Rare species of West Indian aspect in the Holocene of Liverpool Bay and their biogeographic and environmental significance

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ABSTRACT: The Gulf Stream, although not directly responsible for the mild, temperate climate of the British Isles, transports vast quantities of water across the North Atlantic Ocean. An extension of the Caribbean-Loop-Florida current system, this strong current cools and becomes more saline by evaporation as it flows NE across the North Atlantic Ocean. Nevertheless, it is able to transport benthic foraminifera across oceanic distances, the fauna around Bermuda containing many species described from the Caribbean Sea. Examining two cores taken from the shallow middle neritic Holocene Surface Sands Formation of the temperate Liverpool Bay, England, we found rare specimens of eight species recorded also from the neritic of the tropical Caribbean and subtropical Atlantic South Shelf Provinces: *Asterigerina carinata*, *Dyocibicides biserialis*, *Elphidium discoidale*, *Nonionoides grateloupii*, *Quinqueloculina lamarckiana*, *Reussella atlantica* and *Sahulia conica*. We are confident in our identifications of *A. carinata* and *E. discoidale*, but suggest that these names may have been applied to several cryptospecies. Some of these may have been transported on floating phytal debris, *A. carinata*, which supports algal symbionts, having been recorded at abyssal depths in the eastern North Atlantic. Others may have been transported as small propagules (proloculi). Although there may be a constant rain of such specimens into Liverpool Bay, we conclude on the basis of their rarity that the exotic species are unlikely to be able to overwinter there. We suggest, however, that these may have potential as invasive species for Liverpool Bay as climates continue to warm. This is not the earliest instance of transport of exotic species across the North Atlantic. The Late Eocene species *Asterocyclina soldadoensis* has been recorded from both the southern Caribbean region and offshore Ireland.

Keywords: Gulf Stream, Surface Sands Formation, exotic species, propagules.

INTRODUCTION

Murray (2013) wrote that the biogeographic patterns of benthic foraminiferal morphospecies have applications in ecology, palaeoecology and taxonomy. Rare morphospecies must be identified and included in species lists if thorough knowledge of foraminiferal biogeography is to be attained.

Cushman (1948) apparently presaged Murray's (2013) comment when he qualitatively drew a distinction between cold and warm water Recent benthic foraminiferal faunas in the North Atlantic Ocean. He clearly thought that temperature was the principal determinant of benthic foraminiferal distributions (Culver and Buzas 2003). Cushman (1948) suggested that a cold water fauna did not extend south to encompass the entire British Isles (51–59°N, 1°E –10°W), but extended southward into the northernmost North Sea to the east of Scotland. He explicitly showed the nearshore seas elsewhere off the British Isles as supporting a Recent benthic foraminiferal fauna of West Indian aspect (text-fig. 1; see his figure on p. 38). He stated, however, that this fauna was in a 'less characteristic form' than the tropical Caribbean fauna.

Cushman's (1948) figure indicates his West Indian fauna to follow approximately the course of the surficial Gulf Stream /North Atlantic Drift. The Gulf Stream, which is part of the North Atlantic Thermohaline Circulation (Atlantic conveyor), is about 100 km wide and is up to 1000 m deep. It attains its maximum velocity of 2.5 m s^{-1} near the sea surface. Although the Gulf Stream is not directly responsible for the mild climate in the temperate British Isles, (Seager et al. 2002), it carries considerable heat as it departs US waters (Seager 2006). According to Cushman's interpretation, however, his West Indian foraminiferal province did not extent as far north as Cape Hatteras (35°N, 75°W), at which point the Gulf Stream exits the eastern American seaboard (Hogg 1992). At Cape Hatteras there exists a major faunal boundary caused by the warm water to the south and the colder water to the north (e.g., Jones et al. 2009). This is reflected in the biogeography of seaweeds (Searles 1984), bivalves (Jones et al. 2009) and fishes (Mahon et al. 1998).

Schnitker (1971) demonstrated that a form of Cushman's (1948) West Indian benthic foraminiferal province extends northwards to southern North Carolina, where he recovered many species common in the Caribbean Sea. This is reflected in the map of qualitatively-determined benthic foraminiferal provinces published by Boltovskoy and Wright (1976), which extended a West Indian province north to Cape Hatteras. However, these

http://doi.org/10.47894/mpal.69.1.03

authors removed the British Isles from the West Indian province, placing them instead in a temperate-water European Atlantic province. They did not state any provincial placement of Bermuda (32°N, 65°W).

Using a quantitative technique (cluster analysis based on species presence/absence), Culver and Buzas (1980) reiterated that a major benthic foraminiferal provincial boundary at Cape Hatteras is reflected in the biogeographic distributions of benthic foraminifera along the eastern North American seaboard. However, these authors split the West Indian province of Boltovskoy and Wright (1976) into three neritic provinces: a Caribbean Province, a Gulf of Mexico Inner Shelf Province, and an Atlantic Southern Shelf Province (see Culver and Buzas 2003, fig. 6.3). The boundary between the Caribbean and Atlantic Southern Shelf Province occurs at Cape Canaveral, Florida.

