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Quantitative analysis of species distribution of the Mississippian *Zaphrentites delanouei* group from the Vale of Glamorgan, UK

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The evolutionary process of anagenesis is thought to control distributions of members of the *Zaphrentites delanouei* species group, the Tournaisian-Viséan solitary rugose corals, within the Carboniferous Limestone. We present alternative interpretations specific to the Friars Point Limestone Formation, which point to composite evolutionary processes closer to anacladogenesis. We use a Markov Chain Monte Carlo process to organize fossils into matrices representing states of concurrence, where concurrence is the number of species coexisting in each bed. We analyse their distributions according to transitions between states. Data testing by matrix multiplication shows whether stochastic equilibrium or convergence is reached, to determine probabilities of species coexistence. Taking the probabilities from the Markov Chain Monte Carlo process to represent the first generation of a branching process, we proceed to calculate the second to fourth generations. Finally, we model these values in a Galton–Watson process to determine the likelihood of ultimate extinction, and whether the species belong to the same population without immigration or emigration. Results show that the species distribution is both anagenetic (0.725) and cladogenetic (0.275). Therefore, we define the evolutionary process as anacladogenetic with the potential for up to eight species in addition to the six defined in the literature. This represents some evidence for a population unaffected by immigration or emigration, with a high likelihood of ultimate extinction for most localities. We deduce that second or third-generation concurrences are a requisite for survival, even with anacladogenesis. As an environmental corollary, the amplification of extinction rates was exacerbated within a regressive marine system, and our techniques will allow further exploration of evolutionary mechanisms and energy within coral ecosystems.

KEYWORDS
anacladogenesis, branching process, Carboniferous, coral, extinction, Markov Chain Monte Carlo, Rugosa

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1 | INTRODUCTION

1.1 | Stratigraphy and palaeogeography

The *Zaphrentis delanouei* Milne-Edwards and Haime (1851) species group, now known as and synonymous with *Zaphrentites delanouei* Hudson (1941) species group of solitary rugose corals have been studied globally, for example, The UK (Hill, 1940; Thomson, 1880), continental Europe (Aretz, 2010; Poty, 1975, 1986, 2010; Poty et al., 2006, 2014), Russia, Japan, and North America (Fedorowski, Fedorowski). This Tournaisian-Viséan species group is found within the Courceyan-Chadian regional substages (Heckel & Clayton, 2006), represented in South Wales by the Friars Point Limestone (FPL) Formation of the Black Rock Group (BRG) (Waters, 2011; Waters & Lawrence, 1987).

Mississippian outcrop and subcrop have a trend which varies from WNW-ESE to WSW-ENE depending on proximity to inverted thrust faults and regional Variscan folds along the coast of the Vale of Glamorgan (Rutter et al., 2022) (Figure 1). Lithologies within the FPL are varied and include mudstones, skeletal wackestones and packstones, calcarenites, and combinations of these. The depositional environment interpreted for the facies is a sub-wave base within a southerly-thickening sequence, and part of a marine carbonate platform (Waters & Lawrence, 1987) (Figure 2). The local geology of Barry, which is a focus of this study, contains a link system of inverted thrust faults and NW-SE trending strike-slip faults which juxtapose Mesozoic marginal facies and distal facies against the BRG (Figure 3) (Rutter & Miliorizos, 2022).

The Mississippian palaeogeography of the Vale of Glamorgan (Pharaoh, 2018; Waters & Lawrence, 1987) is different to other global settings (e.g., Denayer, 2015), driving alternative local evolutionary trends and mechanisms within the Rugosa. We address the Vale of Glamorgan specifically because although anagenesis was assumed in the literature, the Vale of Glamorgan is omitted from this type of evolutionary study (Aisenverg et al., 1979; de Groot, 1963; Einor, 1979; Poty et al., 2014; Wagner & Higgins, 1979; Waters, 2011; Waters & Lawrence, 1987).

The biostratigraphic succession within the FPL (and BRG) is documented thoroughly by Mitchell (1980, 1989); Mitchell and Green (1965); Ramsbottom and Mitchell (1973); Sibly (1906, 1908); Vaughan (1905); and Waters and Lawrence (1987), so the specific aim herein is to present quantitative data on biozonation and coral distribution from sites at Barry to address the evolutionary mechanisms (Mitchell, 1980, 1989; Mitchell & Green, 1965; Ramsbottom & Mitchell, 1973).

We describe quantitatively the distribution and occurrence of the *Z. delanouei* species group in South Wales further to Poty (1975, 1986) who described the morphology, occurrence, and distribution of rugose and tabulate corals. Furthermore, Poty (2010) discussed the evolutionary processes of the Rugosa and Tabulata which must be considered within their ontogenetic limits following Hill (1940). Poty (1986) and Aretz (2010) inferred changes in the biotic distribution due to facies dependency, climatic fluctuations, and eustacy. Aretz (2010) and Denayer and Hoşgör (2014) agreed that the biostratigraphic ages of the corals are contradicted by the occurrence of microfossils in the Mississippian and Poty et al. (2014) discussed using the foraminiferans with the Rugosa for Eurasian biozonation and correlation of the Mississippian. This presents a worthwhile investigation of the transitional nature of the boundary between biozones and coral distribution in the FPL.

1.2 | Morphology and evolutionary processes

The nomenclature used to describe the species group originates from monographs of the *Z. delanouei* group by Hill (1939, 1940) and detailed descriptions of the species given by Carruthers (1908, 1910), Hill (1940) and Hudson (1940). There are differences in these

