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The mesogastropod *Littorina littorea* (Linné, 1758) in Iceland: palaeobiogeography and migration

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At present, the periwinkle, *Littorina littorea* (Linné, 1758), is not found living in Iceland. The only confirmed occurrence of the species in Icelandic sediments is in the Middle Pleistocene upper littoral conglomerate at Búlandshöfdi, Snaefellsnes, West Iceland. These layers were deposited during an interglacial stage, slightly older than 1.1 Ma. The species apparently evolved from the Pacific *L. squalida* Broderip & Sowerby, 1829, after the trans-Arctic/North Atlantic migration from the Pacific, possibly in response to cooling and increasing environmental energy. The oldest fossil occurrence of *L. littorea* is in the British Red Crag Formation, between 2.55 and 2.4 Ma; it is unknown from the Pliocene Tjörnes deposits in N Iceland, older than 2.6 Ma. This indicates that the species separation postdates the deposition of the uppermost *Serripes* Zone of Tjörnes, after the tide of the migration wave passed Iceland, but before it reached the North Sea area and Britain, between 2.6 and 2.4 Ma. The taxonomic diversity and palaeobiogeography of North Atlantic molluscs were greatly affected by the major climatic changes that resulted in an extensive glaciation at about 2.5 Ma.

KEY WORDS: Mesogastropoda, *Littorina*, Iceland, Middle Pleistocene, speciation, palaeobiogeography, migration.

Introduction

The prosobranch mesogastropod *Littorina littorea* was originally described by Linné (1758), who named it *Turbo littoreus*. In 1822, Férussac established the genus *Littorina*, *T. littoreus* being its type species now. Since the times of these workers, there have been a number of incorrect spelling and minor nomenclatorial complications, but these will not be enumerated here. Several doubtful records of living and fossil *Littorina* exist in Iceland. The aim of the present study is to attempt to clear up the occurrence of *L. littorea* in Iceland and to provide a more precise picture of the palaeobiogeography of the species.

The material studied comprises specimens collected by the authors, as well as specimens kept in geological and zoological museums in Iceland and Denmark.

Abbreviations used in the text are as follows:

IMNH	Icelandic Museum of Natural History, Reykjavík.
NHM	The Natural History Museum, London.

Diagnosis

The typical adult shell of *L. littorea* is solid with a pointed, cyrtoconoid spire and 5-6 whorls, which are slightly tumid to nearly flat in profile (Figure 1a, b). The upper part of the body whorl is straight to concave, especially near the aperture. The suture is shallow, resulting in a flat perimeter. Growth lines are distinctly prosocline and form an angle of about 120° with the axis of the spire. Spiral ridges and grooves are slight and numerous, and especially marked in young individuals, but tend to become obscure in older ones. The numerous ribs are very low and narrow. The aperture is oval and angulate in the uppermost part and lies in a prosocline plane with the peristome. The outer lip meets the periphery of the body at an angle of 125-130° to the axis. The inner lip is thick and lacks an umbilical groove. The white columella is short and inclined towards the shell's axis. Colours of the shell vary from cream to brown, black, brownish black, grey, orange or red, but usually the shell is pale brown with 8-25 narrow black to dark brown lines. The body whorl is around 80-85% of the total height of the shell and the height of the aperture is 60-70%. The adult shell of *L. littorea* is the largest of the genus with a mature shell height between 10.6 and 52.8 mm (Reid, 1996). The protoconch consists of two or more unsculpted whorls (Fretter & Graham, 1980). The snout is broad, slightly tapered and distally truncated. The terminal mouth is slightly ventral on the head and has a radula with a relative length from 1.49 to 2.15 mm (Reid, 1996). The cephalic tentacles each have an eye on a lateral bulge at the base. The foot is elongated and shield-shaped. The operculum has 2-3 turns and a nucleus displaced to the columellar side. There is a linear osphradium and a long gill in the mantle cavity to the left. The penis, with 10-42 mamilliform glands, is sickle-shaped and tapers abruptly distally.

Vermeij (1982) found some patterns in shell thickness on a geographical scale.

