Taxonomy was the foundation of Darwin's evolution

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Darwin's belief in branching evolution was based upon his familiarity with the taxonomy of his day. Facts from biogeography, embryology, and paleontology acquired deep significance because biologists had come to believe that natural classification expressed real relationships. Although Charles Darwin's presentation of his theory in the *Origin of Species*, as well as descriptions of Darwinism after the Modern Synthesis of the 1940s, imply that establishing the causal role of natural selection was essential to proving that evolution has occurred, this is contradicted by Darwin's personal experience and by his own words. It is helpful to compare the history and logical structure of Darwin's revolutionary theory to the Copernican Revolution, for the moving Earth was recognized long before Newton identified causes to explain its motion. Copernicus saw that fixing the Sun as the center of planetary motion explained the appearance of the heavens better than the Ptolemaic system did, and Darwin saw that branching evolution explains the "truly wonderful fact" that a hierarchy of nested groups appears natural.

KEYWORDS: Agassiz, cause, Darwin, evolution, history, systematics, taxonomy, theory

INTRODUCTION

Taxonomy undoubtedly suffers from what the marketing people would call an image problem. Although most taxonomists believe that they are engaged in an enterprise that is scientifically respectable and also valuable to the world at large, many non-taxonomists hold the subject in low esteem. Among the several causes of this problem, there is one that is based on misinformation, namely, taxonomy's ignoble history. Long before the publication of books with titles like *The Poverty of the Linnaean Hierarchy*, the literature was dominated by a story that had naturalists playing the role of drudges mindlessly following the sterile system of Plato and Aristotle. Nowadays some students receive the impression that little of value was understood about systematics before the revolution begun by Willi Hennig. Such views seriously distort history. If blame must be assigned, as a professional historian I accept my share, but other historians, philosophers, and even biologists bear responsibility as well. More important than blame, however, for the sake of taxonomy's reputation, is that its past achievements should be accurately understood and appreciated.

VICTORIAN TAXONOMY

There is abundant evidence that taxonomy was enormously important to Charles Darwin, and the fact that this is not common knowledge is an example of the image problem already mentioned. To examine the subject afresh, there is no better place to begin than with Darwin's own words. This sentence in the *Origin of Species* is key:

> It is a truly wonderful fact—the wonder of which we are apt to overlook from familiarity—that all animals and all plants throughout all time and space should be related to each other in group subordinate to group, in the manner which we everywhere behold—namely, varieties of the same species most closely related together, species of the same genus less closely and unequally related together, forming sections and sub-genera, species of distinct genera much less closely related, and genera related in different degrees, forming sub-families, families, orders, subclasses, and classes. (1859: 128)

The rhetoric in current debates sometimes implies that only an evolutionist can construct a meaningful reference system for living things, but what this key quote highlights is that by Darwin's time, many European naturalists believed that organisms were all "related" and that their classifications should express these relationships. In the decades before 1859, Darwin had canvassed his colleagues and understood perfectly well that they held disparate opinions about organisms' relatedness. Some imagined that the observed similarities and differences flowed from functional necessities, others that embryological forces somehow caused the resemblances, and not a few imagined that the striking closeness of form of species in the same genus or family was evidence of historical derivation from a common ancestor. To us it may seem paradoxical that

naturalists should use the word "related" without agreeing on its meaning, but actually this tolerance enabled them to make progress as a scientific community. Darwin had experienced first-hand in the 1840s how such tolerance could function when he had served on the nomenclature committee of the British Association for the Advancement of Science led by Hugh Strickland (McOuat, 1996).

