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Biogeographic distribution and habitat association of *Ammonia* genetic variants around the coastline of Great Britain

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ABSTRACT

High morphological variation and the lack of clearly defined morphological criteria for identification have led to difficulties in the identification of species in the foraminiferal genus *Ammonia*. It is often difficult to decide if morphological variability is genetic or ecophenotypic and more than 40 species, subspecies and varieties have been described worldwide under the generic name *Ammonia*. This study aimed to add new insight into the genetic diversity, biogeographical distribution and the impact of different environmental conditions in *Ammonia* populations around the coastline of Great Britain. A total of 164 *Ammonia* specimens were examined from 19 different populations. Genetic analysis revealed three distinct large subunit (LSU) ribosomal (r) RNA gene genetic types T1, T2 and T6 in *Ammonia* populations around Great Britain. T6 is the most common genetic type around Great Britain occurring in 14 of the 19 populations. T2 was represented in 6 of the 19 populations and T1 was found in only 5 of the 19 populations. These genetic types were not ubiquitously distributed around the coastline of Great Britain and instead their pattern of biogeographical distribution revealed evidence of geographic structuring of *Ammonia* populations. However, their distribution does not seem to be correlated with habitat. The ability of genetic types to inhabit contrasting intertidal ecosystems is indicative of a non-specific ecological preference. Comparing the *Ammonia* genetic types from Great Britain to those in other regions around the world revealed geographical connectivity. The large scale distribution of *Ammonia* genetic types could result from either passive transport of propagules with Ocean currents or by the anthropogenic transportation of individuals with ships ballast water.

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1. Introduction

Ammonia (Brunnich, 1772) is one of the most extensively studied genera among modern benthic foraminifera. It was the first genus assigned to the foraminifera and was originally described as *Nautilus* from beach sand of Rimini, Italy in 1758 (Chang and Kaesler, 1974). It is a common cosmopolitan genus found from the tropics to the temperate regions in almost every brackish or shallow marine environment (Murray, 1991). The high morphological variation of *Ammonia* and the lack of clearly defined morphological criteria for identification have led to difficulties in the identification of species and, as a consequence, the taxonomy of the genus has remained unresolved (Wang and Lutze, 1986; Walton and Sloan, 1990; Haynes, 1992). Some authors have considered these morphological variations within *Ammonia* to be intraspecific variability and consequently lumped the various morphotypes into one single highly variable species (Chang and Kaesler, 1974; Schnitker, 1974; Poag, 1978; Wang and Lutze, 1986; Jorissen, 1988; Walton and Sloan, 1990). Others have considered the morphological variation to be interspecific with these morphotypes split into several species (Haynes, 1992; Pawlowski et al., 1995; Holzmann et al., 1996, 1998; Hayward et al., 2004). Arnold (1954); Poag (1978); Murray (1991) and Haynes (1992) concluded that it is often difficult to decide if morphological variability is genetic or ecophenotypic.

The idea of ecophenotypes was introduced following Cushman's work in 1926 in which he lumped all *Ammonia* around the world into just three variants of a single species *Ammonia beccarii*: *A. beccarii* forma *beccarii*, *A. beccarii* forma *parkinsoniana*, and *A. beccarii* forma *tepida*. Schnitker (1974) observations of different morphotypes in the offspring of a single cultivated *Ammonia* species that resemble different species supported the conclusion that *Ammonia beccarii* is the only valid species and that the others represent ecophenotypes. However, Haynes (1992) argued that this emphasis on ecophenotype rather oversimplifies the morphological variability and results in indiscriminate lumping without accounting for the underlying genetic variation. Nevertheless, the suggestion that most or all of the identified species and subspecies should be recognised as a number of forms under *Ammonia beccarii* (Cushman, 1926; Schnitker, 1974) became dominant in subsequent studies where their morphological characters tend to vary as clines across gradients of salinity, temperature, food availability and oxygen concentration (Chang and Kaesler, 1974; Wang and Lutze, 1986).

