

Ontogenetic and evolutionary patterns of shape differentiation during the initial diversification of Paleocene acarininids (planktonic foraminifera)

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Abstract.—Previous studies have established a close relationship between the evolutionary origin of new clades of planktonic foraminifera and heterochrony. Studies of the Paleogene radiation of the genus *Morozovella* revealed, for example, a temporal pattern of variation consistent with pedomorphosis. Our study focused on the late Paleocene species of *Acarinina*, sister group of *Morozovella*. Shape variations related to evolution and ontogeny are appraised through a morphometric method based on outline analysis using the elliptic Fourier transform. Patterns of developmental and evolutionary changes are studied and compared within each species (*Acarinina nitida*, *A. subsphaerica*, and *A. mckannai*). As no congruence is found, we suggest that the evolutionary change observed within these species is not related to a heterochronic process. We also test for similarity of both evolutionary and ontogenetic changes among species. Although we observe no significant correlation between temporal patterns of shape change among species, the tight congruence of ontogenetic trajectories suggests that the developmental constraints affecting these trajectories have been preserved in spite of the evolutionary diversification of acarininids. Heterochrony is not clearly involved in the early Paleogene diversification of acarininids and therefore may not be as common as previously claimed. The role of developmental constraints in monitoring morphological evolution therefore needs to be reassessed.

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Accepted: 22 April 2002

Introduction

Following de Beer's (1958) modern reevaluation of the term "heterochrony," Gould (1977) and McNamara (1986) defined heterochrony as representing the changes in timing and rates of the development of morphological features that occur during ontogeny. Gould (1977) presented heterochrony as the chief mechanism of evolutionary change (but see Raff 1996 for discussion), and numerous studies over the past two decades have found evidence for heterochronic processes in many fossil groups (e.g., Alberch et al. 1979; McNamara 1982, 1986; McKinney and McNamara 1991; Crônier et al. 1998; Jones and Gould 1999). Some of these studies promoted the view that heterochrony may be involved in most major evolutionary novelties resulting in the appearance of new taxa (e.g., McKinney and McNamara 1991). In recent years, developmental biologists questioned this as-

sumption (Raff and Wray 1989; Raff 1996; Hall 1998; Klingenberg 1998) and emphasized that little attention had been paid to the developmental mechanisms underlying this evolutionary process.

In paleontology, studying inferred fossil developmental series may allow us to obtain both descriptive and quantitative data that can be used to visualize morphological changes related to the ontogeny and the history of the group under consideration. Under the hypothesis of heterochronic evolution, a tight congruence of ontogenetic changes with phylogenetic ones is predicted, "producing parallelism between ontogeny and phylogeny" (Zelditch et al. 2000). Identification of phenotypic features contributing to the variation among ontogenetic stages and those involved in phylogenetic changes should provide relevant clues to assess the occurrence of such an evolutionary process.

Planktonic foraminifera constitute a particularly relevant group to test the occurrence of heterochronic processes. First, they present the advantage of their exceptionally complete and detailed stratigraphic record. Second, because the ontogeny of metazoan species involves modularity and mosaic development (e.g., Wagner 1996), ontogenetic trajectories of integrated structures result from complex temporal and spatial developmental processes (Reilly et al. 1997; O'Keefe et al. 1999). As compared to metazoans, the development of these unicellular organisms is likely less affected by dissociated heterochrony, which is considered a common phenomenon in metazoans (McNamara 1988; Reilly et al. 1997). Third, test (shell) size in planktonic foraminifera can be considered a relevant proxy for ontogenetic development. The study of heterochrony in fossils is impeded by the fact that the ontogenetic age of individuals at the time of death is not accurately known (McKinney 1999). Even if we cannot determine developmental times for extinct ontogenies (Raff 1996), several studies have shown that size, although imperfect, is a suitable indicator of ontogenetic stage in species of planktonic foraminifera (Brummer et al. 1987; Hemleben et al. 1989; Wei et al. 1992).

Although many scientists have worked on the ontogeny of modern and extinct planktonic foraminifera (Shackleton et al. 1985; Brummer et al. 1987; Hemleben et al. 1989; Wei et al. 1992; D'Hondt et al. 1994; Norris 1996), the occurrence of heterochronic processes has only rarely been investigated in this group. Assuming that test size approximates age, Wei (1994) has shown that the morphological variation and diversification trends in the Pliocene-Pleistocene *Globoconella* clade occurred via several heterochronic modes. Kelly et al. (1996) examined the origin of *Morozovella*, one of the early Paleogene genera of planktonic foraminifera, and identified a complex pattern of heterochronic evolution through the *Praemurica inconstans*/*Pr. uncinata*/*Morozovella angulata* sequence. Kelly et al. interpreted the change in allometric patterns in *Pr. uncinata* and *M. angulata* lineages as reflecting paedomorphosis (i.e., retention of the juvenile features of the ancestor in the adult stage of the

descendant) even though they recognized that the evolution observed did not readily conform to any single heterochronic model. Isotopic analysis suggested, however, that the early morozovellid radiation could be related to the coevolution of photosymbiosis and life history strategies.

This evolutionary framework is partly shared by the early Paleogene planktonic foraminiferal genus *Acarinina*, sister group of *Morozovella* (Norris 1996; Berggren and Norris 1997). Recent studies (Norris 1996; Quillévére et al. 2001) have indicated that the acquisition of photosymbiosis was synchronous with the first major diversification of both *Morozovella* and *Acarinina* during the early Paleogene. These studies showed that the acquisition of algal-photosymbionts for respiration did not trigger an immediate species-level radiation in the acarininids, whereas it dramatically and rapidly boosted the diversification of morozovellids. To appraise the extent of heterochronic patterns in the evolution of *Acarinina*, we have chosen to analyze the relationships between the morphological variations related to the evolutionary trajectories and those related to the ontogenetic ones. Acarininids and morozovellids have been shown to originate from a common ancestor (Olsson 1970; Norris 1996; Berggren and Norris 1997). They also had similar depth ecologies and trophic strategies, as they both harbored algal-photosymbionts (Pearson et al. 1993; D'Hondt et al. 1994; Norris 1996; Quillévére et al. 2001).

