

Review

From descent with modification to the origins of novelty

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ABSTRACT

Descent with modification is the foundational framework of all of evolution. Yet evolutionary novelties are defined as lacking affinities to structures that already existed in the ancestral state, i.e. to somehow emerge in the absence of homology. We posit that reconciling both perspectives necessitates the existence of a type of *innovation gradient* that allows descent with modification to seed the initiation of a novel trait, which once in existence can then diversify into its variant forms. Recent work on diverse, textbook examples of morphological novelties illustrate the value of the *innovation gradient* concept. Innovations as profound and diverse as insect wings, beetle horns, and treehopper helmets derive from homologous source tissues instructed in their development by homologous gene regulatory networks. Yet rather than rendering these traits no longer novel, we posit that discoveries such as these call for a reassessment of the usefulness of defining evolutionary novelty as necessitating the *absence of homology*. Instead, we need to redirect our attention to *how* ancestral homologies scaffold and bias the innovation gradient to facilitate hotspots of innovation in some places, and deep conservation elsewhere.

Descent with modification is the foundational framework of all of evolution (Darwin, 1859). Everything new must, in some way, emerge from the old. Yet when it comes to evolutionary novelties we, paradoxically, tend to view them as somehow existing outside these boundaries. In fact, the most widely used definition of what constitutes a morphological novelty in evolution necessitates the *absence* of homology to structures that already existed in the ancestral state (Müller and Wagner, 1991). Both perspectives cannot be correct simultaneously. Instead their reconciliation must somehow require the existence of a type of *innovation gradient* that allows descent with modification to seed the initiation of a novel trait, which once in existence can then diversify into its variant forms. Yet probing the existence and nature of this gradient has proven challenging.

Insect wings, often viewed as one of the most enigmatic morphological novelties, may now be pointing us in a promising direction. The dual origin hypothesis posits that wings originated once, in the common ancestor of all pterygote insects, from proximal leg segments and dorso-lateral regions of body wall tissues, which merged to give rise to a basic articulated wing similar to what we can see today in dragonflies and damselflies (see Clark-Hachtel and Tomoyasu, 2016 for review). These source tissues themselves predate the origin of wings by >100 Million years and were themselves the subject of much diversification

(Clark-Hachtel and Tomoyasu, 2020). Yet the moment these tissues merged, a novel morphological unit was initiated, able to extend the innovation gradient toward the genesis of the first wing, and ultimately producing the multitude of wing shapes and forms we see today, including halteres in flies, elytra in beetles, and the colorful, scale-covered canvases of butterflies.

Evodevo's contribution to the innovation gradient leading to the origin of wings further revealed that, in addition to the *bona fide* wings on the second (T2) and third (T3) thoracic segment, tissues homologous to those producing wings *also* exist on segments that appear wing-less (Clark-Hachtel and Tomoyasu, 2016). This makes sense, as these segments too possess the same source tissues that in the case of T2 and T3 merged to form wings. Specifically, we now know that in a variety of insect orders tissues exist on the *first* thoracic segment (T1) as well as throughout the abdomen that are genetically underlain by a similar network of genes integral to wing formation in T2 and T3. Not only are these *serially homologous tissues* dependent on wing gene network components but, if genetically induced to do so, they can merge and transform into ectopic T1 or abdominal wings (Clark-Hachtel et al., 2013; Linz and Tomoyasu, 2018). Wing serial homologs thus exist in many segments outside of those that were traditionally viewed as wing-bearing (Fig. 1).

