

## ***Cyprideis torosa* (Jones, 1850) in its type area and stratigraphical context: potential for mapping the freshwater/estuarine boundaries of the Thames–Medway river system in the MIS 9 and MIS 11 interglacials**

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**ABSTRACT:** This study explores the potential of the ostracod *Cyprideis torosa* (Jones, 1850) as a brackish-water indicator for mapping freshwater/estuarine boundaries in Pleistocene interglacials in SE England. Ostracod species records from MIS 9 (Purfleet) and MIS 11 (Hoxnian) interglacial sites are mapped onto established palaeogeographies of the Thames-Medway river system, revealing distribution patterns indicative of a salinity gradient from west (freshwater) to east (brackish estuarine) in both cases. Comparisons with the ostracod biofacies of the present-day Thames Estuary suggest there may be no exact modern analogue for the Thames/Medway palaeoenvironments of the MIS 9 and MIS 11 interglacials. A similar conclusion is drawn from discussion of nodding in *C. torosa*, which is common in the interglacial assemblages but extremely rare in the modern estuary. The value of mapping *C. torosa* onto estuarine palaeogeography is limited by taphonomic considerations because post-mortem transport and mixing in a macrotidal estuary significantly influence the composition of ostracod assemblages. Nevertheless, its use in combination with other brackish-water taxa provides useful insights regarding the palaeosalinity regimes of the lower River Thames and River Medway during the MIS 9 and MIS 11 interglacials.

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In 1850 T. Rupert Jones described eight ostracod species, five of them new, from supposed Pleistocene sediments at Newbury (Berkshire) and Copford, Clacton and Grays (all in Essex). At Grays (the precise locality is, unfortunately, not known) he recorded six species: *Cypris tumida* sp. nov., *Cypris gibba* Ramdohr, *Candona lucens* Baird, *Candona reptans* (Baird), *Candona torosa* sp. nov., and ?*Cythere trigonalis* var. *laevis* sp. et var. nov. Within a few years he had revised his nomenclature a little (Jones 1857). *Cypris tumida* he now considered a variety of *Cypris browniana* (originally described also in 1850 by Jones, but from Clacton), he had synonymised *Candona lucida* with *C. candida* (O.F. Müller), and he placed *Candona torosa* into his new subgenus *Cyprideis*. It was not until later (Jones & Sherborn 1889) that Jones considered his ?*Cythere trigonalis* var. *laevis* to be a species of *Potamocypris*. He originally described *Cyprideis* as a subgenus of

*Candona* (a cypridoidean). Although he suspected already that it would “prove to be a *Cythere*” (Jones 1857, p. 20), in other words a cytheroidean, he was unable to confirm this at the time because he had been unable to examine the appendages of any living specimens (although he was aware of at least one living population on the southern coast of the Thames Estuary near Gravesend). *Candona torosa* Jones, 1850, being the only species assigned to the new genus in its original description, is automatically the type-species of *Cyprideis*.

*Cyprideis torosa* was subsequently transferred to the genus *Cytheridea* by Brady *et al.* (1874) who included in it *Cytheridea torosa* var. *teres*, introduced by Brady & Robertson (1870) for the un-noded form and being the equivalent of *Cyprideis littoralis*, described by Brady (1868) from salt marshes in NE England (*C. torosa* var. *torosa* being the noded form); this assignment was accepted by Jones & Sherborn (1889). The genus *Cyprideis*, subsequently recognized as distinct, is now well-established and in common use (see Kilenyi & Whittaker 1974, who designated and illustrated a lectotype of *C. torosa*).

Today Jones’ six species from the Pleistocene of Grays would be recognised under the following combinations:

*Cypris tumida* = *Scottia tumida* (Jones)

*Cypris gibba* = *Ilyocypris gibba* (Ramdohr)

*Candona lucens* =?? [although synonymised by Jones himself (1857) with *Candona candida* (O.F. Müller), and accepted by Griffiths (1995), the original drawing looks more like a specimen of *Candona neglecta* Sars, which has been found by us in collections from Grays; Baird’s name would be the senior synonym, but as no type specimens are available it must remain uncertain.]

*Candona torosa* = *Cyprideis torosa* (Jones)

?*Cythere trigonalis* var. *laevis* = *Potamocypris* sp. [Griffiths (1995, p. 133) is correct in stating that the species cannot be identified from Jones’ original illustration alone].

The deposits from which these ostracods were collected occupy a former channel of the River Thames (Lynch Hill / Corbets Tey terrace) and are now assigned to the Marine Isotope Stage (MIS) 9 “Purfleet” Interglacial (Penkman *et al.* 2013). The assemblage is essentially of freshwater character with the exception of *C. torosa*, now one of the best-known and most-studied of all ostracods and commonly regarded as an indicator of brackish water.