In Darwin's key sentence, an even more important word for us to consider is "we." To whom did this word refer? To what people was the hierarchical pattern of organisms' similarities so very familiar? Who was positioned to behold relationships between organisms scattered around the globe ("throughout all … space", "everywhere") or long extinct ("throughout all time")? His "we" did not mean you and me, his 21st century readers, he meant Victorians, in concentric circles beginning with Darwin himself, outward to hundreds of zoologists and botanists known to him personally, whether face to face or through exchange of letters, as well as those naturalists, alive or deceased, whose writings he had studied. Darwin knew that in addition to that furthest circle of experts, his book would be read by another dimension of men and women, Victorian readers who were either already aware that naturalists classified organisms using these nested categories, or else were open to learn of it. The enticing word "we" announced to the non-specialist public that there did exist a consensus among the experts that the taxonomic hierarchy reflected nature's reality. Notice how his phrase "throughout all time and space" created a virtual community of palaeontologists, zoologists, botanists, and collectors, for such a wide range of evidence was known to no single person (Darwin, amassing information as best he could, appreciated that these fields were growing at an explosive rate, beyond any man's capacity to master). All this being said, there is also a sense in which Darwin's "we" meant himself at mid-century together with his own younger self of the 1830s, that adventurous twenty-something fellow who had been familiar with taxonomic practice from boyhood, yet only rarely, during the *Beagle*'s voyage, gave a moment's thought to why the Linnaean categories worked so well. He knew first hand how easy it was to overlook the wonderfulness of the shape of nature being recorded by taxonomists.

It is essential to recognize that although the relationships between organisms stretch over all time and space, Darwin's "we" does not. In his day, it covered only people of European education, though these were scattered around the globe by colonization. Nor did his "we" extend back very far, because for several decades before Darwin's own youth, many naturalists would have agreed with the 1749 view of Buffon, the 1778 view of Lamarck, and the 1789 view of Jussieu, that the shape of nature is continuous rather than lumpy, all the distinctions and divisions made by naturalists being merely artificial constructs (Stevens, 1994). Still earlier, although much classification was done, the standardized categories Darwin mentioned—"species," "genus," "family," "order" and "class"—were not the common coin of naturalists. So, Darwin's "we" did not extend to every human being, not even to every serious naturalist, but only to the 19th century heirs of Linnaeus.

PRINCIPLE OF DIVERGENCE

Darwin's "truly wonderful fact" sentence occurs in his chapter on natural selection, where he lays out his argument that not only have species changed, and split, but that selection exerts a pressure that sends them ever further apart, a process he labels the principle of divergence.

> … during the modification of the descendants of any one species, and during the incessant struggle of all species to increase in numbers, the more diversified these descendants become, the better will be their chance of succeeding in the battle of life. Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera. (1859: 128)

His famous tree-like diagram in that chapter illustrates this principle. Yet the order of presentation in the *Origin* has no relation to his order of discovery, nor to the logical steps of his argument. He had sketched tree-like (or coral-like) branching structures in 1837 in the notebook in which he first posited evolution (Barrett & al., 1987: B44), whereas the question of how natural selection could be credited with causing such structures arose later, and nagged at him for years. His solution, the principle of divergence, emerged between 1855 and 1857 (Ospovat, 1981); the few biologists who have given it any thought consider his explanation a failure (Gould, 2002: 63, 224–250). Yet with respect to the role of taxonomy, the principle of divergence is of minor importance, it is the relationship between the Linnaean hierarchy and branching evolution that is primary.

LOUIS AGASSIZ

My own reading of Darwin's words is certainly influenced by my past efforts to understand Louis Agassiz, a zoologist eminent for establishing the concept of an Ice Age, for classifying fossil fishes, and for founding the Museum of Comparative Zoology at Harvard. Agassiz was composing his *Essay on Classification* in 1856 (Winsor, 1991: 6), just as Darwin was starting to write the long first draft of his book (Stauffer, 1975), neither one knowing of

the other's project. Agassiz sent a copy of his publication to Darwin in 1858, and Darwin mailed Agassiz the *Origin* the next year. While courteously thanking each other for the gift, each quietly mumbled their disgust at the other's train of thought. Darwin found Agassiz's essay "all utterly impracticable rubbish…." (Burkhardt & Smith, 1991, vol. 7: 262) while Agassiz scribbled in the margin of his copy of the *Origin*, "This is truly monstrous!" (Lurie, 1960: 255). Yet for all their differences, their attitudes towards taxonomy were strikingly similar. As expert naturalists, both men respected, made use of, and contemplated the meaning of the method inherited from Linnaeus.

