Reply to Aze et al.: Distinguishing speciation modes based on multiple lines of evidence

In a recent study, we present evidence that cladogenesis is the primary driver of long-term phenotypic evolution in planktic foraminifera (1). The phylogeny developed by Aze et al. (2) forms the basis of our study and represents an important contribution to the field. Aze et al. question our methodology (3), but the alternative they advocate, which relies entirely on a lineage-based approach (2), is by itself insufficient to distinguish speciation modes.

In their response, Aze et al. (3) reiterate that their phylogeny does not incorporate findings from genetic studies to ensure its independence. Consequently, they do not consider evidence that may aid in distinguishing anagenesis from cladogenesis. Contrary to the statement of Aze et al. (3), we never claimed to analyze molecular data; rather, we interpret fossil data in light of molecular and other evidence (1). Genetic data (from ∼20 morphospecies) support the simplifying assumption of our study that the vast majority of taxa recognized as distinct morphospecies are reproductively isolated and therefore independently evolving. The one established exception is the recent discovery of genetic homogeneity within the *Globigerinoides sacculifer* plexus (4), where we recognize two morphs, as per Aze et al. (2). This important finding highlights that we still have much to learn about foraminifera diversity, but it does not, by itself, refute our simplifying assumption as appropriate for estimating the relative frequencies of anagenesis and cladogenesis, particularly as it is an example of ecophenotypy, not anagenesis.

The criteria we use to distinguish speciation modes are not based on "just two studies" (3), but rather a comprehensive review of relevant and available evidence. One form is temporal range overlap for ancestor–descendant pairs (5). We agree that the amount of range overlap is partly "an artifact of the typological approach" for defining morphospecies (3), as we show in figure 2A (1), which is why we account for it in our study. Our typological error estimates—one each for the Neogene and Paleogene—were drawn from detailed studies of 20 speciation events. Given the small sample size (20 of 337 Cenozoic events), we acknowledge here and in our paper the need for further work in this area. Within our typological error margins, all events were assumed to be anagenetic in the absence of other evidence. Because such evidence is currently unavailable for the majority of speciation events within our error margins (57 of 105), our method of identifying cladogenetic events is conservative.

As Aze et al. acknowledge (3), many more cladogenetic events have likely occurred than are resolved in their phylogeny. Our methodology was specifically designed to distinguish speciation modes by incorporating other evidence. Because it entails explicit assumptions and is quantitative, it can be modified in light of new findings as they become available. We view our approach as complementary to the lineage-based approach and the detailed morphometric and molecular studies that will be needed to achieve a complete understanding of speciation dynamics in the group.

Luke C. Strotz*[1] *and Andrew P. Allen
Department of Biological Sciences, Macquarie University, Sydney, NSW 2019, Australia

---

1 Strotz LC, Allen AP (2013) Assessing the role of cladogenesis in macroevolution by integrating fossil and molecular evidence. *Proc Natl Acad Sci USA* 110(8):2904–2909.

2 Aze T, et al. (2011) A phylogeny of Cenozoic macroperforate planktonic foraminifera from fossil data. *Biol Rev Camb Philos Soc* 86(4):900–927.

3 Aze T, et al. (2013) Identifying anagenesis and cladogenesis in the fossil record. *Proc Natl Acad Sci USA* 110:E2946.

4 André A, et al. (2013) The cryptic and the apparent reversed: Lack of genetic differentiation within the morphologically diverse plexus of the planktonic foraminifer Globigerinoides sacculifer. *Paleobiology* 39(1):21–39.

5 Eldredge N (1995) Species, speciation, and the context of adaptive change in evolution. *New Approaches for Studying Speciation in the Fossil Record*, eds Erwin DH, Anstey RL (Columbia Univ Press, New York), pp 39–63.

Author contributions: L.C.S. and A.P.A. designed research; performed research; analyzed data; and wrote the paper.

The authors declare no conflict of interest.

[1] To whom correspondence should be addressed. E-mail: luke.strotz@mq.edu.au.