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11 Embryology and Morphology

INTRODUCTION

On December 14, 1859, less than a month after the publication of the *Origin of Species*, Darwin wrote to his confidante Joseph Hooker, "Embryology is my pet bit in my book, & confound my friends not one has noticed this to me" (*Correspondence*, 7: 431–2). Given the overwhelming mass of material presented in the *Origin* and its range across geology, geographical distribution, artificial and natural selection, hybridism, instinct, and classification, perhaps his friends could have been forgiven for having failed to recognize Darwin's pet bit. Indeed, the study of individual development in the *Origin* presents something of a paradox. As a special aspect of morphology, the study of the laws of organic form, embryology offered key evidence for community of descent. Darwin wrote that morphology was "the most interesting department of natural history, and may be said to be its very soul" (*Origin*, 434). The comparative study of the embryo receives similarly heavy rhetorical weight: "community in embryonic structure reveals community of descent" (*Origin*, 449), and "Embryology rises greatly in interest, when we thus look at the embryo as a picture, more or less obscured, of the common parent-form of each great class of animals" (*Origin*, 450). Yet the sections expressly on morphology and embryology together take up less than half of a single chapter (Chapter 13), comprising only 17 of the Origin's 490 pages, or 25 if we add the section on "Rudimentary, Atrophied, or Aborted Organs" and the chapter summary. These topics show none of the weight of detail and example displayed in, for example, the chapters on geographical distribution and hybridism. Although a few references to comparative anatomy and embryology

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may be found scattered elsewhere in the book, the space devoted to these topics seems rather meager compared to the rhetoric attached to their significance.

Yet Darwin insisted on such rhetoric, clinging to it even in old age. In his *Autobiography* he wrote (125), "Hardly any point gave me so much satisfaction when I was at work on the *Origin*, as the explanation of the wide difference in many classes between the embryo and the adult animal, and of the close resemblance of the embryos within the same class." Not only did Darwin's friends fail to recognize it, but historians have not known what to make of this. Just what was it about his embryology that gave Darwin such satisfaction?

As we will see, embryology did indeed hold a key place, both in the *Origin* and in his larger program, for it served as a kind of doorway between existing ways of relating embryology to morphology and classification and Darwin's own picture of the natural world and the problems it posed. Morphologists studied homologies, that is, organs they considered "the same" across different species, with the goal of uncovering the fundamental laws of organic form, which, they hoped, would provide for the organic realm the same kind of foundation that Newton's laws provided for mechanics. They hoped that such laws, in turn, would provide secure grounds for classifying organisms and thus producing (or uncovering) the true "system of nature." Morphology was thus understood by its leading practitioners across Europe and America to be, as Darwin put it, the "very soul" of natural history. For many morphologists, the developing individual presented a particularly compelling problem: what was the connection to be drawn between the course of individual development and the "affinities" or similarities seen among living groups of organisms?

Since the early nineteenth century, naturalists had struggled to discover these connections and wrangled with one another over their differing answers. At one level, Darwin's theory of descent solved this problem straightforwardly: since organisms were related to one another, their embryonic forms, like their adult forms, could be read as a record of their relatedness. The more similar two organisms were in their embryological development, the more closely they were related. Problem solved.

However, embryology was also a focal point of the new problems that Darwin's theory raised. If evolution proceeded by natural

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selection acting upon variations among organisms, then when in development did variation occur? How did variation affect the subsequent course of development? How did natural selection act upon the developing organism? What was the effect on the offspring of the modified parents? And what effects might all these events have upon scientists' reading of the embryo as a record of common ancestry (and thus upon classification)? In the *Origin*, Darwin knitted together the relations of embryology to classification and morphology, on the one hand, and to variation, inheritance, and selection, on the other, as he sought to recast the traditional problems of morphology in his own terms.

CHARLES DARWIN, EMBRYOLOGIST?

Why did Darwin devote so little space in the *Origin* to embryology? Shouldn't we take this absence seriously? One might argue that Darwin was a geologist and breeder and so had much more experience to draw on in those areas than he did in morphology and embryology. This argument falters on the evidence, however: Darwin was interested throughout his career in these topics (Richards 1992). Questions and notes concerning individual development appear in his earliest notebooks; embryology and morphology held a significant place in his essays of 1842 and 1844 and in his researches of the 1850s. Already in the late 1830s and more intensively in the mid-1840s, he began reading closely naturalists who linked classification to the study of form, including English-language writers such as Martin Barry and Richard Owen, French scholars such as the father-son duo Etienne and Isidore Geoffroy St. Hilaire and Henri Milne-Edwards, and German scholars such as Johannes Müller. As he read, he commenced hands-on morphological work as well: from 1846 to 1854, he dissected countless barnacles to establish their morphology and classification. He directed a good deal of his attention to the development of this creature, and he made active use of embryological development to establish the classification of this group (Richmond 1985). Moreover, he was no tyro in vertebrate development, either. He devoted considerable effort in the later 1850s to measuring bird and dog neonates to determine their degree of variation as compared with adults. So although Darwin did not base his authority as a man

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of science on his publications in embryology and morphology, he was certainly deeply acquainted with these subjects, both from his reading and from his own hands-on research.