That the Gulf Stream disperses foraminifera of West Indian aspect across the North Atlantic Ocean aspect is reflected in the composition of the Recent fauna around Bermuda (see Javaux and Scott 2003; Steinker 1980; Steinker and Clem 1984), which is situated ~1000 km east of Cape Hatteras. The Bermudan benthic foraminiferal fauna contains many species common in the Caribbean Sea. Such characteristic nearshore West Indian species as *Disorbis rosea*, however, are not found as far north as Bermuda (Javaux and Scott 2003, table 2; Steinker 1980) or Cape Hatteras (Schnitker 1971), perhaps indicating either that not all West Indian foraminifera species have the same propensity for dispersal, or that changes in the nature (temperature, salinity) of the Gulf Stream, which cools as it flows NE, causes modification of the benthic foraminiferal fauna. Either explanation might account for Cushman's comment that the benthic foraminiferal assemblage around the British Isles is less characteristic of the West Indian province. Cushman (1948) did not, however, elaborate on the 'less characteristic' nature of the British Isles' warm water community.

The occurrence of modified assemblages of West Indian aspect in the Gulf of Mexico (Bandy 1954; Bandy 1956; Parker 1954; Poag 2015), around Florida (Bock 1971) and along the eastern North American seaboard as far north as Cape Hatteras, North Carolina (Schnitker 1971) reflects the flow of the Caribbean-Loop-Florida Current system, which feeds the Gulf Stream/North Atlantic Drift.

To our knowledge, despite Cushman's (1948) indication of a modified West Indian fauna around parts of the British Isles, records of species of West Indian aspect there are few. Heron-Allen and Earland (1930) recorded *Quinqueloculina lamarckiana* d'Orbigny, 1839 around the British mainland, but did not make any biogeographic comment nor illustrate them. This species, originally described from Cuba, is off the eastern American seaboard abundant in the Atlantic Southern Shelf Province, but is found, although rarely, along the coastline farther north (Culver and Buzas 1980). Atkinson (1969, 1971) found *Elphidium discoidale* d'Orbigny (1839), originally described from the Caribbean. He also recorded *Nonionella atlantica* Cushman (1947). This species, like *Q. lamarckiana*, is most commonly encountered on the continental shelf off the SE United States in the Atlantic Southern Shelf Province, but has been encountered, albeit rarely, farther north, along the coastline between Cape Hatteras and Cape Cod (Culver and Buzas 1980, p. 449). Atkinson (1969, 1971) neither made any comment regarding the biogeography of these two species (*E. discoidale*, *N. atlantica*) nor illustrated them.

In a study of Holocene cores taken in Liverpool Bay (text-fig. 2), we recorded rare (<1%) morphospecies of warm water, western North Atlantic aspect, they being recorded from the Caribbean Sea, in the Gulf of Mexico, and off SE North America. We illustrate these species here, outline their biogeographic distributions in the North Atlantic Ocean and adjacent seas, and note their implications for global warming.