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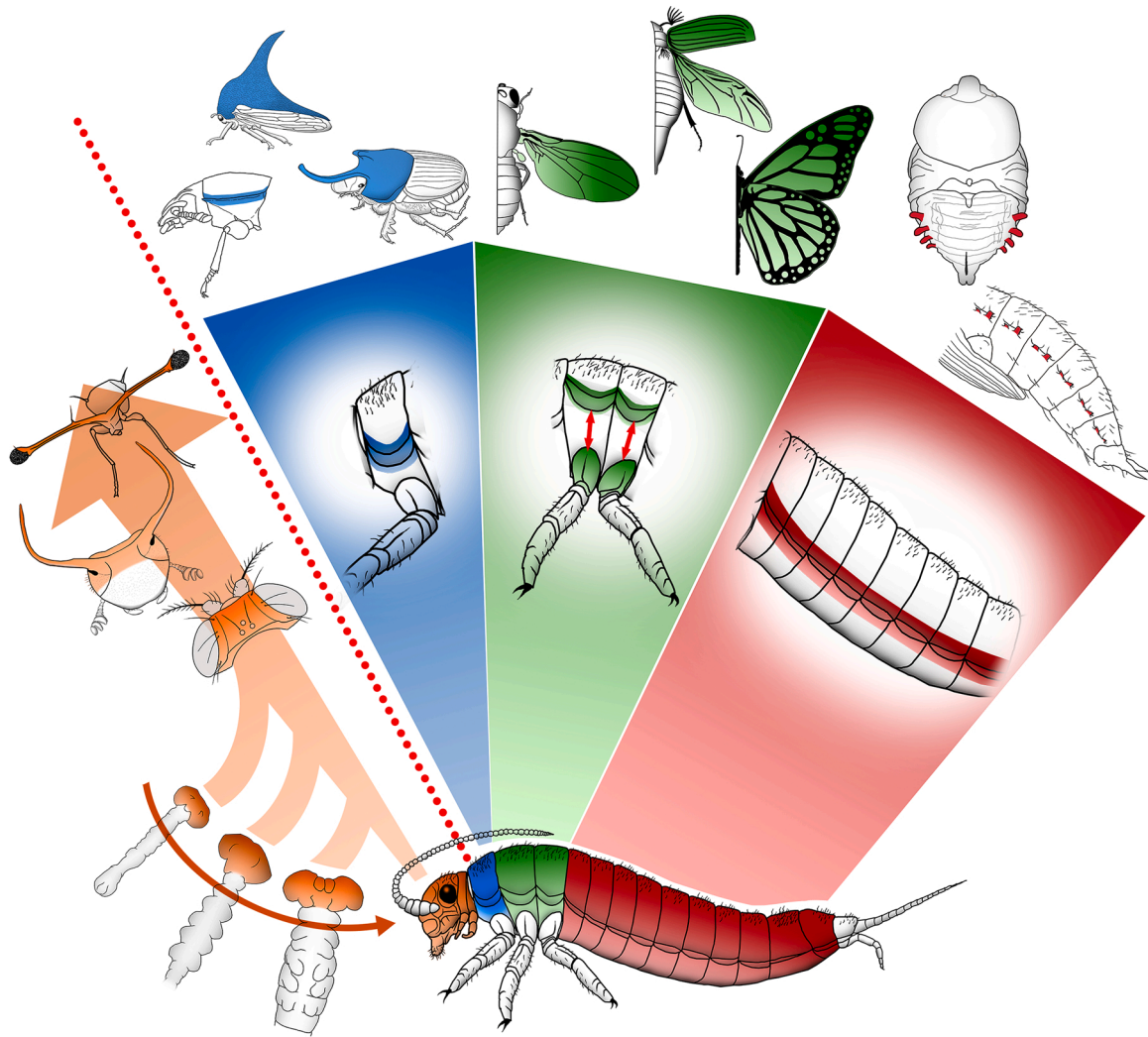


Fig. 1. Innovation gradients connect descent with modification to the initiation and elaboration of novel traits. The origin of *bona fide* wings on T2 and T3 (green) was initiated by the merger of ancestral tergal and pleural tissues (red arrows within green). This event, and those following, then gave rise to the diverse array of present-day wing shapes (green). Tissues serially homologous to the tergal wing origin tissue yet located in the first thoracic segment (blue) or the abdomen (red) also produced a great diversity of structures in their respective domains such as prothoracic horns in dung beetles or gin traps in red flour beetles. Diverse morphological novelties have thus been able to emerge, starting along a shared, but eventually diverging along their own, innovation gradient. Head innovations, in contrast, do *not* rely on wing related tissues. Instead, embryonic head patterning genes are reused and repurposed at later developmental stages to facilitate integration of novel morphologies, including ocelli, horns, and possibly eyestalks (orange). Yet here, too, innovation is guided by ancestral homologies.