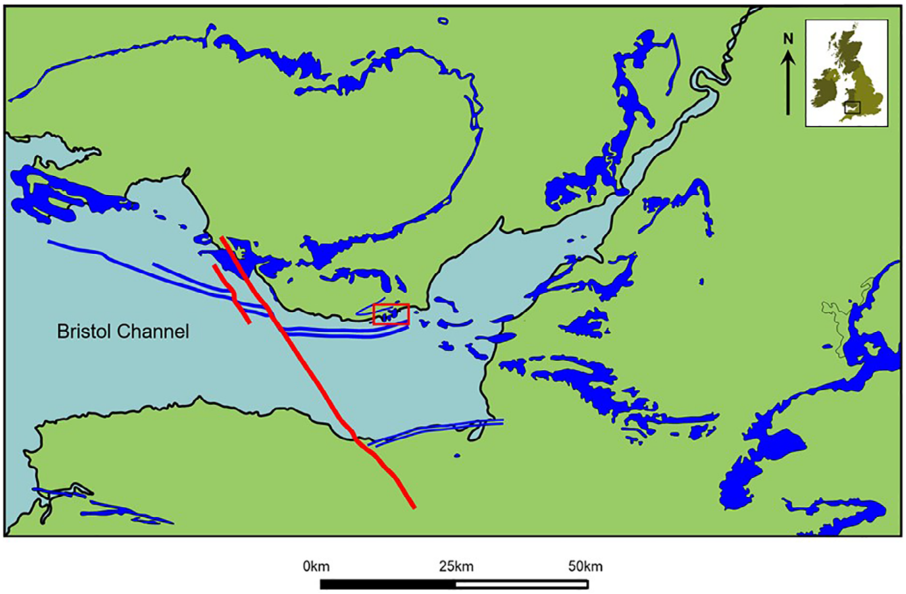

FIGURE 1 Sketch-map of the extent of the Carboniferous Limestone and strata of similar age (in blue) across South Wales, north Somerset and Devon (After Barclay et al., 1989; British Geological Survey, 1986, 1988, 1990; Edmonds et al., 1979, 1979; Kellaway et al., 1993; Whittaker et al., 1983), including the South Scarweather Package contours 0.2 and 0.3 s (seismic reflectors of Carboniferous Limestone). The red box highlights the field sites. The Watchet Cothelstone Hatch Fault is shown by the solid red line between north Somerset and South Wales, indicating the probable extent of the fault trace beneath the inner Bristol channel (Miliorizos, 1992; Miliorizos & Ruffell, 1998).

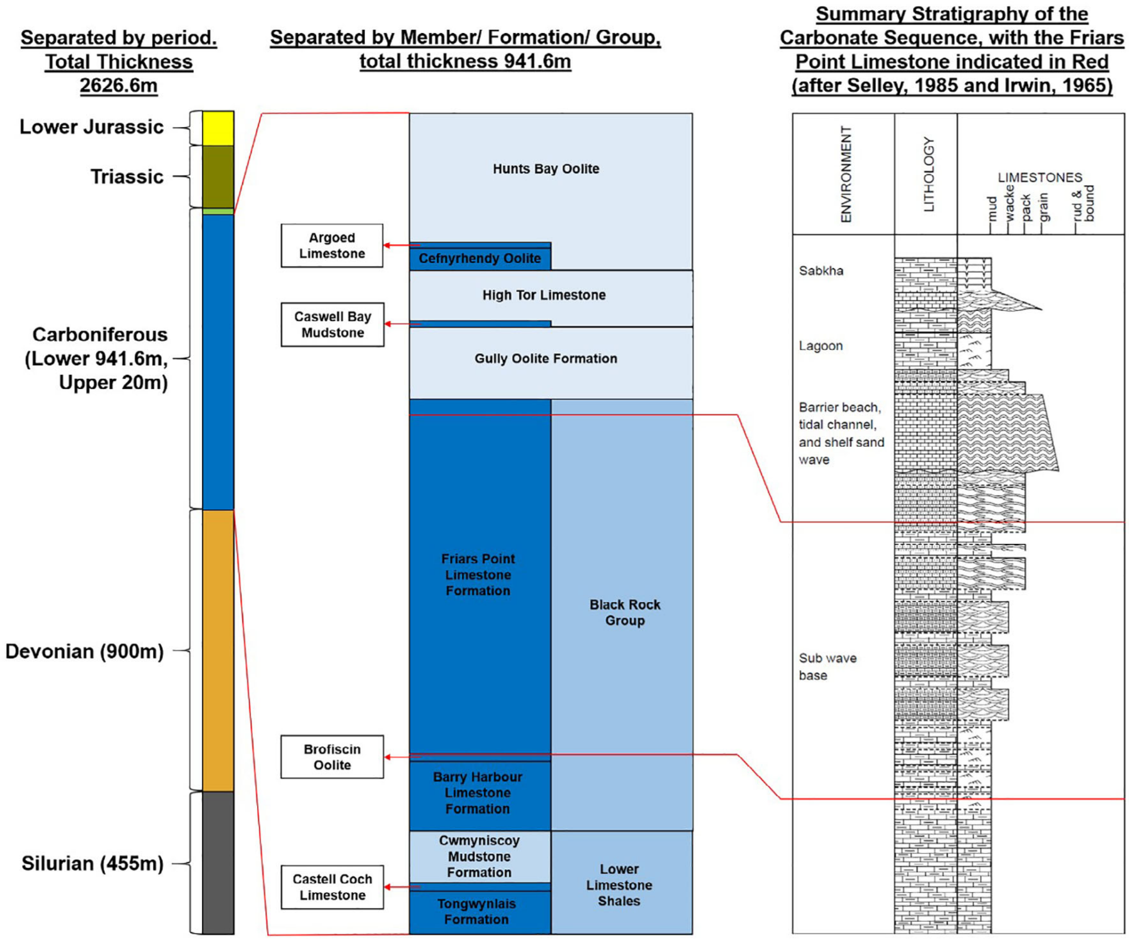

FIGURE 2 The regional stratigraphy in South Wales with thicknesses (Barclay et al., 1988; Waters & Lawrence, 1987; Wilson et al., 1990), and the position of the Friars Point Limestone (FPL, Tournaisian-Viséan) on the summary carbonate sequence from Selley (1985) after Irwin (1965). The *Zaphrentites delanouei* species group can be found throughout the FPL, see documents 1–4 in the data repository at https://doi.org/10.6084/m9.figshare.21779321.v1.

morphological descriptions such as the inclusion and exclusion of species. The *Z. delanouei* group (some of which are shown in Figure 4) is comprised of *Z. delanouei* Milne Edwards and Haime; *Z. constricta* Carruthers; *Z. parallela* Carruthers; *Z. pseudoparallela* Hudson; *Z. disjuncta* Carruthers; and *Z. brevisepta* Hudson. *Z. pseudoparallela* and *Z. brevisepta* have been synonymized into *Z. disjuncta* for the purposes of these statistics, as previously *Z. pseudoparallela* and *Z. brevisepta* respectively were considered the early and late stages of *Z. disjuncta* (op. cit.). Morphological variables, internal structure, and shape of *Zaphrentites* genus corals are shown in Figure 5 (after Clarkson, 1979; Denayer & Hoşgör, 2014; Hill, 1981).

