The Continuation of the Morphological Tradition: American Paleontology, 1880-1910

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One of the most pressing problems facing the study of the history of science is the issue: how has science changed? Scholars from a variety of disciplines have wrestled with that problem, and in most instances they have drawn upon examples from the history of the physical sciences to make their case.[1] Yet the biological sciences have also experienced profound changes in theory, methodology, and technique, and the history of biology likewise affords some insight into the nature of scientific change. Among the more important efforts to explain and describe such scientific change have been Garland Allen's studies of American biology in the late nineteenth and early twentieth centuries.[2] As indicated in the introduction to this set of papers, Allen has characterized the changes in the biological sciences of that period as a "revolt from morphology." That interpretation not only suggests Allen's adherence to a particular philosophy of scientific change, but also colors his historical analysis of turn-of-the-century American biology. My own study of a specific area of the life sciences of that period has brought to light quite a different historical picture and concurrently quite a different conception of the nature of scientific change. In this paper I will present an analysis of certain aspects of American paleontology in the period 1880-1910, an analysis that I believe provides evidence for the persistence of a morphological tradition in paleontology throughout the period and for continuity, not revolution, as the

1. See particularly Thomas S. Kuhn, *The Structure of Scientific Revolutions*, 2nd ed. (Chicago: University of Chicago Press, 1970); Imre Lakatos, "Falsification and the Methodology of Scientific Research Programmes," in Imre Lakatos and Allan Musgrave, ed., *Criticism and the Growth of Knowledge* (Cambridge: Cambridge University Press, 1970), pp. 91-196; and Larry Laudan, *Progress and Its Problems: Toward a Theory of Scientific Growth* (Berkeley: University of California Press, 1977).

2. Among the works by Allen most relevant here are: Garland Allen, "T. H. Morgan and the Emergence of a New American Biology," *Quart. Rev. Biol., 44* (1969), 168-188; *Life Science in the Twentieth Century* (New York: John Wiley, 1975); and "Naturalists and Experimentalists: The Genotype and the Phenotype," *Stud. Hist. Biol., 3* (1979), 179-208.

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best means for understanding the historical development of the biological sciences during those years.

The study of paleontology in late nineteenth-century America embodied some of the principal features of a science of morphology. That branch of biology, first defined by Goethe as the study of the changes in organic structure or form,[3] held an important place in the work of a number of biologists throughout the first half of the last century.[4] Nevertheless, as Allen has pointed out in *Life Science in the Twentieth Century*, morphology had its full flowering in the period following the work of Charles Darwin. According to Allen, morphology drew much of its impetus from Darwin's theory of evolution, and its objectives were directed largely to substantiating some version of that theory. Those aims included the attempts to establish the basic unity that underlay the diversity of forms, to discover the common ancestor that served as the progenitor of latter-day forms, and to trace, usually by constructing phylogenetic trees, the changes in structure that occurred in the evolution from the ancestral forms to their modern-day representatives.[5] Such objectives clearly embraced fields of biology other than paleontology, fields such as embryology and comparative anatomy. Moreover, such morphological issues did not interest the majority of late nineteenth-century paleontologists, most of whom continued to concentrate on the traditional problems of stratigraphy and geological succession.[6] Yet there did emerge in late nineteenth-century America a group of paleontologists who sought to define the origins and evolutionary changes of fossil forms. In the years before 1880 those concerns motivated only a few students of the fossil past, men such as Othniel Charles Marsh (1832-1899), Edward Drinker Cope (1840-1897), and Alpheus Hyatt (1838-1902). Their interest in the embryological and evolutionary changes in fossils not only distinguished their work from that of their contemporaries, but also helped to establish a morphological tradition in American paleontology. The approach and questions that those men formulated with regard to fossil forms were passed on

3. See "Bildung und Umbildung organischer Naturen," an essay that served as the introduction to the 1807 edition of Johann Wolfgang von Goethe's *Versuch die Metamorphose der Pflanzen zu erklaren*.

4. E. S. Russell, *Form and Function: A contribution to the History of Animal Morphology* (London: John Murray, 1916), pp. 45-245.

5. Allen, *Life Science*, pp. 2-6.

6. Stephen Jay Gould, "Eternal Metaphors of Palaeontology," in A. Hallam, ed., *Patterns of Evolution as Illustrated by the Fossil Record* (Amsterdam: Elsevier Scientific Publishing Co., 1977), pp. 12-13.

to a younger generation of paleontologists whose efforts preserved the concern with the issues of morphological science well into the twentieth century. In light of the significance of their paleontological work *vis-à-vis* the larger issue of the changes in late nineteenth-century American biology, it is necessary to examine in some detail the work of Marsh, Cope, Hyatt, and their successors.

Among the three men, Marsh was the oldest, the first in the field, and the one who speculated least on the issues that dominated morphology. Professor of paleontology at Yale from 1867 until his death in 1899, Marsh played a leading role in discovering, collecting, and analyzing a vast number of vertebrate remains from the fossil beds of the American West.[7] These discoveries and analyses led to Marsh's bitter feud with Cope; but more important, they formed the foundation for his contributions to evolutionary theory and the science of morphology. In particular it is Marsh's work on fossil horses, fossil birds with teeth, and extinct orders of large mammals and reptiles that most clearly defines his interest in describing and tracing the changes in vertebrate structure and form.

From the beginning of his career in paleontology, the study of fossil horses held a prominent place in Marsh's work. In his first trip to the West in 1868, Marsh observed the remains of a fossil horse in a Pliocene matrix in western Nebraska. Over the next several years he conducted expeditions of Yale students to that location and others, and by 1874 Marsh and his assistants had collected over thirty individual specimens of horses that were indigenous to North America.[8] Clearly Marsh was not the first scientist to discover such remains nor the first to describe the structural changes that they demonstrated. As early as 1859, the vertebrate paleontologist Joseph Leidy had pointed to the existence of fossil horses in America,[9] and throughout the 1860s and 1870s T. H. Huxley, Ludwig Rütimeyer, and Vladimir Kovalevskii were defining the morphological modifications among the fossil horses of Europe.[10]

7. The most complete study of Marsh's paleontological work remains Charles Schuchert and Clara Mae LeVene, *O. C. Marsh, Pioneer in Paleontology* (New Haven: Yale University Press, 1940).

8. O. C. Marsh, "Fossil Horses in America," *Amer. Nat., 8* (1874), 288-294.

9. Joseph Leidy, "On the Fossil Horse," *Proc. Acad. Nat. Sci. Phil., 11* (1859), 180-185.

10. See T. H. Huxley, "Palaeontology and the Doctrine of Evolution," in T. H. Huxley, *Collected Essays*, VIII (New York: Georg Olms Verlag, 1970), pp. 340-388; Huxley, *American Addresses, with a Lecture on the Study of Biology* (New York: D. Appleton, 1877), pp. 30-96; Ludwig Rütimeyer, "Beitrage zur

Marsh, however, was fortunate enough to discover several new genera of fossil horses, genera that were ancestral to the fossil horses of Europe and that more clearly defined the patterns of descent with modification within that family. Besides providing important documentary evidence for evolution. Marsh's study of those remains offers an insight into the extent to which he was concerned with the problems of evolution and morphology.

Marsh's views on fossil horses were put forth in a number of short articles published during the 1870s. Throughout those studies Marsh relied on comparative anatomy to describe in detail the structural features and the changes in those features indicated by the different species and genera of fossil horses. That approach is most clearly defined in his "Fossil Horses in America" (1874), in which he emphasized the differences in the structure of the skull, neck, teeth, limbs, and overall body size brought to light by comparative anatomical analysis. The changes in limb structure were most apparent, and Marsh discussed the modifications in the scapula and humerus, the expansion of the radius, the reduction of the ulna, and other changes that were necessary to produce the evolution from the four-toed *Orohippus* of the Eocene period to the single-toed *Equus* of today.[11] Such changes in structure offered evidence for defining the patterns of evolution, and Marsh claimed that there was a direct line of descent from *Orohippus* of the Eocene to *Miohippus* of the Miocene, *Anchippus, Hipparion*, and *Pliohippus* of the Pliocene, and finally to *Equus* of the Recent period.[12] On the basis of his morphological analysis, therefore, Marsh was able to define the descent with modification that had occurred within the family of fossil and Recent horses.

In that 1874 essay Marsh maintained that the changes in limb structure indicated that there existed a form of fossil horse that proceeded *Orohippus*, a form that possessed four toes on the back foot and five on the front. In 1879 he defined that organism as *Eohippus*, and thus

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Kenntniss der fossilen Pferd und zur vergleichenden Odontographie der Hufthiere überhaupt," *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 1863, pp. 558-696; Vladimir Kovalevskii, "Sur l'Anchitherium aurelianense Cuv. et sur l'histoire paléontologique des chevaux," *Memoires de l'Academie des Sciences de St. Petersburgh*, 7th ser., *20* (1873), 1-73; and Kovalevskii, "Monographie der Gattung Anthracotherium Cuv. et Versuch einer natürlichen Classification der fossilen Hufthiere," *Paleontographica, 3* (1873), 131-210; *4* (1874), 211-290.

