MARSUPIALS AND MONOTREMES IN PRE-DARWINIAN THEORY

by

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Chapter I

INTRODUCTION

In the mid-nineteenth century a new scientific theory radically altered biological perspectives on nature. The Darwinian theory of evolution provided a new explanatory model for biological phenomena, established new standards as to what constitutes an acceptable biological explanation, and transformed popular attitudes toward nature, God, and man. Early nineteenth-century theorists grappled with problems of paleontology, geographic distribution, and taxonomy which existing explanatory systems failed to satisfactorily explain. For example, the marsupials (pouched mammals, such as the kangaroo and opossum) and monotremes (egg-laying mammals, *viz.*, the platypus and echidna) posed many puzzling problems. These peculiar animals became the focus of an extended scientific controversy and provided empirical tests for new theoretical explanations.

This dissertation is a historical study of the scientific debate provoked by early explanations of marsupials and monotremes. Due to their geographic isolation, they were discovered comparatively late in the development of European science. Scientific theories developed largely without reference to these animals, so theorists were confronted with a number of unexpected facts which did not fit into their theoretical frame of reference. From the first European encounter with marsupials in 1500, they posed special problems, but it was not until the nineteenth century, with the exploration of Australia and the discovery of the monotremes, that the debate became intense. The marsupials and monotremes presented biologists with irregularities of anatomy, classification, geographic distribution, and fossil history which pre-Darwinian biological theories could explain only with difficulty. These same issues were central to the scientific debate leading to the development of the Darwinian theory of evolution and its establishment as an accepted scientific theory. For this reason, marsupials and monotremes became a focus of controversy among the major biological theorists of the nineteenth century, and the problems they presented directly affected the future development of biological thinking.

The failure of the prevailing theories to account for the new discoveries demonstrated the inadequacy of existing explanations and led biologists to search for alternative theories. Each new theory was tested with respect to its ability to explain the empirical evidence. The eventual success of the Darwinian theory is largely attributable to its capacity to explain the previously unexplained. An examination of the case of the marsupials and monotremes will more clearly illuminate this process of theory development and testing.

Chapter II discusses the search for an adequate explanation of marsupial reproduction, an episode which provides the necessary historical background to the nineteenth-century debate about marsupials and monotremes. Although the first opossum specimen to reach Europe attracted immediate attention as an interesting curiosity, there was at first no recognition that its reproduction was unusual. By the seventeenth and eighteenth centuries, however, biologists realized that some features of marsupial reproduction (particularly the small size of the pouch young) could not be explained by the commonly held theories of mammalian reproduction. Seeking to explain marsupial reproduction by analogy with placental reproduction, biologists identified the pouch as the uterus. This erroneous claim originated as a result of a simplistic interpretation of field observation of marsupials with pouch young. Because this notion appealed to common sense, it was prevalent among laymen and persisted among amateur naturalists long after it had been discredited within the scientific community. The peculiar features of marsupial reproduction caused confusion and conflict among biologists until the Comte de Buffon discovered a way to adjust the theory to account for both field observations and laboratory dissections. Buffon explained marsupial reproduction in terms of a two-stage gestation, with part of the foetal development occurring in the uterus and part in the pouch. By thus enlarging the concept of "normal" reproduction to include marsupial reproduction, Buffon was able to explain the phenomenon in terms which related it to placental reproduction. By the beginning of the nineteenth century, the major anomalies presented by marsupial reproduction were largely resolved.

In the first half of the nineteenth century, European biologists were suddenly confronted with another theoretical difficulty, the discovery that marsupials formerly existed in Europe. Chapter III chronicles scientists' attempts to explain the discovery of mammalian fossils from the European Mesozoic. The discovery was puzzling because, according to accepted paleontological theory, mammals should not appear until much later in the fossil record. The evidence was immediately challenged. Opponents argued either that the fossils were not as old as had been claimed or that they were reptiles, not mammals. Paleontologists confirmed that the fossils were Mesozoic and identified them as marsupials. Meanwhile, taxonomists established the marsupials and monotremes as the most primitive of all the mammals. Progressionists quickly adapted these two claims to suggest that the fossil record revealed a gradual increase in organic complexity within the class of mammals. Once this claim had been made, evolutionists were quick to seize upon the argument to support their own version of progressionist theory. At the same time, advocates of organic uniformitarianism used the early appearance of the Mesozoic mammals to argue against any theory of organic progression. The Mesozoic "marsupials" were thus intimately involved in the major theoretical discussions which preceded the acceptance of the Darwinian theory of evolution. Once Darwinism became an established biological theory, the taxonomic arrangement of marsupials and monotremes was used to construct a hypothetical path of mammalian development.

The exploration of Australia revealed even more unexpected and unexplainable facts. At first Australia seemed like a strange new world where the normal laws of nature simply did not apply. Chapter IV outlines biologists' attempts to adapt their theories to the new information. The Australian mammalian fauna was peculiar in that it consisted primarily of marsupials and many of these marsupials seemed strangely similar to placental animals from other parts of the world. There were marsupial "wolves," marsupial "cats," and marsupial "squirrels." Early attempts to explain this unusual feature of geographic distribution appealed to the principle of adaptation. Theorists assumed that there must be peculiar physical features of the Australian environment which made it more suitable for marsupials than for placentals. But this explanation failed because no environmental factor could be identified which was universally and uniquely present in Australia. Moreover, the success of introduced species, such as cats and goats, demonstrated that placentals were eminently suited for life in Australia. Biologists were forced to acknowledge regularities of geographic distribution which confined certain taxonomic groups to certain parts of the world, without having any explanation for these regularities. The Darwinian theory of evolution provided the explanation by referring to past geographic and organic changes.

The first clue to the problem was the realization that the living flora and fauna of Australia bore a striking resemblance to the fossils of the European Mesozoic. This curious fact did not take on any great theoretical significance until Robert Chambers used it as evidence for his own evolutionary theory. Opponents of evolution were compelled to develop an explanation, based on the principle of adaptation, which was consistent with their belief in the stability of species. Their explanation was generally accepted until Darwinists developed an alternative evolutionary explanation. In this new theoretical context, the similarity between existing Australian species and European fossils was transformed from an argument <u>against</u> evolution into an argument <u>for</u> evolution. The Darwinists prevailed because, by employing a single theoretical model, they could explain the isolation of marsupials in Australia, the failure of marsupials to compete successfully against placentals, and the "ancient" appearance of the Australian flora and fauna.

Perhaps the most significant Australian contribution to the development of the Darwinian theory of evolution resulted from the first major discovery of mammalian fossils in the Wellington Caves of New South Wales. Contrary to the expectations of scriptual geologists such as William Buckland, these fossils proved to be marsupials rather than placentals. This fact suggested that the laws of geographic distribution which presently isolate marsupials in Australia operated in the recent past as well. Biologists were later able, based on evidence from other parts of the world, to expand this isolated observation into a general law. The law of succession was a prerequisite to the establishment of a theory of gradual evolution, because it established the necessary organic continuity between past and present. This law was also decisive in convincing Darwin to begin investigations into the question of the origin of species.

The influence of prevailing theories on the interpretation of empirical data is perhaps most clearly seen in the case of nineteenth-century attempts to explain the egg-laying mammals, discussed in Chapter V. When European biologists first encountered monotremes, they did not immediately recognize that their reproduction was peculiar. However, with the first investigation of the internal anatomy of the platypus, it became apparent that this was a very unusual creature. Clearly, the reproductive anatomy was atypical, but biologists were unwilling to accept the idea that mammals could lay eggs. Taxonomists defined the Mammalia as the class of animals which were warm-blooded, gave milk, and gave birth to live young. Rather than alter such a firmly established definition, they tried to force the evidence to conform to existing conceptual categories. Anti-evolutionists denied that there was any anomaly at all, claiming that the monotremes gave milk and gave birth to live young and were therefore mammals in the traditional sense of the term. Evolutionists, on the other hand, wished to challenge the traditional categories, arguing that monotremes formed a transitional class linking mammals with the lower vertebrate classes. They claimed that monotremes laid eggs and did not give milk and therefore were not mammals. Once naturalists had firmly established that monotremes did give milk, biologists assumed that the animals could not lay eggs. This erroneous opinion became so firmly established in scientific circles that biologists ignored Australian reports of platypus eggs. Naturalists were so convinced that monotreme reproduction completely conformed to the normal pattern of reproduction that the belief remained virtually unchallenged for half a century until biologists accidentally stumbled upon monotreme eggs. It was not until 1884, after most scientific opposition to evolution had been overcome, that biologists were forced to enlarge their definition of the class Mammalia to accommodate the egg-laying monotremes.

The development of the modern scientific explanation of marsupials and monotremes was necessarily affected both by the nature of science as an intellectual activity and by the structure of science as a social activity. For this reason, some general considerations from the philosophy and the sociology of science may help to illuminate the case at hand.

The peculiarities of the marsupials and monotremes were of crucial theoretical importance only when they challenged existing theoretical explanations. The philosophy of science can offer insights into the role of anomalies (those phenomena which seem inconsistent with accepted scientific theory) in developing new theoretical explanations.

Willard C. Humphreys argues that nearly all scientific activity focuses on anomalies. He claims that ". . . both the logical structure of scientific theories and their historical evolution are organized around the identification, clarification and explanation of anomalies."[1] Humphreys points out that an anomaly can exist only within the context of a scientific theory. The theory defines the anomaly. An observation is anomalous only if it can be shown to be in conflict with accepted beliefs--the body of observational data, experimental results, and generalizations which composes an accepted scientific theory. Humphreys suggests that it is the ability of scientific theory to single out certain events and facts as anomalies requiring explanation that makes it an effective guide to scientific inquiry. The theory serves as a probing instrument with which to order observation and experiment.[2] Logically, then, the first step in a scientific explanation is to show that something needs explaining. One must "define the anomaly" by demonstrating the incompatibility of theory and observation.

Thomas Kuhn postulates a similarly crucial role for anomaly in producing new scientific discoveries. Kuhn writes,

> In science . . . novelty emerges only with difficulty, manifested by resistance, against a background provided by expectation. Initially, only the anticipated and usual are experienced even under circumstances where anomaly is later to be observed. Further acquaintance, however, does result in awareness of something wrong or does relate the effect to something that has gone wrong before. That awareness of anomaly opens a period in which conceptual categories are adjusted until the initially anomalous has become the anticipated.[3]

Kuhn goes on to argue that the failure to resolve an anomaly can produce a crisis for scientific thought. Such crises can eventually lead to the paradigm shifts which he identifies as scientific revolutions. According to Kuhn, scientists will always try to resolve the anomaly in a manner consistent with the accepted practices and theoretical principles of their discipline. Continued failure to do so may produce discontent and may lead some scientists to challenge the fundamental principles of the prevailing paradigm. He emphasizes, however, that anomalies never cause the rejection of a theory unless an alternative theory is available to take its place.

> The decision to reject one paradigm is always simultaneously the decision to accept another, and the judgment leading to that decision involves the comparison of both paradigms with nature _and_ with each other.[4]

It is this process which we observe in the case of nineteenth-century explanations of marsupials and monotremes. One cannot claim that the anomalies presented by these animals by themselves discredited pre-Darwinian biological explanations nor can one claim that they directly pointed to the new explanatory model which would be developed. Rather, they presented astonished biologists with facts which contradicted their expectations, facts which indicated that there was something wrong with prevailing theories, facts which necessarily had to be accommodated within any new explanatory system. These anomalies were manipulated by scientific adversaries to argue for or against particular theoretical models.

An anomaly, from the scientist's point of view, is disturbing. At best it is a niggling worry, an unpleasant little disorder in an otherwise orderly world. At worst, it is a painful indication of the failure of scientific theory, a serious challenge to scientific orthodoxy. A scientist will attempt, so far as possible and as soon as possible, to get rid of anomalies.

The first step is to evaluate the evidence. It may be possible to deny that the anomaly exists at all. One may be able to explain it away as a result of careless observation or a mistake in reasoning. Anomalous facts are immediately suspect and are subjected to much more rigorous testing than are other phenomena. If further experience fails to unequivocally to confirm the anomaly, it may be rejected solely because it is anomalous. Observations which are inconsistent with a scientist's reasonable expectations because they violate basic theoretical principles which the scientific community holds to be true are not acceptable. For this reason, paleontologists justified (correctly as it turned out) their rejection of the Australian mastodon. And for the same reason (this time incorrectly) European biologists rejected Australian reports of platypus eggs.

If, after careful investigation, it is impossible to deny the existence of the anomaly, then scientists will be forced to adjust their theories to accommodate it. The search for such an adjustment may cause some confusion and conflict, as scientists try to find a resolution which will be consistent with the empirical evidence yet at the same time will preserve, so far as possible, the existing theoretical structure. Thus, although seventeenth and eighteenth century biologists universally sought to explain marsupial reproduction by analogy with "normal" reproduction, it took over a century to construct an explanation consistent with field observations, laboratory dissections, and biologists' understanding of placental reproduction. By making minor adjustments within the theory, scientists may be able to account for the anomaly and at the same time preserve existing theoretical principles. For example, biologists accommodated the monotremes within the Mammalia by enlarging the definition of a mammal to include creatures which lay eggs.

If one fails to eliminate the anomalous observation as an error and one cannot accommodate it by making a minor adjustment within existing theory, then the anomaly becomes a much more serious challenge to the scientific status quo. Anomalies are a sign that something is wrong with existing theories, and repeated failure to explain an anomaly may cast serious doubt on the fundamental assumptions and principles of existing scientific explanations. If scientists encounter a number of apparently unrelated anomalies which resist explanation, as was the case in biology in the early nineteenth century, then they may begin to search for an entirely new theoretical model. Scientific conflict is at its most intense when some scientists propose to substitute a new theory, based on fundamentally different principles, in place of the old, failing theory.

Anomalies play a crucial role in the battle between opposing scientific theories. To attack the validity of a theory, opponents must be able to point to empirical evidence which either contradicts or is unexplained by the theory under attack. If they can propose an alternative theory which explains these same facts, then they have demonstrated that, with respect to these facts at least, their own theory is preferable. Anomalies, then, are the weapons which scientists hurl at their opponents, and theorists must continually adjust their own theories to meet the attacks of the opposition. New scientific theories are constructed in an atmosphere of conflict, and their development is affected by the arguments of the opposition as well as by the empirical evidence they wish to explain. For example, Robert Chambers was not influenced by new empirical evidence when he altered his evolutionary theory to deny that progressive changes in the physical environment were linked to progressive organic changes. Rather, he wanted to invalidate special creationist explanations of organic progression based on the principle of adaptation.

Philosophers of science have emphasized the importance of anomalies in the development of new scientific explanations, but few historians have addressed this issue. In this instance, philosophical speculation on anomalies offers a conceptual framework which will assist in understanding the historical development of theoretical explanations of marsupials and monotremes.

Other considerations of equal importance in understanding this particular case are the special theoretical and social factors involved in colonial science. The isolation of marsupials and monotremes in Australia (with the exception of a few American marsupials) created special problems for European investigators. Few European scientists were able to observe the animals in their natural environment. Therefore they had to depend on anatomical dissections of preserved specimens and on the reports of witnesses, most of whom lacked adequate scientific training. Field research and laboratory investigations were almost always done by different people. Field observers developed theories which differed significantly from those developed by biologists in Europe because they were confronted with different experiences and different "facts." Field and laboratory experience had to be reconciled before a satisfactory scientific explanation could be formulated. The Darwinian theory of evolution was developed by men who combined sound scientific training with considerable field experience. Many leading Darwinists (for example, Charles Darwin, Alfred Russel Wallace, Joseph Dalton Hooker, and Thomas Henry Huxley) had significant experience as naturalists in the Australian region, which suggests the influence of the Australian environment on the development of the new theoretical model.

To a large extent, European scientists had to rely on Australian observers to supply them with specimens and information. The Australians (both amateurs and professional scientists) operated within a different social and intellectual context than the Europeans, and these differences affected their perception and interpretation of the peculiarities they encountered. To understand the operation of science in Australia and the difficulties in communication between the two different scientific communities, we need to examine the nature of colonial science.

George Basalla has proposed a three-stage model for the spread of Western science.[5] Basalla argues that the first stage in the introduction of science into a new country is a "nonscientific" stage. Europeans visit the new land to make collections and observations. The scientific results of their work (as well as the specimens they have obtained) are taken to Europe to be integrated into the corpus of European science. Basalla envisions this stage as an extension of geographic exploration, involving an appraisal of natural resources.

In the second or "colonial" stage, the inhabitants of the new country (either natives or European immigrants) begin to conduct their own scientific investigations. But at this stage the colonial educational system, scientific organizations, and journals are either nonexistent or inadequate to support a strong scientific community. Therefore the colonial scientist is dependent on the institutions and traditions of a European nation with an established scientific culture. His choice of scientific fields and research problems is defined by European science. He seeks institutional attachments, honors, and publication within the European scientific community.

Basalla argues that only at the third stage can the new nation develop an independent scientific tradition. This requires the acquisition of a sophisticated technology, a sound system of scientific education, and strong native scientific organizations and journals.

During the latter part of the eighteenth and the early part of the nineteenth centuries Australia experienced

Basalla's first stage. The voyages of James Cook, for example, long served as a model for European scientific and geographic exploration. By the mid-nineteenth century, however, due in part to the deliberate effort of England to transport all the trappings of British culture to the new continent, local scientific and educational institutions provided a fledgling scientific community with the necessary institutional support to pursue independent scientific research.

Colonial scientists operated under enormous disadvantages. Few of them possessed much previous scientific training, and the scanty library resources available prevented them from remedying this defect. European scientists tended to regard their Australian colleagues as mere collectors who functioned to provide the raw data which would be sifted and interpreted by European professionals. Many colonials consciously and gratefully accepted this role, adopting a Baconian view of science and eschewing theory.

Australian investigators were conscious of their inferior position within the scientific hierarchy. They respected the judgment of their European mentors, and they applied the scientific theories which prevailed in Europe to their own experiences in their own environment. By allowing European theorists to determine the questions they asked and the methods they employed, Australian scientists sometimes completely overlooked important evidence. They failed to solve the problem of monotreme reproduction, for example, because they looked for the wrong things in the wrong places.

Although Australians were generally timid in breaking with the European scientific tradition, some colonial scientists attempted to extend and refine European theories in the light of their Australian experience. However, the structure of colonial science severely hampered their ability to make a personal contribution to theory development and testing. British scientists set up an information-gathering system which facilitated the flow of specimens and information to England, but the return of information from England to Australia was extremely slow and sketchy. Australian scientists repeatedly complained that they could not conduct intelligent investigations because they did not have the current scientific literature about Australian animals. Lacking up-to-date information and isolated from the centers of theoretical speculation, Australian scientists operated with antiquated theories. Australian theorizing was generally ignored in Europe because the theoretical frame of reference was no longer relevant. For example, Frederick McCoy's attack on Darwin, although very influential in Australia, attracted little attention in Europe because the issues he addressed were no longer of any interest to European biologists.

Nineteenth-century Australian scientific institutions suffered numerous political and financial difficulties. There were few positions for professional scientists and few of these insured a steady and dependable income. Australian science was dominated by amateurs, and many members of the small Australian intellectual community, including clerics, politicians, and businessmen, were actively involved in scientific debates. For this reason, the influence of public pressure in restricting scientific speculation was probably greater than was the case in Europe. Certainly the pronounced intellectual and religious conservatism of nineteenth-century Australia was reflected in its scientific theories as well. For example, Australian scientists continued to regard Darwinian theory as scientific and religious heresy long after it had achieved professional acceptance in England.[6]

Given the nature of the colonial scientific enterprise, it is perhaps understandable that European biologists frequently questioned the scientific judgment of the Australian observers. The differences in experience, education, and theoretical perspective between the European and Australian scientific communities caused difficulties in communication and often created misunderstanding between the two groups. European biologists were much less likely to accept anomalous evidence if it originated from outside the European scientific community.

Sociologist Ron Westrum has examined the social dimensions of the reaction of the scientific community to alleged anomalous events by examining the cases of meteorites,[7] sea serpents,[8] and unidentified flying objects.[9] Westrum shows that scientists' rejection of anomaly often takes place on sociological as well as theoretical grounds. Westrum is particularly interested in those kinds of anomalies which amateurs claim to have experienced but which the scientific community rejects as nonexistent.

The scientific community tends to be a closed social group, open only to those with the appropriate educational and professional credentials. Westrum argues that laymen who lack these credentials may in fact possess information of great interest to the scientific community, but they have no access to the normal channels of scientific communication. Scientists are skeptical of information provided by amateurs, because they have no way of testing the reliability of the witnesses. If the alleged event appears to be implausible because it violates accepted scientific theory (as was the case with meteorites and platypus eggs), then the scientific community will reject it on theoretical grounds. Even those scientists who find the alleged event interesting may be induced by the disapproval of their colleagues to abandon investigation. If the scientists cannot personally and independently verify the reports, then they must either reject them as unproven or accept data originating outside the scientific community. As Westrum points out, the latter alternative would place the control of data in the hands of non-scientists, thereby destroying the quality-control system which the professional structure of science is designed to protect. It is reasonable, then, to expect considerable resistance to anomalies if reports of them originate from outside the narrowly defined scientific community.

Westrum's analysis is of relevance to the controversy over marsupials and monotremes because European scientists were reluctant to acknowledge the professional competence of Australian observers. For example, reports of platypus eggs were ignored until a British naturalist testified to their existence. Doubts about the validity of the Australian reports allowed European scientists to accept the evidence which they found reasonable and reject the evidence which contradicted their theoretical expectations. Therefore, European theoretical speculation was less strictly limited by empirical testing than is often the case.

The preceding remarks concerning the nature of colonial science must be kept in mind in the investigation of European explanations of marsupials and monotremes. There are other general considerations which make Australia a particularly promising area of investigation for historians of science. Until very recently, little attention had been paid to the history of Australian science. Consequently, the secondary literature is very limited. But the unique geographic and historical situation of Australia has made possible the preservation of scientific records of extraordinary value to the historian. Australia was explored after (and as a result of) the development of institutionalized science.

No other continent was explored so systematically, with a conscious effort to acquire and transmit new scientific information. The literacy rate of nineteenth-century Europe was higher than ever before, so many Australian colonists could read and write. Records were made and, because there has been no destructive war on Australian soil, they were preserved. As this study shows, the Australian experience can offer valuable lessons concerning the nature of science as an institution and as an intellectual endeavor.

NOTES

[1]Willard C. Humphreys, *Anomalies and scientific theories* (San Francisco: Freeman, Cooper & Company, 1968), p. 12.

[2]*Ibid.*, p. 33.

[3]Thomas Kuhn, *The structure of scientific revolutions* (Chicago and London: University of Chicago Press, 1970), p. 64.

[4]*Ibid.*, p. 77.

[5]George Basalla, "The spread of Western science," *Science* CLVI (1967) pp. 611-622.

[6]Ann Mozley, "Evolution and the climate of opinion in Australia," *Victorian Studies* X (1967) pp. 411-430.

[7]Ron Westrum, "Science and social intelligence about anomalies: the case of meteorites," *Social Studies of Science* VIII (1978) pp. 461-493.

[8]Ron Westrum, "Knowledge about sea-serpents," in Roy Wallis, ed., *On the margins of science: the social construction of rejected knowledge* (Sociological Review Monograph: No. 27) (Keele, England: University of Keele, 1979).

[9]Ron Westrum, "Social intelligence about anomalies: the case of unidentified flying objects," *Social Studies of Science* VII (1977) pp. 271-302.

Chapter II

THE 'POSSUM'S POUCH: AN INCONSISTENCY IN NATURE?

When Europeans encountered the first marsupial in 1500, its pouch was viewed as a curiosity of nature. Early observers assumed that opossum reproduction followed the normal pattern of mammalian development, so the pouch did not immediately offer a serious challenge to biological theory.

Not until the mid-seventeenth century did it become apparent that opossum reproduction possessed many unique features which contradicted accepted explanations of reproduction. Naturalists sought to explain these anomalies by analogy with existing theories of mammalian reproduction. Each attempt at explanation, while contributing to an understanding of marsupial reproduction, raised additional questions and seemingly contradicted the established regularities of mammalian development. Accounts of marsupial reproduction were conflicting and confused until the mid-eighteenth century when the Comte de Buffon resolved the difficulty by postulating a two-stage model of marsupial development. In explaining marsupial reproduction by analogy with placental reproduction, Buffon was able to reconcile the empirical evidence with existing explanations of mammalian development. The problem of reproduction, a prelude to the later debates about marsupials, was largely solved by the beginning of the nineteenth century.

In 1500, when Francisco Pinzón first discovered the opossum in the New World, its pouch attracted immediate attention. A specimen was presented to Queen Isabella of Spain who marvelled at the curious pouch which nature provided for the protection of the young.[1] Until the discovery of Australian marsupials, Europeans believed that this unique anatomical feature distinguished the opossum from all other living creatures.[2] Although it was immediately obvious to European observers that the pouch functioned to protect the young while they were still dependent upon their mother, its special role in reproduction was not immediately perceived. Early writers consistently referred to it merely as an external bag which the young could enter and leave at will.

Peter Martyr's description of the opossum noted that the mother, after the young were born, carried them with her wherever she went in an external belly, something like a large bag.[3] Gesner,[4] Camerarius,[5] and Aldrovandi[6] made similar statements, drawing upon Peter Martyr's account. None of these men had the opportunity to observe a living opossum, although Peter Martyr did examine the first specimen to reach Europe.

Other Europeans who visited the New World supported the view that the opossum gave birth in the customary manner. Francisco Hernández, a Spanish physician and naturalist sent by Philip II of Spain to America to survey the natural products of the New World, specifically stated that the young opossums were conceived in the uterus.[7] José de Anchieta, a Jesuit missionary to Brazil from 1553 to 1597, noted that the young entered the pouch after birth.[8] Bernardino de Sahagún, historian of Aztec civilization and Franciscan missionary in Mexico during the late sixteenth century, believed that the pouch served only as a receptacle to shelter the young after birth.[9] Each of these men lived in the New World for an extended period of time and had the opportunity to make personal observations of living opossums.

Although the possession of a pouch to carry the young certainly aroused curiosity, it did not necessarily imply an exception to the natural order. However, once people began to perceive that the pouch played an important role in the reproductive process itself, it became apparent that marsupial reproduction deviated substantially from the usual process of mammalian reproduction as it was then understood.

One sixteenth-century writer recognized that the opossum's reproductive system was quite unlike that of all other mammals then known to Europeans. Magalhães de Gandavo speculated on the role of the pouch in reproduction as follows:

> Of these animals it is affirmed that they never conceive the young in the belly but only in these pouches, because of all that have been taken none have been pregnant. Moreover, aside from this, there are other very likely conjectures, [according to which] it is considered impossible for them to bear young as all other animals do (according to the laws of Nature).[10]

While this statement demonstrated a realization that marsupial reproduction has unique features, the identification of the pouch as the place of conception failed to recognize that opossums, like all other mammals, conceive their young internally and the fetus begins its development within the uterus. However, marsupials, unlike placental mammals, do not develop an elaborate placenta for nutritional, respiratory and excretory interchange while the fetus is developing. Consequently, the amount of development that can occur within the marsupial uterus is extremely limited. As a result, marsupial young are extremely small at birth, as compared to newborn placental young. For example, a newborn opossum weighs approximately 2.5 grains;[11] twenty will fit in a teaspoon.[12] Due to this small size, there is no visible enlargement of the abdomen and uterus during gestation as occurs in placental pregnancy. Furthermore, much of the development which takes place within the uterus in placental mammals occurs in the pouch in marsupial animals. Thus, marsupials are born in a much more primitive state of development than are placental young.

The scientific revolution of the sixteenth and seventeenth centuries caused a shift in the methods and goals of biology. Previous authorities began to be questioned; experimentation and personal observation became the major criteria of scientific proof. In natural history, the rise of comparative anatomy led to a new emphasis on the anatomical and physiological characteristics of animals.

With respect to beliefs about marsupials, this shift was reflected in the increased interest in the opossum's most outstanding anatomical peculiarity, its pouch. Whereas earlier naturalists concerned themselves with the opossum's usefulness or harmfulness to man, the focus of inquiry shifted in the seventeenth century to the animal itself. Naturalists sought a more accurate description of the opossum and an understanding of its life history, but its location in America made first-hand observation difficult.

Before the mid-seventeenth century, most writers had no difficulty in assuming that opossums reproduced in the same way other mammals did.[13] By 1650, however, it began to be generally recognized that opossum reproduction had some very unusual features. In an effort to explain opossum reproduction in a manner consistent with their understanding of mammalian reproduction, observers made the error of identifying the pouch as the uterus. Finding tiny pouch young in a primitive state of development and observing that they developed within the pouch while attached to the teats, many observers concluded that they originated there.

Much of the European knowledge of marsupials prior to 1648 derived from accounts written by naturalists who had never seen a marsupial. Naturalists in Europe were forced to depend on the reports of travelers, often of questionable reliability. Even those travelers who made careful observations and who refrained from exaggeration lacked the scientific training to know what kind of information was most needed. To remedy this situation, Willem Piso, a physician, and Georg Marggraf, a naturalist, journeyed to Brazil. The scientific results of that expedition, published in 1648, represented the first attempt to investigate the flora and fauna of the New World in a systematic, comprehensive manner.

Marggraf's description of the opossum represented a substantial improvement in accuracy and detail when compared to those of previous writers. He did, however, make a major error in interpreting his observations. He wrote,

> The pouch is itself the uterus of the animal, for it has no other, as I have ascertained by dissection; in this pouch the semen is received and the young are formed. . In this pouch they are kept until they are able to look for food themselves, meanwhile, however, they occasionally go abroad and again return into the pouch.[14]

Marggraf was the first scientifically trained naturalist to observe the opossum in its natural habitat. He was also the first to claim that the opossum had no uterus, as other mammals had, thereby introducing an error into the biological literature which was vigorously debated for a century. Although Marggraf's confusion resulted from inaccurate observation, he did recognize, as so many of his predecessors failed to do, that the marsupial pouch played a critical role in reproduction, a role which was analogous to that of the uterus in all other mammals with which he was acquainted. This recognition could only derive from field observations of living opossums or from dissections of preserved specimens with pouch young. Neither were available in Europe. In drawing the analogy, Marggraf erroneously identified the pouch as the uterus, an error which could only be corrected by careful anatomical investigation. Although Marggraf claimed that he could find no uterus in dissection, he may easily have been confused by the unusual reproductive anatomy of the opossum.

In the same year that Marggraf's description of the opossum appeared, the publishing of François Pelsaert's journal extended this idea to include Australian marsupials. Pelsaert, shipwrecked in the Abrolhos Islands off the coast of Western Australia in 1629, provided Europeans with the first description of an Australian marsupial, the Dama wallaby (Thylogale eugenii binae). From his observations, he concluded that the young grew out of the teats.

> Their manner of generation or procreation is exceedingly strange and highly worth observing. Below the belly the female carries a pouch, into which you may put your hand; inside this pouch are her nipples, and we have found that the young ones grow up in this pouch with the nipples in their mouths. We have seen some young ones lying there, which were only the size of a bean, though at the same time perfectly portioned, so that it seems certain that they grow there out of the nipples of the mammae, from which they draw their food, until they are grown up and able to walk.[15]

Since Marggraf could claim, as could few naturalists, to have personally examined an opossum, he was frequently cited as a major source of information. Willem Piso repeated substantially the same description, including the formation of the young within the pouch and their ability to leave and enter at will. Although he claimed to base his description on personal observation, most of this account, like much of his De Indiae, was lifted from Marggraf without due acknowledgement. Moreover, Piso added that the male, too, was equipped with a pouch so that he could alternately carry the young, relieving the female of her burden.[16] This seems quite contradictory, for, if the pouch is a uterus and the young are affixed to the teats, one can hardly understand how the male could perform this service.[17] Jonstonus, in his survey of zoology, repeated Marggraf's account almost verbatim.[18]

The idea that the pouch was itself the uterus of the opossum raised immediate difficulties. As Magalhães de Gandavo pointed out, it seemed contrary to the laws of nature.[19] John Ray, a distinguished English naturalist who was among the first to attempt to establish a comprehensive modern system of classification, had great difficulty in believing Marggraf's account, and yet had no evidence to contradict it. On the one hand, he seemed to entirely reject it when he wrote that the opossum "is distinguished from all other animals of whatsoever kind by a singular and certainly admirable pouch or open uterus in which the young are received after birth."[20] On the other hand, he cited Marggraf extensively, quoting his remarks (as quoted above) verbatim.[21] Finally he conceded that Marggraf's identification of the pouch as the uterus must be considered, at least until further information was provided from first-hand experience. He remarked,

> We will certainly discern something of the viviparous reproductive process of these animals from repeated inspection of the uteri if we have the means to do so. Indeed, if we may believe Marggraf, the uterus in these animals is not within the trunk of the body but lies outside and is exposed to view.[22]

Although the idea that the opossum's pouch was its uterus did, in a sense, make opossum reproduction consistent with that of other mammals whose young developed within the uterus, it created another anomaly. An external uterus which the young may enter and leave at will was improbable, to say the least, and quite inconsistent with normal mammalian reproduction.

Ray's account of the animal is confusing and self-contradictory. His confusion reflected an unwillingness to believe in an anomaly which contradicted his perception of the regularities of nature, coupled with an unwillingness to deny evidence which claimed to be derived from experience. Obviously the problem demanded further investigation, but there were few in America with the scientific training to resolve the difficulty and few specimens made their way across the Atlantic to Europe.

A living female opossum was presented to the Royal Society by William Bird. When she died, Edward Tyson conducted a detailed anatomical examination and in 1698 published the most complete and detailed description of opossum anatomy yet available.[23] Tyson intended that his examination should conclusively resolve the question of the location of the opossum's uterus. He discovered that even a cursory examination of the internal anatomy revealed an internal uterus, and thus concluded that previous authorities were wrong in stating that the young originated and developed within the pouch.[24] He therefore assumed that opossum young developed internally until birth at which time they had reached a stage of development comparable to that of the newborn young of other mammals. The pouch, then, served only to protect the young while they remained under the mother's care. Concerning the pouch, he wrote,

> Not that it is a Uterus, or the Young Ones are bred there (this Mistake we shall clear up . . .): But Nature has only formed this Part for that Particular Use of receiving or emitting, at Pleasure, the Young Brood, till such time as they are able to provide better for themselves.[25]

Tyson, then, denied that the pouch had any special physiological function in the reproductive process and failed to perceive that opossum reproduction was substantially different from that of all other mammals with which he was familiar. Although a detailed anatomical investigation like that Tyson performed was essential to correct the error of identifying the pouch as an external uterus, an examination of a single dead specimen could not reveal what was apparent to many observers in the field: the presence of tiny pouch young in a primitive state of development and attached to the teats implied a unique reproductive process requiring explanation.

Tyson did not have adequate information to reach this conclusion. Not only did his specimen lack pouch young, but he could not even locate the teats. The teats of a female opossum, especially one who has never given birth, are extremely small; during pregnancy the mammae develop with great rapidity. When a newborn opossum enters the pouch, it seizes the teat in its mouth. The teat swells and the young is thus firmly attached.[26] As a result of his inability to find the teats, Tyson was not even sure that they were located within the pouch. He noted that, although later writers like Piso and Marggraf located them there, the earlier accounts of Pinzón and Gilles specifically indicated that the young must leave the pouch to suckle. Tyson left the question unresolved.[27]

Tyson constructed an explanation of opossum anatomy which was consistent with contemporary theories of reproduction and with the prevailing teleological view of nature. Tyson was the first to carefully examine the skeletal structure which supported the pouch. He discovered two bones extending from the pelvic girdle into the ventral wall of the pouch. These bones serve to support the weight of the litter and the muscles attached to them control the opening and closing of the pouch. They are peculiar to monotremes and marsupials.[28]

Tyson's description of the marsupial bones and his explanation of their function was careful and complete; his interpretation followed the tradition of natural theology, offering the structure as proof of design in nature.

> Nature's Contrivance therefore in placing this *Pouch* here, in this *Hinder* Part of the Body, is very great; her *Mechanisme* in forming these *Two Bones*, the *Janitores Marsupii*, which no *Sceleton* besides has, and so artfully furnishing them with these Muscles, is most admirable; that with the *Philosopher*, there is none but must own θεοσ γεωμετρει.[29]

For Tyson, the anatomist contemplated the mechanisms of God's creation, chronicling His wisdom and benevolence. The idea that nature uses an infinite variety of mechanisms to accomplish a common purpose recurred throughout his work. Of the pouch, he wrote,

> This Contrivance of Nature for securing the *Young Ones* from any Danger, till they are able to shift for themselves, I think, is not to be parallel'd in any *Species* of Animals, at least of the *Quadruped* Kind, besides. Not that she is wanting in abundantly providing for their *Preservation*, but she pleases her self in using infinite *Variety* in attaining the same End.[30]

He gave as examples the stories, common among the ancients, of fish who swallowed their young in times of danger and vomited them forth when the danger had passed. The opossum's pouch was for Tyson no longer an anomaly; it offered but one more variation in nature's design.

Although Tyson readily acknowledged the uniqueness of certain anatomical features of the opossum (for example, the pouch, marsupial bones, and structure of the genital tract),[31] he wished to demonstrate that these anomalies were not inconsistent with the natural order. This concept of regularity in nature was reinforced by his demonstration that opossums, like all other mammals, possessed internal uteri. Tyson disapproved of descriptions of animals which emphasized their aberrations from the norm, making them monstrosities. He was sharply critical of previous authors who described the opossum as a kind of composite animal with a fox's head, human hands, the tail of an ape, and bat's ears. This kind of description led people to marvel at such a monstrous beast. For Tyson, nature produced no monstrosities.