But he was pressed for time. He had not yet gotten to writing up these topics, in his deliberate way, when the threat of being scooped by Alfred Russel Wallace hurried him into publication, causing him to squeeze these important subjects into Chapter 13. Embryology and morphology were undoubtedly more significant for him than the space devoted to them in the *Origin*. His claims for embryology, as for evolution in general, constituted "one long argument" that extended well past 1859 through subsequent editions of the *Origin*, *Variation of Animals and Plants under Domestication* (1868), and *The Descent of Man* (1871).

EMBRYOLOGY IN THE *ORIGIN*

Darwin's main discussion of embryology appears in Chapter 13 of the *Origin*, under the title "Mutual Affinities of Organic Beings: Morphology; Embryology; Rudimentary Organs." The title is unfortunate, for it suggests a certain grab-bag quality to the chapter, as if he were cramming in all the subjects he hadn't gotten to yet in order to finish the book. As true as this may be, in fact the position of the chapter – the very last one before the book's recapitulatory conclusion – offers a clue to its unifying and generalizing quality. This is the chapter in which Darwin connects his theory to the natural system as a whole, in which he argues that indeed the natural system is none other than the genealogy of nature, explained and structured by natural selection. It is the book's punch line.

Morphology, embryology, and rudimentary organs all offer evidence that the natural system is genealogical. Conversely, Darwin's theory explains the known facts in these areas in a new and coherent way. Here Darwin embraces within his system the most intensely pursued questions of philosophical natural history of the previous half-century: What is the order of nature? How are we to understand the similarities and differences in form among different organisms (especially animals)? How is individual development related to the great patterns evinced by the animal world as a whole? His answer, as with everything else in the book, is that these topics are united

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and made coherent through the conception of descent driven by natural selection but are incomprehensible on the theory of separate creation of species.

As he did so often, Darwin worked by first enumerating the various classes of facts that he viewed as requiring an account in his theory. First, there was what he and his contemporaries referred to as "unity of type" and morphological "affinities" – the fact that organisms of the same class resembled one another in structural features that could not be accounted for on strictly functional grounds. These resemblances were strong, consistent, and complete enough that morphologists, following the French museum naturalist Étienne Geoffroy St.-Hilaire, could identify "the same" bones across the different vertebrates and give them the same name. Darwin's compatriot, the leading comparative anatomist Richard Owen, attributed such similarities to a common "archetype," an underlying ideal form. (In 1818, Geoffroy called his theory covering these similarities his "theory of analogues," but in 1843 Owen renamed these similarities "homologues." "Analogous" features, in Owen's recasting, were those that served the same function but used different structures, such as the wings of insects and birds. The distinction stuck.) Geoffroy also provided Darwin with a related idea that the latter would run with: such homologous parts might look entirely different and even serve different functions for different organisms, but they shared a common underlying form. For Darwin, these similarities were inexplicable if one assumed that different species were independently created, but were readily assimilated into his theory: homologies between organisms indicated common ancestry, and their variants demonstrated modifications that were adaptive to particular circumstances, culled by natural selection. His theory of descent thus accommodated both similarities and differences in form at one stroke.

In the case of embryology, comparison also yielded evidence favoring common descent. Animals of different groups within the same class, Darwin argued, often resembled one another more closely in their early embryological stages than in their adult forms. For example, embryos of mammals, birds, and frogs all shared a "peculiar loop-like course of the arteries near the branchial slits" (*Origin*, 440) despite the remarkably different conditions in which they develop – evidence to Darwin, like adult homologies, of common ancestry. A

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close study of embryological stages could reveal surprising commonalities. Darwin's earlier examination of barnacle (cirripede) embryos not only showed that the embryos were much more similar than the adult forms, but also demonstrated to his satisfaction that they were crustaceans, although their widely varying adult forms, most often encased in a calcareous fortress attached to a rock, did not reveal this fact so clearly (*Origin*, 440). (Indeed, Darwin's longtime foe Richard Owen, who favored comparison of adult forms over that of developing forms in establishing homologies, considered cirripedes as a distinct class, which he placed between the Crustacea and Annelida [Richmond 1985, 394]). However, embryos did not always show ancestral resemblances, and sometimes earlier developmental stages could even appear higher in organization than mature ones.

After summarizing these diverse facts, Darwin came to the point:

> How, then, can we explain these several facts in embryology, – namely the very general, but not universal difference in structure between the embryo and the adult; – of parts in the same individual embryo, which ultimately become very unlike and serve for diverse purposes, being at this early period of growth alike; – of embryos of different species within the same class, generally, but not universally, resembling each other; – of the structure of the embryo not being closely related to its conditions of existence, except when the embryo becomes at any period of life active and has to provide for itself; – of the embryo apparently having sometimes a higher organization than the mature animal, into which it is developed. (*Origin*, 442–3)

Not surprisingly, his answer was that "all these facts can be explained, as follows, on the view of descent with modification" (*Origin*, 443). And several pages later, he was still more blunt: "the embryo is the animal in its less modified state; and in so far it reveals the structure of its progenitor. . . . Thus, community in embryonic structure reveals community of descent" (*Origin*, 449).

