Hypothesis

Invasion of the Atlantic Ocean and Caribbean Sea by a Large Benthic Foraminifer in the Little Ice Age

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Invasion of the Atlantic Ocean and Caribbean Sea by a Large Benthic Foraminifer in the Little Ice Age

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Abstract: The larger benthic foraminifera are a group of marine protists, harbouring symbiotic algae, that are geographically confined to shallow tropical and subtropical waters, often associated with coral reefs. The resulting controls on availability of habitat and rates of dispersion make these foraminifers, particularly the genus *Amphistegina,* useful proxies in the study of invasive marine biota, transported through hull fouling and ballast water contamination in modern commercial shipping. However, there is limited information on the importance of these dispersal mechanisms for foraminifers in the Pre-Industrial Era (pre-1850) for the Atlantic and Caribbean region. This paper examines possible constraints and vectors controlling the invasion of warm-water taxa from the Indo-Pacific region to the Atlantic and Caribbean region. *Heterostegina depressa,* first described from St. Helena, a remote island in the South Atlantic, provides a test case. The paper postulates that invasions through natural range expansion or ocean currents were unlikely along the possible available routes and hypothesize that anthropogenic vectors, particularly sailing ships, were the most likely means of transport. It concludes that the invasion of the Atlantic by *H. depressa* was accomplished within the Little Ice Age (1350–1850 C.E.), during the period between the start of Portuguese marine trade with east Africa in 1497 and the first description of *H. depressa* in 1826. The hypothesis is likely applicable to other foraminifera and other biota currently resident in the Atlantic and Caribbean region. The model presented provides well defined parameters that can be tested using methods such as isotopic dating of foraminiferal assemblages in cores and genetic indices of similarity of geographic populations.

Keywords: *Heterostegina depressa*; little ice age; anthropogenic dispersal; range expansion; Caribbean Sea; Atlantic ocean

1. Introduction

The Larger Benthic Foraminifera (LBF), an informal group of protists harbouring algal symbionts of various kinds are an important global component of the marine biosphere, occupying a wide variety of ecological niches in the euphotic zone of the warm-temperate to tropical marine realm (average Sea Surface Temperature (SST) > 18°C) [1]. The nature of these symbiotic relationships can be experimentally related to their habitats through various controlling factors such as nutrients, temperature and available light [2–13]. Their global distribution is well illustrated in the discussion by Prazeres & Renema of the associated symbionts [14].

The cosmopolitan distribution and well-studied physiology and metabolic activities of the diatom symbiont-bearing genus *Amphistegina* has proven it particularly useful in the investigation of the rates of invasion and dispersal of biota that have appeared and spread in the Mediterranean region since the opening of the Suez Canal in 1869, the so-called Lessepsian migration [15–23]. Genetic research has indicated that modern wartime and commercial shipping activities have important vectors for the global dispersion of diverse alien invasive marine and terrestrial species in an increasingly warming world [24–34].

The prime importance of modern shipping as the agent for many of these introductions has been well documented and even taken for granted [35]. However, published information on historical (pre-19th Century) participation of human trade and migration in providing vectors for the dispersal of foraminifers into or out of the Atlantic and Caribbean region (ACR) is sparse. Literature that has explored the importance of such participation among remote ocean islands and other places is based almost exclusively on examples from the Indo-Pacific region (IPR) and Mediterranean/north-west Europe [25,36–38]. The paper presents a hypothesis for a LBF-based invasion of the Atlantic Ocean and the Caribbean to supplement this previous work

2. Methods

Concisely presented data and distribution maps assembled by Langer & Hottinger provided a starting point for the comprehensive literature search and review [7]. Sources and data gleaned from that review were used to determine the nature of potential vectors and barriers that might influence or inhibit the timing, direction and spread of *H. depressa* between the IPR and the ACR. Factors such as sea and ocean temperatures, circulation patterns, ocean transport routes and species presence and absence were key observations while reviewing each source.

3. Hypothesis

Heterostegina depressa d'Orbigny, an easily recognisable, extant, cosmopolitan LBF hosting diatom symbionts, belonging to the family Nummullitidae was selected to test the hypothesis that Holocene, and possibly earlier Quaternary intrusion by LBFs and probably other biota from the IPR into the ACR by natural processes was unlikely due to the physical impediments that exist **(Figure 1)** [7,39]. It was posited that anthropogenic vectors were the most likely means of transport for this species and probably other foraminifera introduced to the ACR from the IPR. The choice of species was guided by two main considerations. Firstly, *H. depressa*, the genus type, was initially described from a remote island in the ACR in 1826 near the end of the Little Ice Age (1350-1850 C.E. [40–42]. Wooden sailing ships were the mode of marine transport at that time. Secondly, the occurrence of *H. depresssa* in the ACR is apparently restricted to Late Holocene sediments. The propositions of our hypothesis are presented sequentially below.

