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Spatiotemporal variation in morphological evolution in the Oligocene–Recent larger benthic foraminifera genus *Cycloclypeus* reveals geographically undersampled speciation

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ABSTRACT

Accurate assessment of location and timing of speciation of species is needed to discriminate between macroevolutionary models explaining large scale biodiversity patterns. In this paper I evaluate fossil evidence of variation in geographical ranges through time, as well as spatio-temporal variation in morphological parameters to examine geographical aspects of speciation and range variation. Specifically I test for geographical morphological stability within time slices and for temporal modes of morphological change within lineages.

Past distribution ranges of all species of the large benthic foraminifera *Cycloclypeus* have been documented on paleogeographic maps. From those samples with sufficiently well preserved specimens internal morphological data were measured and analysed.

Within a small sample of six species in a single genus of reef associated large benthic foraminifera evidence for heterogeneity in geographic speciation modes, including vicariance, peripheral speciation, and sympatric speciation in the centre of the range has been found. Morphological evolution was found to be either homogeneous over large geographic ranges or spatially restricted. In time two gradually evolving lineages were found. Furthermore, an evolutionary transition of two species that previously was regarded as gradual, is shown to be punctuated with intermediate populations occurring restricted in both time and space.

I demonstrate the marked heterogeneity of evolutionary processes and the difficulty to make assumptions regarding tempo and mode of evolution. Furthermore, I introduce the concept of geographically undersampled punctuations. This example exposes some of the pitfalls when conclusions regarding the mode and location of speciation are based on the combination of phylogeny and extant distribution alone.

Introduction

Coral reef organisms show markedly similar patterns of species diversity, with a prominent hotspot in the Indo-Australian Archipelago [42,14,26]. Conflicting hypotheses have highlighted the importance of this area either as a centre of origin, overlap or accumulation, with the presumed geographical locations of origins and extinction of species the primary criterion for testing these hypotheses (e.g., [23,5]). Geographical and temporal variation in species richness is the result of overlapping individual species ranges. The geographic range of species is determined by their location of speciation, potentially followed by range expansion (and subsequent contractions and expansions) and finally by extinction [21]. Here I explore the fossil record to look for evidence of geographic aspects and timing of speciation, extinction, and morphological evolution and the implication of these data for the interpretation of present day distribution patterns.

Commonly speciation modes are identified by the amount of geographic separation of sister-species, usually grouped into allopatric, peripatric, parapatric and sympatric speciation (e.g., [15]; Fig. 1). Even though an overwhelming majority of extant species are millions of years old [4,48], location of origination is often inferred from distribution patterns and the phylogenetic relationship of extant species (e.g., [41,8], but see also [4]). Especially in long lived taxa with high dispersal capacity each of these speciation modes can result in the same distribution pattern (Fig. 1).

Often it is assumed that geographic ranges are small at the time of origination [55,21]. However, Bellwood and Meyer [4] argue that vicariance events in species with large geographic ranges need not result in a spatially restricted speciation event, and that especially

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in wide ranging marine taxa this might be an important speciation mechanism. An example in the fossil record is provided in the planktonic diatom genus *Rhizosolenia*, in which the morphological separation of the ancestral *Rhizosolenia bergonii* and *Rhizosolenia praebergonii* was observed over a 60° longitudinal equatorial transect [52,6]. Very few benthic organism have a sufficiently detailed fossil record to allow the examination of these patterns in sufficient detail to document the relative importance using empirical data.

Large benthic foraminifera are known for their abundance and diversity in the fossil record (e.g., [50,48]). Contrary to many other widespread and abundant taxa which display morphological stasis [36], in many larger benthic foraminifera a repeated, directional morphological change has been inferred (e.g., [30]). *Cycloclypeus* is the largest extant benthic foraminifera, and is represented by a single extant species, *Cycloclypeus carpenteri*. The B-forms, derived from sexual reproduction, can grow to 10 cm in diameter, but most commonly do not grow beyond 5–6 cm diameter. The asexually derived A-forms usually do not grow larger than 1 cm in diameter. *Cycloclypeus* lives within the lower part of the photic zone [27,46]. Koba [33] found that its range encompassed those areas of the South China Sea within the photic zone, with year round temperatures at the sediment–water interface higher than 20 °C, and below the storm wave-base.