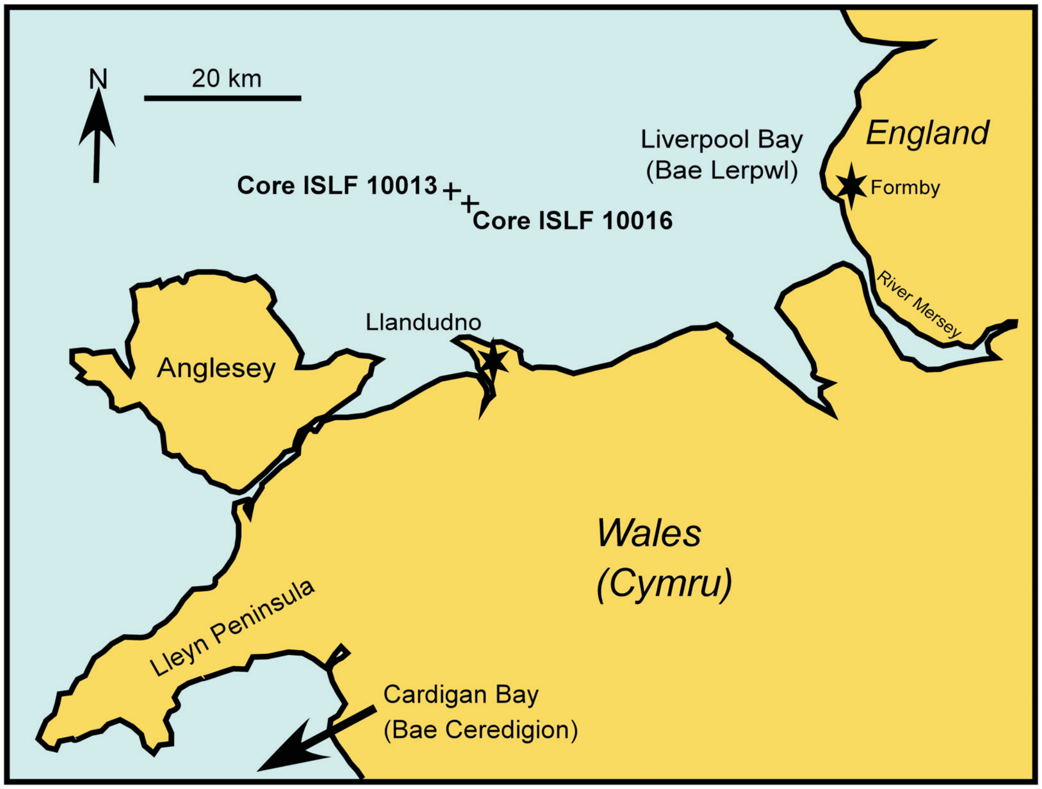
STUDY AREA

Two cores were taken from Liverpool Bay, approximately west of Formby, England, and north of Llandudno, Wales, (water depth ~30 m, estimated from fig. 1 in Polton et al. 2011). It had been hoped for geoarchaeological purposes that these cores would penetrate back to the pre-Holocene surface. Penetration, however, proved insufficient for this (Martin Bates, oral communication). Core ISLF 10013 (53.517°N, 3.807°W) was a 290 cm-long vibrocore. Core ISLF 10016 (53.509°N, 3.785°W), taken to the ESE of Core ISLF 10013, was a ~80 cm long piston core. Vincent et al. (2004, map 12) characterized the two cores' sites as being on a low stress, coarse sediment plain.

The seafloor at the site of these two cores is made of clayey sand with sand grains ~0.5 mm in diameter (Luo et al. 2013, fig. 6A). The cores contain material from the two Members [the overlying Surface Layer 1 Member (SL1) and the underlying Surface Layer 2 Member (SL2)] of the Surface Sands Formation (see Jackson et al. 1995, figs. 69, 71; Mellett et al. 2015).

Core ISLF 10016 for its entire length penetrated dark grey-brown clayey sand of SL 1, with some marine gastropods and broken bivalves. This shelly material and abundant sand was recovered from the upper 202 cm of Core ISLF 10013, but not in that core's lowest 80 cm, which comprised dark brown, structureless clay of SL 2. Martin Bates (oral communication, 2019) suggested that this lower part of Core ISLF 10013 was deposited on a tidal flat. Off Llandudno, the SL2 Member in Borehole 70/07 (see text-fig. 1) consists of peaty silt thought to represent reed swamps adjacent to open water and older than 9.2 ka BP (Roberts et al. 2011). We therefore suggest that the SL 2 in Core ISLF 10013 is probably older than ~9 ka. We conjecture that the SL1 in our cores is younger than ~6,000 cal BP. Our reasoning for this suggestion is that Liverpool Bay (2,528 km^2) currently ranges in depth from mean low water to ~66 m. Much of the bay is comparatively new, a sea-level lowstand of –28 m OD having occurred in the North Welsh region at 12.3 cal BP (Roberts et al., 2011). Sea level within the bay rose rapidly between 12,000 – 9,000 cal BP, inducing the erosional surface that separates the SL 1 from the SL2 Member (Jackson et al. 1995). At 9000 cal BP the rate of sea level rise diminishing markedly, and water depths have increased by only 2 m since ~6,000 cal BP (Roberts et al. 2011, fig. 12). We interpret the upper, sandy clay part of Core ISLF 10013, and the whole of Core ISLF 10016, as being younger than ~9 ka, and perhaps even younger than 6000 cal BP.

Further evidence supports our conjecture regarding the age of SL 1 in our cores. Kershaw et al. (1988) estimated a sedimentation rate of 0.02–0.08 cm a^{-1} for the past 3000–4000 years in the eastern Irish Sea on the basis of age vs. depth profiles of the shells of the gastropod *Turritella communis* (Risso). This depositional rate equates to 60–320 cm of sediment. Thus our



TEXT-FIGURE 1
NE England and N Wales showing the locations of Liverpool Bay (Bae Lerpwl), Cardigan Bay (Bae Ceredigion), and the sites of Cores ISLF 10013 and ISLF 10016.

cores penetrate into sediment older than the Anthropocene, which commenced around 1950, Crickmore and Kiff (1985) finding man-made metals in the open Liverpool Bay only at <10 cm below the sediment surface.

MATERIALS AND METHODS

We had intended to sample the cores at 10 cm intervals in 2 cm slices commencing at the seafloor. This was possible throughout Core ISLF 10016 (7 samples). However, the uppermost 25 cm of the longer Core ISLF 10013 was too sludgy and deformed for accurate sampling (we interpret this as being Layer A [mobile surface sediment] of Pantin and Evans 1984). Therefore, sampling of this core commenced at 30 cm below the seafloor (cmbsf), yielding 26 samples. We conclude that Layer A was either extremely thin in or absent from Core ISLF 10016.

For each sample, 100 g of sediment was soaked in tap water until disaggregated, and then washed over a 63 µm mesh to remove silt and clay. The residue was dried in an oven at 90°C. For each sample the >63 µm residue was split with a microsplitter to give aliquot of >250 specimens, and each aliquot was sieved over 106, 125, 150 and 425 µm meshes. The resulting five fractions were picked clean of foraminifera that were sorted, mounted on micropalaeontological slides, and identified using illustrations and descriptions in the literature. While most specimens could be identified using literature from around the British Isles [Murray (1971, 2000, 2003); Gabel (1971); Haynes (1973); Hofker (1977)], for some of the rarer species we have to use publications from farther afield, within the Caribbean Sea and Gulf of Mexico, and off the SE United States of America (Brady 1884; Cushman 1947; d'Orbigny 1839; Poag 1981, 2015). These rarer, exotic species are the subject of our paper.

The illustrated specimens were photographed using a Neoscope JCM-7000 scanning electron microscope in the College of Petroleum and Geosciences, KFUPM. The plesiotypes will be deposited in the European Micropalaeontological Reference Centre at Micropress Europe in Kraków.