Phylogenetic derivation of early acarininids has long remained an enigma. Berggren and Norris (1997) used cladistic analysis to suggest that the group may have evolved by differentiation of a morozovellid morphology through heterochronic transformation of juvenile representatives of the genus *Praemurica*, clearly identified as the ancestor of the morozovellids (Kelly et al. 1996; Norris 1996; Berggren and Norris 1997). Whereas most of the major evolutionary patterns of the Paleogene planktonic foraminifera became established shortly after the Cretaceous/Paleogene extinction (Berggren and Norris 1997), the acarininids were shown to have appeared only in the middle Paleocene (Selandian), with the evolution of the common ancestor

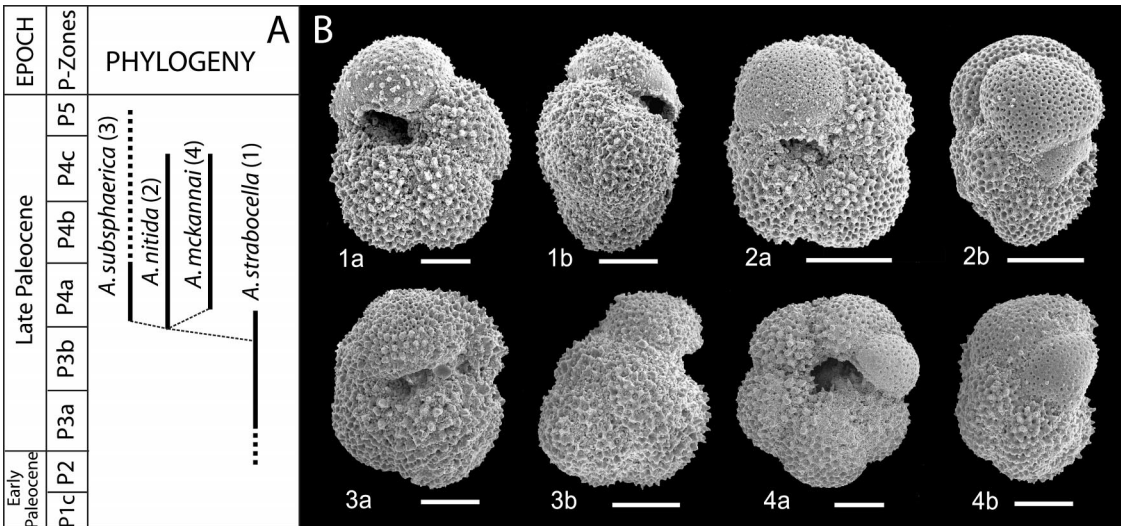


FIGURE 1. A, Phylogenetic reconstruction of Paleocene acarininids studied in this paper (dashed line represents range extension at southern high latitude sites). After Berggren and Norris (1997), Olsson et al. (1999), and Quillévéré et al. (2000). B, Scanning electron photomicrographs of representative Paleocene acarininids from ODP Hole 761B. 1: umbilical (a) and edge (b) views of *A. strabocella* from 761B-18X-2: 10–12 cm. 2: umbilical (a) and edge (b) views of *A. nitida* from 761B-18X-2: 10–12 cm. 3: umbilical (a) and edge (b) views of *A. subsphaerica* from respectively 761B-17X-4, 10–12 cm and 761B-17X-3: 10–12 cm. 4: umbilical (a) and edge (b) views of *A. mckannai* from 761B-17X-1: 10–12 cm. Scale bar, 100 μm .

Acarinina strabocella, considered to be the oldest and most primitive acarininid. Quillévéré et al. (2000) suggested that the genus originated in the high latitudes during the early middle Paleocene (early Selandian) and that the initial diversification of this group (small-sized *Acarinina nitida*, *A. subsphaerica*, and *A. mckannai*), which corresponds to the P3b/P4a biochronal boundary (~59.2 Ma), resulted from a migration event from high to low (sub)tropical latitudes.

The phylogenetic history and patterns of morphological evolution in Paleocene acarininids have been recently established (Pearson 1993; Norris 1996; Berggren and Norris 1997; Olsson et al. 1999; Quillévéré et al. 2000) (Fig. 1A). The group was initially characterized by small and globular taxa with a muricate funnel-pore wall texture (e.g., Berggren and Norris 1997). Subsequently, during the late Paleocene, these taxa acquired a peculiar morphology by developing robust muricae on the umbilical surface. Quillévéré et al. (2000) suggested that two distinctive lineages differentiated during the early late Paleocene (early Thanetian) from the narrow angulo-elongated ancestor *A. strabocella* (Fig. 1B). The first line-

age contained the very divergent *A. subsphaerica* morphology, which added chambers down the coiling axis and did not produce any late Paleocene descendants. The second lineage contained *A. nitida*, which became more involute and axially compressed on the umbilical side, and its first descendant, *A. mckannai*, which developed evolute coiling and a moderately wide umbilicus. The late Paleocene (Thanetian) evolution in all these taxa was accompanied by a size increase (Berggren and Norris 1997; Quillévéré et al. 2001).

To detect any possible heterochronic signal in the evolution of the Paleocene acarininids, we used a geometric morphometric approach that allowed us to quantify and partition the whole morphological variation into several components, e.g., those related to ontogeny and to evolution. Geometric morphometrics has long been shown to be a powerful tool for describing and analyzing shape changes, through both time and space (e.g., Rohlf and Marcus 1993; Reyment and Jöreskog 1993). Here, we used it to describe the relationship between ontogenetic and evolutionary shape variations. To obtain a global ordination and a comparison of such shape changes among

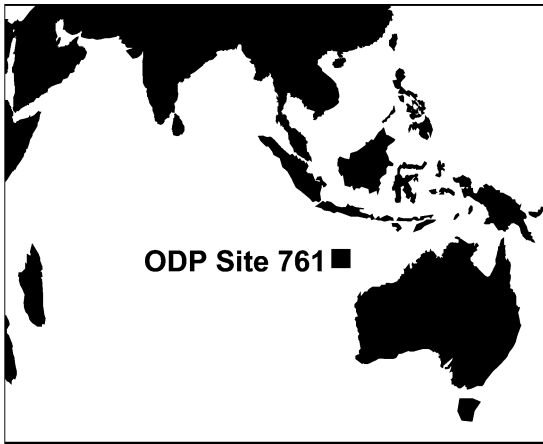


FIGURE 2. Location map of ODP Site 761.

acarininids, we studied several species (*A. nitida*, *A. subsphaerica*, and *A. mckannai*) independently. Obviously, we have focused on the change in allometry (or ontogenetic trajectory) along each lineage, as well as on the congruence between the ontogenetic and evolutionary shape trajectories within each lineage.

