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SYMPOSIUM INTRODUCTION

An Introduction to an Evolutionary Tail: EvoDevo, Structure, and Function of Post-Anal Appendages

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Synopsis Although tails are common and versatile appendages that contribute to evolutionary success of animals in a broad range of ways, a scientific synthesis on the topic is yet to be initiated. For our Society for Integrative and Comparative Biology (SICB) symposium, we brought together researchers from different areas of expertise (e.g., robotosists, biomechanists, functional morphologists, and evolutionary and developmental biologists), to highlight their research but also to emphasise the interdisciplinary nature of this topic. The four main themes that emerged based on the research presented in this symposium are: (1) How do we define a tail?, (2) Development and regeneration inform evolutionary origins of tails, (3) Identifying key characteristics highlights functional morphology of tails, and (4) Tail multi-functionality leads to the development of bioinspired technology. We discuss the research provided within this symposium, in light of these four themes. We showcase the broad diversity of current tail research and lay an important foundational framework for future interdisciplinary research on tails with this timely symposium.

Introduction

Tails are extremely versatile appendages that contribute to the evolutionary success of animals in remarkable ways. They play key roles in mating displays, territorial disputes, and mediating predator-prey interactions (e.g., Andersson 1992; Hawlena 2009; Putman and Clark 2015). They can also be reduced, elongated, prehensile, round or angular, or covered in spines (e.g., Hickman 1979) (Fig. 1). Tails are fundamental to locomotion for many animals as well as bio-inspired robotic designs, providing propulsion in water and on land, stabilisation, maneuvering, and grasping in trees (e.g., Hsieh 2016; Persons and Currie 2017; Vidal and Diaz 2017; Fish et al. 2018; Saab et al. 2018). They are common to all chordates and analogous structures have arisen convergently in numerous invertebrate species. This simple fact that tails persist as a common structure of the basic animal body plan emphasises their evolutionary importance. Yet, compared to appendages such as legs, tails are vastly understudied. In contrast to other parts of the body (i.e., limbs or parts of the axial skeleton other than the tail), tails have not yet been the focus of a scientific synthesis to bring to bear the power of integrative and comparative approaches.

This was the impetus for our symposium, for which we brought together speakers from all over the world, representing a multitude of career stages and research interests, to try to jumpstart a new scientific synthesis. In this and a subsequent issue, authors present cutting edge research that will serve as a foundation on which to build a broader synthesis of tail evolution and function. Contributions from across disciplines provide insightful examples from individual species, while comparative studies hint at potential unifying themes within and across clades. For organizational purposes, the symposium was arranged into broad categories. However, the vast degree of overlap and the challenges of placing individual studies into a single category underscores the interdisciplinarity inherent in tail research. Here, we highlight four main themes which emerged about tail research: (1) "Tail" is a term that is used colloquially, and as such, defies attempts at a formal definition, (2)

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Fig. 1 Selected variation of tail shapes across the animal kingdom. Tails from a primate (A), fish (B), cheetah (C), chameleon (D), kangaroo rat (E), ringworm (F), whale (G), deer mouse (H), alligator (I), and gecko (J). Research related to tails A, B, C, D, E, G, H, and J was highlighted in this symposium. Drawing by Brooke Christensen.

By studying tail development and regeneration, we not only learn about the evolutionary origins of tails but can also use this information to inform our understanding of the rest of the axial and appendicular skeleton, (3) Although tail morphology is tightly correlated with its function, natural selection drives specializations that make identifying the key characteristics critically important, and (4) Tails are highly multi-functional, making them of particular interest for bioinspired technology.

How do we define a tail?

Among all chordates, the tail is defined as the axial portion of the body extending beyond the anus, or the post-anal appendage (Brown et al 2008; Fodor et al. 2021a). Remarkably, the developmental generation of cells to elongate the tail is due to a conserved *wnt/brachyury* signaling mechanism found in a number of animal phyla, including vertebrates and invertebrates (Holland 2002; Martin and Kimelman 2009). Yet, some tail-like appendages in invertebrates defy the established definition for chordates. In the chordate nonfeeding ascidian tadpoles, for example, there is no mouth or anus, but there is a clear head and tail (Fodor et al. 2021b). During metamorphosis in ascidians, the larval tail undergoes apoptosis and is phagocytized, and the sessile adult has a U-shaped gut (Fodor et al. 2021a). For a different example, malacostracan crustacean "tails" (e.g., shrimp and lobsters) are actually an elongate abdomen that is flexed when startled, to promote a rapid retreat (Arnott et al. 1998), but the abdomen is specified developmentally by posterior *Hox* genes (Abzhanov and Kaufman 2000). Similarly, the scorpion "tail", also known as the metasoma, is an extension of the abdomen, with only the enlarged vesicle and stinger comprising the post-anal portion (Farley 2001). Vinegaroons possess a tail-like flagellum which is used for defense via distraction by waving, followed by the ejection of a chemical substance from the flagellar base to ward off potential predators (Schmidt 2009). This brings to question: Should tails be identified by location (i.e., post-anal appendage), developmental mechanism (i.e., expression of posterior *Hox* genes), function, or other characteristics altogether? How do we rectify analogous, "tail-like" structures among invertebrates and vertebrates? We hope that through this collection of papers in this and a subsequent Integrative Comparative Biology (ICB) issue, we highlight the extraordinary morphological, developmental, and functional diversity of tails, and challenge an eventual formalization of what "tail" truly means.

