Accounting For Vertebrate Limbs: From Owen's Homology To Novelty In Evo-Devo

A Review Of Richard Owen's *On The Nature Of Limbs: A Discourse*
Edited By Ron Amundson
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Ingo Brigandt§

This article reviews the recent reissuing of Richard Owen's On the Nature of Limbs and its three novel, introductory essays. These essays make Owen's 1849 text very accessible by discussing the historical context of his work and explaining how Owen's ideas relate to his larger intellectual framework. In addition to the ways in which the essays point to Owen's relevance for contemporary biology, I discuss how Owen's unity of type theory and his homology claims about fins and limbs compare with modern views. While the phenomena studied by Owen are nowadays of major interest to evolutionary developmental biology, research in evo-devo has largely shifted from homology (which was Owen's concern) towards evolutionary novelty, e.g., accounting for fins as a novelty. Still, I argue that questions about homology are important and raise challenges even for explanations of novelty.

KEYWORDS

Richard Owen • Morphological Type • Homology • Vertebrate Limbs • Evolutionary Novelty

On February 9, 1849, Richard Owen gave a public lecture entitled "On the Nature of Limbs," at an evening meeting of the Royal Institution of Great Britain in London. This lecture laid out to a general audience Owen's notion of homology in general, and his account of vertebrate limbs in particular. Earlier, in 1843, Owen had defined a homologue as the "same organ in different animals under every variety of form and function" (Owen 1843, p.379). The 1848 book On the Archetype and the Homologies of the Vertebrate Skeleton had introduced his sophisticated theoretical and observational framework in comparative morphology. Now in the 1849 lecture, Owen forcefully argued for fins as found in different groups of fish and limbs as occurring in different tetrapod taxa being homologous, by pointing to homologies among the individual skeletal parts of fins and limbs. Published in the same year under the title On the Nature of Limbs, this lecture, together with On the Archetype, marks Owen's most innovative contribution to comparative biology, which made him the most prominent naturalist in Britain before Darwin.

Nowadays the evolutionary origin of fins and their transformation into limbs is still a problem motivating ongoing research efforts (Freitas et al. 2006). Major questions include how fins arose and diversified, how they were transformed into limbs, and how in some lineages limbs were transformed into flippers or wings. In general, the explanation of the origin of evolutionary novelties is a major focus of contemporary evolutionary biology, in particular in the context of evolutionary developmental biology. As a result, 19th century morphological studies on fins and limbs are now of interest not only to historians of

§ Department of Philosophy, 2-40 Assiniboia Hall , University of Alberta
Edmonton, AB T6G 2E7 Canada
✉ E-mail: brigandt@ualberta.ca

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science, but also to biologists. This increased recognition of Owen's work is reflected by University of Chicago Press's recent reissuing of On the Nature of Limbs: A Discourse. Edited by Ron Amundson, this volume contains a facsimile of the 1849 text (119 pages plus plates), (1) preceded by a preface by evolutionary developmental biologist Brian Hall and three original essays by philosopher Ron Amundson, paleontologist Kevin Padian, and historians Mary Winsor and Jennifer Coggon (this novel material spans 102 pages). These very well-written introductory essays complement each other by discussing the historical context of Owen's work, explaining how Owen's ideas in this treatise relate to his larger intellectual framework, and pointing to the relevance for contemporary biology. This makes the reedition of On the Nature of Limbs accessible to everyone not familiar with Owen's work and a pleasure to read. (2)

