Francis M. Balfour set the pace on discussions about the evolutionary importance of larvae by addressing many of the fundamental questions regarding larval evolution (Balfour, 1874; Balfour, 1880; Balfour, 1881). He wondered about the ancestry of larvae. Can larvae reveal the ancestral forms of metazoans? He indicated tests to the predictions of recapitulation. Can we find a larva that corresponds to the adult of a related group? He asked whether larvae changed during evolution. How often do larval organs evolve? And what might be the underlying mechanisms for the evolution of development. What guides the maintenance or atrophy of larval organs in adult stages? (Hall and Wake, 1999).

Perhaps, the greatest conceptual advance initiated by Balfour is that larvae are subject to variation and natural selection in the same manner as the adult stage (Balfour, 1874; Balfour, 1881). In other words, he articulated the realization that evolution can occur at any developmental stage. However, if not all embryonic features represent ancestors (or ancestral traits), the foundation of the recapitulation theory is compromised. The evolutionary debate caused by larvae influenced a more informed way to make extrapolations from ontogeny to phylogeny (Hall, 2000; Hall and Wake, 1999). It was no coincidence that one of the most vehement opponents of Haeckel’s recapitulation theory was a larvae affectionate, the biologist Walter Garstang who boldly concluded that “ontogeny does not recapitulate phylogeny, it creates it” (Garstang, 1922).

Present-day research shows that larval traits are evolutionary labile, and often correlate to ecological, developmental and other life-history factors (Strathmann and Eernisse, 1994). Evidence from diverse taxa, including gastropods (Collin, 2004), sea urchins (Raff and Byrne, 2006), ascidians (Jeffery and Swalla, 1992), sea stars (Byrne, 2006; Hart et al., 1997) nemertans (Maslakova and Hiebert, 2014)
and polyclad flatworms (Rawlinson, 2014), indicates that larval forms were modified, gained or lost in different lineages independently, and that the observed similarities are likely the result of convergent evolution.

These observations undermine scenarios about animal evolution that require the homology of larval characters (Jägersten, 1972; Nielsen, 1998; Nielsen, 2001; Nielsen, 2009; Peterson and Cameron, 1997) and are more consonant with the multiple independent evolution of metazoan larvae from a direct-developing ancestor (Page, 2009; Raff, 2008; Sly et al., 2003; Wray, 1995). Yet, the homology of larval characters such as the apical organ (e.g., Hunnekuhl and Akam, 2014; Marlow et al., 2014) or ciliated bands (e.g., Henry et al., 2007; Rouse, 1999) continues to be a central and lively discussed topic. For all the reasons above, larvae are a scandalous epitome of evolution, and the diversity of larval body patterns in marine invertebrates continue to provide a rich framework for evolutionary studies.

This text is a section of my PhD thesis.

REFERENCES