> I think 'tis only our Ignorance makes the Admiration, and that Admiration forms the Monster; for Nature, in her regular Actings, produces no such Species of Animals.[32]

Tyson's view of the inviolability of natural law was a fairly recent development within the history of the biological sciences. Not until the sixteenth and seventeenth centuries did naturalists begin to develop a concept of the regularities of nature which rejected the existence of marvelous creatures like the phoenix, the basilisk, and the barnacle goose. Consequently, early debates about marsupials showed greater tolerance for self-contradiction and anomaly than did the later nineteenth-century debates.

Tyson was somewhat astonished at the peculiar features of the opossum's internal reproductive structures, which differed substantially from those of the placentals with which he was familiar. In most placental mammals of both sexes the urogenital duct and the rectum open separately with an area of body surface between them. In marsupials, however, the urogential organs and the rectum open into a single internal cavity, the cloaca.[33] Placental mammals possess a single vaginal canal and a single uterus. In marsupials, however, the ureters are so placed that there are two lateral vaginal canals and two separate uteri.[34] Tyson could find no similar structures among mammals, although he noted that lobsters, crabs, and rattlesnakes all possessed paired uteri.[35]

Tyson greatly regretted the lack of information on the anatomy of the male opossum. In 1704, due to the death of a male opossum in the possession of the Royal Academy, William Cowper was able to fill this gap. He found the reproductive anatomy of the male to be no less surprising than that of the female.[36] The glans penis is forked, and the right and left prongs are placed in the corresponding lateral vaginal canals during copulation.[37] The forked glans contributed to a popular folk belief that the opossum copulated through the nose. The story probably originated from observing the behavior of the female who, just before parturition, put her nose in the pouch and licked it clean thus preparing it for the reception of the young. This behavior, combined with the bifurcate structure of the glans penis, formed the basis for the Southern folk belief. Allegedly, at birth the female blew the young out of her nostrils into the pouch.[38]

For Cowper, however, the bifurcate structure of the glans penis and the vagina offered new evidence in a continuing debate concerning the nature of mammalian fertilization. He believed that the anatomical structures were designed to insure that the semen reaches both uteri. This being the case, then the seminal aura theory of fertilization had to be in error.[39]

Harvey and Fabricius both claimed that the semen never reached the uterus. Rather, a seminal aura or effluvium was absorbed by the blood and conveyed to the ovary, thus making the ova fertile.[40] Harvey believed this to be the case because, in repeated dissections of various mammals, he could find no semen in the uterus or the oviducts.[41]

In the half century between Harvey's work on generation (1651) and Cowper's treatise on the opossum, much progress was made in the understanding of mammalian fertilization. In 1656 Wharton postulated that the male semen reached the ovaries by means of the uterus and Fallopian tubes,[42] and in 1672 de Graaf succeeded in tracing the course of the ova from the oviduct to the uterus.[43] The discovery of spermatozoa in semen in 1677[44] cast doubt upon the seminal aura theory. In the debate between the ovists and the animalculists most authorities agreed that the semen travelled at least as far as the uterus.

However, the failure to find traces of semen within the uterus continued to present difficulties, and the idea of fertilization by a seminal aura transmitted by the blood was supported by Bartholinus in 1677.[45] As late as 1740 Swedenborg defended this concept of fertilization,[46] and in 1744 Harvey's seminal aura theory was still viable enough that Boerhaave argued against it.[47]

In 1704, then, the theory was very much alive and Cowper used the internal anatomy of the opossum to argue against it.

> They that fancy an *Aura Seminalis* of the Male, passes by the way of the *Bloud of the Female* to their *Ovaria* to faecundate the *Ova*, will here meet with an *Instance I must leave them to* solve. For to what end has Nature been at the trouble of making double Emissaries for the *Semen* of the male *Opossum*, tho she design'd the Impregnation of a double *Uterus* of the Female? Certainly one passage in the *Glans Penis* would have been sufficient to convey the *Semen Masculinum* to the Mass of Bloud of the *Female* in *the manner they* conceive. Nature would never *have* been at the trouble of all this Clutter in this Animal, in making a double *Glans*, and contriving two distinct Apertures in the *Glans*, when its *Penis* is erected, if the Propagation of *the* Species had *not* depended on't: Doubtless 'twas for that end chiefly, that the *Penis* of this Animal differs so much from what we meet *with in* other Creatures.[48]

Cowper assumed an economy in nature which would preclude unnecessary structures. The bifurcate glans existed because it was necessary to assure the transmission of the semen to each uterus.

Tyson had hoped that the dissection of a male opossum would resolve the question as to whether or not it had a pouch. This was not the case. Cowper discovered that, like the female, the male possessed marsupial bones attached to the pelvic girdle, but in the male there were no muscles extending from these bones to the skin of the abdomen.[49] Why should these bones exist if not to support a pouch? Tyson, in a comment published with Cowper's article, noted that the skin of the abdomen was loose so that one could easily turn the skin to form a pouch but, upon release, the skin turned out again. Therefore, he left open to question whether the male might on occasion carry the young as did the females.[50]

Without doubt, Tyson's and Cowper's careful dissections immeasurably furthered knowledge of marsupial anatomy, but both anatomists failed to perceive the unique features of the marsupial reproductive process. Moreover, their investigations did not end the controversy concerning the location of the opossum's uterus. Most trained scientists, familiar with Tyson's and Cowper's dissections, argued that the uterus was internal and that the development of marsupial young did not differ significantly from that of placental young. However, observers in the field could clearly see that the state of development of the new-born pouch young corresponded to that of uterine fetuses. Thus, the identification of the pouch as an external uterus fitted their observations much better than the claim that the pouch served only to protect the young after birth. The controversy continued.

It is clear that some observers were led to the conclusion that the opossums began their development within the pouch from observing the small size and primitive development of the pouch young. Robert Beverley in his history of Virginia (1705) noted that the pouch provided an unusual means of protection for the young.

> But, what is yet stranger, the young Ones are bred in this false Belly, without ever being within the true One. They are form'd at the Teat, and there they grow for several Weeks together into perfect Shape, becoming visibly larger, till at last they get Strength, Sight, and Hair; and then they drop off, and rest in this false Belly, going in and out at Pleasure. I have observed them thus fasten'd at the Teat, from the Bigness of a Flie, until they become as large as a Mouse.[51]

Similarly, John Lawson's account of Carolina (1708) noted, "The Female, doubtless, breeds her Young at her Teats; for I have seen them stick fast thereto, when they have been no bigger than a small Rasberry, and seemingly inanimate."[52] Lawson's work was plagiarized in other travel accounts which repeated the story that the opossum bred at the teats.[53]

Supporters of this view were aware that this method of reproduction was quite peculiar, but experience convinced them that this must be the case. William Byrd, president of Virginia's Council of State, wrote,

> Within the False Belly may be seen seven or eight Teats, on which the Young Ones grow from their first Formation till they are big enough to fall off, like ripe Fruit from a Tree. This is so odd a method of Generation, that I should not have believed it without the Testimony of mine own Eyes. Besides a knowing and credible Person has

> assur'd me he has more than once observ'd the Embryo Possums growing to the Teat before they were completely Shaped, and afterwards wacht their daily growth til they were big enough for Birth.[54]

Pastor François Valentijn's work on Amboina, first published between 1724 and 1726, was important to zoologists because it was one of the first sources of information about the marsupials of the Australian region. Referring to the cuscus (Phalanger orientalis), Valentijn too asserted that the pouch served as a uterus. He compared this kind of generation to that of plants, with the young animal corresponding to the fruit and the teat to the pedicel. He claimed that the young falls from the teat when it has reached the appropriate state of development, just as the fruit falls from a tree. As further evidence of this theory, Valentijn noted that bleeding resulted from pulling the animal away from the teat.[55]

After the anatomical investigations of Tyson and Cowper, those who identified the pouch as an external uterus were amateurs. They were unfamiliar with the scientific literature, but they were acquainted, as were few trained scientists, with living opossums in their natural habitat. European scientists were often forced to rely upon these works as sources of information, at the same time rejecting their statements about the uterus. Thus, Albert Seba used Valentijn's description but castigated him for his careless anatomy. Seba affirmed that "these animals have internal reproductive parts, like cats, dogs, and other species."[56]

Although Seba acknowledged that the pouch was unique to marsupials and conceded that it was in some ways similar to the uterus, he believed that it served only to protect the young after birth. Like Tyson, he cited this mechanism as evidence of God's wisdom and beneficence in insuring the preservation of species.[57]

European scientists rejected the evidence from amateur field observers because it conflicted with their theoretical expectations. Their own research methods were restricted to laboratory investigations, and their methods limited the kind of questions they could ask and the kind of answers they could find. European scientists, unfamiliar with living marsupials, assumed that their reproductive physiology was substantially similar to that of placentals. They ascribed to ignorance all reports to the contrary. Thus, John Hill,[58] Johann Meyer,[59] and Peter Simon Pallas[60] all denied that the pouch served any function other than protection.

The few scientifically trained observers who had an opportunity to see the opossum in its natural habitat or to observe a study specimen with pouch young were puzzled by the apparent contradiction between theory and fact. They affirmed that the marsupial young developed within an internal uterus, but they noted disturbing peculiarities which were not explained by existing theories of reproduction. For example, Folkes, examining a specimen brought from New England, noted that the teat seemed to form a thin cord to which the young was held fast by means of a membrane surrounding the mouth.[61] Dumont de Montigny observed that a mother opossum with pouch young resembled a pregnant placental mammal.[62] Mark Catesby discredited the reports that the pouch served as an external uterus because this would violate the regularities of nature. He did, however, acknowledge that such beliefs could easily arise from the unusual appearance of the young in the pouch.

> Tho' contrary to the Laws of Nature, nothing is more believed in America than that these Creatures are bred at the Teats of their Dams. But as it is apparent from the Desection of one of them by Dr. Tyson, that their Structure is formed for Generation like that of other Animals, they must necessarily be bred and excluded the usual Way of other Quadrupeds; yet that which has given Cause to the contrary Opinion is very wonderful, for I have many Times seen the young ones just born, fixt and hanging to the Teats of their Dams when they were not bigger than Mice; in this State all their Members were apparent, yet not so distinct and perfectly formed but that they looked more like a Foetus than otherwise, and seemed inseperably fixed to the Teats, from which no small Force was required to pull their Mouths, and then being held to the Teat, would not fix to it again.[63]

Until the mid-eighteenth century, accounts of marsupial reproduction continued to be confused, contradictory, and inadequate to explain the observed facts. Those who recognized that the reproductive physiology of opossums differed substantially from that of placentals maintained the false analogy between the uterus and the pouch. Their opponents failed to explain the small size and primitive development of the pouch young. In 1763 the Comte de Buffon in his comprehensive survey of natural history reconciled and synthesized previous authorities. Buffon's explanation was the first to adequately account for both the observations of internal anatomy made in the laboratory and the appearance of the newborn young as reported by observers in the field. He postulated,

> One can suppose, with great likelihood, that in these animals the uterus is only the place of conception, formation, and first development of the foetus, whose birth is more premature than in other quadrupeds; growth is completed within the pouch where they enter at the time of their premature birth.[64]

Buffon noted correctly that the development which occurs within the uterus of placental mammals is divided into two stages in marsupials. Although the conception and first development of the foetus occurs within the uterus, the young are born in a less advanced stage of development than are placental young. They remain attached to the teat until they have reached a stage of development comparable to that of placental mammals at birth. After this time, they continue to suckle for a while, and can enter and leave the pouch until weaned.[65]

Buffon's explanation was particularly perceptive because he recognized that it was this process of development which distinguished marsupials from placentals, not the possession of a pouch. He cited the mouse opossum (Marmosa) as an example of a pouchless marsupial.

> Thus, neither the long adherence to the teats nor the growth of the young in this immobile position depends solely on the comfort or safety which the pouch imparts to the young. I make this remark in order to prevent conjectures which one can make concerning the usage of the pouch, in viewing it as a second uterus or, at the very least an absolutely necessary shelter for the prematurely born young.[66]

Buffon succeeded in shifting attention to the physiology of marsupial reproduction and away from the pouch itself. His explanation also put an end to the scientific controversy as to whether the young marsupials originated within the pouch. Scientists quickly adopted Buffon's explanation. His account was repeated in the Dictionnaire raisonné d'histoire naturelle;[67] Pennant,[68] Alessandri and Scattaglia,[69] and Goldsmith[70] all distinguished between the conception and early development which occurred in the uterus and the later development within the pouch.

Although the explanation considerably advanced understanding of marsupial reproduction, it led to another error, again by a false analogy with placental reproduction. Because the young marsupials were born at such a primitive stage of development, Buffon was convinced that they were born prematurely. Of the mouse opossum, he commented:

> I am persuaded that these animals whelp a few days after conception and that the young at birth are nothing more than fetuses, which, like fetuses, have less than a fourth of their development; the delivery of the mother is always a very premature miscarriage, and the newborn fetuses can only save their lives by attaching themselves to

> the teats and never releasing them until they have acquired the same degree of development and strength that they would have naturally had in the uterus if birth had not been premature.[71]

Buffon suggested that this example of premature birth in nature might serve in the discovery of techniques for the care of prematurely born infants. He exhorted those who had the opportunity to observe living opossums to make careful observations to this effect.[72]

Buffon's explanation resolved one anomaly, only to create another. The idea that opossums gave birth prematurely raised further difficulties concerning an already vexing question: how did the young opossums travel from the uterus into the pouch? Previously, those authors who claimed that marsupial young were expelled from the vagina in the customary manner had assumed either that the mother herself placed the newborn young in the pouch,[73] or that the mother folded her body in such a way that the birth contractions propelled the newborn young into the pouch,[74] or that the young, with maternal assistance, crawled into the pouch.[75] None of these alternatives were very satisfactory, as long as the young opossums were equated with embryos. The newborn young were so tiny that neither the mother's paws nor her lips could handle them; catapulting the young from the vagina into the pouch would require acrobatic contortions; and one could not conceive that a prematurely born fetus could make the trip under its own power. The question was not completely resolved until 1920 when the Hartmans observed a newborn opossum crawl into the pouch.[76]

An eighteenth-century scientist who accepted Buffon's claim that the young were born prematurely would find such a solution impossible. Buffon, comparing the state of development of the newborn opossum to that of the placental fetus, assumed that birth was premature. But this assumption disregarded the fact that the newborn opossum was capable of independent digestion, respiration, and motion.[77] Until the analogy with a placental fetus was abandoned and the newborn marsupial's capability of independent action was recognized, another solution was necessary. M. Roume de Saint-Laurent provided such a solution.

Saint-Laurent reported that "credible" witnesses had seen small opossums, not yet formed, in the pouch. "One saw, at the tip of the nipple, transparent lumps, in which one found the rough outline of the embryo."[78] Saint-Laurent claimed that he had dissected a female mouse opossum and had discovered slender fibers extending from the horns of the uterus to the mammaries. He suggested that the opossums travelled from the uterus to the pouch along these canals.[79]

Although Daubenton, whose anatomical descriptions accompanied Buffon's text in the first edition of the <u>Histoire naturelle</u>, definitely denied the existence of any internal passage between the uterus and the pouch,[80] Buffon believed Saint-Laurent's statements to be worthy of notice. Nevertheless, the discovery was so singular, he stressed the necessity of confirmation by repetition.[81]

The Chevalier d'Aboville and the Marquis de Chastellux, French officers spending the winter of 1781-82 in Williamsburg, Virginia, set out to answer some of the questions Buffon had raised. Chastellux ridiculed the idea, commonly believed in Virginia, that the young entered the pouch through the teats. An army surgeon, who had dissected both sexes, reported to Chastellux that they possessed reproductive organs similar to those of other mammals, although somewhat different in structure.[82] While Chastellux attempted to eradicate a mistake which arose from a combination of erroneous assumptions and careless observations, d'Aboville claimed to have made the following remarkable discovery.

> There are never more teats than young, and when the latter are weaned, the nipples of the mother dry up and fall off, just as the umbilical cord does from the young of other animals; with this difference, that other animals preserve the mark of the place where the umbilical cord was, whereas the female opossum retains no trace of the points where her nipples have been, and which are not, as in other animals, placed in two parallel lines, but irregularly and as if by accident. It seems that the nipples are formed at those places where the embryos happen to touch the mother's belly after she has put them into her pouch, one by one, as she <u>lays</u> them--for that is the most appropriate expression, immature embryos being comparable only to eggs.[83]

Although d'Aboville clearly stated that the mother placed the young in her pouch after birth, his description perpetuated the error of regarding the young as immature fetuses. Further, the analogy between the nipples and the umbilical cord offered indirect support to those who argued that the young passed from the uterus to the pouch internally. The small size of the teats in non-nursing females often led to confusion, and d'Aboville's claim that the nipples formed only where the young touched the belly was cited in support of the view that marsupials gave birth through the teats.[84]

Buffon's two-stage model had substantially resolved all the major problems of marsupial reproduction, but doubts about the way the young were transmitted from the vagina to the pouch continued to cause confusion. As long as the newborn young were regarded as embryos, incapable of independent action, the theory could not be entirely reconciled with the empirical evidence. Unorthodox theorists could seize upon the anomaly to discredit existing theories and support their own, less accepted theoretical arguments.

Etienne Geoffroy Saint-Hilaire was especially interested in marsupial reproduction as evidence to support his biological theories. He cited all arguments he could find from previous authorities to support the claim that the young originated at the teat or passed by an internal passage into the pouch, but he conceded that the evidence was inconclusive.[85] He emphasized Buffon's analogy between marsupial birth and placental premature miscarriage.

In an addendum to his article, he cited recent anatomical investigations by Duvernoy which definitely denied the existence of an internal passage from the uterus to the pouch. Duvernoy described musculature in the opossum which, he believed, served to draw the vaginal opening near the pouch opening so the young could easily be transferred.[86] Geoffroy used Duvernoy's findings to argue that the product of the ovaries was laid (pondu) into the pouch. According to Geoffroy, the uterus, like the vagina, was nothing more than a passage to the outside. The ovule or egg passed immediately into the pouch where it began its development.[87] Thus, for Geoffroy, marsupials united two modes of reproduction: gemmiparous reproduction or budding, by which new individuals were formed at a point on the surface of a parent, and oviparous reproduction by which eggs were formed internally.[88]

This view was consistent with Geoffroy's theory that in the higher animals nature provided two means to accomplish a single function. These operated in a complementary manner; in some taxonomic families, one means predominated; in others, the alternative means prevailed. As additional support for this argument, Geoffroy pointed to the relationship between gestation and lactation in providing nourishment for the young. In placentals, he argued, gestation was at its maximum; lactation at its minimum. The reverse was true in marsupials, where the process of lactation was united with that of incubation, both occurring in the pouch. He drew an analogy between the placental connection with the fetus at the navel and the marsupial connection between the teat and the mouth.[89] He supported this analogy empirically by pointing out that, while in placentals there was a concentration of blood in the reproductive parts, in marsupials there was a concentration of blood in the mammaries.[90] Marsupials, then, differed from placentals in their emphasis on one means of nourishment (lactation) over another (gestation).[91]

According to Geoffroy, marsupial reproduction differed fundamentally from placental reproduction; marsupials, although primarily mammalian in organization, possessed reproductive characteristics which united them with the oviparous animals. Geoffroy later attempted to establish the marsupials as a separate taxonomic group on paleontological grounds (as will be shown in Chapter III) and removed the monotremes from the Mammalia on the basis of reproductive structure (as will be shown in Chapter V). Geoffroy consistently used the peculiarities of the marsupials and monotremes to argue that these creatures were transitional animals, linking the mammals to the lower vertebrate classes. Geoffroy's own evolutionary theory required the existence of such transitional forms.

Geoffroy's theories were imaginative, ingenious and interesting, but, unfortunately, erroneous. He was certainly correct in arguing,

> In Europe, where our opinions are regulated, _a priori_, by what happens ceaselessly under our eyes, and where, in this respect, our theories on generation have been somewhat fixed, we have profited by a certain vagueness which prevails in the observations which travelers have reported

> to us on the subject of marsupials, in order, dissimulating some facts and exaggerating other circumstances, to restore the mode of generation of these animals to a common standard.[92]

He was wrong, however, as to which facts had been exaggerated and which deserved credence. Geoffroy's theoretical speculations on marsupial reproduction collapsed for want of evidence.

Due to the difficulties involved in observing marsupial birth, the question of how the young were conveyed from the vagina to the pouch could not be immediately answered by direct observation. The anomaly was not resolved directly by the acquisition of any new empirical data but was rather eliminated by the rejection of the misleading analogy between pouch young and embryos. Anatomists could find no evidence of aberrant physiological processes. Dissection confirmed that the early development of marsupials followed the normal mammalian pattern, and repeated examinations failed to reveal any means of conveying the young from the uterus to the pouch internally. Moreover, John Morgan established that a young kangaroo, forcibly separated from its position at the teat, could regain its attachment to the teat under its own power.[93] This fact suggested to Richard Owen that the level of development achieved by the newborn marsupial had been underestimated. He noted that

> . . . it is far from being the inert and formless embryo which it has been described to be: It resembles, on the contrary, in its vital powers, the new-born young of the small <u>Mammalia</u> rather than the uterine foetus . . .[94]

Scientists were not able to ascertain how the young reached the pouch until long after the question ceased to be an important issue. After it had been established that the newborn animal was capable of independent existence and action, and after the anatomical evidence failed to support any claims of an internal passage from uterus to pouch, the question ceased to hold any theoretical importance. Thus in 1884 William Caldwell, a British naturalist whose major research interests involved the embryological development of marsupials and monotremes, dismissed the question as insignificant. Although the problem had not at that time been adequately resolved, he did not consider it worth his time to investigate the question.[95]

With the establishment of Buffon's two-stage model of marsupial reproduction and the rejection of the analogy between pouch young and embryos, the major scientific controversy about marsupial reproduction ended. Theorists had developed an explanation which was consistent with existing theory and adequately accounted for the empirical evidence.

Nevertheless, the belief that the young were bred at the teats was never entirely abandoned by laymen. The idea was common among primitive peoples in America[96] and Australia.[97] Amateur naturalists in Australia could never reconcile their observations of pouch young with the scientists' assertion that the young originated in the uterus as in other mammals. Thus, Australian colonist Lockhart Morton, publishing under the pseudonym "An Old Bushman," wrote in the Yeoman in 1861,

> . . . there are the strongest possible reasons for believing that the young are not placed in the pouch, as is commonly supposed, but actually come into existence there. I think the commonly received notion, that the marsupials give birth to their young, and then place them within the pouch to be nursed, is about the most absurd idea that can be entertained. I believe that the offspring of such animals have their origin in the pouch, and are never born at all as other animals. I can conceive it possible for the young to be born and placed in a pouch by the mother; but when I find, as I have hundreds of times done, that the young in the pouch are little bigger than flies and that they are firmly attached by their mouths to the teat, the skin of their body and the skin of the teat being without break, and that the young one cannot be detached from the teat without blood flowing from both, I cannot believe that the mother's instinct has anything to do with their position.[98]

Gerard Krefft, Director of the Australian Museum, complained that most members of the Zoological Society of New South Wales persisted in this erroneous belief.[99]

The belief still remains popular among some Australians who, unfamiliar with scientific theory, rely on their own field experience,[100] and Carl Hartman quotes a Texas frontiersman as follows:

> Zooligy perhaps is nearer right than any other science, but it seems to me its teachers are behind on some variety of snakes as well as some varietys of animals, one of which is the opossom. Though science contradict my theory, I cant surrender an experimental truth, that the opossom delivers its young direct from the womb into the pocket through the old teet. The little fellows bringing a new teet from the womb in its mouth, which it never turns loose while it stays in the pocket. . . . The borning process is very slow, perhaps two weeks making their exit

> from the womb into the pocket. I have seen the little fellows when they were only half borned their hind parts in the pocket while their fore parts were yet in the womb. When they get too large for the pocket they are borned again into the wide world.[101]

Because it was consistent with a common-sense interpretation of their own experience, the belief persisted among amateur naturalists long after it had been abandoned by scientists. Laymen do not hold as conservatively to the regularities of natural law nor are they as personally committed to existing scientific theories as are members of the scientific community. These differences can lead laymen into error (as in the case of marsupial reproduction) or can permit them to perceive facts which the scientific community cannot accept (as in the case of platypus eggs, discussed in Chapter V).

NOTES

[1] Pietro Martire d'Anghiera, Libretto de tutta la navigatione. Angelo Trevigliano, transl. (Paris: Honoré Champion, 1929. [Facsimile of Venice: 1504 edition]) p. 29.

[2] For example, Francisco Hernández stated, "Raro porcierto yadmirable artifico denaturaleza, yque jamas se a visto en otro animal enel mundo." Francisco Hernández, Quatro libros. De la naturaleza y virtudes de las plantas, y animales, Francisco Ximenez, transl. (Mexico: en casa de la viuda de Diego Lopez Davalos, 1615) p. 188.

[3] ". . . quod [illud animal] natos iam filios aliò gestat, quocunque proficiscatur, utero exteriore in modum magnae crumenae . . ." Pietro Martire d'Anghiera, De rebus oceanicis & orbe novo decades tres (Basileae: apud Ioannem Bebelium, 1533) p. [21^r].

[4] Conrad Gesner, Historiae animalium. Lib. I. de quadrupedibus viviparis. (Tiguri: apud Christ. Froschoverum, 1551) p. 982.

[5] Joachim Camerarius the Younger, Symbolorum & emblematum ex animalibus quadrupedibus desumtorum centuria altera collecta ([Nuremberg: P. Kaufman], 1595) p. 59^v.

[6] Ulisse Aldrovandi, De quadrupedibus digitatis. (Bologna: Printed by Nicolaus Tibaldinus for Antonius Bernia, 1637) p. 224.

[7] "Quaternos quinosue parit catulos, quos uteros conceptos . . . " Francisco Hernández, Nova plantarum, animalium et mineralium mexicanorum historia (Romae: sumtibus B. Deversini & Z. Masotti, typis V. Mascardi, 1651) p. 330.

[8] ". . . in quem [folliculum], cum primum editi sunt, ingressi foetus, singuli singulis uberibus adhaerent . . . " José de Anchieta, "Epistola quamplurimam rerum naturalium" in Academia das Sciencias de Lisboa, Colleção de noticias para a historia e geografia das nações ultramarinas (Lisboa: Typografia da mesma academia, 1812) I, num. 3, p. 151.

[9]". . . hace cueva donde mora y donde cria sus hijos, tiene una bolsa entre los pechos y la barriga donde mete sus hijuellos . . . " Bernardino de Sahagún, Historia general de las cosas de Nueva España. Angel Maria Garibay, ed. (Mexico City: Editorial Porrua, 1956) III, p. 229.

[10]Pedro Magalhães de Gandavo, The histories of Brazil. John B. Stetson, Jr., transl. (New York: the Cortes Society, 1922) II, p. 59.

[11]Carl G. Hartman, Possums (Austin: University of Texas Press, 1952), p. 120.

[12]Ibid., p. 90.

[13]Although some sixteenth-century writers used the Latin "uterus" to refer to the pouch, they did not mean to imply that the pouch was equivalent to an external uterus. For example, Trevigliano used the words "venter" and "uterus" interchangeably (Decades, p. [21^r] and Libretto, p. 29) as did Gesner (op. cit., pp. 981-982). Although both words can be used to refer to the womb, they have a more general meaning of "belly" or "paunch." Both authors clearly refer to the placement of the young in the pouch after birth.

[14]"Haec bursa ipse uterus est animalis, nam alium non habet, uti ex sectione illius comperi: in hac semen concipitur & catuli formantur . . . in ea tamdiu retinentur donec ipsi sibi victum quaerere possunt; interea tamen interdum progrediuntur foras & iterum ingrediuntur." Georg Marggraf, "Historiae rerum naturalium Brasiliae" in Willem Piso and Georg Marggraf, Historia naturalis Brasiliae (Lugdun. Batavorum: Apud Franciscum Hackium; Amstelodami: Apud Lud. Elzevirium, 1648) p. 223.

[15]François Pelsaert, as quoted in Gilbert P. Whitley, Early history of Australian zoology (Sydney: Royal Zoological Society of New South Wales, 1970) pp. 10-11. [First published in Nieuwe en vermeerderde ongeluckige Voyagie (Tot Amsterdam: Voor Jan Jansz, 1648)].

[16]Willem Piso, De Indiae utriusque re naturali et medica libri quatuordecim (Amstelodami: apud Ludovicum et Danielem Elzevirios, 1658) p. 323.

[17]The claim that the male opossum possessed a pouch in which he could carry the young also appeared in [Louis de Poincy], The history of the Caribby-Islands. John Davies, transl. (London: Thomas Dring and John Starkey, 1666 [first published, 1658]) p. 70.

[18]Joannes Jonstonus, Historiae naturalis de quadrupetibus [sic] (Francofurti and Moenum: impensis haeredum Math. Meriani, [1650]) p. 137.

[19]Magalhães de Gandavo, op. cit., p. [22^{v}].

[20]"Sequitur jam singulare illud admirabile, quo Animal isthoc ab aliis omnibus cujuscunque generis sunt distinguitur, nimirum marsupium illud seu uterus apertus in quem foetus postquam editi sunt recipit . . ." John Ray, Synopsis methodica animalium quadrupedum et serpentini generis (London: S. Smith and B. Walford, 1693) p. 184.

[21]Ibid., p. 184.

[22]"Horum Animalium si nobis copia facta foret, de processu generationis in viviparis é crebra uteri inspectione certius aliquid disceremus: Siquidem, si Marcgravio fides, in his uterus non intra corporis truncum reductus, sed extrorsum situs & visui expositus est." Ibid., p. 185.

[23]Edward Tyson, "Cariguey, seu marsupiale Americanum, or, the anatomy of an opossum," Royal Society of London. Philosophical Transactions XX (1698) pp. 105-164.

[24]Ibid., p. 116.

[25]Ibid., p. 107.

[26]Hartman, op. cit., p. 83.

[27]Tyson, op. cit., p. 123.

[28]George Stuart Carter, Structure and habit in vertebrate evolution (Seattle: University of Washington Press, 1967) pp. 417-418.

[29]Tyson, op. cit., p. 119.

[30] *Ibid.*, p. 124.

[31] The significance of the marsupial bones, double uterus, forked glans, and other anatomical peculiarities noted by Tyson, Cowper, and later investigators did not become apparent until the nineteenth century. Their role in influencing Blainville's revision of the mammalian system of classification will be discussed in Chapter III.

[32] Tyson, *op. cit.*, p. 109.

[33] Carter, *op. cit.*, pp. 455, 458.

[34] G. B. Sharman, "Reproductive physiology of marsupials," *Science* CLXVII (1970), p. 1223.

[35] Tyson, *op. cit.*, p. 142.

[36] William Cowper, "Carigueya, seu marsupiale Americanum masculum or the anatomy of a male opossum," *Royal Society of London. Philosophical Transactions* XXIV (1704), p. 1582.

[37] Sharman, *op. cit.*, p. 1223.

[38] Carl Hartman, "Traditional beliefs concerning the generation of the opossum," *Journal of American Folk-lore* XXXIV (1921) pp. 321-322.

[39] Cowper, *op. cit.*, p. 1585.

[40] C. W. Bodemer, "History of the mammalian oviduct" in E.S.E. Hafey and R. J. Blandau, eds., *The mammalian oviduct* (Chicago and London: University of Chicago Press, 1969) p. 13.

[41] Elizabeth B. Gasking, *Investigations into generation 1651-1828* (London: Hutchinson & Co., 1967) p. 24.

[42] F. J. Cole, *Early theories of sexual generation* (Oxford: Clarendon Press, 1930) p. 162.

[43] *Ibid.*, p. 163.

[44]Gasking, *op. cit.*, p. 52.

[45]Cole, *op. cit.*, p. 165.

[46]Bodemer, *op. cit.*, p. 15.

[47]Cole, *op. cit.*, p. 174.

[48]Cowper, *op. cit.*, p. 1585.

[49]*Ibid.*, p. 1577.

[50]Edward Tyson, "Some further observations of the opossum," *Royal Society of London. Philosophical Transactions* XXIV (1704), pp. 1573-1574.

[51]Robert Beverley, *The history and present state of Virginia.* Louis B. Wright, ed. (Chapel Hill, N.C.: University of North Carolina Press, 1947 [Reprint of London: R. Parker, 1705]) p. 154.

[52]John Lawson, *A new voyage to Carolina.* Hugh Talmage Lefler, ed. (Chapel Hill: University of North Carolina Press, 1967) p. 125.

[53]John Brickell, *The natural history of North-Carolina* (Raleigh: Reprinted by authority of the Trustees of the public libraries, 1911 [Reprint of Dublin: 1737]) p. 125. William Byrd, *Natural history of Virginia, or the newly discovered Eden.* R. C. Beatty and William J. Mulloy, transl. (Richmond, Virginia: Dietz Press, 1940) pp. 55, 157. This work, attributed to William Byrd, is actually a translation of Samuel Jenner, *Neu-gefundenes Eden* (N.p.: Helvetischen Societät, 1737). See Percy G. Adams, *Travelers and travel liars 1600-1800* (Berkeley and Los Angeles: University of California Press, 1962) pp. 144-145.

[54]William Byrd, *William Byrd's histories of the dividing line betwixt Virginia and North Carolina.* William K. Boyd, ed. (Raleigh: The North Carolina Historical Commission, 1929) p. 248. This account was probably completed in 1738 but was not published until 1841.

[55]François Valentijn as quoted in Albertus Seba, *Locupletissimi rerum naturalium thesauri* (Amstelaedami: J.

Wetstenium, & Gul. Smith, & Janssonio-Waesbergios, 1734) I, pp. 64-65.

[56]"[H]abent enim haec Animantia, aeque ac feles, canes & ejusmodi, partes, generationi servientes, intra abdomen." Ibid., p. 65.

[57]Ibid., p. 57.

[58]John Hill, An history of animals (London: Thomas Osborne, 1752) p. 530.

[59]Johann Daniel Meyer, Angenehmer und nützlicher Zeitvertreib (Nürnberg: Johann Joseph Fleischmann, 1756) III, pp. 2-3.

[60]Peter Simon Pallas, Miscellanea zoologica (Hagae Comitum: Apud Petrum van Cleef, 1766) p. 61.

[61]Folkes, ["Observation et description de l'animal appelé opossum"], Académie des Sciences. Paris. Histoire de l'académie royale des sciences (1746) p. 38.

[62]Lieut. Dumont de Montigny, Mémoires historiques sur la Louisiane (Paris: Cl. J. B. Bauche, 1753) pp. 84-85.

[63]Mark Catesby, The natural history of Carolina, Florida and the Bahama Islands (London: Printed for Charles Marsh, Thomas Wilcox and Benjamin Stichall, 1754 [First published, 1731]) I, p. xxix.

[64]"[O]n peut présumer avec beaucoup de vraisemblance, que dans ces animaux la matrice n'est, pour ainsi dire, que le lieu de la conception, de la formation & du premier développement du foetus, dont l'exclusion étant plus précoce que dans les autres quadrupèdes, l'accroisement s'achève dans la bourse où ils entrent au moment de leur naissance prématurée." Georges Louis Leclerc, comte de Buffon, Histoire naturelle, générale et particulière (Paris: De l'Imprimerie Royale, 1763 [Landmarks of Science Microprint]) X, p. 304.

[65]Sharman, op. cit., p. 1224.

[66]"[C]e n'est donc pas de la commodité ou secours que la poche prête aux petits que dépend uniquement l'effet

de la longue adhérence aux mamelles, non plus que celui de leur accroissement dans cette situation immobile; je fais cette remarque afin de prêvenir les conjectures que l'on pourroit faire sur l'usage de la poche, en la regardant comme une seconde matrice, ou tout au moins comme un abri asolument [sic] nécessaire à ces petits prématurément nés." Ibid., pp. 305-306.

67 Jacques Christophe Valmont de Bomare, ed., Dictionnaire raisonné universel d'histoire naturel (Yverdon: n.p., 1768 [Landmarks of Science Microprint] [First published, 1764]) p. 91.

68 Thomas Pennant, Synopsis of quadrupeds (Chester: Printed by J. Monk, 1771) p. 205; also, Arctic zoology (London: Printed for Robert Faulder, 1792) I, p. 84.

69 Innocente Alessandri & Pietro Scattaglia, Animali quadrupedi (Venezia: All'Insegna delle B.V. della Pace, 1773) III, p. [D2r].

70 Oliver Goldsmith, An history of the earth, and animated nature (London: J. Nourse, 1774 [Landmarks of Science Microprint]) IV, p. 245.

71 "[J]e suis persuadé que ces animaux mettent bas peu de jours après la conception, & que les petits au moment de l'exclusion ne sont encore que des foetus qui, même comme foetus, n'ont pas pris le quart de leur accroissement; l'accouchement de la mère est toujours une fausse-couch très-prématurée, & les foetus ne sauvent leur vie naissante qu'en s'attachant aux mamelles sans jamais les quitter jusqu'à ce qu'ils aient acquis le même degré d'accroissement & de force qu'ils auroient pris naturellement dans la matrice si l'exclusion n'eût pas prématurée." Buffon, op. cit., X, p. 337.