Material

Four samples were collected in deep-sea sediments recovered from Ocean Drilling Program (ODP) Hole 761B (16°44.23'S, 115°32.10'E; 2466 m water depth) on the Wombat Plateau in the eastern Indian Ocean (Fig. 2). These samples from the upper Paleocene (Thanetian) cores 17X and 18X contained exceptionally well preserved representatives of *Acarinina strabocella* (Loeblich and Tappan), *A. nitida* (Martin), *A. subsphaerica* (Subbotina), and *A. mckannai* (White) (Fig. 1B). These species were all involved in the initial diversification of the acarininids.

Age determinations of the samples are based on a temporal interpretation of the Paleocene section recovered at ODP Hole 761B according to the procedure introduced by Aubry (1995). This temporal interpretation was based on an integrated nannofossil and planktonic foraminifer biostratigraphy (Siesser and Bralower 1992; Quillévére et al. 1998), and on magnetostratigraphy (Galbrun 1992), calibrated to the Cenozoic magnetobiochronology of Berggren et al. (2000). The biostratigraphic setting of the section and stratigraphic ranges

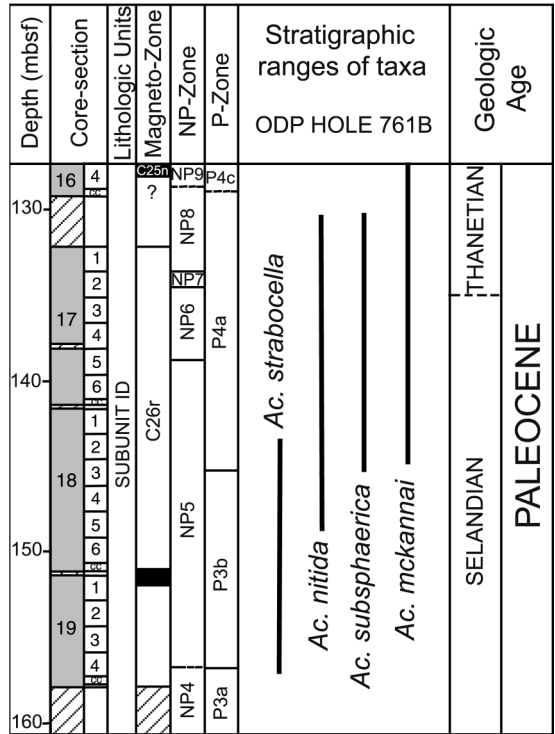


FIGURE 3. Biostratigraphic setting of the section recovered from ODP Hole 761B and ranges of the taxa studied in this paper.

of the species studied in this paper are shown Figure 3.

To reconstitute developmental processes within each species, we sorted individuals into four size classes. Following an ultrasonic cleaning in distilled water, samples were sifted through sieves $1/4$ -phi with mesh sizes of 63, 125, 150, and 250 μm . One additional mesh of 212 μm was used for *A. subsphaerica*. For all species, each size class from each sample consists of 20 right-coiling individuals that one of us (F.Q.) randomly picked without regard for morphologic variation. Altogether, we analyzed 1000 individuals representing 320 specimens of *A. nitida*, 360 of *A. subsphaerica*, 240 of *A. mckannai*, and 80 of *A. strabocella*. *Acarinina strabocella* was recovered only from the oldest stratigraphic horizon considered in this study. At 63 μm , it may be difficult to distinguish between juveniles of closely related sister species of planktonic foraminifera. Juvenile morphotypes of *A. nitida*, like adults, show a compact subcircular to subquadrate test typically with four rounded, radially com-

TABLE 1. Composition, sample size, and age estimates of the acarininids studied in this paper.

Samples	Depth (mbsf)	Age (Ma)	<i>Ac. strabocella</i>	<i>Ac. nitida</i>	<i>Ac.</i>	
					<i>subsphaerica</i>	<i>Ac. mckannai</i>
761B-18X-2: 10–12 cm	143.31	59	80	80	60	
761B-17X-6: 10–12 cm	139.81	58.7		80	100	80
761B-17X-3: 10–12 cm	135.31	58.4		80	100	80
761B-17X-1: 10–12 cm	132.31	57.2		80	100	80

pressed, and axially elongate chambers in the last whorl. Juvenile morphotypes of *A. subsphaerica* show an essentially spherical five-chambered test with highly conical spiral side. The differentiation between juvenile morphotypes in both these species was not a critical issue. The differentiation between juveniles in *A. strabocella* and *A. mckannai* is less obvious. In the last whorl, both taxa show a nearly circular test with five to six (rarely seven for *A. mckannai*) chambers and lobulate outline. In our study, the juveniles morphotypes of *A. strabocella* and *A. mckannai* were, however, clearly related to their adult morphotypes, because the specimens we picked originated from stratigraphic horizons where these species did not co-occur. A summary of the composition, age, sample size, and corresponding reference for each stratigraphic horizon is provided in Table 1.

Methods

Shape Descriptors.—Shape variation among acarininids was appraised by using test outlines in two dimensions. So they could be compared in a relevant way, the outlines considered are those that correspond to the edge view of the test, after all individuals were mounted on glass cover slips with double-sided tape and oriented similarly. Outlines were digitized under the microscope with an optical image analyzer (OPTIMAS v. 4.0). Each outline was semiautomatically traced from a re-locatable starting point, which, in this case, was the acute margin of the antepenultimate chamber. From this origin, the x- and y-coordinates of 100 equally spaced points were extracted for each individual outline.

Any outline can be described in a simple way using a Fourier transform method (Foote 1989). Fourier analysis is a technique for generating a set of shape-representative variables

that are suitable for use in statistical comparisons (Crampton 1995). It has been applied to the study of numerous paleontologic groups including planktonic foraminifera (Healy-Williams and Williams 1981; Healy-Williams et al. 1985; Quillévéré et al. 2000; de Vargas et al. 2001). To appraise shape changes alone, we standardized the size of the specimens by dividing the initial coordinates of the outlines by the area. An elliptic Fourier transform (Kuhl and Giardina 1982) was then performed on the data points with the program NTSYS-PC (Rohlf 1993). The outline of each specimen is thus expressed as a sum of trigonometric functions of decreasing wave-length, the harmonics. The details of the Fourier procedure as performed in this study are described by Renaud et al. (1996) and Crônier et al. (1998).

