

## PERSPECTIVE

# Charles Darwin and the Origins of Plant Evolutionary Developmental Biology

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**Much has been written of the early history of comparative embryology and its influence on the emergence of an evolutionary developmental perspective. However, this literature, which dates back nearly a century, has been focused on metazoans, without acknowledgment of the contributions of comparative plant morphologists to the creation of a developmental view of biodiversity. We trace the origin of comparative plant developmental morphology from its inception in the eighteenth century works of Wolff and Goethe, through the mid nineteenth century discoveries of the general principles of leaf and floral organ morphogenesis. Much like the stimulus that von Baer provided as a nonevolutionary comparative embryologist to the creation of an evolutionary developmental view of animals, the comparative developmental studies of plant morphologists were the basis for the first articulation of the concept that plant (namely floral) evolution results from successive modifications of ontogeny. Perhaps most surprisingly, we show that the first person to carefully read and internalize the remarkable advances in the understanding of plant morphogenesis in the 1840s and 1850s is none other than Charles Darwin, whose notebooks, correspondence, and (then) unpublished manuscripts clearly demonstrate that he had discovered the developmental basis for the evolutionary transformation of plant form.**

## INTRODUCTION

As is so often the reality when tracing the intellectual history of an area of evolutionary biology, one ultimately arrives at the doorstep of Charles Darwin. In the case of the discipline of evolutionary developmental biology, it is tempting to attribute its conceptual roots to Darwin's great book *On the Origin of Species* (Darwin, 1859). Indeed, in Chapter XIII (Mutual Affinities of Organic Beings: Morphology: Embryology: Rudimentary Organs), Darwin explicitly argues that the known facts of comparative morphology and embryology are entirely consistent with evolutionary and developmentally based origins of novelty and biodiversity.

Yet, long before Darwin publicly declaimed his evolutionary views in *On the Origin of Species*, he, along with a small but significant cadre of early evolutionists (Robert Chambers, Herbert Spencer, and Baden Powell) achieved significant and unique insights into the importance of successive modifications of development in the production of new morphologies (Gould, 1977). Darwin's essays of 1842 and 1844 (both unpublished until 1909; Darwin [1909]) as well as his writings in his notebooks in the late 1830s demonstrate a keen recognition of the importance of animal embryology (de Beer, 1958; Richards, 1992) to a transmutationist explanation of biodiversity. While Darwin kept his

early insights into the evolutionary process to himself, Robert Chambers's best-selling (and anonymously published) book on evolution, *Vestiges of the Natural History of Creation* (Chambers, 1844; and subsequent 10 editions through 1860) marked the beginning of a formal and public articulation of an evolutionary developmental perspective. Darwin, Chambers, Powell, and Spencer drew heavily on the abundant and highly synthetic literature from the world of animal embryology (particularly von Baer, 1828; a critical synopsis of von Baer by Carpenter, 1841; and an English translation of key writings from von Baer by Huxley, 1853) and were able to realize the profound importance of developmental modifications as a central mechanism of change in the history of life's diversification.

Fortunately, much has been written about the early history of comparative embryology (e.g., Russell, 1916; de Beer, 1958; Oppenheimer, 1959; Ospovat, 1976; Gould 1977, 2002; Richards, 1992; Raff, 1996) and its influence on the emergence of an evolutionary developmental perspective. Notably, however, this literature has been exclusively focused on the contributions of zoological embryologists, zoological comparative anatomists, and zoologically inclined theorists (e.g., É. Serres, J.F. Meckel, L. Oken, K.E. von Baer, G. Cuvier, É. Geoffroy Saint-Hilaire, H. Milne Edwards, R. Owen, and J.L.R. Agassiz). While most of these workers were not evolutionists, their search for, and analysis of, the laws of development proved to be critical to and ultimately congruent with an evolutionary explanation of transformation and biodiversity among metazoans.

Our goal here is not to go over well-traveled ground regarding the origins of an evolutionary developmental perspective for the diversification of metazoans. Rather, we will focus on the virtually

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www.plantcell.org/cgi/doi/10.1105/tpc.111.084244

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unnoticed contributions of plant morphologists, plant developmentalists, and botanically inclined theorists whose contributions led to the emergence of a plant evolutionary developmental perspective. For all of the dozens of formal examinations of the foundations of zoological evolutionary developmental biology, we are unaware of a single historical treatment of the origins of plant evolutionary developmental biology. With this in mind, we view this attempt to reconstruct the origins of plant evo-devo as but a first (and incomplete) step in illuminating what is most certainly a highly complex and interesting intellectual history.

### WHY ANIMAL AND PLANT EMBRYOLOGY ARE NOT THE SAME DISCIPLINE WITH DIFFERENT ORGANISMS

Although plant embryology was an extraordinarily active and productive discipline in the first half of the nineteenth century (culminating in W. Hofmeister's masterpiece volume on the life cycles of land plants; Hofmeister, 1851), it is essential to recognize that plant embryology is a field entirely distinct from, and intellectually unrelated to, the traditions of metazoan embryology. This key reality is a consequence of the stark contrast between the determinate ontogenies of most animals and the indeterminate growth patterns of most plants. Thus, while animals typically complete the construction of their final bauplan during the embryological phases of development, the formation of a plant embryo constitutes a mere fraction of the entirety of the continuously changing phenotype associated with ongoing organogenesis.

One of the first biologists to reflect explicitly on the ever-changing phenotype of a plant was the botanist and early evolutionist, Matthias J. Schleiden (Schleiden, 1848), who captured the essence of this important insight into plant ontogenies: "Here there is nothing firm, nothing consistent; an endless becoming and unfolding, and a continual death and destruction, side by side and intergrafted—such is the plant! It has a history, not only of its *formation*, but also of its *existence*, not merely of its *origin*, but of its *persistence*. We speak of plants; where are they? When is a plant perfect, complete, so that I may snatch it out of the continual change of matter and form, and examine it as a thing *become*? . . . No individual, persistent, or rather, apparently persistent form, but only the course of its development, can be the object of a study of form in Botany; every system which devotes itself to the isolated formal relations of this or that epoch, without regard to the law of development, is a fanciful air-castle, which has no foundation in actuality, and therefore does not belong to scientific Botany." In essence, the study of plants is inseparable from the study of development.

A plant embryo, with its one to a few leaves (out of an ontogeny that may produce tens of thousands of leaves over the course of an individual's life) typically reveals little of the ultimate course of morphological development and basic architectural features of a plant. Thus, the botanical equivalent to the insights gained by von Baer and others in the field of metazoan embryology must be sought elsewhere. Because plants form new organs from undif-

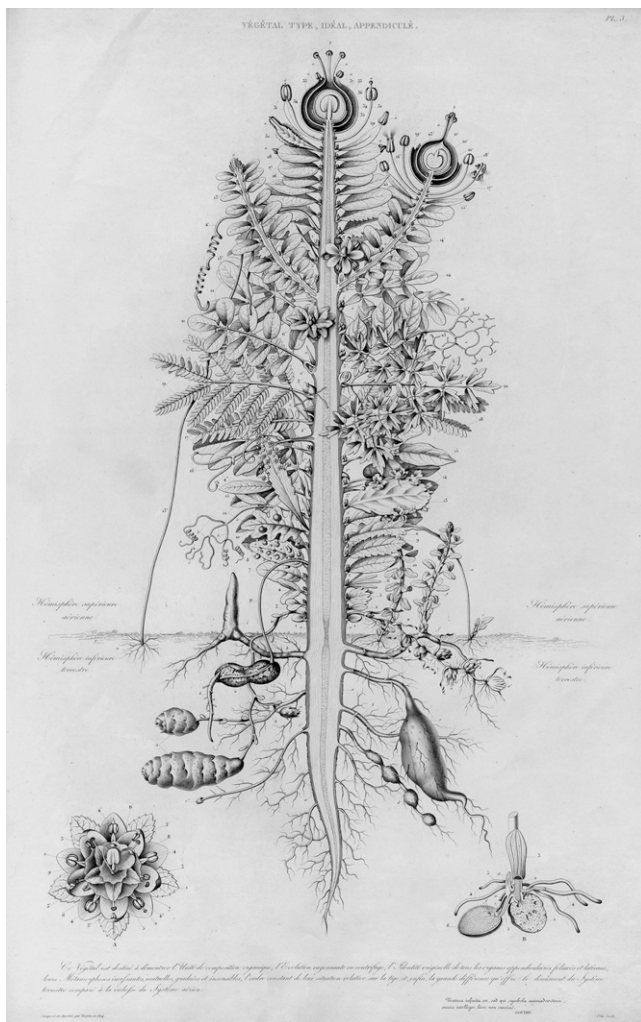
ferentiated populations of cells (meristems) at the apices of roots and shoots, the key to understanding why two closely related plant species have different morphologies and/or architectures must lie in comparative analyses of organ formation and the process of development from meristems. The question is, when did the comparative study of organogenesis in plants first begin?

### THE ORIGINS OF PLANT EVOLUTIONARY DEVELOPMENTAL BIOLOGY: HOMOLOGY AND THE COMPARATIVE METHOD

The genesis of plant (and animal) evolutionary developmental biology requires a key insight: the establishment of a hypothesis of equivalence or what we would now refer to as a concept of homology. The articulation of a statement of equivalence, for example the sepals, petals, stamens, and carpels of flowers are types of leaves, can only emerge from a comparative (though not necessarily evolutionary) examination of plant biodiversity. The origin of such a viewpoint has historically been dated to the late eighteenth century, when Johann Wolfgang Goethe, the German poet, playwright, and natural historian had the seminal insight that "Alles ist Blatt" (all is leaf).