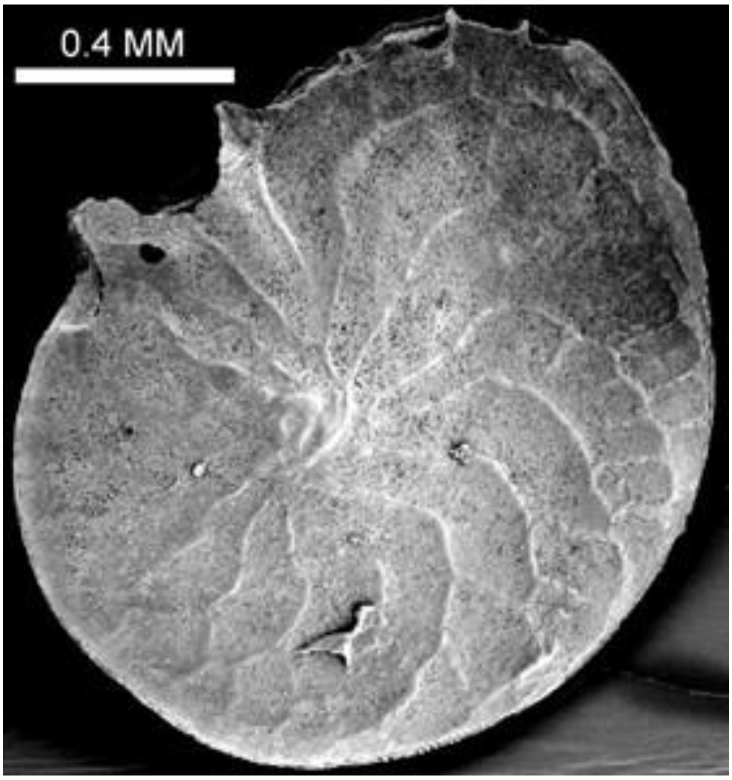

Figure 1. *Heterostegina depressa* d'Orbigny, Recent, Discovery Bay, Jamaica. (Edward Robinson collection, donated by Thomas. F. Goreau).

3.1. Heterostegina Depressa Invaded the Atlantic Caribbean Region from the Indo-Pacific Region But Not via the Central American Seaway

Heterostegina depressa was first described from Recent sediments from St. Helena, one of the remotest islands in the South Atlantic, where Napoleon Bonaparte was exiled following his defeat at the Battle of Waterloo [43–45]. An ACR species, *H. antillarum*, was described by [46] from the Caribbean islands of Cuba and Jamaica and, subsequently, from numerous Recent localities in the Greater Caribbean region and other locations in the tropical ACR (**Figure 2**) [7,47–54]. In 1826 d'Orbigny also described *H. suborbicularis* and one of its variants from the IPR. These are all now considered to be conspecific with *H. depressa* based on genetic studies [39].

The youngest records of fossil species of *Heterostegina* in the Caribbean and Central American region are from the early and early mid Miocene, some 20 to 18 million years ago while the Central American Seaway (CAS), separating North America from South America, was still open [55–57]. For *H. depressa*, Plio-Pleistocene as well as Recent occurrences have been documented from the IPR within the Indonesian region of high nummulitid diversity, from remote Pacific islands and from the west coast of the Americas, frequently as *H. suborbicularis* [8,58–60]. These occurrences include the late Pleistocene Armuelles Formation of the Pacific coast of Central America **Figure 2** [61]. But there are, as yet, no fossil records of *H. depressa* from the Caribbean side of Central America.