One of the characteristics of the Fourier harmonics is that much of the shape information can be summarized by the first few harmonics. The higher the order of the harmonic, the more details of the outline it describes. The content of morphological information added by each harmonic has been estimated by using the cumulative power (Crampton 1995) as a function of the harmonic order. For each acarininid data set, the first eight harmonics reached 99.995% of the average total power. Additional harmonics, accounting for less than 0.005% of the total power, would only be seen as adding high-frequency noise. For example, a specimen-dependent (not species-dependent) character such as the pustules of the muricate texture ranks first from the ninth harmonic. Thus, the Fourier coefficients from the ninth harmonic and higher were not considered for further analyses.

In addition, as pointed out by Rohlf and Archie (1984) and Renaud et al. (1996), (1) the zeroth harmonic represents the starting point of the outlines and is not relevant to the shape

analysis, and (2) the first harmonic, which fits the general contour to a single ellipse, is extremely sensitive to measurement error. The Fourier coefficients corresponding to these harmonics were therefore deleted.

Shape Analyses.—Each harmonic is characterized by four Fourier coefficients. A set of 28 coefficients was then obtained for each individual outline (seven harmonics). We first appraised the significance of the global shape variation among ontogenetic stages, represented by size classes, and among stratigraphic horizons, simultaneously. This was done by applying a multivariate analysis of variance (MANOVA) to (1) the coefficient data set corresponding to the four species (*Acarinina strabocella*, *A. nitida*, *A. subsphaerica*, and *A. mckannai*) considered together and to (2) the coefficient data set of each species. In the latter, “sample” was treated as a single effect, a sample corresponding to a given ontogenetic stage at a given stratigraphic horizon. The significance of the differences in means among samples was tested using Wilk’s Lambda. In association with each of the MANOVAs, a Canonical Variate Analysis (CVA) was performed in order to depict the distribution of sample mean shapes in canonical space (Marcus 1993). The reconstruction of the outline corresponding to any set of Fourier coefficients was obtained by using the inverse Fourier transform (Rohlf and Archie 1984). This procedure permits visualization of morphological changes between the mean shapes of all samples within species.

In order to focus on the significance of morphological change among ontogenetic stages and among stratigraphic levels, respectively, two-way fixed model MANOVAs involving “ontogenetic stage” and “stratigraphic horizon” and their interaction were applied to the species found at more than one stratigraphic horizon. Test of the significance of the interaction effect would indicate whether the pattern of shape change due to the ontogenetic process was conserved or modified along with the evolution of the species. The application of these MANOVAs was standardized by considering, for the three species studied (*A. nitida*, *A. subsphaerica*, and *A. mckannai*), the three chronological stages (58.7, 58.4, and 57.2 Ma)

in which were observed the four or five (*A. subsphaerica*) ontogenetic stages defined for all species (63, 125, 150, 212, and 250 μm meshes).

Congruence between Ontogenetic and Evolutionary Patterns.—We explicitly hypothesized that heterochrony should be evidenced by a significant correlation among ontogenetic variation (i.e., combination of the characters that are modified among ontogenetic stages) and evolutionary change (i.e., combination of the characters that vary among samples from different stratigraphic horizons). The evolutionary trajectory, which corresponds to the morphological changes associated with the evolution of a given species through time, is expressed by its shape modifications across stratigraphic levels. Ontogenetic trajectories were defined as the shape change occurring through the different developmental stages identified as size classes.

To appraise the congruence between these trajectories and to assert the graphical observations that may have been provided by the CVA, we decomposed the total shape variance into ontogenetic and evolutionary components. This required the computation of variance-covariance (VCV) matrices related to both processes and the appraisal of the dependence between those matrices (see below). However, the absolute range and the variance of emerging Fourier coefficients decrease with the rank of the harmonics. Moreover, because each harmonic is computed from the previous one, Fourier coefficients are not independent from each other. Such properties confer on any VCV matrices computed from Fourier coefficients a homogeneous structure that would lead to spurious correlation among these matrices. The use of the correlation matrices prevents such an effect but would then confer a similar weight on any coefficient regardless of the amplitude of the morphological variation they actually express and the significance of this variation. In other words, noise would have been as strong as biologically significant signals.

This bias was avoided by applying a principal components analysis (PCA) to all the coefficients data-set. From the 28 emerging PCs, statistically independent from each other, only

the first few contained relevant information on shape variation and were retained for further analyses. Because the eigenvalues obtained decreased rapidly, we retained the PCs that each accounted for more than 5% of the total variation. This corresponded to the first eight PCs, which together accounted for more than 75% of the total variation. The shape variance supported by these PCs was further decomposed into components directly related to ontogeny and geologic age.

VCV matrices associated respectively with the ontogenetic and evolutionary shape changes were computed for each of the three species found in several stratigraphic horizons, *Acarinina nitida*, *A. subsphaerica*, and *A. mckannai*. For the three species, the correlation between VCV matrices associated with both processes was then computed and tested by using a Mantel *t*-test. One thousand permutations were run. A significant correlation would demonstrate congruence between both patterns of shape variation and thus dependence between morphological evolution and ontogenetic process. This would then be interpreted as a signal of heterochronic evolutionary pattern.

In addition to the intraspecific analysis, we tested for the congruence among species of the patterns of morphologic changes related to each of the effects (ontogenetic and evolutionary). In other words, the procedure used for the correlation test was applied to all species and to the VCV matrices associated with the same effect. This was done in order to compare both evolutionary and ontogenetic patterns of shape changes among species involved in the initial diversification of acarininids. Inasmuch as the VCV matrix related to the ontogenetic change in *A. strabocella* was also computed, the relationships between ontogenetic patterns of *A. nitida*, *A. subsphaerica*, and *A. mckannai* and that of their ancestor were therefore investigated.