RESULTS

A total of 13,450 foraminiferal tests were recovered from the two cores, 10,214 being from Core ISLF 10013, and 3236 from Core ISLF 10016. The samples in the lower part of Core ISLF 10013, deposited as Surface Layer 2 on a tidal flat, yielded quantities of gypsum not sound in the younger Surface Layer 1.

Among these foraminifera, the following seven exotic species from Cushman's (1948) West Indian region were recorded from the Holocene of Liverpool Bay: *Asterigerina carinata* d'Orbigny 1839, *Dyocibicides biserialis* Cushman and Valentine (1930), *Elphidium discoidale* (d'Orbigny 1839) [= *Polystomella discoidalis* d'Orbigny, 1839], *Nonionoides grateloupii* (d'Orbigny, 1839) [= *Nonionina grateloupii* d'Orbigny, 1839], *Quinqueloculina lamarckiana* d'Orbigny, 1839, *Reussella atlantica* Cushman, 1947 [= *Reussella spinulosa* var. *atlantica* Cushman, 1947], and *Sahulia conica* (d'Orbigny, 1839) [= *Textularia conica* d'Orbigny, 1839]. These are collectively represented by 183 specimens (1.4% of total recovery).

Remarks regarding each of these, and details of their biogeography with respect to the Gulf Stream, are given below.

Two specimens of *Asterigerina carinata* d'Orbigny, 1839 (Pl. 1, figs A-C) were recovered, both from upper part of the SL1 Member in Core ISLF 10013, 30–52 cm below the seafloor. The illustrated specimen from 50–52 cmbsf, was the better preserved, showing the chamberlets clearly. That from 30–32 cmbsf showed chamberlets only when wetted. Our specimens clearly show the conical shape seen in d'Orbigny's type illustrations, rather than the more flattened forms shown by Cushman (1931) and Bandy (1954). Poag (2015) also illustrated a highly conical specimen. Cushman (1931) found that *A. carinata* can be up to <750 µm in diameter. Our specimens are only ~250 µm in diameter. This small size might be a factor in the absence of ribbing parallel to the periphery near the aperture, which Bock (1971) noted is not always present. Terquem (1876, p. 440, pl. 5, figs. 6a, b) described and illustrated specimens he called *Asterigerina geometrica* from shore sands at Dunkerque, northern France. However, his illustration does not show the triangular chamberlets in our specimens. Furthermore, Hayward et al. (2021a) regard *Asterigerina geometrica* Terquem, 1875, as being a *nomen dubium*.

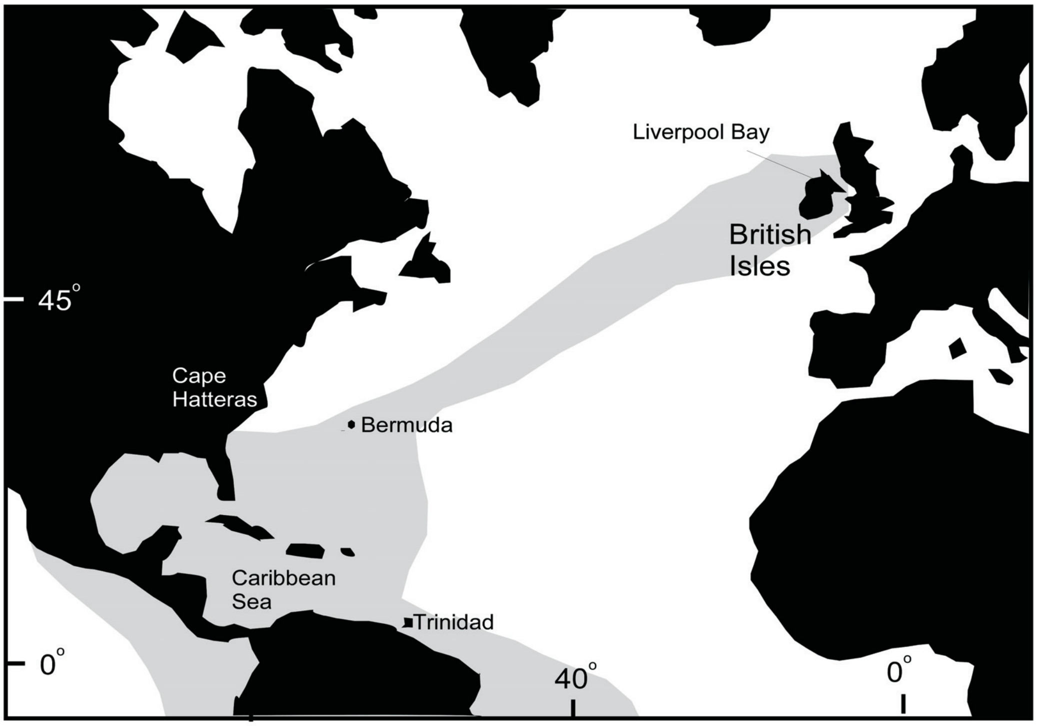
Dyocibicides biserialis Cushman and Valentine, 1930 (Pl. 1, figs. D–F), was represented by nine specimens, all from core ISLF 10013, SL 1 Member. The illustrated specimen, from 40–42 cm bsf, is broken, but the outline of the broken chamber clearly shows the biserial aspect of the more adult portion when compared with the illustration by Cushman (1931, pl. 24, fig. 2). This species was described from shallow waters off California (Cushman and Valentine 1930). It is not a eurythermic species, being found in the Pacific Ocean as far north as Alaska (Culver and Buzas 1985). It was illustrated by Brady (1884; pl. 93, fig. 6), as emended by Barker (1960), from offshore western New Zealand. In the North Atlantic region and adjacent waters, it is associated with warm water. Cushman (1931) illustrated a single specimen found off Georgia, USA, within the Atlantic Southern Shelf Province (see also Culver and Buzas 1980). Sen Gupta and Smith (2013) found the obligate sessile *D. biserialis* in association with hydroids and cornified polychaete tubes in the Gulf of Mexico. It occurs in the Caribbean Sea (Culver and Buzas 1982). Ours is apparently the first record of *D. biserialis* around the British Isles; although Gross (2001) and Costello et al. (2021) state their works to be catalogues of European species, they do not give any European records of this species.