72 Ibid., p. 305.

73 Sahagún, op. cit., III, p. 229.

74 Folkes, op. cit., p. 38.

75 Seba, op. cit., I, p. 65.

[76]Hartman, *op. cit.*, p. 93.

[77]*Ibid.*, p. 113.

[78]"[O]n voyait au bout des mamelons de petites bosses claires, dans lesquelles on trouvoit l'embryon ébauché." Georges Louis Leclerc Comte de Buffon, *Histoire naturelle, générale et particulière* (Paris: De l'Imprimerie Royale, 1782) XII, p. 25.

[79]*Ibid.*, p. 27.

[80]Louis Jean Marie Daubenton in Buffon, *op. cit.*, first edition, 1763, X, p. 324.

[81]Buffon, *op. cit.*, 1782, XII, pp. 27-28.

[82]François Jean, Marquis de Chastellux, *Travels in North America in the years 1780, 1781 and 1782.* Howard C. Rice, transl. and ed. (Chapel Hill: The University of North Carolina Press, 1963) II, pp. 463-464.

[83]François-Marie, comte d'Aboville, as quoted in *ibid.*, p. 468.

[84]Etienne Geoffroy Saint-Hilaire, "Mémoire sur cette question: Si les animaux à bourse naissent aux tétines de leur mère," *Journal complémentaire des sciences médicales* III (1819) p. 198.

[85]*Ibid.*, p. 203.

[86]G. L. Duvernoy, "Note sur la dissection de deux femelles de Didelphe manicou, *Didelphis Virginiana*," *Société Philomathique de Paris. Bulletin* III (1803) p. 160.

[87]Geoffroy, *op. cit.*, p. 205.

[88]*Ibid.*, p. 199.

[89]*Ibid.*, pp. 201-202.

[90]*Ibid.*, p. 204.

[91] *Ibid.*, p. 202. Geoffroy used his theory to explain the parallel between various marsupial families and placental orders.

[92] "En Europe, où nos opinions sont réglées *à priori* par ce qui se passe sans cesse sous nos yeux, et où, pour ce motif, nos théories sur la génération ont quelque chose d'arrêté, nous avons profité d'un certain vague qui régnait dans les observations que les voyageurs nous ont communiquées, au sujet des animaux à bourse, pour, dissimulant quelques faits et exagérant quelques autres circonstances, ramener le mode de génération de ces animaux à une mesure commune." *Ibid.*, p. 194.

[93] John Morgan, "A further description of the anatomy of the mammary organs of the kangaroo," *Linnean Society of London. Transactions* XVI (1833) pp. 458-460.

[94] Richard Owen, "On the generation of the marsupial animals, with a description of the impregnated uterus of the kangaroo," *Royal Society of London. Philosophical Transactions* CXXIV (1834) p. 345.

[95] William H. Caldwell, "On the development of the monotremes and Ceratodus," *Royal Society of New South Wales. Journal* XVIII (1884) p. 121.

[96] Jean Baptiste Dutertre, as quoted in Hartman, *op. cit.*, p. 91.

[97] H. C. Raven, "Strange animals of the island continent," *Natural History* XXIX (1929) p. 94.

[98] Quoted in V. M. Coppleson, "The life and times of Dr. George Bennett," *University of Sydney. Post-Graduate Committee in Medicine. Bulletin* II (1955) p. 248.

[99] Gerard Krefft, "Zoological Society of New South Wales," *Krefft's Nature in Australia* I (1877) p. 4.

[100] Ellis Le G. Troughton, *Furred animals of Australia* (Sydney and London: Angus and Robertson Ltd., 1943) p. 14.

[101] Quoted in Hartman, *op. cit.*, p. 91.

Chapter III

BONES OF CONTENTION

In the early part of the nineteenth century, marsupials (or rather animals alleged to be marsupials) presented a new challenge to accepted theoretical explanations. The discovery of mammalian fossils from the European Mesozoic was greeted with astonishment because, according to accepted paleontological theory, mammals did not appear until much later in the fossil record. The theoretical significance of the discovery and its impact on the development of paleontology must be understood of the context of the major theoretical debates within nineteenth-century paleontology.[1]

At the beginning of the nineteenth century, paleontology was a very young discipline. Before biologists could begin to understand the fossil record, they had to have a method of identifying species from the few fragmentary remains which had been fossilized and preserved. Georges Cuvier provided just such a tool by developing new principles and methods of comparative anatomy. The revolutionary new methodology revealed a startling array of strange animal forms, and paleontologists gradually began to piece together the history of life on earth. Paleontological theory was in a state of flux, as theorists tried to develop an explanatory framework which could accommodate the flood of new information which was being unearthed. The establishment of paleontology as a science during the early years of the nineteenth century laid the groundwork for a theory of organic development through time which, in turn, contributed to the formulation of the Darwinian theory of evolution.

Confronted with a wealth of new and often apparently contradictory data, paleontologists were divided with respect to a number of critical issues: notably, whether geological change was directional, whether organic change was directional, and whether progressive organic changes could be explained with reference to changes in the physical environment, God's design, or natural law. Theories about the history of life on earth were necessarily linked to theories about the physical history of the earth because animals are necessarily affected by the nature of the environment in which they live. One school of thought (the geological progressionists) maintained that environmental change had been progressive. Whether they attributed the changing conditions to a retreating ocean, a cooling earth, or an increase in the amount of atmospheric oxygen, all geological progressionists agreed that the past physical environment was considerably different from the present one and that geological change had been cumulative and directional. The geological uniformitarians, on the other hand, denied that environmental change had been progressive. While recognizing the importance of geological change in transforming the surface of the earth, the uniformitarians argued that these changes had been fluctuating, not directional.

As paleontologists began to decipher the fossil record, a pattern emerged. The new fossil discoveries revealed a gradual progression in the history of life. The lowest vertebrate class (fishes) appeared first, followed by reptiles and birds and finally, mammals. Geological progressionists could easily explain these progressive organic changes by appealing to the principle of adaptation. Biologists believed that each animal was ideally suited to live in the environment it inhabited, so directional environmental change necessarily implied directional organic change.

For the geological uniformitarians, on the other hand, the apparent progression in the fossil record was more difficult to explain. According to the principle of adaptation, fluctuating environmental changes should be accompanied by fluctuating organic changes. Accordingly, some geological uniformitarians were also organic uniformitarians (for example, Charles Lyell). Organic uniformitarians assumed that all the major taxonomic groups (the most advanced, as well as the most primitive) existed from the very earliest beginnings of life on earth, and they attributed any appearance of progressive organic change to the imperfection of the fossil record.

There were other theorists, however, who adopted a progressionist view of the history of life while at the same time advocating a uniformitarian view of geological change. To support this theory, paleontologists needed a mechanism for organic change which was not dependent on geological change. Two major alternatives were proposed: divine miracle and evolution.

Transcendentalists such as Louis Agassiz interpreted organic progression as evidence of the successive miraculous creation of increasingly complex animal forms, culminating in the crowning glory of creation, man. Denying a direct connection between organic and physical changes, Agassiz argued that organic progress revealed the gradual unfolding of the Divine plan of creation. It was dependent upon (and evidence of) the wisdom and foresight of the Creator.

Agassiz believed that each new species was directly created by God, but other equally devout theorists believed that God operated through natural law rather than miracle. Robert Chambers, for example, believed that God had endowed life with a natural creative force so that higher forms evolved from lower forms as a result of the regular operation of natural law. According to Chambers, evolution was a result of God's rational and benevolent design. Organic progression was stripped of its theological significance only after the Darwinian theory rejected the concept of design in nature and postulated a mechanistic model of evolutionary development.

The theoretical conflicts of nineteenth-century paleontology cannot be interpreted (as they sometimes have been) as a simple struggle between evolutionists and anti-evolutionists, another battle in the warfare between religion and science. Rather, they presented a kaleidoscope of shifting theoretical perspectives as paleontologists attempted to construct a scientific theory which would adequately account for both the geological and the paleontological evidence.

With the discovery of the earliest primitive mammals, theories regarding the role of marsupials in the economy of nature were linked with the important problem of the origin of mammals. The Mesozoic "marsupials" were of crucial theoretical significance because they did not fit comfortably within any of the generally accepted theories. The anomaly forced biologists either to discredit the discovery or to attempt to find an interpretation consistent with their own theoretical views.

At first paleontologists were unwilling to accept evidence which violated their theoretical preconceptions. They attempted to discredit the discovery by arguing firstly that the fossils were not as old as had been claimed and secondly that the fossils were reptilian rather than mammalian. In this instance, the empirical evidence was available in Europe, so questions of fact were resolved more quickly and more satisfactorily than was the case with American or Australian marsupials. Once it was firmly established that the bones did belong to Mesozoic mammals, paleontologists were forced to adjust their theories to accommodate them.

For those theorists who denied organic progression, the early appearance of mammals neatly fitted their theoretical predictions. According to this view, paleontologists should expect to find some examples of even the most highly organized taxonomic groups at very early periods. The Mesozoic mammals appeared to discredit progressionist theories and were very influential in inspiring and sustaining Charles Lyell's theory of organic uniformitarianism.

For organic progressionists, on the other hand, the significant fact was that the earliest mammals were primitive in organization. The Mesozoic mammals were identified (erroneously) as marsupials, and taxonomists classified the marsupials among the most primitive mammals. Progressionists could then argue that the fossil record revealed a gradual progression within the class of mammals from primitive groups (monotremes and marsupials) to the more advanced groups (placentals). This argument could be linked to a theory of geological progression (as it was when William Buckland first proposed it) or it could be regarded as independent of progressive environmental change (as in Robert Chambers' revised theory).

After the acceptance of the Darwinian theory, this progressionist view of mammalian development served to provide Darwinists with a hypothetical path of mammalian evolution. Despite the evident lack of paleontological evidence, biologists postulated a phylogenetic succession from reptile to monotreme to marsupial to placental. In the historical discussion which follows, the reader will need to be somewhat familiar with the geological eras listed on the chart on the following page. The chart represents modern geological knowledge, and many of the names and dates were not established until after the period under discussion.

Very early in Georges Cuvier's paleontological investigations, it became apparent that mammals occurred relatively late in the fossil record. Cuvier, in the Discours préliminaire to his Recherches sur les ossemens fossiles (1812), observed that the oviparous quadrupeds (reptiles) appeared in the fossil record earlier than the viviparous quadrupeds (mammals). Noting that numerous reptilian remains from the Jurassic demonstrated the existence of land at that time, he claimed that, nevertheless, no mammals were to be found beneath the layer of chalk which marked the boundary between the Mesozoic and Cenozoic. Marine mammals appeared immediately above the chalk; terrestrial mammals somewhat later.[2]

Cuvier interpreted this evidence according to his theory that the earth had undergone successive catastrophes in which existing continents had been inundated and parts of the ocean floor lifted up to form new continents. Thus, he argued that

> There is every reason to conclude that these animals [viviparous land quadrupeds] have only begun to exist, or

GEOLOGICAL ERAS

ERA	SYSTEM	SERIES (EPOCH)	STAGE
Cenozoic *Age of Mammals*	Quaternary	Recent Pleistocene	——
	Tertiary	Pliocene Miocene Oligocene Eocene Paleocene	——
Mesozoic (Secondary) *Age of Reptiles*	Cretaceous	——	——
	Jurassic	Malm	Portlandian (inc. Purbeckian Kimmeridgian Oxfordian (inc. Corallian)
		Dogger	Callovian Bathonian (inc. Upper Oolite) Bajocian (inc. Middle Oolite) Aalenian (inc. Lower Oolite)
		Lias	Toarcian Charmouthian Senemurian Hettangian
	Triassic	——	——
Paleozoic *Age of Fishes*	Permian Carboniferous Devonian Silurian Ordovician Cambrian	——	——
Proterozoic	Precambrian	——	——

> at least to leave their remains in the strata of our earth, since the last retreat of the sea but one and during that state of the world which preceded its last irruption.[3]

Peter J. Bowler has suggested that Cuvier may have thought of mammals as the first animals adapted to a purely terrestrial habitat. This would have been consistent with the fossil record as Cuvier knew it, for all the Mesozoic reptiles then known (with the exception of the flying *Pterodactylus*) were either aquatic or amphibious.[4] Thus, Cuvier's early paleontological work could have been used to support either the late appearance of terrestrial animals or the late appearance of mammals.

The discovery of mammalian jaws in the Mesozoic strata of Stonesfield, Oxfordshire, challenged generally accepted belief. In 1812 or 1814 a stonemason brought the amateur naturalist, William John Broderip, two fossil mammalian jaws from the Stonesfield slate. Broderip immediately consulted William Buckland, and both men concluded that the fossils were definitely mammalian.[5] However, they wanted further confirmation before publishing a discovery which violated a basic consensus among geologists. In 1818 Cuvier examined one of the fossils (*Amphitherium prevostii*) and pronounced it a marsupial.[6]

English geologists, following the theory that Mesozoic marine animals were succeeded in the Tertiary by creatures adapted to a newly formed terrestrial environment, found the discovery anomalous not only because the fossils were mammalian, but also because they were terrestrial. W. D. Conybeare and William Phillips, announcing the discovery in 1822, indicated:

> We here find the only known instance in which the remains of birds and terrestrial animals have been found in beds of antiquity at all approaching to these; they here occur mingled with winged insects, amphibia, sea shells, and vegetables, presenting at once the most interesting and difficult of problems connected with the distribution of organic remains.[7]

Similarly, in 1824 Buckland noted the fossil as "a case hitherto unique in the discoveries of geology; viz. that of the remains of a land quadruped being found in a formation subjacent to chalk."[8] In the same article Buckland listed the remains of a whale among the Stonesfield fossils.[9] Although the reported discoveries of whale remains from various Mesozoic formations were later identified as belonging to a reptile, Cetiosaurus,[10] Buckland accepted Cuvier's earlier mammalian identification without surprise. The appearance of marine mammals in the Mesozoic would have been consistent with his theory that the late appearance of terrestrial mammals was due to existing physical conditions on land.

Among the Stonesfield fossils, Buckland identified the remains of a "great fossil lizard," actually the first dinosaur. As continued research disclosed the remains of more terrestrial animals in the Mesozoic beds, the supposed progression from aquatic animals in the Mesozoic to terrestrial animals in the Tertiary was abandoned. New explanations emphasized the predominance of reptiles in the Mesozoic and mammals in the Tertiary. But the Stonesfield mammals still did not fit the pattern, and theorists were quick to challenge the evidence.

French geologist Constant Prévost argued that one should be careful about placing too much weight on a single anomalous discovery. When a fact such as the appearance of mammals in the Mesozoic violated generally accepted principles, it should not be accepted without minute investigation.[11] Prévost's argument was the first of a series of attacks on the validity of the Mesozoic mammals. At first, critics claimed the fossils were Tertiary; later they claimed they were not mammals at all.

In 1824 Prévost was able to provide drawings of the Stonesfield fossil from which Cuvier reconfirmed its mammalian nature, concluding,

> . . . if this animal is truly from the Stonesfield slate, it is a notable exception to the rule otherwise so general, that beds of this antiquity do not contain the remains of mammals.[12]

Personal examination of the Stonesfield fossils, combined with the authority of Cuvier's identification, convinced Prévost of their mammalian nature. He could therefore preserve the rule of the late appearance of mammals only by demonstrating that the fossils were Cenozoic rather than Mesozoic. He must show either that the fossils were introduced into fissures in the oolitic strata at a later period, or that the Stonesfield beds were not as old as had been claimed. He chose the latter alternative, despite the fact that Conybeare and Phillips had already examined this possibility and concluded that

> the beds themselves are also most clearly to be traced holding a regular course together with the superior and inferior beds of this oolitic system, and cannot therefore be considered as a local, overlying, and recent deposit.[13]

French geologist J. Desnoyers supported their claim.[14]

Prévost rejected the Mesozoic mammals precisely because they were anomalous; the Stonesfield fossils were the first mammalian remains to be found beneath the chalk.[15] Moreover, Gideon Mantell and Buckland had both alluded to the similarity between the Stonesfield fossil remains and those of the much later (although still Mesozoic) Tilgate Forest beds.[16] Prévost noted that this violated yet another general principle, being the first instance in which widely separated beds contained the same fossils while those in between contained different fossils.[17] Prévost concluded that the identification of the Stonesfield beds as Mesozoic was not proven.[18]

In 1827 Prévost's objections were answered and the existence of Mesozoic mammals strongly confirmed. Broderip, the naturalist who first called attention to the Stonesfield fossils, relocated a specimen he had lost. The fossil not only proved to be that of a mammal, it also belonged to a second genus, allegedly marsupial.[19]

In the same journal, the English geologist William Henry Fitton silenced all doubts concerning the geological position of the Stonesfield beds. After conducting a detailed analysis of the English beds, Fitton concluded that the Stonesfield slate definitely belonged among the Mesozoic strata of the English oolite. He noted that the age of the Stonesfield beds was challenged solely because the fossil remains were anomalous. The positions of other beds, determined by similar methods, remained unchallenged.[20]

The failure of existing paleontological theories to account for the Mesozoic mammals led Charles Lyell to search for a new theory to explain the fossil record. Lyell's early views concerning the Stonesfield fossils are especially interesting because the bones were later influential in his rejection of progressionism. In 1826, Lyell accepted the paleontological evidence for a gradual progression in complexity as one ascends from the lowest to the more recent strata, beginning with the simplest forms of organization and ending with those animals most closely related to man.[21] The Stonesfield "marsupials," however, offered a notable exception. Lyell claimed that the unwillingness of Continental naturalists to accept the Mesozoic mammals far exceeded the bounds of caution. Prévost, who did not himself examine all of the English oolitic sites, could not appreciate the minute correspondences which confirmed the geological identification of the Stonesfield beds.[22] Further, Lyell argued that the Stonesfield fossils were not really as anomalous as many imagined. The existence of marine mammals in the Mesozoic was indicated by reports of whale remains found in various beds.[23] One could not, therefore, argue for the late appearance of mammals. Furthermore, the recent discoveries of terrestrial reptiles negated the theory of the late appearance of terrestrial animals. If marine mammals existed in the Mesozoic, it was not improbable that terrestrial mammals also existed at that time. Few had yet been discovered because nearly all Mesozoic formations were entirely marine.[24] Lyell concluded that mammals, the most perfect class of animals, had existed from a distant, although not from the most remote, period in the earth's history,[25]

While geologists were establishing the existence of the Mesozoic mammals as an exceptional fact demanding explanation, Charles Lyell reversed his position on progression. In 1830, with the publication of the first volume of the Principles of Geology, Lyell launched a major attack against catastrophism and progressionism. Lyell's new theoretical arguments were motivated, at least in part, by a desire to combat early evolutionary theories.[26] Whereas in 1826 he had regarded the Mesozoic mammals as an exception to the general rule, in 1830 he used the Stonesfield fossils as evidence against progression. In the early nineteenth century, the theory of the successive progression of the animal and vegetable world from the simplest to the most perfect forms was explained in connection with progressive changes in the physical history of the earth. Lyell, adopting a strict uniformitarian view in both geology and paleontology,[27] claimed that neither the environment nor the plants and animals living within it had experienced directional change through time. He argued that the appearance of progression in the fossil record was due to accidents of preservation, particularly the predominance of marine deposits in the Mesozoic. The cetacea and marsupials of the Mesozoic were, Lyell claimed, positive proof that a varied population of mammals, the highest class of vertebrates, existed far earlier than most progressionists wished to acknowledge. Lyell asserted,

> The occurrence of one individual of the higher classes of mammalia, whether marine or terrestrial, in these ancient strata, is as fatal to the theory of successive development, as if several hundreds had been discovered.[28]

Lyell pointed to the apparent absence of mammals in the Cretaceous as an example of the dangers of forming generalizations on the basis of negative evidence. In comparing the English Cretaceous beds with those of the early Jurassic,

> . . . we find the supposed order of precedence inverted. In the more ancient system of rocks, mammalia, both of the land and sea, have been recognized, whereas in the newer, if negative evidence is to be our criterion, nature has made a retrograde, instead of a progressive, movement, and no animals more exalted in the scale of organization than reptiles are discoverable.[29]

Of course Lyell wished the reader to conclude that the general appearance of progression in the fossil record was as illusory as this example of apparent regression.

The Stonesfield discoveries exerted considerable influence on Lyell's thinking, for the existence of two separate genera of mammals suggested the presence of a varied mammalian fauna.[30] Moreover, the Mesozoic mammals provided dramatic evidence in favor of biological uniformitarianism. Lyell was able to transform an anomaly into an argument in favor of his theory.

Although Lyell capitalized on the Mesozoic mammals as evidence for uniformitarianism, for other geologists they remained uncomfortable exceptions to the general rule. Thus Gideon Mantell, describing the Mesozoic as the age of reptiles, concluded that the condition of the earth at that time was quite different and probably unfit for the habitation of animals of a more perfect organization. He added, "the occurrence of terrestrial mammalia in beds of this ancient epoch has not been satisfactorily explained."[31] Four years later, he claimed that the fossils did not invalidate any geological principle but only proved that viviparous animals appeared earlier than had been supposed.[32]

The issue was further complicated by the discovery of fossilized footprints from the New Red Sandstone. The animal, whose tracks roughly resembled the shape of a human hand, was named Chirotherium.[33] Early investigators, noting the opposable thumbs, assigned it to the marsupials.[34] If valid, the discovery would have pushed the origin of mammals even further back towards the beginning of the Mesozoic. However, Robert Grant, in a nicely argued article, demonstrated that the shape of the foot and the gait proved the animal to be reptilian.[35] (It is now identified as an amphibian.)

The Mesozoic mammals remained a problem for the progressionists, particularly since they lacked an explanation for the long period of time from the middle Jurassic to the beginning of the Tertiary during which no fossil mammals had yet been found. Why were these two species of terrestrial mammals isolated in a period dominated by huge reptiles?[36] And why should marsupials, now isolated in the New World and Australia, precede the placentals in the geological record?

William Buckland's Bridgewater Treatise attempted to resolve these difficulties in a manner consistent with catastrophism. He attributed the scarcity of early mammalian remains to the scarcity and instability of the land during the earlier periods when the geological forces were more violent.[37] Buckland believed that all four major groups of animals (Cuvier's *embranchements*) were present at an early period, but conditions were unfavorable for the flourishing of mammals.

> . . . it is indeed true that animals and vegetables of the lower classes prevailed *chiefly* at the commencement of

> organic life, but they did not prevail exclusively; . . . it appears, that the more perfect forms of animals become gradually more abundant, as we advance from the older into the newer series of depositions: whilst the more simple orders, though often changing in genus and species, and sometimes losing whole families which are replaced by new ones, have pervaded the entire range of fossiliferous formation.[38]

While relying on the old explanation of adaptation to shifting environmental conditions, Buckland provided the foundations for a revolutionary new model of progression. He suggested that the class of mammals revealed a gradual increase in organic complexity through time. Buckland proposed that marsupials should appear in the geological record before placentals because of their inferior degree of organization. ". the Marsupial Order, so far from being of more recent introduction than other orders of mammalia, is in reality the first and most ancient condition, under which animals of this class appeared upon our planet."[39]

In linking the early appearance of marsupials to their inferior development, Buckland made use of recent advances in taxonomy and comparative anatomy. In 1816 Blainville had established the inferiority of the marsupial reproductive system as a basis for a taxonomic division between two major groups of animals, Monodelphs (placentals) and Didelphs (marsupials and monotremes.)[40] In 1834 Blainville further refined this classification, separating the marsupials and monotremes into two separate subclasses, Didelphs and Ornithodelphs.[41] Blainville arranged his taxa in descending order of complexity from man through the other placentals to marsupials to monotremes. This serial arrangement, while affirming the inferiority of marsupials, did not necessarily suggest a paleontological progression.

Richard Owen's research of 1837 offered an anatomical justification for a progressive taxonomic arrangement. He noted that marsupials, lacking a corpus callosum, possessed a brain intermediate in structure between that of placentals and birds. This fact suggested to Owen that classifications which (like Blainville's) distinguished marsupials as a separate and peculiar group of mammals were more valid than those which (like Cuvier's) integrated them among the placentals.[42] Owen later developed his own progressive classification system based primarily upon brain structure.[43] The work of Blainville and Owen enabled Buckland to construct a new argument for progression, postulating a gradual increase in complexity within the class of mammals.

Buckland suggested that the inferiority of marsupials explained their presence in the Mesozoic beds, as well as accounting for the absence of placental remains.

> As this inferior condition of living Marsupialia shows this order to hold an intermediate place between viviparous and oviparous animals, forming, as it were, a link between Mammalia and Reptiles; the analogies afforded by the occurrence of the more simple forms of other classes of animals in the earlier geological deposites, would lead us to expect also that the first forms of Mammalia would have been marsupial.[44]

Thus Buckland, while supporting the older theory of a transition from marine animals to terrestrial animals, introduced the idea of a paleontological progression from marsupials to placentals. As we shall see, this idea became thoroughly established among progressionists, both evolutionary and anti-evolutionary, and strongly influenced their expectations and their interpretations of new discoveries.

To reinforce his position, Buckland quoted a letter from Owen who interpreted the fossil history of marsupials as evidence of the beneficent foresight of the Creator.

> With an organization defective in that part [the cerebrum] which I believe to be essential to the docility of the horse, and sagacity of the dog, it is natural to suppose that the Marsupial series of warm-blooded quadrupeds would be insufficient for the great purposes of the Creator, when the earth was rendered fit for the habitation of man. They do, indeed, afford the wandering savages of Australia a partial supply of food; but it is more than doubtful that any of the species will be preserved by civilized man on the score of utility.

Owen implied that marsupials, although intelligent enough to protect themselves against enemies no more intelligent than reptiles, were not fitted for survival among placentals.[45] This explanation, used by Owen to support a concept of divinely designed adaptation, was later adapted by Darwinists to provide support for the theory of natural selection.

From 1818, when Cuvier first identified the Stonesfield jaw as that of an opossum, few had questioned the mammalian nature of the fossil. Although Agassiz had at first believed that it might belong to a fish, upon examination he confirmed the mammalian identification.[46]

Attempts to associate the early appearance of marsupials with their primitive nature revived the controversy over the Stonesfield mammals. Thus, in 1838 Blainville renewed the assault, again denying the existence of mammals in the Mesozoic. The position of the Stonesfield beds being firmly established, Blainville chose to challenge the zoological identification. Working from published descriptions and drawings, he argued that the fossils were reptilian.[47]

Mammals have a differentiated dentition consisting of incisors, canines, and molars, the latter generally double-rooted and multicusped. Reptiles, on the other hand, have simple, conical teeth with single roots.[48] If this were universally true, then, Blainville conceded, at least one of the Mesozoic fossils was mammalian. If so, he believed it was more closely allied to the seals than to the opossums.[49] Blainville argued, however, that the recent discovery of a reptile (*Basilosaurus*) with differentiated, implanted, and double-rooted teeth put the problem in a new light. The Stonesfield fossils, he believed, were reptiles like *Basilosaurus*. He concluded that

> . . . the existence of the remains of mammals anterior to the tertiary strata, is not at all proved by the Stonesfield fossils on which we have now treated, although

> we are far from asserting that mammals were not in existence during the secondary period.[50]

Although Blainville was not the first to doubt the mammalian nature of the fossils, Cuvier's identification had previously aroused little controversy. Why, then, did the question suddenly become so significant? True, the established absence of mammals before the Tertiary would provide added support for the occurrence of a major catastrophe, followed by special creation. But catastrophists had, nevertheless, come to accept the existence of mammals in the Mesozoic. Now, however, the Mesozoic mammals posed a more serious threat. The connection, which Buckland wished to establish, between the inferior nature of marsupials and the first appearance of mammals provided a more powerful argument in favor of transmutation. The gradual increase in organic complexity through time suggested to some theorists the existence of a continuous series of fossil forms. According to the transmutationists, the higher mammals were derived from their earlier, more primitive progenitors by descent.

Blainville, in particular, was in a position to recognize this threat, as he himself had established the marsupials as a group intermediate between reptiles and placentals. The gradual appearance of a few marsupials, followed by the later appearance of the more perfect placentals, fitted neatly into an evolutionary interpretation of geological history. As we shall see, transmutationists were quick to seize on this argument.

Blainville's attempt to identify the fossils as reptilian may have been motivated by a desire to destroy this argument for transmutation. Certainly he was concerned about the problem, as the following remarks indicate.

> In effect, depending on whether these fossils belonged to a mammal, terrestrial or aquatic, placental or marsupial, or else to a reptile or a fish, one theory or another concerning the order of formation, or of creation, or of appearance of the species of animals on the surface of the earth follows. The theory of the gradual and insensible development in the complexity of animal organization, generally admitted without sufficient proof, will be disproved or confirmed.[51]

Blainville was specifically concerned about Etienne Geoffroy Saint-Hilaire's use of the Mesozoic mammals to support his own theory of transmutation. Blainville himself, while adopting a serial arrangement of the animal world into a single "chain of being," rejected the occurrence of progression in the fossil record. Blainville argued for a simultaneous and unique creation, attributing all subsequent changes to extinction.[52]

One must also remember that the correct identification of the Stonesfield fossils was nearly impossible in the context of early nineteenth-century biology. Once the fossils were acknowledged to be mammalian, investigators immediately concerned themselves with their identification as marsupials or placentals. Yet Blainville was perfectly correct that these creatures were neither marsupial nor placental insectivores.[53] The ancient Jurassic mammals, more primitive than modern mammals, retained some reptilian characteristics. Buckland's specimen (_Amphitherium prevostii_) was actually a pantothere, among the common ancestors of the marsupial and placental mammals of the Cretaceous and Cenozoic.[54] Although Blainville undoubtedly exaggerated the reptilian affinities to fit his own purposes, the progressionists were equally anxious to exaggerate the marsupial affinities.

In the hope that his critics might be persuaded by personal examination, Buckland took his specimen to Paris. Although Blainville was not in the city, other Franch biologists (notably Achille Valenciennes[55] and A.M.C. Dumeril[56]) were convinced that the fossils were mammalian.

Etienne Geoffroy Saint-Hilaire, under the pretext of reaffirming the absence of mammals in the Mesozoic, provided a novel interpretation which supported his theory of transmutation. Recalling his early taxonomic work on marsupials, he argued,

> Then I could not have suspected that the culmination of these works would be this profound thought, that these creatures are not truly mammals at all in the sense that this term is used in classification, and that it would be necessary to admit them to a different class, _sui generis_, which should be completed, perhaps, by the name _marsupiaire_.
> The new occurrence which has elucidated this is the discovery that some of these animals lived in the antediluvian period: now this result has recently aroused much discussion among naturalists. Marsupials, mistakenly taken for mammals, had broken a magnificent generalization . . . that mammals existed only in the beds of the Tertiary.[57]

Geoffroy claimed that, despite the evidence of the Stonesfield fossils and Cheirotherium, no mammals appear in the Mesozoic. The marsupials, pretended mammals, appeared at this stage in the progressive scale of animals and were later replaced by animals even more advanced. Geoffroy noted that this theory not only explained their early appearance in the geological record, but also resolved the problem as to why so few species are extant.[58]

Although Geoffroy's claim that marsupials were not mammals may seem to be an extreme measure adopted for the purpose of promoting his own theory of transmutation, the idea of a possible reclassification of marsupials based on their presence in the Mesozoic beds was previously suggested by Richard Owen. He argued that, should marsupials continue to be the only mammals found in the Mesozoic beds, they might be considered to be a distinct ovoviviparous sub-class of mammals.[59] Thus the appearance of marsupials in the Mesozoic reinforced their distinctness as a taxonomic group. At the same time, the connection between their inferior organization and their early appearance in the fossil record gave investigators a strong predisposition to identify all Mesozoic mammals as marsupials.

As controversy continued, other biologists joined Blainville in objecting to the Mesozoic "marsupials." Louis Agassiz reversed his former opinion[60] and, with Robert Grant,[61] added his support to Blainville's reptilian identification.

Blainville renewed the battle, again emphasizing the analogy between the Stonesfield fossils and *Basilosaurus*, allegedly a saurian with mammal-like dentition.[62] Duméril countered with the claim that the affinities of the *Basilosaurus* were as yet undetermined, but its vertebrae were similar to those of a cetacean.[63] William Ogilby, after a careful comparison between the Stonesfield fossils and existing marsupials and placental insectivores, contended that the fossils had so many important characters in common with mammals on the one hand and cold-blooded animals on the other that no definitive decision could be made as to which class they really belonged.[64]

Blainville concluded there was so much confusion surrounding the identification of these problematic fossils that they constituted an embarrassment to science

> since, by one party it is referred to the *Mammalia*, by another to the insectivorous monodelphs, or the *Amphibia*; and by a third to the didelphs allied to opossums, or to a genus representing the seals, in the sub-class of *Marsupialia*; whilst others make a saurian, or even a fish of it; which, it may be remarked *en passant*, appears much more in accordance with the age and the geological character of the formation which contains the fossils in question, as well as with the organized bodies with which they are associated.[65]

One writer, frustrated in his attempts to sort out the hodgepodge of conflicting opinions, proposed that the fossils be renamed "*Botheration* - *therium*."[66]

The disputed identity of the Stonesfield fossils was finally resolved by the British comparative anatomist, Richard

Owen. He demonstrated that the convex articular condyle, the coronoid process, and the dentition conclusively identified the fossil as a mammal. Further, he pointed out that Blainville's argument from the compound structure of the jaw, a reptilian characteristic, was based on the mistaken identification of a vascular groove as a suture.[67] By demonstrating that the Basilosaurus was actually a cetacean rather than a reptile, he destroyed Blainville's analogy.[68]

The crucial role of the Mesozoic mammalian remains in influencing the development of the theories of progression and transmutation which preceded the development of the Darwinian theory of natural selection can only be evaluated with the benefit of hindsight. In the nineteenth century the debate assumed a different significance. At the time the controversy was regarded as a crucial challenge to Cuvier's principle of the correlation of parts.

This principle was central to Cuvier's paleontological method, and its value had been dramatically demonstrated in 1804 with the discovery of the first fossil marsupial from Tertiary beds near Montmartre. Cuvier's paleontological research depended on his ability to reconstruct the anatomical features of extinct species by comparing them with living forms. This could be accomplished, Cuvier believed, by careful adherence to the principle of the correlation of parts. Each part of an animal must be understood in terms of its role in sustaining the life of the organism. The parts were so closely interrelated to the function of the whole that no one part could be changed without modifying all the other parts. Cuvier claimed that once this principle was properly understood, one could infer the organization of the remaining parts after careful examination of a single bone, thus identifying the organism according to its class, order, family, genus, and species.

The discovery of an extinct didelphid (now identified as Peratherium) near Paris caused much astonishment, for the living members of this marsupial group were found only in the Americas. Since Cuvier made his identification solely on the basis of the jaw and teeth, many of his colleagues were dubious. But Cuvier was certain, on the basis of past experience, that such teeth could only belong to marsupials. Cuvier invited his associates to witness a crucial test. The pelvis of the animal was still concealed within the matrix. By carefully chipping away the rock, Cuvier exposed the epipubic (marsupial) bones, thus confirming his identification.[69] The achievement was regarded as a triumph for Cuvier's method.[70]

The principle of the correlation of parts provided a basis for the comparative method in nineteenth-century anatomy and paleontology. It was therefore a matter of grave concern when the discovery of new fossils, also identified as marsupials, appeared to challenge the principle. If, as Cuvier claimed, all the parts of an animal form a unified whole each complementing the others, then the paleontologist should be able, upon examination of the fossilized remains of part of an animal (a Stonesfield lower jaw, for example) to determine its affinities (mammalian and marsupial.) Blainville's challenge to Cuvier's identification was regarded as a challenge to basic paleontological methodology. William Whewell gave a brief summary of the conflict in 1839, noting,

> I have dwelt the longer on this controversy, since it involves considerations of the most comprehensive interest to geologists, and, we may add, of the most vital importance. For de summâ reipublicae agitur--the battle was concerning the foundations of our philosophical constitution; concerning the validity of the great Cuverian [sic] maxim--that from the fragment of a bone we can reconstruct the skeleton of the animal. This doctrine of final causes in animal structures, as it is the guiding principle of the zoologist's reasonings, is the basis of the geologist's views of the organic history of the world; and, that destroyed, one half of his edifice crumbles into dust. If we cannot reason from the analogies of the existing, to the events of the past world, we have no foundation for our science.[71]

In the context of early nineteenth-century biology, Owen's victory was interpreted as a victory for Cuvier's methods.

Owen's identification ended all doubts regarding the mammalian nature of the fossils. Henceforth, the existence of Mesozoic mammals was accepted without objection. But they remained anomalous. Biologists attempted, with varying degrees of success, to adjust their theories to accommodate the Mesozoic mammals.

At first, following Buckland's lead, paleontologists related the early appearance of primitive marsupials to explanations involving adaptation. Richard Owen, for example, rested his argument on the common assumption that the earth's atmosphere was less dense and contained considerably more carbon and less oxygen during the Mesozoic than at the present time. He claimed that reptiles, which have a lower level of respiration than mammals, predominated because they were less dependent upon the atmosphere for their existence. According to this view, the first mammals should be small insectivorous marsupials because marsupials were most closely related to the lower vertebrates and Owen believed (erroneously) that insectivores had the lowest respiration of all the mammals. While Owen acknowledged that this explanation was not inconsistent with a theory of transmutation, he himself believed that the most probable cause was the special creation and successive introduction of new animal forms.[72]

In 1844 Robert Chambers adopted a similar argument, also based on adaptation, but he applied an evolutionary interpretation to it. In the Vestiges of the Natural History of Creation Chambers argued that the progression of organic forms revealed in the fossil record was a result of the regular action of God-given natural laws rather than evidence of supernatural intervention by the Creator. Postulating that life was endowed with a "developmental force" which allowed for the gradual appearance of increasingly complex structures, Chambers supported the idea of a gradual evolution of higher forms from lower forms against the views of the special creationists, who believed that God miraculously created each species as it now exists.

