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## Letters

# Different modes of convergent evolution reflect phylogenetic distances: a reply to Arendt and Reznick

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In a recent article in *Trends in Ecology and Evolution* [1], Arendt and Reznick argue that a deeper understanding of the genetics of adaptation blurs the distinction between convergent and parallel evolution based on relative phylogenetic distances. The authors make a compelling case that convergence in closely related lineages – parallel evolution – does not necessarily involve identical genetic processes. Arendt and Reznick also describe how convergence in more distantly related lineages can reflect similar genetic changes [2,3]. The authors conclude that because the genetic underpinnings of convergence are not necessarily more similar in more closely related lineages, distinguishing parallelism from convergence in more distantly related lineages is unjustified and even misleading [1].

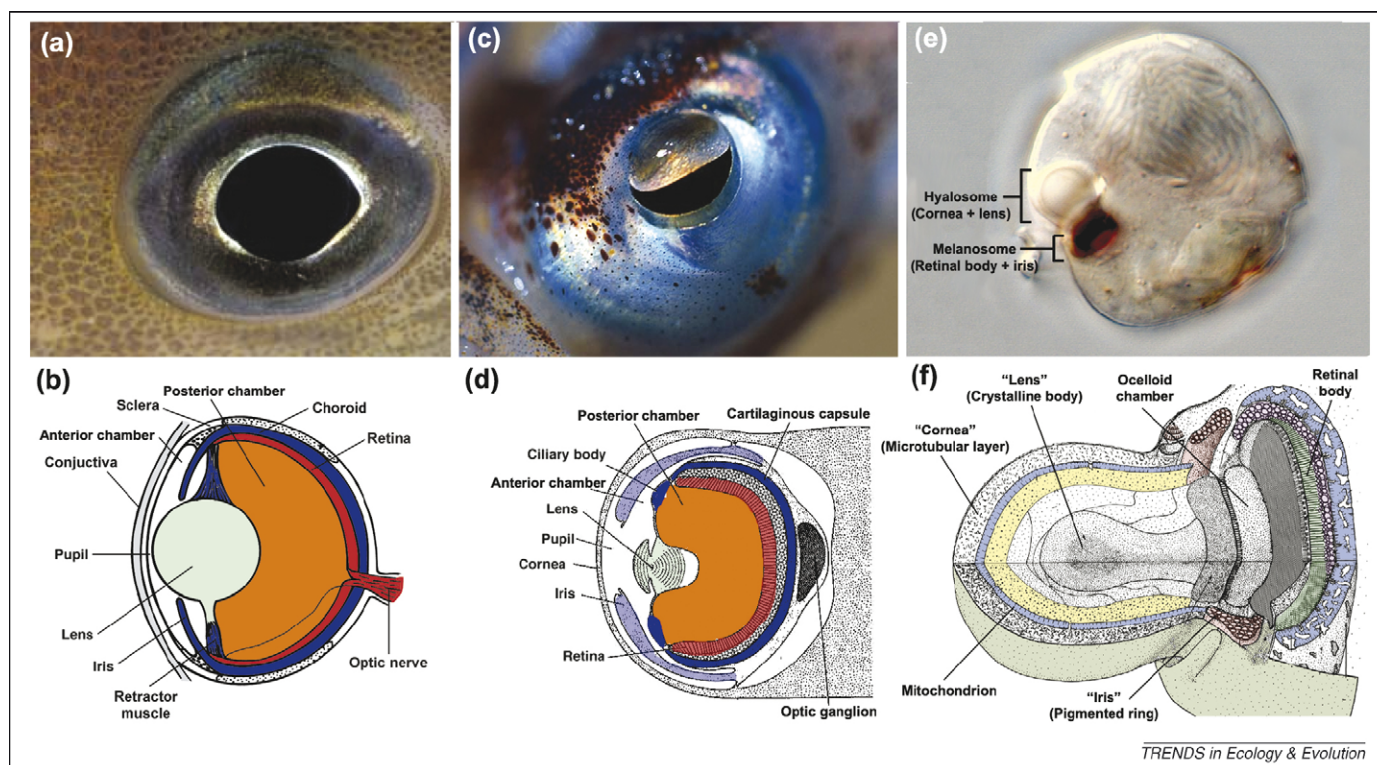
In my view, knowing the genetics of adaptation need not lead to a perspective that downplays the evolutionary significance of morphological variation embedded within complex phenotypes. Detailed analyses of these phenotypes – comparative anatomy – provide the basis for recognizing different degrees of homology, which reflects phylogenetic distance (e.g. the wings of birds, bats and pterosaurs share more homologous characteristics than with the wings of butterflies). Although the general view of phylogenetic distance adopted by Arendt and Reznick conforms to the limited phylogenetic scope traditionally used in evolutionary biology, it is conspicuously narrow when considered within the overall framework of eukaryotic diversity [4,5]. It is not unexpected, for instance, that pelvic reduction in vertebrates (e.g. sticklebacks and manatees) involved a homologous gene(s) [3], because these lineages are very closely related to one another relative to the full scope of the eukaryotic radiation (i.e. divergence times < 450 million years) [6]. The realization that different genetic modifications can produce nearly identical phenotypes in more closely related lineages – parallelism – underscores that most phenotypes (e.g. pale hair color) result from interconnected developmental pathways [1,2,7].