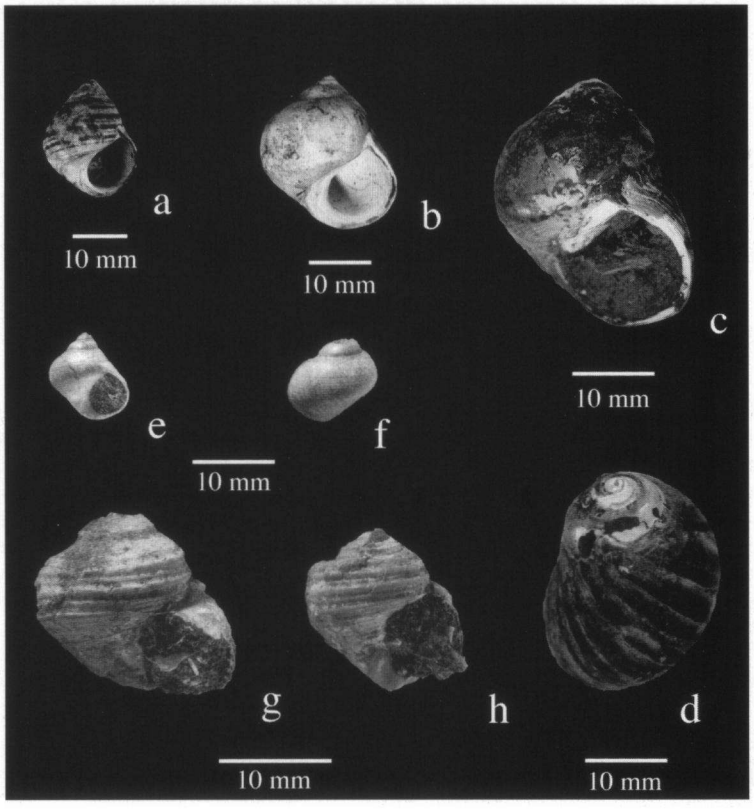

Figure 1. Species of *Littorina*.

a *L. littorea* (IMNH 754), Recent specimen from Rørvig, Denmark;
b *L. littorea* (IMNH 755), from Middle Holocene Stone Age sea deposits in Denmark;
c,d *L. littorea* (IMNH 756), from Middle Pleistocene interglacial deposits at Búlandshöfdi (W Iceland);
e,f *L. squalida* (IMNH 3976), from horizon 11 of the Pliocene *Mactra* Zone of the Tjörnes beds, N Iceland (after Reid, 1996);
g,h *L. islandica* (IMNH 3977, **paratype**), from horizon 25 of the Pliocene *Serripes* Zone of the Tjörnes beds, N Iceland (after Reid, 1966).

In North America, the shells become thinner to the south of Cape Cod, which indicates a relationship between temperature, growth rate and shell form. In brackish habitats, shells are both smaller and thinner with a fainter texture, and the spire height seems to increase with decreasing salinity (Reid, 1996).

Recent distribution

Littorina littorea is widely distributed on European shores (Figure 2) from the White Sea in the north to southern Portugal in the south (Fretter & Graham, 1980; Reid, 1996). The most northerly record from southern Svalbard (Rózycki, 1991) has not yet been confirmed. The species extends into the Baltic as far as Bornholm. Further south it is common along the French Atlantic coast as far as Île d'Olóron. The southern limit in the eastern Atlantic is close to Algarve in southern Portugal. There are some doubtful records from the Mediterranean, but a breeding population has recently been discovered at Castiglioncello, NW Italy (Barsotti & Campani, 1982).

In the western Atlantic, *L. littorea* is distributed from the Strait of Belle Isle (Newfoundland) in the north to Virginia in the south. The coast of Connecticut is the most southerly suitable habitat, but occasionally currents transport larvae south as far as mid-New Jersey and the Delmarva Peninsula where settlement sometimes occurs (Reid, 1996). According to Vermeij (1982), the southernmost occurrence seems to have been at Wachapreague in Virginia.

In the East Pacific, the species has been recorded from the Puget Sound (Washington), San Francisco Bay and Trinidad Bay (California). In these places, the species has not been able to establish populations (Reid, 1996). The vertical range is from 0 m at several localities, to a depth of about 60 m in northern Britain and Skagerrak (Fretter & Graham, 1962, 1980; Reid, 1996). The species prefers the intertidal zone.