At a general level, Darwin's argumentative strategy here was in line with his handling of other classes of facts throughout the *Origin*, in which common descent and natural selection accounted for a wide variety of phenomena in nature for which the theory of independent species creation had a less satisfactory explanation (or none at all). But there was a practical point, too, that tied these subjects together. "We have no written pedigrees," Darwin noted (*Origin*, 425); "we have to make out community of descent by resemblances

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of any kind. Therefore we choose those characters which, as far as we can judge, are the least likely to have been modified in relation to the conditions of life to which each species has been recently exposed." To establish true evolutionary relationships – the now-transformed task of classification – the naturalist must seek clues to ancestry in the commonalities of form, by definition those that had changed least over time. Some of these commonalities would be found in structures so vital to the organism that they could not change much at all, but other characters could also reveal those commonalities, provided they had not been modified through natural selection. Embryonic forms were often protected from selection, in Darwin's view, if they were in eggs or wombs or otherwise not actively exposed to the struggle for existence. Developing forms not only revealed the fact of common descent, then, but could also provide the clues to specific questions of classification.

But there was still more to Darwin's discussion. Right after he listed the main embryological facts he sought to explain (given in the long quotation cited earlier), he introduced some new issues. A long paragraph addressed the question of when variations appear in individual development, and concluded that

> it is quite possible, that each of the many successive modifications, by which each species has acquired its present structure, may have supervened at a not very early period of life; and some direct evidence from our domestic animals supports this view. But in other cases it is quite possible that each successive modification, or most of them, may have appeared at an extremely early period. (*Origin*, 444)

In other words, modifications could appear early on or not. "[A]t whatever age any variation first appears in the parent," Darwin continued, it seemed likely to him that "it tends to reappear at a corresponding age in the offspring." Elevating these two statements – the first quite vague, the second more specific – to principles, Darwin wrote that they could account for "all the above specified leading facts in embryology" (*Origin*, 444).

What was going on here? Why did Darwin insist that the moment at which variation appears is an important issue, and that the corresponding age of appearance in the offspring was also something that needed to be confronted? The answer, I believe, is that introducing these considerations allowed him to do three things that would

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assist in translating embryology into his new framework. First, he sought to account for what had formerly been seen most often as the product of a transcendental Law of Development in historicist and materialist terms, by explaining just how embryos might come to reveal their ancestral history. Second, to do this, he needed to connect his understanding of the embryo-ancestor relationship to other elements of his theory, especially variation, selection, and inheritance. And third, he sought to account in these same terms not only for cases in which embryos revealed the organism's ancestry but also for cases in which they did not, for embryos' developmental stages could bear complex relationships to variation, selection, and the representation of ancestry. Darwin's two principles of embryology and inheritance provided a crucial hinge-point between solving an old problem – the nature of the relationship between embryological development and classificatory affinities – and resituating that problem itself within a framework that decentered its importance.

EMBRYOS AND THE ORDER OF NATURE

Darwin was well aware of the different kinds of relationships his contemporaries and predecessors had drawn between individual development and the order of nature. The choices were far more diverse than the stark opposition between creation and descent that he posed in the *Origin*, and the means of choosing among them not at all clear-cut. Many naturalists, especially in the German-speaking lands, believed that there was a general "law of development" in nature that governed both individuals and the overall history of life. In such formulations, typically, individual development reflected a macrocosmic trend toward increasing progress and complexity. Conversely, naturalists thought (though not without contestation), they could be confident of the overall increase in progress and complexity of the broader organic world that was gradually being revealed in the fossil record in part because they saw a parallel in the individual embryo (Richards 1992; Nyhart 1995; Gliboff forthcoming 2008).

Many naturalists shared this broad conviction, but not all were so certain that simply positing a "law" of development was a satisfying way to account for the parallels. What did it mean to say that such a law "governed" both the development of the organic world as a whole and individual development? Was this law simply