Naturalists all understood that the great question about taxonomic categories was this: "Are these groups real or man-made?" Agassiz described the situation thus:

> There is no question in Natural History on which more diversified opinions are entertained than on that of Classification; not that naturalists disagree as to the necessity of some sort of arrangement in describing animals or plants, for since nature has become the object of special studies it has been the universal aim of all naturalists to arrange the objects of their investigations in the most natural order possible.… [Some naturalists have] plainly acknowledged the artificial character of their systems, while others have urged theirs as the true expression of the natural relations which exist between the objects themselves. (1857: 4)

As we have seen, Darwin too was perfectly aware of his colleagues' "diversified opinions." In the *Origin* he played both sides of the fence; sometimes he made use of the comfort most naturalists felt with the idea that correctly identified groups were natural, as he was doing in his "truly wonderful fact" sentence, while in other places he explained how evolution's gradual change and irregular branching meant that the drawing of division lines will always be arbitrary. In the future, he said, when his theory is accepted, species will be treated "in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience" (Darwin, 1859: 485). Darwin was not being disingenuous, because his theory really explained how far these apparent opposites are both true, but it still requires work to follow his reasoning (Stamos, 2007). Agassiz's answer, otherwise so very different from Darwin's, likewise pronounced correct both opinions, that categories are artificial and that they are natural. For Agassiz, each level of the hierarchy represents a step in God's mental process, so that both taxa and categories are deeply real because the Creator actually conceived them, but neither is real in the material sense enjoyed by individual organisms. Agassiz and Darwin shared the conviction that the living world does exhibit an inherent classifiability. Both men were facing up to the question of the meaning of taxonomic groups, both building upon what Agassiz called the "necessity" and "universal aim" agreed upon by naturalists: that the procedures of taxonomy were appropriate, that scientists ought to give names to species following the conventions that originated with Linnaeus, and that they must strive to situate each species within a nested set of higher categories, or if none fit, propose a new group to contain it.

DARWIN'S DEVELOPMENT

The story of how the young Darwin, who believed in special creation, grew to become the author of the *Origin* has been told countless times, yet the role of taxonomy in the saga is often not appreciated, even by taxonomists. The young Darwin was no different from other naturalists in taking for granted the usefulness of taxonomy without inquiring too closely into the meaning of "natural" groups. His boyhood beetle collecting is an oft-told story, long familiar from his autobiography. Now, thanks to the admirably scholarly publication of his correspondence (Burkhardt & Smith, 1985, vol. 1) we can read his letters to his older cousin, W.D. Fox, another amateur entomologist, letters which nicely show that their hobby was purely taxonomic, with no mention of other aspects of natural history such as adaptation, behavior, or ecology. They used standard texts, they were familiar with the names and appearance of all beetle families and many genera, and they were keen to put a species name on every specimen. As Darwin matured, his interest broadened to include not only the identification of marine invertebrates but also their mode of reproduction, but however much his understanding of science expanded while in university and on the *Beagle*, taxonomy remained its foundation. Calling him a "naturalist," the label he used himself, tends to obscure the centrality of taxonomy, because today the word "naturalist" conjures up images of someone tramping through the woods listening to bird calls and looking at lichens, rather than what it meant then, which was someone experienced in the discipline of carefully collecting and labeling specimens destined for identification and preservation.

How Darwin made the switch from his orthodox acceptance of special creation to believing in branching evolution is now known in great detail (Sulloway, 1982b; Desmond & Moore, 1991; Browne, 1995). During the voyage there were moments of doubt, but what ripened such doubts into the certainty that branching evolution had occurred was the assessment of his specimens by London taxonomists when he got back. Although the actual transition, in March 1837, may have taken a week or two rather than a flashing instant, it certainly did not occur on an exotic island, but in the museum workroom of ornithologist John Gould and the lecture halls

of the Zoological Society and Geological Society where Darwin's specimens were discussed. Still, the old story about the Galapagos finches (Sulloway, 1982a) lingers in our imaginations and our classrooms. The fictional tale highlights the ecological significance of the finches' beaks and was a product of the Modern Synthesis, that is, the agreement of evolutionary biologists in the 1930s and 1940s to concentrate on natural selection and speciation. Disposing of the finch myth has now cleared the way for us to appreciate the central role of taxonomy in the history of Darwin's development.