We define species concurrence as the appearance of multiple species of the same genus within the same bed or depositional unit. High species concurrence means more, and low species concurrence means fewer species are present, in a given layer. For the purpose of Markov chains, these are referred to as states of high species concurrence and low species concurrence (see methodology part below).

Anagenesis, cladogenesis, and anacladogenesis are defined best by Emerson and Patiño (2018). Cladogenesis describes the branching of evolutionary processes whereby an ancestral species can give rise to two or more descendent species. Anagenesis, by contrast, describes the evolutionary change within a single lineage over time. Anacladogenesis (anagenetic speciation) describes the origin of sister species from ancestral species, where a single descendent undergoes character state change (Emerson & Patiño, 2018) (Figure 6).

Consecutive species occurrence can be described as anagenetic, which implies an ordered evolutionary lineage. Species concurrence, the opposite of consecutive species occurrence, can be caused by cladogenesis or anacladogenesis; however, they are not easily linked to these evolutionary mechanisms, due to the problematic phylogeny of the Rugosa (Hill, 1940).

1.3 | Hypotheses

The null hypotheses are (1) There are no differences in species distribution between field sites whilst disregarding facies control; (2) species concurrence does not take place beyond the first generation;

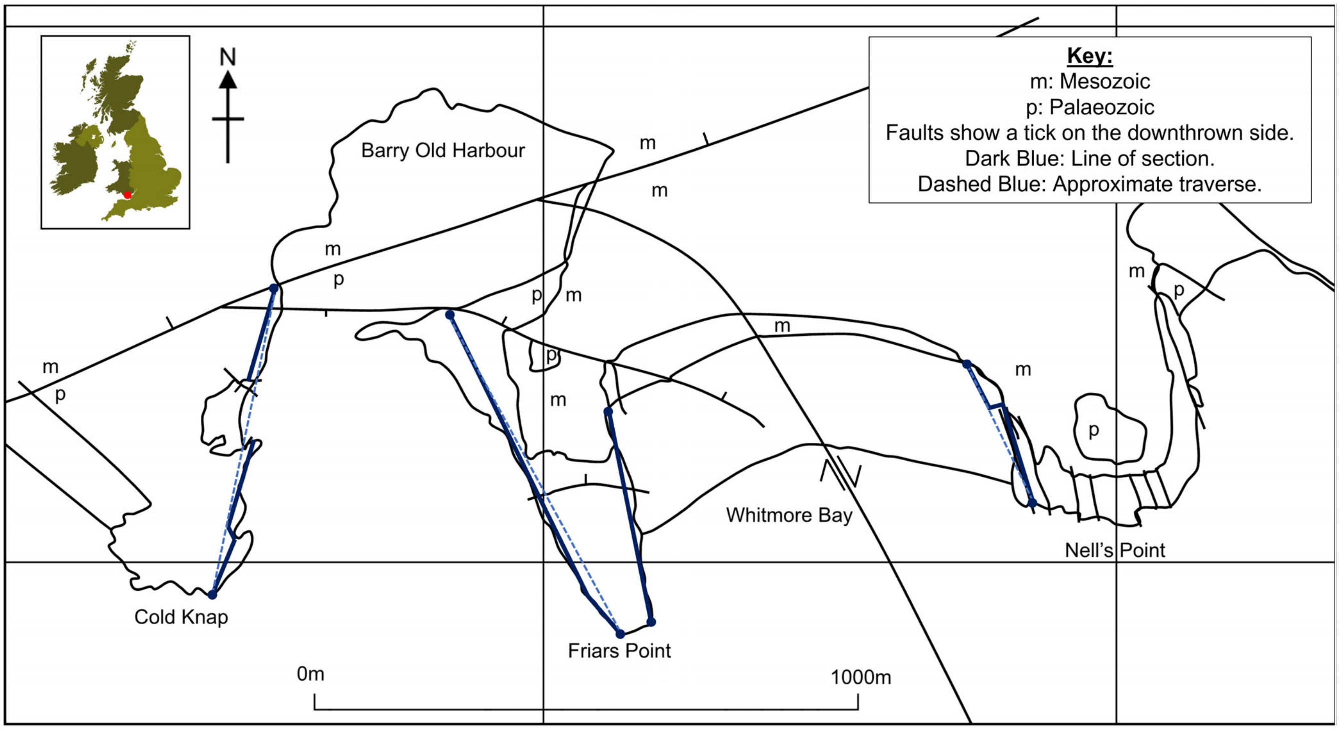

FIGURE 3 Barry Island with key faults highlighted, both subcrop and outcrop. The studied locations are the three headlands of Cold Knap, Friars Point and Nell's Point, which are labelled on the map. This map is the contents of the red box in Figure 1. The Carboniferous Limestone beds dip approximately 35° towards the south–south-east. Lines of the section are highlighted in solid blue and approximated best-fit lines of the section are shown in dashed blue.

(3) regarding the carbonate facies, the palaeoenvironment does not control the distribution, success, or ultimate demise of the corals; and (4) Anagenesis and cladogenesis on their own are not the best descriptions of the evolutionary process for the species group when compared with anacladogenesis (inferred from Bak & Meesters, 1998; Holland, 1995, 2003; Hurst & Pickerill, 1986; Insalaco, 1999; Levinton, 1970; Vermeij, 2002; Waters & Lawrence, 1987; van Woesik, 2002).

Hypothesis (1) can be tested using a Markov Chain Monte Carlo process and a *t*-test. Hypothesis (2) can be tested using a Markov Chain Monte Carlo process, a Branching Process, and a Galton–Watson Ultimate Extinction calculation. Hypothesis (3) can be tested using Markov Chain Monte Carlo processes, with a Branching Process utilizing the results from the Markov Chain, a t-test, and a Galton–Watson Ultimate Extinction calculation. Hypothesis (4) can be tested using Markov Chain Monte Carlo processes, with a Branching Process utilizing the results from the Markov Chain and a Galton–Watson Ultimate Extinction calculation. Each technique is outlined below.

2 | METHODOLOGY

Previous studies have focused on qualitative analysis, with cursory references to quantitative techniques applied to the *Z. delanouei* species group, for example, Swinnerton (1921) did include some quantitative morphology; however, this was not applied in detail to evolutionary trends.