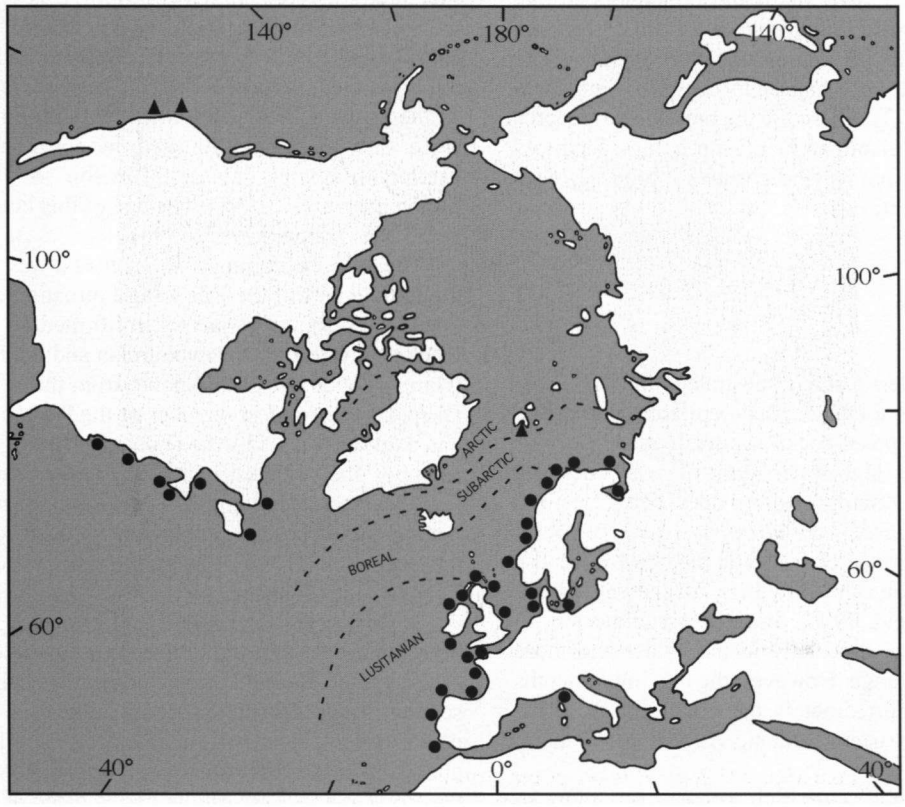

Figure 2. Recent distribution of *Littorina littorea*. Triangles mark either unverified finds or occurrences where the species has not been able to produce established populations. The regional division of northern European seas is based on Feyling-Hanssen (1955), as modified by Símonarson *et al.* (1998).

Littorina littorea was recorded from Greenland by Fabricius (1780), but that was a misidentification of *L. saxatilis* (Olivi, 1792). Another Greenland record was based on incorrectly localised material (Reid, 1996). The species was recorded three times from the Faroe Islands in the 19th century, but it has not been found again despite further collection efforts (Mørch, 1868; Spärck & Thorson, 1933).

From Iceland, *Turbo littoreus* was first mentioned by Mohr (1786). However, it is quite clear from his description that he was actually dealing with *L. obtusata* (Linné, 1758) and *L. saxatilis*, without separating them. Then Mørch (1868, p. 207) stated (in Danish, here translated), 'Some few specimens not more than 15 mm long are found in the Museum of Christian VIII labelled "ex Islandia, Johnsen", but it seems probable to me that a confusion has taken place'. These four specimens are still in the Zoological Museum (Copenhagen). They are all without animals and so fresh looking that they are probably not of subfossil origin (Thorson, 1941). Furthermore, one shell is labelled 'Isld Steenstrup' and Thorson (1941, p. 34) came to the conclusion, ' ..... that it could be subfossil'. The collection also contains two more shells from Iceland labelled *Littorina littorea*. One was found in the tidal zone of Isafjördur (NW Iceland) and the other among stones on the shore in Arnarfjördur (also NW Iceland). These shells are in the

Zoological Museum (Copenhagen), and our re-examination has revealed they all belong to *L. saxatilis*.