The aim of the present study is to explore the potential of *C. torosa*, as an indicator of low-salinity brackish water palaeoenvironments, for mapping the boundaries between freshwater and estuarine water in the Thames-Medway river system in Pleistocene interglacials. A database of ostracod species records has been compiled from ten fluvial sites representing the MIS 9 (Purfleet) interglacial, including Grays (the type locality and horizon of *C. torosa*), as well as four fluvial sites representing the MIS 11 (Hoxnian) interglacial. In addition the lacustrine MIS 11 site at Marks Tey is included because it holds an enigmatic record of *C. torosa*; note, however, that available records from this site most likely do not represent the Hoxnian interglacial but the transition into the succeeding cold stage (Horne *et al.* 2014).

## Methods

We compiled a database of ostracod records from Pleistocene interglacial sites in south-east England and used it to map the distributions of *C. torosa* and other species selected for their palaeosalinity implications, using a Geographical Information System (DIVA-GIS, version 7.5.0; Hijmans *et al.* 2001). Most of the ostracod records were obtained from published literature, but a few are from our own as-yet-unpublished data (see Table 1 for sources). We focused on two interglacials, MIS 9 and MIS 11, because the former includes the type locality and horizon of *C. torosa* and detailed palaeogeographical reconstructions based on palaeochannels are available for both (Bridgland *et al.* 1999; Schreve *et al.* 2002; Roe & Preece 2011). A summary map of modern ostracod biofacies in the Thames Estuary was constructed for comparison with the fossil distributions, using data from Kilenyi (1969). In the absence of evidence to the contrary the fossil ostracod records were assumed to represent *in situ* occurrences, not subjected to significant post-mortem transport, and thus representative of local conditions. This assumption could be validated in a few cases (e.g. MIS 9 Purfleet and Cudmore Grove) by the evidence of a range of adults and juveniles demonstrating autochthonous thanatocoenoses (Boomer *et al.* 2003) but in others there was insufficient evidence to rule out the possibility of transported assemblages such as are common in the modern Thames Estuary. Salinity range information for ostracod indicator taxa was compiled from the available literature.

## Salinity ranges of selected ostracod taxa

Salinity ranges reported in the literature must be treated with a certain amount of caution and attention to the environmental settings in which they were recorded. The salinity ranges of species inhabiting stable brackish waters where there is little variation may be quite different from those of the same species living in a tidal estuary (where marked tidal and/or seasonal fluctuations are experienced) (Smith & Horne 2002). In the stable regime of the Gulf of Finland (Baltic Sea) a number of freshwater taxa are able to extend their distribution into waters of low salinity (Hagerman 1967) where they co-exist with true brackish and marine-brackish species, but this does not provide a valid model for the interpretation of the macrotidal Thames Estuary. The known salinity preferences of the selected indicator taxa are summarised below.

### ***Cyprideis torosa* (Jones)**

This species typically lives mainly in brackish waters connected to marine waters and experiencing significant salinity fluctuations; in certain settings, such as intertidal saltmarsh pools, it can achieve extremely high population densities. It has a wide salinity tolerance, from freshwater to hypersaline (c. 60 ‰), but seems to thrive particularly in low-brackish salinities (2–16.5 ‰); reports of inland freshwater lake occurrences may be misleading as at least some have been shown to be slightly brackish (Meisch 2000; Horne & Boomer 2000; Athersuch *et al.* 1989). Variable carapace nodding in this species is regarded as an indication of low-salinity brackish environments and increases with decreasing salinity, though observations of the actual salinities at which these changes occur are somewhat inconclusive. In microcosm experiments, Frenzel *et al.* (2012) showed a negative linear correlation between salinity and proportion of noded individuals, with a marked increase in the latter below 5–6 (practical salinity units; equivalent to ‰). Field data from the same study found a dominance of noded values from around 2, while other compared studies suggest dominance between 2 and 5. Pint *et al.* (2012) advise caution when attempting to reconstruct absolute salinities, instead suggesting that *C. torosa* may be more effectively used to reconstruct palaeosalinity trends.

### ***Cytheromorpha fuscata* (Brady)**

This appears to be a brackish-water ostracod that also tolerates fresh water. A synthesis of many works on *Cytheromorpha fuscata* is provided by Neale & Delorme (1985; see also references therein), who considered it a brackish-water ostracod found in estuarine and shallow marine environments, with an upper salinity limit of about 20 ‰, but noted that it has been found in freshwater (<1 ‰). They noted its occurrence in freshwater in Finland, citing Alm (1912, 1916), but nevertheless considered their own new records of it from inland freshwater lakes in Canada to be “unique”, and suggested the presence of sodium-chloride-rich brine discharges to be a key factor in the continued existence of *C. fuscata* in the Canadian lakes. Sars (1925-28) recorded it in Norway in the entrance to Drammen Fjord at Svelvik, where the surface water was almost fresh, in association with the brackish/estuarine *Leptocythere castanea*. Hagerman (1967) reported it as a true brackish-water species living in the Gulf of Finland in salinities of 1 to 7 ‰, varying with depth and proximity to the coast. There is only one living record in the UK (Norfolk), from a freshwater lake with brackish incursions on spring tides (Boomer & Horne 1991).