Two topics that interested Darwin during the *Beagle* voyage, important in 1837 and later prominent in the *Origin*, were also part of Agassiz's *Essay on Classification*: fossils and geographic distribution. Usually treated in our literature as separate from taxonomy, their significance depended upon naturalists' confidence in taxonomy. Darwin collected fossils as objects of natural history, but they were food for thought with respect to evolution only when ancient forms of life were placed in the same species, genus, family or order as modern organisms (Rachootin, 1985). He was impressed by the South American megatherium not just because this extinct animal was large, but pointedly because the experts (Cuvier, Owen) classed it in the same family as the sloths that inhabit the same country today. He was impressed by the *Rhea darwinii* not simply because it was a new species of flightless bird but pointedly because it lived adjacent to its nearest relative, the larger common rhea. These sorts of correlations would be termed, by Alfred Russel Wallace two decades later, "the law which has regulated the introduction of new species in space and time." Agassiz was likewise interested in finding an intelligible pattern; when he described the "parallelism between the geological succession of animals and plants and their present relative standing" (Agassiz, 1857: 104) he was also taking for granted taxonomic relationships as the basis for other comparisons.

BRANCHING EVOLUTION PRIOR TO NATURAL SELECTION

Ernst Mayr (1982, 1985, 2004) urged us to recognize not one but five distinct Darwinian theories. Darwin became convinced of the first two, evolution (transmutation) and common descent (branching), beginning in March 1837. Mayr wanted us to realize that others before Darwin had conceived of evolution without branching, but I think it significant that for Darwin himself, these two were simultaneous, because the explanation for the shape captured by the taxonomic hierarchy was repeated branching, leaving gaps and bunches, and the naturalness of classification was Darwin's starting point. Theory number five, natural selection, Darwin worked out between September 1838 and March 1839, which began the long and rich next phase in Darwin's development, culminating in the publication of the *Origin*. (Mayr's third and fourth theories, gradualism and speciation, we may leave aside for another day.) Most narrators give taxonomy a rather inglorious role, for Darwin is said to have earned his spurs as a taxonomist between 1846 and 1854, when he toiled at the classification of barnacles, at the cost of delay in publishing his theory. The picture is worse than that, indeed distinctly negative, if we believe Mayr and the many readers he has influenced, for they maintain that the typological thinking of taxonomists, who believed each species has an essence, committed them to the fixity of species. This claim, which I call the "essentialism story," is at best exaggerated and possibly dead wrong (Atran, 1990; Winsor, 2001, 2003, 2006a, b; Amundson, 2005). Contrary to all this bad press, it seems to me that the record shows overwhelmingly that taxonomy was the main factor causing Darwin to believe in branching evolution.

Darwin devoted the penultimate chapter of the *Origin* to taxonomic topics: "mutual affinities of organic beings; morphology; embryology; rudimentary organs." While writing it he told his friend Joseph Hooker, "the facts seem to me to come out **very** [bold as in original] strong for mutability of species.—I have been much interested in working out this chapter." (Burkhardt & Smith, 1991, vol. 7: 265). Darwin ended the chapter with this firm assertion:

> Finally, the several classes of fact which have been considered in this chapter seem to me to proclaim so plainly, that the inumerable species, genera, and families of organic beings, with which this world is peopled, have all descended, each within its own class or group, from common parents, and have all been modified in the course of descent, that I should without hesitation adopt this view, even if it were unsupported by other facts or arguments. (1859: 457–458)

In the context of that chapter, the meaning of this sentence seems inescapable, namely, that any reasonable person familiar with the data of taxonomy ought to accept branching evolution, even without taking natural selection into account. This certainly agrees with Darwin's own conversion, to which he alluded in the *Origin*'s Introduction:

> … it is quite conceivable that a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species. (p. 3)

This also agrees with the experience of Alfred Russel Wallace, who occupied a similar stage of belief, based on the same kind of evidence, for 13 years before his

independent discovery of natural selection in 1858. A long list of other biologists, including Huxley's nemesis Richard Owen, likewise accepted evolution because of the same sort of evidence.

Yet the taxonomic facts had not already forced a belief in branching evolution upon most of their contemporaries, as Darwin and Wallace keenly understood. Independently, they both decided that the case must be strengthened by adding a plausible cause. As Darwin's introductory statement continued,

> … a naturalist … might come to the conclusion that each species … had descended … from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown *how* the innumerable species inhabiting this world have been modified.… (p. 3; *italics mine*)

The leaders of the Modern Synthesis and their epigones have convinced us that this means that belief in evolution could not be scientific unless it included a cause, which they have achieved by overlooking Darwin's claim that a reasonable person ought to accept branching evolution "even if it were unsupported by other facts or arguments" (Darwin, 1859: 458). In fact, in the years between the *Origin* and the Modern Synthesis, many biologists who accepted evolution withheld assent from natural selection (Bowler, 1983, 1988). Yet after the Modern Synthesis, many writers treat natural selection and evolution as interdependent and inextricable parts of one unified theory. This flies in the face of the historical facts.