Furthermore, it looks like some mixup took place when the shells from Ísafjördur and Arnarfjördur were labelled at the museum, as Johansen (1901), who found them, referred to them as *L. groenlandica* Menke, 1830 and *L. rudis* (Maton, 1797). Finally, it should be mentioned that shells of *L. littorea* were found in an old Danish ship that stranded on Flatey in Breidafjördur, West Iceland. The shells probably came with ballast in the ship from Denmark (Óskarsson, 1973). These are the only known records of *L. littorea* from Iceland, and since no living specimens have been collected from Icelandic waters it probably does not live there at present.

Ecology and biology

Littorina littorea prefers a stable substrate within the intertidal zone where it is a characteristic epifaunal inhabitant of all but the most exposed rocky shores. It usually occurs on rocks between the high-water mark of neap tides and the extreme low-water mark of spring tides, being found in the algal zones of *Fucus* and *Laminaria* (Reid, 1996). It also occurs on the surface of wet mud or, less frequently, on sand where solid objects allow firm attachment (Fretter & Graham, 1980; Reid, 1996). It extends sublittorally to depths of about 60 m, especially in the colder and more northerly parts of its range. However, the maximum depths are recorded from approximately the middle of its distribution range in the eastern Atlantic (Fretter & Graham, 1980).

The species tolerates rather high temperatures, more so in air than in water. Sandison (1967) reported that the animal falls into a coma at 32°C in air and 31°C in water. Heat death occurred at 42°C in air and at 40°C in water for specimens from the Firth of Forth, and Evans (1948) gave 39°C and 46°C for those in Cardigan Bay. When temperature drops below 8°C, most specimens become inactive. They spend part of the winter without feeding (Fretter & Graham, 1980); many appear to migrate down to the shore to avoid cold (Gendron, 1977).

Littorina littorea frequently occurs at river mouths, and may penetrate far into estuaries and fjords, surviving at salinities down to 9-10‰ (Fretter & Graham, 1980). Arnold (1972) reported that the active movement of living specimens apparently decreased markedly at salinities below 20‰ in SW Wales (Milford Have, the Daucleddau) and eastern Canada.

The species is mainly an omnivorous grazer, feeding on a wide range of algae, diatoms, and vegetable detritus, but occasionally it takes animal detritus (Fretter & Graham, 1980; Reid, 1996).

Littorina littorea is oviparous with planktotrophic development (Reid, 1996). Each female lays about 500 capsules at a time, which burst after 5-6 days and release veliger larvae, which swim in the plankton for 4-5 weeks or even 6-7 weeks (Fretter & Graham, 1980). The animal may reach an age of nearly 20 years (Woodward, 1913).

Fossil occurrence

The stratigraphical range of *L. littorea* is apparently from the Pliocene to the present day. For the Plio-Pleistocene boundary we use the boundary between the Reuverian and the Praetiglian stages of The Netherlands, at the beginning of the first major glaciation in the Northern Hemisphere, since this is commonly used in northern and western Europe (Zagwijn, 1992; Morrison & Kukla, 1998; Símonarson *et al.*, 1998). The age of this boundary is close to 2.5 Ma (Funnell, 1995, 1996).

The oldest occurrence of *L. littorea* was recorded from the middle part of the Red Crag Formation of East Anglia (Wood, 1848), subsequently confirmed by Reid (1996), where it is rare in the Newbournian and the Butleyan crags (Harmer, 1920). It is not known from the Waltonian Crag, taken to be the oldest member of the Red Crag Formation, dated at about 2.55 Ma (Funnell, 1996). The Ludham Member, the youngest unit of the upper Red Crag Formation, has been dated at *c.* 2.4 Ma, so it seems that the formation was deposited during Early Pleistocene time, with the exception of the Waltonian Crag, which is of latest Pliocene age (Gibbard *et al.*, 1991; Funnell, 1996).

In continental Europe, fragments of *L. littorea* have been collected from the Ouwerkerk borehole (Zeeland) in sediments of an age corresponding to the Belgian Merksemian Stage, although contamination from overlying deposits cannot be ruled out (Reid, 1996). The species is abundant in the Norwich Crag Formation, which overlies the Red Crag in East Anglia and is dated at 2.0 to 1.6 Ma (Gibbard & Zalasiewicz, 1988; Funnell, 1996). It also is a common fossil in boreholes penetrating contemporaneous deposits in the southern Netherlands, as well as in wells in the middle Tiglian Maas-sluis Formation at Roosendaal (Reid, 1996). Furthermore, it occurs in the *Mya arenaria-Hydrobia ulvae* Zone of similar age in the western and central parts of the Netherlands (Spaink, 1975; Gibbard *et al.*, 1991). A few specimens of *L. littorea* have been found in the Baventian marine clay bed at Covehithe (Suffolk), probably representing the first cold stage of truly glacial intensity in the English marine, Early Pleistocene succession (West *et al.*, 1980). In Morocco, the species occurred as far south as Cape Rhir during cold periods of the Middle Pleistocene (Reid, 1996).