According to Elofson (1969) it is a strictly brackish water form not found in waters with salinity above 18 ‰. McKillop *et al.* (1992) reported on its association with chloride-dominated saline spring waters in the inland Lake Winnipegosis, Canada, together with other ostracods and foraminifera (including *Jadammina macrescens* (Brady), a well-known coastal saltmarsh species); although two ostracod species (*Limnocythere staplini* Gutentag & Benson and *Sarscypridopsis aculeata* (Costa)) were collected alive in saline sites, *C. fuscata* was only found living in a single, freshwater site. Despite this finding they referred to it as a “coastal marine” species, citing Neale & Delorme (1985), and noted that occurrences of empty shells at two Lake Winnipegosis sites probably represented reworking of older marine-brackish water sediments. In the Holocene of the Baltic Sea coast of Poland it was recorded as a monospecific assemblage considered to represent brackish water heralding a marine transgression (Krzywińska & Namiotko 2012).

### ***Sarscypridopsis aculeata* (Costa)**

This species prefers brackish coastal pools (permanent or temporary) up to about 17 ‰ with the optimum around 5–10 ‰; it is rare in fresh water (Meisch 2000). As noted above, McKillop *et al.* (1992) recorded it alive in saline waters in an inland Canadian lake.

### ***Loxoconcha elliptica* Brady**

A true brackish-water species, common in saltmarsh creeks, with an optimum salinity range of 10–20 ‰ although it can tolerate lower and higher salinities for short periods (Theisen 1966; Horne & Boomer 2000).

### ***Leptocythere* spp.**

British *Leptocythere* species have wide salinity tolerances and although they can be valuable palaeosalinity indicators on account of their different salinity ranges, previous taxonomic confusion makes the application of such knowledge difficult in cases where specific identifications cannot be verified by reference to illustrations. For example, *L. castanea*, a common saltmarsh species, is tolerant of salinities ranging from almost freshwater to fully marine (2–35 ‰), while *L. pellucida* and *L. tenera* are exclusively marine (Athersuch *et al.* 1989; Horne & Boomer 2000). Freshwater occurrences of *Leptocythere* species (e.g. in Lake Ohrid, Macedonia) are now considered to belong to the related genus *Amnicythere* (Namiotko *et al.* 2012).

## Distribution of salinity indicator taxa in the Thames-Medway in MIS 9 and MIS 11

The mapping of the selected salinity indicator taxa onto the Thames palaeogeographies for MIS 9 and MIS 11 (Fig. 1) reveals distribution patterns that can be interpreted in terms of a salinity gradient from west (freshwater) to east (brackish estuarine) in both cases, consistent with other evidence including the general west-east flow direction of the palaeo-Thames and the relative proximity of the marine North Sea to the north-east.

Predominantly freshwater assemblages from all ten MIS 9 sites (Fig. 1) include *C. torosa*, with *C. fuscata* also present in both the River Thames and River Medway at two of the five most upstream localities of the palaeochannel. At Purfleet *C. torosa* constitutes c. 50% of the assemblage in some samples (Schreve *et al.* 2002). Additional species indicative of brackish water appear in assemblages downstream from the Thames/Medway confluence, with *L. elliptica* present at Shoeburyness (6), *Leptocythere* spp. present at Barling (7) and North Wick (9), *C. fuscata* present again at Canewdon (8) and *S. aculeata* present at the northernmost MIS 9 site, Cudmore Grove (10), which is interpreted as a tributary of the Thames.

Although there are fewer assemblages from MIS 11, the data similarly show an increased diversity of brackish-water indicators downstream. At the furthest upstream site, Swanscombe (11), *C. torosa* is present in an otherwise freshwater assemblage; at the nearby site of Ebbsfleet (12), the assemblage contains freshwater ostracods only. East Hyde (13) and Clacton (14) possess distinctly more numerous brackish-water indicator species, with *C. torosa*, *C. fuscata* and *Leptocythere* spp. present at East Hyde (13), and *C. torosa*, *C. fuscata*, *S. aculeata* and *L. elliptica* present at Clacton (14). The absence of salinity indicators at Ebbsfleet may be explained by the evidence that this assemblage may have accumulated somewhat earlier in the interglacial than those at other localities (Whittaker *et al.* 2013), when sea-level was lower and saline tidal waters had not reached this far up the palaeo-Thames.

The occurrence of *C. torosa* in MIS 11 lake sediments at Marks Tey, as the sole brackish component of an otherwise freshwater assemblage, was recorded by Robinson (1978) who speculated that it might signify a connection with the saline waters of the Thames estuary. The precise stratigraphical location (Hoxnian Interglacial or post-Hoxnian?) and palaeoenvironmental significance (brackish or freshwater?) of this occurrence are currently being investigated (Horne *et al.* 2014).