What kept both Darwin and Wallace from going public as soon as they arrived at the belief that branching evolution could explain taxonomic affinities (including fossils and geographic distribution) was a heavy load of prejudice against evolution and in favor of species being unchangeable. Although some of the prejudice was religious, based upon the six days of creation or Adam and Eve, there were plenty of scientific reasons at work too. It was common knowledge that offspring belong to the same species as their parents, but recent work by respected scientists had added substantial evidence for the fixity of species. Charles Lyell devoted a chapter of his *Principle of Geology* to countering Lamarck's wild speculations with facts such as that cats and ibises mummified in ancient Egypt were identical to the cats and ibises today.

Yet another objection stood in the way of accepting evolution, and Darwin spelled it out in the rest of the sentence just quoted:

> Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration.… the structure, for instance, of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees. (p. 3)

It was not only clerics like William Paley, but leading philosophers and biologists like Immanuel Kant and Georges Cuvier who had identified teleology, that is, the appearance of having been designed to serve a purpose, as the one special feature of living things that material causes were impotent to explain. This was why most Victorian naturalists considered direct creation by God to be a scientific hypothesis. Thus Darwin was not invoking some formula to the effect that every scientific theory must include a cause, rather he was acknowledging the scope of the theory already on the table, a theory that addressed not only the hierarchical diversity of organisms but their remarkable adaptedness. We can thus understand how Darwin could describe evolution as on the one hand "well-founded," while on the other "unsatisfactory"; it was a perfectly logical inference from taxonomy, but it would need to explain adaptation in order to be superior to divine creation.

COMPARISON TO THE COPERNICAN REVOLUTION

This point may perhaps be clarified by comparing Darwin's situation to the world-altering revolution that culminated with Isaac Newton. Newton famously supplied the causes of planetary motion, inertia and gravity, and Darwin has been called, with good reason, the Newton of biology. There would be good reason to crown Darwin the Copernicus of biology too, if Mayr is correct to claim that he was the first to posit branching evolution. (People who recall Lamarck's branching diagram may dismiss Mayr's surprising claim out of hand, but the presence of extant groups along the trunk and branches of Lamarck's tree signals how confused was Lamarck's view, due to the lingering influence of the old chain of being as well as his reluctance to believe in extinction.) Copernicus proposed the sun-centered system to which Newton, 144 years later, supplied the gears. Contrary to the notion that a theory without a causal mechanism is unsatisfactory, Copernicus was willing to believe in a radically new cosmos even though he had no idea of what drove it. Is it possible that a closer look at Copernicus's reasoning can give us a clue to Darwin's situation between March 1837 and September 1838 (as well as Wallace's between 1845 and 1858)?

I think it can, because the prejudices supporting an immobile Earth were very like those in favor of unchanging species. As Galileo's later trouble with Church authorities would show, religious beliefs played a role, but both ordinary observation and technical details known to

experts endorsed the idea that our Earth sits still while the Sun, Moon, stars and other points of light whirl around us. How could Copernicus have convinced himself that we, along with trees and rocks and seas, are spinning around while dashing forward, and furthermore, since the stars do not retreat and approach, that the entire solar system must be tiny in relation to the cosmos? The answer lies deep within the details of Ptolemy's *Almagest*; to understand it one must know how the Greek and Arabic astronomers measured the positions of the heavenly bodies. They had no telescopes, but they used standard instruments, calibrated into degrees of celestial longitude and latitude, they modeled their predictions using deferents, epicycles and equants, and they had a trigonometry based on chords instead of sines and cosines. Very few people mastered these technicalities, and so it is often imagined that Copernicus was merely toying with mathematical alternatives to the Ptolemaic circles. Copernicus himself knew better (Swerdlow, 2004). He understood that Earth must really be set adrift, otherwise God would be guilty of having planted false witnesses, that is, creating coincidences like the connection between planetary retrograde motion and the position of the sun, which the Earth's orbit explained. Darwin's situation was the same. Too many details were explicable on the hypothesis of common descent for it not to be so. To resist that conclusion by insisting on direct creation would be to convict the deity of salting his creation with deceitful clues.