Littorina littorea is common in several raised beach deposits from the Late Pleistocene in Britain and in continental Europe (Reid, 1996). It is of common occurrence in the Eemian zones of Denmark and the Netherlands (Harmer, 1923), as well as in Upper Pleistocene strata around the White and Barents seas (Knipowitsch, 1900; Merklin *et al.*, 1979). Furthermore, one specimen has been found on Taymyr Peninsula (N Siberia, latitude 32°N), in a deposit from the Kazan-sevskaga Transgression, of about 100,000 years old (Reid, 1996).

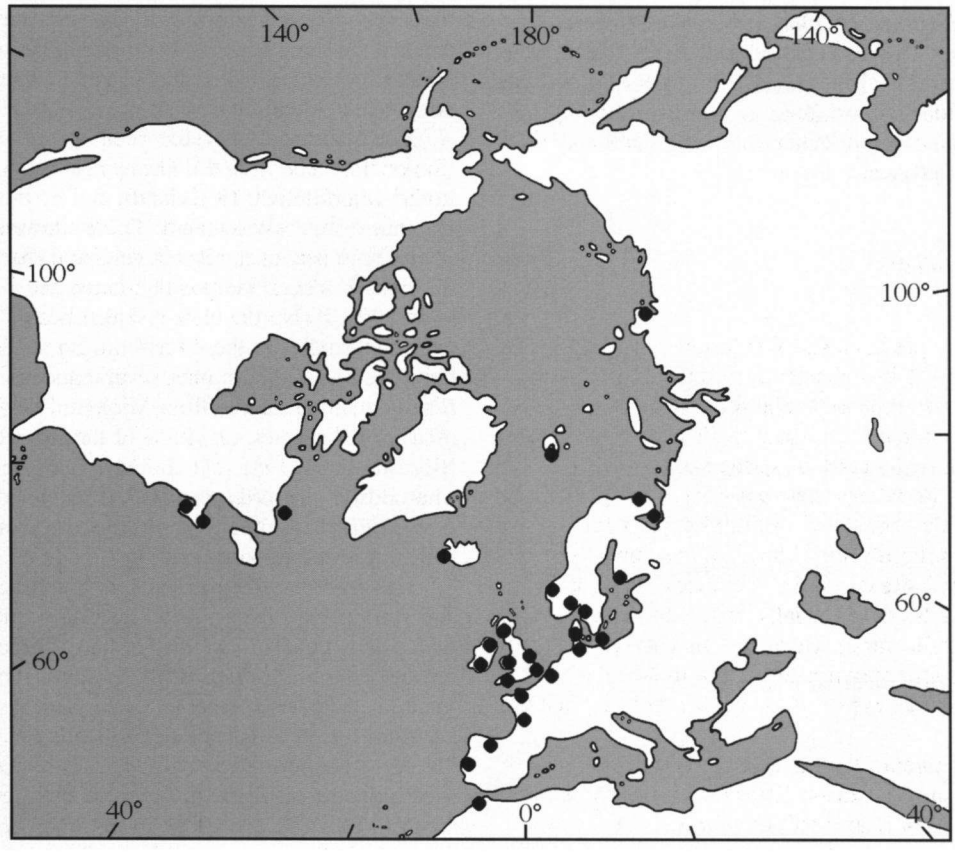

Figure 3. Distribution of fossil *Littorina littorea*.

The species is common in Upper Pleistocene (late glacial) and Holocene sediments in southern Scandinavia, such as the deposits from the Middle Holocene *Littorina* Sea. This sea had an elevated sea temperature and higher salinity than prevailing at present, and during this time the species penetrated far into the Baltic, where it was very common. In Svalbard, the species is considered a good index fossil for littoral deposits from the Middle Holocene warm period (Feyling-Hanssen, 1955).