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an empirical generalization, or did it have causal efficacy? If the latter, how did that causal connection work? Many naturalists sought a more specific connection between the pattern of development of embryos and the larger patterns of organic nature as a whole, even as they were working out the details of both. Two ways of connecting up these two patterns had become prominent by the mid-1840s, when Darwin started to engage the topic with some intensity. One approach, which we will call the recapitulationist approach, took a primarily linear perspective on both the order of nature and the understanding of individual development. This view held that as individuals developed, they worked their way up the chain of being from less to more complex. This was the perspective held by Friedrich Tiedemann, who believed that the brains of mammalian fetuses passed through the adult stages of the lower vertebrate classes as they advanced in development. Darwin would have been familiar with this approach as far back as his reading of Charles Lyell's *Principles of Geology*, for in volume 2, Lyell (1832; reprint 1991) noted Tiedemann's finding, "most fully confirmed and elucidated by M. Serres, that the brain of the foetus, in the highest class of vertebrated animals, assumes, in succession, the various forms which belong to fishes, reptiles, and birds, before it acquires those additions and modifications which are peculiar to the mammiferous tribe." Lyell specifically characterized Tiedemann's views as transformist: "So that in the passage from the embryo to the perfect mammifer, there is a typical representation, as it were, of all those transformations which the primitive species are supposed to have undergone, during a long series of generations, between the present period and the remotest geological era" (Lyell 1991, 63). Tiedemann's argument was reinforced by Serres and several other important French students of development, who interpreted monstrosities as "arrests of development." That is, many monsters resulted from a failure to develop beyond a certain lower stage of development that paralleled the hierarchy of being. The logical connection between monstrosity and transformism was this: monstrosities subtracted levels of complexity from the end of their development, stopping earlier and representing a lower form. Perhaps all a creature needed to do in order to create a newer, higher form was to extend the end of its development. However, Lyell objected, animals in fact "never pass the limits of their own classes to put on the forms of the class above

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them. Never does a fish elevate itself so as to assume the form of the brain of a reptile; nor does the latter ever attain that of birds; nor the bird that of the mammifer" (Lyell 1991, 63). The logic of inversion was false.

This linear view, which had earlier incarnations, had previously been objected to, perhaps most famously by the Estonian "father of embryology" Karl Ernst von Baer. Von Baer's alternative, just becoming available to British naturalists in the early 1840s, did two things. It rejected a single scale from monad to man, supporting instead the view of Georges Cuvier, France's leading zoologist, that there were four basic and distinct kinds of organization in the animal kingdom (called "Types" by von Baer and "Embranchements" by Cuvier). Von Baer's view further interpreted development as a successive process of differentiation that paralleled the successively smaller classificatory groups to which an individual belonged. The embryo first exhibited the characteristics of the vertebrate Type, then its class (e.g., bird), then the order, and so forth down to the individual.

Although Darwin had encountered this view by 1838, he was most struck by the gloss on it presented by Henri Milne-Edwards in an 1844 article, which Darwin read in 1846, just as he was beginning his barnacle work. To the general idea that the embryo first exhibited the broadest characteristics of the Type and then successively the more particular characteristics of the class, order, genus, and species, Milne-Edwards added the corollary that the more characteristics two organisms shared in development, the more closely were they related. Embryology could thus be used to ascertain how closely or far apart two organisms should be classified.

Echoing the divisions of the nineteenth century, historians have long viewed the two systems of linear recapitulation and developmental differentiation as sharply distinct and opposed to one another. Recapitulation went with the linear view and a strong notion of absolute progress; differentiation was associated with branching and specialization. Yet Darwin, and at least one naturalist before him, thought that they could be reconciled. To see how, we must note one key issue to which historians have devoted intense scrutiny. To what, exactly, did naturalists compare the stages passed through by present-day embryos of higher forms?

There are four possibilities. The stages of present-day higher embryos might be comparable to present-day adults (especially of

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lower forms), to present-day embryos, to adults of past forms, or to embryos of past forms. In the pre-Darwinian linear recapitulationist perspective, early stages of present-day embryos were compared to present-day adults of lower forms; in Tiedemann's presentation, these also "represented" or were presumed to be analogous to (or even "the same as") adults of past forms. The differentiationist point of view compared embryos only to other embryos, not to adults. Von Baer and Milne-Edwards were mainly interested in comparisons among living organisms, not in interpreting past organisms. No one was talking about comparing present-day embryos to embryos of past forms – until *Vestiges*, it would appear.

In 1844, the anonymous author of the *Vestiges of the Natural History of Creation* sought to draw explicit parallels (and connections) between fetal brain development, the present-day hierarchy of organic complexity, and the fossil record. The parallels, represented in his accompanying chart, appear clear: the human fetus's resemblance in the fifth month to that of a rodent lines up exactly with the appearance of Rodentia in the lower Eocene. It would seem as though the author of the *Vestiges* wanted the embryological stage to resemble a past adult. Yet the Vestigiarian's language on the analogical target of embryological resemblance was mixed. On the one hand, he declared straightforwardly, "It is only in recent times that physiologists have observed that each animal passes, in the course of its germinal history, through a series of changes resembling the *permanent forms* of the various orders of animals inferior to it in the scale" (Chambers 1994, 198). On the other hand, he later stated (212), "But the resemblance is not to the adult fish or the adult reptile, but to the fish and reptile at a certain point in the foetal progress." Furthermore, as represented in an accompanying diagram (Figure 11.1), his concept of development was not strictly linear: each class within the vertebrates followed a common path to a certain point and then branched off into a path unique to its group. Struggling to accommodate both a linear perspective and a branching one, he imagined a main line of ascent leading to humans, which lower types partially followed before branching during their development.