When imagining the innovation gradient from ancestral variation among arthropod segments to the inception and subsequent diversification of wings, we must therefore include these wing related tissues in our thinking. Amazingly, wing serial homologs *outside* wing bearing segments have also diversified into an array of forms, from the carinated margin (a sort of bilateral reinforcement of T1) of adult *Tribolium* beetles and bilateral gin traps (jawed and contractible defensive structures) in the corresponding pupae, to most likely the extraordinarily gaudy helmets of treehoppers (Membracidae) (Fisher et al., 2020; Prud'Homme et al., 2011) (Fig. 1). Yet perhaps most stunning among these examples are the thoracic horns in *Onthophagus* dung beetles. In 2019 we showed that prothoracic horns, i.e. horns produced from T1, are dependent on members of the core wing gene network and that when ectopic wings are induced in this segment, thoracic horns contribute to the formation of these structures (Hu et al., 2019). Thoracic horns are thus derived from tissues serially homologous to wings. This work suggests that prothoracic horns, considered a textbook example of a morphological novelty (Shubin et al., 2009) and which bear no resemblance to insect wings, are built from the same ancestral set of ancient wing related tissues, instructed in their development by the same core gene network. Does

this mean thoracic horns are no longer a morphological novelty? We posit that instead these discoveries call for a reassessment of the usefulness of defining evolutionary novelty as necessitating the *absence of homology*, and to explore how the innovation gradient allows novelty *to be built through homology*. Yet other horns, one body region over in the head, further nuance this perspective.

Thoracic horns are not the only horns that beetles possess. Rather, many species also form horns that are integrated within the dorsal head capsule. Like their thoracic counterparts, such *head horns* are highly diverse in size, number, and shape, and are typically limited to males where they are used as weapons in combat over females. As such, head horns would seem, morphologically and functionally, to be a segmentally reiterated manifestation of a thoracic horn (or vice versa), and accordingly, one would expect the developmental program underpinning head horns to be the same or similar to that instructing thoracic horns – and, by extension, to rely on wing related tissues. But we now know that “a horn is not a horn is not a horn”. Published in 2020, a large RNAseq project revealed that head horn formation relies on the post-embryonic re-deployment of embryonic head patterning mechanisms (Linz and Moczek, 2020). These mechanisms are largely conserved not

just across insect orders, but bilaterian phyla broadly, and likely instructed components of embryonic head formation in the embryos of our urbilaterian ancestor. Except that in horned beetles they now also, at a much later stage in development, pattern, shape, and position head horns within the dorsal head capsule. Head horns thus fail to relate to the affinities we previously unearthed between thoracic horns and wings. Instead, their innovation appeared to have been enabled at an earlier point in the innovation gradient, though yet again a point marked by the re-use and re-configuration of an ancient gene network and associated ancestral tissues, both pre-dating the invention of head horns by several hundred million years (Fig. 1).

How do these discoveries help us reconcile descent with modification with the origins of novelty? First, they suggest that when we imagine innovation as a gradient, there is no true beginning, at most there may be key events along the way. Second, they underscore that we need to let go of the notion that morphological novelty can somehow exist in the absence of ancestral homologies, and instead redirect our attention to *how* ancestral homologies scaffold and bias the innovation gradient to facilitate hotspots of innovation in some places, and deep conservation elsewhere.

Declaration of Competing Interest

The authors report no declarations of competing interests.

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