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Likewise, Walton and Sloan (1990) reviewed large sets of data on the worldwide geographic distribution including the northern and southern hemispheres of the *Ammonia* genus and their morphological variability. Similarly, to Cushman, they stated that "we recommend that the species *A. beccarii* be retained for all morphotypes and that the three dominant morphotypes be designated as forma: *A. beccarii* forma *tepida*, *A. beccarii* forma *parkinsoniana* and *A. beccarii* forma *beccarii*".

Re-assessment of the taxonomic status of the *Ammonia* genus based on DNA analysis has helped to resolve the taxonomy of *Ammonia* and offered an alternative to the taxonomic criterion based on morphology (Pawlowski et al., 1995; Schweizer et al., 2008). Based on analysis of their rDNA sequences, Pawlowski et al. (1995) asserted that the three previously defined morphotypes of *Ammonia beccarii* (*A. beccarii beccarii*, *A. beccarii parkinsoniana*, and *A. beccarii tepida*, (Cushman, 1926; Walton and Sloan, 1990) are distinct species and cannot be regarded as belonging to a single species. Each of the examined *Ammonia* morphotypes has a unique rDNA sequence. Therefore, Pawlowski et al. (1995) concluded that the assumption of ecophenotypic adaptation as the only interpretation of the morphological variability in *Ammonia* is difficult to uphold, though environmental impact on the morphological variability cannot be completely excluded. Recently, a more comprehensive morphometric analysis based on molecular distinction was undertaken to examine the taxonomic subdivision of *Ammonia* worldwide (Hayward et al., 2004). Thirteen distinct *Ammonia* types (T1–T13) were discriminated both genetically and morphologically, with morphological discrimination based on the assessment of 37 external test characters among worldwide samples (Hayward et al., 2004). Eight of these genetic types were considered an equivalent to pre-described species (Hayward et al., 2004) and they concluded that the widespread use of *Ammonia beccarii* and the recognition of only one species of *Ammonia* should be abandoned.

Taxonomic subdivisions merely based on morphological data are not sufficient for distinction of highly polymorphic species like *Ammonia*, where it has been consistently suggested that morphological variability is the result of environmental influences (Chang and Kaesler, 1974; Schnitker, 1974; Poag, 1978; Wang and Lutze, 1986; Jorissen, 1988; Walton and Sloan, 1990). Thus morphological characterization of *Ammonia* species can only be accurately accomplished after molecular distinction of the different sequence types and this would then facilitate the grouping of each type morphologically. For certain, any further work with extensive sampling on genetic and morphological characterization of the *Ammonia* complex from different ranges of geographic distribution will contribute to our understanding and add more clarity to the chaotic taxonomic state of *Ammonia* worldwide.

This study was set out to add new insight into the genetic diversity and biogeographical distribution of *Ammonia* from around the coastline of Great Britain. It aimed to determine which genetic types of *Ammonia* were present in Great Britain, the pattern of their biogeographical distribution around the coast and to determine if there is a link between their distribution and environmental conditions.

2. Method

2.1. Sample collection

Specimens of *Ammonia* were collected from 19 different near-shore localities around Great Britain between June 2010 and April 2013 (Table 1, Fig. 1 and Supplementary Fig. 1). Sampling localities were situated in a variety of coastal settings representing a wide range of environments in the intertidal zone. Sediment samples were taken by scraping the surface layer (1 cm) of tidal mudflats by hand at low tide. The sediment was sieved through a 53 μm sieve and washed through with seawater. Living *Ammonia* specimens were distinguished under a stereomicroscope by the natural colouration of the protoplasm and pseudopodial activity. *Ammonia* individuals were then picked and cleaned with seawater.