[I]t is apparent that the only thing required for an advance from one type to another in the generative process is that, for example, the fish embryo should not diverge at A, but go on to C before it diverges, in which case

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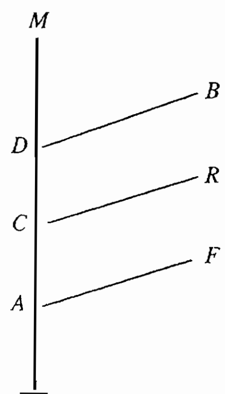

Figure 11.1. Representation of development, in which an embryo (at A) that might develop into a fish (at F), continues to advance (through C, D, and M), giving rise over time to reptiles, birds, and mammals (R, B, and M); from Chambers's anonymously published *Vestiges of the Natural History of Creation* (1844).

the progeny will be, not a fish, but a reptile. To protract the *straightforward part of the gestation of a small space* – and from species to species the space would be small indeed – is all that is necessary. (Chambers 1994, 213)

This was a critical early instance of a scientific writer seeking to combine a linear view of progress with a branching conception of development. As much as Darwin may have detested the *Vestiges*, it constituted part of the picture he was gleaning as he developed his own ideas during the key period of the mid-1840s, and it may have given him something to think about.

So, what did Darwin think? To what did he believe present-day embryological development should be compared?

DARWIN AND EMBRYOLOGICAL RESEMBLANCE

Historians differ in their interpretations of Darwin's views on the recapitulationist versus differentiationist understandings of the embryo. Most follow the argument first set out by E. S. Russell in 1916 and reinforced sharply by Stephen Jay Gould in 1977, that Darwin rejected the former in favor of the latter. In 1981, Dov Ospovat refined this view, arguing that Darwin followed the linear recapitulation model in his early work but that in the mid-1840s he was

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persuaded by more recent work, especially that of Milne-Edwards, arguing that successive differentiation more accurately expressed the parallel between embryos and the larger order of nature. Broadly interpreted within Darwin's developing framework, branching and differentiation in embryonic development mirrored the branching and differentiation in varieties, species, and the larger classificatory hierarchy. In this interpretation, embryos resembled neither the adults of lower present-day types nor historical adults, but only other embryos, present-day and in the past (Ospovat 1981, 166–7).

By contrast, Robert J. Richards has argued (1992) that Darwin believed that present-day embryos tended to resemble ancestral *adults*. In this view, embryonic stages revealed a sequence of adult ancestors–more primitive stages of development in the historical development of life. Critical to this interpretation is a strong reading of Darwin's two principles of embryology and inheritance. If one understands the first principle, that new variations "supervene at a not very early period of life," to mean that such variations appear as end stages of development, and then, following the second principle, they reappear at a "corresponding stage in the offspring," it follows that new *evolutionary* variations will be tacked on to the end of *individual* development in subsequent generations. Stephen Jay Gould dubbed this the doctrine of "terminal addition" (though he excluded Darwin from his list of recapitulationists who took this view). By this logic, a present-day individual will run through adult ancestral stages as it goes through development because that is how the developmental sequence itself came into being, by adding new stages to the end of what was a mature (if primitive) organism. In Richards's reading, Darwin was a recapitulationist, who viewed present-day embryos as primarily comparable to ancestral adults.

Few historians have agreed with this interpretation of Darwin as a recapitulationist, for that would seem to tie his ideas to linear thinking rather than branching, and to a progressive hierarchy rather than a view of change as differentiation (see, e.g., Bowler 2003). After all, Darwin made repeated statements such as "the embryo is the animal in its less modified state. . . . In two groups of animal, however much they may at present differ from each other in structure and habits, if they pass through the same or similar embryonic stages, we may feel assured that they have both descended from the same

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or nearly similar parents. . . . "(*Origin*, 449). Surely this is evidence for differentiation, and for embryos resembling embryos rather than ancestral adults.

But Darwin also offered the example of the forelimbs becoming modified in different directions over evolutionary time from a common ancestral pair of legs, becoming in different descendants hands, paddles, and wings:

> and on the above two principles–namely of each successive modification supervening at a rather late age, and being inherited at a corresponding late age – the fore-limbs in the embryos of the several descendants of the parent-species will still resemble each other closely, for they will not have been modified. But in each individual new species, the embryonic fore-limbs will differ greatly from the fore-limbs in the mature animal; the limbs in the latter having undergone much modification at a rather late period of life, and having thus been converted into hands, or paddles, or wings. (*Origin*, 447)

Clearly, differentiation is occurring here, but the stress on the "rather late age" and on the modifications "being inherited at a corresponding late age" (the two principles) can also be read as Darwin insisting on terminal addition as the means by which this differentiation took place, and as the reason why embryos resemble one another.