The test of *Cycloclypeus* consists of a round initial chamber (proloculus) followed by a partially embracing second chamber. These are followed by a series of undivided operculine chambers and divided heterostegine chambers, before annular chambers develop (Figs. 2 and 3). During evolution the proloculus tends to increase in size, and the number of operculine and heterostegine chambers decreases. The traditional interpretation of morphological variation in *Cycloclypeus* is that they consist of a single morphological cline that evolved gradually over time and synchronously over space [34,16,54]. Several studies noted problems in correlation (e.g., [11,12]) between regions, or the presence of a second lineage of *Cycloclypeus* in the Indonesian/Pacific Middle Miocene (e.g., [54,34]).

This paper presents the spatio-temporal morphological evolution of an entire genus of large benthic foraminifera, *Cycloclypeus* in an attempt to provide empirical data illustrating the above mentioned hypothetical models. This study documents, for the first time, morphological data that can be evaluated across both the entire stratigraphical and geographical range of all species in *Cycloclypeus*. This sheds new light on the morphological stability of species throughout their geographic ranges, and the location of speciation. Specifically, I will first illustrate variation in their geographical range through time, secondly I will test the hypothesis that during any given time interval there is only a single species of *Cycloclypeus* present. If this hypothesis is rejected geographic clustering of the multiple species will be assessed. Finally, I will evaluate the morphological stability of lineages through time.

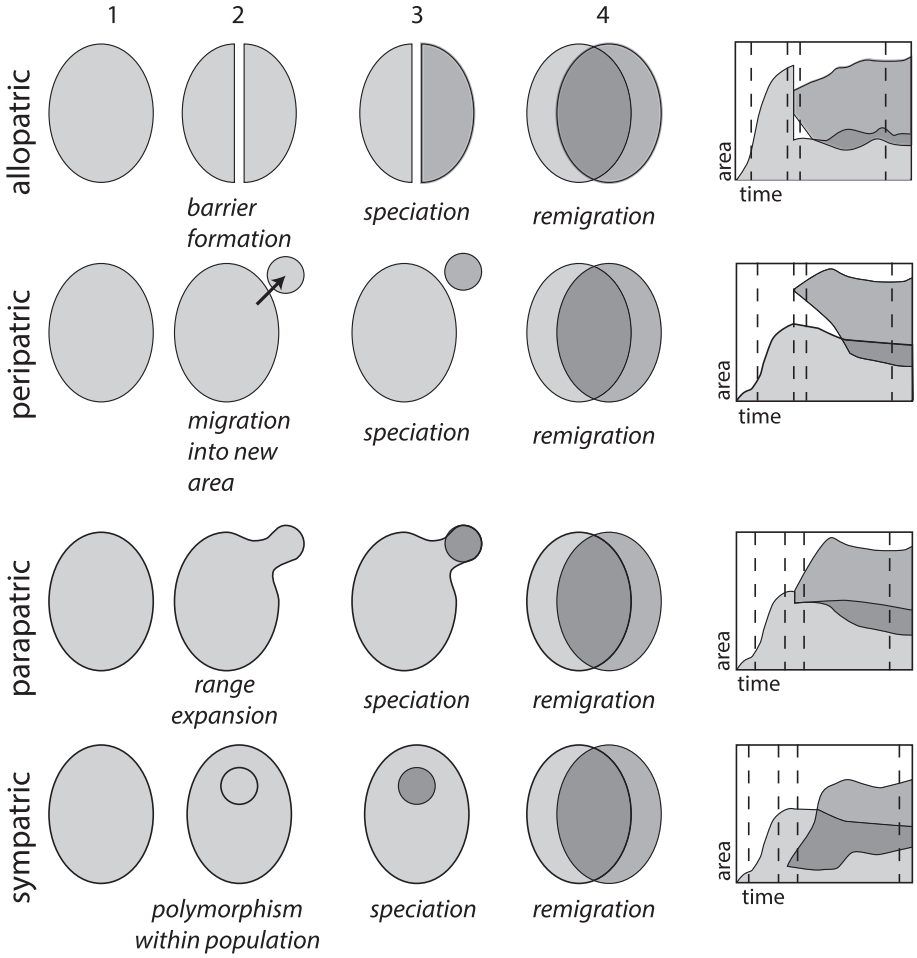

Fig. 1. Hypothetical range variation in the four most frequently used speciation models (from top to bottom: allopatric, parapetric, peripatric and sympatric) can result in near identical present day geographic ranges of species. The fifth column shows how area-time plots of each modes would look like, the dashed lines represent the four steps illustrated in columns 1–4.