## Comparison with ostracod biofacies in the modern Thames Estuary

Of seven ostracod biofacies defined by Kilenyi (1969) in the modern Thames Estuary, the first four are of particular relevance and are summarised below and in Fig. 2. Some taxonomic names have been updated to conform to current usage.

### **Biofacies I**

Biofacies I was defined on the basis of a single sample and is thought to characterise the inner estuarine tidal river where the water is highly variable fresh to brackish but never fully marine. The biocoenosis consists largely of freshwater/oligohaline species dominated by *Ilyocypris gibba*, *Candona neglecta* Sars and *Limnocythere inopinata* (Baird); it also includes the brackish-water taxa *S. aculeata* and *Heterocypris salina* (Brady). The thanatocoenosis is dominated by *C. torosa*, in association with marine/estuarine species including *Leptocythere castanea*.

## **Biofacies II**

Biofacies II occupies the central part of the Inner Estuary where fluctuating brackish-water salinities prevail. The biocoenosis comprises *C. torosa* (very common), marine/estuarine taxa including *Leptocythere* (very common) with several other common or rare taxa, and rare freshwater/oligohaline species. The thanatocoenosis consists of brackish/marine species.

## **Biofacies III**

Biofacies III equates to the eastern or outer part of the Inner Estuary, with salinities varying from brackish to almost fully marine. The biocoenosis is dominated by *C. torosa* (40%) and *Pontocythere elongata* (Brady) (a marine/estuarine species), with other marine/estuarine taxa. The thanatocoenosis comprises two freshwater taxa, *C. neglecta* and *I. gibba*.

## **Biofacies IV**

Biocoenosis IV occupies the largest part of the Outer Estuary where salinities are close to normal marine; the biocoenosis comprises marine/estuarine species dominated by *P. elongata*, with *C. torosa* constituting only 7% of the assemblage overall, although it is the sub-dominant species in the west and decreases in abundance eastwards. The thanatocoenosis consists of one freshwater taxon (*C. neglecta*).

It is important to understand that Kilenyi recorded no living ostracods in his study (which he attributed to the sampling methods used) and determined his biocoenoses using several criteria including staining with Rose Bengal (to identify specimens living at the time of collection; he found this unreliable), valve:carapace ratio, juvenile:adult ratio, mode of preservation, and opacity or colour of shells. Although he stressed that his biocoenoses were interpreted in the widest sense of the term, and equated to Wagner's (1957, 1964) biocoenosis plus thanatocoenosis I, they were considered to represent essentially *in situ* assemblages. Strictly speaking, a biocoenosis (life assemblage) can only be represented by living specimens; Kilenyi's terminology has been followed in the above descriptions of his biofacies, but his "biocoenoses" are in fact thanatocoenoses (*in situ* death assemblages) while his "thanatocoenoses" are really taphocoenoses (transported death assemblages) (Boomer *et al.* 2003).

Despite evidence of an increase in salinity indicator species downstream of the Thames/Medway confluence during both MIS 9 and MIS 11 (Fig. 1), the abundance of freshwater species (cf. "rare freshwater species" in Biofacies II) at all sites suggests a broad palaeoenvironment most similar to Kilenyi's (1969) Biofacies I: a tidal river with highly variable fresh to brackish water and an *in situ* freshwater ostracod assemblage, with estuarine/marine species (including *C. torosa*) being transported post-mortem. The ubiquitous presence of freshwater taxa may partly be the result of their post-mortem transport down the river, but the absence of marine or outer estuarine taxa transported upstream by tidal currents is sufficient to rule out Biofacies II.

If Kilenyi's biofacies are correct, i.e. freshwater-dominated assemblages and *in situ* salinity indicators being mutually exclusive, then there may be no exact modern analogue in the Thames for the palaeochannels of the Thames/Medway system during the MIS 9 and MIS 11 interglacials. However, Biofacies I is defined on the basis of a single sample only. Furthermore, given the lack of true biocoenoses in Kilenyi's definitions, the relationship between the modern biofacies and palaeo-assemblages remains unclear.

It is notable that *C. fuscata*, present in six MIS 9 sites and one MIS 11 site, was not identified in the modern estuary by Kilenyi (1969); indeed its living distribution in Britain is restricted to a single known occurrence in Norfolk (Boomer & Horne 1991).

## Noding

Kilenyi (1972) reported that specimens from the modern Thames Estuary showed a wide range of variation in the development of nodes (swellings on the external surface of the carapace); he cited an example of a sample of living *C. torosa* collected from a ditch behind the sea wall at Decoy Point in the Blackwater Estuary (a tributary of the Thames Estuary) which comprised 296 individuals among which was only a single, juvenile, noded valve. He also stated that in the modern Thames Estuary noded forms only constituted about 1% of the total (41 out of 3,313 specimens). He was unable to find any correlation between salinity and the distribution of noded specimens (bear in mind that he was mainly considering dead assemblages, including some that had been subjected to post-mortem transport, not living specimens).