"While walking in the Public Gardens of Palermo, it came to me in a flash that in the organ of the plant which we are accustomed to call the leaf lies the true Proteus who can hide or reveal himself in vegetal forms. From first to last, the plant is nothing but leaf." These words (written in 1787, but not published until many years later by Goethe (1817) and translated into English by Mueller (Goethe, 1952), launched the modern age of comparative biology and were the basis of a formalized discipline, plant morphology (Engard, 1989; Coen, 2001; Kaplan, 2001; Dornelas and Dornelas, 2005; Friedman, 2009), developed by Goethe and published in 1790 in *Versuch die Metamorphose der Pflanzen zu erklären* (An Attempt to Explain the Metamorphosis of Plants). It is here that Goethe argues that all of the diverse lateral determinate organs of the shoot system are transformed (metamorphosed) manifestations of a true leaf. Many years later, Goethe appealed to the great floral illustrator Pierre Jean Turpin for a representation of plant metamorphosis (Eyde, 1975), but the illustration (Figure 1) did not appear in Goethe's lifetime. In articulating the concept that plants can be broken down into essentially modular and iterative variants of an archetypal structure (the leaf, in the form of bud scales, spines, petals, stamens, and so forth), Goethe provided a key insight that would propel the analysis of plant (and animal) structure for the next two centuries and beyond (Friedman, 2009). At once, Goethe introduced the concept of serial homology of leaves within an individual and of the homology of various manifestations of leaves in plants of different species. However, it is important to note that Goethe's idealist concepts of homology and metamorphosis are neither evolutionary nor are they developmental (Goebel, 1900, 1926; Ganong, 1901; Engard, 1989). Rather, for Goethe, the transformation of one type of leaf into another was viewed as a metamorphosis among

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**Figure 1.** The Plant Archetype by P.J.F. Turpin Appeared in an 1837 Edition of Goethe's Works on Natural History Published in France (Goethe, 1837). (Image courtesy of the Houghton Library of Harvard University.)

mature structures derived from a Platonic or abstract type (Stern, 1993). As forcefully argued by Goebel (1926), Goethe “had no knowledge of the developmental history of leaves, but contented himself with a comparison of the completed stages. This comparison led him to regard metamorphosis not as a real process... [T]o him the different leaf-forms appeared as the different forms of manifestation of an abstract type—of the notion ‘Leaf.’”

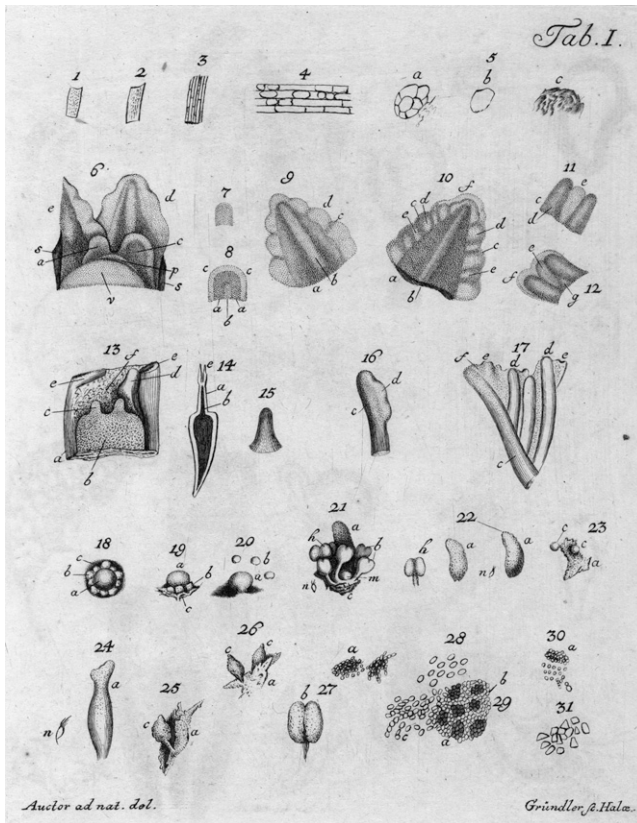
The fact that Goethe did not include a developmental perspective in his concept of metamorphosis among leaves is both interesting and ironic. As Goethe would discover years after publishing his *Metamorphosis of Plants*, he was preceded (indeed anticipated) in the articulation of the hypothesis that the leaf is the basic constructional unit of the plant by the German natural historian Caspar Friedrich Wolff (Goethe, 1817). In 1759, Wolff

published his doctoral thesis, *Theoria Generationis*, on epigenesis in plants and animals (Coen, 2001; see Tooke and Battey, 2003 for a synopsis of Wolff's contributions). Importantly, as Goethe later recognized, Wolff advanced the hypothesis that the leaf is the fundamental building block of the plant and that the organs of the flower (for example, petals) are transformed leaves. “Actually, it does not require a great deal of acuteness to notice that the calyx is only slightly different from the leaves and, to put it briefly, is nothing more than a collection of several smaller and less developed leaves. . . Moreover, from isolated cases it appears at least possible that the corolla and stamens are nothing more than modified leaves. For it is no rarity to see the leaves of the calyx transformed into petals, and conversely to see the petals transformed into sepals. But if the sepals are true leaves and the petals nothing more than sepals, then the petals too are undoubtedly modified genuine true leaves. Similarly, one observes that the stamens. . . are frequently transformed into petals. . . and conversely that the petals are transformed into stamens; from this fact it may be concluded that the stamens, too, are essentially leaves” (Wolff, 1789; English translation in Goethe, 1952). All of this was recorded and published years before Goethe himself would again articulate this foundational concept of plant morphology. As only T.H. Huxley (1853) could put the case, “Wolff demonstrated, by numerous observations on development, the doctrine of the metamorphosis of plants, when Göthe, to whom it is commonly ascribed, was not quite 10 years old.”

The most striking aspect of Wolff's conclusions is that unlike Goethe, who viewed metamorphosis in typological and idealist terms, Wolff, employing a Baconian methodology, was led to his conclusions through direct developmental observation. Wolff was able to determine that the various determinate lateral organs of the shoot system are the same type by observing that vegetative leaves and floral organs all share a similar developmental inception from undifferentiated structures on the flanks of the shoot apex (Huxley, 1853; Tooke and Battey, 2003; Steeves, 2006). Wolff, who proved that leaves are not preformed (that is, the mature structure does not exist in miniature form) but are initiated *de novo* (epigenesis), was the first to illustrate the shoot apex of a plant (Figure 2) with its leaf primordia and to demonstrate the common developmental origin of all mature leaf types. As Wolfe (1789) wrote, “If all plant parts with the exception of the stem can be derived from the leaf form and are nothing more than modifications of it, it follows that it would not be hard to evolve a generation theory of plants. . . First, one must discover through observation the way in which the leaves proper are formed. . . After this has been determined, we must investigate. . . the causes, circumstances, and conditions which modify the general manner of vegetation. . .” (Wolff, 1789; English translation in Goethe, 1952). Wolff went on to do exactly as he proscribed.

Although it is clear that a developmental perspective of plant organs was formally introduced by Wolff in 1759 (republished in 1764, 1774, 1789, and 1889; cited by Goethe, 1817; and reviewed in Huxley, 1853), this empirical approach to the genesis

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**Figure 2.** The First Drawing of the Shoot Apical Meristem of a Plant, from the Dissertation of Caspar Friedrich Wolff (1759).

Wolff called the shoot apex the “punctum vegetationsis” and was the first person to show that vegetative leaves and the organs of a flower (sepals, petals, stamens, and carpels) all have the same developmental origin from the growing tip of a plant and are homologous as leaves. Note in particular, illustrations 6, 13, 18, and 19 of Wolff (1759) for images of vegetative and floral apical meristems and the primordia that they produce. (Image courtesy of the Countway Library of Medicine of Harvard University.)

and generation of plant form had no discernible impact on botanical thought. For example, Erasmus Darwin’s extensive writings on plants and their biology in *The Botanic Garden* (Darwin, 1791) and *Phytologia* (Darwin, 1800) show little understanding of how plants form and develop their basic organs. Forty years later, the widely read botany textbook by John Stevens Henslow (one of Charles Darwin’s most important mentors at Cambridge University), *Descriptive and Physiological Botany* (Henslow, 1835), demonstrates that the study and articulation of basic morphogenetic principles in plants had yet to emerge: “The causes here enumerated, as modifying or disguising the several parts of which flowers are composed, are brought into operation at such early stages of their development, that it is very seldom we can trace the successive steps by which the

metamorphosis has been effected.” Perhaps more importantly, Henslow’s statement provides an important benchmark in one other significant way. His words reveal that by 1835, he (along with others) knew that the explanation for divergent morphologies among floral organs (leaves) could only be gained through an examination of differential patterns of early development at the shoot apex. As with von Baer and his developmental/embryological laws for metazoans, there is no implied evolutionary mechanism associated with Henslow’s rationale for developmental explanation of plant biodiversity.

