three foraminifer species from the genera *Ammonia*, *Cribroelphidium* and *Elphidiella* occurred in the Aral Sea before the large-scale irrigation projects that began in the 1960s.

The Oasis of Tayma is located in arid northern Saudi Arabia close to the An Nafud desert (Fig. 1). A palaeolake formed a continental sabkha in the Early Holocene (Engel *et al.* 2012). *Cyprideis torosa* occurred monospecifically and in very high numbers. Hyperhaline salinities are reconstructed based on sieve pore analysis of *C. torosa* (Engel *et al.* 2012). Four foraminifer species occur in the palaeolake of Tayma, dominated by *A. tepida*.

A ternary plot (Fig. 2) presents the percentages of *C. torosa*, brackish-marine and non-marine ostracods. In lagoons, *C. torosa* occurs mainly together with brackish-marine ostracods, whereas athalassic sites and inner parts of estuaries are characterized by non-marine ostracods and very low percentages of brackish-marine taxa. Only the Aral Sea presents similar proportions of the three groups. The only real monospecific occurrence of *C. torosa* was found in the ancient lake of the Oasis of Tayma. However, the percentages of *C. torosa* in the Turkish lagoons and salt marshes are very high, more than 90%.

Discussion

Cyprideis torosa is known to live in marginal marine and athalassic waters of the Northern Hemisphere (Meisch 2000) and is considered to be an indicator of elevated salinity (Gramann 2000). It populates lagoons, estuaries, coastal ponds and lakes, salt marshes, as well as athalassic water bodies connected to salty springs (Meisch 2000; Pint *et al.* 2012; Fuhrmann 2013), inhabiting a salinity range of 0.4 – 60 (Frenzel *et al.* 2010) or even higher (Meisch 2000). Permanent, brackish and shallow water bodies of only a few metres under relatively warm conditions in summer are required for its

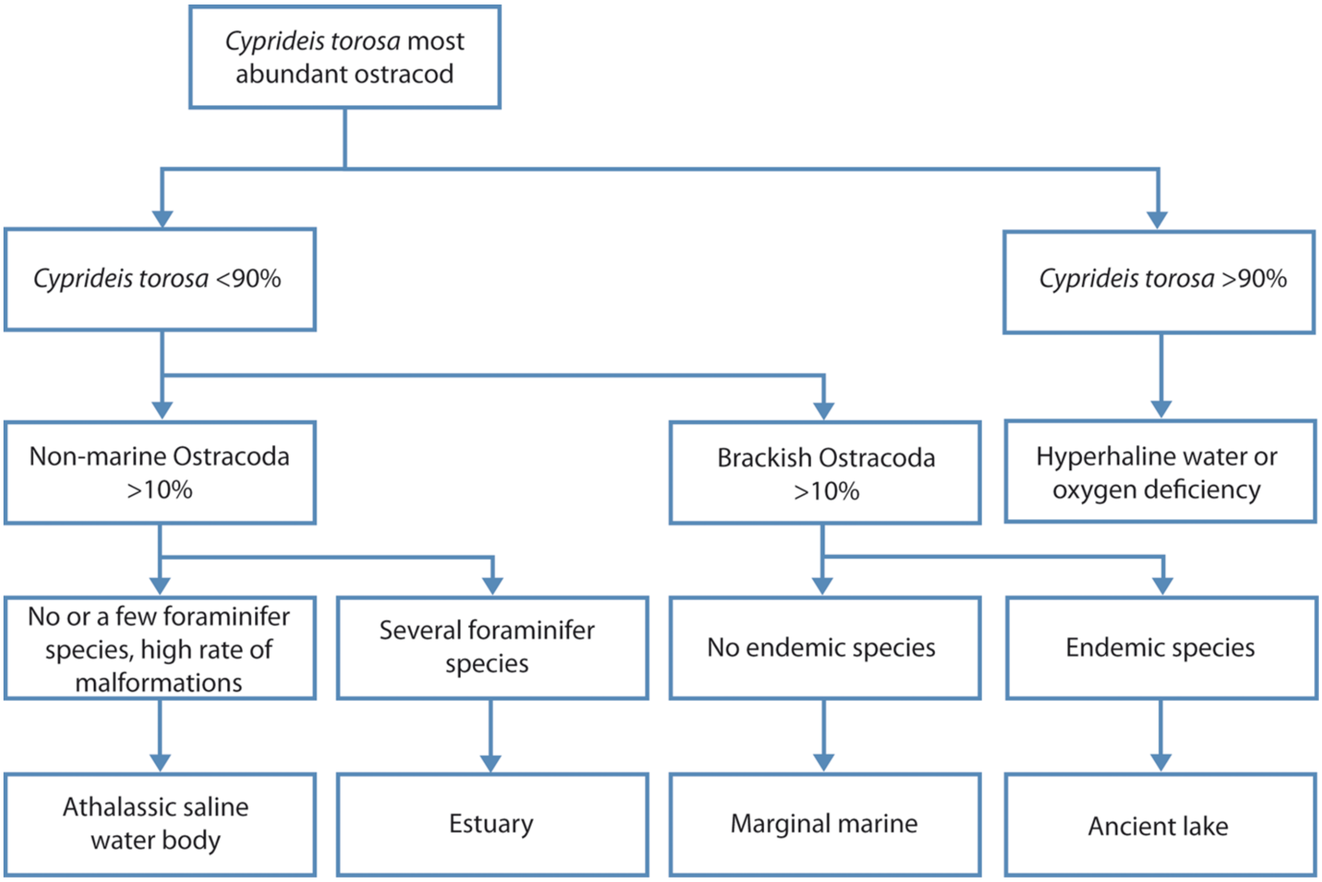

Fig. 3. Flowchart for palaeoenvironmental interpretation of *Cyprideis torosa*-dominated assemblages.

settlement (Pint *et al.* 2012). It can withstand oxygen deficiency and even the presence of H_2S (Gamenick *et al.* 1997). Our study of samples with *C. torosa* as the most abundant ostracod species covers all these general water types with selected examples.