11. Marsh, "Fossil Horses in America," pp. 292-293.

12. Ibid., pp. 291-294.

offered his views on the ancestral origins of the horse family.[13] But Marsh devoted even greater effort to defining the evolutionary origins and changes of other fossil vertebrates, namely, in his examinations of fossil birds with teeth, dinosaurs, and fossil mammals. In his analyses of fossil birds with teeth, summed up most fully in his monograph the *Odontornithes*, Marsh again concentrated almost exclusively on describing the structural characteristics of those extinct birds, noting particularly the dental and vertebral structure. In *Odontornithes* Marsh separated the specimens of fossil birds into two genera: *Ichthyornis*, which possessed a primitive, biconcave vertebral structure, and *Hesperornis*, which had an advanced vertebral structure but a reptilian tooth structure.[14] Marsh further asserted that those features had general evolutionary importance, indicating that those two genera of fossil birds as well as *Archaeopteryx* had branched off from a primitive, generalized form "which gradually lost its reptilian characteristics as it assumed the orthinic type, and in the existing *Ratitae* we have the survivors of this direct line."[15] That morphological analysis clearly defined the structural similarities between birds and dinosaurs, and throughout the 1880s and 1890s Marsh worked to define the evolutionary origins and relationships of those two classes.[16] Similarly, he attempted to establish the evolutionary relationships among the mammals, searching for their origins among the Amphibia and illustrating their phylogeny in his monograph *The Dinocerata.*[17]

In all the principal domains of his paleontological research, therefore, Marsh pursued two of the major objectives of morphological science: the attempt to define the ancestral origins and the effort to outline

13. O. C. Marsh, "Polydactyl Horses, Recent and Extinct," *Amer. J. Sci.*, 3rd ser., *17* (1879), 499-505.

14. O. C. Marsh, *Odontornithes: A Monograph on the Extinct Toothed Birds of North America* (Washington, D.C.: Government Printing Office, 1880), pp. 3-6, 13-87, 125-165, 180-185. See also Marsh, "The Vertebrae of Recent Birds," *Amer. J. Sci.*, 3rd ser., *17* (1879), 266-269.

15. Marsh, *Odontornithes*, p. 189.

16. Among Marsh's works that touched on the structural affinities between birds and reptiles, some of the more important include: O. C. Marsh, "Jurassic Birds and Their Allies," *Amer. J. Sci.*, 3rd ser., *22* (1881), 337-340; "On the Affinities and Classification of the Dinosaurian Reptiles," *Amer. J. Sci.*, 3rd ser., *50* (1895), 483-498; and "The Dinosaurs of North America," *Annual Report of the United States Geological Survey, 16* (1896), 133-414.

17. O. C. Marsh, *Dinocerata: A Monograph of an Extinct Order of Gigantic Mammals* (Washington, D.C.: Government Printing Office, 1886), pp. 170-190; and Marsh, "The Origin of Mammals," *Amer. J. Sci.*, 4th ser., *6* (1898), 406-409.

patterns of descent among fossil vertebrates. Nevertheless, Marsh's views on those issues are found in only a very few places in his work, and such theoretical concerns were distinctly secondary to his interest in describing and classifying extinct organisms. The same is true of his interest in explaining the causes of evolutionary change. In a number of places in his work Marsh advanced his ideas on the causal factors of evolution, often stressing the importance of environmental factors in effecting such change;[18] but such references are brief and scattered throughout the body of his work, and at no time did Marsh put forth a detailed explanation of the causes or mechanisms that produced the evolutionary changes made manifest by his paleontological studies. Marsh clearly helped to establish an interest in the issues of morphology within late nineteenth-century American paleontology, but he reflected on more theoretical morphological problems in a somewhat limited manner. Among the scientists who had more interest in such broad issues, and who had more influence on the next generation of American paleontologists, Cope and Hyatt were especially prominent.

Cope, unlike Marsh, derived his interest in morphology primarily not from paleontology, but from the study of embryology and comparative anatomy. Such studies held an important place in his early work of the 1860s, and in "On the Origin of Genera" (1868), Cope adopted a belief in the doctrine of recapitulation and relied on the study of embryology to explain evolution. In that essay he attempted to account for such morphological problems as the processes and patterns of evolution on the basis of the acceleration and retardation of the stages of individual development.[19] But Cope soon struck out in new theoretical directions. Beginning in 1871 he put forth a new theory of evolution, one that was to provide the framework for his later efforts to describe and explain the changes in fossil vertebrates and that was to have a profound influence on other students of the subject. Because of the importance that his theory was to have for his own paleontological work and that of his successors, I shall describe briefly Cope's later theory of evolution.

Cope's new views on evolution were first set forth in "The Laws of Organic Development" and "The Method of Creation of Organic

18. Marsh, *Dinocerata*, pp. 181-190. See also O. C. Marsh, "Introduction and Succession of Vertebrate Life in America," *Nature, 16* (1877), 490.

19. Edward Drinker Cope, "On the Origin of Genera," in Cope, *The Origin of the Fittest: Essays on Evolution* (New York: D. Appleton, 1886), pp. 41-123. Unless otherwise indicated, the citations and page references for Cope's articles have been drawn from this collection of his early evolutionary and paleontological studies.

Forms." In both pieces Cope focused his attention on the study of an evolutionary problem that he claimed Darwin had neglected: the origin of new variations. Cope contended that such variations, which following embryological acceleration or retardation could be accommodated at the termination of the inherited pattern of individual development, could not be accounted for by natural selection.[20] Rather they were the result of a growth force, a force that he claimed lay dormant in the tissues of organisms and that was actualized only when it existed in excess in a particular locality.[21] While Cope emphasized that such a growth force primarily produced a repetition of cells and segments, he also recognized that such a force had to account for the diversities of structure. In that regard he noted several factors that could influence the growth force, relying most heavily on the effects of use and disuse and effort. The inherited effects of the use and disuse of structural parts, he argued, could direct the growth force and promote new sectors of growth. Yet Cope also realized that something had to direct that use or disuse, particularly in those cases where as yet there existed no structure to be used. That something he defined as conscious choice. Speaking of conscious response on the part of organisms, Cope stated:

> Here we have the source of the fittest – i.e., addition of parts by increase and location of the growth force, directed by the will – the will being under the influence of various kinds of compulsion in the lower, and intelligent option among higher animals.
>
> Thus, intelligent choice, taking advantage of the successive evolution of physical conditions, may be regarded as the *originator of the fittest*, while natural selection is the tribunal to which all the results of accelerated growth are submitted. This preserves or destroys them, and determines the new points of departure on which accelerated growth shall build.[22]

According to Cope, then, external conditions evoked a conscious response or choice from organisms. Such responses in turn promoted the

20. Edward Drinker Cope, "The Method of Creation of Organic Forms," in *The Origin of the Fittest*, pp. 174-175. In light of the fact that this essays contains not only everything expressed in the essay "The Laws of Organic Development," but also much more, I have concentrated my examination on "The Method of Creation of Organic Forms."

21. Cope, "Method of Creation," p. 191. See also Cope's later editorial comment in a footnote at the bottom of that page.

22. Ibid., p. 210.

use or disuse of certain parts, and such use or disuse produced structural modifications that were inherited, accelerated in their development, and ultimately preserved or eliminated by natural selection. That theory could thus account for the origin of new structures as well as the changes in existing structures, and as such it furnished Cope with a means for explaining the evolution of vertebrates.

Cope's belief in the causal efficacy of the reactions of organisms to environmental conditions became a centerpiece of his evolution theory as well as of the theory of many other scientists in late nineteenth-century America.[23] In the years after 1871 he further refined several aspects of that theory, attempting to explain more fully consciousness and its relationship to external conditions, forms of the use and disuse of parts, and inheritance.[24] Of more direct relevance here, however, are the ways in which Cope applied that evolution theory to explain the changes in the hard parts of fossil vertebrates. After 1871 Cope worked increasingly with the data of paleontology, and his studies in that field, particularly on mammalian paleontology, form the basis for his most important and influential contributions to morphology.

In Cope's early work from the 1860s, the data of the fossil record served largely to substantiate his theoretical views, derived from the study of individual development.[25] In the early 1870s, however, Cope participated in a number of paleontological expeditions to the western states, and his findings from those surveys resulted in a number of important theoretical generalizations. Cope's earliest writings on the fossil finds from the American West, articles that stem primarily from the years 1872-1879, offer little analysis of the ways in which use and disuse actually caused structural change among extinct vertebrates.

23. The influence of neo-Lamarckism in late nineteenth-century America is examined in Edward J. Pfeifer, "The Genesis of American Neo-Lamarckism," *Isis, 56* (1965), 156-167; Pfeifer, "United States," in Thomas F. Glick, ed., *The Comparative Reception of Darwinism* (Austin: University of Texas Press, 1974), pp. 198-202; and Elliot R. Gerson, "Natural Selection and Late Nineteenth-Century Paleontologists," *Synthesis, 1*, no. 2 (1973), 14-27.