Chambers argued that the appearance of marsupials in the Mesozoic was consistent with the developmental theory since marsupials were primitive mammals, with many features linking them to the birds, reptiles, and fishes.[73] The gradual progression of life forms was accompanied by parallel geological and atmospheric changes. The more primitive life forms originated in the sea; then, as the land formed, more complex life forms appeared to fit the more varied conditions of existence.

> The huge saurians appear to have been precisely adapted to the low muddy coasts and sea margins of the time when they flourished. Marsupials appear at the time when the surface was generally in that flat, imperfectly variegated state in which we find Australia, the region where they now live in the greatest abundance, and one which has no higher native mammalian type. Finally, it was not till the land and sea had come into their present relations, and the former, in its principal continents, had acquired the irregularity of surface necessary for man, that man appeared. We have likewise seen reason for supposing that land animals could not have lived before the carbonigenous era, owing to the great charge of carbonic gas presumed to have been contained in the atmosphere down to that time.[74]

Chambers suggested that these organic changes may have been prompted by an increase in the available solar radiation.[75]

Consistent with Chamber's proposed progression from sea to land, one would expect the first mammals to be marine. Accordingly, Chambers cited early reports of whale remains found in Mesozoic strata.[76] He persisted in this claim long after these fossils had been conclusively identified as reptilian. This was but one of many scientific errors which served to discredit his argument.

In early versions of the Vestiges, Chambers explained progression as a result of pre-ordained adaptation. The progress of earth history was, he believed, pre-determined by God from the beginning of the universe. Like Buckland, Chambers associated organic change with environmental change, while at the same time suggesting a progressive increase in organic complexity.

In the tenth edition of the Vestiges, Chambers revised his theory considerably. He largely abandoned the appeal to adaptation and argued instead for a gradual increase in organic complexity unrelated to physical conditions. Organic progress represented the gradual unfolding of God's plan for the universe.[77] This explanation divorced organic change from physical necessity and appealed instead to a rational idea in the mind of the Creator.[78] By severing the link between geological progression and organic progression, Chambers negated the special creationist explanation of progression--the principle of adaptation.

Chambers postulated a developmental force, analogous to that controlling normal reproduction, as the mechanism which propelled organic progression. He suggested that embryos possessed an internal impulse such that extended gestation might produce an animal one step further advanced along the evolutionary scale. The linear mammalian taxonomic arrangement suggested a probable line of evolutionary ascent, and Chambers uncritically adopted that model.[79] He hypothesized,

> It is no great boldness to surmise that a super-adequacy [of the developmental force] . . . would suffice in a goose to give its progeny the body of a rat, and produce the ornithorynchus, or might give the progeny of an ornithorynchus the mouth and feet of a true rodent, and thus complete at two stages the passage from aves to the mammalia.[80]

Chambers' choice of example was, to say the least, unfortunate. Such a naive and simplistic notion exposed him to the scathing ridicule of merciless critics. Adam Sedgwick scorned such imaginative genealogies as scientific fantasies which violated all understanding of natural law. Referring to the members attending a recent meeting of the Geological Society of London, he wrote,

> . . . any one of them would have been laughed to scorn who had dared to tell the Society that the march of nature during these morning-hours was plain and easy--that some old Struthio had dropped an egg which by a cunning incubation had been hatched into a Mammal--that it was but a very simple process for a rising Struthio to cast its feathers, to put on a garment of hair, to discharge its old bill, to transform every wheel and cog of its inner mechanism, and then, to hop out of its egg as a full-fledged Mammal. They would have told the vender of such a monstrous fable, that he was deserting the light of analogy and the plain road of physical truth--and that the serious assertion of such a genealogy, while it proved nothing else, proved him incapable either of discussion, or pronouncing a sane judgement on any grave question of organic nature.[81]
>
> What conceptions a man may mature in the teeming womb of his imagination, is not a question for inductive physics. While we trust to Nature, we may send such abortive visions, along with all the idle dreams of ideal or material Pantheists 'into (what Milton calls) a limbo large and broad, since called the paradise of fools.' . . . Cases of organic progress beyond the parental grade

> are cases unknown, and out of all Nature's organic cycles. We may fancy anything; we might make a scheme of Nature out of the wildest Oriental visions. I can fancy a rat to come by hatching from a goose's egg: and I can fancy, with just as much inductive reason (for while I body forth, out of the storehouse of my fancy, the form of things unseen, what have I to do with inductive reason?) a full-dressed, slippered pantaloon to start by natural incubation out of an owl's nest, and begin his pantomimic dances, to the delight of all who love to pry beyond the secrets of nature.[82]

The publication of the _Vestiges_ provoked a bitter controversy. Chambers' evolutionary argument postulated the existence of a God who, with infinite foresight, provided a perfect adaptation between organism and environment through the workings of natural law. But his critics felt that the abandonment of a miraculous creation opened the door to a materialistic, atheistic view of nature. For the special creationists, the Mesozoic mammals represented a unique independent creation, unrelated to the vertebrates which preceded them and the mammals which followed.

Although Sedgwick thoroughly discredited Chambers' argument, he was less successful in his attempts to show the Stonesfield fossils to be inconsistent with transmutation. Sedgwick (and other reviewers[83]) emphasized that the early mammals were isolated in the mid-Mesozoic; no mammalian fossil remains had yet been found in the Cretaceous. Moreover, the mammals found in the lower Cenozoic beds were placentals, apparently unrelated to the "marsupials" of the Mesozoic. Such remains, Sedgwick argued, did not show a gradual development through time. The mammals of the Mesozoic and those of the Cenozoic represented two completely distinct, unrelated creations, the Tertiary mammals had no zoological base in the Mesozoic.

> They were therefore not called into being by any known law of nature, but by a power above nature. They were created by the hand of God, and adapted to the conditions of the period.[84]

James Dwight Dana, attempting to reconcile science and Scripture, adopted a similar argument in favor of successive creations. He claimed that the Mesozoic mammals were not transitional forms leading from reptile to mammal but rather "prophetic types." Few in number and weak, they were harbingers of the great diversity of mammals which would appear in the Tertiary period.[85] As late as 1872 Roderick Murchison persisted in citing the Mesozoic mammals as evidence of successive, progressive creations.[86]

The special creationists failed to provide a convincing argument. They effectively used the imperfections of the fossil record to highlight the weakness of the evolutionist position, but they themselves could offer no better explanation for the appearance of mammals in the Mesozoic. Relying on the argument for adaptation, they had to assume that the early mammals were best fitted to live in the environment of the Mesozoic. Failing that, their early appearance in the geological record depended on the whim of the Creator. Nevertheless, for geologists working within the older tradition of natural theology, this was the only acceptable explanation.

They rejected evolution because it challenged treasured religious and scientific beliefs.

Owen, Chambers, Sedgwick, Dana, and Murchison all interpreted the Stonesfield fossils in the context of a gradual progression in organic complexity throughout geologic history. This view was entirely unacceptable to the organic uniformitarians who believed that the observed changes in plant and animal species at different times merely represented adjustments to fit fluctuating environmental conditions. Attributing geographic and geologic distribution to adaptation to existing physical conditions, they claimed that the physical environment had maintained a state of equilibrium and so, correspondingly, had organic creation. Lyell develope this theory in 1830 and steadfastly continued to support it in 1850, despite increasing paleontological evidence in favor of progression.

For Lyell, the mammals of the Mesozoic offered excellent evidence against progression. Here were mammals, members of the highest class of vertebrates, at a period far earlier than progressionists would have predicted. He attributed their apparent scarcity to environmental conditions and to the imperfections of the fossil record and he confidently predicted that more would be discovered. (It is interesting to note that both Lyell's uniformitarianism and Darwin's evolutionary progressionism relied heavily on gaps in the geological record.) Discoveries of new Mesozoic mammals fulfilled Lyell's expectations. In 1847 Plieninger discovered the remains of a small insectivorous mammal, Microlestes antiquus (now named Thomasia antiqua) in Triassic beds.[87] This fossil pushed the origin of mammals even further back in time. Lyell capitalized on this new discovery as evidence in favor of the existence of mammals in the most remote geological periods.[88]

Progressionists continually emphasized that marsupials, next to monotremes the most primitive of all mammals, appeared first in the geological record. Lyell was therefore most eager to demonstrate the existence of the more advanced placentals in the Mesozoic era. In 1846 Richard Owen provisionally suggested that the Stonesfield Amphitherium might be a placental[89] and in 1854 he tentatively identified a new species, Spalacotherium tricuspidens, as a placental.[90] (He later retracted this opinion, identifying both species as marsupial.[91]) Owen recognized that the Mesozoic mammals displayed many features characteristic of both marsupials and placentals and therefore regarded his identifications as tentative. Moreover, Owen emphatically believed that, despite the evidence of the Mesozoic mammals, the fossil record revealed a gradual progression from general, archetypal features to more specific, specialized characteristics.[92] Nevertheless, Lyell eagerly seized upon his doubtful identifications as evidence in favor of his own theories.[93]

According to Lyell, the occurrence of mammals in the Mesozoic, and especially of placentals,

> seems fatal to the theory of progressive development, or to the notion that the order of precedence in the creation of animals, considered chronologically, has precisely coincided with the order in which they would be ranked according to perfection or complexity of structure.
>
> It was for many years suggested that the marsupial order to which the fossil animals of Stonesfield were supposed exclusively to belong constitutes the lowest grade in the class Mammalia, and that this order, of which the brain is of more simple form, evinces an inferior degree of intelligence. If, therefore, in the oolitic period the marsupial tribes were the only warm-blooded quadrupeds which had as yet appeared upon our planet, the fact, it was said, confirmed the theory which teaches that the creation of the more simple forms in each division of the animal kingdom preceded that of the more complex. But on how slender a support, even if the facts had continued to hold true, did such important conclusions hang! The Australian continent, so far as it has been hitherto explored, contains no indigenous quadrupeds save those of the marsupial order, with the exception of a few small rodents, while some neighbouring islands to the north, and even southern Africa, in the same latitude as Australia, abound in mammalia of every tribe except the marsupial. We are entirely unable to explain on what physiological or other laws this singular diversity in the habitations of living mammalia depends; but nothing is more clear than that the causes which stamp so peculiar a character on two different provinces of wide extent are wholly independent of time, or of the age or maturity of the planet.[94]

For Lyell, the differences between the faunas of different geographic regions and of different time periods can be explained solely on the basis of adaptation to different environments.

> From the earliest period at which plants and animals can be proved to have existed, there has been a continual change going on in the position of land and sea, accompanied by great fluctuations of climate. To these ever-varying geographical and climatal conditions the state of the animate world has been unceasingly adapted. . . . The principle of adaptation above alluded to, appears to have been analogous to that which now peoples the arctic, temperate, and tropical regions contemporaneously with distinct

> assemblages of species and genera, or which independently of mere temperature gives rise to a predominance of the marsupial tribe of quadrupeds in Australia and of the placental tribe in Asia and Europe, or to a profusion of reptiles without mammalia in the Galapagos Archipelago, and of mammalia without reptiles in Greenland.[95]

For Lyell, both environmental conditions and the organic life adapted to these conditions have fluctuated, maintaining a constant equilibrium.

Publicly, Lyell did not swerve in his loyalty to uniformitarianism and his rejection of organic progress. But his notebooks revealed his private doubts. In 1855 Alfred Russel Wallace published a paper, "On the law which has regulated the introduction of new species," which Lyell found profoundly disturbing. On the basis of his knowledge of geographic distribution and paleontology, Wallace argued that "Every species has come into existence coincident both in time and space with a pre-existing closely allied species." This generalization, Wallace argued, explained hitherto unrelated and unexplained facts of classification, geographic distribution, fossil history, and rudimentary organs.[96] Wallace's model of geographic isolation followed by gradual divergence strongly suggested a theory of evolution. Wallace's explanation of the connection between geographic and chronological distribution struck Lyell so forcibly that he began his notebooks on the question of the origin of species.[97] Lyell's doubts increased when, in April of 1856, Charles Darwin first explained his theory of natural selection to Lyell.[98] Lyell felt his uniformitarian convictions failing, but he strongly resisted adopting an evolutionary point of view because he felt it threatened his personal religious beliefs.

In the midst of these doubts, Lyell eagerly grasped any new evidence which confirmed his uniformitarian beliefs. The discovery of a number of new Mesozoic mammals in 1857 provided just such evidence. A thorough exploration of the Wealdon strata of Purbeck revealed the presence of eight or nine genera of mammals. Lyell believed that these new discoveries vindicated his theories, providing proof that a varied mammalian fauna co-existed with the huge reptiles of the Mesozoic. Moreover, the gaps in the record and the scarcity of Mesozoic mammalian remains clearly showed the folly of relying on negative evidence to construct an argument for the non-existence of higher organisms during early geological periods. Once again, he fell back on adaptation to explain geographic and geologic distribution in the context of organic uniformitarianism.[99]

Lyell's journals on the species question reveal a gap from February 1857 to July 1858. Leonard G. Wilson argues that this gap was occasioned by the Purbeck discoveries which led Lyell to retreat from a tentative acceptance of the possibility of transmutation and to reaffirm his earlier theory of uniformitarianism as applied to the organic world.[100] Lyell did not take up the question again until Wallace's independent formulation of the theory of natural selection renewed his doubts regarding the stability of species.

For Lyell, the origin of mammals was a critical problem on which the question of transmutation hinged. He wrote Huxley in June of 1859,

> If we found all the leading Classes, Orders, Families & Genera, or could reasonably hope to find them, or could fairly infer that they did exist in the oldest Periods, then we might by development get the species, or I could conceive the Genera, in the course of millions of ages. But once admit the probable want of Placental Mammalia in the Lower Silurian & we require such an event as the first appearance of that type at some subsequent Period, an event which might compare with the first coming in of any other new type--ending with Man & it becomes difficult to know where to stop . . ."[101]

Lyell was willing to subscribe to a limited evolutionary theory. But, once admit the late appearance of an advanced group of mammals like the placentals, and one can support the argument for the evolution of all higher forms (including man) from lower organisms. This Lyell was unwilling to do.[102]

As Lyell feared, the late appearance of placentals did offer significant support for evolutionary theory. By 1850, the paleontological evidence in favor of organic progression was so overwhelming that Lyell was virtually alone in his continued support of organic uniformitarianism. Lyell clung to the Mesozoic mammals as evidence against progression, but this single apparent exception to the rule could not carry the argument in his favor. Progressionist W. D. Conybeare wrote to Lyell criticizing his uniformitarian views.

> If in the case of the Vertebrata you surely cannot consider the exception of the wretched little marsupials

> of Stonesfield to counterbalance the general bearing of the whole evidence--for all that it would lead to is only this, that in the secondary strata a class of Vertebrata intermediate in their plan between True Mammalia & the lower classes first shewed themselves.[103]

A theory of organic progression through time was a necessary prerequisite to the formulation of a satisfactory evolutionary theory. Difficulties arose, however, when evolutionists attempted to construct a model of evolutionary development consistent with the anatomical and paleontological evidence. Early progressionists had assumed that the fossil record should reveal a linear progression from fish to reptile to bird to mammal. They tried to interpret the data to conform to this view, but by the 1840's a growing body of knowledge from paleontology and comparative anatomy challenged this linear model of progression. The diversity of living forms could not easily be accommodated into a linear taxonomic arrangement, nor did the fossil record reveal a direct linear development. Many forms remained unchanged for long periods of time, some appeared to degenerate, and some developed along lines which could not be defined as progressive. Theorists were forced to alter the model to account for divergence.

Richard Owen, Britain's foremost comparative anatomist and paleontologist, was in a position to appreciate these difficulties. At first, Owen accepted the traditional linear model of progression. Later, increasing evidence in favor of divergence led him to redefine the concept of progression.[104]

In place of a progression from simple to complex forms. Owen substituted a progression from generalized to specialized structures. Owen noted that the older fossil forms adhered closely to the common type, resembling the embryo of modern forms more than the adult. As time went on, organisms approached more closely to the modern types, acquiring specialized adaptations.[105] This model was not inconsistent with the idea of a general progression from lower to higher forms, but it also allowed for numerous side branches leading in various directions.

At first it seemed that the Mesozoic mammals might be inconsistent with even this modified view of progression, for one of the Purbeck species possessed a highly specialized dentition. Falconer cited this as evidence against even the most generalized theory of progression,[106] and Lyell quickly adopted the argument to support his theory of organic uniformitarianism.[107] After the publication of the theory of natural selection, Falconer answered his own objection, suggesting that the specialized nature of the early fossil merely showed that the species had been preceded by a long series of hitherto undiscovered mammalian progenitors.[108] Darwin was predictably eager to adopt the explanation since it eliminated an annoying anomaly.[109]

As Owen gained in scientific experience and theoretical sophistication, he became increasingly skeptical of the special creationists' appeal to miracle to explain the origin of species. Owen argued that the operations of nature, in the creation as well as in the extinction of species, conformed to continuously operating secondary causes.[110] He acknowledged that the pattern of development revealed in the fossil record was not inconsistent with a theory of evolution. According to Owen, traditional Christian belief did not necessarily require the miraculous creation of species. The constant adaptation of organisms to their environment provided incontrovertible evidence of creative foresight. He rejected the Darwinian theory of evolution not because it denied miracles, but rather because it eliminated the argument for design in nature. Owen objected to the mechanism of natural selection because it implied a mindless, mechanical system operating by chance rather than by the wisdom and foresight of a beneficent and intelligent First Cause.[111]

Although Owen's aggressive objections to natural selection and his prestigious reputation in the scientific community combined to offer a formidable challenge to Darwinian theory, Darwinists were quick to adopt those parts of his theory which were consistent with their own view. Owen's model of a gradual progression from generalized forms to specialized structures fitted neatly into the theory of natural selection. As natural selection operates on a generalized organism, those structural variations more perfectly adapted to the environment tend to survive, thus increasing the organism's specialization. Moreover, if members of the species occupy two separate environments, adaptive specialization tends to lead in two separate directions, thus causing a divergence of evolutionary lines. According to Darwinian theory, the fossil record should reveal a divergent pattern leading in numerous directions rather than a single progressive series. Any progress from lower to higher, if it occurs at all, should follow an indirect rather than a linear path.

Alfred Russel Wallace's notebooks reveal that Wallace adopted just such a divergent model to resolve the theoretical difficulties presented by the Mesozoic mammals. Wallace wrote,

> Lyell says the Didelphys of the Oolite is fatal to the theory of progressive development. Not so if low[ly] organized mammalia branched out of low reptiles or fishes. All that is required for the progression is that some reptiles should appear before Mammalia & birds or even that they should appear together. In the same manner reptiles should not appear before fishes, but it matters not how soon after them. As a general rule let Naturalists determine that one class of animals is higher organized than another, & all that the development theory requires is that some specimens of the lower organized group should appear earlier than any of the group of higher organization.[112]

Darwin also fashioned a branching model to explain evolutionary development in the *Origin*.[113] Nevertheless, when it came to tracing the origin of mammals, evolutionists continually returned to the pattern suggested by the pre-evolutionary progressionists. According to the early progressionists, the fossil record should reveal a linear progression from reptiles to monotremes to marsupials to placentals. This model was suggested by the anatomical features of monotremes and marsupials and was reinforced by the identification of the Mesozoic mammals as marsupials. Early Darwinists were never able to completely break away from this hypothetical path of mammalian development, even though their divergent model of evolution did not require it and the fossil evidence failed to support it.

In fact, the failure of the evidence to conform to the standard pattern of mammalian development was the source of some of Lyell's objections to evolution. Attempts to resolve these difficulties led to an extensive correspondence between Lyell and Darwin concerning the genealogy of mammals.

According to Lyell's reasoning, if the marsupials appeared early in the geological record because of their primitive organization, then the more primitive monotremes should appear even earlier. He objected,

> According to the progressive theory, why sh.d there be a living platypus or ornithorhynchus, for we have nothing synthetical or elementary in the coal strata, & if they sh.d be found there how have they escaped being altered, improved, and specialized in 30 periods.[114]

Progressionists commonly assumed that monotremes preceded the marsupials, but that their remains had not yet been discovered. Lyell, whose own uniformitarian theory relied heavily on the insufficiencies of the fossil record, conceded the danger of relying on negative evidence to judge this point.[115] As for the survival of the living platypus, Darwin regarded this as a "strange and inexplicable fact," suggesting that isolation and limited competition among fresh-water forms may have allowed its preservation.[116]

Lyell suggested that, according to Darwinian theory, the reptiles on isolated islands should become primitive non-placental mammals during the course of time. However, Lyell conceded that this objection applied more appropriately to the earlier linear model than to Darwin's divergent pattern of evolution.[117] Darwin responded that, even granting enough time for such a development, no existing reptile could evolve into a mammal as we define the term mammal.[118] He explained, ". . . there must have arrived on the island the necessary and peculiar progenitor, having a character like the embryo of a mammal; and not an already developed reptile, bird or fish."[119] Darwin constantly emphasized that one should not expect to find the progenitors of existing forms among living species. Primitive, unspecialized ancestral forms could not survive competition with their more specialized descendants.

Lyell recognized that the mechanism of natural selection would not lead to a single linear path of progressive development, but he continued to conceive of progression in linear terms and searched for an explanation which would place limited restrictions on divergence. He questioned Darwin,

> Can we assume as at all probable that all mammalia came from one original stock instead of several distinct mammalian types, each developed by small & successive modifications out of lower ornithic, reptilian, or perhaps monotrematous prototypes. It would greatly simplify matters if single & exclusive areas could be assigned or even speculated upon, on some even slight data, or if single periods could be proposed as those of the first coming in of mammalia. But as I understand your views this is not very probable. If for example we found before the Triassic

> Microlestes, some monotremes in Permian or Carbonif.s Beds & fixed on them as the probable starting point of mammalia, what influence would the development of a mammal in Asia or Africa have in preventing some other line of monotremes from improving into a totally different genus of mammal in Australia or America & supposing the mammal first formed, say in Asia, to be extinguished, what is there in your system to cause us to despair of the higher or placental grade from ever being evolved, because after a geological period the earlier formed mammalia died out. . . .
>
> I wish you could give the slightest reason why it should not begin more than once in more than one place. I incline to think it has not, but why? According to the principle of selection, why when once in any one quarter of the globe, at any one period, the step in advance has been taken, are the inferior types elsewhere to be checked, & not to presume to work up into any Gnus of corresponding grade & class? . . . Take some Triassic reptile or bird, I cannot see why they are never to be modified into something higher, because a Microlestes had entered on the stage. Two independent chains of development would not be discordant with your machinery of selection?[120]

Lyell himself clearly expected a linear pattern of development leading directly from reptiles to birds to the marsupials of the Mesozoic to the placentals of the Cenozoic. He proposed to Darwin,

> You would prefer, I conceive to derive Eocene mammalia from the Microlestes of the Trias rather [than] from any reptilian of however high a grade, e.g., a deinosaurian. You wd rather conceive a bird to be turned into a mammal than derive the latter from a reptile. The Microlestes, or its nearest living analogues (marsupials), wd in its embryology go through the bird-state or likeness before it became even a non-placental mammifer?[121]

Darwin responded by proposing a different, divergent model for the origin of the major mammalian groups.

> I see that you do allude in the last page, as a difficulty, to Marsupials not having become Placentals in Australia;

> but this I think you have no right at all to expect; for we ought to look at Marsupials and Placentals as having descended from some intermediate and lower form.[122]

In a later letter, Darwin constructed two alternative models for the development of mammals (reproduced on the following page.) Darwin explained,

> I enclose two diagrams showing the sort of manner I conjecture that mammals have been developed. . . . I have not knowledge enough to choose between these two diagrams. If the brain of Marsupials in embryo closely resembles that of Placentals [sic], I should strongly prefer No. 2, and this agrees with the antiquity of Microlestes. As a general rule I should prefer No. I diagram; whether or not Marsupials have gone on being developed, or rising in rank, from a very early period would depend on circumstances too complex for even a conjecture.
>
> A, in the following diagrams, represents an unknown form, probably intermediate between Mammals, Reptiles and Birds, as intermediate as Lepidosiren now is between Fish and Batrachians. This unknown form is probably more closely related to Ornithorhynchus than to any other known form.[123]

On the basis of this passage, Bowler argues that Darwin rejected the view that marsupial-like creatures were the ancestors of placentals because his evolutionary theory supported a divergent rather than a linear model.[124] In fact, Darwin seems to have developed this argument primarily to counter Lyell's objection that Australian marsupials had not progressed in organization to become placentals. On other occasions, both before and after 1860, Darwin adopted the standard model of development from reptile to monotreme to marsupial to placental.

DIAGRAM I.

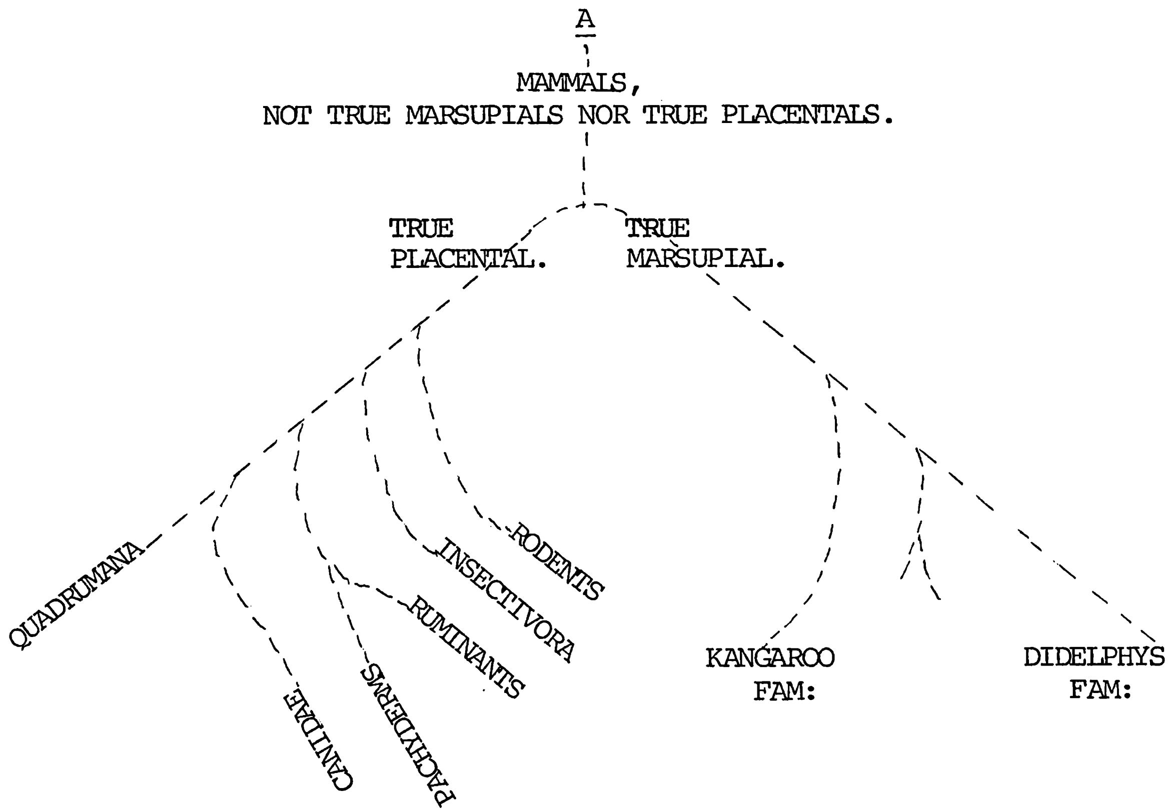
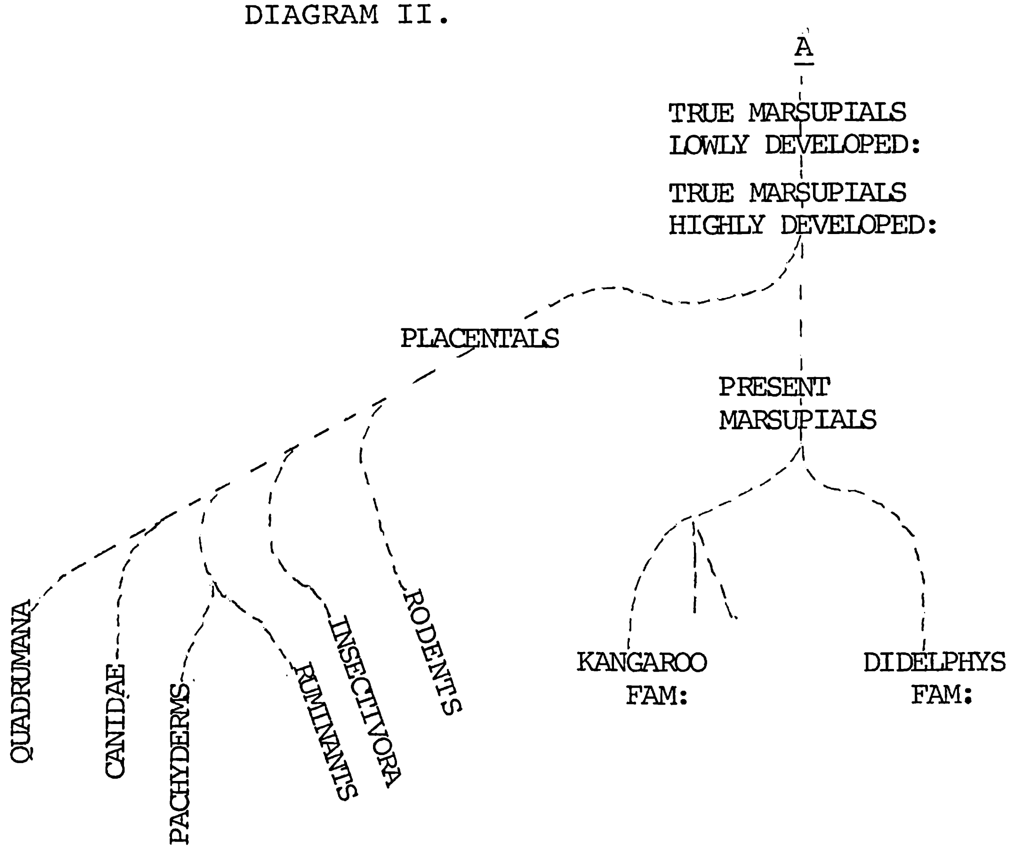


DIAGRAM II.



In Francis Darwin ed., The Life and Letters of Charles Darwin (John Murray, 1887), II, p. 342.

Evolutionists favored this hypothetical path of mammalian development because, despite their commitment to a divergent model of evolutionary development, they continued to be influenced by the old linear concept of progression. In the case of the mammals, they did not consistently apply the theoretical principles of their own theory. This is most clearly seen in their treatment of the monotremes. Darwinists constantly emphasized that one could not reasonably expect to find the progenitors of modern forms among living species, but they constantly referred to the living monotremes as surviving representatives of the primitive mammals. They assumed that the earliest mammals must have been monotremes, despite the complete lack of fossil evidence to support this assumption. The revised model of progression from generalized to specialized structures would not support this assumption either, because the living monotremes are highly specialized. Comparative anatomists had emphasized the affinities between reptiles and monotremes, and taxonomists had established a linear taxonomic arrangement leading from monotremes to marsupials to placentals. Darwinists assumed that the earliest mammals must have been monotremes because they were still influenced by the notion that the "lower" animals must have appeared before the "higher" animals.

The problem of the early development of the mammals attracted Darwin's attention early in his investigations into the origin of species. His notebook of 1837-1838 suggests that, influenced by the then newly proposed theory of a gradual increase in organic complexity through time, Darwin envisioned a primitive marsupial or monotreme as the first mammal from which all other mammalian types descended. He characterized the Stonesfield marsupial as "the father of all mammalia," and suggested that the first mammal may have been as heterodox as the platypus, combining the features of several different classes in a single species.[125]

Even in 1860, when he suggested to Lyell a branching diagram of mammalian evolution, Darwin assumed that the original progenitor of mammals must have possessed monotreme-like features.

> From homologies I should look at it as certain that all mammals had descended from some single progenitor. What its nature was, it is impossible to speculate. More like, probably, the Ornithorhynchus or Echidna than any known form; as these animals combine reptilian characters (and in a lesser degree bird character) with mammalian.[126]

In his early publications on evolution, Darwin declined to propose publicly models for the development of modern taxa because he felt that the existing evidence was too fragmentary to support the construction of such genealogies. With the appearance of The Descent of Man in 1871, Darwin attempted to reconstruct the path of evolutionary development leading to man. Darwin at that time adopted the standard model of mammalian development. He hypothesized,

> In the class of mammals the steps are not difficult to conceive which led from the ancient Monotremata to the

> ancient Marsupials; and from these to the early progenitors of the placental mammals.[127]
>
> The Marsupials stand in many important characters below the placental mammals. They appeared at an earlier geological period, and their range was formerly much more extensive than at present. Hence the Placentata are generally supposed to have been derived from the Implacentata or Marsupials; not, however, from forms closely resembling the existing Marsupials, but from their early progenitors. The Monotremata are plainly allied to the Marsupials, forming a third and still lower division in the great mammalian series. They are represented at the present day solely by the Ornithorhynchus and Echidna; and these two forms may be safely considered as relics of a much larger group, representatives of which have been preserved in Australia through some favourable concurrence of circumstances. The Monotremata are eminently interesting, as leading in several important points of structure towards the class of reptiles.[128]

As evidence supporting the descent of higher mammals from monotremes, Darwin noted similarities between the developing mammary glands of mammalian embryos and the functional glands of the monotremes.[127]

Darwin attributed the characteristics of the living marsupials and monotremes to the earliest mammals, despite the fact that none of the Mesozoic mammals had been identified as monotremes. Moreover, although the marsupial identification of the early fossils was generally accepted, it posed some taxonomic difficulties. The Mesozoic mammals combined the features of marsupials and placentals in such a way that they could not easily be assigned to either group.

Darwin assumed that the existing monotremes were "living fossils," the only survivors of a large group of early mammals, the ancestors of the marsupials. Yet the fossil record as he knew it showed no evidence of the existence of monotremes before the modern period. In fact, modern paleontologists have still not found unequivocal evidence of the existence of monotremes before the mid-Tertiary.

One might expect that the paleontological evidence, coupled with the divergent model of evolution supported by Darwinian theory, would suggest the need to reevaluate the taxonomic position of the Mesozoic mammals. Yet Darwin uncritically retained the old model of mammalian progression which had been developed in a very different theoretical context.

He was supported in this view by other leading evolutionists. Ernst Haeckel, for example, argued that ". . numerous Monotremata, with well-developed teeth and cloaca, must have preceded the advent of Marsupial animals." He even went so far as to suggest that the Microlestes, the earliest fossil mammal then known, may have been a monotreme.[130] He made this claim despite the fact that the Microlestes was identified solely by a few fossil molars and living monotremes possess no teeth with which to compare them. Haeckel maintained that the marsupials developed, probably in the Jurassic, from primitive monotremes, and that placentals evolved from their marsupial ancestors about the beginning of the Tertiary.[131]

Thomas Henry Huxley also assumed, on the basis of comparative anatomy, that the monotremes represented the earliest stage in mammalian evolution. Huxley realized that the Darwinian theory of evolution challenged the philosophical foundations of taxonomy. He redefined the major mammalian taxa to accommodate changes in species (and even orders) through time, but he retained the idea of a phylogenetic progression from reptiles to monotremes to marsupials to placentals. According to Huxley, the reptiles led to the Prototheria (monotremes and their mammalian ancestors), which were succeeded by the Metatheria (consisting of marsupials and their immediate progenitors), which were followed finally by the Eutheria (primitive placentals and their more specialized descendants).[132] Huxley still recognized a linear scale and recalled its origin in the old "great chain of being." He wrote,

> Cuvier's . . . definite repudiation of Bonnet's "échelle des êtres" must be regarded as another unfortunate effort to oppose the development of just biological conceptions. For though no one will pretend to defend Bonnet's "échelle" at the present day, the existence of a "scala animantium" is a necessary consequence of the doctrine of evolution; and its establishment constitutes, I believe, the foundation of scientific taxonomy.[133]

Of course, Huxley substantially modified the progressive series of the early theorists to account for divergence and emphasized that modern marsupials and monotremes were very specialized versions of their primitive prototypes.

Huxley's taxonomic divisions are still in use today, but his model of mammalian phylogeny has been rejected. Modern paleontologists believe that the Prototheria diverged from the rest of the mammals (the Theria) very early in the development of the mammals. At a later date, the Metatheria and Eutheria diverged, pursuing two separate paths of evolutionary development. Metatheria are thus no longer regarded as the middle term in a linear series linking Prototheria and Eutheria.

Early Darwinists maintained a generally linear model of mammalian development even though their theoretical principles did not demand it and the paleontological evidence did not fully support it. They continued to be influenced by theoretical assumptions which had developed within a special creationist, non-divergent theory of progression. The anatomical evidence supported a linear taxonomic arrangement for the major mammalian groups. Moreover, evolutionists frequently referred to the marsupials and monotremes as transitional creatures linking reptiles to placentals. This argument would predispose them to interpret the established progression from reptile to monotreme to marsupial to placental in phylogenetic terms. The lack of paleontological evidence could be attributed to the well known inadequacy of the fossil record. Since they were faced with no clear empirical evidence to challenge the prevailing assumptions, evolutionists did not question the established model of mammalian progression.