Analyses on fossil ostracod associations rely mainly on taphocoenoses. Using preservation and population structure as indicators, allochthonous elements may be identified (Boomer *et al.* 2009), but this criterion is hard to use for well-preserved specimens of rare species. Hence, some portions of the studied associations have to be accepted as unidentified allochthonous elements. This problem is especially serious in estuaries, where inflowing water from the mainland and also the sea carries ostracod shells to the sites. Similarly, athalassic saline lakes and coastal lagoons with abundant *C. torosa* may be affected by transported limnic taxa from rivers or marine taxa from the sea. The produced taphocoenosis is, of course, not completely an assemblage of animals living together or in the same location over the seasons but a mixture of autochthonous and allochthonous elements. This makes palaeoecological interpretation more complicated but tells us something about provenance and, hence, the character and interconnectedness of the studied water body. We confess that we are not able to judge the autochthonous character of every individual registered in our count, but use its presence for the characterization of the waters inhabited by *C. torosa*, thus integrating ecological and taphonomical information.

Coastal lakes or ponds belong to the marine system, but due to its location in the supratidal zone they are often controlled more by freshwater inflow and precipitation than by seawater. In those environments a non-marine ostracod fauna may develop based on the low salinity (Ganning 1971; May *et al.* 2013) and indicate an irregular connnection to the sea.

The plot of proportions of *C. torosa*, brackish/marine water and non-marine ostracods reveals two clearly separated trends along the *C. torosa* axis and along the brackish/marine axis meeting at 100% of *C. torosa* (Fig. 2). The only exception is the sample from the Aral Sea, but some of its ostracod species could not be assigned clearly to an ecological group. The salinity range of the endemic species *L. aralensis* is unknown; the same is true for *Tyrrhenocythere amnicola*, which we suppose is a brackish species. The sample from the Aral Sea falls in the centre of the diagram and may point to the exceptional situation of the Aral Sea: a giant brackish-water lake far from marine coasts but quite stable in salinity and of sufficient size and longevity to allow repeated successful colonization by brackish-water taxa. The long existence of the lake enabled the origination of one endemic species, whereas all other taxa of the brackish waters are widespread or even cosmopolitan. Such endemic species may be used as indicators of ancient lakes. However, *Tyrrhenocythere donetziensis*, probably a synonym of *T. amnicola*, was described from a slightly brackish lake (Griffiths *et al.* 2002) and, therefore, could be classified as a non-marine species. However, it is rare in the Aral Sea and thus its uncertain classification does not change the position of the Aral Sea in the ternary plot. All other athalassic waters studied here group along the *C. torosa* axis with a brackish/marine proportion <10%. In contrast, thalassic sites plot along the brackish/marine-axis with a non-marine proportion <10% (Fig. 2). This means, in general, sites with *C. torosa* as the most abundant ostracod species are from athalassic waters if non-marine taxa prevail or from marginal marine waters if brackish/marine taxa are the more abundant of the two groups. But there are two exceptions – both are estuaries. The Warnow and the Purfleet estuaries both show high proportions of non-marine taxa. This can be explained by strong freshwater input through large rivers and confinement from the open sea. The samples are derived from the inner part of the estuaries, where the salinity is relatively low. In contrast, the sampling of the Alvor estuary was carried out in its outer part. This is reflected by the brackish companions of *C. torosa*, such as *L. elliptica* and *Leptocythere* sp., and point to a greater seawater influence. Distinguishing those associations from athalassic ones is possible by looking into the associated foraminifer fauna. If foraminifera are present they display a very low diversity of one to four species in athalassic sites but, in general, are more diverse in estuaries. But the crucial distinction is that the percentage of foraminiferal malformations is much higher in athalassic sites than in estuaries.

Discriminating associations with more than 90% *C. torosa* is difficult, and hyperhaline conditions or oxygen deficiency can cause such a situation.

Conclusion

The sole occurrence of *Cyprideis torosa* allows no detailed differentiation of salinity ranges. Although morphological valve features, such as nodes and sieve pores (Rosenfeld & Vesper 1976; Frenzel *et al.* 2011, 2012, 2016; Pint *et al.* 2012), may help to determine an estimation of salinity, the associated ostracod fauna may indicate water type and salinity as well. Each taxon associated to *C. torosa* represents an individual salinity range and variability, which could be applied to reconstruct athalassic and marginal marine environments. In athalassic inland waters, the composition of the associated fauna is highly variable and based mainly on salinity, size, structure and permanence of the water body (Fig. 3). Dominating ions also play an important role and climatic conditions cause long-term trends. Waters with low salinity are colonized mainly by non-marine ostracods, whereas marine species migrate into the estuaries or to nearshore ponds with higher salinity. Commonly, ostracods of various origins, such as non-marine, brackish or even marine, appear together in one ecosystem, especially in mesohaline waters. It is possible to differentiate athalassic waters of oligohaline salinity with a relatively diverse non-marine fauna, of mesohaline salinity with a few non-marine and brackish-water species and of hyperhaline salinity with the monospecific occurrence of *C. torosa* from marginal marine waters with higher diversity of brackish-water and a few marine ostracod species.

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