In the preface, Brian Hall—known for his research on the evolution and development of skeletal tissues and as an editor of a volume on the fin-limb transition (Hall 2006a)—highlights the relevance of Owen's treatise to modern research. Building on Owen's clear distinction between homology and analogy and his demonstration of the homology of fins and limbs, Hall documents how we now recognize their homology on all levels of organismal organization, including the cartilage based endoskeleton of fins and fish, conserved tissue and cell interaction in fin/limb buds, and homologous genes and gene regulatory networks. Among other things, Owen was aware of patterns of digit loss in tetrapods, where the "first or innermost digit [thumb or big toe], as a general rule, is the first to disappear … The outer digit ... is the next to disappear" (p.35). This comparative pattern is now interpreted in a strictly phylogenetic framework, and still in need of a detailed mechanistic-developmental explanation, as Hall points out, mentioning also other major current questions about the evolution of fins and limbs. Owen also discussed various theories of his contemporaries that attempted to explain the nature and origin of limbs by hypothesizing them as either modified vertebrae, liberated ribs, or modified gill arches and opercular bones. Given that Owen and his contemporaries studied limb development to shed light on their transformation across various vertebrate taxa, Hall perceives a parallel to current evolutionary developmental biology, which integrates paleontological data with the causal study of developmental mechanisms in order to account for the evolutionary origin and transformation of structures such as fins and limbs.

A typology of Owen's and rival theoretical frameworks

Kevin Padian's essay "Richard Owen's Quadrophenia: The pull of opposing forces in Victorian cosmogeny" relates Owen's theoretical views to several other contemporary or earlier morphological schools. Some aspects of each appealed to Owen, but as a whole most of these traditions were strongly in opposition, so that rather than being perceived as offering an approach that reconciled conflicting views, Owen often faced the difficult task of navigating between all of these rival doctrines. Padian offers a clear exposition of the basic conceptual framework of Owen's morphological theory. This makes Padian's essay especially useful to those readers who have not yet made acquaintance with Owen's theory of homology and archetypes.

In addition to the conceptual distinction between homology and analogy, Owen made successful use of several criteria of homology (the positional, the histological, and the embryological criterion). While the idea of homologies across species—which Owen called special homology—is nowadays known to everyone, Padian emphasizes that Owen's theoretical framework is complete only with his notion of serial homology and general homology, culminating in the theory of the vertebrate archetype. Serial homology is the occurrence of corresponding morphological elements in different parts of the body; and Owen endorsed the vertebral theory of the skull according to which the bones of the skull are modified vertebrae. The most distinctive and innovative element of Owen's theory is the idea of an ideal typical vertebra, which is not just a vertebra (or an individual bone), but a whole body segment consisting of several morphological elements (Fig.1). In an actual organism, a vertebra body corresponds to the centrum, while the attached ribs correspond to further parts of the ideal typical vertebra (e.g. the pleurapophysis and the hæmapophysis). This yields the notion of general homology, the identification of a bone in an organism with the correct morphological part of the ideal typical vertebra. Moreover, Owen assumed that in the skeleton of a vertebrate every segment along its longitudinal axis is an ideal typical vertebra in a transformed fashion.

This idea is encapsulated in the vertebrate archetype as a series of ideal typical vertebrae, transformed according to their position along the axis, in particular when forming the skull (Fig.2). Thus, Owen postulated a unity of type in two dimensions. The skeletons of different vertebrates contained the same morphological elements (transformed in their form and function across species), and the skeleton of one vertebrate contained the same set of morphological elements in each segment along the axis (transformed in their form and function along the axis).