In fact, the contradiction between linearity and branching is only apparent, and may be resolved. Darwin did so, and it is reasonable to believe that he did so via adult ancestors. If two organisms have a common ancestor, then that adult ancestor may be *both* the end product of a particular course of development (up to that point) *and* an earlier stage of the existing course of development of a present-day organism. The doctrine of terminal addition is not necessarily tied to a strictly linear view of nature, but is compatible with a branching one.[1]

To see this most clearly, consider that both development and evolution may be viewed from two ends: from the base of a branching Darwinian tree, or from a twig at the living end. From the base, moving upward, we see branching. But looking back from that twig,

[1] I have made a similar argument in explicating Ernst Haeckel's views on recapitulation (Nyhart 1995, 134–5).

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the organism views a linear history back into the past – the history that led to itself. From another endpoint/twig, a different organism also sees a linear history leading backward. Where these two lines meet in a common ancestor, their two backward-leading histories become one. Branching is what we see as we move forward; linearity and joining are what we see as we move backward in time.

From Darwin's standpoint of evolutionary recapitulation, the same held true in individual development. Individual development, read forward from the deep past, would take place as follows: as evolutionary history proceeded, new variations would tend to be added on to the end of embryonic development. Natural selection would then tend to cause divergent variations to be selected, following Darwin's principle of divergence. Thus as new stages were added on to individual development, incipient evolutionary divergence would simultaneously take place. Suppose that two different end-stage variants eventually resulted in two new, modified species. Each would be able to trace back through its individual development a record of its own evolutionary history, and these two courses of individual development would join up at the point at which the evolutionary histories joined up. So embryos would tend to share a longer common developmental history the more recently they had branched off from one another, and even embryos of the same class (but of different families and orders) would tend to share common features at the very beginning of their development, reflecting their distant and early common ancestry.

Although Darwin said all of these things separately, it is difficult to find him putting the whole picture together – which may be one reason why his friends (and most later historians) did not fully appreciate his achievement. Yet if this reasoning is correct – and I am convinced that this does indeed reflect an important part of Darwin's reasoning – then his achievement respect to embryology was substantial indeed. Darwin resolved the opposition between the linear and differentiationist approaches to the problem of embryonic resemblance, and he did so within his own framework of evolution by natural selection working on variations. All it took was a couple of ancillary principles to make the shift.

And yet I would suggest that this was not what satisfied Darwin himself most about his interpretation of embryology. His two principles of embryology and inheritance not only explained embryos'

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resemblance to other embryos and to ancestral adults but also offered an account of the very nature of development itself.

Consider what Darwin remembered in his *Autobiography*: he was especially proud of his "explanation of the wide difference in many classes between the embryo and the adult animal, and of the close resemblance of the embryos within the same class" (*Autobiography*, 125). What constitutes "the wide difference in many classes between the embryo and the adult animal"? Development. Terminal addition plus inheritance at a corresponding age explained development itself: "This process, whilst it leaves the embryo almost unaltered, continually adds, in the course of successive generations, more and more difference to the adult" (*Origin*, 338). This was why embryos resembled ancestors. But it was also why organisms developed at all: development was a consequence of the process of evolution. By using his two principles, Darwin could derive from evolution the very process of development.

DEVELOPMENT, VARIATION, SELECTION, AND INHERITANCE

Darwin's two principles did not just allow him to establish a material connection between individual development and evolution; they worked to weave this connection deeply into the vocabulary of his overall theory. The idea that modifications tended to supervene at a not-very-early stage of life was a claim about variation, a central component of his theory. That such modifications would tend to be inherited at a corresponding age in the offspring was a claim about heredity. Both were entwined in the physiological problem-complex of development, variation, and inheritance, known at the time as "generation," one of Darwin's most abiding interests, which would culminate in his hypothesis of pangenesis, published in 1868 (see Hodge 1985; Sloan 1985); These concerns plunged him into the nitty-gritty of the material processes by which organisms might become transformed over time.

The mass of facts he had gathered before him did not present a simple picture. Discerning regularities among the varied facts of heredity and variation was one of Darwin's most intractable problems. His need to wrestle with this problem was part of what made Darwin's interest in and claims about development different from

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those of his morphologist predecessors, and ultimately what reduced its place in his overall system from the central topic to one among several important areas of consideration.

Despite the stronger claims he sometimes made at moments of summary, Darwin's discussion of embryology and variation was filled with equivocation. Virtually every single time he discussed the tendency of variations to supervene at a late stage of development, he followed with a counterexample: they could also appear at an early stage. Or development might not proceed very far at all. Everything was qualified; Darwin's language was littered with expectation-lowering phrases. "It is quite possible" that new characteristics "may" have appeared late in life. But then again, it was "quite possible" that they may not have.