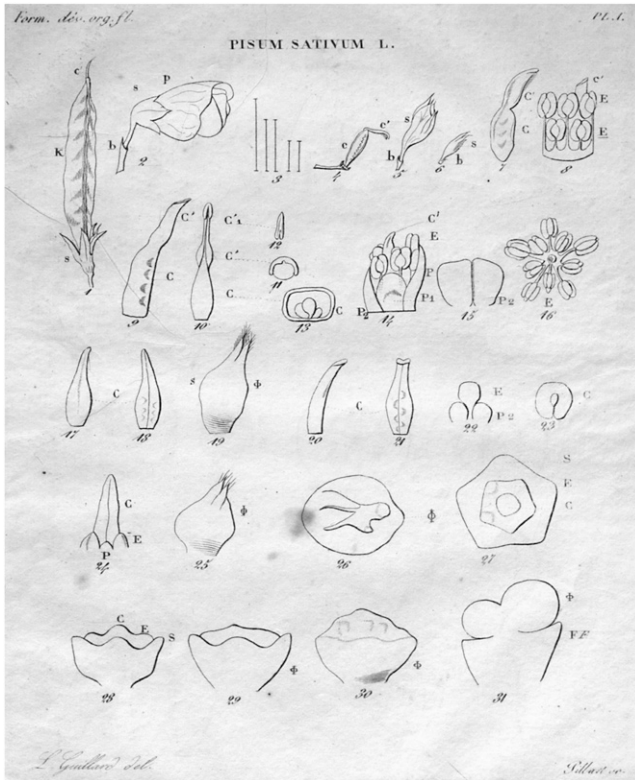
### THE ORIGINS OF PLANT EVOLUTIONARY DEVELOPMENTAL BIOLOGY: ORGANOGENESIS

“Plant organogenesis, that is to say, the study of the various phases through which a plant organ passes before reaching its full development, is a science that is totally new and totally French.” So began the introduction to Jean-Baptiste Payer’s 1857 landmark volume on comparative organogenesis of flowers (*Traité d’Organogénie Comparée de la Fleur*; Payer, 1857). At the heart of this somewhat presumptive statement, there lies a kernel of truth: from the German (Wolff and Goethe) origins of plant morphology, the next phase of the discipline, involving a developmental perspective, was largely, but by no means exclusively, based in France. Beginning in the mid 1830s and continuing through the mid 1850s, a small cadre of French, German, and Russian botanists, benefiting from advances in microscopy, began to systematically study the genesis of vegetative leaves and floral organs at the sites of their initiation on the flanks of the shoot apical meristem.

The stimulus to examine morphogenetic principles that underlie vegetative leaf development can be traced primarily to the expansive studies of plant organography by De Candolle (1827) and the later work of Steinheil (1837). Neither of these botanists directly examined the shoot apical meristem to visualize the formation of leaf primordia (Trécul, 1853b). Rather, their studies (as well as those of other botanists such as Naudin, 1842 and von Mohl, 1845) of later phases of leaf development led to the articulation of hypotheses associated with patterns of directionality of maturation of individual leaves (e.g., acropetal versus basipetal).

The first published work to examine comparative aspects of floral organogenesis was the result of a doctoral thesis in Lyon by Achille Guillard (*Sur la Formation et le Développement des Organes Floraux*, 1835). In this study, Guillard described and figured the initiation of sepal, petal, stamen, and carpel primordia and their subsequent development in floral buds of *Pisum sativum*, *Lathyrus latifolius*, *Papaver somniferum*, *Statice armeria*, and three *Iris* species (Figure 3). He concluded that floral organ primordia begin as colorless and homogeneous structures on the flanks of the shoot apex. Among the many morphogenetic principles articulated, Guillard explicitly discussed the order in which the floral organs are initiated and the differences between the initiation of apocarpous gynoecia and syncarpous carpels

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**Figure 3.** The First Study of Floral Organ Initiation and Development, Undertaken as a Dissertation by Guillard and Published in 1835.

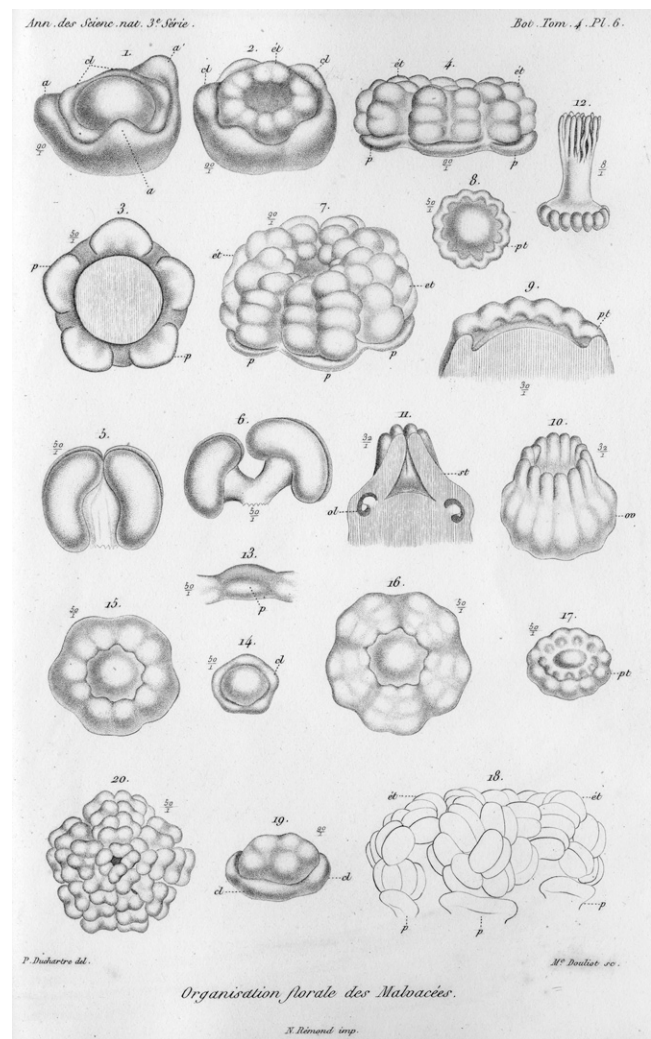
As Guillard (1835) described, his plates of development of pea flower ontogeny could be understood by examining the figures from the last (illustration 31) to the first. Floral organ primordia can be clearly seen in illustrations 27 to 31. (Image courtesy of the Missouri Botanical Garden Library.)

(in essence, the phenomenon of congenital fusion of organs). Guillard's work firmly established an ontogenetic and organogenetic perspective for the study of floral development.

Jacob Mathias Schleiden, while perhaps better known for his widely used textbook (*Grundzüge der Wissenschaftlichen Botanik*; Schleiden, 1842) and as one of the founders of the cell theory, also formulated important generalizations about the nature of floral development. In collaboration with T. Vogel, Schleiden examined legume species with papilionoid flowers and concluded that many of the distinctive features of these monosymmetric (zygomorphic) flowers arise gradually during development (Schleiden and Vogel, 1839). They showed, for example, that floral primordia are initially radially symmetrical and that the organs are initiated individually and are similar in size and shape. The great differences in mature morphology of the banner, wing, and keel petals arise during growth, and the fusion of the keel petals occurs quite late in the development of the flower.

Beginning in 1841, P. Duchartre published a series of papers on the earliest (and later) phases of flower development in a

variety of angiosperm taxa (Figure 4). He was clearly focused on gaining insights into floral diversity through the study of comparative organogenesis as well as extending the initial morphogenetic observations of Schleiden and Vogel (1839). "To know the parts of plants, it is not sufficient to observe them carefully when their forms are mature. . . It is necessary to reach back to when they appear for the first time, to study them in all phases of their progressive development, report at each instant the changes they experience in their form and their relationships. . .



**Figure 4.** Floral Organ Development in *Lavatera trimestris* of the Malvaceae (from Duchartre, 1845).

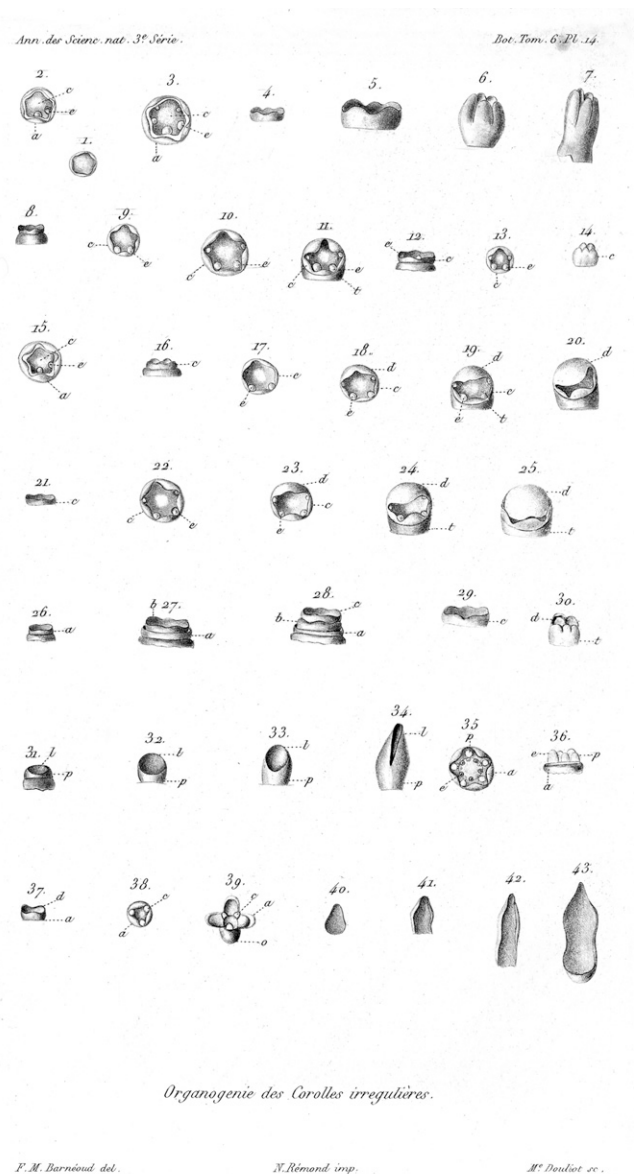
Darwin read this paper at some point between 1853 and 1857. In illustrations 1 to 4, the epicalyx, calyx, and stamens can be seen as extremely young primordia. (Image courtesy of the Library of the Arnold Arboretum of Harvard University.)