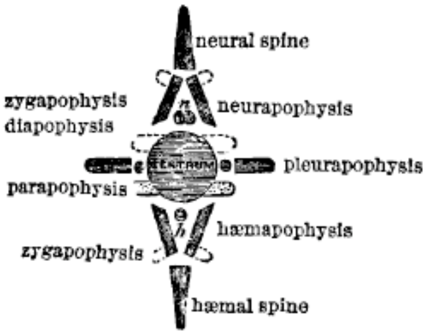

Fig 1: Ideal typical vertebra

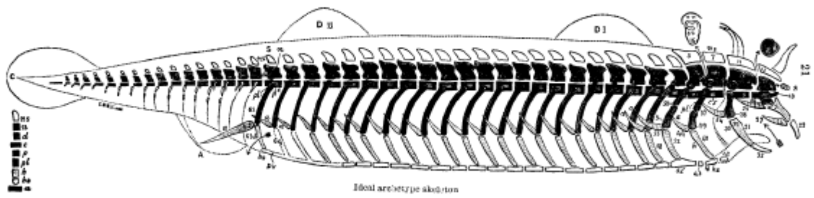

Fig 2: The vertebrate archetype

As a result, a morphological account of an individual bone consists in a three-fold task: 1) to identify it with corresponding bones in other species (special homology), 2) to identify the segment along the body axis to which it belongs, and 3) to identify the part of the ideal typical vertebra which it represents (general homology). Owen's account of the nature of limbs attempted to answer these questions for the fins in different fish and the limbs in different tetrapods. (3) Owen admitted strongly transformed and even shifted segments, and attempted to identify the skeletal elements of fins and limbs in various species with particular parts of the ideal typical vertebra and the archetype by working from the most proximal elements (e.g. the shoulder blade) toward the most distal elements (digits and fin rays), using relative position as a guide. For instance, the human shoulder blade is a pleurapophysis element (of the ideal typical vertebra). The shoulder blade is homologous to a specific bone of the pectoral fins in lungfish (the rib of the occipital vertebra), which is likewise a pleurapophysis, so that a correct establishment of general homology permits an inference to other species (p.71).

Padian is impressed by the amount of detailed comparative data presented and discussed by Owen, who moved "among a tremendous variety of features and taxa, with an intimate understanding of development, connections, variation within groups, and anomalies" (p.LXVII). There are also examples where Owen considered structures to be homologous while pointing out that they develop out of different precursors. This foreshadows the important fact that homologies on different levels of organization (genes, developmental processes, anatomical structures) need not align (Brigandt 2006). While to us it may seem very odd to think of the skull as fused, transformed vertebrae, Padian notes that this grows out of an in principle legitimate practice of Owen's, namely focusing on the most simple forms to establish homologies, as these have undergone the least modification (p.15). "This is why he used the fishes so extensively" in his discussion of limb homology and transformation (p.LIX), including the lungfish Lepidosiren (pp.51, 55)—from a contemporary phylogenetic perspective likewise an essential data point. While Owen's archetype has often been construed as a Platonic ideal form (see below), it is in fact the very opposite of the most perfect and complex form, by representing a very primitive condition and looking "rather like a bony amphioxus" (p.LXII). (4) Even though Owen packaged his public lecture in pious references to a creator, Padian points out that Owen's perspective was broadly evolutionary by discussing in detail the transformation of skeletal elements across different vertebrates and endorsing the progression of fossil life through geologic time.

The most insightful aspect of Padian's introductory essay is how he locates Owen within rival contemporary approaches. Padian is well aware of the fact that Owen took over several ideas from earlier approaches, but as these were conflicting intellectual schools, Owen faced the constant need to hide or rhetorically denounce some of their controversial aspects while at the same time pandering to his forebears whenever opportune. The ingenious title "Richard Owen's Quadrophenia" reflects that (according to Padian) there were four opposing forces which Owen was drawn to as well as repulsed by. This phrase stems from The Who's rock opera "Quadrophenia", wherein the young protagonist, being torn by loyalty to different people and ideas, exclaims "Schizophrenic? I'm bleedin' quadrophenic!" In the case of Owen, the two parties on the side that Padian characterizes as more evolutionist and developmentalist were Geoffroy Saint-Hilaire, who earlier had emphasized homology and the unity of type, and the German transcendentalists, who had defended the notion of developmental transformation and the vertebral theory of the skull. The two influences on the more anti-evolutionist side were Cuvier and the British Paleyites, the latter forming a major source of career support for Owen. Geoffroy and Cuvier had of course conducted the largest scientific dispute in the first half the 19th century, with one emphasizing homology and form over function, and the other privileging function (Appel 1987; Russell 1982[1916]). The German transcendentalists worshipped pantheism, rejected authority, and favored speculative intellectual intuition, very much in opposition to the Christian conservatism of the Paleyites and the careful empiricism of British philosophy. As a fifth possible player Padian identifies the London medical school morphologists, who favored a materialistic philosophy and possibly even atheism (Desmond 1989). This discussion nicely illustrates that Owen's intellectual development and the presentation of his scientific views was also contingent on philosophical and religious considerations.