24. Among Cope's articles on the subject contained in *The Origin of the Fittest* are: "Consciousness in Evolution" (1875), pp. 390-404; "The Origin of the Will" (1877), pp. 437-457; "On Archaesthetism" (1882), pp. 405-421; and "On Catagenesis" (1884), pp. 422-436. Other articles by Cope on consciousness and its relationship to evolution and inheritance include: "The Energy of Evolution," *Amer. Nat., 28* (1894), 205-219; "Evolution and Consciousness," *Science*, n.s., *3* (1896), 119-120; "Psychic Evolution," *Amer. Nat., 31* (1897), 91-92; and "The Inheritance of Acquired Characteristics," *Amer. Nat., 31* (1897), 176-177.

25. Cope, "On the Origin of Genera," pp. 112-113.

Instead, Cope concentrated on documenting and describing the kinds of changes that had occurred among fossil mammals. That approach enabled him to develop several morphological and evolutionary principles, perhaps most evident in two essays from the years 1874-1875: "The Homologies and Origin of the Types of Molar Teeth of the Mammalia Educabilia" and "The Relation of Man to the Tertiary Mammalia."[26] Those essays were among Cope's first attempts to use the data derived from his field work of 1872-1873 to define certain morphogenetic principles that characterized the changes among fossil mammals.

The earlier essay (1874) was an attempt to employ the comparative anatomical analysis of mammalian molar teeth to establish the ancestral origins and evolutionary relationships of the fossil ungulates. In that essay, based upon his studies of extinct mammals from the lower and middle Eocene of the present states of Colorado, Utah, and Wyoming, Cope claimed that the modern ungulate molar was an evolutionary modification of the simple, single tubercle that characterized the most primitive fossil mammals.[27] According to Cope, there were two principal ways for that primitive tooth to become complicated: by the development of a crown with additional tubercles, or by the folding of the sides or the summit of the crown. Cope associated the two different means of complication with two different mammalian types, the Bunodont and Lophodont, respectively. The several species and genera of the Bunodont type belonged to one of the older geological epochs of the Eocene period, and Cope identified the primitive genus *Achaenodon* as the ancestral form of the type. He further asserted that the Bunodonts, which possessed a quadritubercular form of molar tooth, were ancestral to the Lophodonts, and much of the essay was devoted to describing and tracing that evolutionary transition.[28] In the same essay Cope also tried to correlate the homological relationships defined by dental structure with those defined by foot structure.

26. In "The Homologies and Origin of the Types of Molar Teeth of the Mammalia Educabilia," Cope used the term "Educabilia" to refer to the ungulates, or mammals with hoofed feet, and what he called the unguiculates, or mammals with clawed feet. See Cope's preface to *The Origin of the Fittest*, p. ix; and Cope, "On the Extinct Vertebrata of the Eocene of Wyoming," *Sixth Annual Report of the United States Geological and Geographical Survey of the Territories* (1873), p. 643.

27. Edward Drinker Cope, "On the Homologies and Origin of the Types of Molar Teeth of the Mammalia Educabilia," *J. Acad. Nat. Sci. Phil.*, 2nd ser., *8* (1874), 71.

28. Ibid., pp. 77-84.

Again the evidence of comparative anatomy demonstrated connecting points among such orders as the Artiodactyla, Perissodactyla, and Proboscidea; and Cope concluded the essay by claiming that his study of the Mammalia Educabilia indicated "that the primitive genera of this division of mammals must have been Bunodonts with pentadactyle [*sic*] plantigrade feet."[29] In later essays, such as "The Relation of Man to the Tertiary Mammalia," Cope defined in detail the changes in the bones of the feet of fossil and recent mammals.[30] Thus by the mid 1870s Cope had defined the ancestral form of a major division of the mammals, had established the principal structural changes that had occurred from the ancestral to the more modern forms, and had provided tables and illustrations of the patterns of descent defined by those changes in structure. In short, Cope's work fulfilled the major objectives of a science of morphology.

Cope continued his interest in those aspects of morphology, producing in later years a number of more detailed analyses of the phylogenies of many different orders of fossil and recent mammals.[31] His work, coupled with that of Marsh, thus helped to define the origins and evolutionary histories of major groups of those extinct organisms. But perhaps even more important were Cope's efforts to explain the changes that he and others discerned in the fossil record. Although Cope made little effort to apply the principles of his 1871 evolutionary theory to the fossil data he analyzed in the mid 1870s, by the end of that decade and throughout the 1880s and 1890s he explicitly used the doctrine of the inherited effects of use and disuse to explain the morphological changes manifested in the fossils. He did so in

29. Ibid., p. 88.

30. Edward Drinker Cope, "The Relation of Man to the Tertiary Mammalia," in *The Origin of the Fittest*, pp. 268-280.

31. Throughout the 1880s and 1890s Cope produced a number of studies on the phylogenies of a wide variety of fossil vertebrates. Some of the more important were: "On the Extinct American Rhinoceroses and Their Allies," *Amer. Nat., 14* (1880), 771a-771j; "On the Genera of Felidae and Canidae," *Proc. Acad. Nat. Sci. Phil., 31* (1879), 168-194; "On the Extinct Cats of America," *Amer. Nat., 14* (1880), 833-858; "On the Extinct Dogs of North America," *Amer. Nat., 17* (1883), 235-249; "The Extinct Rodentia of North America," *Amer. Nat., 17* (1883), 43-57, 165-174, 370-381; "The Amblypoda," *Amer. Nat., 18* (1884), 1110-1121, 1192-1202; "The Classification and Phylogeny of the Artiodactyla," *Proc. Amer. Phil. Soc., 24* (1887), 377-400; and "The Perissodactyla," *Amer. Nat., 21* (1887), 985-1007, 1060-1076. See also Stephen Jay Gould, *Ontogeny and Phylogeny* (Cambridge, Mass.: Harvard University Press, 1977), p. 423 n 19.

a number of essays, most notably the papers on the origin of the specialized teeth of the Carnivora (1879), the origin of the ungulate foot (1879), and, somewhat later, the origin of the mammalian molar teeth (1883-1884). Although Cope had examined all those subjects previously, he now did so with the intention of explaining the causes of the origins and changes of specific structures. In each instance he explained the new variations as a result of organic responses to external conditions, adaptations that resulted in the use and disuse of particular morphological parts. This explanation clearly applied to variations in mammalian molar teeth, changes that he now maintained stemmed from a primitive tritubercular form. Writing of the changes in the dentition of the Amblypoda, an ancient mammalian order, Cope noted:

> The tritubercular is the primitive [form of molar tooth], and is adapted for softer food, as flesh, so that primitive placental Mammalia were carnivorous or nearly so. The mastication of hard food was impossible until the molars of the two series opposed each other, and this was not accomplished until the quadritubercular superior molar was produced. This was accomplised, as I have pointed out, by the addition of a posterior internal tubercle, and I suspect that the mechanical cause of its origin was the attempt of the animal in mastication to crush substances harder than flesh against this posterior edge of the superior molar, by applying to it the anterior edge of the lower molar.[32]

In Cope's opinion it was the mechanical effects of such use or disuse, the notion of parts against other parts, that resulted in the evolution of a new tubercle and a quadritubercular form of molar tooth. Moreover, such motion, particularly the motions that produced friction, strains, or impacts, had similar effects in other cases, giving rise to the blade-form of grinding tooth in the Carnivora and a reduction in the number of digits in the Ungulata.[33] Cope later defined the doctrine based on the effects of motion as kinetogenesis, and in his last major work, *The Primary Factors of Organic Evolution*, he claimed that kinetogenesis could explain the evolution of the entire vertebrate

32. Edward Drinker Cope, "On the Mechanical Origin of the Dentition of the Amblypoda," *Proc. Amer. Phil. Soc., 25* (1880), 80.

33. Edward Drinker Cope, "The Origin of the Specialized Teeth of the Carnivora," in *The Origin of the Fittest*, pp. 363-367; and Cope, "On the Origin of the Foot Structure of the Ungulates," in *The Origin of the Fittest*, pp. 368-372.

skeleton.[34] Thus Cope, in addition to exploring the central problems of the science of morphology, advanced a theory to explain the origin and evolution of the changes in vertebrate structure, a theory that rivaled Darwin's and that profoundly influenced American biologists at the turn of the century.

Cope's attempt to explain as well as to describe the origin and evolution of structures in fossil vertebrates found a parallel in the invertebrate work of his close friend and colleague Alpheus Hyatt. A student of Louis Agassiz's, Hyatt was trained in biology and brought an interest in biological issues to the geologically dominated science of invertebrate paleontology. Like Cope, Hyatt drew much of his inspiration from embryology, particularly from Agassiz's belief that there were parallels between embryonic growth, the structural gradation among living forms, and the geological succession of extinct forms.[35] Throughout his career, Hyatt relied on the study of embryology and comparative anatomy to describe and explain the changes in structure that occurred in both individual development and group history. In much the same way that Marsh and Cope brought a concern with morphological issues into vertebrate paleontology, Hyatt infused an interest in ancestral origins, evolutionary histories, and evolutionary mechanisms into invertebrate paleontology.