In this analogy, taxonomy in Darwin's day occupies the role of astronomy when Copernicus was a student, and by this we must mean not only the mathematical techniques, instruments, and recorded observations of centuries, but the objects being studied, that is, what can be seen in the sky without a telescope. Astronomy changed radically after Copernicus, and only partly because of his revolutionary new theory. Not just scientific curiosity but the needs of navigators stimulated researchers and funded the improvement of instruments, even before Galileo's telescope. Now, jumping forward, we come to a time when even people who could not tell you the meaning of ecliptic or equinox can hold up a device and read off their position, in degrees and minutes of longitude and latitude. This is also a time, perhaps not coincidentally, when most points of light in the night sky visible to everyone in Copernicus's day are blotted out from the view of most of us. Clearly the noun "astronomy" should always have an adjective, "modern" or "16th Century," or "post-Newtonian." Changes no less momentous have transformed taxonomy. Our culture is so far removed from the one in which Darwin grew up that nowadays to postulate an intelligent designer impresses people as a new idea. Computers never entered Darwin's wildest dreams. Still, the taxonomy of today is descended, by an unbroken chain, back through the Victorian era to the Renaissance (Ogilvie, 2006).

CONTEMPLATION

What has happened to Darwin's "truly wonderful fact," the way that most of the organisms known to science, this vast number of living kinds plus some fossils, resemble one another by degree, forming clusters and clumps of clusters? Once again, it is important to ask, to whom does the key word "we" apply? A "fact" is hardly a fact at all, much less a familiar or wonderful one, except in the minds of particular people at certain times and places. In today's world there are professional biologists who are less familiar with the sort of taxonomy Darwin took for granted than today's amateur birdwatchers or serious gardeners are. Most ironically, the triumph of Darwin's theory has undermined, twice over, the foundation upon which that theory was based. First of all, the process of speciation has focused interest on those cases, so very essential to Darwin's own argument, where the distinction between variety and species is thoroughly blurred. Furthermore, because evolutionary biologists hold the whole past history of life so fondly in their imaginations, the shape of nature for them becomes continuous, as if those billions of ancestors were available to answer a roll call. That seamless tree of vanished life, with its branches so irregular, sometimes even reticulating, cannot be fairly represented in any classification, because the act of naming groups of organisms must slice it up. By no means does this replicate the vision of Buffon or Jussieu, however, for those men were predicting, based on samples of plants and animals from around the world that were pouring into European gardens and museums, that gaps between extant kinds would be filled in with other extant kinds. They lived to see their expectation disappointed. The continuity envisioned today postulates missing links that can never actually be collected. With respect to the actual living things around us, however, the shape of nature is not so very different from what it was 150 years ago. What has been lost is our familiarity with it.

ACKNOWLEDGEMENTS

I dedicate this essay to the memory of my beloved mentor, Asger Aaboe, historian of astronomy and lifelong enemy of cant. For technical advice I thank Noel M. Swerdlow, another Aaboe student, as well as my colleague Craig Fraser. Numerous other colleagues and students from the Institute for the History and Philosophy of Science and Technology at the University of Toronto helped me to refine my argument. The two people most directly responsible for the existence of this paper are Tod Stuessy, who invited me to address the topic, and David Hull, first for recommending me to Tod, then for giving me a home in Chicago, and finally for spurring me on with his penetrating critique. For helpful suggestions I am also indebted to Ron

Amundson. I am particularly grateful to Michael Ghiselin for many stimulating conversations. I acknowledge with gratitude the financial support of the International Association for Plant Taxonomy.

LITERATURE CITED

Agassiz, L. 1857. *Essay on Classification*, 1962 reprint. Harvard University Press, Cambridge.

Atran, S. 1990. *Cognitive Foundations of Natural History: Towards an Anthropology of Science*. Cambridge University Press, Cambridge.

Amundson, R. 2005. *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo.* Cambridge University Press, Cambridge.

Barrett, P.H., Gautrey, P.J., Herbert, S. & Smith, S. (eds.). 1987. *Charles Darwin's Notebooks, 1836–1844*. British Museum (Natural History) and Cambridge University Press, London.