Here we use the well-established mathematical technique of Markov Chain analysis (Brooks, 1998; Chung, 1960; Orey, 1991) for species concurrence and occurrence in carbonate facies. We determine the probability of the number of different species occurring simultaneously in a bed, and in each carbonate facies, and extrapolate them using branching processes involving various models of growth. Previous biological use of Markov Chain analysis explains and predicts modern species distribution but again, has not been applied to the Rugosa (Aldous & Popovic, 2005; Alfaro et al., 2003; Huelsenbeck et al., 2004; Lakner et al., 2008; Link et al., 2002; Pagel & Meade, 2006). We then determine the likelihood of ultimate extinction at each generation using a Galton–Watson process, and a *t*-test to determine whether immigration or emigration had an impact on the population distribution.

2.1 | Markov Chain Monte Carlo

The Markov Chain Monte Carlo process (Brooks, 1998; Brooks et al., 2011; Chung, 1960; Geyer, 1992; Gilks et al., 1995; Hastings, 1970; Kendall, 1953; Larget & Simon, 1999; Neal, 1993; Orey, 1991; Shumway, 1987; Winkler, 2012) is carried out for species concurrence and species occurrence in a carbonate facies using field data from systematic stratigraphic logs. The Markov Chain Monte

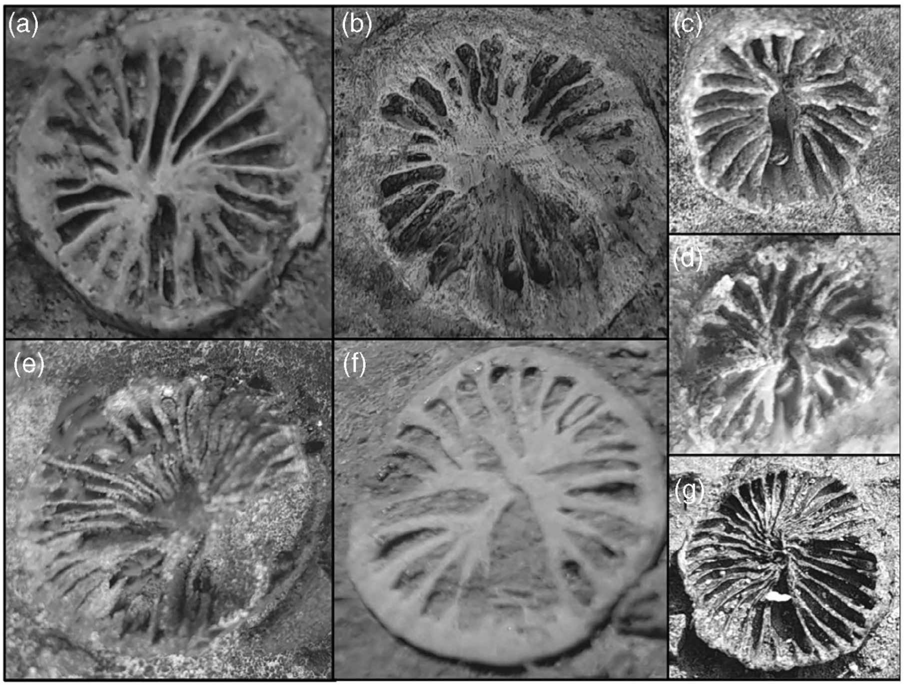

FIGURE 4 Photographs of some members of the *Zaphrentites* genus in situ with maximum dimensions (a) *Z. parallela*, 10 mm; (b) Morphotype between *Z. constricta* and *Z. disjuncta*, 9 mm; (c) *Z. parallela*, 7 mm, next to; (d) *Z. delanouei*, 6 mm; (e) *Z. constricta*, 9 mm; (f) Morphotype of *Z. delanouei* based on the position of the alar fossula, 11 mm; (g) *Z. parallela* with elements of constriction, 12 mm. All photographs are in transverse sections with slight obliquity indicated by their ellipticity.

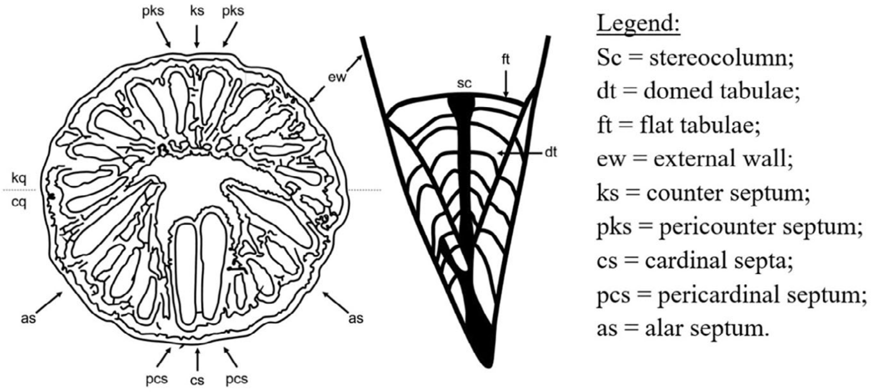

FIGURE 5 The morphological variables, internal structure and shape of *Zaphrentites* genus corals (Partly adapted after Clarkson, 1979; Denayer & Hoşgör, 2014; and Hill, 1981). Scale of transverse section is 12 mm in diameter and the scale of the longitudinal section is 35 mm.

Carlo process is a standard technique in mathematical analysis which results in stochastic equilibrium only being achieved if the dataset is convergent, giving invariant probabilities of species concurrence or consecutive species occurrence. In the event of non-convergent data, the Markov Chain Monte Carlo process cannot be used unless data points are amalgamated. If data are amalgamated, then the anomalous results must be categorized between two equal bins as near as possible to the original values based on morphological variables.

The calculation requires data on the change in the number of species between beds, herein referred to as transitions between states in the Markov Chain Monte Carlo process. For example, in Table 1, a change from two species to one species across successive beds is expressed as one transition from two to one. These counts of transitions between states are written into a count matrix and normalized into proportions (Table 1). These form a transition matrix (Kendall, 1953; Pakes & McGuire, 2001) and iterative matrix multiplication is continued until stochastic equilibrium is reached (p^5 Table 1) (Cao et al., 2017; Laverty et al., 2002).

The number of transitions between states, n, utilized in the Markov Chain Monte Carlo process is listed here, with n being 57 at Cold Knap, 84 at Friars Point (west), 74 at Friars Point (east), and 81 at Nell's Point, and for example, calculated as the sum of transitions in Table 1 (count) for Friars Point (east). Full datasets are available in a digital repository at: https://doi.org/10.6084/m9.figshare.21779321.v1.