Throughout much of his paleontological career, Hyatt concentrated on the study of fossil cephalopods. From the time of his first examination of the group, presented in an 1866 lecture to the Boston Society of Natural History, Hyatt focused his attention on the correlation between the structural changes that occurred in the individual development and the group history of cephalopods. Emphasizing the importance of examining the entire course, not just the early stages, of cephalopod development, Hyatt pointed out that changes in the septa, whorls, and other features of shell structure corresponded closely to the evolutionary changes that characterized the extinct order of ammonites. Shell structure, he argued, was particularly important, and the development from a shell with a smooth external surface to a shell with ribs or tubercles and the eventual return to a shell with no ornamentation constituted a series of developmental changes that were quite similar to those that occurred among the fossil ammonites of the Jurassic and

34. Edward Drinker Cope, *The Primary Factors of Organic Evolution* (Chicago: Open Court Publishing Co., 1896), pp. 246-384.

35. Agassiz's views on this parallelism were put forth most fully in his *Essay on Classification*, ed. Edward Lurie, (Cambridge, Mass.: Harvard University Press, 1962).

Cretaceous periods.[36] Hyatt traced those changes in shell structure on both the individual and group levels, and claimed that the evolutionary history of the ammonites and nautiloids was in fact a result of the acceleration of the developmental process.[37] Furthermore, Hyatt, unlike Cope, held that such acceleration could account for retrogressive as well as progressive evolutionary change, arguing that retrogression was a result of the acquisition of degenerative features late in evolutionary history and the subsequent accelerated deterioration of those features to earlier and earlier stages of development.[38] That thesis, which Hyatt termed his "old age theory," drew a marked parallel between the process of individual aging and the stages of evolutionary decline and ultimate extinction. Indeed, Hyatt held that individual development, besides providing the mechanism for evolutionary change, was also the key to the pattern of phylogeny. As he stated in an essay on another family of fossil cephalopods, the Arietidae:

> The individual grows by constant addition of characteristics, or parts, and declines by the loss in those characteristics or parts, first of the power to perform their functions, and then by their obsolescence. Series of species, on the other hand, progress by the evolution of forms which, in the adult condition, add certain common or parallel characteristics in regular order, and then decline by the evolution of a series of forms exhibiting the obsolescence of the same parts or organs, each form inheriting at an earlier age the old age characteristics of the parent until finally none of the adult characteristics remain even in the young.[39]

According to Hyatt, evolution was partly a linear, partly a cyclical, process of change, a pattern of morphological advance through the addition of parts up to a certain point, followed by an equally well-defined pattern of decline toward extinction. Drawing both his model and his mechanism from individual development, Hyatt was able to point to the ancestral species of fossil cephalopods as well as to define the processes and patterns of their evolutionary change.

36. Alpheus Hyatt, "On the Parallelism between the Different Stages of Life in the Individual and Those in the Entire Group of the Molluscous Order Tetrabranchiata," *Mem. Boston Soc. Nat. Hist., 1* (1866), 196.

37. Ibid., pp. 199-203.

38. Ibid., pp. 203-207. See also Gould, *Ontogeny and Phylogeny*, pp. 91-96.

39. Alpheus Hyatt, "Evolution of the Arietidae," *Proc. Boston Soc. Nat. Hist., 16* (1873-1874), 170.

Throughout the 1870s Hyatt extended his interest in morphological questions to other groups of cephalopods, attempting to define the ancestral origins and homological relationships in such groups as the Angulatidae and Stephanoceras.[40] His studies in the early 1880s of freshwater snails reflected those concerns as well as Hyatt's growing interest in the causal mechanisms of evolution. His work with those snails focused on an extensive deposit of fossils from a dry lake bed in Steinheim, Germany, and Hyatt charted the several lines of descent from the ancestral species, *Planorbis levis*. Hyatt recognized certain uniform tendencies in the lines of descent, and concluded that the responses of those snails to changes in external, particularly environmental, conditions caused structural change and controlled the patterns of evolution.[41] Further studies of those organisms helped to define more clearly Hyatt's views on evolution, but it is his most famous paper, "Phylogeny of an Acquired Characteristic," that most fully defines Hyatt's concern with the objectives of a science of morphology.

Published in 1893, that essay was essentially a detailed examination of the evolutionary history of one feature of the ammonites and nautiloids: a groove called the impressed zone that runs along the inner surface of each whorl of the shell. According to Hyatt, it was the tightening of the coils of the shell that brought the whorls into contact and produced the impressed zone, and that character, like any other character, was inherited and in later geological periods accelerated to earlier and earlier stages of development.[42] In his study of the anatomy and development of the major features of external shell structure among fossil and living forms of ammonites and nautiloids, Hyatt addressed such problems as the ancestral origins, phylogeny, and causes of evolution. He put forth a detailed argument for the evolution of those two orders from a common, early Paleozoic, radicle. Based on his study of the development of the shell of living nautiloids, Hyatt claimed that the ancestral form of the cephalopods must have possessed

40. In addition to Hyatt's "Evolution of the Arietidae," see his "Genetic Relations of the Angulatidae," *Proc. Boston Soc. Nat. Hist., 17* (1874); pp. 15-23 and Hyatt, "Genetic Relations of Stephanoceras," *Proc. Boston Soc. Nat. Hist., 18* (1876), 360-400.

41. Alpheus Hyatt, "Transformations of *Planorbis* at Steinheim, with Remarks on the Effects of Gravity upon the Forms of Shells and Animals," *Proc. Amer. Assoc. Adv. Sci., 29* (1880), 527-550. See also an article with the same title but somewhat different and more extensive conclusions in *Amer. Nat. 16* (1882), 441-452.

42. Alpheus Hyatt, "Phylogeny of an Acquired Characteristic," *Proc. Amer. Phil. Soc., 32* (1893), 372-380, 589-615.

a straight or uncoiled shell, a feature characteristic of the genus *Orthoceras.*[43] He also claimed that during their evolutionary history, at a time when there were many unoccupied niches, the early cephalopods diverged widely from the original form, producing several separate lines of descent. Beyond that early divergence, however, there was little room for further variation; instead, later cephalopod evolution became a function of the accelerated development of existing structures and presented a picture of regular, parallel lines of descent. Such accelerated development was, according to Hyatt, largely responsible for the creation of the impressed zone. He contended that "the more generalized of each genetic series show in their ontogeny that they were derived from the more loosely coiled, and the more specialized show that they were derived from forms which were tightly coiled. In other words, the tendency to closer and closer coiling gains in the organization of the different genetic series and is manifested more intensely in the young of more specialized forms and makes them coil more quickly and closer."[44] Hyatt described the pattern of that accelerated development in the different lines of cephalopod descent, and in two essays in 1893 suggested a terminology for the different stages of such development and evolution.[45] In so doing Hyatt defined and explained the characteristics of fossil and recent cephalopods in evolutionary, morphological terms.

The work of Marsh, Cope, and Hyatt had by 1880, therefore, established an interest in morphological problems in the two principal domains of paleontology. Their work, particularly the more speculative aspects concerning the causes and paths of evolutionary change, did elicit objections from younger American biologists. Moreover, as Garland Allen has pointed out, those objections served as a stimulus for the development of a new philosophy, methodology, and technique in certain fields of biology.[46] Those new views and new objectives, however, did not encompass the whole of biology, and their later successes should not imply that a concern with morphological issues ceased or in some sense lost out to the new experimental biology. On the contrary, Marsh, Cope, and Hyatt continued to pursue their interest in morphology undaunted, producing some of their most important studies

43. Ibid., pp. 359-365.

44. Ibid., pp. 589-590.

45. Ibid., pp. 380-433; Alpheus Hyatt, "Bioplastology and the Related Branches of Biological Research," *Proc. Boston Soc. Nat. Hist., 26* (1893), 59-125.

46. Allen, *Life, Science*, pp. 8-72.

in the last decade of the nineteenth century. More important, their work, particularly that of Cope and Hyatt, had a profound, affirmative effect on a number of younger scientists. In the years between 1890 and 1910 there emerged in America a new generation of paleontologists, many of whom adopted the approach taken by their predecessors and continued the interest in morphological, particularly evolutionary questions. It is their work that provides the evidence for the persistence of a morphological tradition in turn-of-the-century American paleontology.

The continued interest in morphological questions and issues within vertebrate paleontology was largely a result of the influence of Marsh and, especially, Cope. In his paleontological laboratory at Yale, Marsh headed a large team of research assistants, many of whom, such as Erwin H. Barbour, John Bell Hatcher, and Samuel Wendell Williston, carried on his tradition in the study of fossil vertebrates. While Hatcher was perhaps best known for his discoveries and the development of new field techniques,[47] Barbour and Williston provided morphological descriptions and classifications of numerous groups of fossil mammals and reptiles. Those men, much like Marsh, had relatively little interest in the problems of ancestral origins or the causes of evolution, yet their descriptive work served as a basis for establishing the changes in vertebrate structure and the patterns of descent among vertebrates.[48] Another assistant of Marsh, Georg Baur, had a more active interest in the study of evolutionary questions, and in his paleontological and comparative anatomical work he addressed the standard questions

47. See the chapter on Hatcher in Url Lanham, *The Bone Hunters* (New York: Columbia University Press, 1973), pp. 197-213.