Results





Morphological Differentiation among Species.—The MANOVA performed on the 28 Fourier coefficients of the four acarininid species considered together provides a highly significant differentiation among samples (Wilk's Lambda = 0.80, $df_1 = 100$, $df_2 = 6749.2$, $p < 0.001$)

indicating an important variation among species, ontogenetic stages, and stratigraphic horizons. From the projection of the sample means on the plane formed by the first two canonical variate axes (70.2% of the total variance), phylogenetic and ontogenetic trajectories may be viewed as combinations of the first two canonical axes (Fig. 4). Shape changes inferred from the reconstructed mean outlines correspond to a narrow angulo-elongated shape in edge view and more umbilically inflated chambers for juvenile forms of each species (higher scores), and a more concave shape, associated with relatively more involute coiling, for adults (lower scores). The morphological pattern associated with the evolution and the ontogeny of *Acarinina subsphaerica* could partly be interpreted as peramorphosis (Alberch et al. 1979), the adults of the early representatives (59.0 Ma) resembling the juveniles of its first descendant (58.7 Ma). However, such a pattern is not retrieved either in the later representatives of *A. subsphaerica* or in the other species (see Fig. 4). The graphical representation of morphological differentiation among acarininids does not show any clear relationship between ontogeny and phylogenetic evolution consistent with an unequivocal heterochronic pattern. Incidentally, the phylogenetic and ontogenetic trajectories, expressed respectively by the species recovered at different stratigraphic horizons and by the different size classes, appear to be globally orthogonal.

Morphological Differentiation within Species.—Within each species considered, the MANOVA on the Fourier coefficients indicates a significant morphological differentiation among samples (see below). For each species, the pattern of differentiation is depicted by the mean location in the canonical plane as defined by the first two axes. These axes, which express between 56.7% and 90.3% of the total among-group variance (see Figs. 5–8), provide a reliable depiction of the relationships between ontogenetic trajectories and evolutionary changes in morphology through geologic time.

The MANOVA on the Fourier coefficients of the common ancestor *A. strabocella* indicates a morphological differentiation along ontogeny

SYMBOL CAPTIONS

	<i>Ac. strabocella</i>	circles: 59.0 Ma
	<i>Ac. nitida</i>	squares: 58.7 Ma
	<i>Ac. subsphaerica</i>	diamonds: 58.4 Ma
	<i>Ac. mckannai</i>	triangles: 57.2 Ma

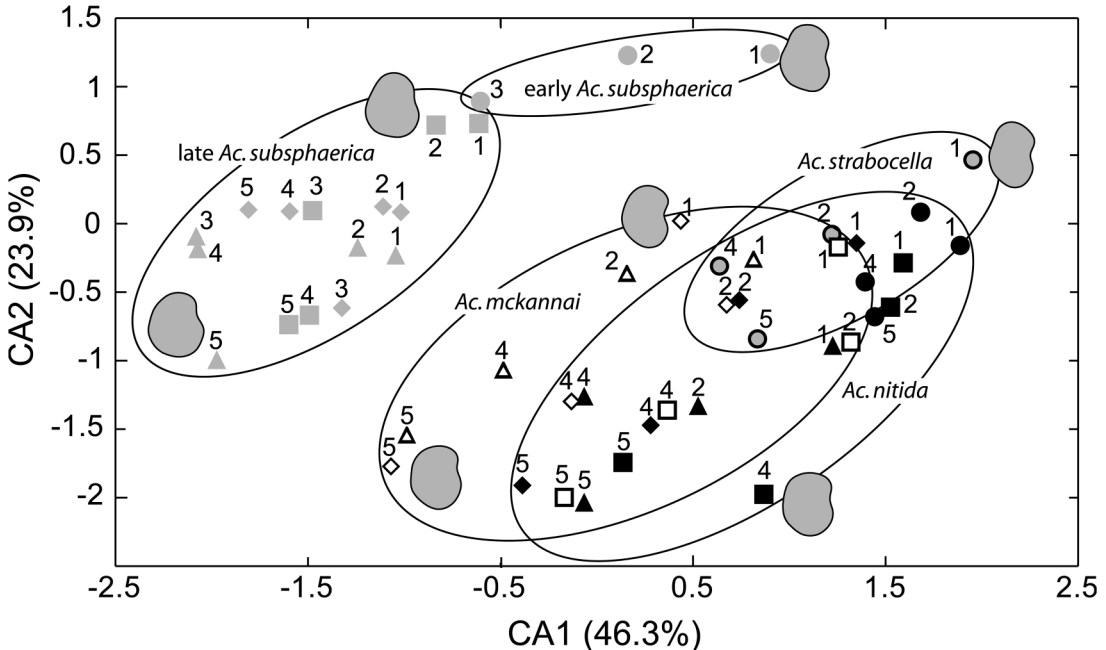


FIGURE 4. Location of the sample means in the canonical plane of the MANOVA performed on standardized Fourier coefficients of ontogenetic stages and stratigraphic horizons of the acarininid species considered in this study. The species name is expressed by the color of the symbols. The age of the samples analyzed is expressed by the shape of the symbols. Labels correspond to the different test size fractions (1 = 63–125 μm ; 2 = 125–150 μm ; 3 = 150–212 μm ; 4 = 212–250 μm ; and 5 > 250 μm). Reconstructed outlines for some group means visualize shape changes in the plane defined by the first two canonical axes. These reconstructed mean outlines of selected groups have been obtained using inverse Fourier Transform.

(Wilk's Lambda = 0.107, $\text{df}_1 = 84$, $\text{df}_2 = 147.5$, $p < 0.001$). The shape change is mainly expressed by the first canonical axis (77.6% of the among-group variance), which distinguishes a narrow angulo-elongated shape in edge view and umbilically inflated chambers for the juvenile forms (lower scores) from a more concave shape for the adults (higher scores) (Fig. 5).

Unlike *Acarinina strabocella*, which was found only in the oldest stratigraphic horizon considered in this study, the other species were found in several samples. Thus, the Wilk's Lambda statistics tested not only the significance of the shape differentiation among ontogenetic groups but also the significance of global shape differentiation among group means as defined above.