We recovered three specimens of *Ephidium discoidale* (d'Orbigny 1839), all from the SL 1 Member. The illustrated specimen (Pl. 1, figs. G–I) came from Core ISLF 10013, at 160–162 cm below sea floor. The other two specimens came from Core ISLF 10016, at 60–62 cm below the seafloor. All came from below the mobile surface layer A. We identified our specimens using the type illustration in d'Orbigny (1839), which shows a rather acute periphery, an imperforate umbilical boss and recurved sutures, and a aperture at the base of the apertural face. This is well illustrated using SEM photographs of *Elphidium discoidale* forma *typicum* by Poag (2015). The specimen illustrated by Cushman (1930, pl. 8, fig. 9) is not *E. discoidale* (see Le Calvez 1977), having a somewhat rounded periphery, rather than the acute one of the type illustration. The specimen illustrated by Bock (1970, pl. 20, figs. 9, 10) is also not *E. discoidale*, having straight sutures and an almost rounded periphery. Despite the occurrence of these apparent cryptomorphospecies, we are confident that our specimens are *E. discoidale* sensu stricto, given their close resemblance to the type illustration.

Cushman (1930) suggested *E. discoidale* to have a generally West Indian distribution, and Gross (2001) did not list it as being present in the eastern North Atlantic Ocean. Culver and Buzas (1980), however, mapped it as being widespread in the Atlantic Southern Shelf Province. It is thus associated with the warm water of the Gulf Stream. The acceptance by Culver and Buzas (1980) of Schnitker's (1971, pl. 7, fig. 6) illustration of *Elphidiella* sp. cf. *mexicanum* (Kornfeld, 1931) as their concept for *E. discoidale* warrants further investigation, this morphotype having a rather subrounded periphery. Javaux and Scott (2003) listed *E. discoidale* as occurring around Bermuda, but did not illustrate it. Atkinson (1969) recorded *E. discoidale* in association with macroalgae in the littoral zone of Cardigan Bay, especially in a holdfast of *Laminaria* sp. He did not, however, illustrate his specimens. Ours is the first illustrated specimen of *E. discoidale* around the British Isles.

A single specimen of *Nonionoides grateloupii* (d'Orbigny, 1839) (Pl. 1, figs. J–K) was recorded from 220–222 cm below the seafloor in core ISLF 10013. It was cracked when found, and broke during preparation for SEM photography. We have provided a picture of the largest fragment. The type locality of this species is around Cuba. It is widespread in the Caribbean Sea and along the eastern Atlantic seaboard of North America as far north as Cape Cod. Culver and Buzas (1980) noted it to move into deeper water off the eastern American seaboard with increasing latitude, and stated that this shift in distribution pattern correlates with where the Florida Current leaves the continental margin at Cape Hatteras to become the Gulf Stream. This distribution north of Cape Hatteras might reflect the discarding of dead specimens from floating plant debris; Wilson and Ramsook (2007) found *N. grateloupii* on phytal substrates in the eastern Caribbean Sea.

Quinqueloculina lamarckiana d'Orbigny 1839 (Pl. 1, Figs. L–N) was represented by 155 specimens, 13 from Surface Layer 2 in core ISLF 10013, the remainder from Surface Layer 1. This was the most abundant exotic species in our samples. There is evidently much confusion regarding distinguishing *Q. lamarckiana* from *Q. auberiana* d'Orbigny 1839 and *Q. cuvieriana* d'Orbigny, 1839. The type illustration shows *Q. lamarckiana* from Cuba and Jamaica as having a neck, but Bock (1970), working in Florida Bay, USA, found this feature to be variably developed, even being non-existent in some specimens. Cushman (1921, 1929) thought *Q. lamarckiana* and *Q. auberiana* to be synonymous. Parker (1954) stated that her concept for *Q. lamarckiana* may represent a 'species group', there being much variation in the acuteness of the chamber angles and the extent to which they project. Drooger and Kaasschieter (1958) likewise stated that not all *Q. lamarckiana* have an acute periphery, some being rounded. Hofker had difficulty with *Q. lamarckiana*; he (Hofker, 1964) placed in it specimens with a rounded periphery and indistinct longitudinal striae, but later (Hofker 1976) suggested it to have a short carina on each chamber and to be smooth (see also Andersen, 1961). Culver and Buzas (1980) used as their concept for *Q. lamarckiana* the specimen illustrated by Schnitker (1971) from the North Carolina continental shelf, which has sharp chamber angles and faint longitudinal striae. Our specimens vary from having sharp, angular chamber peripheries to more rounded ones, and we cannot with



TEXT-FIGURE 2
The North Atlantic Ocean, showing the locations of Liverpool Bay, Bermuda, Trinidad and Cape Hatteras, and the West Indian fauna according to Cushman (1948).

confidence split our specimens into two groups on the basis of peripheral angularity. We use the name *Q. lamarckiana* as it has precedence over *Q. auberiana*. The longitudinal striations are faint on our specimens, which are small.