The central contribution of paleontology to the development of evolutionary theory was the concept of organic progression through time. At first the Mesozoic mammals seemed to disprove progression, and paleontologists struggled to adjust their theories to explain this apparent anomaly.

Biologists necessarily interpreted new evidence within the context of prevailing theoretical preconceptions. The earliest mammals were erroneously identified as marsupials, because biologists believed that all mammals must fit within existing taxonomic categories. They assumed that no mammal could combine the characteristics of marsupials and placentals. Once the marsupial identification became firmly established as a universal characteristic of all Mesozoic mammals, this generalization itself became an accepted theoretical principle. The "primitive," marsupial character of the early mammals contributed to the development of a theory of organic progression in time which, in turn, led to the erroneous assumption that the earliest mammals must have been monotremes.

NOTES

[1]For a discussion of the development of theories of progression, see Peter J. Bowler, *Fossils and progress* (New York: Science History Publications, 1976), and Martin J. S. Rudwick, "Uniformity and progression: reflections on the structure of geological theory in the age of Lyell," in D. H. D. Roller, ed, *Perspectives in the history of science and technology* (Norman, Oklahoma: University of Oklahoma Press, 1971), pp. 209-237.

[2]Georges Cuvier, *Recherches sur les ossemens fossiles de quadrupèdes* (Paris: Deterville, 1812) I, p. 69.

[3]Georges Cuvier, *Essay on the theory of the earth* (Edinburgh: W. Blackwood, 1813 [Landmarks of Science Microprint]) p. 109, which is Robert Kerr's translation of Cuvier, *Ossemens fossiles*, I, p. 70.

[4]Bowler, *Fossils and progress*, pp. 19-20.

[5]George Gaylord Simpson, *A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum* (London: British Museum (Natural History) Department of Geology, 1928) p. 3.

[6]William Buckland, "Notice on the Megalosaurus or great fossil lizard of Stonesfield," *Geological Society of London. Transactions* I (1824) p. 391.

[7]William Daniel Conybeare and William Phillips, *Outlines of the geology of England and Wales* (London: William Phillips, 1822) p. 207.

[8]Buckland, "Notice on the Megalosaurus," p. 391.

[9]*Ibid.*, p. 394.

[10]Richard Owen, "Report on British fossil reptiles, part 2.," *British Association for the Advancement of Science. Reports* (1841) p. 102.

[11]Constant Prévost, "Note sur une *Ichthyolithe* des rochers des Vaches-Noires," *Annales des Sciences Naturelles* III (1824) p. 244. Reijer Hooykaas has argued that Prévost

intended to defend the theory of organic progression by linking the chronological order of fossils with the taxonomic order reflected in contemporary systems of classification. ("Geological uniformitarianism and evolution," Archives Internationales d'Histoire des Sciences XIX (1966), p. 12.) Bowler has argued, more convincingly, that Prévost merely wished to reestablish Cuvier's rule concerning the late appearance of mammals. Bowler claims that Prévost could have incorporated the Mesozoic mammals into a simple hierarchy of ascent, since it was widely accepted that the marsupials were the lowest mammals. That he did not do so can be attributed, according to Bowler, to the relative lack of emphasis on progression in the paleontological theories of the 1820's. (Fossils and progress, p. 21.) In fact, Prévost does not connect the early appearance of marsupials with their primitive level of organization, nor would the accepted taxonomic theories of the day have supported such a connection. True, Blainville proposed in 1816 a revolutionary classification which, once accepted, provided the taxonomic basis for a progressive theory of development, reflecting an increasing complexity of organization. But Cuvier did not perceive the differences in marsupial and placental reproduction to be of high taxonomic significance. His classification of 1817 still integrated the marsupials among the placentals as a division of the order Carnivora. Cuvier's views were almost universally adopted and Blainville's classification gained little acceptance until Owen's studies of comparative anatomy provided justification for them. (W. K. Gregory, "The orders of mammals," American Museum of Natural History. Bulletin XXVII (1910) pp. 79-80, 86.) As we shall see, the later identification of marsupials as primitive mammals transformed the controversy concerning the Mesozoic mammals into an argument over evolution.

[12]Georges Cuvier, Recherches sur les ossemens fossiles (Paris and Amsterdam: Chez G. Dufour et Ed. d'Ocagne, 1824) V, ii, p. 349. ". . . si cet animal est vraiment du schiste de Stonesfield, c'est une exception bien notable à la règle, d'ailleurs si générale, que les couches de cette ancienneté ne recèlent point de restes de mammifères."

[13]Conybeare and Phillips, Outlines, p. 207. Although Prévost tried to support his argument for the doubtful position of the Stonesfield beds by drawing quotations from this work out of context, Conybeare and Phillips clearly accepted Buckland's conclusions but made no attempt to explain the anomaly.

[14]Jules Desnoyers, "Observations sur quelques systèmes de la formation Oolitique de nord-ouest de la France; et

particulièrement sur une Oolite à Fougères de Mamers," Annales des Sciences Naturelles IV (1825) p. 388.

[15]Constant Prévost, "Observations sur les schistes calcaires oolitiques de Stonesfield en Angleterre, dans lesquels ont été trouvés plusieurs ossemens fossiles de Mammifères," Annales des Sciences Naturelles IV (1825) p. 396.

[16]Gideon Mantell, The fossils of the South Downs (London: L. Relfe, 1822 [Landmarks of Science Microprint]) p. 59. Buckland, "Notice on megalosaurus," p. 394.

[17]Prévost, "Observations sur les schistes," p. 396.

[18]Ibid., p. 415.

[19]William John Broderip, "Observations on the jaw of a fossil mammiferous animal, found in the Stonesfield slate," Zoological Journal XI (1827) pp. 408-412.

[20]William Henry Fitton, "On the strata from whence the fossil described in the preceding notice (fossil jaw from Stonesfield) was obtained," Zoological Journal XI (1827) pp. 412-413.

[21]Charles Lyell, "Art. IX.--Transactions of the Geological Society of London Vol. i, 2d. Series. London. 1824," Quarterly Review XXXIV (1826) p. 513.

[22]Ibid., p. 530.

[23]These were later identified as the reptilian Cetiosaurus.

[24]Ibid., p. 531.

[25]Ibid., p. 539.

[26]Michael Bartholomew, "Lyell and evolution: an account of Lyell's response to the prospect of an evolutionary ancestry for man," The British Journal for the History of Science VI (1973) pp. 261-305.

[27]On the connection between Lyell's uniformitarian geology and his rejection of progression in the organic world see Reijer Hooykaas, Natural law and divine miracle (Leiden: E. J. Brill, 1959); Martin J. S. Rudwick, The meaning of fossils (New York: Science History Publications, Inc., 1976) p. 179 ff.; Peter J. Bowler, Fossils and progress, pp. 4-6, 69ff.

[28]Charles Lyell, Principles of geology (New York and London: Johnson Reprint Corporation, 1969 [reprint of London: John Murray, 1830]) I, p. 150.

[29]Ibid., p. 152.

[30]See Leonard G. Wilson's introduction to Sir Charles Lyell's Scientific Journals on the Species Question (New Haven and London: Yale University Press, 1970) pp. xxv-xxvi.

[31]Gideon Mantell, "The geological age of reptiles," Edinburgh New Philosophical Journal XI (1831) pp. 181, 183.

[32]Gideon Mantell, "Opossum in the Stonesfield slate, near Oxford, England," The American Journal of Science and Arts XXVII (1835) p. 412.

[33]Alexander von Humboldt, ["Offre au nom de M. Buckland, des planches représentant des traces de pieds de quadrupèdes,"] Académie des Sciences. Comptes rendus VII (1838) pp. 604-605.

[34]The opposable thumb appears on all four feet. Thus the animal, if attributed to the mammals, should have been included among the Quadrumana, the order which includes the primates. However, believing that the first mammals should be primitive in organization, biologists chose to ignore a significant diagnostic character and placed it among the marsupials.

[35]Robert Grant, ["On the impressions of footsteps of Chirotherium in the Storton quarries at Liverpool,"] Magazine of Natural History n.s. III (1839) pp. 43-48.

[36]Modern paleontologists attribute the scarcity of Mesozoic mammalian fossils to their small size. As long as reptiles were dominant, mammals remained small and evolved slowly. With the extinction of the large Mesozoic reptiles,

mammals evolved to fill the vacated ecological niches. Edwin H. Colbert, Evolution of the Vertebrates (New York, etc.: John Wiley & Sons, Inc., 1969) p. 232.

[37]William Buckland, Geology and mineralogy considered with reference to natural theology (Philadelphia: Carey, Lea and Blanchard, 1837) pp. 63-64.

[38]Ibid., pp. 95-96.

[39]Ibid., p. 64.

[40]Henri Ducrotay de Blainville, "Prodrome d'une distribution systématique du règne animal," Société Philomathique de Paris. Bulletin s.3, III (1816) p. 109.

[41]Paul Gervais, "Mammalogie ou mastologie," in Félix Edouard Guérin-Méneville, ed., Dictionnaire pittoresque d'histoire naturelle et des phenomènes de la nature (Paris: au Bureau de souscription [Impr. de Cosson], 1836) IV, p. 619.

[42]Richard Owen, "On the structure of the brain in marsupial animals," Royal Society of London. Philosophical Transactions CXXVII (1837) p. 92.

[43]Richard Owen, "On the characters, principles of division, and primary groups of the class Mammalia [1857]," Linnean Society of London. Journal (Zoology) II (1858) pp. 1-37.

[44]Buckland, Geology and mineralogy, p. 65.

[45]Richard Owen, quoted in ibid., p. 65.

[46]Louis Agassiz, "[Letter from Neufchatel, Switzerland, June 20, 1835]," Neue Jahrbuch für Mineralogie und Geologie III (1835) pp. 185-186.

[47]Henri Ducrotay de Blainville, "Doutes sur le prétendu Didelphe fossile de Stonesfield," Académie des Sciences. Comptes rendus VII (1838) pp. 402-418.

[48]Some advanced, mammal-like reptiles have differentiated dentition, but this is an exception to the rule. Colbert, Evolution of vertebrates, pp. 251-252.

[49]Blainville, "Doutes," p. 418.

[50]Ibid., p. 418. Translated in Magazine of Natural History II (1838) p. 654.

[51]"En effet, suivant que ces restes fossiles auraient appartenu à un mammifère terrestre, ou aquatique, monodelphe ou didelphe, ou bien à un reptile ou un poisson, telle ou telle théorie de l'ordre de formation, ou de création, ou d'apparition, des espèces animales à la surface de la terre, celle du développement graduel et insensible dans la complication de l'organisation des animaux, généralement admise sans preuves suffisantes, se trouverait infirmée ou confirmée," Henri Ducrotay de Blainville, "Réclamation de M. de Blainville à l'occasion de Compte rendu de la dernière séance," Académie des sciences. Compte rendu VII (1838) p. 750.

[52]Toby Appel, "Blainville, Lamarck and the chain of being," Paper delivered at the 1978 Annual Meeting of the History of Science Society, Madison, Wisconsin, October, 1978.

[53]Blainville, "Doutes," p. 411.

[54]Colbert, Evolution of vertebrates, p. 258.

[55]Achille Valenciennes, "Observations sur les mâchoires fossiles des couches oolithiques de Stonesfield nommées Didelphis Prevostii et Didelphis Bucklandii," Académie des sciences. Comptes rendus VII (1838) p. 578.

[56]A. M. C. Duméril, "Remarques sur les didelphes fossiles de Stonesfield," Académie des sciences. Comptes rendus VII (1838) p. 633.

[57]"Alors je ne pouvais soupçonner que le couronnement de ces travaux deviendrait cette profonde pensée, serait que ces êtres ne sont véritablement point des mammifères eu [sic] égard à l'idée qu'on attache à cette expression dans la classification, et qu'il les faudrait admettre d'une classe différente et sui generis; laquelle il faudra finir peut-être par nommer marsupiaire.

"Ce qui est venu m'éclairer tout nouvellement, c'est qu'une partie de ces animaux se trouve avoir vécu dans les âges antédiluviens: or ce résultat vient d'agiter tout récemment l'opinion des naturalistes. Les marsupiaux pris mal à propos pour des mammifères, auraient rompu une magnifique généralisation, . . . que les mammifères existeraient uniquement dans des couches de troisième formation." Etienne Geoffroy Saint-Hilaire, "De quelques contemporains des Crocodiliens fossiles des âges antédiluviens, d'un rang classique jusque alors indéterminé," _Académie des sciences. Comptes rendus_ VII (1838) pp. 630-631.

[58]_Ibid._, pp. 632-633.

[59]Owen, quoted in Buckland, _Geology and mineralogy_, p. 65.

[60]Louis Agassiz, "Sur les ossements fossiles de Stonesfield qui avaient été rapportés à des Didelphes," _Académie des sciences. Comptes rendus_ VII (1838) p. 537.

[61]Robert Grant, "General view of the characters and distribution of extinct animals," in Robert D. Thomson, ed., _British annual and epitome of the progress of science for 1839_ (London, Paris: J. B. Baillière, 1838) III, p. 263.

[62]Henri Ducrotay de Blainville, "Nouveaux doutes sur le prétendu Didelphe de Stonesfield," _Académie des sciences. Comptes rendus_ VII (1838) p. 734.

[63]A. M. C. Duméril, "Remarques de M. Duméril à l'occasion du Mémoire de M. de Blainville," _Académie des sciences. Comptes rendus_ VII (1838) p. 736. (The order of aquatic mammals Cetacea includes whales, dolphins and porpoises.)

[64]William Ogilby, "Observations on the structure and relations of the presumed marsupial remains from the Stonesfield oolite," _Magazine of Natural History_ n.s. III (1839) p. 209.

[65]Blainville, "Nouveaux doutes," pp. 735-736. Translated in _Magazine of Natural History_ n.s. III (1839) p. 57.

[66][E. Charlesworth], ["Unsigned note,"] _Athenaeum_ (1838) p. 731.

[67]Richard Owen, "Observations on the fossils representing the _Thylacotherium Prevostii_, Valenciennes, with reference to the doubts of its mammalian and marsupial nature recently promulgated, and on the _Phascolotherium Bucklandi_

[1838]," *Geological Society of London. Transactions* VI (1842) pp. 47-67.

68 Richard Owen, "Observations on the teeth of the *Zeuglodon*," *Magazine of Natural History* n.s. III (1839) p. 213.

69 Georges Cuvier, "Mémoire sur le squelette presque entier d'un petit quadrupède du genre des sarigues trouvé dans la pierre à plâtre des environs de Paris," *Paris: Muséum national d'histoire naturelle. Annales* V (1804) pp. 277-292. The same species had been discovered two years earlier but was erroneously identified as a bat. See Jean Claude Delamétherie, "Note sur une machoire inférieure d'un carnivore analogue à la chauve-souris," *Journal de physique, de chimie, d'histoire naturelle des arts* LV (1802) p. 404.

70 François Pictet, *Traité élémentaire de paléontologie* (Paris: Langois et Leclerq, 1844) I, pp. 329-330. Richard Owen, "Paleontology," in *Encyclopaedia Britannica* (8th ed.) XVII (1859) p. 165.

71 William Whewell, "Extracts from the anniversary address of the Rev. Wm. Whewell, before the Geological Society of London," *American Journal of Science* XXXVII (1839) p. 231.

72 Owen, "Report on British fossil reptiles, pt. 2," pp. 202-204.

73 [Robert Chambers], *Vestiges of the natural history of creation* (New York: Humanities Press, 1969 [reprint of first ed., 1844]) p. 112.

74 *Ibid.*, pp. 149-150.

75 *Ibid.*, pp. 229-230.

76 [Robert Chambers], *Explanations* (London: John Churchill, 1846) p. 87. Spurious reports of Mesozoic whales later caused both Lyell and Darwin some difficulty.

77 [Robert Chambers], *Vestiges of the natural history of creation* (London: John Churchill, 1853 [10th ed.]) pp. 117-118.

[78]Peter Bowler notes the striking similarity between this argument and the transcendental theory of progression of Louis Agassiz, a confirmed opponent of transmutation. See Fossils and progress, chapter 3.

[79]In later editions of the Vestiges, Chambers denied the existence of a simple, single evolutionary path. Rather, to account for observed irregularities in the fossil record, he postulated a number of parallel lines of development, each progressing independently. He ascribed a dual origin to mammals. According to his theory, the higher mammals developed directly from reptiles (from cetiosaur to whale, for example), and marsupials and monotremes derived from birds. The oviparous reproduction, duck-bill, and webbed feet of the platypus revealed this close relationship. According to Chambers, rodents and insectivores merely represented further stages in this ornithic line of descent, thus explaining the obvious similarity between Australian marsupials and their placental counterparts. According to this view, cows and kangaroos did not possess a common mammalian ancestor, the former having developed from reptiles and the latter from birds. See [Chambers], Vestiges (1853) pp. 238-239.

[80][Chambers], Vestiges [reprint of the first ed.] p. 219.

[81]Adam Sedgwick, A discourse on the studies of the University of Cambridge (London: John W. Parker; Cambridge: John Deighton, 1850 [5th ed.]) p. 261.

[82]Ibid., p. 272.

[83][David Brewster], "Art. IX--Vestiges of the natural history of creation. Fourth edition," North British Review III (1845) p. 493 and "Geology versus development," Fraser's Magazine XLII (1850) p. 369.

[84][Adam Sedgwick], "Art. I.-Vestiges of the natural history of creation. 8 vo. London: 1845," The Edinburgh Review LXXXII (1845) p. 60.

[85]James Dwight Dana, "Science and the Bible," Bibliotheca Sacra XIII (1856) pp. 125-126.

[86]Roderick I. Murchison, Siluria (London: John Murray, 1872 [5th ed.]) pp. 482-484.

[87]Theodor Plieninger, "Abbildungen von Zähnen aus der oberen Grenzbreccie des Keupers bei Degerloch und Steinenbronn vor, mit folgenden Bermerkungen," Verein für vaterländische Naturkunde in Würtemberg, Stuttgart. Jahreshefte III (1847) pp. 164-165.

[88]Charles Lyell, A manual of elementary geology (London: John Murray, 1852 [4th ed.]) pp. xiii-xviii.

[89]Richard Owen, A history of British fossil mammals, and birds (London: John van Voorst, 1846) p. 61.

[90]Richard Owen, "On some fossil reptilian and mammalian remains from the Purbecks," Geological Society of London. Quarterly Journal X (1854) p. 431.

[91]Richard Owen, Researches on the fossil remains of the extinct mammals of Australia (London: J. Erxleben, 1877) I, pp. 14, 27.

[92][Richard Owen], ["Lyell on life and its successive development,"] Quarterly Review LXXXIX (1851) pp. 439-442.

[93]Charles Lyell, "Anniversary address of the president," Geological Society of London. Quarterly Journal VII (1851) p. lxiv.

[94]Charles Lyell, Principles of geology (London: John Murray, 1853 [4th ed.]) pp. 139-140.

[95]Lyell, Manual, pp. xxi-xxii.

[96]Alfred Russel Wallace, "On the law which has regulated the introduction of species," Annals and magazine of natural history s.2, XVI (1855) p. 196.

[97]Wilson, Introduction to Lyell's journal of species, p. xli.

[98]Ibid., p. xliv.

[99]Charles Lyell, Supplement to the fifth edition of a manual of elementary geology (London: John Murray, 1857) pp. 27-29.

[100]Wilson, Introduction to *Lyell's journals on species*, p. liv.

[101]Quoted in *ibid.*, p. lvi.

[102]Bartholomew, "Lyell and evolution."

[103]Quoted in M. J. S. Rudwick, "A critique of uniformitarian geology: a letter from W. D. Conybeare to Charles Lyell, 1841," *American Philosophical Society. Proceedings* III (1967) p. 282.

[104]For a discussion of Owen's divergent model of evolution, see Bowler, *Fossils and progress*, pp. 98-107. Also see Roy M. MacLeod, "Evolutionism and Richard Owen, 1830-1868: an episode in Darwin's century," *Isis* LVI (1965) pp. 259-280.

[105][Owen], ["Lyell on life,"] pp. 449-450.

[106]Hugh Falconer, "Description of two species of the fossil mammalian genus *Plagiaulax* from Purbeck," *Geological Society of London. Quarterly Journal* XIII (1857) p. 276.

[107]Lyell, *Supplement*, p. 24.

[108]Hugh Falconer, "On the disputed affinity of the mammalian genus *Plagiaulax*, from the Purbeck Beds," *Geological Society of London. Quarterly Journal* XVIII (1862) p. 365.

[109]Darwin to Falconer, 14 November 1862, in Charles Darwin, *More letters of Charles Darwin*, Francis Darwin, ed. (London: John Murray, 1903) I, p. 210.

[110]Richard Owen, "On the extinction and transmutation of species," published as an appendix to *On the classification and geographical distribution of the Mammalia* (London: John W. Parker and Son, 1859) p. 60.

[111]Richard Owen, *Paleontology* (Edinburgh: Adam and Charles Black, 1860) pp. 403-413. This is substantially the same as the earlier article in the *Encyclopaedia Britannica* with some additions regarding Darwin's theory of natural selection.

[112]Quoted in H. Lewis McKinney, Wallace and natural selection (New Haven and London: Yale University Press, 1972) p. 41.

[113]Charles Darwin, The origin of species, J. W. Burrow, ed. (Harmondsworth: Penguin Books, 1968) pp. 160-161.

[114]Lyell to Darwin, 8 September 1860, in Lyell's Journals, p. 474.

[115]Ibid., p. 189.

[116]Darwin to Lyell, 12 September [1860], in Charles Darwin, The life and letters of Charles Darwin, Francis Darwin, ed. (London: John Murray, 1887) II, p. 340.

[117]Lyell to Darwin, 28 August 1860, in Lyell's Journals, pp. 467-468.

[118]Darwin to Lyell, [23 September 1860], in Life and letters II, p. 344.

[119]Darwin to Lyell, 1 September [1860], ibid., p. 335.

[120]Lyell to Darwin, 18 September 1860, in Lyell's Journals, p. 475.

[121]Lyell to Darwin, 28 August 1860, ibid., p. 468.

[122]Darwin to Lyell, 12 September [1860], in Life and letters II, p. 339.

[123]Darwin to Lyell, [23 September 1860], in Life and letters II, p. 342.

[124]Bowler, Fossils and progress, p. 126.

[125]Charles Darwin, Notebooks on transmutation of species, Gavin de Beer, ed. (London: British Museum (Natural History), 1969) p. 51.

[126]Darwin to Lyell, 1 September [1860], in Life and letters II, p. 335.

[127]Charles Darwin, *The Descent of Man* (London: John Murray, 1888) p. 165.

[128]*Ibid.*, pp. 157-158.

[129]*Ibid.*, p. 162.

[130]Ernst Haeckel, *The history of creation* (New York: D. Appleton and Company, 1876) II, pp. 233-234.

[131]*Ibid.*, p. 291.

[132]Thomas Henry Huxley, "On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia," *Zoological Society of London*. *Proceedings* (1880) p. 658.

[133]*Ibid.*, p. 652.

Chapter IV

AUSTRALIA: LAND OF "LIVING FOSSILS"

The Stonesfield fossils presented yet another anomaly which attracted the attention of English naturalists. Biologists noted that the closest living analogues to the Stonesfield "marsupials" inhabited Australia. Moreover, fossil plants and marine animals bearing a close resemblance to living Australian species were found with the remains of the Mesozoic mammals. As theorists struggled to explain the puzzling distribution of marsupials in space and time, attention shifted to the peculiarities of the Australian environment. The general similarity between the flora and fauna of the English oolite and contemporary Australia led to the hypothesis that Australia represented an ancient world, preserving life forms which had disappeared from other parts of the world long ago.

This suggestion was generally accepted and aroused little discussion until Robert Chambers cited it as evidence in favor of his developmental theory. Then the "ancient" appearance of the Australian flora and fauna became the focus of a struggle between evolutionists and anti-evolutionists, with each side eager to find an explanation consistent with its own theories.

Evolutionists suggested that Australia, with its primitive plants and animals, represented an early stage in the development of life. Anti-evolutionists, on the other hand, suggested that the oolitic fossils and living Australian species merely represented similar adaptations to similar environments. As it became increasingly apparent that the principle of adaptation failed to account for the regularities of present and past geographic distribution, this explanation failed. Darwinists reinterpreted the problem, explaining the observed similarities as a result of migration, geographic isolation, and reduced competition. By applying a single theoretical model, Darwinists could explain the isolation of marsupials in Australia, the failure of marsupials to compete successfully against placentals, and the "ancient" appearance of the Australian flora and fauna. Efforts of concerned and devout Australian naturalists to combat this theoretical interpretation failed, and the "ancient" appearance of the Australian flora and fauna became a powerful argument in favor of evolution.

In 1830 the discovery of a number of mammalian remains in the Wellington Caves of New South Wales provided the first evidence of past mammalian distribution in Australia. Biologists were surprised to find that the peculiar character of living Australian mammals (their marsupial reproduction) extended to the extinct mammals of the recent geological past. This fact, combined with first-hand observations in South

America, suggested to Darwin the law of the succession of types, which provided important evidence in favor of evolution. It was, in fact, the law of succession which first attracted Darwin's attention to the problem of the origin of species.

As biologists gradually pieced together the available information concerning the biogeography of Australia, they began to conceive of Australia as a land of "living fossils," inhabited by primitive forms of plants, invertebrates, and mammals. Péron's discovery in 1802 of *Neotrigonia*, a marine clam found only in Australian waters, disconcerted paleontologists who had assumed that *Trigonia*[1] had been extinct since the Mesozoic. This was the first of the famous "living fossils" to be recognized as such, and it did not immediately suggest a general pattern.[2] The discovery of "marsupials" associated with *Trigonia* in the Mesozoic strata of Stonesfield suggested a further similarity between Australia and the European Mesozoic.[3]

Richard Owen extended this comparison even further. He suggested that Australia, with its marsupials, *Araucaria* and cycads (primitive plants), and its living *Clavagella*, *Terebratula* and *Trigonia* (marine invertebrates) "presents us with the picture, as it were, of the last remains of an old and worn-out world,--of one that has long been superseded in this hemisphere by other strata and a higher type of mammiferous organization. . . ."[4] It was not until 1837 that biologists first attributed the early appearance of Mesozoic "marsupials" to their primitive nature. A year later Owen suggested that the entire Australian flora and fauna was characterized by a similar primitive organization.

Until 1844, the similarity between the flora and fauna of the European Mesozoic and that currently living in Australia was noted with interest, but it was not regarded as a particularly important scientific observation, nor was it the subject of debate. In 1844, however, this situation changed dramatically. Chambers appropriated the observation as evidence in favor of his developmental theory. From this point on, debate focused on Australian animals as evidence for or against evolution.

As evidence in favor of his theory, Chambers referred to the observed similarity between the fossils of the European Mesozoic and the plants and animals living in Australia. He argued that Australia was younger than the other continents. According to Chambers, each continent progressed through the same series of developmental stages. Australia was at an early stage of that development, a stage Europe had experienced during the Mesozoic.

> Altogether, the plants and animals of this minor continent [Australia] convey the impression of an early system of things, such as might be displayed in other parts of the earth about the time of the oolite. In connexion with this circumstance, it is a fact of some importance, that the geognostic character of Australia, its vast arid plains, its little diversified surface and consequent paucity of streams, and the very slight development of volcanic rock on its surface, seem to indicate a system of physical

> conditions, such as we may suppose to have existed elsewhere in the oolitic era . . . . Australia thus appears as a portion of the earth which has, from some unknown causes, been belated in its physical and organic development. And certainly the greater part of its surface is not fitted to be an advantageous place of residence for beings above the marsupialia, and judging from analogy, it may yet be subjected to a series of changes in the highest degree inconvenient to any human beings who may have settled upon it.[5]

Chambers predicted that Australia would in the future undergo vast geological changes, similar to those Europe experienced during the Mesozoic and Cenozoic. In developing this argument, Chambers elaborated on the conclusions of naturalists like René Primevere Lesson who had earlier argued that Australia was the youngest continent, only recently elevated above the sea.[6]

In Explanations, a sequel to his Vestiges, Chambers clarified his ideas and defended his theory against its many vocal critics. According to Chambers, the perfection of the flora and fauna of an area was proportionate to the time it had existed as dry land. He claimed that the continuity in the chain of life (a continuity necessary for any evolutionary theory) implied that other continents had continued without submergence since at least the beginning of terrestrial life. Australia must have emerged from the sea some time later, because it was absurd to claim that geological change and organic life stood still in Australia while progressing on other continents.[7] According to Chambers' theory, Australian marsupials would, in the course of time, evolve into the higher placentals.

Gideon Mantell elaborated on the parallels between the living flora and fauna of isolated areas and the fossils of the European Mesozoic. He argued that the plants and animals of New Zealand corresponded to those of the Carboniferous and Triassic, Australia represented the English oolite, and life as it exists in the Galapagos Islands was comparable to that of the Age of Reptiles. For Mantell these similarities did not imply an evolutionary development but rather demonstrated that the same natural laws applied throughout all geological periods. Mantell wished to show that, whatever the cause of present geographic distribution, the same cause produced similar effects in the Mesozoic.[8]

Faced with Chambers' evolutionary interpretation of these parallels, special creationists were compelled to offer an alternative interpretation consistent with their own theories. Sedgwick suggested such an alternative in his anonymous review of the Vestiges. Sedgwick argued that the parallel between European oolitic fossils and living Australian flora and fauna did not imply that Australia was a younger continent. On the contrary, one might argue that it was extremely old, as old as the oolite.[9]

Sedgwick later elaborated on this theory. He agreed with Chambers that there had been a gradual progression in organic life through time, a progression paralleled by geological changes in the structure of the earth. This was entirely consistent with the theory of special creation, which held that the perfect adaptation of organisms to the environment in which they live necessarily implies the appearance of new plants and animals to fit new physical conditions. Sedgwick and other special creationists argued that the creation of new life forms was beyond the power of nature. New creations required the miraculous intervention of a Creator who acted outside the realm of natural law.

Sedgwick explained the correspondence between the European Mesozoic and present Australia as an example of similar adaptations to fit similar environments. He noted that no Mesozoic deposits had so far been discovered in Australia. This fact, he suggested, implied that Australia has existed as dry land since the Mesozoic and that it was one of the oldest continents on earth.[10]

Sedgwick was, however, reluctant to claim that the current flora and fauna of Australia was related to Mesozoic forms by direct descent. He noted that the living forms represented different species and often different genera from their oolitic counterparts. To accept living Australian marsupials as descendants of Mesozoic mammals, one must deny the stability of species. Sedgwick attributed the similarity in forms to a similarity in climate. It was the conditions of existence, rather than time, which determined the character and distribution of species.[11]

Sedgwick claimed that the correspondence between the plants and animals of the English Mesozoic and those living in Australia, far from supporting the development theory, offered a new argument against it, for the developmentalists failed to explain the absence of organic change on the ancient continent of Australia.[12] As long as organic changes were necessarily linked to geological changes, Sedgwick and other special creationists could explain organic progression as a natural consequence of adaptation of form to environment.

J. B. Jukes, in his Sketch of the physical structure of Australia (1850) carried the argument one step further. On the basis of his field experience in Australia, Jukes concluded that the physical character of Australia had remained nearly unchanged for a vast period of time. He suggested that the flora and fauna represented by the fossils of the English Mesozoic had at that time a world-wide distribution. The plants and animals of Australia may be descendants of Mesozoic species which survived due to the absence of extensive geological change.[13]

In the tenth edition of Vestiges (1853), Chambers responded to the attacks of his opponents by revising his argument considerably and rejecting his former claim that organic progress was linked to geological change. Development, Chambers now argued, was entirely dependent on time, not on external circumstances. If, as Chambers now claimed, organic progress proceeded independent of changes in the physical environment, it could no longer be explained as a product of adaptation of organisms to their environment. Chambers no longer referred to the geography and climate of Australia to explain the primitive nature of its flora and fauna; he rested his whole argument on its age.

> The hypothesis is equally applicable to the imperfect developments of life upon the more recently raised lands, such as the Galapagos islands and Australia. Development is a matter of time, and in the case of these regions, the full time has not yet elapsed. It is therefore exactly what we might expect, upon the natural hypothesis, that, in these regions, animals [sic] life should have yet hardly reached the mammalian stage, the point which was attained in our elder and greater province about the time of the oolite. On the other hand, no rational cause for this imperfect zoological show can be presented in consonance with the plan of special exertions.[14]

According to this view, the Australian mammalian fauna was largely limited to marsupials because they were the first mammals to evolve, not because the Australian environment was better suited to support marsupials than placentals. With this revised theory, Chambers could claim that Australia was anomalous only with respect to the theory of special creation; it was entirely consistent with his theory of development. By eliminating the concept of adaptation, he eliminated the only explanation special creationists could offer.

Chambers' idea of creation by law rather than by miracle was unacceptable with respect to both religious dogma and scientific theory. Special creationists adopted a theoretical explanation of the correspondence between the European Mesozoic and contemporary Australia which was specifically designed to refute Chambers' arguments. They attributed the observed similarities to adaptations to similar environments, rejecting Chambers' claim that organic progress occurred independent of environmental change.

These arguments were generally accepted in Australia as well. Colonial scientists adopted the theoretical views of their more conservative European colleagues and interpreted their own Australian experiences in a manner consistent with these theories. William Sharp Macleay believed that the gradual progression revealed in the fossil record was linked to physical changes in the earth's history. He attributed the absence of mammals in the early geological periods to the presence of large amounts of carbonic acid in the atmosphere.[15] He argued that Australia has existed as dry land since the Mesozoic,[16] and appears to have expected an almost identical correspondence between the species of the English Mesozoic and those recently living in Australia, e.g., he expected that wombats and Diprotodon would be found in the Mesozoic deposits of England.[17] Although W. B. Clarke believed that Australia had been subject to violent catastrophes within recent geological history, he, too, agreed that it was a continent of enormous antiquity.[18]

Ludwig Becker, German artist and self-educated naturalist, emigrated to Australia in 1851. He is best remembered in Australian history for his tragic (and unnecessary) death as a member of the Burke and Wills expedition.[19] Becker developed his own theory to explain the primitive nature of

Australian plants and animals. He agreed with Jukes that the primitive flora and fauna of Australia represented the survival of Mesozoic species which became extinct elsewhere, that Australia preserved aspects of an older order of things.[20] Like the English theorists, he attributed this survival to the absence of geological change in Australia and to the similarity of physical conditions in the English oolite and contemporary Australia. Becker hypothesized that light was the primary factor affecting development. Animals living in conditions where light is in short supply display a primitive organization. In the English Mesozoic, as in contemporary Australia, the climate was very hot. Animals were forced by the heat to seek cover during the day. They were active at night, and so did not receive the benefit of sunlight.[21] In support of this thesis, Becker pointed out that nearly all Australian marsupials are nocturnal. Becker believed that Australia, unlike other continents, had experienced so little geological activity since the time of the oolite that the plants and animals had been little affected. He attributed this lack of geological change to the existence of volcanoes which acted as ventilating ducts to relieve underground stresses before they built up to catastrophic proportions.[22] Becker's explanation, emphasizing the adaptation of organisms to their environment, remained consistent with the theory of special creation.

Richard Owen had been the first to suggest that nature in Australia represented the last remains of a worn-out world, its flora and fauna superseded elsewhere by plants and animals of a higher level of organization. He continued to support that view in 1859.[23] Owen constantly emphasized the appearance of design in nature, as manifested by the adaptation of each organism to the environment in which it lives. In fact, he suggested that failure to perceive design in nature signified an unhealthy, abnormal condition of the mind, perhaps a congenital defect.[24]

Owen sought to explain the isolation of marsupials in Australia as a special adaptation to the unique Australian environment. He claimed,

> The premature birth of the offspring, and its transference to the tegumentary pouch, in which it remains suspended to the nipple for a period answering to that of uterine life in higher mammals, relate to the peculiarities of the climate of Australia.
>
> The adventurous and much-enduring explorers of that continent bear uniform testimony to the want of water as the chief cause of their sufferings and danger. During the dry season the rivers are converted into pools, 'few and far between;' and the drought is sometimes continued so long as to dry up these. An ordinary non-marsupial quadruped, such as the wild cat or fox, having deposited her young in the nest or burrow, would in such a climate, at the droughtiest period of her existence, be compelled to travel a hundred, perhaps two hundred miles, in order to quench her thirst. Before she could return her blind and helpless litter would have perished. By the marsupial modification the mother is enabled to carry her offspring with her in the long migrations necessitated by the scarcity of water.
>
> With the climatal peculiarities of Australia, therefore, we may connect the peculiar modifications of those members of the mammalian class which are most widely distributed over that continent.[25]

Owen's explanation did not survive examination, because the conditions he described were not unique to Australia nor did they prevail in all parts of the continent. Darwin rejected Owen's claim that the Australian environment was particularly suited to support marsupials. He objected, "I have always thought it a gigantic hallucination of Owen. there are many marsupial species in Brazil; also, New Guinea, although humid, is tenanted by marsupials as exclusively as Australia."[26] Andrew Murray further objected that the deserts of other continents were successfully populated by placentals. Moreover, the luxuriant vegetation of the Mesozoic proved that the earliest marsupials existed in areas of abundant rainfall.[27]

Owen proposed that extinction could be largely attributed to gradual changes in physical geography which created new environmental conditions for which existing species were not suitably adapted.[28] These views suggest that Owen agreed with the prevailing view of Australia as an ancient continent which had experienced little geological change, and so preserved a primitive flora and fauna.