Littorina littorea has been found in North America, but the only Pleistocene record is from SW Nova Scotia. The shell was collected from a deposit of Middle Wisconsian age, 33,000-44,000 years old (Wagner, 1977). Additionally, specimens have been collected in Indian middens in the Canadian Maritimes, dated at 500-1,000 BP (Reid, 1996). In northern Newfoundland, two specimens have been found at a site of Norse settlement. A few shells have also been found in Nova Scotia and New Brunswick which have been radiocarbon-dated between 1,000 and 1,500 BP (Clarke & Erskine, 1961).

Thus, *L. littorea* has been recorded as a fossil from several places outside the present area of distribution,

which indicates shifts in geographical range, apparently linked to climatic oscillations (Figure 3). One of these places is Iceland, but the Icelandic occurrence will be dealt with below.

Occurrence in Iceland

Mørch (1871) recorded *L. littorea* from the Pliocene *Serripes* Zone of the Tjörnes beds in northern Iceland. Much later, Gladenkov *et al.* (1980) recorded it from horizons 10 and 12 of the older *Mactra* Zone and horizons 18, 23 and 25 of the younger *Serripes* Zone, following the division of Bárdarson (1925) (see also Figure 4).

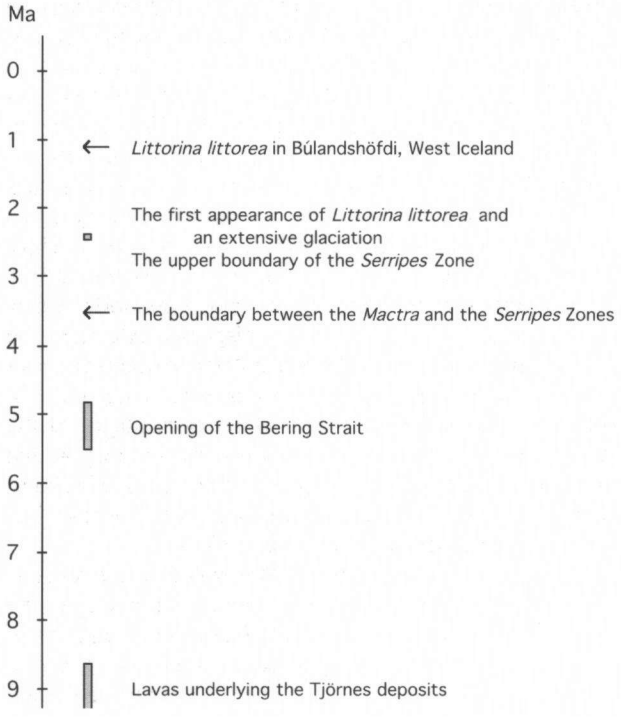

Figure 4. Chronology of main events. The ages of the lavas underlying the Tjörnes beds (N Iceland) are from Aronson & Saemundsson (1975); that of the *Serripes* Zone of the Tjörnes beds is from Einarsson *et al.* (1967) and Albertsson (1978).

Reid (1996) identified the specimen mentioned by Mørch as *L. squalida*, on account of its typical rounded whorls, more swollen last whorl, more impressed sutures, and more raised ribs of irregular size as compared to *L. littorea* (Figure 1e, f). He also identified the specimens that Gladenkov *et al.* (1980) recorded from the *Mactra* Zone as *L. squalida*. Recently, specimens of *L. squalida* have also been collected in horizon 9 of the *Mactra* Zone. Then the specimens of *L. littorea* that Gladenkov *et al.* (1980) recorded from the *Serripes* Zone were ascribed by Reid (1996) to a new species, *L. islandica*, having more distinct sutures and an ornament of rounded ribs, of which up to three may become more prominent and carinate than in *L. littorea* (Figure 1g, h). Thus, Reid (1996, p. 247) concluded, when dealing with *L. islandica*, that, 'The only other *Littorina* species recorded as a Pliocene fossil from Iceland .... is *L. squalida*.' The present authors have reached the same conclusion regarding the identification of *Littorina* from the Tjörnes beds, namely that *L. littorea* has not yet been found there.