For *A. nitida*, *A. subsphaerica*, and *A. mckannai*, the MANOVAs yielded highly significant statistics (*A. nitida*: Wilk's Lambda = 0.057, $\text{df}_1 = 420$, $\text{df}_2 = 3727.7$, $p < 0.001$; *A. subsphaerica*: Wilk's Lambda = 0.064, $\text{df}_1 = 476$, $\text{df}_2 = 4656.9$, $p < 0.001$; *A. mckannai*: Wilk's Lambda = 0.060, $\text{df}_1 = 308$, $\text{df}_2 = 2095.4$, $p < 0.001$), indicating an important variation among samples in each of the species considered.

Regarding *A. nitida*, the location of the group means in the plane of the first two canonical axes (Fig. 6), which represents 63.5% of the among group variance, shows a pattern of shape changes consistent with both the morphological evolution through geologic time and the ontogeny. However, neither the evolutionary shape change nor the ontogenet-

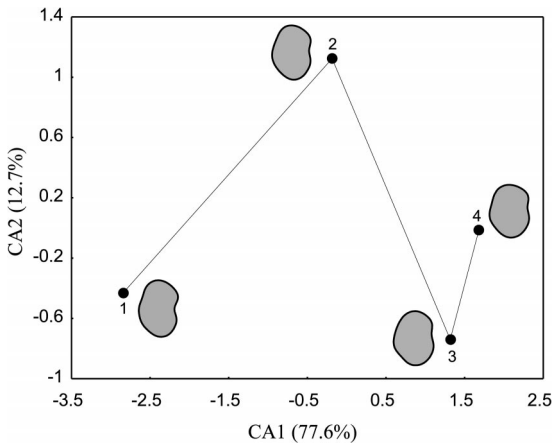


FIGURE 5. First two canonical axes and corresponding outlines for *A. strabocella*. The age of the sample is 59.0 Ma. Labels correspond to the different test size fractions (1 = 63–125 μm ; 2 = 125–150 μm ; 3 = 150–250 μm ; and 4 > 250 μm). The solid lines denote the ontogenetic trajectory. The reconstructed mean outlines of group means are obtained using the inverse Fourier Transform, which permits visualization of the shape changes in the morphological plane defined by the first two canonical axes.

ic change can be clearly associated with one of the two first axes, but both appear to be expressed by a combination of these two axes. The evolutionary trajectory seems to differentiate a narrow angulo-elongated test in edge view (higher scores on CA1), characteristic of ancestors, from a more involute coiling test characteristic of the descendants (lower scores on CA1). The ontogenetic trajectory differentiates a more elongate and umbilically inflated shape for the juveniles, and the higher the ontogenetic stage is, the more concave and less axially compressed the shape becomes.

The canonical analysis of the *A. subsphaerica* data set indicates that the shape variation is satisfactorily displayed in the plane of the first two canonical axes, which express 56.7% of the among-group variance (Fig. 7). From juvenile to adult morphologies, the test tended to develop more involute coiling. The evolutionary pattern differentiates younger representatives of the species (lower scores on CA1), which added chambers down the coiling axis (the test becoming more and more conical in edge view through time) and reduced the inflation of the umbilicus, from the oldest representatives (higher scores on CA1), which retained a relatively axially compressed

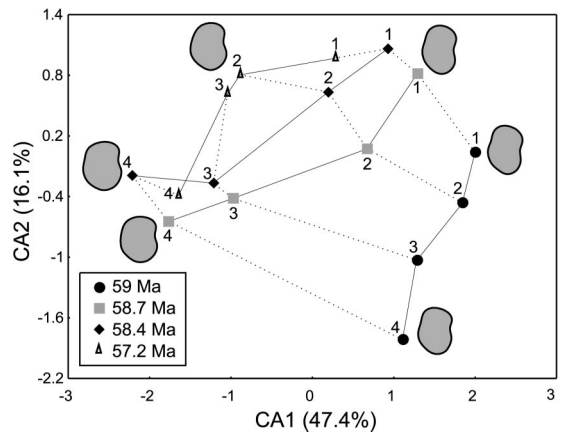


FIGURE 6. First two canonical axes and corresponding outlines for *A. nitida*. Labels correspond to the different test size fractions (1 = 63–125 μm ; 2 = 125–150 μm ; 3 = 150–250 μm ; and 4 > 250 μm). Solid lines denote the ontogenetic trajectory between the different size classes within the same stratigraphic horizon. Dashed lines denote evolutionary trajectories within the same size class. Reconstructed mean outlines of selected group means obtained using inverse Fourier transform.

coiling. Note that early *A. subsphaerica* were confined to small size fractions. In the sample dated at 58.8 Ma, we did not find a sufficient number of specimens of *A. subsphaerica* larger than 150 μm .

Finally, regarding *A. mckannai*, the location

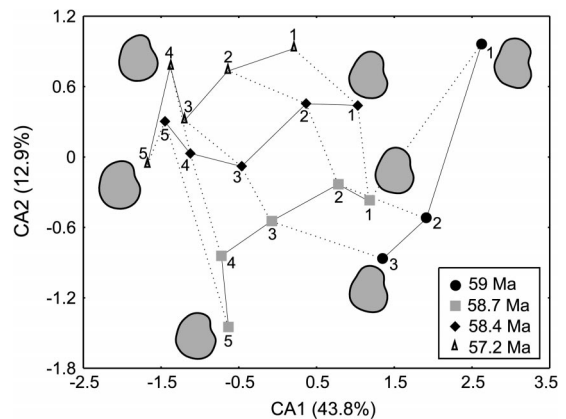


FIGURE 7. First two canonical axes and corresponding outlines for *A. subsphaerica*. Labels correspond to the different test size fractions (1 = 63–125 μm ; 2 = 125–150 μm ; 3 = 150–212 μm ; 4 = 212–250 μm ; and 5 > 250 μm). Solid lines denote the ontogenetic trajectory between the different size classes within the same stratigraphic horizon. Dashed lines denote evolutionary trajectories within the same size class. Reconstructed mean outlines of selected groups obtained using inverse Fourier Transform.