Convergent evolution between lineages of microbial eukaryotes, by contrast, often involves very distantly related lineages (i.e. divergence times > 950 million years)

[8], which severely weakens, and perhaps eliminates, the role of ancestral developmental programs in subsequent evolution [5]. Examples of large-scale convergent evolution consist of few, if any, homologous components (genetic or structural) and include subcellular analogues (e.g. centric diatoms and prorocentroid dinoflagellates), multicellular analogues (e.g. bifurcating body forms in bryozoans and coralline rhodophytes) or subcellular analogues to multicellular systems (e.g. haplozoan dinoflagellates and marine tapeworms) (illustrated in Ref. [5]). I argue that convergence between such distantly related lineages – ultimate convergence – is fundamentally different from convergence between closely related lineages. Ultimate convergence is also consistent with a hierarchical view of convergent evolution that emphasizes, rather than downplays, the significance of relative phylogenetic distances. Nonetheless, the perspectives expressed by Arendt and Reznick and those that I emphasize here inform one another and, together, should help facilitate the construction of a theoretical framework for understanding convergent evolution.

For instance, warnowiid dinoflagellates inhabit marine planktonic communities and use one of the most sophisticated photoreception apparatuses known – called ocelloids – consisting of a cornea, iris, lens and retina (Figure 1e). Although these organelles have converged on the overall structure of the multicellular eyes of vertebrates and cephalopods, ocelloids are composed entirely of subcellular components (Figure 1a–f). In fact, the retinal bodies of ocelloids appear to be highly modified plastids, which are, in turn, highly modified cyanobacterial endosymbionts (Figure 1e,f) [9–12]. The spatial scale at which ocelloids and camera eyes function is completely different, and the evolutionary trajectories that led to ocelloids and the camera eyes of animals could hardly be more dissimilar. Yet, it would not be surprising if certain genes involved in photoreception (e.g. retinals and opsins) were present in both the retinal body of ocelloids and the retina of camera eyes, either as the result of molecular convergence, horizontal gene transfer or distant homology; this is because opsin and retinal genes have already been characterized in a diverse array of organisms that span the entire ‘tree’ of life [13]. However, we should not lose sight of the fact that the structural modification of a

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**Figure 1.** An example of ultimate convergent evolution involving the subcellular ocelloids of warnowiid dinoflagellates and the multicellular eyes of vertebrates and cephalopods. (a) The eye of an Atlantic cod. (b) An illustration of the general anatomy of the teleost (vertebrate) eye. (c) The eye of a squid (cephalopod). (d) An illustration of the general anatomy of the cephalopod eye. (e) Light micrograph of a warnowiid dinoflagellate (*Proterothropsis* sp.) showing an ocelloid consisting of two main components: the hyalosome and the retinal body (cell 45  $\mu\text{m}$  wide). The retinal body appears to be a highly modified cyanobacterial endosymbiont (image taken by M. Hoppenrath). (f) An illustration of the general anatomy of the warnowiid ocelloid. (f) Modified, with permission, from Ref. [12].

cyanobacterial cell, and its associated subcellular systems, into a functioning ocelloid involves fundamentally different components and processes from those that led to the independent origins of multicellular eyes in vertebrates and cephalopods.

Therefore, I question the notion expressed by Arendt and Reznick that understanding the genetics of adaptation leads to the rejection of an unambiguous relationship between phylogenetic distance and different modes of phenotypic convergence. Studies of convergent evolution traditionally compare species within a limited portion of the full tree of life, and an improved understanding of the diversity of microeukaryotes will allow for broader comparisons. When considering lineages with phylogenetic distances that are much greater than those found in vertebrates, and animals as a whole, there are many examples of evolutionary convergence that are not constrained by homologous developmental networks. These examples reflect ultimate convergence, which occurs over vast timescales and great phylogenetic distances. In my view, distinguishing between ultimate convergence and more proximate cases of convergence – parallel evolution – is appropriate and informative, if for no other reason than to help guide future research on the genetics of adaptation.

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