Noding (or lack of it) in *C. torosa* at Pleistocene sites within the Thames-Medway river system is of great interest, and seems to present a rather different picture from what might be found at the present day. Jones (1850) originally described *C. torosa* from the MIS 9 ("Purfleet Interglacial") site at Grays, where the valves are exclusively noded, with the maximum seven positions of noding being exhibited. In all the sites of this interglacial (Fig. 1), in our experience, the ostracod is similarly noded, although in the North Wick (North Wycke) borehole we have seen smooth forms beginning to appear and outnumbering noded forms towards the top of the sequence. In the MIS 9 assemblage at Purfleet, Huw Griffiths (in Schreve *et al.* 2002) found the majority of *C. torosa* specimens to be well noded, as did Bridgland *et al.* (2013). In the earlier MIS 11 (Hoxnian Interglacial) Thames-Medway sites (Fig. 1) *C. torosa* is again highly noded, with all seven nodes developed on each valve.

*Cyprideis torosa* also occurs in younger Pleistocene sites of the Thames-Medway system. Of the MIS 7 ("Aveley") interglacial, only two sites (from Aveley itself) are known to us. The major collection of Eric Robinson (formerly of University College London), now housed in the Natural History Museum, London, has been revisited. We also have access, thanks to Simon Parfitt (Natural History Museum, London), to material from a section prepared for a Geologists' Association fieldtrip to Aveley in 1994. In both sets of samples, when it occurs, the valves of *C. torosa* are invariably entirely smooth. Most recently, one of us (JEW) has had the opportunity, again through the good offices of Simon Parfitt, to examine MIS 5e (Ipswichian Interglacial) material from the famous Trafalgar Square site in London (in particular an excavation at Canadian Pacific House, collected some time ago); in this case *C. torosa* is strongly noded.

What are we to make of this? Clearly, part of the explanation must be the salinity. As already discussed above, the highly noded forms indicate low brackish conditions, on or near the limit of tidal reach within the Thames-Medway system. This is corroborated by the fact that these same sections, where noded *C. torosa* occurs, also contain non-marine ostracods which can tolerate such conditions, but the tidal limit may have been variable, moving up and down the estuary perhaps on a seasonal basis. At North Wick farm within the Burnham Channel the upper part of the MIS 9 sequence, with a preponderance of smooth valves, also contains *Leptocythere lacertosa* (Hirschmann) and small foraminifera and this suggests the site could have been a little more saline (see Fig. 1). With regard to MIS 7, we have few localities and little is known of the palaeogeography of the river at that time, as is also the case in the Ipswichian, but with smooth forms at Aveley and noded ones at Trafalgar Square, *C. torosa* is suggesting there is a salinity regime difference between the two sites. This, however, cannot be the full answer. Is substrate also part of the picture? The facies of the MIS 11 and MIS 9 sediments always seems to indicate a sandy substrate, as does MIS 5e. Unfortunately, we have little of the original sediment from Aveley (there is none left of the original sediment that Robinson studied so

extensively), and the brick pit is now flooded. In the Geologists' Association section we have recorded silt and silty sand for the samples containing smooth *C. torosa*.

Today, in our experience, noded *C. torosa* is not found within the Thames-Medway estuaries. However, we have mainly sampled the soft mud of tidal creeks and saltmarsh. Kilenyi's (1972) exceedingly rare records of noded forms probably represent reworking. For that matter, whether relevant or not, *C. fuscata*, another ostracod of tidal rivers and a common associate of *C. torosa* in the Pleistocene (see above, and Fig. 1), is (as far as we know) completely absent in the modern Thames-Medway. Something in the ecological dynamics has clearly changed.

## Conclusions

In spite of the widely recognized value of *C. torosa* as a precise palaeosalinity indicator, its use in mapping palaeosalinity regimes onto estuarine palaeogeography is constrained by taphonomic considerations. Nevertheless, its use in combination with other palaeosalinity indicators has provided valuable insights regarding the palaeosalinity regimes of the lower River Thames and River Medway during the MIS 9 and MIS 11 interglacials. All of the assemblages considered in this study are best matched to Biofacies I of Kilenyi (1969) which, although poorly defined, is indicative of predominantly freshwater river conditions with some limited tidal influence; the main estuary must have existed further east and north-east than the present study area and all of its deposits must be submerged today. Assemblages such as that recorded at Purfleet (MIS 9), comprising *in situ* noded *C. torosa* in association with an otherwise freshwater fauna, appear to have no recorded modern analogue in the present-day Thames Estuary. Whether this is due to different conditions in the past, or simply a lack of adequate sampling in the upper reaches of the modern estuary, may be a suitable question for future research.

