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- 1 Title: Ontogenetic constraints on foraminiferal test construction
- 2 Running title: Ontogenetic constraints on test construction
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8   **ABSTRACT**

9   Developmental processes represent one of the main constraints on the generation of adult
10   form. Determining how constructional and energetic demands operate throughout growth is
11   essential to understanding fundamental growth rules and trade-offs that define the framework
12   within which new species originate. In organisms producing spiral shells, coiling patterns can
13   inform on the constructional constraints acting throughout development that dictated the
14   diversification of forms within a group. Here we use Synchrotron radiation X-Ray tomographic
15   microscopy (SRXTM) reconstructions of eight planktic foraminifera representative of the major
16   morphotypic groups to determine disparity of coiling patterns by measuring Raupian
17   parameters. The results show that foraminifera are a morphologically highly conservative
18   group, exploiting a limited range of potential coiling patterns. Very similar coiling patterns
19   during early ontogeny, regardless of species, point towards strong constraints in early
20   ontogeny and to common developmental processes acting across all morphogroups.
21   Dispersion and lateral displacement of taxa in morphospace are limited to the adult stage.
22   Accretion with low translation down the coiling axis in juveniles may maximise lateral growth
23   and metabolic efficiency in light of costly calcification. Increased translation in the adult stages
24   allows growth to accommodate new chamber shapes, mediated by changes in aperture
25   location and the site of accretion over ontogeny. These constructional constraints, and the
26   accretion of a small number of discrete chambers, limit the potential for novel forms within
27   the foraminifera compared to other groups of coiling organisms and may explain the repeated
28   evolution of similar morphotypes throughout the evolutionary history of the group.

29

INTRODUCTION

The evolution of new forms by changes in morphology is directed by the limitations imposed by developmental programmes on the phenotype (Raff, 2000). Developmental processes are powerful mechanisms to generate disparity, i.e., morphological diversity at and above the species level, through changes in timing, rate and location of developmental events (heterochrony and heterotopy, (Zelditch & Fink 1996; Zelditch et al. 2003)). Understanding what developmental requirements need to be fulfilled at each stage of growth can inform us on the potential for action of these mechanisms, and thus the evolvability of the group. In most groups, the study of developmental processes and their influence on adult form is restricted to the living organisms due to the difficulty in obtaining complete ontogenetic sequences. Several groups, however, such as gastropods, cephalopods, bivalves and foraminifera, preserve a record of their entire ontogeny in their shells through incremental growth (Jablonski & Lutz 1983). Their extinct counterparts can also be included in the investigation of disparity and its generation, giving a more complete overview of the realised developmental patterns employed through time (Gerber et al. 2007). Furthermore, in many cases, shells offer a representation of the size and volume of the organisms that retract into them, allowing us to infer biological processes.

Planktic foraminifera, a group of unicellular organisms, secrete a calcium carbonate test, whose structure changes throughout growth due to the accretion of new chambers at each successive stage of growth (Huang 1981). Species are defined by aspects of coiling geometry, chamber shape and number, surface and wall texture, aperture shape and position, suture shape, and any modifications such as keels or apertural lips (Norris, 1991a). Most modern species have either spinose globular forms (globigerines) or non-spinose lenticular or conical forms (globorotaliids). In the evolutionary history of the group, each of the three major radiation events since their origination in the mid-Jurassic saw the evolution of similar adult

morphologies (Figure 1; Cifelli 1969; Norris 1991a). Following the end-Cretaceous and end-Eocene extinctions, diversity was reduced to small unkeeled forms with globose tests, from which large species and species with keels subsequently re-evolved convergently (Norris 1991a, b). This suggests the potential for restrictions to shape innovation that could arise from intrinsic constraints.