Development and regeneration inform the evolutionary origins of tails

Key to understanding the functional diversity of tails is a deeper knowledge of their evolutionary history and development. Vertebrate animals are divided into three regions that differ in the way that they develop: Head, trunk, and tail (Burke et al. 1995). Developmentally, the brain is formed first, then neural crest cells move outward and form the skull. The trunk region is where the major organs are housed, protected by the ribs, and the posterior tail is formed last, as all vertebrates develop from anterior to posterior (Burke et al 1995; Fodor et al 2021b). Anterior–posterior development in vertebrates is determined by the developmental gene *Hox* complex (Burke et al. 1995) and the tail is also specifically dependent on posterior *Hox* gene expression and *caudal* expression, as *caudal* mouse mutants lack a tail (Mallo 2010). In tetrapods, the posterior limb forms at the Hox 9/10 boundary in the somites, and the tail is determined by the posterior *Hox* genes, 10–13. Vertebrates have had two genome duplications, so they have four Hox complexes, A–D, except in teleost fish, that have an extra genome duplication and contain eight *Hox* complexes (Fodor et al 2021b). By this criteria, some invertebrates, for example, *Saccoglossus* hemichordate larvae, express posterior *Hox* genes in their tail (Lowe et al. 2003; Fodor et al 2021b). Remarkably, this posterior tail is used to wrap around sand grains to tether the larva on the ocean floor (Lowe et al. 2003). The invertebrate cephalochordates (amphioxus) also determine their chordate post-anal tail by a *Wnt/brachyury* posterior gene network, including *caudal* (Holland 2002) and delayed expression of the posterior *Hox* genes in the tail tissues at the larval and late larval stages (Pascual-Anaya et al. 2012).

Developmental mechanisms also play a key role in appendage regeneration and the retention of these developmental pathways into adulthood is believed to be at least partially responsible for observed differences in regenerative abilities among various taxa. For example, metamorphosis relies on similar developmental processes, so invertebrates and amniotes that undergo different life stages are more commonly capable of regenerating structures morphologically indistinguishable from the original, with minimal, if any, detectable loss of function (Alibardi 2020; Stocum and Cameron 2011). This includes salamanders and newts, which can replace a lost tail or limb with full segmentation and anatomical complexity intact (Joven et al. 2019). In contrast, regeneration in predominantly terrestrial amniotes—which notably lack metamorphic life stages—is limited to imperfect appendage regeneration with reduced function, as is seen among lizards (Alibardi 2020). Among lizards, the regenerated tail consists of a cartilaginous rod with significantly simplified neuromuscular morphology (e.g., Gilbert et al. 2013). Such morphological simplification can be correlated with decreased functional breadth, having differential impacts on performance. For example, tail autotomy may change the kinematics of prey capture for some geckos, but it does not necessarily alter success rate (Vollin and Higham 2021). And in another species of gecko, tail regeneration is associated with neuroplasticity, potentially underlying changes in neural control patterns required for locomotion or other tasks with a regenerated tail (Bradley et al. 2021).

Why regenerative capabilities differ and how they relate to evolutionary and ecological histories remain active areas of exploration. The ability to regenerate all body parts is ubiquitous among basal metazoan lineages, suggesting that the act of regeneration has deep evolutionary roots (Bely and Nyberg 2010; Alibardi 2020). This is further supported by the observation that general stages of healing and regrowth are mostly conserved across phylogeny (although see Ramon-Mateu et al. 2019), suggesting a strong presence of phylogenetic constraint (Dunoyer et al. 2020), with clear divergences that may indicate novel evolution of regenerative processes (Bely and Nyberg 2010). Among vertebrates, limb and tail regeneration follow what appear to be similar molecular mechanisms (Stocum and Cameron 2011), making tails an excellent model for understanding regeneration processes for both axial and appendicular appendages. Much remains to be discovered about the mechanisms, physiological impacts, and behavioral implications of tail loss and regeneration, and it has been identified as a key area of focus for future tail research.