48. Barbour, a mammalian paleontologist, produced a number of studies, including: Erwin Hinckley Barbour, "Nature, Structure, and Phylogeny of Daemonelix," *Bull. Geol. Soc. Amer., 8* (1897), 305-314; "Evidence of Loess Man in Nebraska," *Publ. Geol. Surv. Nebraska, 2* (1907), 331-348; "Skeletal Parts of Moropus," *Publ. Geol. Surv. Nebraska, 3* (1908), 219-222; "The Skull of Moropus," *Publ. Geol. Surv. Nebraska, 3* (1908), 1-10; and "Skeletal Parts of the Columbian Mammoth, *Elephas maibeni*, sp. nov.," *Bull. Nebraska State Museum, 10* (1925), 95-118. Williston was one of the premier students of fossil reptiles, and his major publications include: Samuel Wendell Williston, "North American Plesiosaurs, Part I," *Publ. Field Museum Nat. Hist.,* geological ser. *73* (1903), 1-77; *American Permian Vertebrates* (Chicago: University of Chicago Press, 1911); *Water Reptiles Past and Present* (Chicago: University of Chicago Press, 1914); "Synopsis of the American Permocarboniforous Tetrapoda," *Contribution of the Walker Museum, 1* (1916), 193-236; "Phylogeny and Classification of Reptiles," *J. Geol., 25* (1917), 411-421; and *Osteology of the Reptiles,* ed. William King Gregory (Cambridge, Mass.: Harvard University Press, 1925).

posed by morphology.[49] Although Baur died in 1898, his influence as a teacher and researcher extended to several of his students at the new University of Chicago, most notably Ermin C. Case and Oliver P. Hay. Perhaps even more noteworthy were two other scientists, both of whom were influenced by Cope and both of whom examined the theoretical as well as descriptive problems related to fossil vertebrate morphology, William Berryman Scott (1858-1947) and Henry Fairfield Osborn (1857-1935).

Scott, who for over fifty years taught geology and paleontology at Princeton University, was for a time a classmate and instructor with Osborn at that institution, and early in their careers both young men were befriended by Cope.[50] Apparently the older man's impact was more than social, for Scott and Osborn adopted not only Cope's general interest in the problems of morphology and evolution, but also many of his explanations for the changes in fossil vertebrate structure. An interest in such problems and explanations is evident in one of Scott's earliest works. In a collaborative study with Osborn, "The Mammalia of the Uinta Formation (1889)," Scott defined the systematic and homological relationships among such fossil mammals as the genera *Protoreodon* and *Oreodon*, and the separate family Agriocherinae. In that same paper Scott also concerned himself with a specific morphegenetic issue: the origin and evolution of rodent dentition. Well aware of Cope's work on mammalian molar teeth, Scott was struck by the fact that one genus of fossil rodent, *Plesiarctomys*, exhibited a tritubercular pattern in its superior molar teeth. According to Scott, that evidence "seems to show that the rodents are to be derived from the same generalized group of primitive placental mammals, the Bunotheria, to which we refer the origin of the types just mentioned."[51] The principal features of that early work, the search for ancestral origins, the effort to describe changes in vertebrate structure, and the effort to use such changes to produce phylogenies, all took on an added importance in Scott's later work of the 1890s.

In the years between 1885 and 1891 Scott continued his field work

49. In the course of his short career Baur produced a large number of comparative anatomical and paleontological studies that contributed to the morphological tradition. For a listing of his many works see William Morton Wheeler, "George Baur's Life and Writings," *Amer. Nat., 33* (1900), 15-30.

50. See the biography of Scott by G. G. Simpson, "William Berryman Scott, 1858-1947," *Biog. Mem. Nat. Acad. Sci., 25* (1949), 177.

51. William Berryman Scott, "The Mammalia of the Uinta Formation," *Trans. Amer. Phil. Soc.*, n.s., *16* (1889), 478.

and laboratory analysis on the skeletal hard parts of fossil artiodactyls. His descriptive analysis of those organisms as well as his views on the modes and factors of their evolutionary change were presented in two essays published in 1891: "On the Osteology of *Poebrotherium*" and "On the Osteology of *Mesohippus* and *Leptomeryx*." Those essays, which Scott considered a unit, were his most ambitious attempts to examine the anatomical structure of fossil vertebrates in order to determine the modes and factors of evolution. Scott opened the first essay with a set of questions concerning the nature of the evolutionary process, though he delayed answering those questions until the conclusion of the second essay. Instead, he concentrated first on describing the major structural characteristics of *Poebrotherium* and the changes in those characteristics that had occurred in the family Camelidae. Examining the changes in the teeth, skull, vertebral column, forelimbs, and hindlimbs, Scott described the evolutionary history of the Camelidae and the systematic relationship of the members of that family to the Ruminantia.[52] He did much the same for *Mesohippus* and *Leptomeryx* in the second essay, concluding with an effort to answer the questions laid out at the start.

In his paleontological studies, Scott, more than Cope, was interested in examining the patterns of evolutionary change that were suggested by his descriptive work. In his 1891 accounts of the osteological struture of different fossil mammals, Scott was struck by the widespread occurrence of evolutionary parallelism and convergence. Such parallelism was particularly evident in the evolution of the selenodont molar teeth, but, as Scott noted, it was also demonstrated in the evolution of the cerebral convolutions of the brain and in the reduction of the number of teeth, feet, and ribs of extinct mammals. Indeed, Scott cited Cope's views to substantiate his belief that identical or nearly identical changes of osteological structure had supervened in distinct lines of descent.[53]

The widespread occurrence of evolutionary parallelism provided Scott with a perspective on several questions, and in answer to one he suggested that many genera of fossil mammals had a polyphyletic origin.[54] Although he did not explicitly define the common ancestor of

52. William Berryman Scott, "On the Osteology of *Poebrotherium*: A Contribution to the Phylogeny of the Tylopoda," *J. Morph.*, *5* (1891), 10-78.

53. William Berryman Scott, "On the Osteology of *Mesohippus* and *Leptomeryx*, with Observations on the Modes and Factors of Evolution in the Mammalia," *J. Morph.*, *5* (1891), 363-365.

54. Ibid., p. 363.

the different families of extinct artiodactyls, Scott did assert that the use of comparative anatomy could enable one to establish their origins as well as to trace the separate, parallel lines of descent. Scott's emphasis on parallelism led him, as it had led Cope and Hyatt, to define those lines as essentially linear, as

> advancing steadily in a definite direction, though with slight deviations . . . On the whole we are impressed by the steady march of differentiation; thus, in the equine series the premolars one by one become molariform, the molar pattern more complex, the face elongated, the digits are continually reduced in number, the median digit becomes more and more enlarged, and the carpal and tarsal bones adjusted to the new character of the strains, the limbs become more and more elongated, and the stature of the whole animal increased.[55]

Thus Scott not only defined the phylogenies of fossil mammals in terms of parallel, orthogenetic changes in structure, he also suggested a possible explanation for such change.

Although Scott did not speculate on the causes of evolutionary change to the same extent as did Cope and Hyatt, he did consider such issues and he adopted the general explanation put forth by those men. At the conclusion of his essay "On the Osteology of *Mesohippus* and *Leptomeryx*," Scott argued that the theory of evolution by natural selection could not account for the definite, parallel trends evident in the fossil record. Instead, Scott adopted the neo-Lamarckian thesis advanced by Cope and Hyatt, claiming that the changes in vertebrate structure were a result of the mechanical adaptations of organisms to their surroundings. The increase or reduction of parts, he wrote, occurs "just as *if* the direct action of the environment and the habits of the animal were the efficient cause of the change, and any explanation which excludes the direct action of such agencies is confronted by the difficulty of an immense number of the most striking coincidences."[56] Although Scott did not attempt to explain precisely how such external factors or organic habits could produce structural change, it is clear that he believed that the evidence of the paleontological record could provide some insight into the issues of the origins, directions, and mechanisms of the morphological modifications that occurred over time.