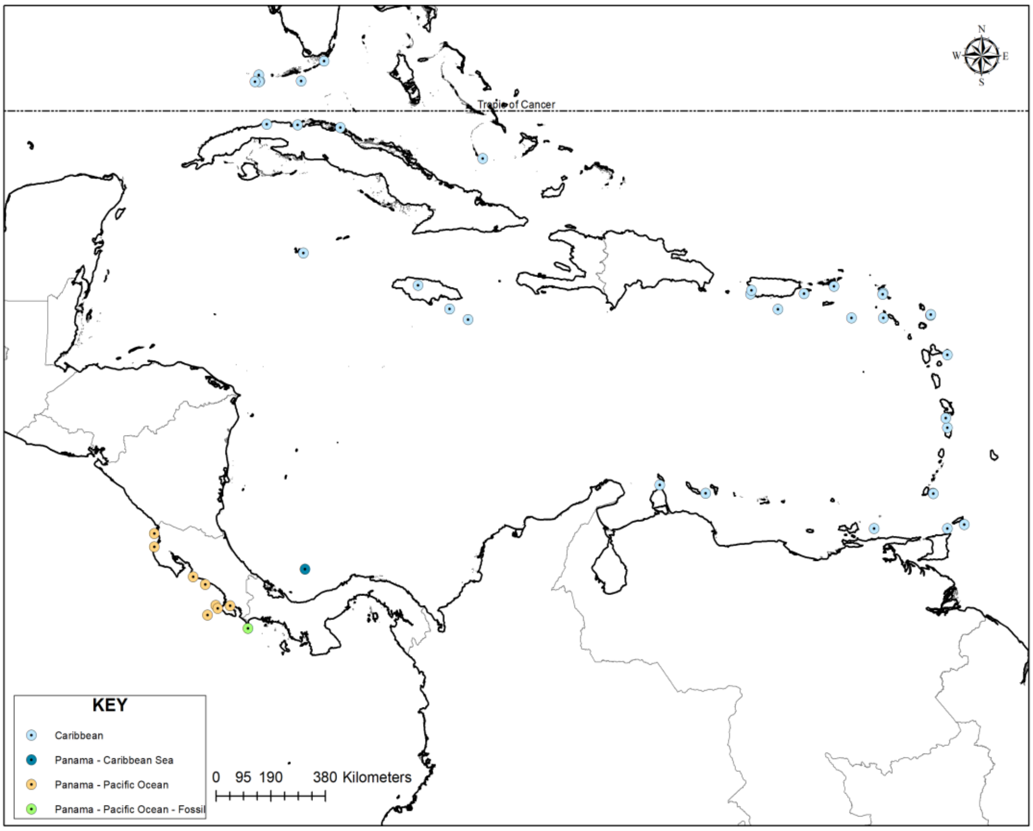

Figure 2. Caribbean and Central American localities for Heterostegina depressa. See Appendix A1.

The absence of pre-Late Holocene records of *H. depressa* can also be attributed to insufficient sampling of appropriate Holocene facies and localities. However, as of now such records are apparently lacking in ACR sedimentary strata, including Pleistocene cores from southeast Florida, in which the endemic Caribbean LBF soritid genera are well-represented [62]. This species has not been reported in Pliocene to Pleistocene formations in Jamaica ([63] nor in the Ruth Todd Library's card catalogue at the Smithsonian Institute. Nor was it recorded in radiometrically dated mid-Holocene (~6 kyr BP) sedimentary deposits from Caribbean Panama [64].

This leads to the conclusion that *H. depressa* was introduced to the ACR from the IPR and not the other way around as suggested by [61] (p. 163), sometime within the Holocene, well after closure of the CAS 3 million years ago [65].

3.2. The Only Other Available Invasion Route Was Around South Africa

In examining other possible routes into the ACR besides the CAS, the Suez Canal opened in 1869. Since then, several genera of foraminifera have entered the Mediterranean Sea from the Gulf of Aqaba (Red Sea), including *H. depressa* and other LBF, providing future potential for *H. depressa* to reach the ACR via the Mediterranean [18,59]. But the descriptions of *H. depressa* from the ACR antedate the Suez Canal opening by 44 years and the Panama Canal opening in 1914 post-dates these descriptions by 88 years.

A seaway extending from the Indian subcontinent through the Mediterranean region to the Atlantic (the Tethyan Seaway) existed for much of the Cenozoic Era, allowing interchange of LBF genera and species between the ACR and the Tethyan/IPR, leading to LBF centres of diversification in several shifting locations through time [66,67]. This seaway became restricted and was eventually closed off in the Miocene, well before the emergence of *H. depressa* in the IPC and ACR [68,69].

Two other naturally existing corridors linking the IPR with the ACR have remained open for millions of years. Around the southern tip of South America sea surface data indicate temperatures of 6-10°C thus greatly inhibiting the survival prospects of tropical symbiont-bearing foraminifera invading the ACR from that direction. The nearest IPC source today, Rapa Nui (Easter Island), is at the northern edge of the temperate zone, well over 4000 km away from the tip of South America [7,70]. The other route is around the southern tip of Africa. As related below, although sea surface temperatures there are marginally unfavourable for the existence of the tropical *H. depressa.* it remains the most probable marine corridor from the IPR to the ACR.

3.3. South Africa Presents Barriers for LBF Invasion of the ACR Through Natural Vectors

The two most widely accepted natural processes promoting expansion or invasion of a marine species are either by expansion of its range through local interaction with its environment [23] or by dispersal through transport by ocean currents, including rafting on seaweed or other floating debris [71–74]. Other less likely natural vectors include transport in tsunami debris [75]; lateral and vertical dispersal of debris and animals by storm events [76,77]; transport on or in the feet/feathers/guts of birds; and on, or in, fish [78,79]

Turning first to possible range expansion from the East African coast, where *H. depressa* is widely recorded [7,80], the journey around the Cape of Good Hope (CGH) and up the west coast of South Africa into the ACR presents difficulties. *H. depressa* was recorded as tolerating the lowest SST among the Nummulitidae, based on its distribution pattern, at about 18°C [7]. Langer & Hottinger's isotherms indicate that temperatures at the southern extremity of South Africa were just outside *H. depressa*'s range of tolerance. While today's SSTs are noticeably higher [20], south Atlantic SSTs at the time the species was first described, near the termination of the Little Ice Age, are estimated variously to have been about 0.3° to 0.9°C even up to more than 2°C lower than the those of the latter part of the 20th Century [42,81,82].

For any LBF that might reach the CGH from the tropical east African coast via coastwise migration, the southwest coast of Africa presents a region of unfavourable temperatures for some 2000 km north, from the CGH to [7]. At an average natural invasion rate in shallow coastal waters of around 11–13 km per year, using *Amphistegina* as a proxy [20], it would take as much as 150 years for *H. depressa*, migrating along a coast with variable temperature conditions as low as 14°C [70], to reach the LBF tolernace zone, assuming that reproduction was possible. Evidential support for this proposition is available through the study by [83] concerning the changes in distribution of *Amphistegina* on the southeast coast of South Africa, especially Figure 1 showing the absence of *Amphistegina* on the southwest coast of Africa. Additionally, the predictive model shown in their Figure 2 suggests that, even in today's immediate warming future, conditions along that southwestern shore form an important barrier, restricting intrusion of *H. depressa* into the ACR by this route (see also a similar argument for the goatfish *Mulloidichthys* [84]*)*. Therefore, the main alternative method of dispersal of *H. depressa* into the South Atlantic must be by surface currents or other suitable ocean vectors.