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The flower is especially important to study from this point of view; because it may become the source of important considerations, and, also, it may be the site of major alterations. The number and shape of its parts, their position, their relationships can be changed more or less during the course of its development, and, thenceforth, the study of its development, can let us know the nature and extent of perturbations it has undergone. . .” (Duchartre, 1841). Duchartre (1841) began his work with an examination of floral organogenesis in *Helianthus annuus* and *Dipsacus sylvestris* to decipher how fused organs in flowers are initiated. Duchartre would go on to study the developmental basis of free central placentation in Primulaceae, Theophrastaceae, and Myrsinaceae (Duchartre, 1844) and floral organogenesis (with emphasis on developmental processes associated with stamen connation) in members of the Malvaceae (Duchartre, 1845) and the Nyctaginaceae (Duchartre, 1848).

Also drawing upon (and responding to) the morphogenetic studies of zygomorphic flowers in legumes by Schleiden and Vogel (1839), Marius Barnéoud initiated an extraordinarily broad analysis of floral development among angiosperms with monosymmetric flowers, including members of the Ranunculaceae, Violaceae, Labiatae, Scrophulariaceae, Aristolochiaceae, Piperaceae, Verbenaceae, Leguminosae, and Fumariaceae (Barnéoud, 1846). His goal was to determine whether the morphogenetic findings of Schleiden and Vogel (1839) on papilionoid flowers, that morphologically different petals within a monosymmetric flower begin as similar primordial structures and become progressively more divergent in form during the course of development, could be extended to most or all flowering plants (Figure 5). Barnéoud (1846) concluded, “with respect to organogenesis of the calyx and corolla. . . all [floral organ] parts are equal and regular at their origin” despite the tremendous variation of mature forms among petals in individual zygomorphic flowers. Moreover, Barnéoud proposed that the more dissimilar two mature floral organs in a flower are, the earlier in development they diverge from one another. Barnéoud also was able to demonstrate that in certain cases when floral organs are absent from the adult flower, these structures are initiated and remain in a rudimentary state (Brongniart, 1846).

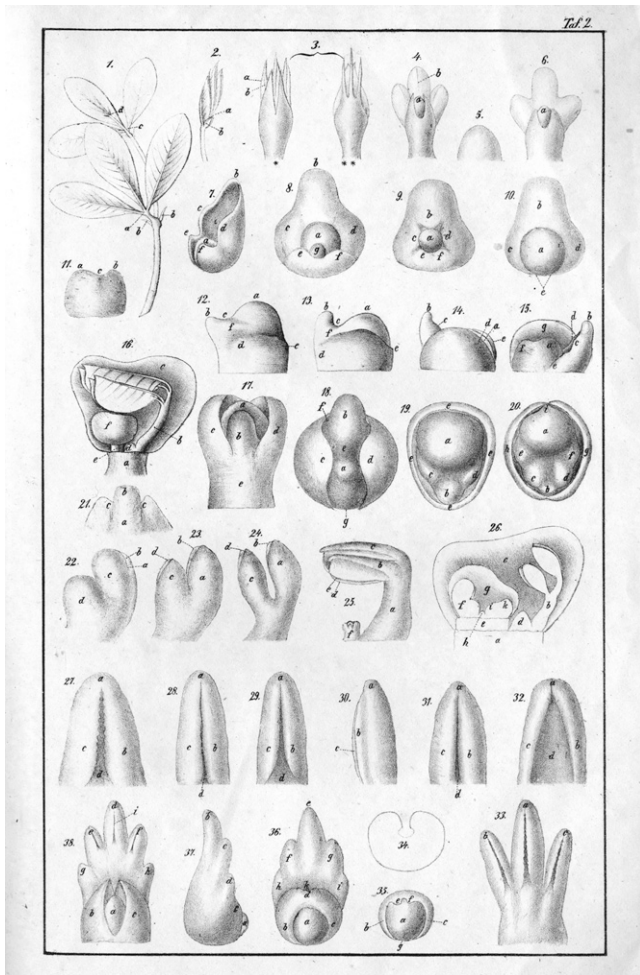
The first truly observational and comparative analyses of vegetative leaf initiation and early organogenesis can be found in the elegant studies of Carl Mercklin (1846a, 1846b). Mercklin examined leaf development from inception at the shoot apex, through the differentiation of upper and lower leaf zones, and to maturity, in a variety of flowering plant taxa (*Acer*, *Liriodendron*, *Hordeum*, *Melanthus*, *Costus*, *Ceratophyllum*, *Baptisia*, and *Amica*). From this broad survey, Mercklin formulated a number of generalizations about the development of leaf form. Importantly, because Mercklin studied the early development of leaves with simple and dissected lamina, he was able to demonstrate that in both cases, leaf primordia are initially simple and homogeneous, and the development of compound morphology is established secondarily. His illustrations are remarkable for their detail and accuracy (Figure 6).



**Figure 5.** Floral Organ Initiation and Development in Irregular (Zygomorphic) Flowers.

Plate from Barnéoud (1846): *Collinsia bicolor*, Plantaginaceae (illustrations 1 to 7); *Antirrhinum majus*, Plantaginaceae (illustrations 8 to 14); *Lamium garganicum*, Lamiaceae (illustrations 15 to 20); *Phlomis fruticosa*, Lamiaceae (illustrations 21 to 25); *Scabiosa ucranica*, Dipsacaceae (illustrations 26 to 30); *Aristolochia pistolochia*, Aristolochiaceae (illustrations 31 to 34); *Cytisus nigricans*, Fabaceae (illustrations 35 to 36); *Orchis galeata*, Orchidaceae (illustrations 37 to 43). (Image courtesy of the Library of the Arnold Arboretum of Harvard University.)

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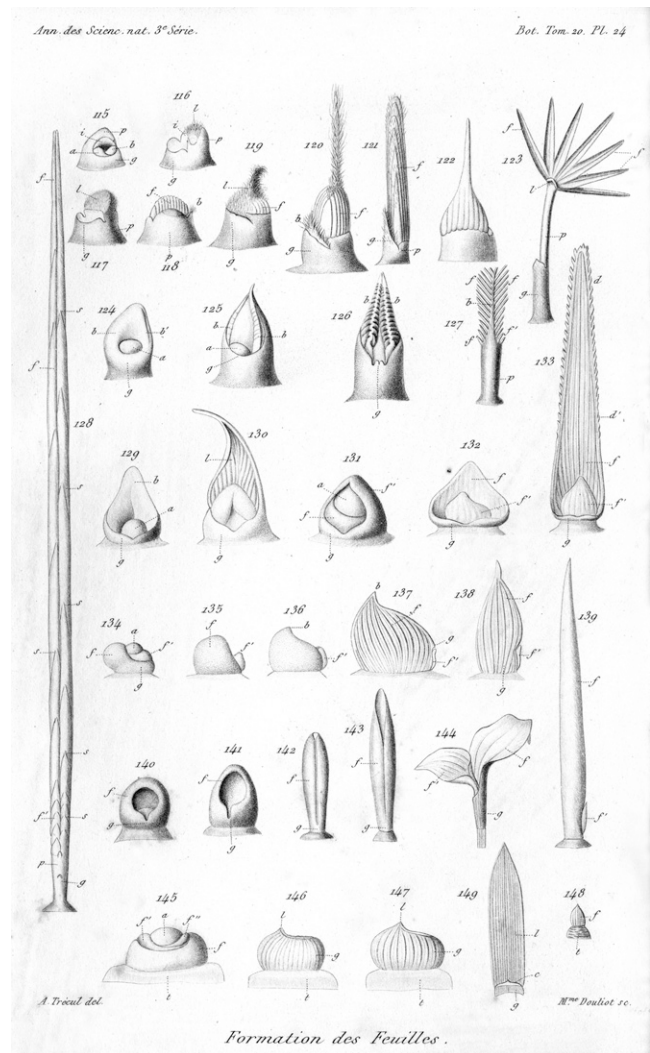
**Figure 6.** Development of Leaves with Dissected Lamina.

Plate from Mercklin (1846a): *Baptisia minor*, Fabaceae (illustrations 1 to 11), *Amicia zoffomeris*, Fabaceae (illustrations 12 to 26, 30 to 32, and 34), *Melianthus major*, Melianthaceae (illustrations 27 to 29, 33, and 35 to 38). Note the careful observations of the formation of leaflets from an initially simple upper leaf zone. (Image courtesy of the Botany Libraries of Harvard University.)

The culmination of this early period of plant morphogenesis research can be found in the publications of Auguste Trécul (1853a, 1853b, 1853c), Herman Schacht (1854), and Jean-Baptiste Payer (1851, 1852, 1853a, 1853b, 1857). Regrettably, the contributions of these workers (as well as those of Duchartre, Mercklin, and Barnéoud) would be largely overlooked (or relegated to minor status) in later historiographies of plant morphology (e.g., Goebel, 1900; Sachs, 1906; Kaplan, 2001). Trécul, Schacht, and Payer pushed the limits of microscopy (as did Mercklin, who was the author of a widely circulated book on microscopy for plants, which was translated from the original

German into English and published in several editions) and focused on processes at the shoot apical meristem to connect the mature morphologies of leaves and floral organs with their developmental origins as undifferentiated primordia on the flanks of the shoot apex.