55. Ibid., p. 371.
56. Ibid., p. 396.

In subsequent years Scott made few additional efforts to define further his understanding of the causal factors of evolution, virtually abandoning that enterprise in despair after 1894.[57] Yet he did continue to pursue other objectives of morphological science, in particular the goal of defining the common progenitors and the patterns of evolutionary change of the different orders and families of fossil vertebrates. Throughout the 1890s he produced a number of studies that described in detail the structural features and phylogenies of such fossil mammals as *Hyaenodon* (1894), *Protoceras* (1895), and *Elotherium* (1898).[58] Furthermore, his pursuit of those objectives continued well into the twentieth century. Indeed, Scott's most famous work, *A History of Land Mammals in the Western Hemisphere* (1913), was, as the title suggests, an attempt to describe the patterns of descent with modification among the principal orders of mammals. Working backward from recent forms, Scott traced the changes in the skeletal hard parts and defined the common ancestors of mammals. Although he no longer wrestled with the problem of the causes of such change, Scott by no means gave up the pursuit of other stated objectives of morphology.[59]

In addition to Scott, his more famous colleague Osborn also helped to preserve interest in morphology. He too was influenced by Cope, and in his own research as well as in his institutional efforts at the American Museum of Natural history, New York, Osborn pursued the search for ancestral forms that would help explain the process of evolution. Like Scott, Osborn had an avid interest in constructing phylogenies of fossil vertebrates, and like Cope he worked to erect a comprehensive theory that would explain the causes of such evolution. Osborn, in fact, adopted many of the evolutionary and morphogenetic principles put forth by Cope, and in that respect he kept alive not only many of the specific concerns of his predecessor but also the morphological tradition within vertebrate paleontology that Cope had done so much to define.

57. Simpson, "William Berryman Scott," pp. 186-191. One of Scott's last and most stimulating studies of the causes of evolution was his critical review of William Bateson's book *Materials for the Study of Variation* (1894) in Scott, "On Variations and Mutations," *Amer. J. Sci.*, 3rd ser., *48* (1894), 355-374.

58. William Berryman Scott, "The Osteology of Hyaenodon," *J. Acad. Nat. Sci. Phil.*, 2nd ser., *9* (1894), 499-536; "The Osteology and Relations of *Protoceras*," *J. Morph.*, *11* (1895), 303-374; "The Osteology of Elotherium," *Trans. Amer. Phil. Soc.*, n.s., *19* (1898), 273-324. Other phylogenetic and taxonomic studies by Scott are listed in Simpson, "William Berryman Scott," pp. 188, 196-200.

59. William Berryman Scott, *A History of Land Mammals in the Western Hemisphere* (New York: Macmillan, 1913).

Like most other vertebrate paleontologists of the day, Osborn analyzed the teeth, feet, and other hard parts of fossil vertebrates, and his study of those structures provided the underpinnings of his effort to define the origins, processes, and patterns of mammalian evolution. As early as 1887 Osborn independently confirmed Cope's theory of the trituberculár origin of mammalian molar teeth, and in his later work Osborn extended and further refined that morphogenetic doctrine.[60] In addition, he adopted Cope's explanation for the changes to and from that primitive form, claiming that the use and disuse of parts, in effect kinetogenesis, offered a better means of explaining such changes than did Darwin's theory.[61] Similarly, Osborn accepted the general features of Cope's understanding of the evolution of the ungulate foot, describing the five-toed plantigrade form as the common ancestor of more modern ungulates and explaining the evolution from that primitive form to a digitigrade form as a result of the effects of the use and disuse of parts.[62] Unlike Cope or Hyatt, Osborn did not accept the belief that such effects were inherited according to the neo-Lamarckian principle of the transmission of acquired characteristics. He did, however, emphasize that the cumulative and regular effects of such change were evident in the fossil record, and in addition to describing the findings from that record he provided a means for explaining them.

In a number of his studies of the late 1880s and early 1890s Osborn maintained that the neo-Lamarckian principle of the inheritance of acquired characteristics, although it did not provide a workable theory of heredity, was nonetheless a necessary assumption in order to explain the evolutionary trends found in the fossil record.[63] By the mid-1890s, however, Osborn, as the director of a new research program in vertebrate paleontology at the American Museum, was becoming much more involved with the study of the fossil past, and his increased reliance

60. Osborn's first statement on the tritubercular theory was "The Origin of the Tritubercular Type of Mammalian Dentition," *Science, 10* (1887), 300. His later studies of the subject include: "The Evolution of Mammalian Molars to and from the Tritubercular Type," *Amer. Nat., 22* (1888), 1067-1079; "The History of the Cusps of the Human Molar Teeth," *Int. Dent. J.*, 1895, pp. 1-26; "The Origin of the Teeth of the Mammalia," *Science*, n.s., *5* (1897), 576-577; "Trituberculy: A Review Dedicated to the Late Professor Cope," *Amer. Nat., 31* (1897), 993-1016; and *Evolution of Mammalian Molar Teeth to and from the Triangular Type*, ed. W. K. Gregory (New York: Macmillan, 1907).

61. Osborn, "Evolution of Mammalian Molars," pp. 1074-1075.

62. Henry Fairfield Osborn, "The Mammalia of the Uinta Formation," *Trans. Amer. Phil. Soc.*, n.s., *16* (1889), 531-569.

63. Osborn advanced such views in "The Palaeontological Evidence for the

on the data derived therefrom led him to emphasize the importance of evolutionary parallelism much more than he had in the past. Largely on the basis of that data, and on the basis of his desire to develop a comprehensive evolution theory that did not draw exclusively on neo-Lamarckism or neo-Darwinism, Osborn put forth in 1895 a new explanation for the evolution of fossil vertebrates. He claimed that such orderly evolutionary change could only be the result of the interrelationship of four processes: heredity, environment, ontogeny, and selection. Those four processes, he claimed, worked together in some unknown manner to produce the regular, indeed purposive changes that Osborn by then believed characterized phylogenetic evolution.[64] The doctrine of the interrelated working of those four factors, which Osborn eventually termed the tetra-plastic theory of evolution.[65] became a hallmark of his later work, and helped to explain his understanding of the patterns of vertebrate evolution.

From the time of his early work in the 1880s, Osborn had been interested in tracing the evolutionary histories of different groups of fossil mammals. In the mid-1890s, however, he had a much larger data base and a theory of evolution at his disposal, and he stepped up his efforts to construct phylogenies. In almost all his studies of that period Osborn pointed out that in addition to the occurrence of a good deal of evolutionary parallelism there also was a certain amount of adaptive radiation and morphological divergence.[66] Osborn claimed that most groups of fossil mammals diverged from a hypothetical common ancestor early in their evolutionary history, and thereafter those groups followed orthogenetic, parallel lines of descent. In the years after 1897 Osborn made a distinction between the kinds of characters affected by such early divergence and those that later evolved in definite, orderly

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Transmission of Acquired Characteristics," *Amer. Nat., 23* (1889), 561-566; "Evolution and Heredity," *Biol. Lect., 1* (1890), 130-141; "Are Acquired Variations Inherited?" *Amer. Nat., 25* (1891), 191-216; "The Present Problem of Heredity," *Atlantic Monthly, 67* (1891), 353-364; and "Difficulties in the Heredity Theory," *Amer. Nat., 26* (1892), 537-567.

64. Henry Fairfield Osborn, "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," *Biol. Lect., 4* (1894), 79-100.

65. Henry Fairfield Osborn, "Tetraplasy, the Law of the Four Inseparable Factors of Evolution," *J. Acad. Nat. Sci. Phil.*, 2nd ser., *15* (1912), 275-309.

66. The concept of adaptive radiation, which previous scientists had discussed, was defined most clearly and fully in Osborn's work. See Osborn, "The Rise of the Mammalia in North America," *Proc. Amer. Assoc. Adv. Sci., 42* (1893), 187-227; "The Origin of Mammals," *Amer. J. Sci.*, 4th ser., *7* (1899), 92-96; and "The Law of Adaptive Radiation," *Amer. Nat., 36* (1902), 353-363.

ways. He associated the occurrence of early adaptive radiation with changes in the form, size, and proportions of characters, while he described the changes that took place after such divergence as affecting only the evolution of new, additional characters. He further associated such changes with a distinction between variations and mutations, a distinction that had been made earlier in the century by the German invertebrate paleontologist Wilhelm Waagen. According to Waagen, there existed two quite different kinds of organic modifications: changes that occurred in the same period of time, changes in space or variations; and changes that took place over the course of time, mutations.[67] Waagen defined the latter as gradual, orderly changes that characterized extensive fossil series, and Osborn did much the same, asserting that such mutations were not the result of natural selection but rather were due to the unknown factor that coordinated the four other factors of evolution.[68] Such a distinction had significance for Osborn's evolution thoery; furthermore, it influenced the way in which he defined the evolutionary history of the organisms he studied. According to Osborn, the early differentiation of variations was important taxonomically, enabling him to distinguish clearly different lines of descent and thus put forth highly polyphyletic evolutionary histories. Furthermore, mutations were important for the subsequent pattern of evolution, producing parallel lines of descent. In the early years of the twentieth century, Osborn applied those views to several families of fossil mammals, revising the standard phylogenies of such groups as the horses, rhinoceroses, and titanotheres with illustrations and classifications that emphasized the evolution of separate, parallel phyla from unknown progenitors.[69] Indeed, Osborn devoted much of the rest of his life to working out in greater detail those evolutionary histories, pursuing in effect the goals of morphology.

Osborn's interest in the problems of morphology also went beyond the bounds of his own work, extending to the efforts of his students and associates at the American Museum. The problems of the origins

67. Wilhelm Waagen, "Die Formenreihe des *Ammonites subradiatus*," *Benecke geognostische-paleontologische Beitrage, 2* (1868), 179-257.