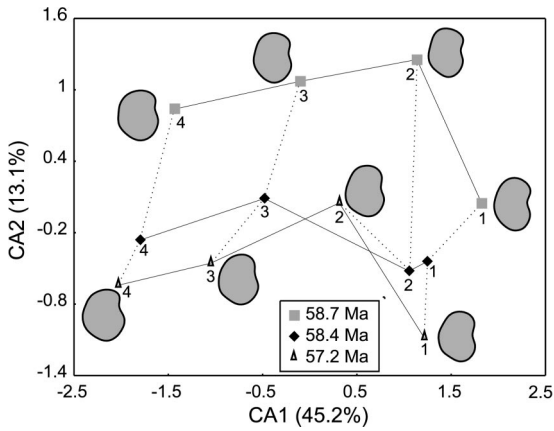


FIGURE 8. First two canonical axes and corresponding outlines for *A. mckannai*. Labels correspond to the different test size fractions (1 = 63–125 μm ; 2 = 125–150 μm ; 3 = 150–250 μm ; and 4 = >250 μm). Solid lines denote the ontogenetic trajectory between the different size classes within the same stratigraphic horizon. Dashed lines denote evolutionary trajectories within the same size class. Reconstructed mean outlines of selected groups have been obtained using inverse Fourier Transform.

of the group means in the canonical space (Fig. 8) shows that the first canonical axis (45.2% of the among group variance) noticeably represents the ontogenetic trajectory from juveniles (higher scores) to adults (lower scores). The juveniles tended to have umbilically inflated chambers and a relatively axially compressed and evolute coiling, whereas the adults tended to have a relatively more involute coiling and concave shape. Remarkably, the evolutionary change may be well expressed by the second canonical axis (13.1% of the among-group variance). It essentially separates early (higher scores) and later (lower scores) representatives of the species, which

tended to develop evolute coiling through geologic time.

Relationships between Ontogeny and Phylogeny.—The two-way fixed MANOVAs performed on each species except the ancestor show that both the stratigraphic origin and the size classes are highly significant sources of variation (see Table 2). Interestingly, the interaction between these two effects is not significant in *A. subsphaerica*, suggesting that, in this lineage, the pattern of shape change related to the ontogenetic process is preserved across stratigraphic levels. Conversely, the interaction term is significant for the two other species (*A. nitida* and *A. mckannai*). However, the level of significance for the interaction is trifling, with regard to the significance of each main effect, so we conclude that the ontogenetic processes were only moderately modified along these two lineages. Consequently, although the shape changes related to the evolution of species and to the ontogenetic processes are shown to be clearly significant in the three species considered, the developmental trajectories in terms of shape change appear to be either poorly modified or not modified during the evolution of the species.

Because the shape changes related to time and those related to ontogeny are highly significant within each lineage, it was interesting to test whether the modification of shape across the stratigraphic levels was dependent on those corresponding to the developmental trajectories. This required the use of variance-covariance matrices of shape descriptors related to both stratigraphy and ontogeny within each species. As stated in the method section, from the 28 principal components com-

TABLE 2. Two-way MANOVAs applied to the sets of Fourier coefficients for each sample.

Samples	Effects	Wilk's lambda	df1	df2	p-level
<i>Ac. nitida</i>	Stratigraphic	0.67	56	402	0.009
	Ontogenetic	0.29	84	602	$\ll 0.0001$
	Interaction	0.39	168	1190	0.033
<i>Ac. subsphaerica</i>	Stratigraphic	0.51	56	402	$\ll 0.0001$
	Ontogenetic	0.39	84	602	$\ll 0.0001$
	Interaction	0.41	168	1190	0.112
<i>Ac. mckannai</i>	Stratigraphic	0.57	56	402	$\ll 0.0001$
	Ontogenetic	0.26	84	602	$\ll 0.0001$
	Interaction	0.37	168	1190	0.009

TABLE 3. Within-sample comparisons between ontogenetic and stratigraphic VCV matrices. Mantel tests were used to test for the significance of the correlations.

Sample	Correlation	<i>p</i> -value
<i>Ac. nitida</i>	<i>r</i> = 0.25	0.119
<i>Ac. subsphaerica</i>	<i>r</i> = 0.08	0.29
<i>Ac. mckannai</i>	<i>r</i> = -0.14	0.17

puted from the PCA, the first eight were retained for the multivariate decomposition of variance. These eight PCs accounted for 76.5% of the total variation. The VCV matrices related to each effect (i.e., ontogenetic and evolutionary ones) were therefore computed from the scores of these eight first PCs. For the three species of acarininids, matrix correlations were computed. Results of the Mantel *t*-tests performed within species between VCV matrices of ontogenetic and evolutionary variation are provided in Table 3. No correlation was found to be significant, suggesting independence between morphological patterns related to both sources of variation, and thus a lack of evidence for heterochronic evolutionary processes.

Shape Variations among Species.—Results of the permutation tests are summarized in Table 4. No correlation was found to be significant between the VCV matrices associated with evolutionary changes. This suggests that the species evolved relatively independently from each other in terms of morphology. However, several ontogenetically related patterns were found to be congruent between species. Ontogeny-related matrices appear to be highly correlated between *A. strabocella*, *A. nitida*, and *A. mckannai* suggesting that these species partly shared a common ontogenetic trajectory. However, the ontogenetic VCV matrix of *A. subsphaerica* is marginally correlated only with that of *A. mckannai* suggesting that the former species presents the most differentiated development.

Discussion

For each of the three species *Acarinina nitida*, *A. subsphaerica*, and *A. mckannai*, the patterns of shape changes associated with the ontogeny at several steps of the evolution of the species were shown to be dissociated from those

TABLE 4. Comparisons of ontogenetic and stratigraphic VCV matrices among samples. Mantel tests were used to test for the significance of the correlations. (a) = *Ac. strabocella*, (b) = *Ac. nitida*, (c) = *Ac. subsphaerica*, (d) = *Ac. mckannai*.