The similarity between the flora and fauna of Australia and that of the European Mesozoic suggested to Owen yet a further generalization. Noting the great geographic distance separating Australia and Europe, Owen proposed the following rule:

> that the deeper we penetrate the earth, or, in other words, the further we travel in <u>time</u> for the recovery of extinct

> mammals, the further we must travel in <u>space</u> to find their existing analogue.[29]

That is, the older fossil forms were to be found in places far removed from the living species which most closely approached them. Owen appealed to this rule to explain why the closest living analogues of the Mesozoic mammals existed only in Australia. Owen formulated the rule when little was known about paleontology outside of Europe. At the time, it seemed valid, but later evidence failed to confirm it.

As paleontological research continued, the exceptions to Owen's rule became more apparent. Darwinists were able to reinterpret his observations to conform to the theory of evolution by natural selection. They explained his conclusion as the predictable result of the combined effects of natural selection and isolation. The longer two continents had been isolated from one another, the more their flora and fauna diverged, and the further back in time one must go to find their common origin. Thus, once again, Darwinian evolutionists appropriated Owen's observations as evidence for a theory which directly contradicted his most cherished beliefs.

Sedgwick and Owen were compelled by Chambers' argument to construct a theoretical explanation for the observed similarity between the English Mesozoic and contemporary Australia which was consistent with progression but which would not lend added support to Chambers' developmental hypothesis. Lyell was faced with a different problem. He must construct an interpretation consistent with geological and organic uniformitarianism. First, Lyell denied that the flora and fauna of the Mesozoic represented a primitive stage of development. Although he conceded that the Araucaria and ferns (common in the European Mesozoic and in Australia) might be more primitive than the later dicotyledons, he argued that the presence of monocotyledons of a perfect structure in the Mesozoic strata refuted the argument for progression.[30] Further, Lyell denied that the fauna of Australia was in fact comparable to that of the European oolite, pointing out that Australia lacked the huge reptiles which predominated during the Mesozoic period. Lyell denied that Australia resembled an ancient order of nature, and explained the observed similarities as a result of similar adaptations to similar environments. He suggested that the lack of large reptiles might be due to differences in physical conditions. No area of the world today combines a tropical climate such as existed during the English Mesozoic with the unequal days and nights of European latitudes.[31]

Lyell specifically rejected Chambers' claim that organic progress was solely dependent on time. Denying progression entirely, he attributed all differences in geographic distribution to adaptations to different environments, suggesting

> that at certain periods of the past, as in our own days, the predominance of certain families of terrestrial mammalia has had more to do with conditions of space than of

> time, or in other words has been more governed by geographical circumstances than by a law of successive development of higher and higher grades of organisation, in proportion as the planet grew older.[32]

Like Owen, Lyell wished to ascribe the isolation of marsupials in Australia to the uniqueness of the Australian environment.

For those who rejected the evolutionary explanation, yet believed that the principle of adaptation was insufficient to explain the regularities of geographic distribution, the observed similarities between the species of the European Mesozoic and those of contemporary Australia became inexplicable. Louis Agassiz, for example, denied that organic change was linked to changes in the physical environment. Rather, he believed that the progression of organic life as observed in the fossil record revealed the gradual unfolding of God's plan for His creation. Agassiz agreed that Australia reflected an ancient aspect of organic nature. He conceded that the isolation of marsupials in Australia and their resemblance to the mammals of the Mesozoic was "not to be explained" but affirmed that it was not related to the physical environment.[33]

Before the publication of the Darwinian theory of natural selection, then, most naturalists explained the observed similarities between the fossils of the European oolite and the flora and fauna of Australia with reference to the principle of adaptation. Most readily conceded that the Mesozoic fossils represented a primitive stage of organization and that this ancient order of things was represented in the living plants and animals of Australia. Some, like Jukes and Becker, even suggested that Australian species were direct descendants of Mesozoic forms. These arguments developed as a deliberate attempt to refute the developmental theory of Robert Chambers, and most naturalists had little difficulty in formulating an explanation consistent with their theoretical beliefs.

With the development of the theory of natural selection, the problem acquired a new significance. According to Darwinian theory, one would hardly expect to find such a marked similarity between the flora and fauna of two different areas, widely separated in both space and time. Anti-evolutionists argued that the plants and animals of Australia served as a counter-example disproving the theory of evolution. Darwinists hastened to reinterpret the evidence within an evolutionary framework, thus transforming an argument against evolution into an argument in favor of it. As the dispute focused on the theory of natural selection, each side adjusted its approach to the problem to fit the new area of conflict.

At first the similarity between the European oolite and contemporary Australia seemed to provide a powerful argument against descent with modification. Anti-evolutionists emphasized the difference between the two groups of species and the discontinuities in the fossil record. John Phillips, arguing in favor of the fixity of species, perceived nature as the expression of the Divine Idea. Phillips challenged those who claimed that Australian species had descended from Mesozoic progenitors to explain how they came to be placed on the other side of the world. Moreover, for some species the process of evolution seemed to have stalled, showing very little change over a vast expanse of time and space, while other forms had entirely disappeared and new ones had appeared. Still less could one imagine that such similar associations of species could be derived by modification from different branches of life. According to Phillips, the fossils of the European Mesozoic and the flora and fauna now living in Australia were "really separate creations suited to partially similar conditions in very different periods of time . . ."[34]

David Page presented a similar argument based upon the adaptation of organisms to conditions of existence. According to Page, the resemblance must be explained by analogy, not by descent, for nature never repeats herself in time. Furthermore, the immediate predecessors of existing Australian species were huge marsupial herbivores like Diprotodon rather than small insectivores allied to the Mesozoic "marsupials."

> In some of its minor features the oolite may find an analogue in existing nature, but in its entirety it stands alone . . . a great life-epoch, whose forms are not to be confounded either with what has gone before, or with what has yet to follow.[35]

To explain the observed similarities, special creationists continually returned to the concept of adaptation. Meanwhile, progress in the study of geographic distribution demanded a better explanation. Old explanations based on adaptation to similar environments were no longer adequate as it became more and more apparent that species were limited to a single place of origin. If the characteristics of a given animal depended solely on its adaptation to its environment, one might expect to find the same species occupying the same environment in widely separated parts of the world. Such was not the case. Franz Unger, a German botanist whose work on plant geography and paleobotany had made him a convinced evolutionist by 1852, noted this difficulty.

> And why should not similar, or even perfectly identical plants originate in two or several parts of the globe, provided external circumstances are favorable? Theoretically speaking, there is, indeed, nothing to oppose to this, provided that the origin of species is brought about exclusively by external circumstances. But we are led to quite an opposite view by what we know of the distribution of existing plants. We know that every species . . . as a collection of countless individuals related by their mutual descent . . . was originally more or less confined to a circumscribed space, whence it spread centrifugally. Not a single species has as yet been found occupying two distinct territories which are evidently the result of two centres of creation . . . Nothing remains but to assume that either the New Holland plants emigrated to Europe, or (what is less probable) the former European plants which had an Australian character passed from Europe to New Holland.[36]

Unger argued that the facts of geographic distribution demonstrated the former existence of a continental link between Europe and Australia. Plants migrated into Europe across this land bridge, later to be replaced by new immigrants from Asia and elsewhere. Australia, now isolated due to the disappearance of the land bridge, escaped these later migrations.[37] This explanation, first applied to plant distribution, was readily extended to account for marsupial distribution.

The peculiarities of geographic distribution, particularly as exemplified in Australia, troubled Darwin as well. His letters reveal something of his attempts to deal with this issue. Darwin adopted the theory that the Australian flora and fauna represented the survival of Mesozoic forms.

> The view which I should have looked at as perhaps most probable . . . is that the whole world during the Secondary ages was inhabited by marsupials, araucarias . . . Banksia, etc.; and that these were supplanted and exterminated in the greater area of the north, but were left alive in the south. Whence these very ancient forms originally proceeded seems a hopeless enquiry.[38]

Darwin explained the survival of these ancient forms as a result of isolation and reduced competition. He believed that competitive superiority led to the dominance of Cenozoic species over Mesozoic species and of European species over Australian species.

> On our theory of Natural Selection, if the organisms of any area belonging to the Eocene or Secondary periods were put into competition with those now existing in the same area (or probably in any part of the world) they (i.e., the old ones) would be beaten hollow and be exterminated; if the theory be true, this must be so. In the same manner, I believe, a greater number of the productions of Asia, the largest territory in the world, would beat those of Australia, than conversely.[39]

Darwin attributed the competitive inferiority of Australian species to the comparative lack of competition in small, isolated areas. In the same way he explained the survival of "living fossils" like the platypus.[40]

Darwin suggested the outlines of this explanation in the first edition of the Origin. He emphasized the competitive superiority of plants and animals from larger areas where selection was more severe and thus explained the rapid migration of introduced European and Asian species into Australia.[41] In addition, he suggested that reduced competition, leading to a slower rate of evolutionary change, explained the greater uniformity among marsupials than among placentals.

> A set of animals, with their organization but little diversified, could hardly compete with a set more perfectly diversified in structure. It may be doubted for instance, whether the Australian marsupials, which are divided into groups differing but little from each other, and feebly representing, as Mr. Waterhouse and others have remarked, our carnivorous, ruminant, and rodent mammals, could successfully compete with these well-pronounced orders. In the Australian mammals we see the process of diversification in an early and incomplete stage of development.[24]

In 1862 Searles V. Wood elaborated on Darwin's suggestions to develop an explanation of the observed similarity between the flora and fauna of the European Mesozoic and living Australian forms. Wood used the concept of isolation to answer the arguments of the anti-evolutionists, reinterpreting the evidence to fit within the framework of Darwinian theory. Wood adapted earlier claims that the Australian flora and fauna were the descendants of Mesozoic forms, unchanged due to the absence of environmental change in Australia. He claimed that nearly all the land masses of the Mesozoic had been transformed by later geological and climatic changes, but a small remnant remained intact in Australia. The ancient fauna survived in Australia due to its isolation. Unequal rates of change experienced by different species did not, according to Wood, present serious difficulty because the influence exerted by changing physical conditions was greater on some forms of life than on others. In the small isolated Southern areas competition for existence had been less severe than on the larger land masses of the Northern hemisphere and as a result change had been slower.[43] The geological and geographical evidence could only be understood by a branching model of evolution, allowing for differing rates of change.

Wood attacked previous attempts to explain the character of Australian species as a special creation perfectly designed to fit the special nature of the Australian environment. This explanation obviously failed in the light of experience with introduced species such as cats and rabbits which thrived so well in the Australian bush that they seriously threatened the survival of indigenous species.[44] Natural selection works precisely because adaptation is not perfect.

With the failure of the explanation based on adaptation, Wood claimed that the resemblance between existing

Australian species and those of the English Mesozoic could only be explained as a result of isolation and natural selection.

> If, therefore, it can be shown with any degree of probability that there exist remnants of an earlier state of being, preserved in a state of complete isolation, which belong exclusively to one or more of the simpler forms, as is the case with implacental mammalia of Australia, another link is added to the chain of evidence that all forms of life have originated, by a natural course of reproduction and slow variation, from one common root.[45]

Thomas Henry Huxley independently developed a similar argument in 1870. Huxley sought to explain the sharp break between the flora and fauna of the Mesozoic and that of the Cenozoic, a discontinuity in the fossil record which presented great difficulties for evolutionists. Huxley hypothesized that geographic changes occurred at the end of the Mesozoic which made possible the migration of a new flora and fauna into Europe. These species, which had evolved elsewhere, replaced the Mesozoic forms previously existing there. Australia escaped this migration because it had become isolated from the rest of the world during the Mesozoic and so preserved the remnants of the plants and animals of the era.[46] Alfred Russel Wallace supported these views as well, explaining the primitive nature of the Australian species as a result of migration and subsequent early isolation.[47]

Darwin, Wood, Huxley, and Wallace all sought an explanation for the peculiarities of Australian nature which would provide evidence for the Darwinian theory of natural selection.

In this they were only partially successful. Andrew Murray, for example, accepted the argument as evidence in favor of evolution, but rejected the mechanism of natural selection.[48] By placing the emphasis on the effects of isolation rather than on adaptation, evolutionists were able to reverse Chambers' argument. Australian animals were peculiar, not because they were younger but because they were older. In so doing, they took advantage of the arguments of the special creationists, so carefully constructed to combat Chambers' developmental theory. Thus they were able to transform an argument against evolution into an argument in favor of it.

Such explanations did not meet with favor in Australia, where scientific activity was strongly influenced by religious belief. Among the few men who turned aside from practical concerns to the more esoteric realm of science, many were clergymen who devoted themselves to the study of nature in order to achieve a better understanding of the Creator. Moreover, the general lack of advanced scientific training, coupled with the difficulty of acquiring new publications from Europe, led to a staunch conservatism with respect to scientific theory.[49]

Frederick McCoy entered the Australian scientific community in 1854 as the Professor of Natural History at Melbourne University. McCoy had already established a sound reputation as a paleontologist in Ireland and England. While at the University of Cambridge, he worked in close association with Adam Sedgwick who may have contributed to McCoy's resistance to Darwinian theory. Like Sedgwick, McCoy believed in special creation and interpreted the evidence of design in nature as proof for the existence of God.

As a paleontologist, McCoy faced some special problems peculiar to the study of Australian fossils. The uniqueness of the living flora and fauna suggest that Australia may have displayed noticeable peculiarities throughout its entire geological history. This posed many problems for geologists, because the identification of the age of a given strata could only be determined by comparison with similar strata of known age. For these reasons, W. S. Macleay argued that Australian fossils should not be classified by scientists in England, but should be studied independently by naturalists living in Australia. Since marsupials, now extinct in England, continue to survive in Australia, he argued that other fossil forms might have inhabited the two different hemispheres at two very different time periods.[50] W. B. Clarke expressed a similar concern to McCoy who was working in England on the classification of the fossil plants of New South Wales.

> Of course here in Australia geology owing to want of means of comparison, has difficulties in its way: the peculiar condition of this portion of the earth apparently at all times since the commencement of its dry land, renders some of its phenomena peculiar.[51]

Once in Australia, McCoy began to find evidence which challenged the assumption that Australian forms displayed a peculiar organization from an early geological period. Before the appearance of Darwin's Origin, McCoy did not attach any special theoretical significance to these discoveries. Sedgwick suggested that they offered yet further evidence against Lyell's uniformitarian views on paleontology. Writing to McCoy in 1858, he commented,

> Your account of the fossils is most interesting. Do not the facts you mention prove that the Fauna of the northern and southern hemisphere were far more alike during the paleozoic period than they are now? Lyell fights against this but I think to no purpose.[52]

Sedgwick argued that the fossil record did not reveal a static equilibrium in organic nature, as Lyell claimed, but rather demonstrated a gradual progression toward the present system of things.

With the delineation of the theory of natural selection, McCoy's discoveries acquired a new significance. As Melbourne's Professor of Natural History and the first Director of the National Museum of Victoria, McCoy had become the chief representative of institutionalized science in Victoria. As such, he felt called upon to present a coherent theoretical interpretation of Australian natural history which would defeat the Darwinian theory, so damaging to treasured religious beliefs. On the basis of his paleontological researches in Australia, McCoy launched a concerted attack against the view that Australia preserved the remnants of an ancient world.

McCoy argued that Australian fossils revealed a general uniformity of plants and animals over the entire world during the Paleozoic period. Moreover, the same uniformity could be traced through Australian Mesozoic deposits. McCoy's identification of the Australian coalfields as Mesozoic,[53] contradicted previous claims that Australia had remained elevated above the ocean since the Mesozoic. McCoy argued that Australia, like the rest of the world, was almost totally covered by water during the early Tertiary. Every trace of previous creations had been destroyed, to be replaced by a totally new set of plants and animals, represented in Australia by huge marsupials like Diprotodon.[54]

McCoy's conclusions were immediately seized upon by Henry Barkly, the President of the Royal Society of Victoria and Governor of that colony, as ammunition in the holy war against Darwinian theory. Barkly used McCoy's work to refute Darwinian claims and called upon geologists to join in "the refutation of errors so pernicious to the very existence of Christianity."[55]

In 1870 a series of newspaper articles popularizing these ideas appeared over the pseudonym "Microzoon," written by McCoy himself.[56] Microzoon specifically attacked Huxley's argument that Australia had remained isolated and unaltered for a vast period of time, its plants and animals the surviving remnants of Mesozoic forms. He emphasized the differences between the European oolite and contemporary Australia, notably the presence of placental bats, rodents, and dingos in Australia. He argued that the peculiar plants and animals of Australia constituted a new flora and fauna specially created to replace the species destroyed when Australia sank beneath the sea in the early Tertiary. According to Microzoon, the sharp contrast between Australia's ancient and living fauna disproved any theory of descent with modification.[57] To combat Darwinian evolution McCoy revived Sedgwick's argument of discontinuous progression and applied it to the Australian fossils.

Such views were generally accepted in Australia where they confirmed prevailing religious and scientific opinions. For example, the Catholic priest Julian Tenison-Woods read the Vestiges with interest, accepting many of Chambers' theoretical opinions. But he perceived Darwin's natural selection, with its reliance on chance rather than God to propel organic progression, as a serious threat to religious truth. He adopted McCoy's argument against evolution, reversing his former geological opinions.

In 1862, while apparently still unfamiliar with Darwin's work, Tenison-Woods published Geological observations in South Australia. Tenison-Woods perceived no real conflict between science and the certainty of revelation. Apparent conflicts arose, he argued, when scientists drew conclusions from insufficient data or theologians insisted on a literal interpretation of Scripture. Tenison-Woods rejected diluvialist attempts to explain fossil deposits as a result of the

Biblical flood, arguing that revelation was better off without the equivocal support of misinterpreted facts.[58] He adopted the assumptions of natural theology, studying the Creation in order to understand the Creator.

Tenison-Woods noted that the fossil record revealed a progression in organic complexity through time. But in Australia development lagged behind the rest of the world. He attributed the observed similarity between living Australian forms and the fossils of the European Mesozoic to adaptation to similar conditions.

Tenison-Woods adopted Chambers' idea that Australia had only recently emerged from the sea (although he did acknowledge the possibility of its continued existence as dry land from the Mesozoic onward), thus accounting for its poor soil and its meagre, primitive flora and fauna.[59] Tenison-Woods found Chambers' concepts of natural law and transmutation unobjectionable, for both depended upon the rational foresight of the Creator.

Tenison-Woods' major objection to Chambers' argument was that it limited the Creator's freedom of choice. Most progressionist theories, Tenison-Woods complained, seemed to imply that the order of fossils was dictated by necessity, not by choice. If plants and animals were perfectly adapted to their environment and if organic progression could thus be linked to a directional change in physical conditions on earth, then it followed that the plants and animals of any given period were the only ones suited to live in that environment. In fact, Tenison-Woods claimed, the presence of man in Australia proved otherwise.

Conditions in Australia approximated those existing in the Mesozoic, yet Australian aborigines survived among the primitive plants and animals. This in itself, argued Tenison-Woods, proved that God could have created man at an earlier geological period if he chose to do so.

> The very fact that man finds an easy, nay, comfortable subsistence in Australia which . . . is far behind other countries in natural development, proves, on the one hand, the perfect adaptability of the earth as a residence for man at other periods--besides our small conception of the plans of the Creator; while, on the other, the better adaptation of the other parts of the earth, more advanced and developed, proves the beneficence of the Author of it all in perfecting man's habitation to the highest degree before He placed him upon it.[60]

Tenison-Woods suggested that the wretched, degraded condition of the aborigines may be attributed to the primitive environment in which they lived. Early European settlers in Australia found the climate harsh and uninviting. The primitive flora and fauna, it was claimed, could not support the demands of civilized man. According to Tenison-Woods, the importers of sheep and cattle improved the environment by introducing the blessings of a more advanced (Tertiary) fauna.[61] Berthold Seemann echoed this view, asking, "Is the whole of this vegetation, and the animals dependent upon it for support, to disappear before the continent becomes a fit abode for the white man?"[62] To bring Australia the benefits of civilization, Europeans found it necessary to alter the environment considerably. Thus, the attempts of the early acclimatization societies to introduce economically useful and aesthetically pleasing European plants and animals may be seen as a deliberate effort to "modernize" the primitive environment.[63]

By 1876 Tenison-Woods, influenced by McCoy's anti-Darwinist argument, reversed his opinion. He now argued that Australia and Europe had possessed similar plants and animals during the Mesozoic, that Australia was subsequently submerged beneath the sea and, upon emergence, was populated with a new, distinct flora and fauna unrelated to any which preceded it. Tenison-Woods claimed,

> . . . in all my examinations of our fossil and living fauna I have carefully sought for any reasonable evidence in favour of evolution or clue to its mode of operation, and have found none--none whatever. I must add that Australian geology, whether reluctantly or not, must admit that she can urge nothing in favour of that theory being true, the true explanation of nature as we find it.
>
> But in the supposition that in our land fauna and flora we have a relic of secondary epoch, there is something not easy to reconcile with the evolution hypothesis. Types remaining stationary during such long periods of time appear, to my imperfect knowledge of evolution, inconsistent with the necessary postulates.[64]

In Australia special creation survived as a scientific hypothesis long after it had been abandoned by European theorists.

However influential McCoy may have been in Australia, in Europe his views were generally ignored. If mentioned at all, his arguments were dismissed without discussion.[65] McCoy represented the older tradition of natural theology, an approach to nature which was fast becoming obsolete in Europe. European scientists were eager to acquire observational data from their colonial colleagues, but they paid little attention to Australian scientific theories which they tended to regard as naive and simplistic. Moreover, McCoy's observations did not seriously threaten Darwinian theory. The general uniformity of organisms at early geological periods followed by an increasing peculiarity in Australia flora and fauna remained consistent with the Darwinian explanation of isolation followed by gradual modification.

Despite the efforts of concerned and devout Australian naturalists, the "ancient" appearance of the Australian flora and fauna became a powerful argument in favor of evolution. The expanding body of knowledge about present and past geographic distribution provided evolutionists with a structured set of observations which could be explained as a logical consequence of Darwinian evolution. With the failure of explanations based on adaptation, special creationists were unable to explain the peculiarities of geographic distribution, especially the anomalies presented by the species of the Southern hemisphere.

In the early decades of the nineteenth century Australia was sparsely settled and its colonists had little time to devote to scientific investigation. Paleontological discoveries were rare and the colonists themselves lacked the scientific expertise necessary to interpret their significance, but the Australian fossil evidence provided European biologists with the key to a fundamental law of distribution. The exploration of the Wellington Caves of New South Wales in 1830 led to the first major discovery of mammalian fossils in Australia. This discovery aroused a great deal of interest and speculation in Europe because it provided the first evidence of past geographic distribution in Australia, a continent known for its biological peculiarities. The Wellington fossils challenged some of the treasured assumptions of the Scriptural geologists, particularly belief in the universal Deluge. More significantly, the fact that the recently extinct Australian mammals were marsupials and thus clearly related to the living mammals of Australia led to the formulation of the "law of the succession of types," a generalization of fundamental importance in the development of evolutionary theory.

The first report of fossil vertebrates from Australia appeared in the Sydney Gazette of 1829. Naval surgeon Peter Cunningham concluded that these fossils were very old, dating from before the time of the Biblical flood. Their large size coupled with their similarity to human vertebrae led to the suggestion that a race of giants or gigantic humanoid animals lived on the continent before the Deluge. Such an interpretation reflected the traditional religious assumptions and the scientific naivete of many Australians of that time.[66]

Colonist George Ranken first discovered the fossil remains of the Wellington Caves[67] and brought them to the attention of the Surveyor-General of New South Wales, T. L. Mitchell, who conducted further explorations.[68] John Dunmore Lang first announced the discovery, interpreting the fossils in the context of traditional Christian belief as proof of the literal truth of Scripture and evidence of the wisdom and foresight of the Creator. Lang, a Presbyterian clergyman with an amateur interest in geology, was eager to show that the facts of science were not in conflict with the Mosaic account of creation and the Deluge.[69] Relying on the aborigines to identify the animals,[70] he noted that many of them were extinct or at least were no longer to be found in New South Wales. Lang attributed their extinction to natural catastrophe, a catastrophe which did not materially change the external appearance of the country, i.e., a flood. Lang regarded this discovery as further evidence of the antiquity of Australia, and concluded,

> While this very interesting discovery supplies us, therefore, with another convincing proof of the reality and universality of the deluge, it supplies us also with a powerful motive of gratitude to Divine Providence for that long-forgotten visitation. For if this territory were over-run with such beasts of prey as the antediluvian inhabitants of the cave at Wellington Valley, it would not have been so eligible a place for the residence of man as it actually is. The tiger or hyaena would have been a much more formidable enemy to the Bathurst settler than

> the despicable native dog, though indeed they would certainly have afforded a much nobler game to the gentelmeu [sic] of the Bathurst Hunt. And if the huge rhinoceros had inhabited the lagoons of Hunter's River, it might have been a much more serious work to displace him than to shoot the pelican or emu.[71]

Just as the European colonists sought to explain the huge fossils in a manner consistent with their Christian beliefs, so the aborigines explained them within their own frame of reference. The aborigines of Eastern Australia were very fearful of the bunyip, a legendary aquatic monster inhabiting deep waterholes and roaming the billabongs at night. Confronted with the fossil remains of gigantic animals, the natives often identified these as the remains of the bunyip. As one colonist observed,

> It may not be amiss to state that all the Natives throughout these Northern Districts have a tradition relative to a very large animal having at some time existed in the Creeks & Rivers & by many it is said that such animals now exist & several of the Fossil bones which I have at various times shown to them they have ascribed to them. Whether such animals as those to which they refer be yet living is a matter of doubt, but their fear of them is certainly not the less & their dread of bathing in the very large waterholes is well known--[72]

J. W. Gregory, Professor of Geology at the University of Melbourne (later at the University of Glasgow), suggested that the Aboriginal legends of gigantic monsters might be based upon a knowledge of the living Diprotodon.[73]

Examples of the Wellington Cave fossils were sent to Robert Jameson, Professor of Natural History at Edinburgh

University, for identification by European experts. Jameson forwarded them to W. Clift, Curator of the Hunterian Museum, who identified the remains of a dasyurid, wombat, kangaroo, phalangers, and koala. All the bones belonged to marsupials of the Australian type with one apparent exception. Lang had suggested that a large thigh bone found in the caves belonged to an Irish elk, rhino, or elephant.[74] Clift compared it to the thigh of an ox or hippo,[75] and W. Pentland claimed that it represented the remains of an elephant.[76] From these data, Jameson observed that Australia, like Europe, was formerly populated with gigantic animals which have since become extinct. Moreover, he argued that the cause of extinction was the same in Europe and Australia, but he did not identify this cause as the Biblical flood. Most significantly, he concluded ". . that New Holland was, at a former period, distinguished from the other parts of the world, by the same peculiarities in the organization of its animals, which so strikingly characterize it at the present day."[77]

This conclusion challenged catastrophist theories. If all the plants and animals of the Tertiary were destroyed by a universal deluge and subsequently replaced by a specially created, entirely new set of plants and animals, why should there be any continuity between existing species and recently extinct species? In fact, from the principle of adaptation one would expect that organic changes would accompany drastic changes in the physical environment.

Scriptural geologists like William Buckland seized on the single placental exception in an effort to reconcile geology and Scripture. In Reliquiae diluvianae (1824) Buckland argued that the recent fossilized remains of large mammals, especially elephants, which are now extinct revealed the action of a universal deluge. These inhabitants of the antediluvian world were, he argued, destroyed by a world-wide flood, as described in Genesis.[78] Australian naturalists adopted Buckland's argument. Thomas Mitchell's cave explorations were inspired by a desire to dicover antediluvian remains which would further support Buckland's theory,[79] and Lang's interpretation of the Wellington fossils represented a conscious attempt to make the Australian evidence conform to these theories. Buckland wished to emphasize the discontinuities in fossil distribution. He argued that as one set of plants and animals became extinct, it was replaced by another, unrelated association of species. Thus Buckland eagerly publicized the alleged discovery of large fossil placentals in Australia.[80] Similarly, he seized upon later announcements of an ostrich-like bird in New Zealand and an elephant in Australia.[81] If the presence of placentals in Australia during the Tertiary could be established, then the discontinuities between these recently extinct mammals and those now living in Australia would support catastrophist geology. In addition, it would cast doubt on any theory of transmutation, which was the lesson which the English geologist Roderick Murchison wished to draw from it.[82]

In fact, the Wellington fossils led to quite the opposite conclusion. Most European scientists were struck with the similarities between the fossils and living species rather than with the differences. Pentland, for example, observed,

> . . . with a single exception, all the genera to which these fossils are referable, are now found inhabiting the Australasian Continent, a remarkable coincidence with the fossil animals of the same geological epoch in Europe, where, with few exceptions, the animals which have been found in what have been called Diluvial Deposits, belong to genera still inhabiting our countries.[83]

This fact was taken to cast doubt on Buckland's diluvialist theories. Mitchell wrote to George Ranken concerning the significance of their discovery at Wellington,

> I understand Buckland's nose is put completely out of joint by the bones from Australia, their not being those of lions and hyenas is, I find, a fact which is considered in England to entirely upset his theory. And I have now heard from the best authority that the fact of their fossil bones belonging to animals similar to those now existing has worked a great change in all their learned speculating on such subjects at home.[84]

European scientists were surprised to find the peculiarities of the living Australian flora and fauna reflected in the fossil species as well. This discovery suggested that the laws of geographic distribution which currently confine particular groups of animals within particular geographic regions applied in the recent geologic past as well. The Wellington discoveries, coupled with Darwin's observations in South America, led him to formulate the law of the succession of types. This law provided important evidence in favor of evolution and, indeed, turned Darwin's attention toward the problem of the origin of species.

Darwin is credited with developing the law in 1837 as a result of his fossil discoveries in South America. Finding the remains of giant mammals related to sloths, llamas, and armadillos, he noted that these extinct mammals are now represented by smaller animals, also confined to South America, which display the same peculiarities of anatomy as their larger prototypes.[85]

> The most important result of this discovery, is the confirmation of the law that existing animals have a close relation in form with extinct species . . . The law of the succession of types, although subject to some remarkable exceptions, must possess the highest interest to every philosophical naturalist, and was first clearly observed in Australia, where fossil remains of a large and extinct species of Kangaroo and other marsupial animals were discovered buried in a cave. In America the most marked change among the mammalia has been the loss of several species of Mastodon, of an elephant, and of the horse. . . . If Buffon had known of these gigantic armadilloes, llamas, great rodents, and lost pachydermata, he would have said with a greater semblance of truth, that the creative force in America had lost its vigour, rather than that it had never possessed such powers.[86]

Contemplating the Wellington fossils, Thomas Mitchell offered a similar suggestion with regard to the waning power of Australian nature.

> It is consolatory here to find that Australia did once support herbivorous animals of such magnitude--and that an animal so well provided for a country of burning woods and fallen timber--by its young = [sic] protecting pouch and saltatory power has always belonged to Australia--although the curious gradation of species--and the diminutive character of existing classes seem to indicate the energies of animal nature here to be on the wane--unless indeed this is a wise provision of providence for the introduction of those other large animals by man's agency--which have been found better suited to his wants.[87]

The influence of the Australian fossils on the development of the law of the succession of types has not been generally recognized. It is, however, doubtful that Darwin could have developed a comprehensive generalization on the basis of a single South American example. In fact, Darwin himself cited Clift's work on the Wellington fossils as evidence for the law of succession.[88] Clift's work was also cited favorably in Lyell's Principles of Geology,[89] which Darwin had studied while on the Beagle.[90] In 1831 E. W. Brayley suggested the possibility of such a correlation in distribution, but the Wellington Caves provided the first and most dramatic evidence of the law.[91]

Richard Owen developed a similar law, again based on the fossils of the Wellington Caves. In 1844 Owen cited the Australian fossils as evidence

> that, with extinct as with existing Mammalia, particular forms were assigned to particular provinces, and, what is still more interesting and suggestive, that the same forms were restricted to the same provinces at a former geological period as they are at the present day.[92]

This generalization was frequently repeated in Owen's publications[93] and, together with his work on Darwin's "Beagle" fossils, formed the basis of his claim to priority in formulating the law of succession. Although Darwin readily acknowledged that Owen had extended the law to apply to the Old World, Owen's attempt to steal credit for the law annoyed him. In a letter to Lyell, he complained,

> Why I gave in some detail references in the . . . [Origin] is that Owen (not the first occasion with respect to myself and others) quietly ignores my having ever generalised on the subject, and makes a great fuss on more than one occasion at having discovered the law of succession. . . . Long before Owen published I had in MS. worked out the succession of types in the Old World (as I remember telling Sedgwick, who of course disbelieved it).[94]

As further research provided additional evidence for the law of succession,[95] it became an accepted rule of geographic distribution. The close relationship between existing species and recently extinct species strongly suggested an evolutionary connection. Such a connection was, of course, denied by the anti-evolutionists, although they could offer no alternative explanation. Agassiz, for example, acknowledged the law but specifically denied any genetic connection between living and fossil species on the grounds that they belonged to different genera.[96]

The law of succession is, in fact, a special case of Wallace's broader law of 1855, which asserted that "every species has come into existence coincident both in time and space with a pre-existing closely allied species.[97] Wallace's argument that present distribution could be explained as a result of isolation and divergence provided the foundation for an evolutionary explanation of past and present geographic distribution.

Although the discoveries at Wellington Caves led to the formulation of the law of succession, they also offered a major exception to it. Naturalists wished to establish that the laws of geographic distribution which confined marsupials to Australia and excluded large placentals applied before existing species appeared. Reports of a fossil elephant clearly violated this rule. Thomas Mitchell had already questioned the identification. He wrote to Ranken, "They find most of them [the Wellington fossils] to be wombats and kangaroos, but Cuvier[98] calls your large bone an elephant's. The London surgeons, however, seemed puzzled about it, and I have doubts . . ."[99]

In 1838 Owen resolved this anomaly by identifying the large Wellington fossil as that of Diprotodon australis (Owen), a giant, wombat-like marsupial.[100] But this was not the end of claims that elephants once roamed the Australian bush. In 1843 Owen identified a fossil from the Darling Downs as a Dinotherium, an extinct placental pachyderm.[101] The following year he corrected this error, noting that these bones, too, belonged to the Diprotodon. At the same time, however, he identified a fossil tooth, ostensibly from Australia, as that of a Mastodon.[102] This tooth, which the Polish explorer

Strzelecki claimed to have acquired from an Australian Aborigine, served as the basis for later accounts of mastodons in Australia.[103] These false identifications and conflicting reports caused a great deal of confusion. In Europe, as in Australia,[104] the former existence of an Australian placental pachyderm was generally accepted.

The Australian mastodon remained an anomaly until 1863 when the British paleontologist Hugh Falconer challenged its existence. Falconer wished to confirm the generalization that Australia represented a fragment of an older world where development had been suspended while it progressed on other continents. The presence of a large placental like the mastodon challenged this. Falconer agreed that Strzelecki's tooth belonged to a mastodon, but noted that it appeared to belong to a South American species. Moreover, Strzelecki had on a previous occasion confused specimens of Australian and South American origin. Since claims for the existence of mastodons in Australia rested solely on this isolated example, Falconer concluded there must be an error respecting the origin of the fossil.[105] Owen quietly abandoned his claims.[106]

The controversy surrounding the Australian mastodon has been documented in some detail because it offered a serious challenge to the law of succession.[107] A naturalist whose sole concern was to establish the rule that current laws of geographic distribution applied in the recent geological past as well might explain the Australian mastodon as the proverbial "exception which proves the rule." After all, as Owen pointed out, the mastodon is the most cosmopolitan extinct mammalian genus, and so one might expect it to have an unusually wide distribution.[108] If, however, one wished to explain the unique character of the Australian fauna as a result of isolation and natural selection, then such an explanation is unacceptable. Darwinists claimed that Australia had at an early geological period become separated from the rest of the world by vast oceans. Darwin's mechanisms of chance dispersal could hardly account for the migration of the huge mastodons. For this reason, Darwin rejoiced at Falconer's attack on the Australian mastodon, commenting, "I never did or could believe in him."[109]

The law of succession, now firmly established, provided a powerful argument in favor of evolution. With the failure of explanations based on adaptation, the similarity between living animals and recent fossil species could not be explained solely on the basis of adaptation to similar environments. In fact, the observed similarities further discredited the adaptation argument, since extensive environmental changes had occurred during the intervening time. Thus, the law of succession provided yet another important rule of geographic distribution which the theories of the anti-evolutionists failed to explain. Moreover, the law of succession played an important role in convincing

Darwin of the validity of evolution. He wrote to Lyell, "In fact, this law, with the Galapagos distribution, first turned my mind on the origin of species."[110]

NOTES

[1]*Neotrigonia* was at first classified in the genus *Trigonia*.

[2]The existence of such a living fossil was recognized as an anomaly requiring explanation. Various contemporary theories adopted differing explanations for this singular fact. See Stephen Jay Gould, "*Trigonia* and the origin of species," *Journal of the History of Biology* I (1968) pp. 41-56.

[3]William John Broderip, "Observations on the jaw of a fossil mammiferous animal, found in the Stonesfield slate," *Zoological Journal* XI (1827) p. 411.