2.2 | Branching process

The branching process is applied to the probabilities obtained from the Markov Chain analysis, for example, Table 2, which is a well-documented process in literature (Agresti, 1974; Aldous & Popovic, 2005; Cardy & Täuber, 1998; Haccou & Iwasa, 1996; Matsumoto & Aizawa, 1999; Przeworski & Wall, 1998; Raup, 1977; Wei & Winnicki, 1990). The data are inserted into differently sized matrices that allow for the concurrence of up to five species at each

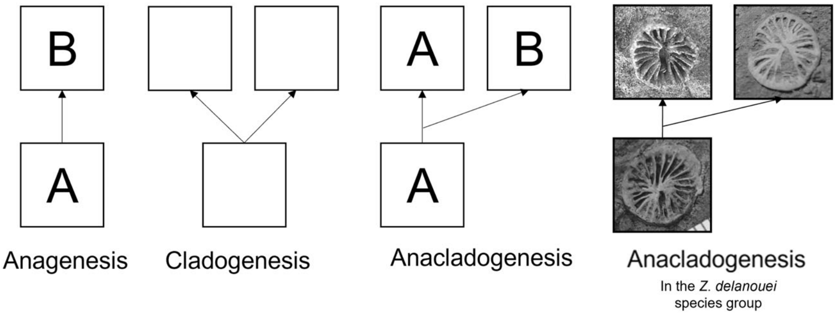

FIGURE 6 A schematic showing the three considered evolutionary methods: anagenesis, cladogenesis, and anacladogenesis (After Emerson & Patiño, 2018). The example species are from Figure 6, showing *Zaphrentites parallela* as A and a morphotype of *Z. delanouei* as B.

site (Table 5) and here for example at Friars Point (east), there is a concurrence of three at the first generation (Tables 5 and 7). The maximum number of permutations in the branching process is determined and values of the likelihood of species concurrence are generated for the second, third and fourth consecutive evolutionary stages. The outcomes at the third generation are shown in Table 2, with up to six concurrent species, where $z = 0–6$.

Simple algebra is also used to manually calculate approximations for the potential outcomes of a given permutation and arranged them into a form that permits their summation representing an abbreviated version of the results obtained from the matrix method. For example, Tables 2 and 3, where *r*, *q*, *p*, and *k*, represent the probabilities $P(Z_1 = z)$ for $z = 0–3$ and pp, 2pq, 2pr and 2pk represent examples of probability multiples for $P(Z_2 = z)$.

Multiplication of *r*, *q*, *p*, and *k*, with the probability multiples, gives the estimates for $P(Z_3 = z)$ (Table 5). The estimates for *z* and the probabilities are given in Table 2 at the third generation for $z = 0–3$. This gives the probabilities from the first generation to the second generation and is similarly used up to the fourth generation.

2.3 | *t*-tests

For the purpose of this work, data are amalgamated for each site and two sites are compared, enabling a *t*-test to be carried out using the method described by Gossett (Student., 1908). The test statistic (*t*-Stat) is calculated using sample size, standard deviation and mean to determine the difference between two datasets. Friars Point and Cold Knap are compared using the results of a Markov Chain Monte Carlo process for species occurrence in a carbonate facies, for each species of the *Z. delanouei* group. Data are amalgamated for *Z. pseudoparallela*, *Z. disjuncta*, and *Z. brevisepta* under the label *Z. disjuncta* as previously stated. The purpose of the t-test is to determine whether there is a difference in species distribution across the field sites and whether the observed occurrences are from different populations.

The t-Stat is compared to a standard two-tailed distribution at 95% significance, to obtain the critical values and hence the rejection region for the test. If the t-Stat (equal variance) is too extreme, then the null hypothesis is rejected. If the t-Stat (equal variance) falls between the positive and negative critical values, then the null hypothesis is accepted. There are 10 degrees of Freedom, and the sample numbers are eight and four; an example is shown in Table 4. The results are shown in Table 8.

2.4 | Galton–Watson ultimate extinction

The probabilities for each generation of the branching process are multiplied by the generation index and then summed to calculate a value for ultimate extinction (μ).

$$\mu = z(0) \times [z(0)P(Z_1 = z)] + z(1) \times [z(1)P(Z_1 = z)] + z(2) \times [z(2)P(Z_1 = z)] + z(3) \times [z(3)P(Z_1 = z)].$$

The values from Table 2 (column 1) are inserted into this equation.

$$\mu = (0 \times 0.484214756) + (1 \times 0.313245664) + (2 \times 0.188710416) + (3 \times 0.013829164) = 0.732153988$$

If μ ≤ 1 then ultimate extinction is the result; however, if μ > 1 extinction is a possibility but not guaranteed. The higher the value of μ, then the lower the likelihood of reaching ultimate extinction. Therefore, ultimate extinction is the outcome for the first generation of the branching process on Friars Point (east).

3 | RESULTS

The Markov Chain for Species Concurrence indicates the probability of the number of species that will occur in a given stratigraphic horizon after traversing a given sequence. Table 5 outlines the stochastic equilibrium reached for each field site, for between zero and five coral species and P^n refers to the number of lithological units to pass through before stochastic equilibrium can be reached. This gives the first generation of the branching process in Figure 7. The percentages of species occurrence and concurrence are also outlined in Table 5, where species occurrence is ≤1 species in a given horizon, and species concurrence is >1 species in a given horizon. Table 6 shows the results of the Markov Chain process for species occurrence in carbonate facies, using the same method as for species concurrence, taking coral species within facies types at each site. Species were absent in certain facies, for example, calcarenite beds which contain extraformational bioclasts.

TABLE 1 An example of species concurrence (Friars Point, eastern side) marked Count, an example of normalized data based on the Count (P1), and an example of convergent data in five iterations (P5)

	Count				P^1				P^5			
Count	0	1	2	3	0	1	2	3	0	1	2	3
0	15	13	6	1	0.429	0.371	0.171	0.029	0.484	0.313	0.189	0.014
1	15	4	5	0	0.625	0.167	0.208	0.000	0.484	0.313	0.189	0.014
2	6	5	3	0	0.429	0.357	0.214	0.000	0.484	0.313	0.189	0.014
3	0	1	0	0	0.000	1.000	0.000	0.000	0.484	0.313	0.189	0.014

TABLE 2 An example of the first generation of the branching process for Friars Point (east) based on Table 1

	Matrix multiplication		Algebraic
z	$P(Z_1 = z)$	$P(Z_3 = z)$	$P(Z_3 = z)$
0	0.4842147559	0.1135308946	0.1135308945
1	0.3132456640	0.3936085740	0.4378543598
2	0.1887104163	0.1911886587	0.1469428728
3	0.0138291639	0.2707632511	0.2707632510
4	0.0000000000	0.0168360854	–
5	0.0000000000	0.0091676597	–
6	0.0000000000	0.0049048769	–
Sum	1	1	0.9690913781

Note: z represents the transitions between states and $P(Z_1 = z)$ represents the probability of each of these outcomes at the first generation and $P(Z_3 = z)$ represents the probability of each of these outcomes at the third generation of the branching process for Friars Point (east) based on Table 1. The Algebraic result for $P(Z_3 = z)$ is comparable to the matrix multiplication results.