Identifying the key characteristics highlights functional morphology of tails

Driven by the great diversity of tail form and function, much of the research on tails has focused on the underlying functional morphology. Given the importance of tails in the aquatic environment for propulsion, fish have provided an ideal model for exploring these structure–function relationships. It has long been known that body and fin morphology, and especially tail shape are reliable predictors of swimming performance and even habitat preference among fish (Webb 1982). Because tail shape strongly influences vortex wake structure (Wilga and Lauder 2004; Fish et al. 2021), it is possible for a tail to simultaneously produce thrust, stabilise, and generate lift during a single stroke (Lauder 2000; Nauen and Lauder 2002). Furthermore, the flexible nature of the tail and coordination of the fine intrinsic musculature facilitates nimble modulation of tail shape, further increasing its importance for rapid maneuvering (Flammang and Lauder 2009). Although somewhat less common, fish tails are also used for propulsion on land (Hsieh 2010; Hsieh 2013; Ashley-Ross et al. 2014; Gibb et al. 2013; Bressman et al. 2015). More recent work examining details of tail morphology and kinematics among fish and tetrapods, taking into account their drastically different material properties and flexibilities, have given additional nuance to how tail morphology affects function, as well as insight into the drivers for evolutionary, ecological, and behavioral patterns (Donatelli et al. 2021; Fish et al. 2021; Giammona 2021; Mekdara et al. 2021; Naughton et al. 2021).

Surprisingly, tails can also perform non-locomotor tasks underwater, most commonly used as an anchor, to help animals grasp stationary objects within their environments (e.g., seahorses and pipefish: Weber 1926; Blake 1976; Porter et al. 2015). Such prehensility has fascinated scientists for centuries. Animals such as opossums (e.g., Hamilton 1958) and new world primates (Karrer 1970) are just some additional models that have been used to examine this behavior. Currently, cutting edge analyses of chameleon tails have begun to identify how vertebral shape and muscle arrangement enable force production during prehensile grasping (Luger et al. 2021).

While tails are fundamental for locomotion for many species in a wide range of environments, their role in providing balance and maneuverability has received particular attention. In arboreal environments, tails are key to maintaining stability (Shield et al. 2021; Smith and Hilliard Young 2021; Young et al. 2021). When animals jump from elevated surfaces or leap high in the air, tails are able to control orientation, perform self-righting maneuvers, and provide dynamic stability to ensure a safe landing (Gillis et al. 2009; Libby et al. 2012; Clark et al. 2021; Fukushima et al. 2021; Schwaner et al. 2021a; Siddall et al. 2021).

Considering the importance of tails for all types of locomotion, it becomes even more important to understand the evolutionary drivers that may lead to tail length variability (Mincer and Russo 2020; Hager and Hoesktra 2021; Smith and Hilliard Young 2021) or why they may be lost, altogether (Fish et al. 2021).

Tail multi-functionality leads to the development of bioinspired technology

The extraordinary robustness and functional breadth of an object as externally apparently simplistic as a tail have attracted the attention of biologists and engineers who seek to emulate their performance in robotic systems (Fish et al. 2021; Liu and Ben-Tzvi 2021). For example, fish tails have long inspired investigations striving to understand their incredible efficiency of thrust production (e.g., Triantafyllou et al. 1993). This has also led to multiple groups to develop fish-like robots that can achieve or exceed the performance of an actual fish (e.g., Anderson and Chhabra 2002; Liao and Du 2014; White et al. 2021). On land, their utility for both stabilisation and maneuvering has led to tails being fitted to wheeled robots, both to better understand the physical mechanism of aerial stabilisation (Jusufi et al. 2010; Libby et al. 2012), as well as to emulate the hunting behavior of cheetahs replete with rapid directional changes (Patel and Braae M 2014). This, in turn, has inspired researchers to explore tail shapes and their effect on stability in maneuvers (Shield et al. 2021; Lui and Ben-Tzvi 2021). Combining these data with mathematical and physical modeling approaches can help define the limits of tail performance and explore the capacity of inertial reorientation maneuvers (Schwaner et al. 2021b).

Conclusion

The most recent comprehensive review of animal tails was by Hickman in 1979, which examined only mammalian tails (although Saab et al. 2018 more recently reviewed robotic tails). This shows that despite a common interest, there has been no opportunity to bring tail related research together. Research on tails continues in a broad range of fields, from evo-devo to behavior to robotics, but these fields remain largely isolated from one another. This symposium and ICB special issue are a first step towards a foundation of scientific synthesis of tails and tail-related research with an interdisciplinary approach.

Tails are key to the evolutionary success of many animals and yet, the topic of tails has not received similar attention as other appendages, such as limbs, for example. Here, we lay a small foundation for what can be great interdisciplinary and collaborative research endeavors. Much about tails remains to be discovered. For example, mechanisms of tail development and evolution, regeneration, functional morphology, their role in sensorimotor control, and their application in physical and computational models. These topics have been identified as key areas of focus for future tail research and are highlighted in a forward-looking article at the end of this issue (Schwaner et al. 2021b).

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Data Availability

No data available for the article.

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