In a classic and highly synthetic article on the formation of leaves, Trécul (1853b) presented the results of his studies of



**Figure 7.** Leaf Development in Diverse Monocotyledonous Flowering Plants.

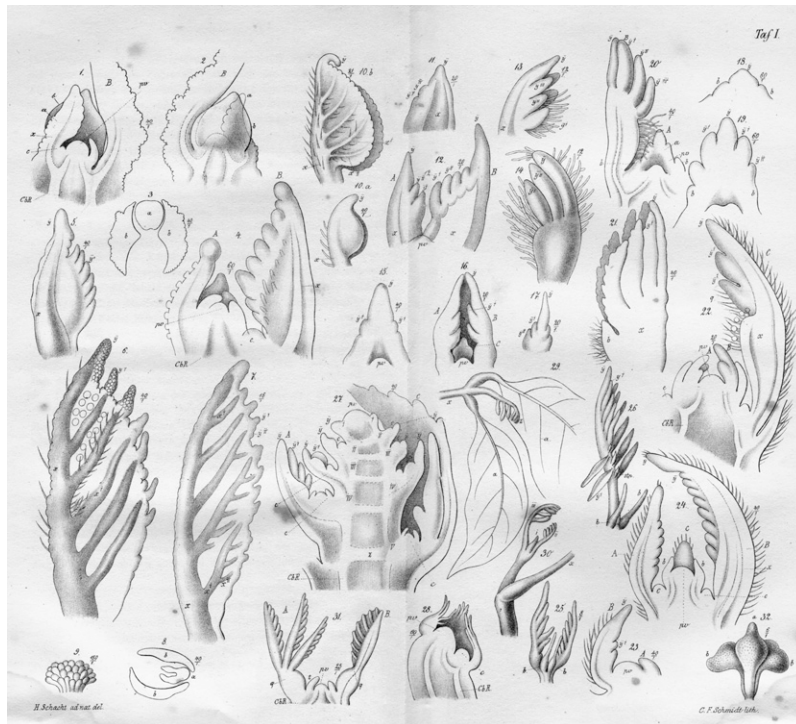
Plate from Trécul (1853b): *Chamaerops humilis*, Arecaceae (illustrations 115 to 123); *Chamaedorea martiana*, Arecaceae (illustrations 124 to 128); *Geonoma baculum*, Arecaceae (illustrations 129 to 130); *Carex riparia*, Cyperaceae (illustrations 131 to 133); *Iris germanica*, Iridaceae (134 to 139); *Tradescantia zebrina*, Commelinaceae (illustrations 140 to 144); *Glyceria aquatica*, Poaceae (illustrations 145 to 149). (Image courtesy of the Library of the Arnold Arboretum of Harvard University.)

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nearly fifty different species of plants (Figure 7). Trécul concluded with a set of 18 basic generalizations governing the shoot apical meristem and leaf morphogenesis. Importantly, his developmental analyses demonstrated that patterns of leaf differentiation (acropetal, basipetal, or a combination of both) are highly variable across diverse taxa and that the rigid morphogenetic rules articulated by earlier workers had so many exceptions as to not constitute rules at all. At the same time that Trécul was formulating his principles of leaf development, Herman Schacht (1854) was examining similar questions. Schacht (1854) predicted “that all leaves, no matter how diverse, will agree in basic mode of development” and set out to test this hypothesis by examining an array of species with diverse mature leaf morphologies (Figure 8). “Now that we have gained a firm understanding from a comparative history of development, we will see how leaves emerge from the shoot tip and how they gradually develop into full grown leaves. From a large number of case studies, I have selected those leaf forms that are quite dissimilar from each other in their adult condition and are indistinguishable when they are initiated.” Schacht also considered cases in which similar

forms can arise by very different developmental patterns (what would later be viewed as homoplasy).

While Trécul and Schacht were analyzing morphogenetic rules for vegetative leaves, Payer (1851, 1852, 1853a, 1853b) began to publish a series of highly influential articles on floral morphogenesis (with some asides on vegetative leaf development). Payer (1852) proposed hypotheses about the metamorphosis of petals into stamens (in essence, homeosis), examined the developmental nature of inferior ovaries, and studied the morphological basis for perigyny. Payer also demonstrated that the order of initiation of organs in flowers may be decoupled from relative amounts and rates of subsequent growth; hence, stamens may surpass petals in their development, but are still initiated after petals (Payer, 1853b). The culmination of Payer’s extraordinary dissections and microscopic examinations of developing flowers is his masterpiece two volume systematic compendium of more than a decade of observations (Payer, 1857). The figures (154 plates in total) are so well executed that current studies of floral morphogenesis drawing upon the technology of the scanning electron microscope appear to be only marginally more



**Figure 8.** Leaf Development in a Broad Diversity of Eudicotyledonous Flowering Plants.

Plate from Schacht (1854). *Alnus glutinosa*, Betulaceae (illustrations 1 to 9), *Tilia grandifolia*, Tiliaceae (illustration 10), *Juglans regia*, Juglandaceae (illustrations 11 to 14), *Sambucus nigra*, Adoxaceae (illustrations 15 to 17), *Rosa canina*, Rosaceae (illustrations 18 to 21), *Acer campestre*, Sapindaceae (illustration 22), *Robinia pseudoacacia*, Fabaceae (illustrations 23 to 26), *Ampelopsis quinquefolia*, Vitaceae (illustrations 27 and 28), *Guarea trichilioides*, Meliaceae (illustrations 29 and 30), *Aesculus hippocastanum*, Sapindaceae (illustration 31), *Betula alba*, Betulaceae (illustration 32). (Image courtesy of the Library of the Arnold Arboretum of Harvard University.)



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informative (Figure 9). Payer concluded this work with a highly synthetic analysis of principles across angiosperms that govern the generation of form in each of the floral organs (sepals, petals, stamens, and carpels) and argues that only with a developmental/organogenetic approach can the true affinities (taxonomic, but not phylogenetic) of plant groups be determined.

By the mid 1850s, the discipline of comparative plant developmental morphology was in full bloom. The basic concept of homology of different forms of leaves had been firmly established by Goethe and Wolff. Extensive surveys of organogenesis of

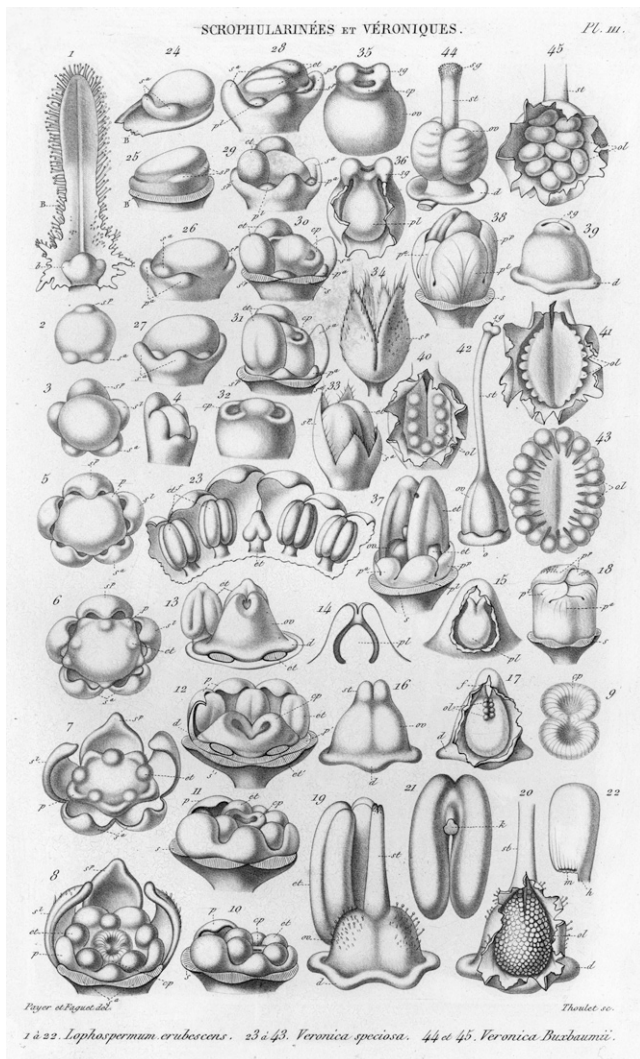
vegetative leaves and floral organs among angiosperms had resulted in the establishment of a basic set of developmental principles that govern the generation of plant form. Yet, none of this scholarship was evolutionary in nature. The question thus remains: When did the diversity of plant form come to be viewed as an evolutionary result of the transformation of ontogenies over time?

### THE ORIGINS OF PLANT EVOLUTIONARY DEVELOPMENTAL BIOLOGY: EVOLUTION

Charles Darwin was by no means the first evolutionist. The concept of evolution was discussed, written about, and widely disseminated as early as the second half of the eighteenth century (e.g., De Maillet, 1748; Diderot, 1754). Indeed, Charles Darwin was not even the first Darwin to espouse evolutionist ideas. That honor belongs to his grandfather, Erasmus Darwin, whose *Zoonomia* (Darwin, 1794) contained the first English language discussion of the concept of organic evolution. Between 1748 and 1859, perhaps as many as 40 (or more) individuals in France, Germany, England, Scotland, Belgium, Switzerland, and the United States had formally published on the fact and process of evolution. Yet, with very few exceptions, none of this early evolutionist literature can be shown to have intersected with the plant developmental literature of the first half of the 19th century.

Robert Chambers, the anonymous author of the sensational and best-selling book on evolution, *Vestiges of the Natural History of Creation* (1844) was the first person to link a developmental view of the world with the process of evolution. Drawing upon the embryological and developmental (but not evolutionary) rules of von Baer (and possibly Martin Barry, 1837a, 1837b), as circumscribed in William Carpenter's *Principles of General and Comparative Physiology* (first edition, 1838; second edition, 1841), Chambers argued that the modification of ontogenies over time was a central mechanism of (and means of understanding) biological diversity (Gould, 1977). "I suggest then, as an hypothesis already countenanced by much that is ascertained, and likely to be further sanctioned by much that remains to be known, that the first step was an *advance under favour of peculiar conditions, from the simplest forms of being, to the next more complicated, and this through the medium of the ordinary process of generation [development]*" (Chambers, 1844).