Two approaches have traditionally been taken in the literature to consider constraints on shell development: deducing the ontogeny as preserved in real specimens (e.g., Gerber 2011; Raup 1967; Schindel 1990), and creating theoretical ontogenies according to predetermined growth parameters (e.g., Raup 1966; Rice 1998; Tyszk 2006; Urdy et al. 2010a, b). These methods are complementary, as theoretical modelling can manipulate aspects of growth independently to provide geometrically possible forms against which to compare empirical observations.

Theoretical modelling of incremental growth in spirally coiled shells was most prominently defined by Raup (1966), who described coiling by four parameters summarising the shape and expansion rate of the generating curve, and its displacement along and away from the coiling axis. Although Raup's model has subsequently been critiqued (Schindel 1990; Tursch 1997) and numerous studies have attempted to improve on his approach by adding or modifying characters (e.g., Rice 1998; Schindel 1990; Tursch 1997), these merely express the same four parameters differently (e.g., Gerber et al. 2008; Gerber et al. 2007; Noshita et al. 2012).

Several theoretical models have attempted to investigate the spectrum of possible forms in foraminifera via hypothetical morphospace construction (Berger 1969; Labaj et al. 2003; Signes et al. 1993; Topa & Tyszk 2002; Tyszk 2006; Tyszk & Topa 2005; Tyszk et al. 2005; Webb & Swan 1996). Foraminiferal growth differs from that of other organisms, as material is added onto the test as discrete morphological units rather than along a continuous generating curve. A number of studies have described the ontogeny of selected species of planktic foraminifera (e.g., Bé et al. 1969; Brummer et al. 1986, 1987; Caromel et al. 2016; Huang 1981; Huber 1994;

Sverdlove & Bé 1985). Following on from the proloculus, the first chamber, the juvenile stage is morphologically conservative, characterised by the addition of a number of uniform chambers (Brummer et al. 1987). The subsequent neanic stage is a transitional stage during which species-specific morphological features are gradually developed (Brummer et al. 1987), such as changes in aperture position, changes in allometry in globigerines and changes in chamber shape in globorotaliids (Caromel et al. 2016). The adult stage is signalled by distinct features in globigerines, such as secondary apertures and wall texture (Brummer et al. 1987), and a change in allometry in globorotaliids (Caromel et al. 2016). Empirical analyses of coiling throughout the entire ontogeny, however, are lacking, because the methods used to back-track the ontogeny, such as low-resolution X-Ray microscopy (Bé et al. 1969), scanning and transmission electron microscopy (Brummer et al. 1986, 1987; Sverdlove & Bé 1985) and serial dissection (Huber 1994), restricted the ability to resolve morphology in three dimensions. Using virtually reconstructed specimens from Synchrotron radiation X-Ray tomographic microscopy (SRXTM) scans, we quantify coiling patterns in tests of eight specimens from six species of planktic foraminifera across the morphological spectrum. We use Raup-like parameters to seek an understanding of constructional constraints within the group, in light of comparisons with other groups of coiled organisms.

MATERIALS AND METHODS

Specimen preparation, scanning and reconstruction

Eight specimens from six species across the globigerines (spinose globular forms) and globorotaliids (non-spinose lenticular or conical forms) were chosen for imaging and analysis, representing most of the main morphologies in the planktic foraminifera: globose *Globigerina bulloides*, *Globigerinoides sacculifer*/*Globigerinoides trilobus* (morphotypes of this species complex with and without a sac-like final chamber respectively), and biologically-determined

Globigerinella siphonifera types I and II considered to be distinct cryptic species (Darling & Wade 2008; Huber et al. 1997); discoidal *Globorotalia menardii* and *Globorotalia tumida*; and conical *Globorotalia truncatulinoides* (Figure 2). For each species, a specimen that was well-preserved and representative of the adult morphology, having undergone full ontogenetic growth and exhibiting all of the species-specific diagnostic features, was selected for scanning.

The full details of the scanning and 3D model generation process are described in Caromel et al. (2016). Provenance for each specimen and scan parameters are presented in Table 1.