Apart from a few, scattered references farther north, Culver and Buzas (1980) noted that *Q. lamarckiana* has off eastern North America been found in the Atlantic Southern Shelf Province. Gross (2001) listed *Q. lamarckiana* and *Q. auberiana* as occurring in the Mediterranean Sea, but not in the eastern Atlantic Ocean. This species was suggested by Cushman (1928), however, to have been recorded around the British Isles as *Q. auberiana* d'Orbigny 1839. However, he provided no further details. Heron-Allen and Earland (1909) recorded, but did not illustrate, *Miliolina auberiana* d'Orbigny sp. from the shore sands at Bognor, England, and later (Heron-Allen and Earland, 1916) from the west coast of Scotland, where they noted specimens to be small and obscure. Heron-Allen and Earland (1930) recorded *Miliolina lamarckiana* (d'Orbigny) around Plymouth, and stated that it was "Frequent everywhere, but rather small." They also stated this theirs was the first record under this name. They did not, however, illustrate their specimens. Our Liverpool Bay specimens are the first to be illustrated from around the British Isles.

Reussella atlantica Cushman 1947 (Pl. 1, figs. O–Q) was represented by 3 specimens between 212–60 cm bsf (SL1 member) in Core ISLF 10013, two being very poorly preserved. The illustrated specimen came from 60–62 cm below the seafloor. *Reussella atlantica* was described by Cushman (1947, 91; pl. 20, figs. 6–7) from off Cape Canaveral, Florida. The type figure does not show any spines, although a re-photograph of the type specimen (see Hayward et al. 2021b) shows weakly developed, short, stumpy spines. Such a specimen was illustrated from the Orinoco-Trinidad-Paria shelf off NE South America (Drooger and Kaasschieter 1958).

Culver and Buzas (1980) mapped *R. atlantica* off the eastern coast of North America as being most abundant in the Atlantic Southern Shelf Province, but with only a single occurrence east of southern Virginia. This closely matches the distribution of the Florida Current and its extension into the Gulf Stream. It is also found in semi-protected lagoons around Bermuda (Javaux and Scott 2003). Gross (2001) did not list *R. atlantica* as occurring in either the eastern North Atlantic Ocean or the Mediterranean Sea, but recorded the more distinct *Reussella spinulosa* (Reuss, 1850) in both areas. To our knowledge, however, this is the first record of any species of *Reussella* from around the British Isles.

We recovered 10 specimens of *Sahulia conica* (d'Orbigny, 1839), two being from between 72–50 cm below the sea floor in Core ISLF 10013, the remainder being recovered from throughout Core ISLF 10016. All specimens came from the SL1 Member. The illustrated specimen (PL. 1, Fig. O–S) was recovered from 70–72 cm below the seafloor in Core ISLF 10013. We include this species in our record of exotic species in Liverpool Bay because of its distinctive biogeography. Ours is not, however, the first illustrated record from around the British Isles. *Sahulia conica*, though originally described from Cuba, and widespread in the Atlantic Southern Shelf Province (Culver and Buzas, 1980, fig. 136), was listed by Heron-Allen and Earland

(1916, 1930) from around the British Isles (see also Cushman 1922) and illustrated by Gabel (1971). It has recently been illustrated from Falmouth, southern England (Fenwick, no date), though Gross (2001) did not list it as living in the eastern North Atlantic Ocean. The foraminifer illustrated as *Textularia conica* from Bermuda by Javaux and Scott (2003) is not this species. Its test is much more elongate and its aperture is a simple basal arch without lateral re-entrants. Ours is apparently the first record of *S. conica* for the Central Irish Sea.

Murray (1971) illustrated specimens of what he termed a *Textularia sagittula* Defrance group. None of these resemble *Sahulia conica* in side view. He stated that the aperture in members of this group is "a short interomarginal arch without a lip." However, at least one specimen shown in apertural view (see Murray 1971, pl. 8, fig. 9) has a *Sahulia* type of aperture, with a lip and re-entrants at either side. It is not clear how this specimen might relate to *Sahulia conica*.

DISCUSSION

We have recorded seven species of benthic foraminifera in Liverpool Bay that were originally described from the Caribbean Sea or the Atlantic Southern Shelf Province. It might be suggested that these exotic species were been introduced by human activity, such as in ship's ballast water (cf. Calvo-Marcilese and Langer 2010). There has historically been much shipping between the port at Liverpool and the Caribbean region (Clover 2011; Drake 1976). However, such transport might not be the case for all species. Some *Quinqueloculina lamarckiana* and the sole *Nonionella grateloupii* were recovered from the older Surface Layer 2 Member of the Surface Sands Formation. This member, which was deposited on a tidal flat, overlays an erosional surface that, dated at 10.2 ka BP, developed shortly after the start of post-glacial rapid sea-level rise in the North Wales region, which commenced 11,000 cal BP (Roberts et al. 2011, fig. 11). Recovery of all rare morphospecies recorded here extended below the 10 cm below the seafloor limit for man-made metals within Liverpool Bay.