The results of these Markov Chain processes show species occurrence and concurrence in support of null hypotheses (1) that there are no differences in species distribution between field sites whilst disregarding facies control and (4) anagenesis and cladogenesis on their own are not the best descriptions of the evolutionary process for the species group when compared with anacladogenesis. These results also support the rejection of null hypotheses (2) species concurrence does not take place beyond the first generation and (3) regarding the carbonate facies, the palaeoenvironment does not control the distribution, success, or ultimate demise of the corals; and as outlined in Tables 5 and 6.

Calculations of the potential number of species in each generation of the Branching Process (Table 7) are given for each location, alongside each other in Figure 7. Peaks in potential concurrence for up to four generations occur at 1, 3, and 6. Noteworthy are peaks at 1 and 3 at Cold Knap and Friars Point, whereas Nell's point has a consistently high level of species occurrence and concurrence for up to 7 species after which the probability diminishes. The results of the branching process show species concurrence to multiple generations in support of null hypothesis (4) and in rejection of null hypotheses (2) and (3) (see above).

Markov Chain analysis followed by *t*-tests disregarding facies control shows that sample data are from the same population without the influence of immigration or emigration, but do not preclude some displacement, especially within calcarenaceous storm beds with extra-formational bioclasts (Rutter, 2020). Null hypothesis (1) (above) is accepted for each case (Table 8) under the condition: -*t*-Critical two-tail < *t* Stat < *t*-Critical two-tail. These *t*-test results, whilst showing no difference in species distribution between field sites disregarding facies control, necessitate null hypothesis (3) (above) to be rejected because, by inspection of the probabilities in Table 6, there are unequivocally different species distributions between carbonate facies.

Branching process results for each generation used in a Galton–Watson calculation, show that the relationship between the number of generations (d) and the likelihood of extinction μ may not be simply proportional (Table 9). Therefore, ultimate extinction at the first generation is particular to Friars Point (east and west) and Cold Knap. The results of the Galton–Watson calculation show that whilst ultimate extinction is likely after the first generation, this is not the case at all field sites and necessitates the rejection of null hypotheses (2) and (3), and acceptance of null hypothesis (4) (above).

4 | DISCUSSION

Based on the Markov Chain for species occurrence in a Carbonate Facies, the results of the t-test, and the derived p-values are consistently greater than 0.05, we have strong evidence to accept the null hypothesis (1) that there are no differences in species distribution between field sites whilst disregarding any facies control. At face value, the Markov Chain for species occurrence in carbonate facies shows large differences in the distribution between the different coral species and the facies in which they occur; however, whilst there are differences, they are not statistically significant when they are averaged across a sequence and across multiple sites.

The Markov Chain for species concurrence, and subsequent Branching Process and Galton–Watson calculations, give evidence to reject null hypothesis (2) because the branching process can be demonstrated to multiple generations (Table 7, Figure 7). The stochastic equilibria reached in the Markov Chain Monte Carlo processes represented the probabilities of species concurrence for the first generation of the branching process. The estimates of the likelihood of extinction, using the Galton–Watson calculation, founded on the results of the branching process, suggest a higher likelihood of extinction at Cold

TABLE 3 An example of an algebraic expression of the branching process, when multiplying the values indicated by the letter in the first column, by the values in the second row which are from the corresponding multiplications above

	pp 0.0356116212	2pq 0.1182254393	2pr 0.1827527363	2pk 0.0052194145	Summation of *r*, *q*, *p* and *k*, and different terms in P($Z_2 = z$).			
r	0.0172436725	0.0572465022	0.0884915716	0.0025273175	2	3	2	5
q	0.0111551859	0.0370336062	0.0572465022	0.0016349590	3	3	3	6
p	0.0067202839	0.0223103719	0.0344873449	0.0009849579	2	3	2	5
k	0.0004924789	0.0016349590	0.0025273175	0.0000721801	5	6	5	5

Note: The final two columns show an example of the number of species obtained with the algebraic method, by summation of *r*, *q*, *p*, and *k*, and the different terms in P($Z_2 = z$).

TABLE 4 The *t*-test method for *Z. delanouei* and *Z. constricta* based on the results of the Markov Chain Monte Carlo for Species Occurrence in Carbonate Facies

Species	*Z. delanouei*		*Z. constricta*	
Location	FP	CK	FP	CK
Data taken from Markov Chain Analysis for Species Occurrence in a Carbonate Facies	0.078	0.072	0.029	0.057
	0.243	0.155	0.031	0.053
	0.113	0.092	0.032	0.000
	0.000	0.000	0.000	0.000
	0.092		0.026	
	0.113		0.120	
	0.096		0.029	
	0.016		0.016	
Mean	0.094	0.080	0.035	0.028
Difference in means	−0.014		−0.008	
Observations	8	4	8	4
Hypothesized Mean Difference	0		0	
Degrees of Freedom	10		10	
t-Stat	−0.442		−0.495	
t-Stat two-tail assuming equal variance	0.325		0.181	
p = P(*T* ≤ *t*) two-tail	0.752		0.718	
t critical two-tail	2.228		2.228	

Knap and Friars Point but a markedly lower likelihood at Nell's Point (Table 9). For the second and third generations, this likelihood is low which implies that if a second or third generation were produced, then ultimate extinction would be unlikely unless influenced by significant environmental factors. We attribute this difference to a higher stratigraphic level at Nell's Point and its more proximal depositional environment, relative to those of other sites. Environmental factors include water clarity, light, water temperature and energy, as expected in our log (Figure 2) based on Selly (1985; from Irwin, 1965), as Nell's Point represents a sequence near the wave base, compared to Friar's Point and Cold Knap which represent sequences from lower to middle part of the sub-wave-base, with upward increasing wave activity.