SRXTM was performed at the TOMCAT beamline tomography station at the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland. Slice data from the scans were imported into the 3D visualisation and reconstruction software Avizo 6.3 (Mercury Computer Systems Ltd., Chelmsford, MA, USA, www.tgs.com) for analysis. The internal cavity of each chamber (incorporating any residual sedimentary or organic infilling, to represent the true internal space) was manually isolated and assigned to separate elements to create each ontogenetic step as an independent 'material', or segmented unit. Each ontogenetic step of every foraminiferal species was classified into juvenile, neanic and adult stages following the classification by Brummer et al. (1987) (Caromel et al. 2016).

Morphometrics: Raupian framework and measurements

Raup (1966) described shells as successive positions of a generating curve rotation about a coiling axis. The generating curve represents a cross-sectional outline of the body whorl when the shell is sectioned in a plane passing through the coiling axis (Urdu 2015). Raup (1966) pointed out that the system is most easily applied when the generating curve approximates a simple geometric figure such as a circle or ellipse, and defined a series of parameters which allowed this three dimensional structure to be quantified: the shape of the generating curve, approximated as the outline of the growth edge of the shell (S), the expansion rate (W), the

position of the generating curve, i.e. the edge of the shell, in relation to the axis (D) and the rate of whorl translation (T).

Raup's system was generated for organisms which have a continuous generating curve, and hence we had to adapt the approach to foraminifers which grow by the addition of discrete chambers. Whilst a cylindrical coordinate system was preferred by Raup (1966), in which a point is expressed by its distance and angular increment from the coiling axis and plane, the benefit of digital visualisation is that the reconstructed specimen can be placed in a Cartesian coordinate system, where a point is defined by 3 positional coordinates (x, y, z), from which any number of linear measurements and angles can be computed. By enabling the visualisation of the interior and high power magnification, the 3D models also allow precise orientation of the specimens and thereby accurate measurements of the growth parameters. The origin of the coordinate system was taken as the centre of the proloculus, and the specimens were rotated such that the x-y plane bisected the proloculus through this centre and several lateral points along its equator. The z-axis therefore constituted the coiling axis along which growth proceeds, and which passes through the umbilicus (Figure 3). Homologous points or features used in deriving the measurements were identified. Points along the chamber surface could not be deemed homologous because of the incremental growth in foraminifera and because chamber shape can change throughout growth (see Caromel et al. (2016)). Chamber centroids were thus chosen as homologous reference points from which to calculate measurements as prescribed by Arnold (1983). The chamber centroids were determined as the region centres of the internal cavities and their coordinates extracted via a specific automatic function in the *Avizo* software. Note that the internal cavity is the realised shape taking into account overlap between chambers, and therefore the shape centroid is different to the centre of the spheres as used in theoretical accretion models. The dorso-ventral height (H) and radial length (L) of each chamber were also measured in side view.

The distance (r) of each centroid to the coiling axis in an x-y plane, was calculated as the resultant of the x and y components (coordinates from the origin, i.e. the proloculus centroid) (Figure 3):

$$r = \sqrt{x^2 + y^2}$$

The position of the chamber in relation to the coiling axis, D' , is equivalent to the relative distance of the chamber centroid to the coiling axis, and is given by the ratio of the distance of the inner edge of the chamber from the axis to the distance of the chamber centroid to the coiling axis (r), with the distance of the inner edge being calculated as the difference between r and the chamber radius (i.e. half the chamber length L):

$$D' = \frac{r - \frac{L}{2}}{r}$$

Note that this definition of D' allows for negative values, while [Raup's model only generates values between 0 and 1 for \$D\$ because it is restricted to cases where the inner margin of the generating curve is in contact with or moving away from the axis. In reality, the inner margin may overlap the coiling axis, generating a negative value for the distance between the inner margin and coiling axis](#) (e.g., Noshita et al. 2012). ~~the original definition of D in Raup (1966) only generates values between 0 and 1.~~

The rate of translation down the coiling axis, T' , was calculated as the ratio of the distance from the origin along the coiling axis (z-coordinate) to the distance from the coiling axis (r) and deviates from Raup's original definition of T by taking the entire test rather than only the last whorl into account. S' , a measure of chamber shape, was summarised by the ratio of maximum chamber height (H) to maximum chamber length (L).