Regarding the question of what Owen has to teach modern biology, Padian notes that most elements of Owen's theoretical framework are not endorsed any longer, in particular the vertebral theory of the skull and the more general theory of the vertebrate archetype based on the notions of general homology and the ideal typical vertebra. Apart from the idea of serial homology, which continues to resonate for some morphologists, Padian views Owen's criteria of homology—that permit the reliable establishment of homologies even in the absence of well-confirmed phylogenetic trees—as his main heritage.

Interpreting animal form, interpreting the history of science

"Richard Owen and animal form" by Ron Amundson is my favorite among the introductory essays. For it works closely to Owen's text and relates various passages to the historical background and modern interpretations of Owen. Like Padian, Amundson addresses how Owen's scientific development and the presentation of his ideas were influenced by his efforts at career building. Amundson's main aim is to dispel modern misinterpretations of Owen's views, including their motivation and relevance. In particular Owen's notion of the archetype has often been denounced as an idealistic version of the argument from design, thereby erroneously suggesting that Owen was primarily engaged in a debate between special creation and evolution rather than between form and function. By doing so Amundson does not present novel historical discoveries, as the earlier work of Owen's intellectual biographer Nicolaas Rupke (1994) has provided a good deal of the material for a reevaluation of Owen. But Amundson spreads recognition for a recent historiographic perspective that has come to reject the idea that pre-Darwinian taxonomy and morphology was governed by essentialism (Winsor 2003; Amundson 2005).

Whereas functionalists explain morphological features in terms of adaptive considerations—thereby viewing animal form as being due to functional demands—structuralists emphasize morphological unity across species—conceiving the adaptive modification of structures as secondary. Amundson views Owen's achievement as turning British biology to structuralism based on three steps. First, Owen showed that a functionalist or teleological approach cannot account for many biological facts. Second, he tried to show that structuralism—despite its transcendentalist and pantheist roots—can be construed so that it accords with British empiricism and Christian piety. Third, Owen raised controversy by hinting at the fact that a structuralist approach can contribute to an understanding of the natural causes of species origins.

Amundson points to various passages and examples of Owen's where he argued that a comparative approach and the notion of unity of type is needed to understand biological facts that cannot be accounted for based on the idea that the characters of a species are created for certain functions or adaptive purposes.

For instance, the bones of a human infant's skull are not fused, which does in fact aid in child birth. Yet a look beyond a single species shows that in a bird the corresponding bones are present in the same arrangement, a fact which a teleological approach cannot explain (p.40). While a functionalist may explain the reduced number of phalanges in the big toe based on its use in human walking, Owen points out that in seals and elephants this digit is likewise reduced, even though it faces the same functional demands as the animals' other, non-reduced digits (p.37).

In spite of Owen's anti-functionalist considerations ("I think it will be obvious that the principle of final adaptation fails to satisfy all the conditions of the problem", p.39), some of his writings did construe the vertebrate archetype as a Platonic form, suggesting that it is an abstract idea in the mind of the creator. To relieve this tension, Amundson points to what Rupke (1994) earlier uncovered. In contrast to his earlier discussions, Owen started to give a Platonic interpretation of the archetype from 1848 on; and he did this based on the explicit suggestion by the Cambridge conservative William Conybeare. So Owen Christianized the archetype as part of his career efforts, which involved appeasing or gaining the patronage of the Oxbridge Paleyites, to whom the structuralist aspects of Owen's theory were suspect, especially given their pantheist heritage. (5) Amundson makes plain that despite these theoretical concessions and the pious rhetoric used, On the Nature of Limb contains several passages that show that Owen did not view the Platonized archetype as an idealistic version of the argument from design. For Owen argued explicitly that a difference between human inventions designed for a purpose and morphological organization in nature is that an artifact is directly adapted to its purpose, so that different artifacts are independently designed and exhibit no common plan. When stating that "There is no community of plan or structure between the boat and the balloon" (p.10), Owen referred to the shipwright analogy that Conybeare had suggested to him, but actually turned Conybeare's argument from design on its head, as Amundson points out. On the penultimate page, Owen reiterated that "The fallacy lies in judging of created organs by the analogy of made machines" (p.85). (6)