An important possibility for the natural transport of *H. depressa* by ocean currents westward into the ACR, beyond South Africa, would be via a 'piggy-back' vector or as propagules caught in one or more of the westerly drifting current eddies (Agulhas Rings) spun off into the South Atlantic by the warm Agulhas Current of southeast Africa [85,86]. However, based on the information indicated by [86] (Figure 1), such Rings weaken and dissipate while the surrounding ocean SST is still below 20°C. Even if the Rings intercepted the warmer surface waters of the southward flowing Brazil Current, east of South America, any contained propagules would face the prospect of being carried southwards into the cold waters of the South Atlantic Malvinas (Falkland) Current and Southern Ocean (formerly Antarctic Ocean) [87]. The NASA SVS video illustrates this situation clearly (https://svs.gsfc.nasa.gov/3912).

3.4. Anthropogenic Vectors Transported H. depressa to the ACR

A review of anthropogenic vectors shows hull fouling and ballast water contamination in shipping to be the most common vector-related mechanisms for the modern (post 1850 CE) invasion of non-endemic species of foraminifers and other biota into northern European waters, the northeast coast of North America and the central and northeast Pacific [24,26,28,88]. Gollasch attributed nearly 40% of species invasive to European waters as resulting from hull fouling and ballast water contamination, and about a further 25% from processes resulting from deliberate or inadvertent interventions in the aquaculture and stocking industries [38]. Only 6% were judged to result from species range expansion, while about 25% probably arrived via Lessepsian migration, vector not stated.

At the time *H. depressa* was described by d'Orbigny, wooden-hulled sailing ships carrying dry ballast were the common mode of transport. Experimental investigations in the Pacific Ocean using a replica of a 16thCentury wooden sailing ship, showed that many kinds of marine organisms were transported through attachment to the hull exterior [89]. Fouling of the hull was probably enhanced by the niches produced by boring species such as *Teredo*, dry rot, and local scraping of the hulls against rocks while ships were anchored or beached for maintenance or repairs [25,90,91] and [92] (illustration p. 49). The dry ballast carried in these ships would have varied depending on the purpose of the voyage and nature of the cargo. Frequent dumping of non-commercial ballast in exchange for new materials was, and still is, commonplace [93]. Ballast ranged from rocks and sand collected from the local coastline or beaches, commercial supplies of rock for construction, even spare cannons (Wenzlhuemer, 2020). Ballast collected from Indo-Pacific coastlines, particularly coral reefal coasts would almost certainly have included LBF and other biota, including coral fragments, either directly in the associated sediments or attached to other organisms such as seagrass [54,72] and algae growing on the ballast. Although this is admittedly still conjectural, archaeological investigation of medieval shipwrecks, including assessment of ballast materials, has become an important field of research [93,94]. Sailing ships have the enormous advantage over natural ocean currents of being steerable vectors, able to choose their destinations, including remote ocean islands. Therefore, we regard most of the natural mechanisms discussed in section 3 above as being relatively unlikely compared with the transport opportunities offered by the shipping trade [95].

3.5. Heterostegina Depressa Invaded the ACR After the Late 15th Century

Before the late 15th Century, trans-ocean shipping in the central and southern ACR was non-existent. Only local operations originating from the Mediterranean along the northwest and west African coasts were active [96]. Ocean-going vessels refined by the Portuguese led to the first European ship venturing around the Cape into the Indian Ocean by the Portuguese navigator Bartelomeu Diaz in 1488, who sailed as far as Algoa Bay [97]. A replica of Diaz's caravel "Boa Esperanca", launched in 1990, provides an example of the trading vessels of the late 15th Century. With a length of 28.8 m and a beam of 6.6 m, it has a draught of 3.3 m and can accommodate 22 people (fundacionnaovictoria.org/caravel-boa-esperanca).

Vasco da Gama's successful follow-up voyage into the Indian Ocean in 1497 (Russel-Wood,1998) brought the Portuguese into direct contact with the Swahili traders who had been sailing up and down the east African coast and lands further east for several centuries **Figure 3** [92,96,98]. Simultaneously it also brought the Portuguese into tropical coastal areas that, today at least, and almost certainly then, contained *H. depressa* as an important component of the shallow-water foraminiferal assemblages [7,19,80,99]. After 1497 there was constant passage of ships between the Atlantic and Indian Oceans for trade and colonisation, frequently with conflict [97], extending to India, the South China Sea and present-day Indonesia, the "Coral Triangle", where *H. depressa* probably evolved[10,96,100].