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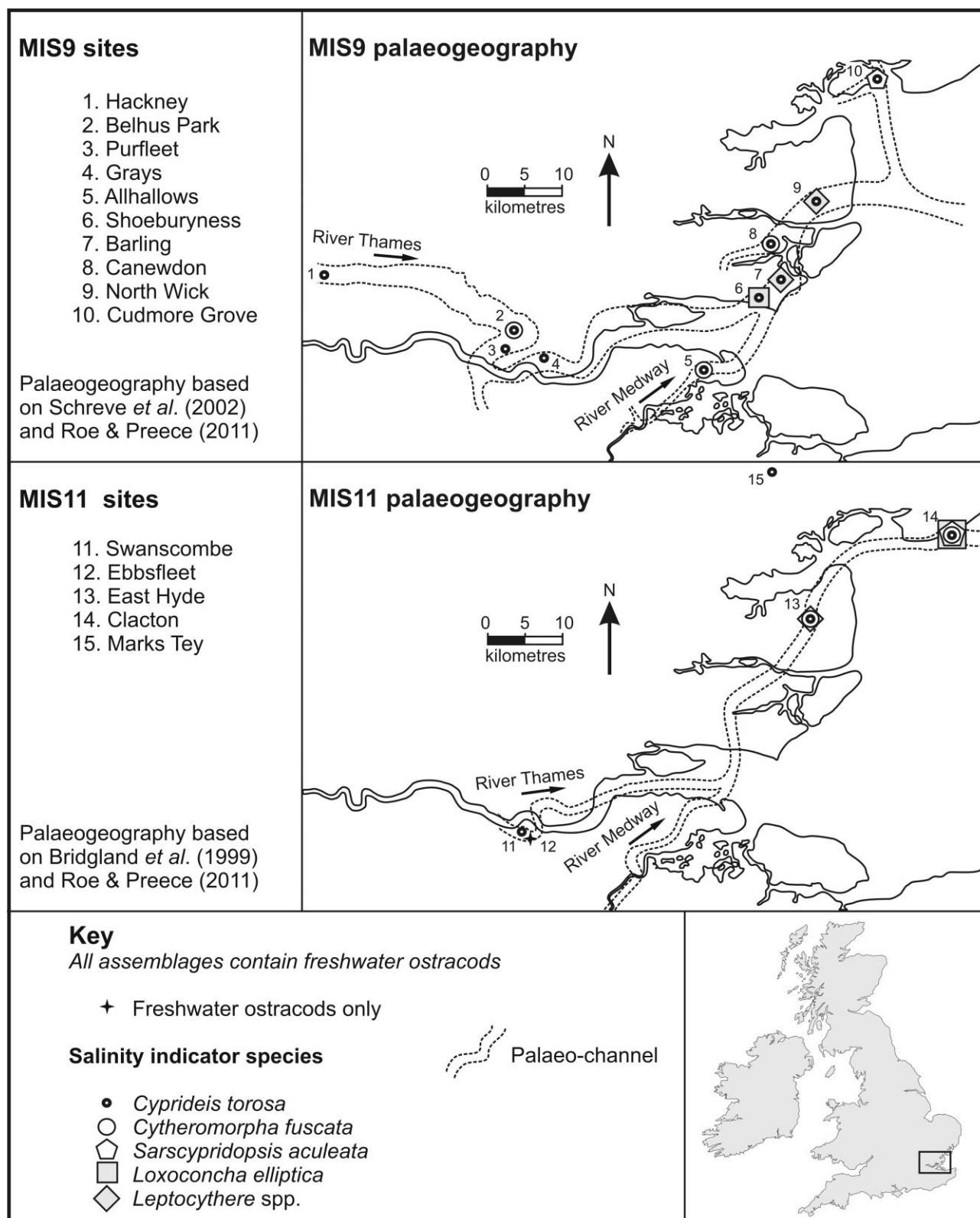


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## Figures and tables



**Fig. 1.** Distribution of ostracod species indicative of brackish water in otherwise freshwater assemblages of MIS9 (ten sites) and MIS11 (five sites) age.