Murray (2013, fig. 36) suggested *Asterigerina carinata* to be a low latitude, warm-water species, with live specimens confined to nearshore environments in the Caribbean Sea and on the shelf off the southern USA and Nicaragua. However, its distribution is not so restricted. Although *A. carinata* was described from Cuba and Jamaica by d'Orbigny (1839, p. 118) and is widespread in shallow waters in the Caribbean Sea and around the Bahamas (Culver and Buzas 1982), it is also found in the Gulf of Mexico (Culver and Buzas 1983), and along the SE North American seaboard as far north as Cape Hatteras (Culver and Buzas 1980; Schnitker 1971). Javaux and Scott (2003) illustrated a high spired specimen from Bermuda. There is thus a close correlation between the distribution of *A. carinata* and the warm waters of the Caribbean, Loop and Florida Currents, and the Gulf Stream. The significance of the low-spired nature of the specimens illustrated by Cushman (1931) and Bandy (1954) is unclear. These might be either ecophenotypic variants or members of a cryptospecies.

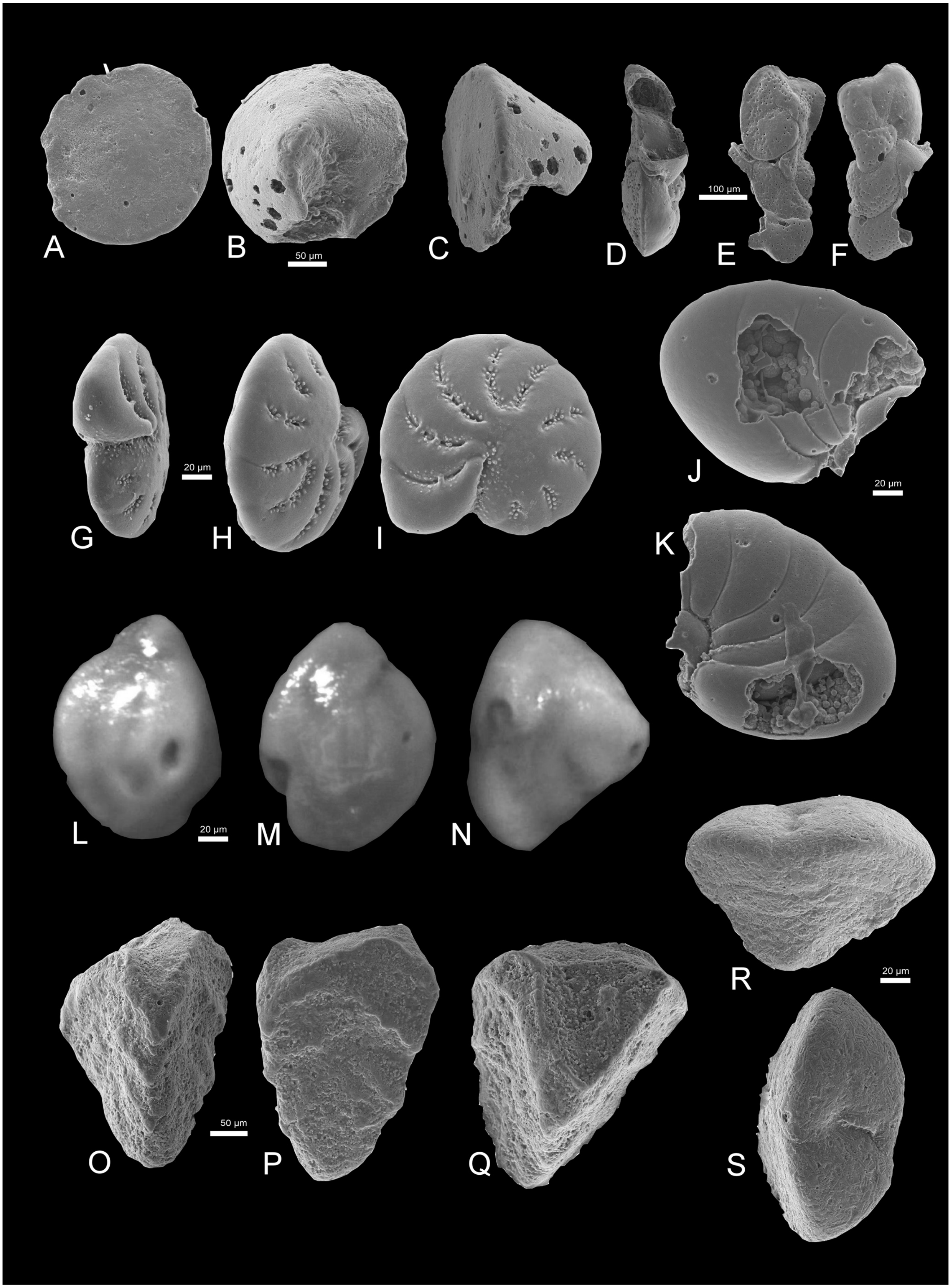
Although ours is the first record of *A. carinata* from around the British Isles, it is not the first from the eastern Atlantic Ocean. McCave (2004) recorded it in a piston core taken from the abyssal plain ~1000 km west of Ireland (50.69°N, 21.86°W, water depth 3547.0 m). *Asterigerina carinata* is a nearshore, epiphytal species with a flat attachment surface, It is commonly associated with coral reefs (Wilson et al. 2012), seagrasses and algae (Fischel et al. 2018), and is symbiotic with algae (Hallock et al. 1992) and so limited to the photic zone. We suggest that McCave's (2004) abyssal specimens are allochthonous, perhaps being transported and dropped from floating seagrass debris carried NE on the Gulf Stream (cf. Fiorini and Lokier 2020), similar to the offshore transport noted in the Caribbean Sea by Wilson (2008).