Thoroddsen (1892) recorded *L. littorea* from two Lower Holocene littoral deposits near the Urridafoss Falls in the Thjórsá River (S Iceland), and by the Laxá River in Hvammsfjördur (W Iceland). These sites are 31 m and 20-26 m above sea level, respectively, and shell material from the latter has been radiocarbon-dated as 9,755±90 BP and 9,765±90 BP (Norddahl & Ásbjörnsdóttir, 1995). Despite extensive studies at these localities no shells of *L. littorea* have been found, but rather several specimens of *L. saxatilis*. In a single sample from Mjóhylur we found 39 specimens of the species, or 35.4% of the sample (Jónsdóttir & Björnsdóttir, 1995). Therefore, our opinion is that Thoroddsen's records were based on misidentification of *L. saxatilis*. Unfortunately, Thoroddsen's material has not been traced for a re-examination.

The records of Spjeldnaes & Henningsmoen (1963) and Reid (1996) from the Middle Holocene warm period in Iceland are obviously based on Thoroddsen's above-mentioned samples reported in 1892. Therefore, some mixup in time has apparently taken place, as these samples are from Lower Holocene deposits and not from the Middle Holocene warm period. We have identified several shell samples from Icelandic sediments deposited during the Middle Holocene climatic optimum and have never found *L. littorea* in any of them. Some of these samples consist of up to 800 specimens of *Littorina* (Leifsdóttir & Símonarson, 1999). Therefore, we assume that *L. littorea* did not live in Iceland during the Holocene.

The last record of *L. littorea* from Iceland is that of Leifsdóttir (1999). The species was collected in the upper littoral conglomerate of the Búlandshöfdi interglacial sediments at Snaefellsnes (W Iceland). It was found in a molluscan assemblage together with the bivalves *Mytilus edulis* Linné, 1758 and *Arctica islandica* (Linné, 1767), as well as several other shallow-water species. The shell-bearing deposits at Búlandshöfdi rest on glacially eroded Cainozoic lavas and are overlain by a lava sheet that has been K/Ar-dated as 1.1±0.12 Ma (Albertsson, 1976). The sediments are held to be from the Middle Pleistocene, slightly older than the lava cover, that nevertheless is thought to be from the same interglacial stage. The species identification (Figure 1c, d) was confirmed by David G. Reid in the Spring of 2000 (pers. comm.).

The conclusion seems to be that the only confirmed occurrence of *L. littorea* in Iceland is that from the Middle Pleistocene deposits at Búlandshöfdi (Figure 4).

Evolution and migration

Shell characteristics, several anatomical details, allozyme frequency and mitochondrial DNA sequences all suggest that among Recent species the closest relative of *Littorina littorea* is *L. squalida*, now restricted to the Pacific (Reid, 1996). Although the fossil record is hardly sufficiently complete to provide certain details of the speciation process, it appears that *L. squalida* migrated from the Pacific to the Atlantic through the Arctic Ocean, at the latest during deposition of the *Mactra* Zone of the Tjörnes beds, older than 3.5 Ma (Einarsson *et al.*, 1967). Apparently, the species did not reach the North Sea area and Britain, as its occurrence in the Red Crag Formation, as well as in other British or continental European formations has not been confirmed (Reid, 1996). Distinct Pacific molluscs have been found both in the *Mactra* Zone and in the underlying Early Pliocene *Tapes* Zone of the Tjörnes beds (Durham & MacNeil, 1967; Backman, 1979; Símonarson *et al.*, 1998). Furthermore, Marincovich & Gladenkov (1999) and Marincovich (2000) suggested an early opening of the Bering Strait, between 5.5 and 4.8 Ma, and based their conclusion on the occurrence of molluscs of Atlantic-Arctic origin found in southern Alaska with North Pacific diatoms. This conclusion contrasts with previous studies (Einarsson *et al.*, 1967; Durham & MacNeil, 1967) that suggested an age of 4.1-3.1 Ma for the initial opening of the Bering Strait. The well-documented invasion of Pacific molluscs into the Arctic and North Atlantic (Durham & MacNeil, 1967) during the deposition of the uppermost *Serripes* Zone of the Tjörnes beds, older than 2.6 Ma (Albertsson, 1978), evidently resulted from a change to northerly flow through the Bering Strait, when the Central American Seaway became closed at about 3.5 Ma (Backman, 1979).