An interesting and scholarly novel aspect of Amundson's essay is his discussion of how Owen successfully argued that his structuralist approach was compatible with British empiricist philosophy—highlighting the need for Owen to dissociate himself from the transcendentalist philosophy of German idealism and Naturphilosophie as a major historical root of the unity of form notion. In earlier decades the cross-species identification of morphological elements that differ substantially in form and function may have been viewed as an identification or transformation carried out in the imagination only. But now Owen was in a position to make recourse to clear-cut criteria of homology, so as to argue that an observational practice in line with a careful empiricism permits homologizing morphological elements in taxonomically quite unrelated species. In contrast to earlier schools of comparative anatomists who referred to morphological structures by lengthy descriptions of their form or position, Owen introduced a short name for each bone across all vertebrates, following Lockean philosophy according to which names are arbitrary symbols devoid of theoretical interpretation.

Amundson also mentions aspects of Owen's work where he discussed causes of morphological diversity and hinted at natural causes of species origins. Especially in his earlier work, before interpreting the archetype as a Platonic form (as in On the Nature of Limbs) Owen had offered an explicitly causal approach to structural diversity within vertebrates, more precisely an explanation in terms of differential development in different taxa. Owen postulated two basic forces governing development. The first one generates the repetition of morphological elements and accounts for the unity of type both across species (special homology) and within organisms (serial homology). The second force adapts each of these parts to its specific functional contingencies, accounting for why a homologue varies in form and function across species and why serially homologous structures differ (e.g. vertebrae along the body axis). Of course this falls short of a genuinely historical explanation. Yet Amundson points out that Owen's account in terms of phenomenal laws had the advantage of sticking to what Owen could empirically back up based on detailed comparative observation rather than engaging in speculations about historical or ultimate causes. Even in On the Nature of Limbs, Owen hints in the concluding sentences at the idea that there are natural causes of species origins: "To what natural laws or secondary causes the orderly succession and progression of such organic phænomena may have been committed we are as yet ignorant. But … we learn from the past history of our globe that she [i.e. nature] has advanced with slow and stately steps … from the first embodiment of the Vertebrate idea under its old Ichthyic vestment, until it became arrayed in the glorious garb of the Human form" (p.86). Many modern interpreters have overlooked this passage's evolutionary implications. But a few of Owen's contemporaries did not and went on to criticize him on this point.

While acknowledging that Owen and Darwin pursued distinct research goals (the explanation of form vs. the explanation of change), Amundson points to some positive influences Owen had on Darwin. In his 1844 essay, Darwin had lacked Owen's clear conceptual distinction between homologies and analogies. Darwin had known that the unity of type can be explained by common descent, but Owen's anti-functionalist arguments helped Darwin to see that the unity of type is independent of adaptive considerations and why homologies but not analogies establish taxonomic relatedness. In the Origin of Species, Darwin used Owen's work on the unity of type to argue against the idea that species are independently created, as the argument from design of the Paleyites had it. Finally, Amundson hints at the fact that while Darwin is viewed as the founder of evolutionary biology, in the second half of the 19th century evolutionary morphology made scant use of the notion of natural selection, so that its comparative studies and phylogenetic explanations owed a good deal to Owen. Many contemporary evolutionary developmental biologists view evolutionary morphologists as intellectual precursors, and Amundson rightly hopes that the reedition of On the Nature of Limbs will contribute to Owen be seen in the lineage to evo-devo.