2.2. DNA extraction, PCR amplification and sequencing

A total of 164 *Ammonia* specimens were examined with 5–10 individuals from each of the populations. DNA was extracted using Guanidinium extraction buffer (Seears and Wade, 2014). This extraction procedure has the advantage of preserving the shells intact thereby permitting morphological examination of the specimens being used in genetic analysis.

An approximately 650 bp fragment of the 5′ terminal region of the LSU rRNA gene was amplified using a nested PCR approach for the identification of genetic types. In the first round of PCR, 3 μl of template DNA was used for amplification using foram specific primer 2TA (5′-CAC ATC AGC TCG AGT GAG-3′) (Pawlowski et al., 1995) coupled with universal primer Rib0 (5′-GCT ATC CTG AG(AG) GAA AC-3′) (Pawlowski et al., 1995). 1 μl of product from the first round was then used as a template for reamplification in the second round using two specific foram primers 2TA and LIF (5′-ACT CTC TCT TTC ACT CC-3′) (Pawlowski et al., 1995). PCR amplification was performed in a total volume of 50 μl using 1 unit DNA Polymerase (Qiagen or New England Biolab) with 200 μM dNTPs, 1.5 mM $MgCl_2$ and 0.2 μM each primer. Thermal cycling was carried out with an initial denaturation step of 96 °C for 2 min followed by 35 cycles of 94 °C for 30 s, 50 °C for 30 s and 72 °C for 2 min and 72 °C for 4 min for final extension. All positive amplifications were purified from an agarose gel using QIAquick® Gel Extraction Kit (Qiagen), ligated in the pGEM-T vector system (Promega) and cloned using DH5α competent cells (Bioline) prior to sequencing. Following plasmid extraction using a Spin Miniprep kit (QIAgen®), the sense strand of the LSU rDNA was sequenced on an Applied Biosystems 377 DNA sequencer using universal M13 Forward and M13 reverse primers.

2.3. Sequence analysis

The LSU rDNA sequences generated in this study were aligned manually within the Genetic Data Environment (GDE) (version 2.2) package (Smith et al., 1994) and 379 nucleotides that could be unambiguously aligned across sequences were retained for use in sequence analyses. Pairwise distances were calculated in PAUP using the general time-reversible (GTR) model with among site rate variation accounted for by incorporating a gamma (+Γ) correction (Lanave et al., 1984; Yang, 1993). Nucleotide diversities (π) were estimated in DNAsp v3.53 with correction using the Jukes Cantor 1969 model (Rozas and Rozas, 1999). The relationships among the LSU rDNA *Ammonia* sequences were visualised using a median-joining (MJ) network using the Network (version 4.6.1.1) package (Bandelt et al., 1999). An equal default Networks weight of 10 was applied to each character. The epsilon, which is a weighted genetic distance measure, was set to 10. The maximum parsimony (MP) option was run on a full median network which contains all possible shortest trees to remove unnecessary median vectors and links. To further generate additional information to assist in determining underlying genetic structure and diversity within *Ammonia*, Principal Component Analysis (PCA), as implemented in ADE4 and Adegenet packages (Dray and Dufour, 2007; Jombart, 2008) in the R-environment (R Core Team, 2006), was performed. PCA portrays the relationship between individuals or populations and accordingly clusters them into groups based on allele frequency information derived from the LSU rDNA sequence data where the traits being tested are nucleotide bases.

The *Ammonia* sequences generated in this study were included in a phylogenetic analysis alongside all currently available *Ammonia* LSU rDNA sequences on GenBank as well as LSU rDNA sequences of *Pararotalia nipponica* and *Neorotalia calcar* which were used as outgroups. 178 nucleotide sites were unambiguously aligned across all taxa and retained for tree building. A neighbour joining (NJ) phylogenetic tree (Saitou and Nei, 1987) was constructed using Paup version 4.0 (Swofford, 1998) and a maximum likelihood (ML) tree (Felsenstein, 1981) was constructed using PhyMl version 3.0 (Guindon and Gascuel, 2003). In order to correct

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