The oldest fossil occurrence of *Littorina littorea* in the upper part of the Red Crag Formation in East Anglia, between 2.55 and 2.4 Ma, strongly suggests that the differentiation of the two species postdates the opening of the Bering Strait. This might support a vicariant speciation and transformation of an Atlantic isolate of *L. squalida* into *L. littorea*, during the latest phases of the trans-Arctic/North Atlantic migration (Reid, 1996), possibly as a result of cooling at the onset of major and widespread glaciation at about 2.5 Ma (Shackleton *et al.*, 1984; Chen *et al.*, 1995). Since *L. littorea* has not been found in the Tjörnes deposits, this transformation probably occurred after the tide of the migration wave passed Iceland, but apparently prior to it reaching the North Sea and Britain. Thus, *L. littorea* possibly originated after 2.6 Ma, which indicates a somewhat lower age for the separation than proposed by Zaslavskaya *et al.* (1992), who placed the separation at 3.45 Ma. The onset of the extensive glaciation at about 2.5 Ma is also an important event affecting the diversity of Mediterranean molluscs of tropical affinity at the beginning of the Gelasian (Monegatti & Raffi, 2001). This glaciation also remarkably affected the diversity of the molluscs in the north, resulting in the first appearance of several new species in the N Greenland Kap København marine fauna, dated at 2.45 Ma (Símonarson *et al.*, 1998). Thus, the first appearance of *L. littorea* in the Red Crag Formation is no isolated event, but linked to a cooling event (glaciation) of considerable global impact on marine molluscs.

Littorina littorea probably spread from the North Sea to the present area of distribution during the Early Pleistocene. Several occurrences outside the present area show that the species is a sensitive indicator of climatic change. Thus, it reached Iceland during a rather mild Pleistocene interglacial stage (Chen *et al.*, 1995), about 1.1 Ma ago. Then it disappeared from Iceland, probably during the following glaciation, and we have no indication of its return during younger interglacial stages or during the Holocene. Drifting of planktonic larvae or rafting of adults on floating algae, driftwood, or other pieces of debris from the North Sea area, the British Isles or continental Europe might have taken place from time to time. However, it is more likely that after the disappearance of shallow-water areas on the Iceland-Faroe Ridge and the Wyville Thomson Ridge, between 3.3 and 2.4 Ma, the currents only occasionally carried the larvae, or rafting, floating or swimming adults to Iceland, but mainly in a northeasterly direction into the Norwegian Sea (Símonarson, 1981). Thus, stepping-stone migration of *L. littorea* via Iceland during the Late Pleistocene or the Holocene, *e.g.* to North America, is not as probable as earlier dispersal. Although the present current system in the North Atlantic seems to make passive pelagic dispersal from east to west rather improbable, there are indications that during early stages of the last deglaciation conditions were different and may at that time have facilitated such dispersal (Kellogg, 1980; Buckland *et al.*, 1986). This might also have been the case during earlier Pleistocene deglaciation periods.

There has been much debate as to whether *L. littorea* is native or introduced in North America. Surprisingly, the oldest fossil occurrence in eastern North America is from the middle part of the last glaciation in SW Nova Scotia (Wagner, 1977). Also, two specimens have been recorded from sediment beneath the surface of a beach terrace in northern Newfoundland, where a Norse house was built, and presumably predates the settlement (Bird, 1968). Several shells have also been found in two Indian middens in Nova Scotia, and two more in New Brunswick, radiocarbon-dated to between 1,000 and 1,500 BP (Clarke & Erskine, 1961). These finds show that the local populations were established in northeastern America before European settlement. Although *L. littorea* has not been found in North America in older deposits, migration earlier from Europe cannot be excluded. On the other hand, it is not impossible that repopulation from Europe might have occurred occasionally, also after the last glaciation (Ingólfsson, 1992). Spjeldnaes & Henningsmoen (1963) even came to the conclusion that *L. littorea* was introduced to North America by man. However, it is more likely that Vikings introduced some live specimens that genetically affected and strengthened the native population that rap-

idly increased its area of distribution. As a result, *L. littorea* became the dominant intertidal herbivore on many rocky shores in the region. European shipping may also have helped a native race to disperse from the Gulf of St Lawrence (Clarke & Erskine, 1961; Clarke, 1971). The records from the west coast of North America are taken to represent accidental introductions with the bivalves *Crassostrea* or *Mercenaria* from the Atlantic Coast (Carlton, 1969).

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