From Owen's homology to novelty in evo-devo

The introductory essays to the University of Chicago Press reedition of On the Nature of Limbs nicely set the stage for Owen's original 1849 text by laying out and analyzing the relevant intellectual and historical background. This makes this volume of particular interest to biologists and philosophers. At this point I offer some additional considerations on the relevance of Owen's work for contemporary research.

After the advent of Darwinian evolutionary theory, the notion of homology continued to be of central importance to comparative biology. However, while this clearly holds for Owen's special homology—homologies across species—the idea of serial homology became increasingly less relevant for a phylogenetic approach. In the last few decades, however, developmental approaches to homology have taken a more favorable view of serial homology (Wagner 1989). The idea is that different structures of an individual develop by the same basic developmental processes operating in different part of the body, or that different structures are governed by similar developmental constraints. If it is the case that two structures develop based on a basic ancestral developmental mechanism that was reused, these two serial homologues show a similar range of possible intergenerational phenotypic variation and thus are similar in their morphological evolvability. To the extent that some sort of duplication of developmental processes can generate an additional body segment or a repeated morphological unit, this sheds light on the generation of some kinds of evolutionary novelties. Thereby contemporary discussions of homology tap into modularity and novelty as core notions of evolutionary developmental biology (evo-devo).

A major aim of current evo-devo is to account for evolvability, the ability of developmental systems to generate heritable phenotypic variation. While Owen and other morphologists of his time have been accused of being typologists that ignore variation, their transformational approach was in fact predicated on the idea that a homologue can vary substantially across different vertebrates, being the "same organ in different animals under every variety of form and function" (Owen 1843, p.379). In the Nature of Limbs, Owen even saw the possibility of vertebrate forms beyond those of organisms that have inhabited the earth (p.83). Yet he was less concerned with explaining how it is possible for a homologue to exhibit variation; instead he started out with the comparative study of variation in order to detect the natural morphological units that vary across species. Finding a developmental-mechanistic explanation of evolvability as the potential for morphological variation is a focus of current research. While some features of an organism vary in a correlated fashion, other parts can vary largely independently of each other, so that they are different modular variational units. In this fashion, Owen's idea of a body being composed of different homologues as units of morphological variation is germane to contemporary explanations of evolvability and morphological covariation structure (Brigandt 2007; Jamniczky 2008).

Owen's account of the nature of limbs was a detailed comparative application of his theoretical framework on homology and the archetype. Despite the awareness in contemporary thinking of homologies on all levels of organization and regular use of the notion of conserved body plans, Owen's understanding of the unity of type—extending in two dimensions—is not acceptable to us any longer. Along the body axis, the idea that the skull and limbs are just transformed parts of ideal typical vertebrae strikes us as outlandish. Across species, we are more cautious by not assuming that all fin and limb elements in different vertebrates can be homologized. For instance, nowadays it is often assumed that the digits of tetrapod limbs are not homologous to any part of fish fins, and thus arose as a morphological novelty (Hall 2006b). Accounting for 'the nature of limbs' makes it necessary to explain how they originated in evolution. Thus, unlike Owen we are aware of the prevalence of genuine novelties in evolution, in the sense of structures that are neither homologous to any ancestral structure, nor just a duplication of a feature that already existed in another part of the body (Müller and Wagner 1991). To the extent that there are shared body plans ('archetypes'), their very evolutionary origin—an instance of morphological novelty—is likewise in need of explanation. However, it is easy to criticize Owen's vision of a unity of type, and it does not yield a positive account of a structure deemed a novelty. Explaining the evolutionary origin of a structure that is not just a transformation of a homologous ancestral structure is a demanding task, and a mechanistic explanation of the generation of novelty is a largely open problem for contemporary biology. This also holds for the explanation of the evolution of fins and limbs.