Although Robert Chambers was not a practicing natural historian (he was a Scottish publisher of middlebrow journals, encyclopedias, and books; Secord, 2001), he read widely and wrote prodigiously on many aspects of biology and geology. Perhaps because he was neither a practicing botanist nor zoologist, his brilliant insight of linking development of the individual with the development (evolution) of life was proposed for both animals and plants (in the chapter "Hypothesis of the Development of the Vegetable and Animal Kingdoms"). However, there are no specific references to, or examples from, the emerging field of plant developmental morphology; his arguments are almost exclusively drawn from the metazoan embryological literature.



**Figure 9.** Floral Development.

Plate from Payer (1857). *Lophospermum erubescens*, Plantaginaceae (illustrations 1 to 22), *Veronica speciosa* (= *Hebe speciosa*), Plantaginaceae (illustrations 23 to 43), *Veronica buxbaumii*, Plantaginaceae (illustrations 44 and 45). (Image courtesy of the Botany Libraries of Harvard University.)

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The next book to be published on the topic of evolution, *Essays on the Spirit of the Inductive Philosophy, the Unity of Worlds, and the Philosophy of Creation* (Powell, 1855), also draws heavily on the embryological principles of von Baer as well as the developmental perspectives of the evolutionist Robert Knox (1852). By integrating development into an understanding of diversity, Baden Powell forcefully confronts the creationist alternatives to the explanation of closely allied species in place and subsequent time. “And the only question is as to the sense in which such *change of species* is to be understood; whether individuals naturally produced from parents, were modified by successive variations of parts, in any stage of early growth or rudimental development, until, in one or more generations, the whole species became in fact a different one; or whether we are to believe that the *whole race* perished without re-producing itself, while, independent of it, *another new race*, or other new individuals (by whatever means), came into existence, of a nature closely allied to the last, and differing often by the slightest shades, yet *unconnected with them by descent*. . .” Powell was fully aware of the powerful mechanistic explanation of evolutionary diversification that development provides for metazoans but was unaware of (or not focused on) the similar but separately derived laws of plant organogenesis.

In the end, the first articulation of the concept that plant (namely floral) evolution results from successive modifications of ontogeny would come from the mind of Charles Darwin. As Darwin (1859) wrote in *On the Origin of Species* (pp. 436–437), “we can actually see in embryonic crustaceans and in many other animals, *and in flowers* [emphasis added], that organs, which when mature become extremely different, are at an early stage of growth exactly alike.” This seemingly minor (and odd—crustaceans and flowers!) statement reveals that Darwin was aware of the developmental principle of the homogeneous and similar to the heterogeneous and dissimilar, not only for animals, but also for the organs of flowers. Although this passage from *On the Origin of Species* suggests a merely incidental interest by Darwin in an evolutionary developmental perspective on plants, as we will demonstrate, this sentence is the product of many years of intellectual analysis of how modifications of development in the flower could explain, mechanistically, the origin of the vast diversity of floral forms among angiosperms.

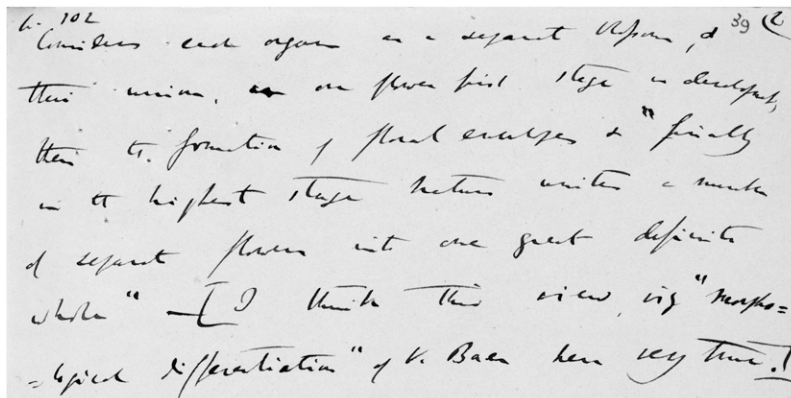
Although previously unnoted (at least to our knowledge), Darwin’s notebooks reveal that he was keenly interested in the emerging frontiers of French and German plant developmental morphology. Darwin’s abstracts of scientific books (Cambridge University Library, DAR 72) record that he carefully read many volumes from the 1830s through the early 1850s of *Annales des Sciences Naturelles, Botanique*; in essence, Darwin read the journal at the center of the advances being made in the study of floral and vegetative leaf development. Specifically, Darwin read and summarized the key findings from the seminal papers on principles of organ initiation and development in flowers by Schleiden and Vogel (the 1840 French summary of their paper from 1839, *Sur le développement des fleurs des Légumineuses*),

Duchartre (1845; *Observations sur l’organogénie de la fleur dans les plantes de la famille des Malvacées*), Barnéoud (1846; *Mémoire sur le développement de l’embryon et des corolles anormales dans les Renonculacées et les Violariées*; here, Darwin records nearly two full pages of notes), Brongniart (1846; *Rapport sur un Mémoire de M. Barnéoud*; Darwin extracts another two pages of notes from this overview of recent advances and developmental principles inferred from the study of floral development, including the results from Barnéoud’s paper on Ranunculaceae and Violaceae), Barnéoud (1847; *Seconde mémoire sur l’organogénie des corolles irrégulières*), Barnéoud (1848; *Mémoire sur l’anatomie et l’organogénie du *Trapa natans**), and Duchartre (1848; *Observations sur l’organogénie florale et sur l’embryogénie des Nyctaginées*). Darwin grasped the significance of the principle articulated by Barnéoud that in zygomorphic flowers, sepals, and petals that will ultimately diverge in form begin as very similar and symmetrically arranged primordia. More generally, Darwin understood that plant organ development proceeds from the similar and homogeneous to the diverse and heterogeneous.

It is unclear precisely when Charles Darwin made his way through the entire second series and first 19 volumes of the third series of *Annales des Sciences Naturelles, Botanique*. These volumes cover the years from 1834 through 1853. A reasonable assumption, in light of the continuous pagination of Darwin’s notes, is that he read through these critical volumes of French botanical literature at some point after the publication of series three, volume nineteen, in the middle of 1853. In his notes “Books to be certainly read,” dated May 2, 1856 (Cambridge University Library, DAR 91: 88a1), Darwin records “*Annales des Sc. Nat.* 3<sup>d</sup> series Tom VII et seq.” Thus, by May of 1856, Darwin had read and digested the articles of interest that predate the seventh volume of the third series of *Annales des Sciences Naturelles, Botanique*. These papers included a French overview of Schleiden and Vogel (1840) on floral development in legumes (Darwin records in his notebook, Cambridge University Library, DAR 72: 97, “the flowers are perfectly regular in their origin - the parts united are born as free extremities”), the work of Duchartre (1845) on floral development in Malvaceae, and the seminal paper on organ development in zygomorphic flowers by Barnéoud (1846; along with the overview paper by Brongniart, 1846). Additionally, it is possible to constrain the latest date that Darwin perused these volumes through his correspondence with T.H. Huxley in July of 1857.

In July of 1857, after Darwin had completed the seventh chapter (Laws of Variation: Varieties and Species Compared) of his manuscript *Natural Selection* (begun in 1856, abandoned in 1858 when he initiated *On the Origin of Species*, finally published by R.C. Stauffer in 1975), he sent T. H. Huxley a fair copy of four folio pages from this chapter (Stauffer, 1975). These four pages of the manuscript dealt specifically with principles (laws) of development that had been articulated in a series of papers by Marius Barnéoud (see discussion above), Gaspard Auguste Brullé, and Henri Milne Edwards. Brullé (1844) examined the

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**Figure 10.** Charles Darwin's Notes about Schleiden's Book *The Plant; A Biography*.

Here, Darwin makes the connection between flower and inflorescence development, as described by Schleiden, and the laws of morphological differentiation of von Baer. The text reads: "Consider each organ as a separate blossom, & their union as one flower first stage in development, then the formation of floral envelopes & finally in the highest stage nature unites a number of separate flowers into one great definite whole" [I think this view viz 'morphological differentiation' of V. Baer here very true.]. (Image courtesy of Cambridge University Library.)

early development of crustaceans (nota bene) and concluded that ontogenetically, the most complex organs are initiated prior to those organs that are simpler in structure. Henri Milne Edwards (Milne Edwards, 1844) pressed the case for the importance of embryological features among metazoans for purposes of identifying natural groups and proposed a series of principles about the relative timing of organ initiation in ontogeny in relation to degree of specialization.

In Darwin's July 5, 1857 letter to Huxley that accompanied the four evolutionary developmental pages of manuscript, he asks if "there is any truth in MM Brullé and Barneoud. . . I was long ago much struck with the principle referred to [Milne Edwards' views on classification]: but I could then see no rational explanation why affinities should go with the more or less early branching off from a common embryonic form. But if MM Brulle and Barneoud are right, it seems to me we get some light on Milne Edwards views of classification; and this particularly interests me." Darwin was struggling to understand how basic principles of embryology and organogenesis might be associated with the identification of evolutionary relationships among organisms.