68. See Henry Fairfield Osborn, "Evolution as It Appears to the Paleontologist," *Science*, n.s., *26* (1907), 744-749.

69. For Osborn's earliest revisions of those phylogenies see his "Phylogeny of the Rhinoceroses of Europe," *Bull. Amer. Mus. Nat. Hist., 13* (1900), 229-276; "The Four Phyla of Oligocene Titanotheres," *Bull. Amer. Mus Nat. Hist., 16* (1902), 91-109; and "Fossil Wonders of the West: The Evolution of the Horse in America," *The Century Magazine, 69* (1904), 3-17.

and evolutionary history of numerous orders and families of fossil mammals played a prominent part in the work of such men as William King Gregory and William Diller Matthew.[70] Furthermore, Osborn's work had institutional implications, defining the major objectives of some of the principal paleontological expeditions conducted by the American Museum. Indeed, the 1907 expedition to Egypt and, more important, the famous Central Asiatic Expedition of the early 1920s were both inspired in part by Osborn's views on the origin and adaptive radiation of mammals.[71] In terms of contributions beyond his own work, therefore, Osborn, perhaps more than any other individual, helped to infuse morphological concerns into early twentieth-century American paleontology.

At much the same time that Scott, Osborn, and other students of fossil vertebrates were pursuing the questions raised by morphology, a group of invertebrate paleontologists were adopting many of the tenets of Hyatt's program and preserving the interest in morphological issues in that field. Those scientists, many of whom actually worked with Hyatt, accepted the doctrine of recapitulation and employed the study of individual development to define the evolutionary origins and histories of fossil invertebrates. Among the most prominent of the scientists who adopted that approach were Charles Emerson Beecher (1856-1904), John M. Clarke (1857-1924), Amadeus W. Grabau (1870-1946), Robert Tracy Jackson (1868-1949), Charles Schuchert (1858-1942), and James Perrin Smith (1864-1931). Whereas Hyatt had employed the study of individual development to determine the causes and patterns of evolution among fossil cephalopods and snails, the younger men

70. Gregory's most important work for the period up to 1910 was William King Gregory, "The Orders of Mammals," *Bull. Amer. Mus. Nat. Hist., 27* (1910), 3-524. Among Matthew's more important studies for that same period were: "A Revision of the Puerco Fauna," *Bull. Amer. Mus. Nat. Hist., 9* (1897), 259-323; "The Ancestry of Certain Members of the Canidae, the Viverridae, and Procyonidae," *Bull. Amer. Mus. Nat. Hist., 12* (1899), 109-139; "The Evolution of the Horse," *Amer. Mus. J., 3*, supplement (1903), 1-30; "The Arboreal Ancestry of the Mammalia," *Amer. Nat., 38* (1904), 811-818; "Osteology of Blastomeryx and Phylogeny of the American Cervidae," *Bull. Amer. Mus. Nat. Hist., 24* (1908), 535-562; "On the Osteology and Relationships of Paramys and the Affinities of the Ischyromyidae," *Bull. Amer. Mus. Nat. Hist., 28* (1910), 43-72; and "Phylogeny of the Felidae," *Bull. Amer. Mus. Nat. Hist., 28* (1910), 289-316.

71. Henry Fairfield Osborn, "The Fayum Expedition of the American Museum," *Science*, n.s., *25* (1907), 513-516. For an assessment of Osborn's influence on the Central Asiatic Expedition, see Roy Chapman Andrews, *On the Trail of Ancient Man* (Garden City, N.Y.: Doubleday, 1922), pp. vii-ix, 3; and *idem, Under a Lucky Star: A Lifetime of Adventure* (New York: Viking Press, 1944), pp. 158, 163-164.

took up a similar approach and similar questions in their studies of other major groups of invertebrates. Far from rejecting the biogenetic law or a concern with the problems of morphology, those scientists sought to define the relationship between individual development and group history and to establish the changes in structure and form that had occurred in the course of that history.

One of the first areas of research that was brought into line with the concerns of morphological science was the study of fossil brachiopods. Earlier students of the subject, notably the Englishman Thomas Davidson and the Frenchman Joachim Barrande, had denied the occurrence of evolutionary change among those organisms.[72] But in the early 1890s a group of American paleontologists attempted to document such evolution. Particularly prominent in that regard were Beecher, Clarke, Schuchert, and James Hall, all of whom sought to establish the origins, phylogenies, and systematic relationships of the members of the order on the basis of the study of the individual life histories of fossil and recent brachiopods.

The earliest efforts in the field were made by Beecher and Clarke, who in the late 1880s were working at Hall's paleontological laboratory in Albany, New York. In 1889 they published "The Development of Some Silurian Brachiopoda," a study that marked a new departure in the analysis of that order. In their work Beecher and Clarke were fortunate enough to obtain from a formation in Waldron, Indiana, some 50,000 fossils specimens that represented all stages of individual development. As a result they were able to examine in detail the ontogeny of fossil brachiopods; in addition, they correlated ontogeny to the evolutionary history of the order. According to Beecher and Clarke, analysis of the early stages of development demonstrated that the Brachiopoda had evolved from an ancestor related to the genus *Orthis*, one line of descent leading through the genera *Strophomena, Scenidium, Orthisina, Lectaena, Chonetes, Productus*, and *Strophalosia*, the other through *Rhynchonella, Spirifer, Atrypa, Retzia*, and *Terebratula.*[73] By means of their study of ontogeny as revealed in a remarkable collection of fossil inverstebrates, therefore, Beecher and Clarke were able to fulfill two primary objectives of morphology: identification of

72. For an assessment of the works of Davidson and Barrande, see the article by Davidson's student and associate Agnes Crane, "The Evolution of the Brachiopoda," *Geol. Mag.*, 4th ser., *2* (1895), 71-73.

73. Charles E. Beecher and John M. Clarke, "The Development of Some Silurian Brachiopoda," *Mem. N.Y. State Mus., 1*, no. 1 (1889), 85-93.

the ancestral form and delineation of the lines of evolutionary descent of the Branchiopoda.

In succeeding years both Clarke and Beecher continued and modified their work in the field. In the early 1890s Clarke joined with his mentor Hall to produce a thorough study of the Brachiopoda in volume 8 of *The Natural History of New York*. In his previous paleontological studies Hall had concentrated primarily on stratigraphic problems;[74] but he and Clarke now focused their attention on the structural development of the brachiopods in an effort to determine their evolutionary history. Concentrating on the development of the pedicle passage, Hall and Clarke defined the genus *Paterina* as the progenitor of later forms, and thus provided one of the first phylogenies of the order.[75] At about the same time, Beecher was defining the evolutionary origins and history of brachiopods in a similar way. He claimed that the initial part of the brachiopod pedicle valve, the protegulum, was the principal defining characteristic of the early embryo and common ancestor, and his work was also largely an attempt to trace the changes in that structure.[76] Yet Beecher, more than Hall and Clarke, acknowledged an interest in the causal factors of the evolution of such a structure as well as an explicit debt to the work of Hyatt. In another study of the Brachiopoda published in 1891, Beecher focused on the study of the entire life history of individual specimens. In so doing, he adopted Hyatt's scheme for naming and classifying the stages of development; more important, he also adopted Hyatt's views concerning evolution and classification. As Beecher wrote in that essay: "The value of the stages of growth and decline in work relating to phylogeny and classification is now generally admitted. The memoirs of Hyatt, Jackson, and others amply show that the clearest and simplest understanding of a group may thus be reached. The application of the principles of growth, acceleration of development, and mechanical genesis, form the main factors in the studies here made."[77] Indeed, Beecher did make those

74. This is made evident by analysis of the previous seven volumes of James Hall's *Natural History of New York: Palaeontology*.

75. James Hall and John M. Clarke, "An Introduction to the Study of the Genera of Palaeozoic Brachiopoda," *Nat. Hist. N.Y.: Palaeontology, 8*, pt. 1 (1892), 35-185. See also the conclusion in pt. II of the report (1894), pp. 319-358.

76. Charles E. Beecher, "Development of the Brachiopoda, Part I," *Amer. J. Sci.*, 3rd ser., *41* (1891), 343-357; see also Beecher, "The Correlations of Ontogeny and Phylogeny in the Brachipoda," in Beecher, *Studies in Evolution* (New York: Charles Scribner's Sons, 1901), pp. 286-289.

77. Beecher, "Development of the Brachipoda," p. 343.

factors the basis of his study, attributing the variations in the pedicle valve to mechanical adaptations and the long-term evolutionary trends to the subsequent inheritance and accelerated development of those adaptations.[78] In later studies, most notably "Origin and Significance of Spines," Beecher adopted additional particulars of Hyatt's theory, explaining organic responses to external conditions as the causal factors of evolutionary change and maintaining that such change followed parallel lines of change as well as a general pattern of growth and decline.[79] Furthermore, Beecher emphasized that the study of individual development had importance for understanding not only evolution but also taxonomy; and in his own work as well as that of the Schuchert ontogeny became the basis for a new classification of the brachiopods.[80] In their work on that order, which continued into the early twentieth century, Beecher, Schuchert, and, to a lesser extent, Clarke and Hall extended Hyatt's program of fossil research, and thereby not only preserved but expanded the morphological tradition in turn-of-the-century American invertebrate paleontology.