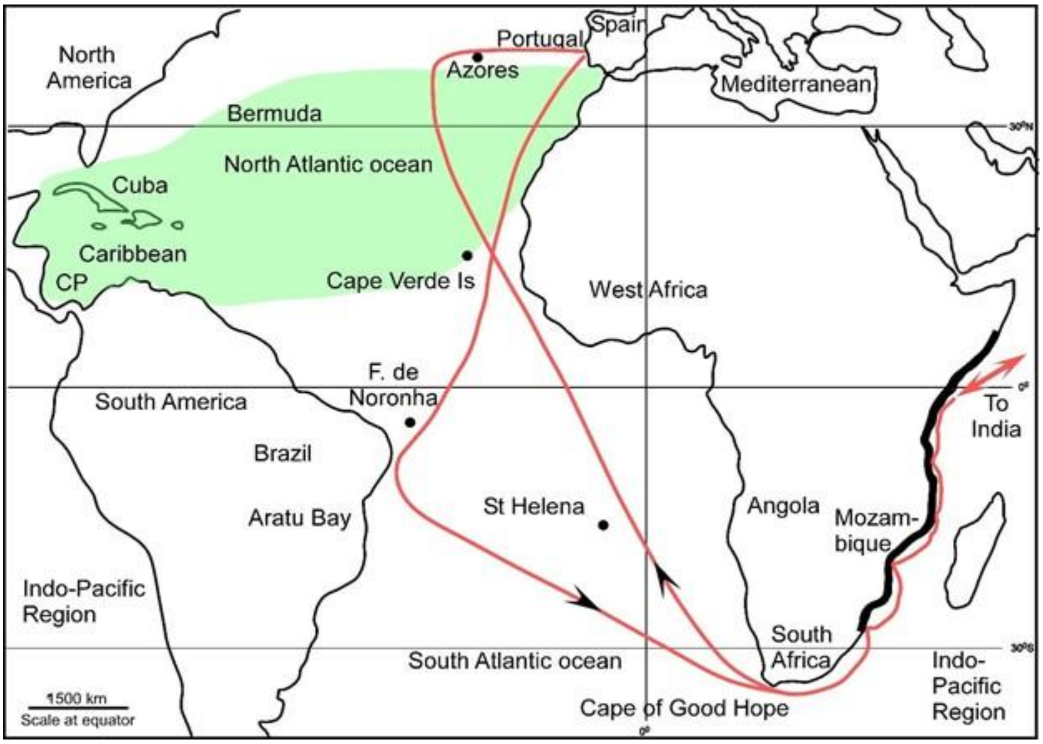

Figure 3. Introduction and spread of shipping activity in the Atlantic and Caribbean at the end of the 15th Century. Bold Black Line - the Swahili Coast of east Africa. Red Lines - routes opened by Portuguese traders to the Swahili Coast and Indo-Pacific,[96] 9p. 390. Green Area - approximate area of Spanish trading and expansion to the Caribbean and Central America, based on the routes of Columbus' four voyages [101] (p. 80).

The return journey to Portugal from the IPR after rounding South Africa was north through the central South Atlantic Ocean to maximise the wind patterns [96] (p. 39) **(Figure 3).** On one of these voyages the remote subtropical South Atlantic island of St. Helena (type locality for *H. depressa*) was discovered by the Portuguese in 1502 only four years after trade commenced [102]. It quickly became an important stopover for the repair and revictualing of the Portuguese merchant ships [102,103]. The central Atlantic Portuguese island colonies of Cape Verde and the Azores also provided important in transit stops [96]and [[97] (pp. 214 &234).

About the same time trans-Atlantic shipping activity in the tropical ACR between maritime Europe, particularly Spain, and the Greater Caribbean sprang into life and flourished from the end of the 15th Century, following Columbus's 1492 voyage to the New World [101] (pp. 77-88). This development introduced a host of additional vectors to favourable LBF habitats within the tropical ACR (**Figure 3**). Trade was driven by European colonisation, accompanied by immigrant ships, naval rivalry, privateers and piracy [101]; by the growth of the transatlantic slave trade [104]; by the establishment of botanical and other centres across the growing colonies to collect and secure supplies of plants and other produce for agricultural and medical use [105,106]. By the mid-17th Century, the Dutch, French and British, using the same general ocean routes, had caught up and surpassed Portugal as the primary global traders and colonisers [97]. In 1659 St. Helena became a British colony but the island continued to be an important staging post [102].

The route of Portuguese traders from South Africa and the IPR intersected with some of the routes of Caribbean-bound European shipping, pioneered by Columbus's third voyage in 1498, within the tropical Cape Verde Islands an important entrepot for the slave trade and goods [96] (p.138) and [97]. This would have provided in transit and vector exchange opportunities for *H. depressa.* This is evidenced by the several localities recorded there for the species [48] and [107] (p. 746).

This suggests that the window of opportunity for invasion by *H. depressa* of the ACR from the IPR existed from sometime after about 6 kyr BP, the youngest dated ACR sediments in which *H.*

depressa was not encountered, until sometime before 1826, the date of the first description of the species. As the beginning of the 16th Century coincided with a revolutionary change for the better in the options for vectors via South Africa and within the tropical ACR, it leads to the conclusion that the introduction of *H. depressa* to the ACR occurred shortly after that date, perhaps even as early as 1502, when St. Helena was discovered. The probable route of the *H. depressa* invasion of the Caribbean is illustrated in **Figure 4**.