We also reject null hypothesis (3), based on the Markov Chain analysis for species occurrence in a carbonate facies, the results of the *t*-test on these data, the Markov Chain for species concurrence, and the subsequent Branching Process and Galton–Watson extinction calculations. The sequence at Nell's Point is indeed from a higher stratigraphic level (Waters & Lawrence, 1987), based on the varieties and abundance of the bioclasts, and the results of the Markov Chain analyses support this by showing a greater concurrence, and a higher likelihood of coral occurrence, at Nell's Point (Table 5). This suggests the palaeoenvironment had a quantifiable effect on the distribution and success or demise of the *Z. delanouei* species group.

We accept the final null hypothesis (4) as we find anagenesis and cladogenesis on their own are not the best description of the evolutionary processes controlling the *Z. delanouei* species group, based on the two Markov Chains, the Branching Process, and the Galton–Watson extinction calculations. In the case of anagenesis, we would not expect species concurrence to happen in an ordered ancestor-descendent familial line. Instead, we have established species concurrence does happen and indeed to multiple generations. However, some horizons only contain one species, and some contain no species, so we cannot state cladogenesis as the only alternative evolutionary mechanism. Therefore, by exhaustion, we take anacladogenesis as the controlling evolutionary process, as this most closely aligns with the patterns from the statistical analyses and observations made in the field.

Branching process analysis suggests there can be up to 14 species in a given horizon (Figure 7); however, only six species are

TABLE 5 The resultant probabilities of species concurrence across the field study sites. The final two columns are the percentages of species concurrence and consecutive species occurrence across each field site.

		The probability of the number of species occurring within a given bed.							
Location	P^{n}	**0 species**	**1 species**	**2 species**	**3 species**	**4 species**	**5 species**	**% ≤1**	**% >1**
Cold Knap	P^{12}	0.437	0.366	0.150	0.032	0.015	0.000	65.0%	35.0%
Friars Point (west)	P^{8}	0.602	0.229	0.121	0.036	0.012	0.000	57.5%	42.5%
Friars Point (east)	P^{5}	0.484	0.313	0.189	0.014	0.000	0.000	60.7%	39.3%
Nell's Point	P^{8}	0.136	0.333	0.309	0.185	0.025	0.012	38.5%	61.5%

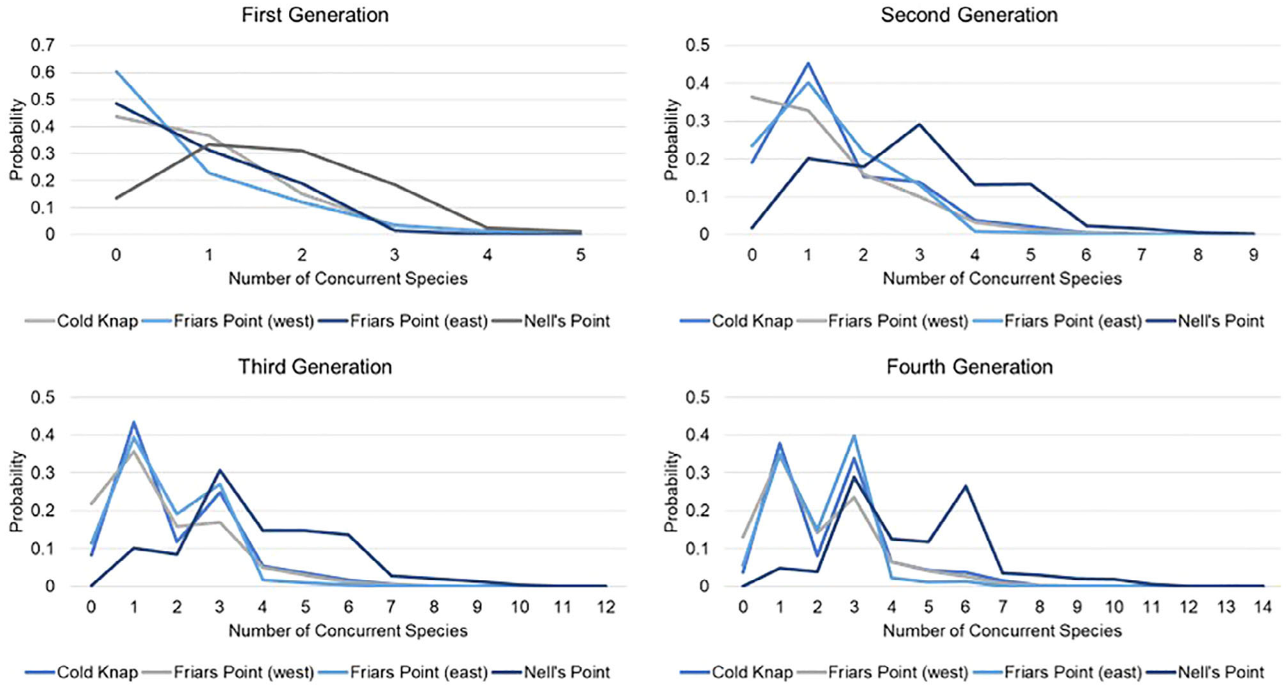

FIGURE 7 The probabilities of species concurrence within the Friars Point Limestone (FPL) at each field site to four generations

documented in the literature. This is due to the numbers of observed species and concurrences, where higher concurrence in the first-generation leads to higher concurrence in further generations as at Nell's Point. Such a hypothetical progression with a significant increase in biodiversity is known from Davis and Hollingsworth (2019) who used a branching process based on the Galton–Watson methodology to estimate the likelihood of ultimate extinction. However, as extinction is not always certain, based on counts within the branching process, there are other multivariate factors controlling extinction. For example, sequence progradation, environmental energy, competition with *Caninophyllum patulum*, and predation (Mitchell, 1980).

Furthermore, the t-tests indicate at a 95% confidence level that the *Z. delanouei* species group on Cold Knap, Friars Point, and Nell's Point are from the same population unaffected by immigration and emigration, but are controlled by lithology and environment of deposition, and governed by facies. According to Hubbard and Pocock (1972), Kleypas et al. (1999), and Shinzato et al. (2011), energy, storm transportation, depth, light, clarity, and temperature are the controlling variables in both occurrence and concurrence of the corals. The exact influence of each variable is as yet unknown but may be quantified using entropic studies based on Markov Chain analyses (e.g., Daly, 2005; Hattori, 1976; Hoque & Nwajide, 1985 and Tewari et al., 2009).