Raup's fourth parameter, a measure of the whorl expansion rate, W , was measured based on

chamber volume and angle of rotation about the axis from the previous chamber (W'). However, a Principal Components Analysis using all four parameters showed variation along PC2 (representing 25.2% of the variance) being dominated by W' , reducing the signal from the other three parameters to variation along PC1 (representing 50.8% of the variance). As it was our goal to assess the overall morphological variation, W was therefore not included further in the study in contrast to other studies using Raup's coiling model. The loading of W' on a separate PC axis to the other coiling measures indicates that the latter three represent a separate signal and are not just a result of a change in expansion rate, justifying their study separate to W .

Disparity metrics and statistical analyses

Each ontogenetic step was treated as a separate entity, independent from others within its group. While these ontogenetic steps are clearly not independent in a statistical sense, this approach allowed us to quantify both within and amongst species morphological variance. Analyses of variance (ANOVA) followed by post-hoc pairwise comparisons by t-tests were carried out on the individual parameters to assess the significance of inter-species and inter-stage differences. Standard Bonferroni corrections to significance levels were applied to correct for multiple comparisons.

~~To assess changes of the parameters with growth, regressions of the log transformed coiling parameters against log transformed test length were performed for each one and the residuals plotted against log test length.~~

RESULTS

Although the ANOVAs indicate an overall statistically significant difference between species group means (D' $p=0.009$; T' $p=0.035$; S' $p=0.001$), a high degree of morphological overlap between all species (Figure 4) is reflected in the post-hoc pairwise comparisons on species D' ,

T' and S' means, which do not isolate any groups from each other across all three parameters (Table 2). The overlap between species is the result of the disparity amongst ontogenetic stages rather than adult species (Figure 5): juvenile stages across all species cluster together in morphospace, exhibiting low translation T' and high displacement D' and chamber aspect ratios S'. In general, neanic and adult stages show a shift to a greater T' and an increase in spread in D' and S'. Consequently, juvenile stages occupy a significantly different location in morphospace (ANOVAs on group means, D' p=0.002; T' p<0.001; S' p<0.001; t-tests on group means: juvenile-neanic D' p=0.156, T' p<0.001, S' p=0.044; juvenile-adult D' p=0.002, T' p<0.001, S' p<0.001; neanic-adult D' p=0.763, T' p=0.011, S' p=0.025). ~~The regression residuals of the coiling parameters against log-normalised size show an overall increase in variation with growth in the case of chamber aspect ratio, reflected in the larger variance of the residuals in the adult form (Figure 6). The linear relationships between the residuals and size suggest that there is still size-related, allometric variation in the shape descriptors (Figure 6).~~

To test whether the similarity in the juvenile stages is obscuring the differences between the morphospace of the adult species, the differences between species within each ontogenetic stage were tested. At each ontogenetic stage, species group means for parameters T' and S' are significantly different (ANOVAs; juvenile stages, D' p=0.458, T' p=0.073, S' p=0.004; neanic stages, D' p=0.004, T' p=0.004, S' p=0.025; adult stages, D' p=0.169, T' p<0.001, S' p<0.001), but t-test comparisons do not isolate groups, even at the adult stage, implying that a high degree of overlap between species remains within each ontogenetic stage. For all species except *Globorotalia truncatulinoides*, juvenile and adult stages are significantly different in at least T' (Table 3); in all but *Globigerinella siphonifera* type I and *Globigerina bulloides*, this difference is already established between the juvenile and neanic stages (Table 3).