Effect	Samples	Correlation	<i>p</i> -value
Ontogenetic	(a)/(b)	<i>r</i> = 0.87	0.001
	(a)/(c)	<i>r</i> = -0.03	0.48
	(a)/(d)	<i>r</i> = 0.68	0.001
	(b)/(c)	<i>r</i> = -0.03	0.43
	(b)/(d)	<i>r</i> = 0.65	0.012
	(c)/(d)	<i>r</i> = 0.41	0.068
Stratigraphic	(b)/(c)	<i>r</i> = -0.19	0.22
	(b)/(d)	<i>r</i> = 0.26	0.11
	(c)/(d)	<i>r</i> = 0.01	0.37

related to the morphological evolution of the species across these steps. This is deduced from the perpendicularity of the major direction of ontogenetic and evolutionary trajectories in the three species considered, as shown in Figures 6–8. Additionally, the non-significance of the Mantel test results on VCV matrices related to both ontogenetic and evolutionary stages (Table 3) corroborates the hypothesis that both effects are independent. Heterochronic evolution has been defined as a morphological change inscribed within an ontogenetic trajectory that produces parallelism between ontogeny and phylogeny (Zelditch and Fink 1996). The independence between the direction of evolutionary change and that related to the ontogeny precludes consideration that the evolution of Paleocene acarininids displays a heterochronic signal affecting the whole shape of these unicellular organisms, at least as assessed through the analysis of outline variations. Conversely, the moderate changes in ontogenetic trajectories along the lineages of two species (*A. nitida* and *A. mckannai*), as suggested by the slightly significant interaction term in the MANOVAs, can be interpreted as a heterotopic process in the sense of Zelditch and Fink (1996) and Zelditch et al. (2000). It is not possible to test or assume that these changes have occurred at particular stages of the ontogeny. However, the examination of canonical planes for these two species (Figs. 6 and 8) suggests a certain parallelism—and thus moderate changes—of ontogenetic trajectories among the different stratigraphic horizons. However, the fact that

no change was detected for *A. subsphaerica* does not preclude that such a divergence might have occurred at earlier stages than those considered in this study; in such case, the divergence could have been preserved throughout growth despite similar ontogenetic transformations, leading to the observed parallelism of developmental trajectories.

Using the permutation tests on VCV matrices, we have shown that the morphological evolution of *A. nitida*, *A. subsphaerica*, and *A. mckannai* displayed significantly different patterns of variation in the shape space (Table 4). This result suggests that although these species resulted from the same diversification event, the subsequent morphological evolutionary changes were partly independent among the emerging lineages. Interestingly, despite this independence, the morphological changes related to ontogenetic process are shared by most of the species under consideration. In particular, the pattern of morphological variation associated with the ontogenetic trajectories in *A. nitida* and *A. mckannai* is the same as that of their common ancestor, *A. strabocella*. This preservation of shape variation associated with the ontogenetic trajectories in descendant species may be an expression of the developmental constraints inherited from their ancestor (see Raff 1996 for review).

Nonetheless, the developmental constraints did not prevent the species from evolving towards a different morphology. *Acarinina subsphaerica* displays the most divergent developmental trajectory since the ontogenetic variation is marginally correlated only with that of *A. mckannai*. This may reflect the fact that *A. subsphaerica*, which had an initially low spire similar to *A. strabocella* and *A. nitida* (Berggren and Norris 1997), later on added chambers down the coiling axis to become almost conical in edge view (see Fig. 1B) and developed a lower trochospire, as did some of the representatives of *A. mckannai*. The mechanisms selected to lead to a viable adult morphology might be globally preserved despite micro- and macro-evolutionary events.

Recent studies (Norris 1996; Quillévére et al. 2001) indicated (1) that the evolution of photosymbiosis was synchronous with the

abrupt evolution of both genera *Morozovella* and *Acarinina* during the early Paleogene and (2) that the acarininids inherited this trophic strategy from the common ancestor they shared with morozovellids. The acquisition of algal-photosymbionts for respiration did not trigger an immediate species-level radiation in the acarininids, which remained a low-diversity group restricted to the high latitudes for nearly 1.7 Myr before migrating into low-latitude environments and radiating. On the contrary, the diversification of morozovellids was dramatically and rapidly boosted by this novel ecologic strategy (Norris 1996). The acarininid diversification was consequently delayed relative to that of the morozovellids.

Heterochrony is often cited as a pathway for the appearance of evolutionary novelties (McKinney and McNamara 1991; Raff 1996). In the case of the Paleocene planktonic foraminifera, the evolutionary origin of the genus *Morozovella* revealed a temporal pattern of variation consistent with paedomorphosis (Kelly et al. 1996). Moreover, as pointed out by McKinney (1999), all of the examples including heterochronoclines in marine organisms (McNamara 1997; Crônier et al. 1998; Jones and Gould 1999) seem to result from progressive adaptation to environmental changes in water masses through time. By harboring algal-photosymbionts, both acarininids and morozovellids expanded their ecologic niches into new low-nutrient habitats, such as the oligotrophic tropical gyres. In this context, one could have expected heterochrony to be detected in the morphological diversification of *Acarinina*, as it was stated for *Morozovella*.

Conclusions

The morphological patterns observed for shape variations during ontogeny and evolution of late Paleocene (early Thanetian) species of *Acarinina* indicate that ontogenetic stages differ from each other within each species and with geologic age. The ontogenetic trajectories of *A. nitida*, *A. subsphaerica*, and *A. mckannai* are shown to be distributed along a morphological pathway orthogonal to the evolutionary-related shape trajectories. Heterochrony has been defined as a related pattern between evolutionary change through time and onto-

genetic differentiation; this result therefore advocates a non-heterochronic evolution of the shape of the entire organism during the initial diversification of the acarininids. It is possible, however, that some characters may be concerned by heterochronic processes but the related morphological signals remained too localized to be detected by our integrative approach. In addition, our results showed that patterns of phylogenetic evolution were independent between species and, conversely, patterns related to ontogeny were shared. This indicates that developmental constraints affecting ontogenetic changes have been preserved, in spite of the evolutionary divergence among species. Our study suggests that even if heterochrony is thought to be a common process, it may not have been properly investigated in most cases. Moreover, as claimed by Raff (1996), heterochronic process may not be suitable for explaining an evolutionary pattern. Developmental differences observed between very close clades such as acarininids and morozovellids, which shared a common ancestor, used the same trophic strategies, and finally inhabited the same environments, set limits to extrapolations of the heterochronic evolutionary process.

Acknowledgments

We thank M.-P. Aubry, R. D. Norris, R. Reymont, and C. P. Klingenberg for discussion on an early version of this manuscript. We gratefully acknowledge M. Zelditch, B. Malmgren, P. Pearson, and an anonymous reviewer for critical and useful comments that materially improved the manuscript. This work has been supported by the GDR 2474 CNRS "Morphométrie et Evolution des Formes" and by a Marie Curie Fellowship.

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