This equivocation has two important aspects: one has to do with Darwin's confidence in his claims, the other with their generality. First, at the time of writing the *Origin*, Darwin appears not to have been fully confident about the temporal relationship of variation to development. He hinted at the difficulty he faced in coming to a resolution at the beginning of the passage introducing his two principles of embryology and inheritance, when he treated the assumption that "variations necessarily appear at an . . . early period" – a view he opposed, but without complete conviction. It turns out that his equivocation was significant, and that Darwin had changed his mind from an earlier, opposing position. The story of Darwin's shifting stance shows his lack of certainty about the relation of modification to development, his continued efforts to link this problem up with classificatory relationships, and his desire to connect both issues to selection.

As early as his "Sketch" of 1842, Darwin had suggested that variations could enter in at different times during development, but that it did not matter just when they did so if they were protected from selection (*Foundations*, 42). In his 1844 "Essay," he elaborated upon the point, noting that all that counted was that an adaptive structure be in place at a time when selection could act to preserve it, which typically occurred only in the mature state. Thus if it could be shown that variation did not always take place early on in development but tended to take place later on, and that selection too tended to take place at later stages, this would account for differences in the adult organism; at the same time, the lack of selection at early stages would leave those early stages resembling one another more

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than their mature forms (*Foundations*, 220-7). Darwin's measurements of newborn greyhounds and bulldogs showed their legs and noses to be the same length, confirming that even greatly varying breeds resembled one another more closely at birth. (In the 1850s, he would gain further confirmation of his views with measurements of neonate pigeons.) Using his characteristic analogy between artificial and natural selection, he argued that if nature's selective hand worked on mature individuals as human selection did, then it would make sense that in nature, too, younger individuals would tend to resemble one another more than adults.

However, in the manuscript of his "Big Book" – the one for which the 490-page *Origin* served as a mere abstract – Darwin changed his position, based on reading he had done just after his 1844 essay. There he wrote that "modifications in the mature state will almost necessarily have been preceded by modification at an earlier age" (*Species Book*, 302). He then cited the French entomologist Gaspard Auguste Brullé, who in 1844 had argued that the more complex an organ would become in its adult stage, the earlier it must appear in development. The botanist François Marius Barneoud had found something similar in plants. Darwin then immediately turned to discussing Milne Edwards's 1844 paper, which used the criterion of embryological differentiation to establish classificatory affinities. As Darwin interpreted Milne Edwards, "the more widely two animals differ from each other, the earlier does their embryonic resemblance cease" (*Species Book*, 303). Darwin concluded the section with the following:

> If the foregoing principle be really true & of wide application, it is of importance for us; for then we might conclude that when any part or organ is greatly altered through natural selection it will tend either actually first to appear at an earlier embryonic age or to grow at a quicker rate relatively to the other organs than it did before it had undergone modification.: consequently, . . . this early formation will tend to act on the other & subsequently developed parts of the system. (*Species Book*, 304)

Darwin copied out this section of his manuscript and sent it to Huxley for review on July 5, 1857.

> Especially I want your opinion how far you think I am right in bringing in Milne Edwards['] view of classification. I was long ago much struck with the principle referred to: but I could then see no rational explanation why affinities should go with the *more or less early* branching off from a common

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embryonic form. But if MM Brullé and Barneoud are right, it seems to me we get some light on Milne Edwards['] views of classification; and this particularly interests me. (*Correspondence*, 6: 420–1)

What exactly Darwin thought that light would be remains unclear. In his reading notes on Milne Edwards's article in the mid-1840s, Darwin had written that "to mature an organ, a certain time is required, & that the earlier changes can alone be hurried. This at once nearly explains the gradual loss of embryonic characters. . . . " (*Correspondence*, 4: 393). By 1857, his worrying over the problem may have made its implications more expansive: perhaps he inferred that complex forms–those most modified from an ancestral one–would share an embryonic resemblance only early in development. This would associate early branching from a common ancestor (Darwin's interpretation of Milne Edwards) with modification at an early stage of development. In any case, it is clear that Darwin was working to combine and reconcile the results of Brullé and Milne-Edwards while also translating them into his own terms. At this moment, in 1857, he was thinking that new variations normally supervened early in development, not at the end. (Rachootin [1984] treats at length how Darwin developed Brullé's ideas.)

Huxley's reply was scathing– as he put it, he "brûler'd Brullé," arguing that every bit of the latter's evidence was wrong and that his logic was, if anything, worse. Moreover, he corrected Darwin's apparent interpretation of Milne-Edwards: "he seems to me to say that, not the *most highly complex*, but the most *characteristic* organs are the first developed" (*Correspondence* 6: 424–7). Thus Brullé's argument did not reinforce Milne Edwards's, as Darwin would have it.

Darwin not only omitted the passage in the *Origin* but, as we have seen, tilted in the opposite direction, returning to his views of the early 1840s. Significant new variations tended to appear not early in development but late. This he put to work to explain embryos' resemblance to ancestors (and, significantly, this discussion appeared in the chapter on affinities, morphology, and classification, not in the chapter on laws of variation, as had the earlier version in the big species book). Yet the uncertainty remained – Brullé had found cases where modifications seemed to supervene early, and Darwin continued to take those instances seriously. The general rule that he came up with in the end was not one in which embryos *must*

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mirror ancestors or *must* retrace the successive features of the class, the order, the genus, and the species. Instead, it was one that emphasized contingency, variation, and the intervening hand of natural selection.