DISCUSSION

Constraints on juvenile disparity

Juvenile planktic foraminifera display a limited diversity of shell coiling patterns, leading to a small occupation of morphospace indicating a high degree of similarity in early ontogeny with subsequent significant spreading of taxa as forms transition to the adult stage. A shift in morphospace to greater translation during the juvenile stage occurs in all species, although in the later stages it can be slowed or reversed in species such as *Globigerinella siphonifera* types I and II and *Globorotalia truncatulinoides*. These differences in morphospace occupation point towards pervasive constraints, both in early ontogeny and in developmental patterns across all morphogroups within the planktic foraminifera. Gerber et al. (2007) documented a similar trend of increased disparity from juvenile to adult stages in postembryonic ammonoids; as they noted, this is unexpected as flexibility is usually thought to be higher in early ontogeny, with counterbalancing between different ontogenetic novelties ultimately reducing adult disparity (Gerber 2011; Zelditch et al. 2003). Our results would suggest that development in planktic foraminifera is constrained to limit the amount of possible novelties in early ontogeny, thereby reducing the potential for compensation between them (Zelditch et al., 2003) and potentially allowing a greater diversity of adult forms.

The lower T' in juvenile planktic foraminifera results in a greater overlap between chambers, which decreases the living space, but also decreases the total amount of material necessary to enclose the organism by using part of the surface of preceding whorls (Raup, 1967; Noshita et al., 2012). In ammonoids and gastropods, coiling character constraints have been placed in light of constructional efficiency and trade-offs with metabolic requirements (Noshita et al. 2012; Raup 1961, 1966, 1967; Saunders & Shapiro 1986; Schindel 1990; Stone 1999; Ubukata et al. 2008). The amount of overlap between successive whorls dictates the compromise necessary between soft body expansion and shell construction (Noshita et al. 2012; Raup 1961, 1966, 1967; Stone 1999; Ubukata et al. 2008). In any organism, the amount of material saved, i.e. the reduced need for additional calcification, needs to be weighed against the potentially

smaller living space and its negative impact on cell volume, as calcification effort, a measure of the amount of material required relative to the organism volume available to produce it, will increase with very high or very low overlap. Greater overlap in the juvenile foraminifer is counterintuitive as the organism should seek to minimise the calcification effort by minimising the calcite surface to cytoplasm volume ratio. Surface area-to-volume ratios are in fact higher in the juvenile stages (see Caromel et al. (2016)) which seems costly when considering that foraminifers grow by enclosing the whole test in a new layer of calcite with the addition of a new chamber (Bé & Lott 1964). A large proportion of the energy acquired by the organism is thus likely to be devoted to calcification, with little left for volumetric expansion of the cytoplasm, potentially making these early stages as constructionally efficient as possible given the mode of calcification.

Across foraminiferal species, transition from the juvenile to the neanic stage predominantly occurs around 100µm (Figure 67) regardless of the number of chambers. The most rapid and efficient way to attain this size is by growing predominantly along a single plane, achieved by coupling a low translation rate with greater displacement (Norris 1992). We therefore suggest that the mode of accretion in juvenile planktic foraminifera is an attempt to reach this threshold size as rapidly as possible. Changes in growth curves, which mark the transition between ontogenetic stages (Caromel et al. 2016), may hence be partly a reflection of coiling patterns. Similarly, reaching this threshold size may allow juvenile foraminifers to increase their foraging potential, change their food source, evade predators, or induce a shift in metabolic processes and requirements.