In the second half of the 19th century, the thriving discipline of evolutionary morphology established relationships between species and studied morphological evolution. Around the turn of the century, however, it lost in significance, largely ceding to experimental embryology as an approach concerned with the experimental study of model organisms but not with comparative or phylogenetic questions. A major reason for the decline of evolutionary morphology—which is also instructive in the context of novelty in evo-devo—were disputes about the proper method of arriving at phylogenetic scenarios that could not be resolved (Nyhart 1995). Some researchers favored the comparison of adult morphological structures to establish homologies and relations between taxa. Others preferred using embryological data. Yet morphological and embryological methods led in some cases to conflicting interpretations as to which structures were homologous and from which ancestral features extant structures had evolved. The symptomatic debate concerned the evolutionary origin of paired fins in fish—still a core issue for contemporary studies (Freitas et al. 2006). The gill-arch theory claimed fins to be derived from the two hindmost gill arches, which had migrated from the head to form the pelvic and pectoral fin girdles, with the rays of the gill arches becoming fins. This hypothesis was supported by the comparison of adult fins and girdles. The rival side-fold hypothesis assumed that paired fins had evolved from lateral folds that had formed (originally in a continuous manner) lengthwise along the fish's side, and which later evolved rays and were broken up into pectoral and pelvic fins. This theory was favored by embryological methods, viewing other taxa as representing the basal condition compared to the gill-arch theory. The clash between morphological and embryological methods was never resolved; and there was no resort to interpretation-free comparative data: phylogenies were questioned by homology assessments, and revised phylogenies led to changed accounts of homology and character evolution.

Similar to 19th century evolutionary morphology studying evolutionary novelties, which used embryology to theorize about the patterns and processes of phylogenetic transformation, contemporary evo-devo uses development to explain the evolutionary origin of novelties. For this reason Günter Wagner (2007) points to the fate of evolutionary morphology as a lesson for current evo-devo. Yet while evolutionary morphology fell because of unsolved conflicts about how to infer patterns of morphological evolution, given modern reliable cladistic methods Wagner does not view this issue as a serious possible pitfall for current accounts of novelty. Instead, Wagner emphasizes that currently there is disagreement about the mechanisms accounting for various changes in the evolution of development. It is unclear which genetic, cellular, and developmental features account for evolutionary transformations and the origin of different novelties. For instance, are changes in homeotic genes and their regulation driving the transformation, or are they just the result of secondary developmental modifications that took place after the key evolutionary transformation? Even more worrisome, according to Wagner there is also no agreement about which data and inference methods are best suited to arrive at a theory of the developmental-mechanistic basis of evolution.

Despite the currently popular focus on mechanisms of variation generation, there are still open challenges regarding the assessment of particular homologies. Well-confirmed phylogenies are a precondition for any account of novelty, yet in some cases classical and molecular data lead to conflicting phylogenies, and there are currently no generally agreed upon methods of combining both kinds of data (Gura 2000). Claims about actual patterns of structural transformation and whether or not structures in a descendant are homologous to some ancestral features can also be controversial in many cases. For instance, while the neural crest is considered a novelty of vertebrates, it may have some precursor in urochordates (Jeffery et al. 2004). Yet even if a morphological structure's components on lower levels of organization (tissues, cells, gene expression patterns) are homologous to ancestral features, this does not imply that the morphological structure itself—the neural crest as a character found in vertebrates in this case—is homologous to some ancestral character (Stone and Hall 2004). Characters exist on several levels of organization, and homologies on different levels can be decoupled, which raises questions as to what delineates a character from other characters on the same and lower levels (Brigandt 2007). It is often assumed that in the transition from fish fins to tetrapod limbs, the bones of the fin (except the fin rays) were transformed into the stylopodium and zygopodium of the limb (upper and lower arm/leg), with the fin rays being lost and the limb autopodium (hand/foot)—especially the bones of the digits—originating as a genuine novelty (Wagner and Larsson 2006). However, recent paleontological evidence suggests that tetrapod digits are derived from pre-existing fin radials (Boisvert et al. 2008).