And this brings us to the other aspect of Darwin's equivocation over the timing and nature of the appearance of heritable modifications in development: the question of their generality. Darwin wanted to account not only for those cases in which embryos of related forms resembled one another, but also for cases in which they did not, as well as for different amounts and moments of resemblance. To succeed, his framework had to accommodate all the different cases. So he proceeded to show how they all might be understood as the product of evolution by natural selection acting on variations, whenever they might appear.

Sometimes embryological development exhibited a succession of modified ancestral adults. This would be the case in many vertebrates, especially in those organisms, such as birds and mammals, that were protected from the pressures of selection in the egg or womb, where there had been much modification from an original primitive ancestor, and where successive modifications were inherited at a corresponding age in the offspring. But in some organisms, early developmental stages did not benefit from the protections of egg or womb and had to fend for themselves. The pressure of selection on these free-living larval forms meant that adaptations would appear earlier on in development, tending to efface ancestral connections (*Origin*, 440) and also in some cases producing distinct metamorphic stages (*Origin*, 448). In yet other cases, embryos could display variations early on in their development that made them resemble more closely the adult forms. Drawing on his own research measuring pigeon neonates, Darwin noted that this was the case in the short-faced tumbler pigeon, which revealed its adult facial characteristic at the moment of hatching, whereas other pigeon varieties all closely resembled one another when newly hatched. He used this case to move away from the question of ancestral resemblance to focus more closely on a larger group of cases in which there was little developmental difference between young and adults; and again, he explained these cases via the pressure of selection. If the young, instead of being protected from selection, were exposed to the same environmental pressures as their parents, they would tend to display early on in development the same adaptive characteristics.

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In this discussion, the resemblance of some embryos to ancestors represented one pattern among many – the only one that required modifications to supervene at "a not very early period of life." It may have been Darwin's default pattern, but the others were also significant and demanding of explanation. One way or another, evolution by natural selection could account for all the various patterns of development seen in the organic world.[2] Embryo-ancestor resemblance was one important consequence of evolution, and Darwin's theory explained it in a nonidealistic way. But in Darwin's scheme, all those other developmental patterns required – and received – explanation in evolutionary terms.

In the fourth edition of the *Origin* (1866), Darwin clarified and strengthened his claims about recapitulation, while also broadening his discussion of nonrecapitulatory cases. Thus he explicitly mentioned that embryonic resemblance corresponded to an adult ancestor:

> [I]t is probable, from what we know of the embryos of mammals, birds, fishes, and reptiles, that [these animals] are the modified descendants of some one ancient progenitor, which was furnished in its adult state with branchiae, had a swim-bladder, four simple limbs, and a long tail fitted for an aquatic life. (*Variorum*, 702, *306.10.d*)

Crustaceans showed a similar phenomenon. Here Darwin leaned heavily on a small book, *Für Darwin*, published in 1864 by the German émigré zoologist Fritz Müller, who lived in Brazil and had closely studied the crustacea there. In his book, Müller demonstrated a common larval stage for a range of crustaceans with widely differing adult states and argued that this larval stage represented an adult common ancestor. His position, based on impeccable embryological research, so pleased Darwin that he paid for the translation and publication in English of Müller's little book (Müller 1869; West 2003, 120–1). The fourth and later editions would be peppered with new references to Müller.

Even as he clarified his claim that embryos resembled adult ancestors, however, he also expanded his discussion of cases in which they did not. Again, the fourth edition elaborated further on cases

[2] Darwin included plants in his discussion but devoted much less space and attention to them.

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of early adaptation, especially in insects – cases, for example, in which the need to survive in unprotected environments produced distinct metamorphic stages, which might sometimes be "higher" than later ones. Thus, to his first-edition declaration that "community in embryonic structure reveals community of descent" (*Origin* 449), he added, "but dissimilarity in embryonic development does not prove discommunity of descent, for in one of two groups all the developmental stages may have been suppressed, or may have been so greatly modified as no longer to be recognized, through adaptations, during the earlier periods of growth, to new habits of life" (*Variorium* 703, *312:d*) Adaptation and selection would account for cases in which embryos did not reveal their ancestral heritage.

From first to last, Darwin believed that when embryos resembled others of related classificatory groups, they did so because they shared a common ancestry. But his understanding of variation, selection, and the general contingency of nature led him away from an understanding of morphology as the study of the *laws* of form in the strict sense of earlier (and later) continental morphologists. Nature did not make laws of form. She might have some rules governing form – frequent regularities – but these could be broken, and the organic world was littered with such breakage. The only law was evolution; all else was contingent. Even as Darwin solved the problem of embryology and ancestral affinity, he dissolved it into the larger complex of evolution by natural selection.