Bowler, P.J. 1983. *The Eclipse of Darwinism: Anti-Darwinian Evolution Theories in the Decades Around 1900*. The Johns Hopkins University Press, Baltimore.

Bowler, P.J. 1988. *The Non-Darwinian Revolution: Reinterpreting a Historical Myth*. The Johns Hopkins University Press, Baltimore.

Browne, J. 1995. *Charles Darwin Voyaging: A Biography.* Princeton University Press, Princeton.

Burkhardt, F. & Smith, S. (eds.). 1985 onwards. *The Correspondence of Charles Darwin*. Cambridge University Press, Cambridge.

Darwin, C.R. 1859. *On the Origin of Species*, 1964 reprint. Harvard University Press, Cambridge.

Desmond, A. & Moore, J. 1991. *Darwin: The Life of a Tormented Evolutionist*. W.W. Norton, London.

Ghiselin, M.T. 1997. *Metaphysics and the Origin of Species.* State University of New York Press, Albany.

Gould, S.J. 2002. *The Structure of Evolutionary Theory.* Harvard University Press, Cambridge.

Lurie, E. 1960. *Louis Agassiz: A Life in Science*. University of Chicago Press, Chicago.

Lyell, C. 1830–1833. *Principles of Geology*, 3 vols. John Murray, London.

Mayr, E. 1982. *Growth of Biological Thought.* Harvard University Press, Cambridge.

Mayr, E. 1985. Darwin's five theories of evolution. Pp. 755–772 in: Kohn, D. (ed.), *The Darwinian Heritage.* Princeton University Press, Princeton.

Mayr, E. 2004. *What Makes Biology Unique?* Cambridge University Press, Cambridge.

McOuat, G.R. 1996. Species, rules and meaning: the politics of language and the ends of definitions in 19th century natural history. *Stud. Hist. Philos. Sci.* 27: 473–519.

Ogilive, B.W. 2006. *The Science of Describing: Natural History in Renaissance Europe.* University of Chicago Press, Chicago.

Ospovat, D. 1981. *The Development of Darwin's Theory: Natural History, Natural Theology and Natural Selection 1838–1859.* Cambridge University Press, Cambridge.

Rachootin, S.P. 1985. Owen and Darwin reading a fossil: *Macrauchenia* in a boney light. Pp. 155–183 in: Kohn, D. (ed.), *The Darwinian Heritage*. Princeton University Press, Princeton.

Stamos, D.N. 2007. *Darwin and the Nature of Species.* State University of New York, Albany.

Stauffer, R.C. 1975. General introduction. Pp. 1–14 in: Stauffer, R.C. (ed.), *Charles Darwin's Natural Selection being the Second Part of his Big Species Book Written from 1856 to 1858*. Cambridge University Press, Cambridge.

Stevens, P.F. 1994. *The Development of Biological Systematics: Antoine-Laurent de Jussieu, Nature, and the Natural System*. Columbia University Press, New York.

Swerdlow, N.M. 2004. An essay on Thomas Kuhn's first scientific revolution, *The Copernican Revolution*. *Proc. Amer. Philos. Soc.* 148: 64–120.

Sulloway, F. 1982a. Darwin and his finches: the evolution of a legend. *J. Hist. Biol.* 15: 1–53.

Sulloway, F. 1982b. Darwin's conversion: the *Beagle* voyage and its aftermath *J. Hist. Biol.* 15: 325–396.

Winsor, M.P. 1991. *Reading the Shape of Nature: Comparative Zoology in the Agassiz Museum.* University of Chicago Press, Chicago.

Winsor, M.P. 2001. Cain on Linnaeus: the scientist-historian as unanalysed entity. *Stud. Hist. Philos. Biol. Biomed. Sci.* 32: 239–254.

Winsor, M.P. 2003. Non-essentialist methods in pre-Darwinian taxonomy. *Biol. & Philos.* 18: 387–400.

Winsor, M.P. 2006a. The creation of the essentialism story: an exercise in metahistory, *Hist. Philos. Life Sci.* 28: 149–174.

Winsor, M.P. 2006b. Linnaeus's biology was not essentialist. *Ann. Missouri Bot. Gard.* 93: 2–7.