Huxley's reply (July 7, 1857) was severely critical of the embryological principles of Brullé ("And now having *brûler*'d Brullé"), whose analyses of development contained factual errors. Nevertheless, Huxley reminded Darwin of the well-established principle "that 'the more widely two animals differ from one another the earlier does their embryonic resemblance cease' but you must remember that the differentiation which takes place is the result not so much of the development of new parts as of the *modification of parts already existing and common to both of the divergent types*." In the course of this reasonably long letter, Huxley did not specifically allude to Barnéoud and his analyses of floral organ development.

In response to Huxley's strong dismissal of Brullé, Darwin recorded a note in his manuscript pages for the seventh chapter of *Natural Selection* (Stauffer, 1975) in which he distinguishes between the (erroneous) developmental principles articulated by Brullé and those of Barnéoud, who had demonstrated that the most widely different forms of petals (and sepals) in zygomorphic flowers diverge in morphology very early in development. This note was then developed by Darwin into a response to Huxley sent on July 9, 1857 (Stauffer, 1975). "There is only one point in your letter which at present I cannot quite follow you in: **supposing** that Barneoud's (I do *not* say Brulle's) remark were true & universal, ie that the petal which have [sic] to undergo the greatest amount of development & modification begins to change the soonest from the simple & common embryonic form of the petal, if this were a true law, then I cannot but think that it would throw light on Milne Edwards' proposition that the wider apart the classes of animals are, the sooner do they diverge from the common embryonic plan, which common embryonic [plan] may be compared with the similar petals in the early bud—the several petals in *one* flower being compared with the distinct but similar embryos of the different classes. I much wish, that you w<sup>d</sup>. so far keep this in mind, that whenever we meet, I might hear how far you differ or concur in this. I have always looked at Barneoud's & Brulle's proposition as only in some degree analogous."

There is one final piece of evidence that makes absolutely clear that Darwin was the first to link the principles of metazoan embryology that he already viewed as explanatory in an evolutionary context to the rapidly advancing field of comparative developmental plant morphology. In Darwin's abstracts of scientific books (Cambridge University Library, DAR 71), he records four pages (Cambridge University Library, DAR 71: 38–42) of

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notes in response to having read the English edition of Schleiden's lectures, *The Plant; a Biography* (1848). These lectures include a chapter on plant morphology in which Schleiden discusses the development of flowers and inflorescences in angiosperms. Darwin writes (Figure 10): "Considers each organ as a separate blossom, & their union as one flower first stage in development, then the formation of floral envelopes & 'finally in the highest stage nature unites a number of separate flowers into one great definite whole' [I think this view viz 'morphological differentiation' of V. Baer here very true.]" The date of this entry is unknown, but Darwin, the evolutionist, has unequivocally drawn the critical inference that floral development, from homogeneous primordia to differentiated mature sepals, petals, stamens, and carpels, is directly analogous to the developmental principles articulated by von Baer for metazoans.

### THE ORIGINS OF PLANT EVOLUTIONARY DEVELOPMENTAL BIOLOGY: CONCLUSIONS

Charles Darwin is well known as the codiscoverer (along with Alfred Russel Wallace, 1858) of the mechanism of natural selection to account for the process of evolution. What has long been much underappreciated, is that natural selection is but one of two critical mechanisms that Darwin proposed to account for transformation over time, the other being the modification of development. Darwin understood the centrality of development in a deep and profoundly important way, both for animals and for plants.

His notebooks record his careful reading and interest in animal embryology and plant leaf and floral organ morphogenesis. By 1857, Darwin had directly linked the embryological laws of von Baer and Milne Edwards for metazoans to the recently revealed principles of organogenesis of floral organs in plants. Moreover, Darwin had integrated the rules of floral development into the explanatory context of developmental evolution, just as he had done many years earlier for metazoans. Thus, while Darwin may have been puzzling primarily over questions of metazoan development and evolution (and indeed, this is a major emphasis of the chapter on morphology and embryology in *On the Origin of Species*), his earlier readings of the plant developmental morphology literature provided him with key insights into the evolutionary implications of the modification of structure through development. Unfortunately, as a consequence of the interchange of views with Huxley, this specific section of "Laws of Variation" from the seventh chapter of *Natural Selection* would not be used in what became the fifth chapter, "Laws of Variation," in *On the Origin of Species* (1859). All that remains of Darwin's intense consideration of Brullé and Barnéoud is the single enigmatic sentence referring to the developmental evolution of crustaceans and flowers.

In the final analysis, Charles Darwin is unique among the early evolutionists who discussed the importance of ontogenetic modifications to understanding the process of biological diver-

sification. He alone, among the many early evolutionists (including Chambers and Powell), extended his discussion of the evolution of development specifically to plants. Without question, Darwin clearly recognized the explanatory power of an evolutionary developmental perspective for both animals and plants. Plant evo-devo had been born.

### ACKNOWLEDGMENTS

We thank Peter Stevens and Nancy Dengler for many helpful suggestions in tracking the earliest plant developmental morphologists, Janet Browne for feedback on Darwin and his botanical pursuits, Peter Endress and Daniel Medeiros for feedback on the manuscript, Susanne Renner for assistance with translations from German, Julien Bachelier for assistance with translations from French, and Lisa Pearson and Lisa DeCesare for assistance acquiring digital images for the plates. Finally, we thank Marianne Bronner-Fraser for the original invitation to speak on the topic of the history of plant evo-devo at the 2009 Society for Developmental Biology meeting.

Received February 11, 2011; revised March 17, 2011; accepted March 29, 2011; published April 22, 2011.

### REFERENCES

- Barnéoud, M.** (1846). Mémoire sur le développement de l'embryon et des corolles anormales dans les Renonculacées et les Violariées. *Ann. Sci. Nat. Bot. 3rd Series* **6**: 268–296.
- Barnéoud, M.** (1847). Seconde mémoire sur l'organogénie des corolles irrégulières. *Ann. Sci. Nat. Bot. 3rd Series* **8**: 344–356.
- Barnéoud, M.** (1848). Mémoire sur l'anatomie et l'organogénie du *Trapa natans* (Linn.). *Ann. Sci. Nat. Bot. 3rd Series* **9**: 222–244.
- Barry, M.** (1837a). On the unity of structure in the animal kingdom. *Edinburgh New Phil. J.* **22**: 116–141.
- Barry, M.** (1837b). Further observations on the unity of structure in the animal kingdom, and on congenital anomalies, including "hermaphrodites;" with some remarks on the embryology as facilitating animal nomenclature, classification, and the study of comparative anatomy. *Edinburgh New Phil. J.* **22**: 345–364.
- Brongniart, A.** (1846). Rapport sur un mémoire de M. Barnéoud ayant pour objet le développement de l'ovule et de l'embryon dans les Renonculacées et les Violariées, et celui du calice et de la corolle dans ces familles et dans plusieurs autres à corolle irrégulière. *Ann. Sci. Nat. Bot. 3rd Series* **6**: 297–303.
- Brullé, A.** (1844). Recherches sur les transformations des appendices dans les articulés. *Ann. Sci. Nat. Zool. 3rd Series* **2**: 271–374.
- de Beer, G.** (1958). Darwin's views on the relations between embryology and evolution. *J. Linn. Soc. Lond. Zool.* **44**: 15–23.
- De Candolle, A.P.** (1827). *Organographie Végétale, ou Description Raisonnée des Organes des Plantes*, Vol. 2. (Paris: Deterville).
- Carpenter, W.B.** (1841). *Principles of General and Comparative Physiology*, 2nd ed. (London: John Churchill).
- Chambers, R.** (1844). *Vestiges of the Natural History of Creation*. (London: John Churchill).
- Coen, E.** (2001). Goethe and the ABC model of flower development. *C. R. Acad. Sci. III Vie* **324**: 523–530.