5 | CONCLUSIONS

From Table 6 showing species distribution and Table 8 with $p > .05$ consistently, we conclude that there are no differences in species distribution between field sites but by inspection of Table 6, there are significant differences in species distribution due to facies control, and we, therefore, accept null hypothesis (1).

We conclude species concurrence does take place beyond the first generation from between and we, therefore, reject null hypothesis (2).

Regarding carbonate facies, we conclude that the palaeoenvironment does control the distribution, success, or ultimate demise of the corals, and we, therefore, reject null hypothesis (3). The occurrences and concurrences are markedly different in these tables.

TABLE 6 The results of a Markov Chain for species occurrence in carbonate facies, using the same method as for species concurrence

	Location	P^n	*Z. delanouei*	*Z. constricta*	*Z. parallela*	*Z. disjuncta*	*Zaphrentites* Sp.
Mudstones	Cold Knap	P^{11}	0.109	0.072	0.116	0.105	0.153
	Friars Point (west)	P^{13}	0.078	0.029	0.035	0.111	0.067
	Friars Point (east)	P^{12}	0.014	0.026	0.013	0.000	0.043
	Nell's Point	P^{9}	0.078	0.053	0.062	0.078	0.058
Wackestones	Cold Knap	P^{11}	0.155	0.053	0.013	0.098	0.055
	Friars Point (west)	P^{13}	0.243	0.031	0.091	0.075	0.017
	Friars Point (east)	P^{12}	0.270	0.120	0.071	0.112	0.074
	Nell's Point	P^{9}	0.057	0.037	0.045	0.063	0.110
Packstones	Cold Knap	P^{11}	0.092	0.000	0.015	0.008	0.015
	Friars Point (west)	P^{13}	0.113	0.032	0.030	0.008	0.023
	Friars Point (east)	P^{12}	0.096	0.029	0.029	0.038	0.035
	Nell's Point	P^{9}	0.065	0.028	0.053	0.035	0.029
Calcarenites	Cold Knap	P^{11}	0.000	0.000	0.000	0.000	0.000
	Friars Point (west)	P^{13}	0.000	0.000	0.000	0.000	0.017
	Friars Point (east)	P^{12}	0.016	0.016	0.000	0.000	0.000
	Nell's Point	P^{9}	0.005	0.000	0.000	0.000	0.000

TABLE 7 The potential number of species in each generation of the branching process

	Potential maximum number of species (in each generation)			
	First	Second	Third	Fourth
Cold Knap	4	7	9	10
Friars Point (west)	4	7	9	10
Friars Point (east)	3	5	6	6
Nell's Point	5	9	12	14

TABLE 8 The results of the t-tests for Species Occurrence between Friars Point (FP) and Cold Knap (CK); Friars Point (FP) and Nell's Point (NP); and Nell's point (NP) and Cold Knap (CK). The t-Stat assumes equal variance.

	Species	(−) *t* critical two-tail	t-stat	(+) *t* critical two-tail	*p*-value	Accept null hypothesis?
FP-CK	*Z. delanouei*	−2.228	0.325	2.228	.752	Yes
	Z. constricta	−2.228	0.181	2.228	.718	Yes
	Z. parallela	−2.365	−0.023	2.365	.967	Yes
	Z. disjuncta	−2.365	−0.578	2.365	.411	Yes
	Zaphrentites sp.	−2.228	−0.489	2.228	.443	Yes
FP-NP	*Z. delanouei*	−2.201	0.820	2.201	.269	Yes
	Z. constricta	−2.228	−0.043	2.228	.922	Yes
	Z. parallela	−2.306	0.120	2.306	.908	Yes
	Z. disjuncta	−2.306	−0.167	2.306	.871	Yes
	Zaphrentites sp.	−2.228	−0.558	2.228	.206	Yes
NP-CK	*Z. delanouei*	−2.365	−0.844	2.365	.426	Yes
	Z. constricta	−2.447	0.194	2.447	.584	Yes
	Z. parallela	−2.571	−0.060	2.571	.918	Yes
	Z. disjuncta	−2.571	−0.455	2.571	.479	Yes
	Zaphrentites sp.	−2.447	0.060	2.447	.941	Yes

TABLE 9 The results of the Galton–Watson process indicate whether ultimate extinction is likely for the first three generations of the branching process. CK Cold Knap, FP(w) Friars Point (west), FP(e) Friars Point (east), and NP Nell's Point

	First generation			Second generation			Third generation		
Site	*d* value	μ	Extinction likely?	*d* value	μ	Extinction likely?	*d* value	μ	Extinction likely?
CK	104	0.8226298	Yes	51	1.4624393	No	42	1.9752592	No
FP (w)	44	0.6264818	Yes	118	1.4624393	No	38	1.6373017	No
FP (e)	65	0.7321539	Yes	69	1.2943881	No	30	1.7308875	No
NP	26	1.6666466	No	13	2.9255630	No	8	3.8777459	No

We conclude, from the particularly high probability of concurrence at Nell's Point, that due to the occurrence of ancestral species in the same horizons as descendants, neither anagenesis nor cladogenesis on their own is an appropriate description of the evolutionary process and mechanism. Hence, anacladogenesis becomes the best description of the style of evolution and we accept null hypothesis (4), that anagenesis and cladogenesis on their own are not the best descriptions of the evolutionary process for the species group when compared with anacladogenesis.

Furthermore, from the Markov Chain analyses, we conclude that since species occurrence was markedly different across depositional facies, then the whole anacladogenetic lineage was significantly controlled by the palaeoenvironment.

Finally, it is worth making a conjecture to pursue in further work, that since the branching process analysis reveals up to 14 species of *Zaphrentites* whilst only six species are known, an avenue of investigation opens up in the search for the occurrence of morphotypes and sub-species, especially at Nell's Point where abundance is high. At Nell's Point, many *Zaphrentites* species may well have continued to subsequent generations, even without the influence of immigration and before their ultimate extinction. Perhaps the likelihood of extinction at Cold Knap and Friars Point, where ultimate extinction after the first generation was inevitable, is explained by the commencement of the *C. patulum* Zone and the competition that may have ensued between both genera.

AUTHOR CONTRIBUTIONS

W.A.J.R. and M.N.M. designed and conceived the research. W.A.J.R. carried out fieldwork and data collection. W.A.J.R. and M.N.M. processed data, formulated results and conclusions. W.A.J.R. and M.N.M. wrote the manuscript together.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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