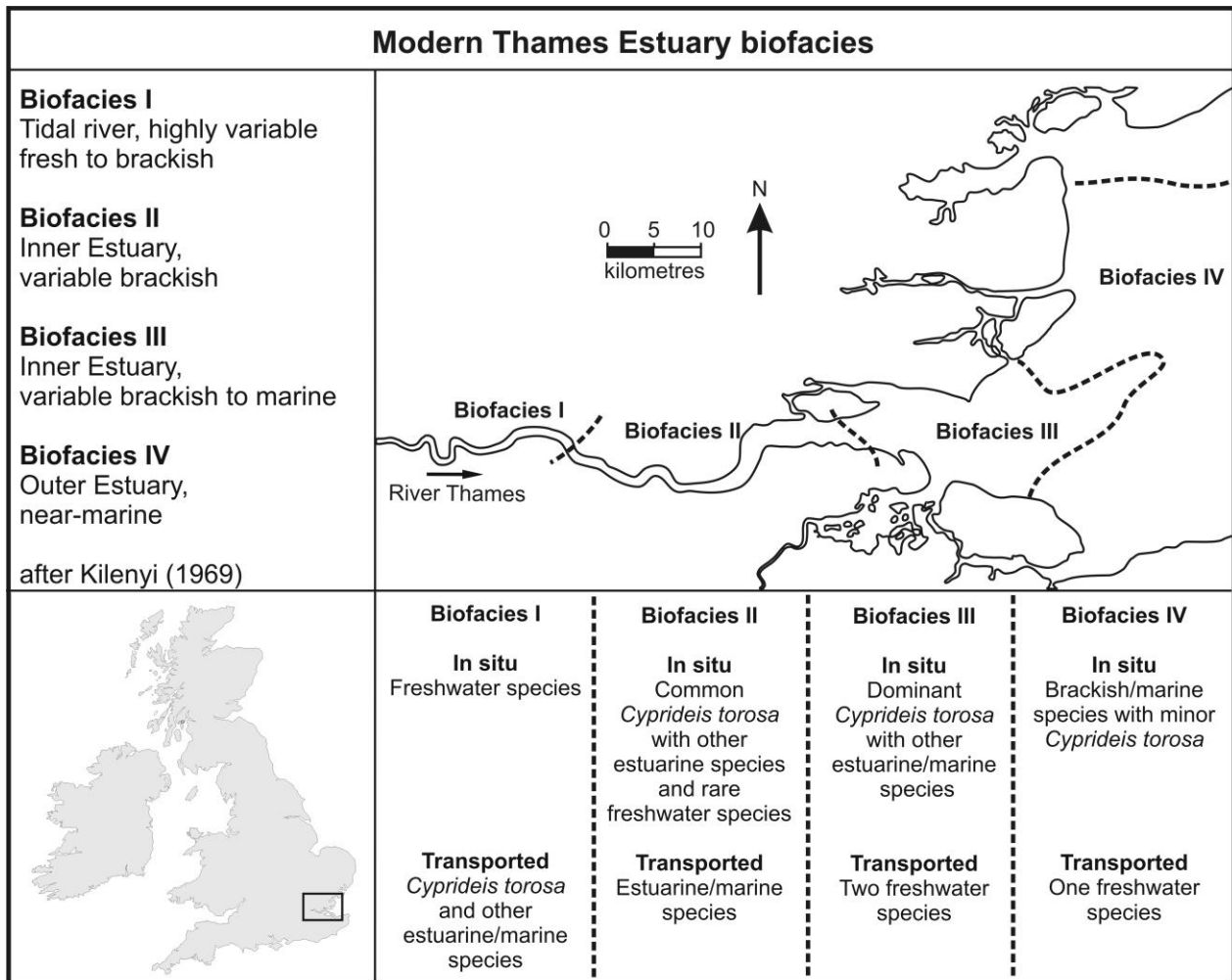


Fig. 2. Ostracod biofacies of the modern Thames Estuary (after Kilenyi 1969).

**Table 1.** Records of ostracod taxa in the Pleistocene deposits assigned to MIS 9 and MIS 11 in the Thames-Medway region. Species occurrences are coded F = Freshwater or B = Brackish water. Sources of data are listed below.

MIS 9: Hackney (Green *et al.* 2006, including supplementary data), Belhus Park (J.E. Whittaker, unpublished data), Purfleet (Schreve *et al.* 2002; Bridgland *et al.* 2013), Grays (Jones 1850, 1857; J. E. Whittaker, unpublished data), Allhallows (Bates *et al.* 2002), Shoeburyness (Roe *et al.* 2011), Barling (Bridgland *et al.* 2001), Canewdon (Roe & Preece 2011), North Wick (Roe & Preece 2011), Cudmore Grove (Roe *et al.* 2009).  
MIS 11: Swanscombe (White *et al.* 2013), Ebbsfleet (Whittaker *et al.* 2013), East Hyde (Roe 2001), Clacton (Bridgland *et al.* 1999), Marks Tey (Robinson 1978; Lord *et al.* 1988; Horne *et al.* 2014).