Adult disparity

The high degree of overlap between species across different morphogroups, when considering all ontogenetic stages, suggests that planktic foraminiferal coiling patterns are highly

conservative. This observation is confirmed when comparing with the coiling patterns of other groups. Even with a cautious interpretation given the differences in the parameters used to describe the morphospace due to the differences in methodologies between Raup and our approach, foraminifera occupy a greater region than typical planispiral ammonoids, but a more restricted area than gastropods ([Figure 7; Noshita et al. 2012; Raup 1967](#))(~~[Figure 8; Noshita et al. 2012; Raup 1967](#)~~). Noshita et al. (2012) found that the more extreme edges of the gastropod space are more sparsely populated, with the average gastropod shell having a higher spire at $T=2$ and $D=0$. An increase in translation rate while keeping other parameters constant leads to a high trochospire and tight coiling around the axis as chamber size increases; increasing the distance to the coiling axis on its own, on the other hand, leads to an increasingly flatter shape with looser coils. In both the foraminiferal and gastropod morphospace, the low T - low D region is unfilled ([Figure 78](#)), implying that a shift in D to more negative values could not occur without a concurrent shift in T . If growth is constrained to low translation rates in the early ontogeny of foraminifera, it limits the amount by which translation can increase throughout one individual's lifetime, inevitably constricting the foraminiferal occupation of morphospace compared to gastropods ([Figure 78](#)).

Accretion site and aperture location

The combination of a low translation rate and high displacement in juvenile foraminifers not only influences the overall geometry but also leads to a wider umbilicus. In gastropods, low-spired forms with higher displacement and lower translation appear to have a more flexible system of internal trade-offs and morphogenetic pathways upon which to call to maintain overall shell shape than high-spired forms, by varying the shape, inclination and angle of the aperture, which in turn dictates the shape of the accreted shell (Schindel 1990). As the aperture is located on the umbilical side in foraminiferal tests, it is possible that the retention of a wider umbilicus similarly allows greater flexibility in adjusting aperture position, and

therefore new chamber position and shape, to regulate growth. Changes in the coiling pattern and growth curves marking the transition of ontogenetic stages are generally accompanied by the migration of the aperture along the chamber margin (Caromel et al. 2016). In early chambers, the aperture is always extraumbilical, leading to accretion in a low trochospire. In contrast, in adults the aperture either migrates to a more umbilical position, causing accretion to occur in a tighter coil and increase T' and closing the umbilicus, or a subequatorial or marginal position, facilitating accretion with low T' . As the chamber shapes characteristic of each species or morphogroup are acquired during the neanic stage retention of a wider umbilicus in the juvenile could allow for more flexibility in chamber shape in the later stages of development, accommodating more complex elongate or triangular chambers.

CONCLUSIONS

Planktic foraminiferal have a conservative morphology, with large overlap between morphogroups but differentiation between ontogenetic stages. Disparity in coiling increases from the juvenile to the adult stages, demonstrating a constraint in early ontogeny which is subsequently relaxed in later stages. Low rates of translation along the coiling axis and higher distance from the axis in juveniles result in morphological overlap between successive stages. This restricted morphology may represent an attempt to minimise constructional costs and to maximise metabolic efficiency while at the same time facilitating growth to larger sizes rapidly by concentrating growth in one direction. At the neanic stage in all species, an increase in translation rates implies a pervasive constraint in developmental patterns. A migration of the location of the aperture towards umbilical and marginal positions may be modulated by, or potentially cause, a displacement of the site of new chamber addition, allowing new chamber shapes. Planktic foraminifera exploit a more limited amount of coiling options than gastropods; whether this is because of the discrete nature of growth combined with early ontogenetic constraints, or as a functional constraint due to their surface water environment,

remains an open question. Developmental mechanisms invoked in speciation, such as heterochrony, must therefore operate within this constructional framework, limiting the potential disparity within the group.

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430 **TABLES**

431 Table 1. Age, provenance and Synchrotron Radiation X-Ray Tomographic Microscopy specifications for each of the specimens scanned.