The study of fossil brachiopods was perhaps the most prominent but clearly not the only field of paleontology to be brought within the framework of the morphological tradition. While Beecher, Schuchert, Clarke, and Hall defined the importance of ontogeny for the study of phylogeny and classification among the brachiopods, other contemporary scientists worked to establish the evolutionary origins and histories for other groups of invertebrates. Among those men, Robert Tracy Jackson, a student of Hyatt's at the Museum of Comparative Zoology, took the lead in applying the questions of morphology, in particular Hyatt's views on those questions, to the Pelecypoda and Echinoidea. In his first major study, "Phylogeny of the Pelecypoda" (1890), Jackson explicitly acknowledged his acceptance of the doctrine of recapitulation and his intention of employing the study of the entire life history of individual living molluscks to determine their

78. Ibid., pp. 344-351.

79. Charles E. Beecher, "The Origin and Significance of Spines," in his *Studies in Evolution*, pp. 3-105.

80. Beecher, "Development of the Brachiopoda," pp. 351-357. Charles Schuchert, "A Classification of the Brachiopoda," *Amer. Geol., 11* (1893), 141-167. For a contemporary assessment of the importance of that classification see Agnes Crane, "New Classification of the Brachiopoda," *Geol. Mag.*, 3rd ser., *10* (1893), 318-323. The classification of that order on the basis of ontogenetic development still holds today. See Raymond C. Moore, Cecil G. Lalicker, and Alfred G. Fischer, *Invertebrate Fossils* (New York: McGraw-Hill, 1952), p. 219.

evolution. Jackson followed the approach used by Hyatt and Beecher, employing the study of one major feature of shell structure as the means of understanding ontogeny, evolution, and classification. Whereas Hyatt had looked to the proteconch among the cephalopods and Beecher to the protegulum among the brachiopods, Jackson held that the prodissconch was the significant feature among the pelecypods. He claimed that on the basis of his study of the anatomy and development of those organisms he could "trace, to *Nucula* or a *Nuculoid* form as a probable type-ancestor, the prodissconch which I have found to be characteristic of developing *Avicula, Perna, Ostrea, Pecten, Anomia*, and their allies."[81] Not only did Jackson use that feature to define the progenitor of the group, he also traced the developmental and evolutionary changes in that structure over time. Like Beecher and Schuchert, Jackson adopted Hyatt's classification of the stages of individual growth and decline, and he also understood phylogeny to be a process that closely followed such developmental maturation and eventual degeneration. Jackson also accepted several other features of Hyatt's evolution theory, including the belief that mechanical adaptations to external circumstances were the foremost cause of evolutionary changes and the belief that such changes were inherited and later accelerated in their development.[82] So similar were Jackson's views to Hyatt's that in his later studies of fossil pelecypods and echini Jackson described himself as a member of a Hyatt school, as a scientist who along with other scientists was working actively to apply Hyatt's methodology and theory to the study of fossil invertebrates.[83]

In addition to Jackson and Beecher, there were others who worked to apply those principles. James Perrin Smith, a student of fossil ammonites, worked with Hyatt in the later 1890s, and in his later analyses Smith relied on the study of the process of individual development to establish the phylogenies and systematic relationships of several genera of extinct ammonites. Like Jackson, Beecher, and others, Smith accepted not only Hyatt's terminology for the stages of individual growth and decline, but, more important, Hyatt's contention that it was the

81. Robert Tracy Jackson, "Phylogeny of the Pelecypoda: The Aviculidae and Their Allies," *Mem. Boston Soc. Nat. Hist.*, *4* (1890), 379.

82. Ibid., pp. 277-400. See also such other studies by Jackson as Robert Tracy Jackson, "Localized Stages in Development in Plants and Animals," *Mem. Boston Soc. Nat. Hist.*, *5* (1898), 89-153; and "Phylogeny of the Echini," *Mem. Boston Soc. Nat. Hist.*, *7* (1912), 1-491.

83. Jackson, "Localized Stages in Development," p. 90; and Jackson, "Alpheus Hyatt and His Principles of Research," *Amer. Nat.*, *47* (1913), 195-205.

study of those stages that offered the means for understanding taxonomy as well as evolutionary origins and histories.[84] So too did Amadeus Grabau, another student of Hyatt's who in the first decade of this century applied the working principles of his mentor's program to the study of fossil gastropods.[85] In the work of Hyatt's students as well as in the work of others,[86] Hyatt's views loomed large, forming the foundation of their understanding of the processes and patterns of evolution. More generally, the work of those men also reflected a continued commitment to morphology, a commitment to study the features of structure and form in order to answer questions concerning the evolutionary origins and histories of extinct organisms.

The continuation of the morphological tradition as indicated in the work of these vertebrate and invertebrate paleontologists provides some insight into the nature of turn-of-the-century American biology and the larger issue of the nature of scientific change. In the first place, the evidence of a continued adherence to the questions and methods of morphological science within paleontology, while it may not fully discount Allen's notion of a "revolt from morphology," does nonetheless limit the usefulness Allen's conception. It is true that in the 1890s there were in certain fields of biology reactions against precisely the kinds of programs that were put forth by men such as Cope or Hyatt. At the same time, however, it is equally clear that such reactions did not extend

84. Smith's more important works include: James Perrin Smith, "Comparative Study of Palaeontology and Phylogeny," *J. Geol., 5* (1897), 507-524; "The Development of Glyphioceras and the Phylogeny of the Glyphioceratidae," *Proc. Calif. Acad. Sci.*, 3rd ser. (Geology), *1* (1897), 105-126; "The Development of Lytoceras and Phylloceras," *Proc. Calif. Acad. Sci.*, 3rd ser. (Geology), *1* (1898), 129-160; "The Biogenetic Law from the Standpoint of Paleontology," *J. Geol., 8* (1900), 413-425; "The Development and Phylogeny of Placenticeras," *Proc. Calif. Acad. Sci.*, 3rd ser. (Geology), *1* (1900), 181-240; "The Carboniferous Ammoniods of America," *U.S. Geol. Surv. Mono., 42* (1903), 1-211; and "Acceleration of Development in Fossil Cephalopoda," *Stanford U. Publ., 30* (1914), 1–30.

85. See Amadeus W. Grabau, "Studies of Gastropoda. I," *Amer. Nat., 36* (1902), 917-945; "Studies of Gastropoda. II. Fulgur and Sycotypus," *Amer. Nat., 37* (1903), 515-539; "Studies of Gastropoda. III. On Orthogenetic Variation in Gastropoda," *Amer. Nat., 41* (1907), 607-646; and "Studies of Gastropoda. IV. Value of the Protoconch and Early Conch Stages in Classification of Gastropoda," *Proc. Seventh Int. Zool. Cong.*, 1910, pp. 753-766.

86. The incorporation of Hyatt's principles in the work of others is pointed out in Jackson, "Alpheus Hyatt," pp. 201-205; and P. E. Raymond, "Invertebrate Paleontology," in *Geology, 1888-1938. Fiftieth Anniversary Volume of the Geological Society of America* (Geological Society of America, 1941), pp. 90-94.

to all areas of biological inquiry, and in fact the pursuit of paleontology in the period 1880-1910 demonstrates quite the reverse: a continued commitment to the questions, methods, and in many cases even the theoretical views laid out by Marsh, Cope, and Hyatt. The notion of a "revolt from morphology," insofar as it is even applicable, must be restricted in its scope. Certainly it does not apply to turn-of-the-century American paleontology, where there existed an ongoing tradition with regard to both methodology and objectives.

Nor was that tradition merely an intellectual backwater. Clearly paleontology has changed dramatically since the early years of this century, and the theoretical views of men such as Cope and Hyatt as well as the search for archetypes and common ancestors have been set aside.[87] Yet paleontology is still today based largely on the study of fossil structure and form, and many of its practitioners still pursue questions about the mechanisms and patterns of evolution. The fact that paleontology, a science that did not embrace the new analytical, experimental philosophy and method, has nonetheless retained its distinctive aims and methods, suggests that the concept of revolution does not fully explain the changes that occurred in late nineteenth- and early twentieth-century American biology. It is perhaps possible to understand the changes in biology in terms not of revolution, but of an increasing specialization and proliferation of different research programs, each of which pursued its own distinctive problems and developed in its own distinctive ways. The idea of separate, contemporary research programs allows for the spectacular intellectual and institutional growth of experimental biology and genetics without asserting that such a program triumphed over or supplanted other programs of biological research. More important, that idea accounts for the continued significance of paleontology, a science that has certainly abandoned some of its older morphological objectives but that still retains a concern with the problem of evolutionary changes in fossil structure and form.

87. That modern paleontologists have largely abandoned the search for archetypes and common ancestors is stated by George Gaylord Simpson in *The Major Features of Evolution* (New York: Simon and Schuster, 1953), pp. 340-349.