In the case of the bird wing where two of the five digits have been lost in evolution, there are remaining uncertainties about the homology of the other three digits. Paleontological evidence suggests that the extant digits are DI, DII, and DIII, while developmental evidence suggests that DII, DIII, and DIV remain because in bird ontogeny the digits develop from what seems to be condensations CII, CIII, and CIV. One way to solve this apparent conflict is to postulate a developmental frame shift, according to which condensation CII ancestrally developed into DI not DII, and likewise for CIII giving rise to DII and CIV developing into DIII (Wagner 2005). There is now molecular developmental evidence supporting this scenario and new paleontological support has become available (Xu et al. 2009). While this largely resolves the earlier conflict, without a mechanistic explanation of how such a developmental frame shift is possible—or in case of the emergence of evidence that it is developmentally very unlikely—the frame shift hypothesis may be challenged again. This shows that answering a question that seems to be purely about patterns of character transformation may make it necessary to consider additional information about processes, leading to additional complications for assessing homology and the identity of characters.

We no longer buy into Owen's overarching unity of type theory and his homology claims about fins and limbs; and the focus of explanation has shifted from homology towards novelty. Yet a mechanistic explanation of novelty in evo-devo does make it necessary to first get clear about which structures evolved out of which ancestral features and which other structures originated as genuine novelties. Owen could back up many of his homology tenets by a consensus within his community (p.46), while the above examples show that in the last few decades views about some structures have oscillated between homology and non-homology. Thus, we still have to ponder hard questions about homology and character identity just like Owen did.

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NOTES

(1) The plates are also available at http://www.press.uchicago.edu/books/owen.

(2) Another expression of the current interest in Owen is the publication of a revised version of Nicolaas Rupke's intellectual biography of Owen by University of Chicago Press (Rupke 2009, originally published as Rupke 1994).

(3) See Plate 1 at http://www.press.uchicago.edu/books/owen for how Owen identified skeletal elements in different vertebrates with parts of the ideal typical vertebra and the vertebrate archetype.

(4) Despite the usefulness of model organisms for modern developmental biology, their relevance for phylogenetic studies such as evolutionary developmental biology is more contentious, as they are highly derived species. Within evo-devo there are still debates as to how to chose alternative model organisms whose development better represents basal forms (Jenner and Wills 2007).

(5) The way in which social context influenced Owen's framing of his ideas is also addressed in the third introductory essay "The mystery of Richard Owen's winged bull-slayer," wherein Mary P. 'Polly' Winsor and Jennifer Coggon uncover a historical nugget. On the frontispiece of On the Nature of Limbs is a drawing showing the outlines of a winged angel who is about to cut the throat of a kneeling bull (see http://www.press.uchicago.edu/books/owen). Within the outlines of these two beings the skeleton of a human and a bull are shown, with the bones of the limbs being numbered and homologous bones having identical numbers. Owen clearly used this to illustrate to the general audience of his lecture the various homologies among the parts of the human arm and the forelimb of a non-human species and likewise for the leg and the hindlimb. However, it has been unknown why Owen chose an angel and a bull and what artistic image or story (a biblical motif?) was his inspiration and likely to be recognized by his audience. Due to recent research in London by Coggon, it turns out that the 'angel' is not a Christian image at all. To avoid spoiling the fun of reading Winsor and Coggon's actual essay, I carefully refrain from revealing the image's meaning. Owen got the image from a marble sculpture, which still exists. Furthermore, Winsor and Coggon discuss why the image would have captured the attention of Owen's audience, in part because bulls were prominently featured in the London news of the late 1840s.

(6) Just like the Paleyites, in their 'argument from design' current proponents of intelligent design claim organisms to be like artifacts, portraying even cellular and molecular structures as machine-like. But cellular features exhibit differences from machines as well, which are essential to understanding the developmental plasticity and evolvability of organisms (Kirschner et al. 2000).

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