Species	Age and Provenance	X-Ray beam energy (keV)	X-Ray microscope magnification	Binning of pixels	Isotropic voxel size (µm)	Nº of slices
<i>Globigerina bulloides</i>	Holocene, sediment sample, west coast of South Africa, Walvis Ridge Transect (ODP Leg 208, site 1264A-1H-1, 0-2cm)	9.87	x20	x1	0.35	929
<i>Globigerinoides sacculifer</i> , 'sacculifer' morphotype	Miocene-Pliocene Boundary, sediment sample, Caribbean (ODP Leg 165, site 1000A-20H-3, 147-149cm)	9.87	x20	x2	0.7	577
<i>Globigerinoides sacculifer</i> , 'trilobus' morphotype	Holocene, sediment sample, west coast of South Africa, Walvis Ridge Transect (ODP Leg 208, site 1264A-1H-1, 0-2cm)	17.5	x10	x2	1.4	427
<i>Globigerinella siphonifera</i> types I and II	Recent, surface water sample, SCUBA collected by Brian Huber and Jelle Bijma off coast of Curaçao	15	x20	x1	0.35	1259 1245

<i>Globorotalia menardii</i>	Holocene, sediment sample, west coast of South Africa, Walvis Ridge Transect (ODP Leg 208, site 1264A-1H-1, 0-2cm)	17.5	x10	x2	1.4	200
<i>Globorotalia truncatulinoides</i>	Holocene, sediment sample, north-west coast of Africa (RV Meteor cruise, core sample GeoB1802-10, 0-1cm)	15	x20	x1	0.35	1541
<i>Globorotalia tumida</i>	Pliocene, sediment sample, west of Panama Isthmus, Southeast Pacific Transect (ODP Leg 202, site 1241A-8H-2, 10- 12cm)	9.87	x20	x2	0.7	747

432 Table 2. Probabilities (p-values) for pairwise comparisons of group means between species by t-tests following ANOVA. Significance following Bonferroni

433 correction for multiple comparisons indicated in bold.

	<i>G. bulloides</i>			<i>G. sacculifer</i> 'sacculifer'			<i>G. sacculifer</i> 'trilobus'			<i>G. siphonifera</i> typel			<i>G. siphonifera</i> typell			<i>G. menardii</i>			<i>G. trun-</i>	
	D'	T'	S'	D'	T'	S'	D'	T'	S'	D'	T'	S'	D'	T'	S'	D'	T'	S'	D'	
<i>G. sacculifer</i> 'sacculifer'	1.000	1.000	1.000	-	-	-														
<i>G. sacculifer</i> 'trilobus'	1.000	0.384	0.999	1.000	0.693	0.891	-	-	-											
<i>G. siphonifera</i> typel	0.103	0.107	0.889	0.652	0.164	0.585	0.026	1.000	0.066	-	-	-								
<i>G. siphonifera</i> typell	0.077	0.171	0.004	0.562	0.292	0.001	0.015	1.000	0.022	1.000	1.000	<0.001	-	-	-					
<i>G. menardii</i>	0.209	0.541	0.459	1.000	1.000	0.386	0.064	1.000	0.124	1.000	0.248	1.000	1.000	0.693	0.003	-	-	-		
<i>G. trunca-</i> <i>tulinoides</i>	0.038	0.209	0.044	0.284	0.359	0.027	0.009	1.000	0.226	1.000	1.000	0.001	1.000	1.000	1.000	0.710	0.862	0.010	-	
<i>G. tumida</i>	0.120	1.000	1.000	0.646	1.000	1.000	0.039	0.260	1.000	1.000	0.004	0.725	1.000	0.032	0.255	1.000	0.239	0.357	1.000	

434 Table 3. Probabilities (p-values) for pairwise comparisons of group means between ontogenetic
 435 stages within species by t-tests following ANOVA. Significance following Bonferroni correction for
 436 multiple comparisons indicated in bold.