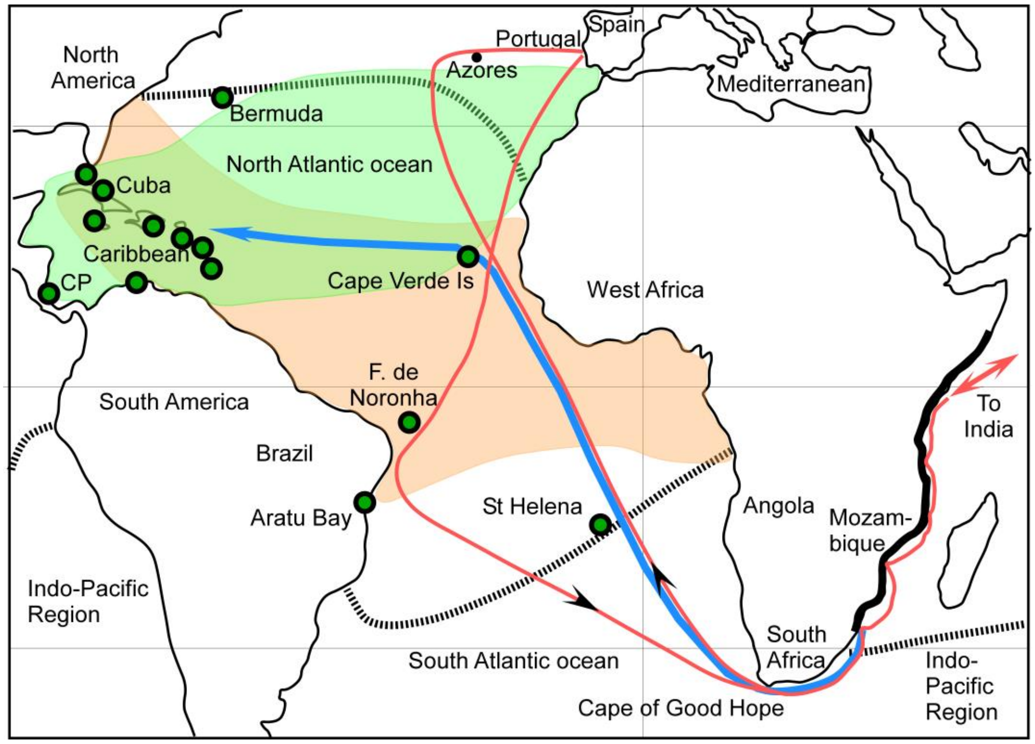

Figure 4. Suggested route of the invasion of the Caribbean by *Heterostegina depressa*, Blue Line -. Green Points, locations yielding Recent *H. depressa* based on [7] with additions of Bermuda & some Caribbean localities (Panama, CP). Orange Area - routes of the Atlantic Slave Trade as described in [101,108]. Dashed Lines - approximate limits of the tropical zone with year-long SSTs above 20°C, based on data from [109]. Other symbols as for Figure 3.

4. Discussion

In suggesting the Portuguese trade route around South Africa as the most likely avenue for the introduction of tropical *H. depressa* to the ACR, the response of the species to various factors, including light and temperature tolerances [4,12,13,23] as well as vector velocities requires comment [110–112].

Survival Times. Experiments by [12] showed that the photosymbionts of *H. depressa* remained active even after 15 days without light, while experimental studies over a 4-week period by [13] showed that survival at temperatures as low as 15.6 °C occurred. Alve & Goldstein demonstrated that some shallow water benthic foraminiferal propagules can survive quiescently for up to two years in many cases before growth starts [113], while [21,114] have shown that foraminifera that have diatom endosymbionts (*Amphistegina*) may become dormant and mostly survive for as long as 12 months of darkness and, with slower and less complete recovery, as long as 20 months. Most studies have been concerned with LBF survival in in a warming world, with less attention directed to research specifically concerned with the survival prospects of tropical LBF subjected to extended decreased water temperatures, such as might be encountered during transit between two geographically separated tropical regions [115,116]

Although the light tolerances of members of the Nummulitidae favour a relatively deep habitat, *H. depressa* is an exception [1,111]. This species is found living in a wide range of water-depth

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situations, ranging from a cryptic sensu [112] in intertidal pools, where it protects itself from the strongest sunlight by living in crevices and other sheltered habitats, down to the base of the euphotic [112,118,119]. It has also been found attached to algae and seagrasses [61], as well as in sediments associated with seagrass meadows [54]. This would favour involuntary transport for the species as fouling on wooden vessels that were anchored or beached in the intertidal zone in the source region. This paper offers that the sheltered living ability of *H. depressa* might be a factor which has resulted in the successful intrusion of the species into the ACR, in contrast to the current absence of other members of the Nummulitidae, which tend to be restricted to greater depth habitats (pers. comm. Geoffrey Adams, November 13, 1973) [1] (Figure 2).