## PERSPECTIVE

- Darwin, C.** (1859). On the Origin of Species by Means of Natural Selection. (London: John Murray).
- Darwin, C.** (1909). The Foundation of the Origin of Species: Two Essays Written in 1842 and 1844. (Cambridge, UK: Cambridge University Press).
- Darwin, E.** (1791). The Botanic Garden; A Poem in Two Parts. (London: J. Johnson).
- Darwin, E.** (1794). Zoonomia. (London: J. Johnson).
- Darwin, E.** (1800). Phytologia. (London: J. Johnson).
- De Maillet, B.** (1748). Telliamed ou entretiens d'un philosophe indien avec un missionnaire françois, sur la diminution de la Mer, la formation de la Terre, l'origine de l'Homme, etc. Mis en ordre sur les Mémoires de feu M. de Maillet. (Amsterdam: L'Honoré et Fils).
- Diderot, D.** (1754). Pensées sur l'Interprétation de la Nature. (Paris).
- Dornelas, M.C., and Dornelas, O.** (2005). From leaf to flower: Revisiting Goethe's concepts on the "metamorphosis" of plants. *Braz. J. Plant Physiol.* **17**: 335–344.
- Duchartre, P.** (1841). Observations sur quelques parties de la fleur dans le *Dipsacus sylvestris* Mill. et dans l'*Helianthus annuus* Lin. *Ann. Sci. Nat. Bot. 2nd Series* **16**: 1–15.
- Duchartre, P.** (1844). Observations sur l'organogénie de la fleur et en particulier de l'ovaire. *Ann. Sci. Nat. Bot. 3rd Series* **2**: 1–23.
- Duchartre, P.** (1845). Observations sur l'organogénie de la fleur dans les plantes de la famille des Malvacées. *Ann. Sci. Nat. Bot. 3rd Series* **4**: 123–161.
- Duchartre P.** (1848). Observations sur l'organogénie florale et sur l'embryogénie des Nyctaginées. *Ann. Sci. Nat. Bot. 3rd Series* **9**: 263–284.
- Engard, C.J.** (1989). Introduction. In *Goethe's Botanical Writings/Johann Wolfgang Goethe*, translated by Bertha Mueller, with an introduction by Charles J. Engard. (Woodbridge, CT: Ox Bow Press), pp. 3–18.
- Eyde, R.H.** (1975). The foliar theory of the flower. *Am. Sci.* **63**: 430–437.
- Friedman, W.E.** (2009). Evolution. Auxin at the evo-devo intersection. *Science* **324**: 1652–1653.
- Ganong, W.F.** (1901). The cardinal principles of morphology. *Bot. Gaz.* **31**: 426–434.
- Goebel, K.** (1900). Organography of Plants, Especially of the Archeogniata and Spermaphyta, Parts 1 and 2, authorized English ed. (Oxford, UK: Clarendon Press).
- Goebel, K.** (1926). Wilhelm Hofmeister: The Work and Life of a Nineteenth Century Botanist. (London: Ray Society).
- Goethe, J.W.** (1790). Versuch die Metamorphose der Pflanzen zu erklären. (Gotha, Germany: Ettinger).
- Goethe, J.W.** (1817). Goethe's Werk, Italienische Reise. (Stuttgart, Germany: Dreizehnter Band).
- Goethe, J.W.** (1837). Oeuvres d'Histoire Naturelle de Goethe. Translated and annotated by C.F. Martins. (Paris: A.B. Cherbuliez).
- Goethe, J.W.** (1952). Botanical Writings, translated by Bertha Mueller, with an introduction by Charles J. Engard. (Honolulu, HI: University of Hawaii Press).
- Gould, S.J.** (1977). Ontogeny and Phylogeny. (Cambridge, UK: Harvard University Press).
- Gould, S.J.** (2002). The Structure of Evolutionary Theory. (Cambridge, UK: Harvard University Press).
- Guillard, A.** (1835). Sur la Formation et le Développement des Organes Floraux. (Lyon, France: D.L. Ayné).
- Henslow, J.S.** (1835). The Principles of Descriptive and Physiological Botany, Vol. 54 of Cabinet Cyclopædia: Natural History. (London: Longman, Hurst, Rees, Orme, Brown, and Green).
- Hofmeister, W.** (1851). Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen (Moose, Farne, Equisetaceen, Rhizocarpeen and Lycopodiaceen) und der Samenbildung der Coniferen. (Leipzig, Germany: Friedrich Hofmeister).
- Huxley, T.H.** (1853). The cell theory. *Brit. Foreign Medico-Chirurgical Rev.* **12**: 221–243.
- Kaplan, D.R.** (2001). The science of plant morphology: Definition, history, and role in modern biology. *Am. J. Bot.* **88**: 1711–1741.
- Knox, R.** (1852). Great Artists and Great Anatomists; A Biographical and Philosophical Study. (London: John Van Voorst).
- Mercklin, C.E.** (1846a). Entwicklungsgeschichte der Blattgestalten. (Jena, Germany: Carl Hochhausen).
- Mercklin, C.E.** (1846b). Observations sur l'histoire du développement des feuilles. *Ann. Sci. Nat. Bot. 3rd Series* **6**: 215–246.
- Milne Edwards, H.** (1844). Considérations sur quelques principes relatifs à la classification naturelle des animaux, et plus particulièrement sur la distribution méthodique des mammifères. *Ann. Sci. Nat. Zool. 3rd Series* **1**: 65–129.
- Mueller, B., and Engard, C.J.** (1952). Goethe's Botanical Writings. (Honolulu, HI: University Press of Hawaii).
- Naudin, C.** (1842). Résumé de quelques observations sur le développement des organes appendiculaires des végétaux. *Ann. Sci. Nat. Bot. 2nd Series* **18**: 360–365.
- Oppenheimer, J.** (1959). An embryological enigma in the Origin of Species. In *Forerunners of Darwin: 1745–1859*, B. Glass, O. Tempkin, and W.L. Strauss, Jr., eds (Baltimore, MD: Johns Hopkins University Press), pp. 292–322.
- Ospovat, D.** (1976). The influence of Karl Ernst von Baer's embryology, 1828–1859: A reappraisal in light of Richard Owen's and William B. Carpenter's "palaeontological application of 'Von Baer's Law'." *J. Hist. Biol.* **9**: 1–28.
- Payer, J.-B.** (1851). Organogénie végétale. Familles des Nitrariées (*Nitraria*, des Morées (*Morus*, *Ficus*) et des Anacardiées (*Mangifera*, *Rhus*). *C. R. Hebd. Acad. Sci.* **32**: 936–940.
- Payer, J.-B.** (1852). Organogénie de la classe des Cactoidées (*Cactées*, *Ficoïdes* et *Tétragoniées*) et de celle des Berbérinées (*Berbéridées*, *Ménispermées*). *Ann. Sci. Nat. Bot. 3rd Series* **18**: 234–256.
- Payer, J.-B.** (1853a). Organogénie végétale. Organogénie de la famille des Myrtacées (*Myrtus*, *Eucalyptus*, *Callistemon*) et de celle des Umbellifères (*Heracleum*, *Eryngium*). *C. R. Hebd. Acad. Sci.* **37**: 417–422.
- Payer, J.-B.** (1853b). Organogénie des familles des Myrtacées, Punicées, Philadelphées, Loasées et Omellifères. *Ann. Sci. Nat. Bot. 3rd Series* **20**: 97–128.
- Payer, J.B.** (1857). Traité d'Organogénie Comparée de la Fleur. (Paris: Librairie de Victor Masson).
- Powell, B.** (1855). Essays on the Spirit of the Inductive Philosophy, the Unity of Worlds, and the Philosophy of Creation. (London: Longman, Brown, Green and Longmans).
- Raff, R.A.** (1996). The Shape of Life. (Chicago: University of Chicago Press).
- Richards, R.J.** (1992). The Meaning of Evolution. (Chicago: University of Chicago Press).
- Russell, E.S.** (1916). Form and Function: A Contribution to the History of Animal Morphology. (London: John Murray).
- Sachs, J.** (1906). History of Botany (1530–1860), authorized translation by H.E.F. Garnsey. (Oxford, UK: Clarendon Press).
- Schacht, H.** (1854). Beiträge zur Anatomie und Physiologie der Gewächse. (Berlin: G.W.F. Müller).
- Schleiden, M.J.** (1842). Grundzüge der Wissenschaftlichen Botanik

## PERSPECTIVE

- nebst einer Methodologischen Einleitung, Zweiter Theil, Morphologie. (Leipzig, Germany: Organologie).
- Schleiden, M.J.** (1848). *The Plant; A Biography*. (London: Hippolyte Bailliere).
- Schleiden, M.J., and Vogel, T.** (1839). Beiträge zur Entwicklungsgeschichte der Blüthentheile bei den Leguminosen. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum **11**: 59–84.
- Schleiden, M.J., Vogel, T.** (1840). Sur le développement des fleurs des Légumineuses. Ann. Sci. Nat. Bot. 3rd Series **13**: 377–378.
- Secord, J.A.** (2001). *Victorian Sensation: The Extraordinary Publication, Reception, and Secret Authorship of Vestiges of the Natural History of Creation*. (Chicago: University of Chicago Press).
- Stauffer, R.C.,** ed. (1975). *Charles Darwin's Natural Selection; Being the Second Part of His Big Species Book Written from 1856 to 1858*. (Cambridge, UK: Cambridge University Press).
- Steinheil, A.** (1837). Observations sur le mode d'accroissement des feuilles. Ann. Sci. Nat. Bot. 2nd Series **8**: 25–304.
- Stern, W.L.** (1993). The uses of botany with special reference to the 18th-century. Taxon **42**: 773–779.
- Steeves, T.A.** (2006). The shoot apical meristem: An historical perspective. Can. J. Bot. **84**: 1629–1633.
- Tooke, F., and Battey, N.** (2003). Models of shoot apical meristem function. New Phytol. **159**: 37–52.
- Trécul, A.** (1853a). Note sur la formation des feuilles. Ann. Sci. Nat. Bot. 3rd Series **20**: 183–190.
- Trécul, A.** (1853b). Mémoires sur la formation des feuilles. Ann. Sci. Nat. Bot. 3rd Series **20**: 235–314.
- Trécul, A.** (1853c). Organogénie végétale—Formation des feuilles. C. R. Hebd. Acad. Sci. **37**: 482–486.
- von Baer, K.E.** (1853). Fragments relating to philosophical zoology. In *Scientific Memoirs Selected from the Transactions of Foreign Academies and From Foreign Journals, Natural History*, A. Henfrey and T.H. Huxley, eds (London: Taylor and Francis), pp. 176–238.
- von Baer, K.E.** (1828). *Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion*. (Königsberg, Germany: Bornträger).
- von Mohl, H.** (1845). *Vermischte Schriften botanischen Inhalts*. (Tübingen, Germany: Ludwig Friedrich Fuchs).
- Wolff, C.F.** (1759). *Theoria Generationis*. Halae ad Salam: Litteris Hindelianis.
- Wolff, C.F.** (1789). Von der eigenthümlichen und wesentlichen Kraft der vegetabilischen sowohl als auch der animalischen Substanz. In *Zwo Abhandlungen über die Nutritionskraft welche von der Kayserlichen Academie der Wissenschaften in St. Petersburg den Preis getheilt erhalten haben. Die erste von Herrn Hofrath Blumenbach, die zweite von Herrn Prof. Born. Nebst einer ferneren Erläuterung eben derselben Materie, von C. F. Wolff der Akademie Mitgleid*. (St. Petersburg, Russia: Kayserliche Akademie der Wissenschaften).