Ostracod taxa	MIS 9 sites									MIS 11 sites				
	Hackney	Belhus Park	Purfleet	Grays	Allhallows	Shoeburyness	Barling	Canewdon	North Wick	Cudmore Grove	Swanscombe	Ebbsfleet	East Hyde	Clacton
<i>Candona angulata</i> G.W. Müller			F				F						F	F
<i>Candona candida</i> (O.F. Müller)	F		F	F										F
<i>Candona neglecta</i> Sars	F		F		F	F	F	F	F	F	F	F	F	F
<i>Candona</i> sp.	F		F						F			F	F	
<i>Candonopsis scourfieldi</i> Brady														
<i>Cyclocypris laevis</i> (O.F. Müller)							F							
<i>Cyclocypris ovum</i> (Jurine)											F			
<i>Cyclocypris serena</i> (Koch)													F	
<i>Cypria opthalmica</i> (Jurine)														F
<i>Cyprideis torosa</i> (Jones)	B	B	B	B	B	B	B	B	B	B	B	B	B	B
<i>Cypridopsis hartwigi</i> G.W. Müller													F	
<i>Cypridopsis vidua</i> (O.F. Müller)	F	F	F			F	F			F	F		F	
<i>Cypris pubera</i> (O.F. Müller)	F													
<i>Cypris marginata</i> (Strauss)							F							
<i>Cytherissa lacustris</i> (Sars)			F		F	F	F					F	F	F
<i>Cytheromorpha fuscata</i> (Brady)		B			B	B		B	B	B		B	B	
<i>Darwinula stevensoni</i> (Brady & Robertson)	F	F	F		F	F	F	F	F	F	F	F	F	
<i>Dolerocypris fasciata</i> (O.F. Müller)							F							
<i>Eucypris dulcifons</i> Diebel & Pietrzeniuk							F							
<i>Eucypris elliptica</i> (Baird)							F							
<i>Eucypris pigra</i> (Fischer)										F				
<i>Eucypris</i> sp.														F
<i>Fabaeformiscandona balatonica</i> (Daday)			F								F			
<i>Fabaeformiscandona caudata</i> (Kaufmann)	F		F		F					F				
<i>Fabaeformiscandona levanderi</i> (Hirschmann)							F						F	F
<i>Fabaeformiscandona siliquosa</i> (Brady)													F	
<i>Herpetocypris reptans</i> (Sars)	F			F		F	F		F	F	F	F	F	
<i>Herpetocypris</i> sp.			F		F									F
<i>Heterocypris salina</i> (Brady)														F
<i>Heterocypris</i> sp.	F													
<i>Ilyocypris bradyi</i> Sars											F	F	F	F

<i>Ilyocypris cf grabschuetzi</i> (Fuhrmann & Pietrzeniuk)																			F							
<i>Ilyocypris cf monstifica</i> (Norman)																			F							
<i>Ilyocypris decipiens</i> (Masi)			F	F															F							
<i>Ilyocypris gibba</i> (Ramdohr)	F			F	F	F	F	F	F	F	F	F						F	F	F						
<i>Ilyocypris inermis</i> Kaufmann				F																						
<i>Ilyocypris lacustris</i> (Kaufmann)?																			F							
<i>Ilyocypris lacustris</i> (Kaufmann)			F	F				F																		
<i>Ilyocypris quinculminata</i> (Sylvester-Bradley)																	F			F						
<i>Ilyocypris salebroza</i> Stepanaitys				F		F		F																		
<i>Ilyocypris</i> sp																	F			F						
<i>Leptocythere castanea</i> (Sars)																		B		B						
<i>Leptocythere pellucida</i> (Baird)								B																		
<i>Leucocythere batesi</i> Whittaker & Horne ( <i>L. mirabilis</i> (Kaufmann)?)																				F						
<i>Leucocythere</i> sp																			F							
<i>Limnocythere falcata</i> (Diebel)																			F		F					
<i>Limnocythere inopinata</i> (Baird)	F	F	F		F	F	F	F	F	F	F								F		F					
<i>Limnocythere suessenbornensis</i> (Diebel)																					F					
<i>Limnocytherina sanctipatricii</i> (Brady & Robertson)								F											F		F					
<i>Loxococoncha elliptica</i> Brady																				B						
<i>Metacypris cordata</i> (Brady & Robertson)				F				F	F										F		F	F				
<i>Paralimnocythere compressa</i> (Brady & Norman)								F	F										F		F	F				
<i>Paralimnocythere</i> sp.																						F				
<i>Potamocypris aff. producta</i> (Sars)																						F				
<i>Potamocypris cf arcuata</i> (Sars)																						F				
<i>Potamocypris trigonalis</i> var. <i>laevis</i> (Jones)																			F							
<i>Potamocypris villosa</i> (Jurine)	F																									
<i>Potamocypris zschokkei</i> (Kaufmann)																				F	F		F			
<i>Potamocypris</i> sp.																							F			
<i>Prionocypris zenkeri</i> (Chyzer & Toth)																					F		F	F		
<i>Pseudocandona albicans</i> (Brady)																							F			
<i>Pseudocandona compressa</i> (Koch)																							F?			
<i>Pseudocandona marchica</i> (Hartwig)	F			F			F		F														F			
<i>Pseudocandona rostrata</i> (Brady & Norman)	F																									
<i>Pseudocandona sarsi</i> (Hartwig)	F																									
<i>Pseudocandona</i> sp																							F			
<i>Sarscypridopsis aculeata</i> (Costa)																							B		B	
<i>Scottia browniana</i> (Jones)																							F		F	F
<i>Scottia tumida</i> (Jones)																							F	F		