	<i>G. bulloides</i>			<i>G. sacculifer</i> 'sacculifer'			<i>G. sacculifer</i> 'trilobus'			<i>G. siphonifera</i> type I			<i>G. siphonifera</i> type II	
	D'	T'	S'	D'	T'	S'	D'	T'	S'	D'	T'	S'	D'	T'
Juvenile-Neanic	0.568	0.088	0.082	0.012	0.018	0.629	1.000	0.003	1.000	1.000	0.071	0.062	1.000	0.03
Neanic-Adult	1.000	0.207	0.307	1.000	0.591	1.000	1.000	0.008	1.000	0.975	0.322	0.415	1.000	1.000
Juvenile-Adult	0.002	0.001	0.014	0.473	0.001	0.873	0.291	<0.001	1.000	1.000	0.004	0.754	1.000	0.02

437

	<i>G. menardii</i>			<i>G. truncatulinoides</i>			<i>G. tumida</i>		
	D'	T'	S'	D'	T'	S'			
Juvenile-Neanic	1.000	0.009	0.331	1.000	0.047	0.639	0.190	0.008	1.000
Neanic-Adult	0.789	1.000	0.010	1.000	0.935	0.079	0.027	0.003	0.011
Juvenile-Adult	1.000	0.010	<0.001	0.880	0.057	1.000	0.285	<0.001	0.002

FIGURE LEGENDS

Figure 1. Spindle diagram of species diversity of planktic foraminifera through geologic time, and representative homeomorphs from each of the three major radiations (redrawn, with permission, from Norris (1991a)).

Figure 2. Spiral and side views of the selected specimens, with each colour representing a separate ontogenetic step. Top row from left: *Globigerina bulloides*; *Globigerinoides sacculifer*, 'sacculifer' morphotype; *Globigerinoides sacculifer*, 'trilobus' morphotype. Middle row from left: *Globigerinella siphonifera* types I and II. Bottom row from left: *Globorotalia menardii*; *Globorotalia truncatulinoides*; *Globorotalia tumida*. White scale bars represent 100µm.

Figure 3. Schematic representation of a specimen of *Globigerina bulloides* illustrating the coiling parameters measured. The relative distance of the chamber centroid to the coiling axis, D' , normalises the distance of the inner edge of the chamber to the coiling axis ($(r-L/2)$) with the distance of the chamber centroid to the coiling axis (r). The rate of translation down the coiling axis, T' , was calculated as the ratio between the distance from the origin along the coiling axis (z) and the distance from the coiling axis (r). Chamber shape, S' , was calculated as the ratio of chamber height (H) to chamber length (L). A) Face view, with the coiling axis extending orthogonally to the page through the proloculus centroid; B) Side view.

Figure 4. Displacement rate from the coiling axis, D' , chamber aspect ratio, S' , and translation rate along the coiling axis, T' , of the analysed foraminiferal species. Each point represents an ontogenetic step.

Figure 5. Displacement rate from the coiling axis, D' , chamber aspect ratio, S' , and translation rate along the coiling axis, T' , of the ontogenetic stages for all analysed foraminiferal species. Each point represents an ontogenetic step.

Figure 6. Residuals from regressions of the log-transformed coiling parameters against log-transformed test length.

Figure 7. Translation rate along the coiling axis, T' , versus test length of selected foraminiferal species. Each point represents an ontogenetic step.

Figure 8. A) Morphospace occupation of foraminifera in the T' - D' plane; B) Morphospace occupation in the Raupian T-D plane for planispiral ammonoids and gastropods. Ammonoid zone defined for planispiral ammonoids, excluding heteromorphic, helicoid and orthoconic forms, after Raup (1967). Gastropod data from Noshita et al. (2012).

NEOGENE

PALEOGENE

CRETACEOUS

A)

B) x-y plane

SPECIES

- *Globigerina bulloides*
- △ *Globigerinoides trilobus*
- + *Globigerinoides sacculifer*
- △ *Globigerinella siphonifera* type I
- ▽ *Globigerinella siphonifera* type II
- × *Globorotalia menardii*
- ▽ *Globorotalia truncatulinoides*
- *Globorotalia tumida*

STAGE

- adult
- × juvenile
- + neanic

A)

B)