[4]Richard Owen, "Observations on the fossils representing the *Thylacotherium Prevostii*, Valenciennes, with reference to the doubts of its mammalian and marsupial nature recently promulgated, and on the *Phascolotherium Bucklandi* [1838]," *Geological Society of London. Transactions* VI (1842) p. 63.

[5][Robert Chambers], *Vestiges of the natural history of creation* (New York: Humanities Press, 1969 [reprint of first ed., 1844]) p. 258.

[6]René Primevere Lesson, *Histoire naturelle générale et particulière des mammifères et des oiseaux découverts depuis 1788 jusqu'à nos jours. Vol. III Races humaines, orangs et gibbons* (Paris: Baudouin Frères, 1829) p. 179.

[7][Robert Chambers], *Explanations* (London: John Churchill, 1846) pp. 163-164.

[8]Gideon Mantell, *The wonders of geology* (London: Henry G. Bohn, 1848 [6th ed.]) II, p. 894.

[9][Adam Sedgwick], "Art. I.-*Vestiges of the natural history of creation*. 8vo. London: 1845," *The Edinburgh Review* LXXXII (1845) p. 58

[10]Adam Sedgwick, *A discourse on the studies of the University of Cambridge* (London: John W. Parker; Cambridge: John Deighton, 1850 [5th ed.]) pp. 263-264.

[11] Ibid., [p. 324].

[12] Ibid., p. 264.

[13] J. Beete Jukes, A sketch of the physical structure of Australia (London: T. & W. Boone, 1850) pp. 89-90.

[14] [Robert Chambers], Vestiges of the natural history of creation (London: John Churchill, 1853 [10th ed]) pp. 117-118.

[15] William Sharp Macleay to W. B. Clarke, 26 June 1842, Clarke Correspondence, Mitchell Library, Uncat. MSS set 139, item 11.

[16] William Sharp Macleay, ["Letter to the editor,"] Sydney Morning Herald, 2 December 1847, p. 3.

[17] William Sharp Macleay to Richard Owen, 9 March 1858, Owen Correspondence, British Museum, folio 345.

[18] W. B. Clarke, "Mr. Turner's Diprotodon," Sydney Morning Herald, 6 December 1847, p. 2.

[19] Ludwig Becker, "On the age of the animal and vegetable kingdom of Australia relatively to that of the rest of the world; and some remarks on the changes of this land by upheavals," Philosophical Institute of Victoria. Transactions I (1856) pp. 15-16.

[20] See Marjorie Tipping, The life and work of Ludwig Becker, M.A. Thesis, University of Melbourne, 1978.

[21] Ludwig Becker, "Über das Alter der lebenden Thier-und-Pflanzen-Welt in Australien," Neues Jahrbuch für Mineralogie, Geognosie, Geologie, und Petrefakten-kunde (1858) p. 536.

[22] Ibid., p. 539.

[23] Richard Owen, "Paleontology," in Encyclopaedia Britannica (8th ed.) XVII (1859) p. 159.

[24] Ibid., p. 160. This remark was specifically intended to disparage the theoretical views and intellectual abilities of Etienne Geoffroy Santi-Hilaire.

[25]Richard Owen, On the classification and geographical distribution of the Mammalia (London: John W. Parker and Son, 1859) pp. 28-29.

[26]Charles Darwin to Charles Lyell, 23 [September 1860], quoted in P. Thomas Carroll, Annotated calendar of the letters of Charles Darwin in the library of the American Philosophical Society (Wilmington, Delaware: Scholarly Resources Inc., 1976) #227, p. 85.

[27]Andrew Murray, The geographical distribution of mammals (London: Day and Son, Limited, 1866) p. 285.

[28]Owen, "Paleontology," p. 175.

[29]Richard Owen, "On the geographical distribution of extinct Mammalia," Annals and Magazine of Natural History XVII (1846) p. 201. This generalization played a prominent part in Owen's later discussions of geographic distribution and fossil history. See "On the extinction and transmutation of species," published as an appendix to On the classification and geographical distribution of the Mammalia (London: John W. Parker and Son, 1859) p. 55 and Paleontology (Edinburgh: Adam and Charles Black, 1860) p. 397.

[30]Charles Lyell, A manual of elementary geology (London: John Murray, 1852 [4th ed.]) pp. 270-271.

[31]Charles Lyell, Principles of geology (London: John Murray, 1853 [4th ed.]) pp. 140-141.

[32]Charles Lyell, Supplement to the fifth edition of a manual of elementary geology (London: John Murray, 1857) p. 29.

[33]Louis Agassiz, Essay on classification, Edward Lurie, ed. (Cambridge, Mass.: The Belknap Press of Harvard University Press, 1962 [abridgement of London, 1859]) p. 122.

[34]John Phillips, Life on earth; its origin and succession (Cambridge and London: Macmillan and Co., 1860) pp. 172-174.

[35]David Page, The past and present life of the globe (London: William Blackwood and Sons, 1861) p. 141.

[36]Franz Unger, Neu-Holland in Europa (Wien: Wilhelm Braumüller, 1861) pp. 16-17. English translation taken from Journal of botany, British and foreign III (1865) p. 46. Unger's views were popularized by B. Seemann, "Australia and Europe formerly one continent," Popular Science Review V (1866) pp. 18-28.

[37]Unger, Neu-Holland in Europa, p. 20.

[38]Darwin to Hooker, [before 9 December 1859], in More letters of Charles Darwin, Francis Darwin, ed. (London: John Murray, 1903) I, p. 454.

[39]Darwin to Hooker, 30 December [1858], in More Letters I, p. 114.

[40]Darwin to Lyell, 18 [February 1860], in More Letters I, p. 143.

[41]Charles Darwin, On the origin of species (London: Watts & Co., 1950 [reprint of 1st ed.]) pp. 92-93, 322.

[42]Ibid., p. 101.

[43]Searles V. Wood, "On the form and distribution of the land-tracts during the Secondary and Tertiary periods respectively; and on the effects upon animal life which great changes in geographical configuration have probably produced," Philosophical Magazine s.4. XXIII (1862) p. 391.

[44]Ibid., pp. 391-392.

[45]Ibid., p. 393.

[46]Thomas Henry Huxley, "Anniversary address of the President," Geological Society of London. Quarterly Journal XXVI (1870) pp. lix-lxi.

[47]Alfred Russel Wallace, "The comparative antiquity of continents, as indicated by the distribution of living and extinct animals," Royal Geographical Society of London. Proceedings XXI (1877) p. 530.

[48]Andrew Murray, The geographical distribution of mammals pp. 23-24.

[49]Ann Mozley, "Evolution and the climate of opinion in Australia, 1840-76," Victorian Studies X (1967) esp. pp. 413-419.

[50]Andrew Murray, The geographical distribution of mammals pp. 23-24.

[51]W. B. Clarke to Frederick McCoy, 14 February 1851, McCoy Correspondence, Mitchell Library, A675.

[52]Adam Sedgwick to Frederick McCoy, 2 July 1858, McCoy Correspondence, Mitchell Library, A675.

[53]While still in England, McCoy reached the conclusion that the Australian coalbeds dated from the Mesozoic. Throughout his career he engaged in a lengthy and often bitter debate with W. B. Clarke who argued that the coal was Paleozoic. This debate is documented in Ann Mozley Moyal, Scientists in nineteenth century Australia: a documentary history (Melbourne: Cassell Australia, 1976) pp. 130-140.

[54]Frederick McCoy, "Note on the ancient and recent natural history of Victoria," Annals of Natural History s.3, IX (1862) pp. 138-145. This essay was first published as part of the Catalogue of the Victorian Exhibition, 1861 (Melbourne: John Ferres Government Printer, 1861) pp. 159-174.

[55]Henry Barkly, "Anniversary address of the President, 8 April 1861," Royal Society of Victoria. Transactions VI (1861-64) pp. xxiv-xxvi.

[56]D. J. Dickison, ("The naming of the pilot-bird" The Australian Bird Watcher I (1960) p. 78) identifies "Microzoon" as McCoy, a judgement confirmed by G. P. Whitley ("Who was 'Microzoon'?" Australian Zoologist XV (1969) p. 121.)

[57][Frederick McCoy] Microzoon, "Why is Australia odd?" Australasian 6 August 1870, p. 168; 17 September 1870, p. 359; 24 September 1870, p. 392.

[58]Julian Edmund Tenison Woods, Geological observations in South Australia (London: Longman, Green, Longman, Roberts & Green, 1862) pp. 349-350.

[59]Ibid., pp. 143-146.

[60]Ibid., p. 144.

[61] *Ibid.*, pp. 145-146.

[62] Seemann, "Australia and Europe one continent," p. 28.

[63] There is an interesting parallel between the idea that Australian flora and fauna are ancient and primitive and the post-Darwinian view that Australian aborigines are "a stationary remnant of primitive humanity." Both theories are based on the assumption that "primitive" may be equated with "primeval." See D. J. Mulvaney, "The Australian aborigines 1606-1929: opinion and fieldwork," *Historical Studies* (*Melbourne University*) VIII (1958) pp. 131-151, 297-314.

[64] Julian Tenison Woods, "The history of Australian tertiary geology," *Royal Society of Tasmania. Papers and Proceedings* (1876) pp. 76-79.

[65] See, for example, Murray, *Geographical distribution of mammals*, p. 24.

[66] Peter Cunningham, "Fossil bones; letter to the editor," *Sydney Gazette*, 14 May 1829, p. 3.

[67] For a thorough discussion of the Wellington Cave discoveries, see Edward A. Lane and Aola M. Richards, "The discovery, exploration and scientific investigation of the Wellington Caves, New South Wales," *Helictite, Journal of Australasian Cave Research* II (1963) pp. 1-53. Unfortunately, the authors make a number of serious historical errors.

[68] For a discussion of Mitchell's cave explorations and fossil discoveries, see William Foster, "Colonel Sir Thomas Mitchell, D.C.L., and fossil mammalian research," *Royal Australian Historical Society Journal* XXII (1936) pp. 433-443.

[69] John Dunmore Lang, *John Dunmore Lang: Chiefly Autobiographical 1799 to 1878*, Archibald Gilchrist, ed. (Melbourne: Jedgram Publications, 1951) II, p. 393.

[70] Although generally colonists tended to view the aborigines as ignorant savages, they were quick to take advantage of their superior knowledge of the natural environment. Lang noted that, although it is presumptuous of one who is not acquainted with comparative anatomy or osteology to identify fossils, ". . . the aborigines are very good authority on this point in the absence of such men as Professor Jameson, or Professor Buckland, or Baron Cuvier . . ." "L" [John

Dunmore Lang], "Letter to the editor," Sydney Gazette, 25 May 1830, p. 3. Repeatedly, Europeans relied on aborigines for technical information as well as manual labor to assist in their scientific endeavors.

[71] Ibid. This letter was reprinted in its entirety as "Account of the discovery of bone caves in Wellington Valley," Edinburgh New Philosophical Journal X (1831) pp. 364-368.

[72] F. N. Isaac, "An account of some fossil bones found in Darling Downs," Unpublished Ms. British Museum (Natural History) Owen Correspondence, Vol. 16, folios 26-27.

[73] J. W. Gregory, The dead heart of Australia (London: John Murray, 1906) p. 7.

[74] John Dunmore Lang, "Letter to the editor," p. 3.

[75] W. Clift, "Report . . . in regard to the fossil bones found in the caves and bone-breccia of New Holland," Edinburgh New Philosophical Journal X (1831) p. 394.

[76] W. Pentland, "Further notices in regard to the fossil bones found in Wellington Country, New South Wales. By Major Mitchell," Edinburgh New Philosophical Journal XI (1831) p. 180. [This is attributed to Mitchell, but is is actually an editorial note in which all the new material is directly quoted from Pentland.]

[77] Robert Jameson, "On the fossil bones found in the bone-caves and bone-breccia of New Holland," Edinburgh New Philosophical Journal X (1831) p. 395. As Clift identified the fossils, Darwin and others frequently attributed the article to Clift. As the article was published, it appears that Jameson wrote the conclusions.

[78] William Buckland, Reliquiae diluvianae (London: John Murray, 1824) esp. pp. 183-184.

[79] Foster, "Thomas Mitchell," p. 434.

[80] William Buckland, ["Sur les ossemens découvertes a la Nouvelle Hollande,"] Société Géologique de France. Bulletin I (1830) p. 227.

[81] Buckland to W. S. Macleay, 26 Feb.[?] 1843, Macleay Correspondence and Miscellaneous Papers, Linnean Society of London. Microfilm in Mitchell Library, FM 4/2699.

[82] Roderick Murchison, "Address to the Geological Society," Geological Society of London. Proceedings I (1832) p. 367.

[83] W. Pentland, "On the fossil bones of Wellington Valley, New Holland, or New South Wales," Edinburgh New Philosophical Journal XII (1832) p. 308.

[84] Thomas Mitchell to George Ranken, 24 July 1833, quoted in C. G. Ranken, The Rankens of Bathurst (Sydney: S. D. Townsend, 1916) p. 29.

[85] Charles Darwin, "A sketch of the deposits containing extinct Mammalia in the neighbourhood of La Plata [1837]," Geological Society of London. Proceedings II (1838) p. 544.

[86] Charles Darwin, Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle, from 1832 to 1836 (London: Henry Colburn, 1839) pp. 209-210.

[87] Thomas Mitchell to Richard Owen, 28 January 1843, British Museum (Natural History), Owen Correspondence, Vol. 19 folios 242-247.

[88] Darwin, Origin, p. 287.

[89] Lyell, Principles [reprint of 1st ed.] III, p. 144.

[90] For further discussion concerning the influence of Clift's work on Darwin's formulation of the law of succession, see Camille Limoges, La sélection naturelle (Paris: Presses Universitaires de France, 1970) pp. 17-18.

[91] E. W. Brayley, "On the odour exhaled from certain organic remains in the Diluvium of the Arctic Circle, as confirmatory of Dr. Buckland's opinion of a sudden change of climate at the period of destruction of the animals to which they belonged; and on the probability that one of the fossil bones, brought from Eschscholtz Bay, by Captain Beechey, belonged to a species of Megatherium," Philosophical Magazine IX (1831) pp. 411-418.

[92] Richard Owen, "Report on the extinct mammals of Australia, with descriptions of certain fossils indicative of the former existence in that continent of large marsupial representatives of the order Pachydermata," British Association for the Advancement of Science. Reports (1844) p. 240.

[93] See Owen, A history of British fossil mammals and birds (London: John van Voorst, 1846) p. xliv; "On the geographical distribution of extinct Mammalia," p. 201; On the classification and geographical distribution of the Mammalia p. 55.

[94] Darwin to Lyell, 27 [December 1859], in More Letters I, p. 133.

[95] See, for example, P. W. Lund, "Liste des mammifères fossiles du bassin du Rio das Velhas, avec un extrait de quelques-uns des caractères qui les distinguent," Académie des Sciences. Comptes- rendus VIII (1839) p. 577.

[96] Louis Agassiz, Essay on classification, pp. 99-100.

[97] Alfred Russel Wallace, "On the law which has regulated the introduction of species," Annals and magazine of natural history s.2, XVI (1855) p. 196.

[98] The identification has been attributed to Pentland as Cuvier probably died before he could study the Wellington fossils.

[99] Thomas Mitchell to George Ranken, 30 October 1831, quoted in Ranken, Rankens of Bathurst, p. 25.

[100] Thomas Mitchell, Three expeditions into the interior of Eastern Australia (Adelaide: Library Board of South Australia, 1965 [facsimile of London: T. & W. Boone, 1839]) II, p. 369.

[101] Richard Owen, "On the discovery of the remains of a mastodontoid pachyderm in Australia," Annals and Magazine of Natural History XI (1843) p. 7 and "Additional evidence proving the Australian pachyderm . . . to be a Dinotherium," ibid., p. 329.

[102]Richard Owen, "Description of a fossil molar tooth of a mastodon discovered by Count Strzlecki in Australia," Annals and Magazine of Natural History XIV (1844) pp. 268, 270-271.

[103]Richard Owen, Descriptive and illustrated catalogue of the fossil organic remains of Mammalia and Aves contained in the Museum of the Royal College of Surgeons of England (London: Richard and John E. Taylor, 1845) p. 308 and "Presidential address," British Association for the Advancement of Science. Reports XXVIII (1858) pp. lxxxvi, lxxxviii.

[104]Owen's opinions on the subject were adopted and promulgated by the Australian physician and naturalist, Edmund Charles Hobson. See Hobson, "Extract from a letter 'On some fossil bones discovered at Mt. Macedon, Port Phillip,'" Tasmanian Journal of Natural Science, Agriculture, Statistics, etc. II (1846) p. 208; "On the fossil bones from Mount Macedon, Port Phillip," ibid., p. 346.

[105]Hugh Falconer, "On the American fossil elephant," Natural History Review X (1863) pp. 96-101.

[106]Richard Owen, Researches on the fossil remains of the extinct mammals of Australia (London: J. Erxleben, 1877) I, p. viii.

[107]It offers, in addition, another example of the function of anomaly in challenging accepted scientific doctrines. Falconer's refusal to accept the existence of a mastodon in Australia precisely because it was anomalous is, after all, not very different from Prévost's refusal to accept the existence of a mammal in the Mesozoic.

[108]Richard Owen, "Report on the extinct mammals of Australia," p. 239.

[109]Darwin to Falconer, 14 November [1862], quoted in More Letters I, p. 211. Also see Charles Darwin to Hugh Falconer, 4 January 1863, ibid., p. 228.

[110]Darwin to Lyell, 27 [December 1859], ibid., p. 133.

Chapter V

THE PARADOXICAL BIRD-BILLED BEAST

The discovery of the platypus (*Ornithorhynchus anatinus*) in 1797 astounded the scientific community. According to accepted anatomical, physiological, and taxonomic principles, such a creature should not exist. The appearance of a duck's bill on a mammal's body was a surprising combination, but it was readily explained by teleological principles relating form to function. Naturalists were less able to explain or willing to accept the existence of a warm-blooded quadruped which gave milk and brooded its eggs in a nest.

The egg-laying mammals, or monotremes,[1] challenged fundamental concepts of taxonomy. Prior to the discovery of the platypus, all lactiferous animals were placed among the viviparous mammals; all warm-blooded, egg-laying animals were classified as birds, and all oviparous quadrupeds were identified as reptiles. The platypus challenged these neat taxonomic divisions by combining essential characteristics from three different classes. Such fundamental conceptual changes were not accepted without resistance. For nearly a century naturalists tried to force the platypus to fit into the established taxonomic framework.

The extensive controversy concerning whether the platypus gave milk and whether its generation was oviparous, ovoviviparous, or viviparous was fundamentally a taxonomic debate. The eventual resolution of the problem was a modification of the definition of the class Mammalia to include a special subclass of egg-laying mammals, the Prototheria. But before taxonomists would adopt such a radical change in commonly accepted assumptions, the milk-giving and egg-laying characteristics of the monotremes had to be undeniably established.

The pertinent anatomical, physiological, and taxonomic questions could not be answered without a combination of laboratory and field investigation. These investigations were hampered by the remoteness of Australia and the difficulty of keeping monotremes in captivity. Since the evidence was scarce and often contradictory, naturalists could select or reject evidence on the basis of its agreement with their own theoretical preconceptions. As transitional animals, the monotremes supplied pre-Darwinian evolutionists with ammunition in the debate over the stability of species. To a large extent, a naturalist's interpretation of the evidence depended on his position with respect to this issue. Naturalists favoring transmutation emphasized the anomalous aspects of the animal, and naturalists who supported the stability of species attempted to force the monotremes to conform to the traditional definition of a mammal.

The debate was temporarily resolved in 1834 when naturalists concluded that the platypus was a mammal just like other mammals, giving milk and giving birth to live young.

This conclusion remained virtually unchallenged for the next fifty years. Following an argument from analogy, naturalists erroneously assumed a closer relationship between monotremes and other mammals than actually exists. The primary cause of the error was the unwillingness of biologists to readjust their taxonomic categories and to sever the assumed connection between lactation and viviparity.

When the first egg-laying mammal (the echidna, *Tachyglossus aculeatus*) was discovered by Europeans in 1792, it attracted little attention. Its peculiarities remained unnoticed, and naturalists assumed that its reproductive anatomy followed the standard placental pattern. The echidna is an Australian spiny anteater, so taxonomists immediately classified it in Linnaeus' order Bruta among the other anteaters. Distinguished from them by its spines, the echidna was seen as a link between the distant groups of the porcupine and the anteater, thus demonstrating the beautiful gradations within the animal kingdom.[2]

This classification remained unchallenged until after the discovery of the platypus, a much more obviously anomalous creature. Although eighteenth-century exploration introduced Europeans to a vast array of new animal species, none of these discoveries challenged the commonly accepted divisions between the major vertebrate classes: mammals, fish, birds, and reptiles.[3] In 1799 naturalists were astonished by the announcement of the discovery of an animal with the body of a mammal and the beak of a duck. George Shaw, examining a specimen sent to Joseph Banks by the Governor of New South Wales, at first suspected that the specimen was an artificially prepared deception, a duck's beak engrafted on the body of a quadruped. On closer inspection, he concluded that the animal was genuine. Although he confessed ignorance of its real nature, the absence of true teeth led him to place it in the order Bruta next to the anteaters.[4] Shaw believed that the existence of such a paradoxical creature confirmed Buffon's observation that whatever can exist does exist.[5] C. R. W. Wiedemann, editor of the *Archiv für Zoologie und Zootomie*, repeated this remark, emphasizing that the platypus presented a challenge to generally accepted taxonomic principles. Combining essential characteristics of two different classes, the platypus demonstrated the deficiencies of existing theories; it fitted into none of the major class divisions.[6]

Johann Friedrich Blumenbach named this peculiar mixture of bird and mammal *Ornithorhynchus paradoxus*, or paradoxical bird-billed beast. He noted that naturalists had not seriously conceived of an animal combining distinct parts from birds and mammals since the English writer and physician Sir Thomas Browne had discredited the existence of the griffin, a mythological beast with the head and wings of an eagle and the body of a lion. In 1648, Browne wrote,

> if examined by the doctrine of animals, the invention is monstrous, . . . for though some species there be of a

> middle and participating natures [sic], that is, of bird and beast, as we finde the Bat to be, yet are their parts so confirmed and set together that we cannot define the beginning or end of either, there being a commixtion of both in the whole, rather then an adaptation, or cement of the one unto the other.[7]

Blumenbach cautioned his readers that the strange Australian mammal with a duck's beak instead of teeth should teach us the truth of Pliny's statement that we ought to judge nothing incredible in nature.[8]

On closer investigation, however, the creature did not seem especially paradoxical. Although at first glance the beak appeared to be identical to that of a duck, a more careful examination revealed substantial differences. Anatomist Everard Home established that the beak was not a part of the mouth but extended beyond it. The soft, fleshy, sensible edges served as a sense organ,[9] enabling the animal to feel in the mud for the small crustaceans and water insects which constitute its food. Blumenbach perceived that the beak is an exploratory organ for touching and tasting, serving in place of smell and sight which are useless under water.[10] He attributed the similarities between the bill of the platypus and that of the duck to similarity in function. He concluded that the possession of similar, specialized sense organs by different species of animals from two different classes was most enlightening for comparative anatomy, but it did not necessarily signify a close taxonomic relationship between these animals.[11]

Blumenbach noted that the discovery of the platypus at first seemed to confirm Bonnet's conception of the gradations of nature. Bonnet postulated that all living beings were connected to one another in a single, great chain of being. Blumenbach objected that the platypus and the bat both represented transitional forms between birds and mammals. Only with difficulty could these very different forms fit into a single chain.

The true explanation for these apparent transitions, Blumenbach argued, was the subordination of form to function. Teleological principles applied even in the case of so anomalous a creature as the platypus.[12] In its general form the platypus conformed to the normal mammalian plan of organization. He naturally assumed that the young were nourished with milk, like other mammals, although he questioned how the young could suckle with their beaks.[13] The internal anatomy of the beak was also mammalian, but its external form resembled a duck's bill because both structures performed the same function. The apparent paradox of the duck-billed platypus was thus resolved when one understood that nature's products reflect nature's goals.[14] Noting similarities in form between the echidna and the platypus, Blumenbach assigned both animals to the family of edentates with the anteaters, sloths, and armadillos. He predicted (erroneously) that the edentates, although rare in other parts of the world, would, like the marsupials, be represented by a wide variety of Australian forms.[15]

The inadequacy of Blumenbach's explanation and classification was dramatically demonstrated in 1801. Early descriptions of the platypus were based upon dried specimens. When Governor Hunter sent two specimens preserved in spirits to Joseph Banks, naturalists discovered that its internal structure was even more extraordinary than its outward appearance. The announcement that its reproductive structure more closely resembled that of a lizard than a bird or a mammal, coupled with the apparent absence of mammary glands, led to astonished speculations that the animal was oviparous.[16]

Everard Home's complete anatomical dissection revealed reptilian characteristics possessed by no other mammals. The structure of the ear and the shoulder girdle combine reptilian and mammalian traits. The organization of the urogenital system displays the most remarkable deviation from normal mammalian anatomy. As in reptiles and birds, the intestinal tract and the urinary and genital ducts open into a common chamber, the cloaca. In the male, urine empties into the cloaca from an opening at the base of the penis, thus reserving the penis for the passage of the semen. In the female, the absence of nipples and the lack of a well developed uterus led Home to compare the reproductive system to that of birds and reptiles. He argued that the animal could not be oviparous, because an eggshell could not form in the vagina due to the presence of urine. (Actually, the shell is formed as the egg passes down the oviduct.[17]) Home concluded that the reproductive process must be similar to that of the ovoviviparous reptiles which produce eggs which are hatched within the mother's body.[18]

Home's dissection of the echidna revealed similar anatomical peculiarities, thus conclusively demonstrating that the two species were closely related. The substantial differences in stomach and mouth parts could be attributed to the difference in food sources. The similarities between the echidna and the South American anteaters (Myrmecophaga) led Home to postulate the existence of a graded series of forms from bird to platypus to echidna to anteater. He argued that the platypus and echidna belonged to a tribe outside existing vertebrate classes. Animals lacking nipples and a common uterus and possessing a cloaca could not be considered mammals.

> These characters distinguish the Ornithorhynchus, in a very remarkable manner, from all other quadrupeds, giving this new tribe a resemblance in some respects to birds, in others to the Amphibia; so that it may be considered as an intermediate link between the classes Mammalia, Aves, and Amphibia; and, although the great difference that exists between it and the Myrmecophaga, the nearest genus we are at present acquainted with, shows that the nicer gradations towards the more perfect quadrupeds are not at present known, . . . between it and the bird, no link of importance seems to be wanting.[19]

At the beginning of the nineteenth century, the platypus' duck-like bill represented a curiosity of nature which could be adequately explained by accepted anatomical principles relating form to function. Its internal structure, however, presented a serious challenge to fundamental principles of comparative anatomy, physiology, and taxonomy. Its peculiar reproductive anatomy inspired an 82-year-long controversy concerning its reproductive process. Comparative anatomists were unable to determine whether the animal was oviparous, ovoviviparous or viviparous. The apparent absence of nipples and mammary glands led to further doubts about its identification as a mammal. Nineteenth-century naturalists assumed that lactation was necessarily accompanied by viviparous generation. As we shall see, this assumption led naturalists to reject significant evidence in an effort to force the platypus to fit their preconceived notions of the natural order.

The platypus, combining essential characteristics of birds, reptiles, and mammals, provided an ideal transitional form. Friedrich Tiedemann suggested that the monotremes were oviparous, basing his argument on the reproductive anatomy and the absence of nipples.[20] He agreed with Home in excluding them from existing mammalian orders and assigning them a position intermediate between mammals, birds, and reptiles. He cited them as proof that nature passes from one class to another by imperceptible gradations.[21]

Such a transitional form was particularly attractive to evolutionists because the sharp, well defined divisions between the vertebrate classes constituted a major objection to theories of transmutation. Lamarck, seeking to arrange all animals in a single linear scale of increasing organic complexity, cited the monotremes as evidence to support his evolutionary theory in the Philosophie zoologique, first published in 1809. He argued that the monotremes formed a special class intermediate between birds and mammals.

> We now pass to the birds; but I must first note that there is no gradation between mammals and birds. There exists a gap to be filled, and no doubt nature has produced animals which practically fill this gap, and which must form a special class if they cannot be comprised either among the mammals or among the birds . . .
>
> They are not mammals, for they have no mammae and are most likely oviparous.
>
> They are not birds; for their lungs are not pierced through and they have no limbs shaped as wings.
>
> Finally, they are not reptiles; for their heart with only two ventricles removes them from that category.
>
> They belong then to a special class.[22]

William Elford Leach cited similar reasons for establishing a separate class.[23] One anonymous reviewer even suggested placing the monotremes in the Reptilia despite their hair, warm blood, and four-chambered heart.[24]

Although most taxonomists adopted a more conservative approach, they readily recognized that the classification of the platypus and echidna presented special problems. Etienne Geoffroy Saint-Hilaire suggested that they be placed in a separate order, which he called Monotremata (literally "one-hole") because they possessed a cloaca.[25] André Duméril listed the echidna and the platypus as two genera in the family of edentates. However, he noted that many of their anatomical characteristics, particularly the absence of mammary glands, were more similar to reptiles and birds than to mammals. He regarded his classification as temporary, pending further investigation.[26] Carolus Illiger placed the monotremes in a newly created order, Reptantia, so named because of their reptilian stance and their affinities to reptiles. Illiger suggested that the marsupials and the Reptantia presented peculiarities of organization which tended to be confined to the Australian region.[27] Cuvier included the monotremes as a tribe of edentates, but he emphasized their anatomical peculiarities, especially their extraordinary generation. "As it has been so far impossible to discover their mammaries," he remarked, "one does not know if these animals are viviparous or oviparous."[28] Although each of these taxonomists classified the monotremes as mammals, all emphasized their anomalous organization. The failure to discover mammary glands constituted a major obstacle to their identification as mammals.

Henri Ducrotay de Blainville differed from other taxonomists by placing the monotremes unequivocally in the class of viviparous, milk-giving mammals. He objected to previous taxonomic systems on the grounds that their authors classified by instinct and analogy rather than by rigorous anatomy.[29] He noted that the apparent absence of mammary glands had caused taxonomists to ignore fundamental affinities with mammals and to exaggerate superficial resemblances to reptiles and birds.[30] He believed that the mammalian nature of monotremes was so apparent that one could not doubt that they had mammary glands, although perhaps these were readily observed only during lactation.[31] Continuing the analogy with other mammals, Blainville assumed that monotremes gave birth to live young and predicted that the young were born in a more fully developed state than were marsupials.[32]

Blainville concluded his investigations with suggestions concerning the appropriate position of the monotremes in a classification scheme. If one distinguished taxonomic groups on the basis of digestion, then monotremes belonged among the Edentata. If, on the other hand, the most basic taxonomic divisions were decided on the basis of reproduction, then monotremes should be grouped with the marsupials.[33] This question was of crucial importance to the establishment of a natural system of classification. Blainville was trying to discern the distinction between taxonomic affinities and adaptive similarities.

Blainville's careful anatomical studies of marsupials and monotremes led him to propose in 1816 a revolutionary system of classification based upon characters of the reproductive system and the skull. Blainville divided mammals into two subclasses: the "monodelphs" or placentals and the "didelphs" which included both marsupials and monotremes.[34] This division provided the foundation for present classifications and paleontologist and comparative anatomist W. K. Gregory has described it as "perhaps the most important [step] in the history of the classification of mammals."[35] Blainville's classification attributed the similarity between the tongue of the echidna and the anteater or the beak of the platypus and the duck to functional adaptations. Similarities in reproductive structures, on the other hand, indicated natural affinities. According to this arrangement, monotremes were more closely related to marsupials than to the Edentata with which other taxonomists grouped them.

Blainville arranged his orders according to "degrees of organization" beginning with the primates and descending with gradually decreasing complexity through marsupials to the monotremes. This taxonomic scheme introduced the idea that monotremes were the most primitive form of mammals. The anatomical investigations of Everard Home gave further support to this linear arrangement. Home sought to link placentals to birds through a series of gradations. He argued that comparative studies of reproduction revealed a descending series of gradual transitions from placental to kangaroo to opossum to platypus (which he believed to be ovoviviparous) to bird.[36] This generally linear arrangement was adopted by transmutationists as a basis for the construction of hypothetical lines of evolutionary development.

Blainville's taxonomic treatment of the monotremes represented a major advance in the understanding of the natural system of mammalian classification, but the question as to whether the group was viviparous, ovoviviparous, or oviparous could not be resolved by anatomical studies in the laboratory. The problem could only be solved by field observations in Australia. European scientists turned to observers in Australia for assistance, but few colonists had the leisure to engage in scientific studies and fewer still had the necessary scientific training. What little information was available directly from Australia seemed to confirm that the monotremes laid eggs. Joseph Banks appealed to his botanical collectors, George Caley[37] and Robert Brown[38] for specimens and information. Caley questioned a number of aborigines who separately confirmed that the platypus laid eggs.[39] This claim was independently supported in 1818 by Australian colonist John Jamison.[40] Members of Bellingshausen's Russian expedition to the Antarctic seas (1819-21) found an egg inside the body of a female platypus and concluded that the reproductive system resembled that of birds.[41] Patrick Hill, a surgeon in the Royal Navy, sent a specimen of an impregnated uterus to England in 1822. Hill found a round, yellow ovum in the left ovary and noted that the natives informed him that the platypus laid two eggs.[42]

These reports, coupled with the failure to find mammary glands in monotremes, gradually convinced European scientists that these strange Australian creatures could not be accommodated within traditional taxonomic groupings. Support grew for the idea of a special, transitional class of mammal-like creatures which possessed an oviparous, or at least ovoviviparous, form of reproduction and did not give milk. When a report arrived from Australia claiming that Jamison had himself seen platypus eggs, Etienne Geoffroy Saint-Hilaire became convinced that the platypus must be oviparous. As a result, he revised his taxonomic system, establishing a special class for monotremes intermediate between mammals and birds.[43]

Everard Home reversed his former opinion and now argued for oviparous reproduction. As evidence, he cited new anatomical dissections and reports from aborigines.[44] Fleming agreed, claiming that platypus eggs had been sent to London.[45]

Jan van der Hoeven also supported the formation of a new vertebrate class, basing his argument primarily on the apparent absence of mammary glands. Van der Hoeven criticized taxonomists for trying to force the platypus to fit into one of the four existing classes. It could not be a bird because it had no wings; it could not be a reptile because it was warm-blooded; and it could not be a fish because it breathed through lungs. So taxonomists called it a mammal, "as if what we know was the rule of all that nature could create."[46] Van der Hoeven argued that it was absurd to call a creature without mammary glands a mammal. He conceded the possibility that they might later be discovered, but believed it to be unlikely because the structure of the platypus' beak was ill-suited for suckling. Van der Hoeven cited Home's previous claims that monotremes were ovoviviparous as further evidence that they lacked mammary glands.[47]

In 1823 most biologists agreed that monotremes represented a serious challenge to existing taxonomic principles.

Clearly the definition of mammals as warm-blooded, viviparous, lactiferous quadrupeds failed to account for these peculiar Australian creatures. James Prichard summarized the problem as follows:

> The great class of warm-blooded quadrupeds, or quadrupeds with a double heart and double circulation, was assumed by Linnaeus to be, without exception, viviparous and mammiferous. Hence it received the denomination of mammalia, which has been generally adopted by naturalists; but is liable to objection, since its application to the whole class of warm-blooded quadrupeds is founded on an opinion assumed without proof. It is taken for granted, that the peculiarity which gives rise to the term Mammalia, has been, universally, conjoined with another more important one, by which the class is constituted; whereas it is very possible, though Linnaeus was not aware of any such fact, that Nature may, in some instances, have separated these characters. It appears, indeed, that a tribe of animals has been discovered in New Holland, which furnishes an example of this separation. Now, if the great department of quadrupeds with warm blood be distinguished, as a particular class, by this circumstance only, by having warm blood, and the structure on which this depends, namely, a double heart, and corresponding organs of respiration, it will be proper afterwards to subdivide the class thus constituted with reference to the mode of reproduction. The first order may contain those tribes which are oviparous, or ovo-viparous [sic]; and, like other oviparous animals, unprovided with organs for suckling their young. The second may comprise such as produce their offspring in an immature state, and keep them for a time attached to their bodies, chiefly in abdominal pouches, which Nature has provided for this purpose. These animals have been termed the marsupial tribe. The third order must receive all those which produce their offspring in what may be termed a mature state.[48]

Prichard's conclusions and his assumption that oviparous animals did not give milk were called into question in 1824 by the announcement that Johann Friedrich Meckel had discovered mammary glands in the platypus.[49] The glands had previously escaped notice because their structure differed markedly from analogous glands in other mammals. The mammary glands of monotremes were more primitive in organization, consisting of a great number of caeca placed side by side, all directed to the same point of the skin. They opened directly onto the skin, without any trace of a nipple. The discovery of mammary glands in the platypus completely transformed biologists' understanding of the reproductive physiology and the taxonomic position of the monotremes.

Meckel argued that the existence of mammary glands in monotremes destroyed the argument for placing them in a special class, but it did not resolve the question of their reproductive process. Meckel reviewed the reports from Australian observers alleging that monotremes laid eggs, but he did not believe that these claims had been adequately demonstrated. Further, the existence of an oviparous mammal was improbable because it was inconsistent with experience with other mammals.[50] Nevertheless, he had previously acknowledged that these animals might prove to be oviparous,[51] and he now argued that the possession of mammaries did not preclude this possibility.

