

FROM THE ARCHIVES

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Revisiting “Genetic Diversity of Symbiotic Dinoflagellates in the Genus *Symbiodinium*”



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We are both humbled and honored that our review on the genetic diversity of symbiotic dinoflagellates in the genus *Symbiodinium* (Coffroth and Santos 2005; Fig. 1A–E) qualifies as a Citation Classic in *Protist* and sincerely thank the journal's patrons for their continued interest in our article long after its publication. The sizeable number of citations it has accumulated to date (227 citations [by June 28, 2018] according to Clarivate Analytics Web of Science) likely derives from the multi-faceted interest in, and importance of, the coral reef ecosystem, particularly in light of the recent plights it has experienced. Given that the underpinnings of this ecosystem are the relationships *Symbiodinium* form with various protists and invertebrates (Fig. 2) and that understanding these symbioses is contingent upon an awareness of the diversity within the group, the initial incentive for authoring our review was the opportunity to summarize the field's long history as well as to distill and synthesize the current knowledge of the time provided by approaches such as molecular genetics. Here, we revisit a small fraction of the ideas and hypotheses pertaining to *Symbiodinium* diversity presented in our review and briefly discuss how a number have been upheld and others have evolved, while many still remain relatively unexplored over a decade later.

Firstly, it is not surprising that one of the large-scale ecological and evolutionary patterns we highlighted which has sustained the test of time is that levels of diversity within *Symbiodinium* are as great as what they were originally alluded to be. Specifically, previous estimates from molecules such as the ribosomal internal transcribed spacers (ITS) that hypothesized the existence of 100s of *Symbiodinium* ‘types’ across eight clades (i.e., divergent, monophyletic groups within the genus) have been substantiated. Moreover, additional distributional (i.e., bathymetrical, geographical, host-community) surveys and the employment of other genetic markers since 2005 has led to the detection of even greater diversity, including the recognition of a ninth clade (i.e., Clade I; Pochon and Gates 2010) following our review. Furthermore, some *Symbiodinium* ITS ‘types’ themselves, like the Caribbean-dominating B1, can be resolved into 10s–100s of lineages each with specific genetic, physiological, ecological and evolutionary attributes that substantially distinguish them from one another. For example, at least four species have been subsequently recognized from the likely Pleistocene radiation of B1, with many more awaiting formal description (LaJeunesse et al. 2012; Parkinson et al. 2015). Thus, overall diversity within *Symbiodinium* as a whole and across a wide variety of measures is considerably greater than has been previously anticipated and the tremen-

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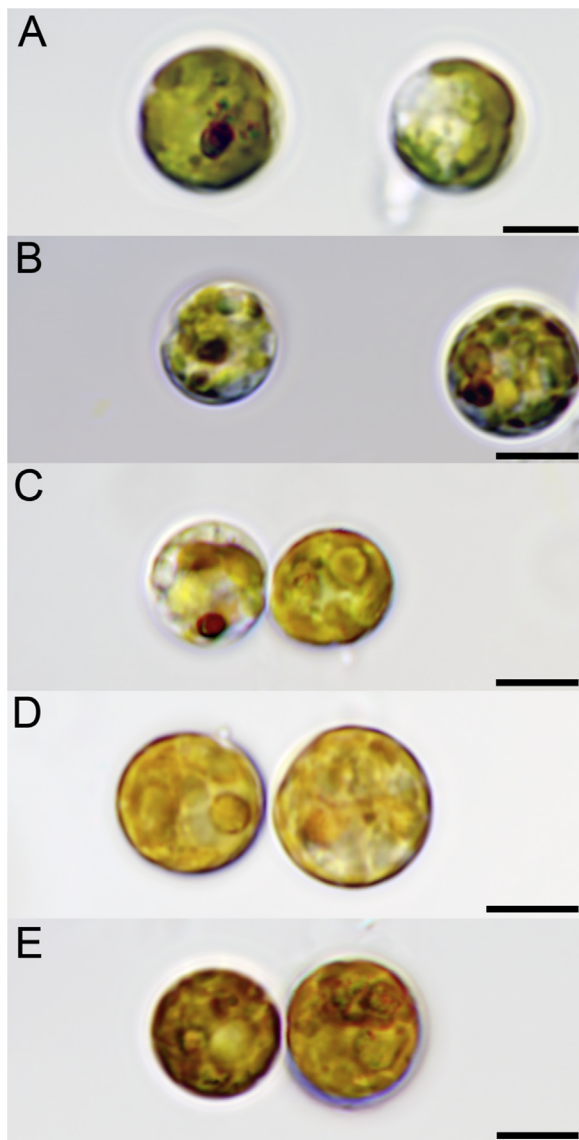


Figure 1. Photomicrographs of cultured *Symbiodinium* spp. from different clades. **A.** *S. microadriaticum* (CassKB8; A1). **B.** *S. antillogorgium* (SSPE; B1). **C.** *S. minutum* (Mf1.05b; B1). **D.** *S. trenchii* (Mf2.2b; D1a). **E.** *S. voratum* (rt-383; E1). Culture designation and cladal type (as defined by internal transcribed spacer 2 (ITS2)-rDNA genotyping) provided in parentheses. Scales: A–E = 5 μ m. Photo credit: A. Siegel, State University of New York at Buffalo.

dous variation both between and within clades of these symbiotic dinoflagellates should lead to the simple realization that one cannot, and should not, generalize particular traits (e.g., genetic, phenotypic, physiological, etc.) as belonging solely to a

specific “clade” unless overwhelming evidence supports such a conclusion.

On the other hand, some aspects of quantifying and conceptualizing *Symbiodinium* diversity have substantially changed as knowledge and data have accumulated or become newly available in the 13 years since our review. A notable illustration of this is the renaissance in formal species descriptions for members of the genus. Historically, such descriptions for *Symbiodinium* have been challenging due to culturing difficulties and a reliance upon diagnostic morphological and biochemical traits proving problematic to identify and score in a reliable fashion. In contrast, informative variability from sequences of nuclear and organellar loci as well as an increased awareness of distinct attributes like geographic distributions, ecological preferences, host affinities, and/or population genetics have contributed to the unambiguous recognition of reproductively isolated lineages (i.e., biological species) within *Symbiodinium* that formal nomenclature can be (and has been) assigned (see above). Furthermore, analyses of transcriptomic and genomic resources, facilitated by recent advancements in low(er)-cost DNA sequencing technologies, have proven powerful tools in the study of the evolution and function of these diverse group of symbionts (Aranda et al. 2016; Lin et al. 2015; Shoguchi et al. 2013) and quantified significant levels of evolutionary divergence separating members of different *Symbiodinium* ITS ‘types’ (Parkinson et al. 2016), offering additional support to the now widely accepted view that they (and by extension the clades encompassing them) represent diversity well above that of species.

As noted earlier, the coral reef ecosystem in general, and these symbioses in particular, have been significantly and negatively impacted by a range of anthropogenic insults, most notably increased sea surface temperatures due to global climate change. Because of this, one question asked in our review is still highly relevant today – Can the diversity within *Symbiodinium* provide these symbioses with some capacity to survive such onslaughts? Supporting this possibility, an increasing number of studies have demonstrated among- as well as within-clade associations between genetic identity and physiological capability and ITS ‘types’ have been identified within most clades that show some degree of variation in traits like thermal tolerance. Along with this, appreciable functional differences can exist between apparently closely related genotypes or clones within specific *Symbiodinium* ITS ‘types’ (e.g., Díaz-Almeyda et al. 2017) and recent work has sought to determine their adaptation

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