Rates of Dispersal. The average speed of the Portuguese traders, and similar 16th and 17th Century ships, was about 3.5 knots, sometimes up to 7 or 8 knots, depending on wind and current speeds and directions, or about 160 km per day [89,96]. At that speed the average 16th Century nao would reach subtropical St. Helena with average SST 20-22^{o}C from the vicinity of the CGH, South Africa, in 3 to 4 weeks [120]. These transit times are well within the reported survival times of quiescent foraminifers mentioned above. The intertidal habitat tolerance of *H. depressa* would also favour dispersal from the same wooden ships, anchored or beached, or wrecked in storms, or driven ashore, or from drifted floating remains of ships sunk by unfriendly adversaries, while in transit through favourable shallow marine habitats in the tropical and subtropical ACR [101]. On average about one in four ships was lost on each Portuguese voyage [97].

5. Conclusions

The particular problems accompanying invasion of the ACR from the IPR through the natural processes outlined above suggest that anthropogenic vectors appear to be the only likely means of dispersal for *H. depressa.* These vectors only became available at the end of the 15th Century, hence it is concluded that *H. depressa* was introduced into the South Atlantic and Caribbean as hull fouling and/or as a contaminant of solid ballast material on Portuguese or later commercial shipping via South Africa, commencing about the end of the 15th Century, when the trans-Atlantic shipping trade in general rapidly expanded from non-existence, and ending before 1826 when the first formal description of the species was recorded, a period of about 330 years.

When one considers the expansion of the LBF *Amphistegina* into and through the Mediterranean within the last 150 years, there appears to have been adequate time for *H. depressa* to have achieved its present-day distribution in the ACR, especially in terms of colonisation of remote islands, such as St Helena and Bermuda [47], and into the favourable environmental conditions of the Caribbean, initially via commercial trade between the Indo-Pacific and the ACR and subsequent dispersal within the tropical ACR.

This paper did not examine or review the paleobiogeography of the LBF *Borelis pulchra* [46], initially described from Cuba in the ACR. However, it is possible to apply a similar reasoning to the timing and method of its introduction into the ACR as it does not appear to be present there in sediments aged between its doubtful reported occurrence in the late Miocene around St Martin [121,122] and the late Holocene [62] and [123] (p.1417).

Culver & Buzas remarked that 53 of 878 species of modern benthic foraminifera on the North and Central American Atlantic coasts have no fossil record but are geographically widespread, suggesting recent evolution and rapid dispersal [124] (p.102). Based on this remark this paper offers that the distribution pattern could also be related to an invasion event such as the one described.

The hypothesis and its propositions presented in this paper provide a first exploration of some of the factors that might inhibit the introduction of LBF from the IPR to the ACR regions (and perhaps vice versa) by natural processes. This model has an advantage over most other early historical biotic dispersion accounts in supplying specific temporal parameters that can be tested using such methods as radiocarbon dating of foraminiferal assemblages and other organisms from cores [116] and comparative studies of genetic diversity [84].

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org, Figure S1: title; Table S1: title; Video S1: title.

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Data Availability Statement: We encourage all authors of articles published in MDPI journals to share their research data. In this section, please provide details regarding where data supporting reported results can be found, including links to publicly archived datasets analyzed or generated during the study. Where no new data were created, or where data is unavailable due to privacy or ethical restrictions, a statement is still required. Suggested Data Availability Statements are available in section "MDPI Research Data Policies" at https://www.mdpi.com/ethics.

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Conflicts of Interest: "The authors declare no conflicts of interest."

Abbreviations

The following abbreviations are used in this manuscript:

ACR	Atlantic and Caribbean region
BP	Before Present
CAS	Central American Seaway
CE	Common Era
CGH	Cape of Good Hope
DOAJ	Directory of open access journals
IPR	Indo-Pacific region
LBF	Larger Benthic Foraminifera
MDPI	Multidisciplinary Digital Publishing Institute
NASA	National Aeronautics and Space Administration.
SST	Sea Surface Temperature
SVS	Scientific Visualization Studio

Appendix A

Appendix A.1 Source Documents Heterostegina antillarum (depressa) locations

Table A1. Locations of Heterostegina antillarum (depressa) shown in Figure 2.

Record No	Publication	Year	Genus	Species	Locality	Lat	Long	Site Desc	Country
12802	BROOK S 1973	1973	Heterostegina	antillarum	S PUERTO RICO	17.56	-66.31		Puerto Rico
12803	BERMUD EZ 1935	1935	Heterostegina	antillarum	NORTHERN CUBA	23.08	-81.33		Cuba