Although *Reussella spinulosa* (Reuss, 1850) has been recorded living epiphytally in the Mediterranean area (Murray 2013), and *R. mortensi* Hofker, 1956 in the Caribbean Sea (Wilson and Ramsook 2007), we are not aware of any such records for *R. atlantica.* Attachment to floating marine plant debris is, however, not the only means by which benthic foraminifera might have been transported from the SE North Atlantic Ocean to Liverpool Bay. Many benthic foraminifera on reproduction form propagules (both sexually and asexually produced young, and perhaps only the proloculus; see Alve and Goldstein 2003; Alve and Goldstein 2010). These propagules have been cultured to produce adults from sediment <32 µm in size, which indicates the propagules' maximum size. The sexually produced (microspheric) young appear to have a greater potential for dispersal. Murray (2013) suggested that propagules are a likely mechanism by which benthic foraminifera across oceans, the being transported in suspension. The high velocity of the Gulf Stream near the surface may be sufficient to allow such transport.

PLATE 1

Foraminifera of Caribbean aspect from Cores ISLF 10013 and ISLF 10016 from Liverpool Bay.
Figures A–K and O–S are SEM photomicrographs, while figures L–N are digital micrographs.

A-C *Asterigerina carinata* d'Orbigny 1839.
D-F *Dyocibicides biserialis* Cushman and Valentine 1930.
G-I *Ephidium discoidale* (d'Orbigny 1839).
J-K *Nonionoides grateloupii* (d'Orbigny 1839).
L-N *Quinqueloculina lamarckiana* d'Orbigny 1839.
O-Q *Reussella atlantica* Cushman 1947.
R-S *Sahulia conica* (d'Orbigny 1839).


A
B
50 µm
C
D
100 µm
E
F
G
20 µm
H
I
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S

Wilson (2008) suggested that *A. carinata* and *E. discoidale* may be members of the same guild, a guild being a functional cluster of species that interact among themselves more strongly than with other species in the assemblage (Jaksic 1981). Wilson and Ramsook (2007) recorded live (rose Bengal-stained) *E. discoidale* and *A. carinata* on marine algae and seagrasses in the back-reef around Nevis, NE Caribbean Sea. It is possible that this guild membership is in some way responsible for the co-occurrence of these two species in Liverpool Bay.

The Gulf Stream might deliver a constant rain of propagules throughout the year. However, given the rarity of the West Indian species, it appears probable that they may be able to survive only during warmer summer months around the British Isles, not being able to overwinter. However, the occurrence of these rare species suggests they have potential as future invasive species as the British climate warms due to climate change.

This is not the oldest instance of foraminiferal transport by the Gulf Stream, evidence for which exists in rocks as old as Early Eocene (Pinet et al. 1981). Kugler and Caudri (1975) examined the stratigraphy of Soldado Rock, a slump exposed subaerially in the Gulf of Paria, which separates Trinidad from Venezuela. They distinguished 13 beds, of which beds 3–10 are of Late Eocene age. They were thus deposited at a time when waters in western Europe were warm, in comparison to those in eastern Europe (Pożaryska 1978). *Asterocyclina soldadoensis* Caudri, 1975 was described from Bed 9a on Soldado Rock (Caudri 1975). Dobson et al. (1976) recorded *Astercyclina* cf. *stellata* (d'Archiac) from Porcupine Bank, west of Ireland, but this was later re-identified as *A. soldadoensis* (Haynes, oral communication, 1980; Wilson 1981). We conclude that this species was transported NE across the paleo-Atlantic Ocean from Trinidad to offshore British Isles by the proto-Gulf Stream.

CONCLUSIONS

Some rare species in Liverpool Bay have affinities with the Caribbean and Atlantic Southern Shelf Provinces. Their occurrence around the British Isles apparently reflects transport by the Caribbean-Loop-Florida Current system and its extension into the surficial Gulf Stream, which flows NE across the North Atlantic Ocean. The occurrence of *Asterigerina carinata*, which is of nearshore aspect, at abyssal depths in the eastern North Atlantic, suggests transport on floating marine plant debris, from which the specimens were shed. However, transport as propagules in suspension seems equally likely for the remaining rare West Indian species. Such transport has apparently ranged back at least to Late Eocene times, when *Asterocyclina soldadoensis* lived on both the shelf around Trinidad and off Ireland.

ACKNOWLEDGMENTS

Thanks are due to Martin Bates (Lampeter University, Wales) who kindly provided us with the samples on which this paper is based. The late John Murray kindly provided BW with much of the British literature cited. BW would also like to thank the staff at the Cardigan Bay Marine Wildlife Centre (Sarah Parry, Gemma Woodford, Laura Evans) for discussions and encouragement.

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