12804	0 'OR Bl GNY 1839	1839	Heterosteginaantillarum	CUBA	23	-80	Cuba
12805	S EIGLIE 1970 A	1970	Heterosteginaantillarum	SE PUERTO RICO	18.03	-65.49	Puerto Rico
12806	S E JGLIE 1971 A	1971	Heterosteginaantillarum	SW PUERTO RICO	18.02	-67.16	Puerto Rico
12807	S EN GUPT A SC HAFER 1973	1973	Heterosteginaantillarum	NW ST LUCIA	14.02	-61	St Lucia
12808	D 'OR BI GNY 1839	1839	Heterosteginaantillarum	JAMAICA	17.57	-76.58	Jamaica
12809	HOFK ER, SR . 1956	1956	Heterosteginaantillarum	ST. CROIX	17.3	-64	St Croix
12810	D ROOGE R K A ASS CHJE TER 1958	1958	Heterosteginaantillarum	TRINIDAD SHELF	11	-61	Trinidad
12811	HOFK ER, SR. 1964	1964	Heterosteginaantillarum	GRENADA	12.05	-61.45	Aruba
12812	HOFK ER, SR. 1964	1964	Heterosteginaantillarum	ARUBA	12.3	-70	Aruba
12813	R AOF CR O 1976B	1976	Heterosteginaantillarum	TOBAGO ISLAND	11.12	-60.48	Tobago
12814	HOFK ER1 SR. 1976	1976	Heterosteginaantillarum	LA DESIRADE	16.2	-61	La Desirade
12815	HOFK ER , SR . 1976	1976	Heterosteginaantillarum	ST. MARTIN	18.05	-63.02	St Martin
12816	HOF K ER, SR. 1976	1976	Heterosteginaantillarum	CURACAO	12.05	-68.57	Curacao
12817	HOFK ER1 SR . 1 976	1976	Heterosteginaantillarum	GRAND CAYMAN	19.25	-81.15	Grand Cayman
12818	HOFK ER1 SR . 1976	1976	Heterosteginaantillarum	HAVANA, CUBA	23.1	-82.3	Cuba
12819	HOFK ER, SR . 1964	1964	Heterosteginaantillarum	ST. MARTIN	18.01	-63.03	St Martin
12820	HOFK ER , SR . 1964	1964	Heterosteginaantillarum	ST. EUSTATIUS	17.3	-63.01	St Eustatius
12821	HOFK ER, SR. 1976	1976	Heterosteginaantillarum	VIRGIN ISLANDS	18.25	-64.55	Aruba
12822	HOFK ER1 SR . 1976	1976	Heterosteginaantillarum	W PUERTO RICO	18.13	-67.13	Puerto Rico
12823	HOFK ER1 SR . 1976	1976	Heterosteginaantillarum	MARTINIQUE	14.3	-61.05	Martinique
12824	HOFK ER, SR . 1976	1976	Heterosteginaantillarum	GRENADA	12.04	-61.44	Grenada
12825	ILL ING 1952	1952	Heterosteginaantillarum	BAHAMA BANKS	22.08	-75.54	Bahamas
12826	BERMUDEZ 1937	1937	Heterosteginaantillarum	MORANT CAYS, JAMAICA	17.25	-76	Jamaica
12827	B R AS IE R 1975 B	1975	Heterosteginaantillarum	BARBUDA	17.38	-61.53	Barbuda

12828	B A S IER 1975 A	1975	Heterosteginaantillarum	BARBUDA	17.4	-61.52		Barbuda
12829	CUSHMAN 1921	1921	Heterosteginaantillarum	MONTEGO BAY, JAMAICA	18.28	-77.56		Jamaica
12830	S E IGLIE 1967	1967	Heterostegina antillea	ARAYA-LOS TESTIGOS SHELF	11	-63.3		Araya Los Testigos
19087	NOR T ON 1930	1930	Heterosteginaantillarum	TORTUGAS, FLA	24.4	-82.52		Tortugas Florida
19068	CUSHMAN 1930	1930	Heterosteginaantillarum	TORTUGAS, FLA	24.58	-82.55		Tortugas Florida
19089	CUSHMAN 1922A	1922	Heterosteginaantillarum	TORTUGAS	24.38	-82.54		Tortugas
14797	HOWAR D 1965	1965	Heterostegina depressa	S. FLORIDA KEYS	24.4	-81.22		Florida Keys
14798	BOCK 1971	1971	Heterostegina depressa	FLORIDA BAY	25	-80.5		Florida Bay
MO64322	Bock. 1971. Miami Geol.Soc.Mem. (n.1): 57, pl.21,f.3.	1958	Heterostegina depressa	GULF OF MEXICO	24.38	-82.67		Gulf of Mexico
	Weinmann &Langer	2011		Malindi 1 (Kenya)	-3.2161	40.1337	Outer lagoon (exposed)	Kenya
	Weinmann &Langer	2011		Malindi 2 (Kenya)	-3.2196	40.1263	Inner lagoon	Kenya
	Weinmann &Langer	2011		Kilifi (Kenya)	-3.6425	39.8631	Rock pool, beach	Kenya
	Weinmann &Langer	2012		Coco Beach (Tanzania)	-6.7752	39.2843	Beach (exposed)	Tanzania
	Weinmann &Langer	2012		Kilwa 1 (Tanzania)	-8.8893	39.5267	Outer lagoon (sheltered)	Tanzania
	Weinmann &Langer	2012		Kilwa 2 (Tanzania)	-8.8978	39.5191	Inner lagoon	Tanzania
	Weinmann &Langer	2012		Carrusca (Mozambique)	-15.0049	40.773	Rock pool, beach	Mozambique
	Weinmann &Langer	2012		Mafamete (Mozambique)	-16.3517	40.0305	Beach (exposed)	Mozambique

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