Meckel noted that "the difference between the bringing forth of live young and of eggs is really small, and not in any way essential."[52] He claimed that "in experiments with birds, the egg had been caused to hatch within the abdomen and the young bird to be born alive. Furthermore, in marsupial reproduction the young were born in an almost embryonic state of development. In this way, marsupial reproduction approached that of oviparous animals. Since the platypus was even more closely allied to birds and amphibians, one might expect that its reproduction would even more closely approach the oviparous type. Meckel argued that his discovery had conclusively demonstrated that monotremes were mammals. If they should prove to be oviparous, then they represented a transitional form linking the rest of the mammals to birds and amphibians.[53]

Meckel's discussion of monotreme reproduction was particularly perceptive because, unlike other naturalists, he did not see a necessary connection between lactation and viviparous reproduction. Monotreme reproduction posed a difficult problem to naturalists, because the question could only be resolved by field observations. Lacking the necessary empirical data to decide the issue, naturalists argued the question on the basis of their own theoretical preconceptions. Most naturalists unquestioningly adopted the conceptual framework implied by the traditional taxonomic definitions arguing that the possession of mammary glands necessarily eliminated the possibility of oviparous generation.

Henri Ducrotay de Blainville eagerly accepted Meckel's discovery because he believed that it confirmed his claim that the platypus was viviparous. Blainville assumed that viviparity was an essential feature of mammalian organization but lactation was not. Before the discovery of the mammary glands, Blainville had suggested that the platypus foetus lived so long in the placental stage that lactation was unnecessary. Meckel's discovery had eliminated the need for such an hypothesis and, Blainville argued, had discredited second- or third-hand reports of platypus' eggs.[54]

Naturalists who supported the idea of a separate taxonomic class for the monotremes greeted Meckel's announcement with considerably less enthusiasm; they tried to discredit the discovery. Van der Hoeven acknowledged that the presence of mammary glands in the platypus would completely destroy his argument in favor of a special class. He conjectured, however, that the primitive glands discovered by Meckel might merely be useless vestiges of mammalian organization, since monotremes clearly had close affinities with mammals.[55] Everard Home was unable to locate the glands at all.[56]

Etienne Geoffroy Saint-Hilaire raised more serious objections. Like Blainville, Geoffroy assumed that all lactiferous mammals must be viviparous, but he challenged Meckel's interpretation of his findings. The glands Meckel described could not be mammary glands, Geoffroy argued, because their structure was so anomalous. They had no nipples, although these would be especially necessary to an animal with a mouth so ill-suited for sucking. They displayed enormous variations in size in different individuals. Geoffroy suggested that Meckel's glands must be analogous to the scent glands of mustelids or the lubricating glands of salamanders. In any case, they were not mammary glands and so did not affect the arguments for a separate taxonomic class and oviparous generation.[57] Geoffroy published a detailed description of the uro-genital anatomy of the platypus arguing that such anomalous structures justified the establishment of a special class, the Monotremata.[58]

Meckel defended his claims against Geoffroy's arguments, noting that at least Geoffroy had confirmed the existence of the disputed glands, even though he objected to their identification as mammary glands. Meckel argued that the presence of a nipple was not necessary in a mammary gland. In fact, its absence was a pathological condition in some women. Since nipples were not present in embryos, one might expect that they would also be missing in primitive mammals like the platypus. Meckel believed that the structure of the mouth would not necessarily prevent sucking; the flexible lips could be formed into a long tube.[59] He admitted that the mammaries of monotremes differed markedly in structure from those of other animals, but he argued that differences in structure did not necessarily imply differences in function. They were quite large in older females, but almost completely lacking in younger females and males. Other kinds of secreting glands displayed considerably less variation in individuals of different sexes and ages.[60]

The German anatomist Karl Ernst von Baer examined the glands in an effort to resolve the argument. Von Baer conclusively identified them as mammary glands, noting that they were quite similar in structure to the mammae of cetaceans such as the porpoise.[61] Von Baer underscored Meckel's remark that the mode of generation still remained undetermined, noting that the reproductive structures of egg-laying and viviparous reptiles were so similar that sometimes two similar species from the same genus differed from each other in this respect. One could not resolve the question on the basis of anatomical dissection; one needed to see the animal emerge from the egg. Von Baer suggested that the primary difference between oviparous and viviparous generation was the length of gestation. Animals with a short gestation period laid eggs; those with a longer gestation gave birth to live young.[62]

The nature of monotreme reproduction and the function of glands discovered by Meckel were the central issues in a major controversy between Geoffroy and the English comparative anatomist Richard Owen, Primarily the debate revolved around a question of taxonomy. Owen wished to integrate the monotremes into the Mammalia by establishing that they were lactiferous and that their mode of generation was not inconsistent with mammalian physiology. Geoffroy wished to establish a transitional class between mammals and birds, characterized by oviparous reproduction and the absence of lactation. Each man ignored significant evidence in an effort to force the evidence to conform to his theoretical model.

Each allowed his theoretical preconceptions to determine the kinds of questions which could be asked and the kind of evidence which could be accepted.

Geoffroy argued that zoologists identified Meckel's organs as mammary glands, despite their anomalous structure, because they wanted to force the platypus to fit the mammalian mold. In fact, by naming the class of warm-blooded quadrupeds "mammals," taxonomists had attributed unwarranted significance to the mammary glands. No organ which displayed such great variation in size, number, and distribution should serve as an essential criterion for distinguishing major taxonomic groups.[63]

Zoologists such as Owen who identified Meckel's glands as mammary glands noted their appropriate position in the abdomen of females and their absence in males. Their extensive variation in size in different individuals indicated that they served a temporary function,[64] and their larger relative size in mature individuals suggested a sexual function.[65] Moreover, Owen argued, one could expect the platypus to give milk like other mammals because its respiratory, circulatory, nervous, and tegumentary systems were all mammal-like.[66]

Geoffroy's major objection to these arguments was based on the anomalous structure of the alleged mammary glands. He pointed out that young animals could not suckle from a breast that lacked a nipple.[67] Owen attempted to meet this objection by remarking that the unusual shape of the platypus' mouth would demand a similarly abnormal mammary structure. He suggested that the muscles around the gland contracted to force the milk out, thus eliminating the need for suction.[68] The question was not satisfactorily resolved until 1834 when Owen was able to examine specimens of platypus nestlings. Although the tongue of the adult platypus was lodged far back in the mouth, in very young animals it was advanced to the end of the lower mandible, enabling them to lick milk from the mother's fur.[69]

Reports from Australia supported claims that the platypus gave milk. Lauderdale Maule, a military officer in New South Wales, set out to investigate the truth of the "generally accepted belief"[70] that the platypus laid eggs and suckled its young. Maule dissected a female whose glands exuded milk.[71] His report was confirmed a year later by another observer.[72]

Geoffroy objected to these observations because they offered no proof that the fluid secreted was milk. If those glands produce milk, Geoffroy challenged, let's see the butter.[73] He denied that the fluid was milk, arguing that glands of such a simple structure could not produce it. Simple glands must produce a simple fluid: mucus.[74] Owen responded to this objection by observing that the Cetacea possessed similar glands which produced rich milk. The simpler structure of the glands did not necessarily imply a difference in function. Mammary glands varied in complexity in different species, and one would expect to find the simplest structure in the most primitive mammals.[75]

If Geoffroy could show that monotremes lacked mammary glands, then they could not be classified as mammals. If he could demonstrate that these glands served a function other than lactation, then the anatomical peculiarities of monotremes would justify their establishment as a separate class. At first he suggested that the glands were analogous to the lubricating glands on the sides of aquatic reptiles and fish.[76] But, as Owen pointed out, the size and functioning of lubricating glands did not vary in accordance with the sexual cycle.[77]

Then Geoffroy argued, on the basis of anatomical similarities, that the glands were analogous to the musk glands of shrews. They served as scent glands to attract a mate.[78] He found similar "monotrematic" glands in the water rat (Arvicola terrestris). But Owen argued that if the secretion served to attract the male, then it should be at its greatest just before impregnation. This was not the case; the glands were at their greatest development immediately after gestation.[79] Morevoer, the so-called "monotrematic glands of the water rat appeared in both sexes in all seasons.[80]

Rather than believe that the glands discovered by Meckel secreted milk, Geoffroy suggested that they might secrete carbonate of soda to form a shell around the egg. He admitted that this would be an extraordinary arrangement, but what was extraordinary in other animals was ordinary for so anomalous an animal as the platypus.[81]

To explain reports that the glands contained a milky fluid, Geoffroy hypothesized that the monotrematic glands secreted a nutritive mucus which was eaten by the young. Geoffroy suggested that there were two major modes for supplying nourishment to newborn young. Mammals secreted milk from mammary glands from which the young suckle. Monotremes, in contrast, expelled mucus into the water. The mucus absorbed moisture, becoming a gelatin-like substance which the young ate. Monotrematic glands consisted of a mass of caeca with no erectile tissue and no nipple.[82] Such an unusual mode of nutrition was not inconsistent with nature, he argued, because other oviparous animals such as frogs nourished their young with a mucus secretion.[83] (This assertion has no factual basis.)

Since Geoffroy based most of his arguments on the anomalous structure of the disputed glands, von Baer's argument that the mammary glands of monotremes were analogous to those of cetaceans presented serious difficulties. Geoffroy's proposed solution demonstrated his talent for constructing imaginative theories as well as his tendency to bend the facts to conform to these theories.

Geoffroy maintained that zoologists assumed that the porpoise gave milk only because they had never carefully examined the nature of its alleged mammary glands. Perhaps the porpoise, like the platypus, fed its young on mucus. Rather than assign the platypus to the class Mammalia, Geoffroy removed the porpoise from it. He argued that the Cetacea formed a second order in the class of Monotremata. Their skulls, tegument, teeth, and limbs all differed significantly from the normal mammalian pattern.[84]

Geoffroy noted that the porpoise, like the platypus, had a beak-like mouth which was ill-suited for suckling. Its nourishment must therefore be released into the water. Milk would be lost. Mucus, however, absorbed the water to form a gelatin-like food with many of the properties of egg-yolk. As evidence for this theory, Geoffroy cited reports from whalers who had observed masses of a gelatin-like substance floating in the ocean.[85]

Duméril and Blainville objected to Geoffroy's unorthodox claim that whales were not mammals, arguing that they suckled their young like all other mammals. Although the teats were normally quite small, they became enlarged during lactation. Blainville further objected to Geoffroy's claim that monotrematic glands differed substantially in function from mammary glands. The essential characteristic of mammary glands was not the fluid they produced, i.e., milk, but rather their function in providing nourishment for the newborn mammals. Blainville argued that whatever substance the glands secreted they should still be identified as mammary glands because they performed the same function.[86]

Owen pointed out that it was impossible for all monotremes to nourish their young with mucus ejected into the water; the echidna lives in a dry, sandy habitat.[87] Geoffroy replied that he saw no reason that the function of the glands could not be modified in accordance with the nature of the environment,[88] but he did not suggest an appropriate modification. Owen further objected that the young platypuses he dissected had not yet opened their eyes and so could not see to follow their mother into the water.[89] Moreover, shrews and water rats possessed Geoffroy's "monotrematic" glands in addition to normal, lactiferous mammary glands.[90] Owen administered the final blow to Geoffroy's theory when he extracted coagulated milk from the stomach of a young platypus. A microscopic examination confirmed that the substance was milk.[91] In 1834 Geoffroy conceded the argument, disavowing his former belief regarding the mucus secretion.[92] No longer did naturalists question the existence of mammaries in monotremes, thus effectively ending the attempt to establish a separate class of Monotremata.

Geoffroy was equally unsuccessful in his attempt to convince other naturalists that the platypus laid eggs. Just as comparison with other mammals led to the conclusion that the platypus must give milk, so the same argument convinced naturalists that the platypus must give birth to live young. It never occurred to most naturalists to question the assumption that lactation and viviparity were linked.

Blainville continued to maintain that the generation of monotremes must be analogous to that of other mammals. He suggested that lactation must be especially well developed, as it is in marsupials, to make up for the absence of a placenta.[93]

Richard Owen, on the other hand, noted that the many anatomical similarities with reptiles pointed to ovoviviparous reproduction. Owen defined viviparity as a reproductive process in which the fetus is attached to the mother through a placenta.[94] Following this definition, the only truly viviparous animals were the placental mammals. By applying the term "ovoviviparous" to all animals in which the eggs were incubated and hatched within the mother's body without the formation of a placenta, Owen established that at least one order of mammals, the implacental marsupials, was ovoviviparous. He applied the term "oviparous" to all animals which laid eggs that were hatched outside the body. Owen's use of the word "ovoviviparous" differs substantially from the modern definition. Zoologists now apply the term, if they use it at all, only to species within a group in which the predominant mode of generation is oviparous. In those reptiles and fish which give birth to live young there is no prolonged maternal-fetal link, thus justifying the term "ovoviviparous."

Owen maintained that monotreme reproduction was probably analogous to that of marsupials. Since at that time he had no evidence that monotremes possess a pouch, he suggested that the period of gestation within the uterus was probably longer than in marsupials.[95] Owen believed that mammals displayed a regular gradation toward the ovoviviparous mode of reproduction.[96] He argued that marsupials and monotremes formed a primitive subclass of ovoviviparous mammals.[97] This taxonomic arrangement integrated monotremes into the Mammalia and emphasized the close affinities between marsupials and monotremes.[98] Owen stressed that monotreme reproduction was in no way inconsistent with mammalian organization.

Owen observed that the theory that monotremes were oviparous was first proposed before the discovery of the mammary glands on the assumption that the egg yolk was necessary to provide nourishment for the young. Once monotremes were to be lactiferous, such an assumption was unnecessary.[99] Owen argued that monotremes must be ovoviviparous rather than oviparous because he could not determine how the shell was added to the egg.[100] Moreover, Owen argued, the alleged eggs of the platypus would have to be disproportionately small to pass through the pelvis.[101] Such a small egg would not be large enough to contain the nutriments necessary for the nourishment of the foetus. If the platypus was oviparous, the eggs must be formed in a manner quite different from the eggs of reptiles or birds because the monotreme ovary was essentially mammalian.[102]

The strongest argument in favor of the oviparity of monotremes was based on reports from observers in Australia. A colonist claimed in 1825 to have found platypus eggs the size of hen's eggs.[103] In 1829, when Geoffroy heard that four platypus eggs had arrived in England, he eagerly seized upon the report as proof of the oviparous (and therefore non-mammalian) nature of the platypus. Robert Grant, professor of zoology at London, acknowledged that he had seen the eggs but had assumed that they were reptilian. Grant believed that Meckel's discovery of the mammary glands necessarily implied that monotremes must be viviparous. Geoffroy's arguments changed his mind and Grant returned to England to pursue the question.[104] Grant's account described the egg as similar to that of a snake or lizard but larger. Geoffroy added that the general resemblance of the reproductive organs of monotremes to those of reptiles supported the claims of oviparity.[105] Unfortunately for Geoffroy, the eggs displayed in England were those of the Australian common long-necked turtle (Chelodina longicollis).[106] Their erroneous identification as platypus' eggs discredited Geoffroy's theory and contributed to serious misconceptions about the nature of monotreme reproduction.

When Lauderdale Maule observed milk in the mammaries of the platypus, he also found remnants of eggshell among the debris in the nest.[107] Owen suggested that the alleged eggshells were really excrement coated in urine salts.[108]

As Geoffroy pointed out,[109] Owen was inconsistent in his treatment of the evidence. He accepted those accounts which confirmed his own theories and rejected those which contradicted his preconceptions.

Nearly all Australian observers confirmed that the platypus laid eggs. The single major exception was George Bennett, a physician who served as Owen's collector in Australia. Bennett received his medical training at the Royal College of Surgeons where he became a close friend of Richard Owen. After immigrating to Australia, he set out to investigate marsupial and monotreme reproduction in order to provide Owen with the necessary evidence to prove his theories. For fifty years Bennett searched for a solution to the problem of monotreme reproduction, but his theoretical assumptions prevented him from finding it.

Bennett was already fully convinced that the platypus was ovoviviparous when he questioned the aborigines regarding their knowledge of monotreme reproduction. He wrote,

> The various contradictory accounts that have been given on the authority of the aborigines . . . as to the animal laying eggs and hatching them, induced me to take some pains to find out the cause of the error; and being now perfectly satisfied that ova were produced in the uteri, I could the more readily determine the accuracy or inaccuracy of the accounts which I might receive from the natives.

Bennett reported that the native accounts were contradictory, sometimes claiming that the platypus laid eggs, and later claiming that it gave birth to live young. Bennett interpreted these inconsistencies as evidence that the animal was probably ovoviviparous, although he conceded that some confusion might have resulted from difficulties in communication. Bennett cited the reports of aborigines as evidence that the platypus gave milk, but he concluded that native accounts of oviparous reproduction were unreliable.[110]

Bennett wished to provide Owen with specimens which would conclusively resolve the issue, but his preconceptions led him to conduct his research in such a way that he could not succeed. To prove definitely that monotremes were viviparous, Owen needed a female with an internal, shell-less foetus. Bennett attempted to obtain one by shooting live platypuses as they came out to feed. He did not undertake the laborious, time-consuming task of searching the burrows where the eggs were laid. His research was not designed to find platypus eggs because he "knew" they did not exist.

Owen himself provided some anatomical evidence supporting oviparity in monotremes, but he was unprepared to acknowledge its significance. While dissecting a very young platypus, Owen discovered a structure on the upper mandible similar to the egg tooth with which young birds break out of the shell. At first Owen was nearly convinced by this analogy,[111] but he later concluded that the similarity between the two structures did not necessarily imply similarity in function. He argued that the balance of the evidence still favored ovoviviparous generation.[112] Of course Geoffroy maintained that the egg tooth of the platypus conclusively demonstrated its oviparous origin.[113]

A major obstacle to the acceptance of oviparity in monotremes was the prevailing belief that lactation was always accompanied by viviparous generation. Cuvier, Blainville, and Geoffroy all shared this opinion, although Meckel, von Baer, and Owen argued against it.

Owen claimed that the arguments for oviparous reproduction and the arguments for lactation should be examined independently. Lactation only implied that the young were nourished with milk; it did not necessarily follow that they were born live.[114] The young of oviparous animals sometimes needed additional nourishment after hatching, as was the case with birds. Owen maintained that marsupials combined lactation with ovoviviparous reproduction.[115] Despite these general theoretical considerations, Owen allowed the arguments that monotremes gave milk to reinforce his claims that they gave birth to live young.

Geoffroy, on the other hand, criticized Maule's claim that the platypus was both oviparous and lactiferous. He argued that the combination of these two traits was inconceivable because it violated the principle of correlation of parts. He objected that Owen wanted to combine organs from one class with organs from another. But if part of the organization was modified, the rest of the anatomy must be modified accordingly. Oviparous animals could not be lactiferous. Geoffroy criticized other naturalists for forcing the facts to fit their theories, accusing them of trying to make a mammal out of an oviparous animal.[116]

In 1834, in the face of overwhelming evidence that the platypus gave milk, Geoffroy reversed his position. This isolated example of the union of oviparity and lactation should teach us the power of nature to destroy arguments from analogy, he remarked.

> If it is an incomprehensible fact, of the same sort, for example, as the fall of stones from the sky, one should accept it with submission; explanations will come later, and perhaps not at all, but what reason justifies our disbelief? Is there a valid reason to believe that oviparity is a thing necessarily different from lactation? I admit that I know of none other than this; the association has never been encountered.[117]

Meanwhile, Geoffroy was having increasing difficulty defending his claim that the platypus was oviparous. When it was pointed out that the eggs described by Grant were too large to pass through the pelvis of the platypus, he conceded that the egg must be hatched within the body. After hatching, the young passed through the pelvis with the broken shell. He compared this process to the ovoviviparous reproduction of some fish and reptiles.[118]

It seemed that Geoffroy had conceded the argument to Owen. For the next fifty years naturalists agreed that monotremes were ovoviviparous, giving birth to live young. Yet Geoffroy's use of the term "ovoviviparous" differed substantially from Owen's. Owen wished to apply the term to marsupials as well as monotremes, but Geoffroy emphasized that, with respect to reproduction, monotremes differed as much from marsupials as they did from placentals. He argued that Owen's taxonomy failed to take into account substantial differences in reproductive physiology.[119]

By 1835 the question appeared to be resolved. Monotremes were classified among the mammals. They appeared to conform to the traditional definition of a mammal: a warm-blooded quadruped which gives milk and bears its young live. Naturalists abandoned the argument for oviparity in monotremes.

In 1844, the amateur Robert Chambers resurrected the idea of monotreme oviparity in support of his theory of evolution. Chambers proposed that the platypus represented a transitional step linking birds and mammals. He argued that a developmental force propelled organisms along a foreordained path of evolutionary progress. His claim that a goose-egg might produce a platypus which might in turn give birth to a rat was never scientifically respectable.[120] Naturalists responded to the suggestion with scorn. Adam Sedgwick argued that such a transformation was against the observed laws of nature. Conceding that the anatomy of the platypus was similar to that of birds in some respects, he cited Owen's proof that the animal gave birth to live young.[121]

For half a century, no one seriously challenged Owen's conclusions. In 1848 Jules Verreaux travelled to Australia to study the platypus. He confirmed that the animal gave milk and claimed that his specimens demonstrated that the platypus was ovoviviparous and not oviparous, as some had claimed.[122] Owen remarked that all that was lacking for conclusive proof was a specimen of a uterine fetus. He calculated that the period of gestation was about six weeks.[123] When Owen reviewed the literature in 1865 he still maintained this opinion, even in the face of substantial evidence to the contrary.

The discovery of the echidna's pouch further emphasized the affinities between marsupials and monotremes and supported the belief that both groups were ovoviviparous. James Ruddall, a Melbourne physician, and Ferdinand Mueller, an Australian botanist, sent Owen a specimen of a mother echidna with a young in its pouch, concluding that the animal could not be oviparous.[124] Owen concurred, emphasizing the similarity between the young echidna and the newborn kangaroo.[125]

In 1864 Owen received a letter from a physician in Victoria offering important evidence that the platypus was oviparous. He reported that workmen had captured a platypus and tied it up for the night. The next morning they discovered that the animal had laid two eggs. Owen rejected this evidence, noting that the eggs had not been preserved, so one could not examine their contents. He accepted the suggestion that the female's fright during captivity might have induced her to abort.[126]

It was not until nearly a century after the discovery of the echidna that the true nature of monotreme reproduction was generally recognized. W. H. Caldwell, a Cambridge zoologist, was sent to Australia by the Royal Society of London to study the embryology of Australian mammals. On August 29, 1884, he sent a telegram to the British Association at Montreal reporting, "Monotremes oviparous, ovum meroblastic."[127] The discovery was confirmed in the same month by Haacke who displayed an eggshell from the pouch of an echidna to the Royal Society of South Australia.[128] Presented with conclusive proof, Owen finally acknowledged the existence of egg-laying mammals.[129]

Naturalists had resisted the evidence for oviparity in monotremes because they tried to fit the animals into preexisting conceptual categories. As long as they could assume that the platypus gave birth to live young, it fitted within the existing definition of a mammal. The link between lactation and viviparity was preserved. Biologists accepted the view that monotremes were ovoviviparous, despite evidence to the contrary, because it was consistent with existing taxonomic theory. The discovery of the monotremes forced taxonomists to revise their definition of the Mammalia to accommodate the egg-laying mammals. Such a revision was resisted because major changes in taxonomic groupings require a major shift in the conceptual model with which biologists explain the natural order.

NOTES

[1]There are only three monotypic genera: the platypus (*Ornithorhynchus*) and the spiny anteaters (*Tachyglossus* and *Zaglossus*).

[2]George Shaw, *The naturalist's miscellany* (London: Nodder & Co., [1792?]) III, pl. 109.

[3]The Amphibia were at that time usually treated as a subdivision of the Reptilia.

[4]This classification was adopted and integrated into the Linnean system in William Turton's edition of Linnaeus' *A general system of nature* (London: Lackington, Allen and Co., 1802) I, p. 30.

[5]Shaw, *Naturalist's miscellany*, [1799?], X, pl. 385-386.

[6][C. R. W. Wiedemann], "Nachricht von einem äusserst sonderbaren, neuentdeckten Säugethiere, *Platypus anatinus*," *Archiv für Zoologie und Zootomie* I (1800) pp. 175-176.

[7]Thomas Browne, *Pseudodoxia epidemica* (London: Edward Dod, 1646) p. 129.

[8]Johann Friedrich Blumenbach, *Abbildungen naturhistorischer* Gegenstände (Göttingen: bey Johann Christian Dieterich, 1800) pl. 41.

[9]Everard Home, "Some observations on the head of the *Ornithorhynchus paradoxus*," *Royal Society of London*. *Philosophical Transactions* XC (1800) pp. 433-435.

[10]Johann Friedrich Blumenbach, "Anatomical observations on the structure of the *Ornithorynchus paradoxus*," *Philosophical Magazine* XI (1801) p. 367.

[11]Johann Friedrich Blumenbach, "Einige anatomisch Bemerkungen über den *Ornithorhynchus paradoxus* aus Neu-Südwallis," *Magazin für den neuesten Zustand der Naturkunde* II (1800) p. 289-290.

[12]Johann Friedrich Blumenbach, ["Ueber das Schnabelthier ein neu entdecktes Geschlecht von Säugethieren des fünften Welttheils,"] Göttingische Gelehrte Anzeigen I (1800) p. 611.

[13]Johann Friedrich Blumenbach, "Über das Schnabelthier (Ornithorhynchus paradoxus) ein neuendecktes Geschlecht von Säugthieren des fünften Welttheils," Magazin für das neuesten Zustand der Naturkunde II (1800) p. 211.

[14]Ibid., pp. 213-214.

[15]Johann Friedrich Blumenbach, "Sur un nouveau genre de quadrupède édenté, nommé, Ornithorhynchus paradoxus," Société Philomathique de Paris. Bulletin II (1800) p. 113.

[16]"Zur Anatomie des Schnabelthiers," Magazin für den neuesten Zustand der Naturkunde III (1801) pp. 724-725. This article is an unsigned extract from a letter. Oldfield Thomas in British Museum (Natural History) Department of Zoology, Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum (Natural History) (London: Printed by order of the trustees, 1888) p. 386 attributes it to Joseph Banks. Alexander Strauch, De loco Monotrematibus in systemate zoologico assignando et de Ornithorhynchi anatini Shaw. Calcari (Dorpati Livonorum: Typis Henrici Laakmanni, 1859) pp. 91, 95 attributes it to both Banks and Blumenbach. It is probably an extract of a letter from Banks to Blumenbach.

[17]George Stuart Carter, Structure and habit in vertebrate evolution (Seattle: University of Washington Press, 1967) p. 400.

[18]Everard Home, "A description of the anatomy of the Ornithorhynchus paradoxus," Royal Society of London. Philosophical Transactions XCII (1802) pp. 69-82.

[19]Everard Home, "Description of the anatomy of the Ornithorhynchus hystrix," Royal Society of London. Philosophical Transactions XCII (1802) pp. 360-361.

[20]Friedrich Tiedemann, Zoologie (Heidelberg: Landshut, 1809) I, p. 589.

[21]Ibid., p. 592.

[22]Jean Baptiste de Lamarck, Zoological philosophy. Hugh Elliot, transl. and ed. (New York and London: Hafner Publishing Company, 1963) p. 74.

[23]William Elford Leach, The zoological miscellany (London: E. Nodder and Son, 1815) pp. 89-90.

[24]"Art. XIII. A description of the anatomy of the Ornithorhynchus Paradoxus," Edinburgh Review II (1803) p. 436.

[25]Etienne Geoffroy Saint-Hilaire, "Extrait des observations anatomiques de M. Home sur l'échidné," Société Philomathique de Paris. Bulletin III (1803) p. 125.

[26]André Marie Constant Duméril, Zoologie analytique (Paris: Allais, 1806) p. 21.

[27]Carolus Illiger, Prodromus systematis mammalium et avium (Berlin: C. Salfeld, 1811) pp. 113-116.

[28]"Comme enfin il a été impossible jusqu'à présent de leur découvrir des mamelles, on en est à savoir si ces animaux sont vivipares ou ovipares." Georges Cuvier, Le règne animal (Paris: Chez Deterville, 1817) I, p. 225.

[29]Henri Ducrotay de Blainville, Dissertation sur la place que la famille des ornithorhynques et des échidnés doit occuper dans les séries naturelles (Paris: Lebeque, 1812) p. 72.

[30]Ibid., p. 92.

[31]Ibid., p. 97.

[32]Ibid., p. 100.

[33]Ibid., p. 101.

[34]Henri Ducrotay de Blainville, "Prodrome d'une nouvelle distribution systématique du règne animal," Société Philomathique de Paris. Bulletin. s.3., III (1816) p. 109.

[35]William K. Gregory, "The orders of mammals," American Museum of Natural History. Bulletin XXVII (1910) p. 76.

[36]Everard Home, "On the ova of the different tribes of opossum and Ornithorhynchus," *Royal Society of London. Philosophical Transactions* CIX (1819) p. 234.

[37]Joseph Banks, letter to George Caley, 8 April 1803, in Banks Papers--Brabourne Collection, Vol. 8, Caley, p. 120, in Mitchell Library, Sydney (A79-1).

[38]Robert Brown, letter to Joseph Banks, September, 1803, in *Historical Records New South Wales. Vol. 5: King, 1803, 1804, 1805.* F. M. Bladen, ed. (Sydney: William Applegate Gullick, Government Printer, 1897) p. 228.

[39]George Caley, letter to Joseph Banks, 12 March 1804, in Banks Papers--Brabourne Collection, Vol. 8, Caley, p. 141, in Mitchell Library, Sydney (A79-1).

[40]John Jamison, ["Observations on *Ornithorhynchus paradoxus*"] *Linnean Society of London. Transactions* XII (1818) p. 584.

[41]Thaddeus Bellingshausen, *The voyage of Captain Bellingshausen to the Antarctic Seas, 1819-21.* Frank Debenham, tr. & ed. (London: Hakluyt Society, 1945) II, p. 353.

[42]Patrick Hill, ["Observations on *Ornithorhynchus*"] *Linnean Society of London. Transactions* XIII (1822) pp. 623-624.

[43]Etienne Geoffroy Saint-Hilaire, "Note où l'on établit que les monotrêmes sont ovipares, et qu'ils doivent former une cinquième classe dans l'embranchement des animaux vertébrés," *Société Philomathique de Paris. Bulletin* (1822) p. 95.

[44]Everard Home, *Lectures on comparative anatomy* (London: Printed by W. Bulmer for G. and W. Nicol, 1823) III, pp. 364-365.

[45]John Fleming, *The philosophy of zoology; or, a general view of the structure, functions, and classification of animals* (Edinburgh: Archibald Constable & Co.; London: Hurst, Robinson & Co., 1822) II, p. 215.

[46]". . . comme si ce que nous connaissons était règle de tout ce que la nature pourrait créer." Jan van der Hoeven,

"Mémoire sur le genre Ornithorhinque," Deutsche Akademie der Naturforscher. Nova acta Leopoldina XI (1823) pp. 366.

[47]Ibid., p. 368.

[48]James Cowles Prichard, Researches into the physical history of mankind (London: Printed for John and Arthur Arch, 1826) pp. 57-58.

[49]Johann Friedrich Meckel, "Die Säugthiernatur des Ornithorynchus," Notizen aus dem Gebiete der Natur- und Heilkunde VI (1824) p. 144.

[50]Johann Friedrich Meckel, Ornithorhynchi paradoxi descriptio anatomica (Lipsiae: Gerhard Fleischer, 1826) p. 58.

[51]Johann Friedrich Meckel, ["Omnium eorum, quae ad id tempus de Ornithorhyncho promulgata erant, complexus,"] in Christ. Fridericus Campe, Dissertatio inauguralis medica hydrocephalo acuto (Halae: Typis Orphanotrophei, 1823) p. 40.

[52]". . . discrimen inter partum vivorum foetuum et ovorum revera minimum est, nec ullo modo essentiale." Meckel, Ornithorhynchi paradoxi descriptio, p. 58.

[53]Ibid., p. 58.

[54]Henri Ducrotay de Blainville, "Sur les mamelles de l'Ornithorhynque femelle, et sur l'ergot du mâle," Société Philomathique de Paris. Nouveau Bulletin (1826) p. 138.

[55]Jan van der Hoeven, "Corrections au mémoire sur le genre Ornithorhinque," Deutsche Akademie der Naturforscher. Nova acta Leopoldina XI (1825) pp. 369-370.

[56]Everard Home, "Facts adduced in refutation of the assertion that the female Ornithorhynchus paradoxus has mammae," Royal Society of London. Proceedings III (1831) p. 71.

[57]Etienne Geoffroy Saint-Hilaire, "Sur un appareil glanduleux récemment découvert en Allemagne dans l'Ornithorhynque situé sur les flancs de la région abdominale et faussement considéré comme une glande mammaire," Annales des Sciences Naturelles IX (1826) pp. 458-460.

[58]Etienne Geoffroy Saint-Hilaire "Sur les appareils sexuels et urinaires de l'Ornithorhynque," Paris. Muséum d'Histoire Naturelle. Mémoires XV (1827) pp. 1-48.

[59]Johann Friedrich Meckel, "Ueber die Brustdrüse des Ornithorhynchus," Archiv für Anatomie und Physiologie (1827) pp. 23-24.

[60]Ibid., pp. 25-26.

[61]Karl Ernst von Baer, "Noch eine Bemerkung über die Zweifel, welche man gegen die Milchdrüse des Ornithorhynchus erhoben hat, und Betrachtung über das Eierlegen und Lebendiggebären," Archiv für Anatomie und Physiologie (1827) p. 569.

[62]Ibid., pp. 571-575.

[63]Etienne Geoffroy Saint-Hilaire, "Analyse d'un mémoire intitulé: propositions de philosophie anatomique au sujet des glandes mammaires et des glandes monotrémiques," Institut I (1833) p. 52.

[64]Richard Owen, "On the mammary glands of the Ornithorhynchus paradoxus," Royal Society of London. Philosophical Transactions CXXII (1832) p. 531.

[65]Meckel, "Ueber die Brustdrüse . . .," p. 25.

[66]Richard Owen, "Observations sur les jeunes de l'Ornithorhynque," Annales des sciences naturelles (Zool.) II (1834) pp. 305-306.

[67]Etienne Geoffroy Saint-Hilaire, "Analyse d'un mémoire intitulé: Découverte de glandes monotrémique chez le rat d'eau, et dissertation sur l'essence, les rapports, et le mode de formation de ce nouveau système d'appareils glanduleux," Institut I (1833) p. 28.

[68]Owen, "On the mammary glands of the Ornithorhynchus," pp. 532-533.

[69]Richard Owen, "On the young of the Ornithorhynchus paradoxus, Blum.," Zoological Society of London. Transactions I (1835) p. 223.

[70]Although this belief may have been generally accepted among Australian inhabitants, most professional zoologists rejected the combination as impossible or at least highly improbable.

[71]Lauderdale Maule, ["Habits and oeconomy of the Ornithorhynchi,"] Zoological Society of London. Committee of Science and Correspondence. Proceedings II (1832) p. 145.

[72]Henri Ducrotay de Blainville, ["Sur les glandes mammaires de l'Ornithorhynque,"] Société Philomathique de Paris. Bulletin (1833) pp. 69-70.

[73]Geoffroy, "Découverte du glandes monotrémique chez le rat d'eau," p. 28.

[74]Etienne Geoffroy Saint-Hilaire, "New observations on the nature of the abdominal glands of Ornithorhynchus," Zoological Society of London. Proceedings I (1833) p. 92.

[75]Richard Owen, "Response to 'New observations on the nature of the abdominal glands of Ornithorhynchus' by E. Geoffroy Saint-Hilaire," Zoological Society of London. Proceedings I (1833) pp. 95-96

[76]Etienne Geoffroy Saint-Hilaire, "Considérations sur des oeufs d'Ornithorinque, formant de nouveaux documens pour la question de la classification des Monotrêmes," Annales des Sciences Naturelles XVIII (1829) p. 160.

[77]Owen, "On the mammary glands of the Ornithorhynchus," p. 531.

[78]Etienne Geoffroy Saint-Hilaire, "Sur les glandes abdominales des Ornithorhynques, faussement présumées mammaires, lesquelles secrètent, non du lait, mais du mucus, première nourriture des petits nouvellement éclos," Gazette Médicale de Paris, s.2, I (1833) p. 156.

[79]Owen, "On the mammary glands of the Ornithorhynchus," p. 531.

[80]Owen, "Response to 'New observations . . .,'" p. 95.

81 Etienne Geoffroy Saint-Hilaire, ["Reflections on Dr. Weatherhead's communication respecting the Ornithorhynchus,"] Zoological Society of London. Proceedings I (1833) p. 15.

82 Etienne Geoffroy Saint-Hilaire, "Mémoire sur les glandes mamellaires pour établir que les Cétacés n'allaitent point comme à l'ordinaire leurs petits, et qu'ils pourraient s'en tenir à les nourrir de mucus hydraté!" Annales des Sciences Naturelles, (Zool.) s.2, I (1834) p. 176.

83 Geoffroy, "Sur les glandes abdominales . . faussement présumées mammaires," pp. 158-159.

84 Etienne Geoffroy Saint-Hilaire, "Mémoire sur la structure, la capacité de sécrétion et la manière d'être des glandes monotrémiques a l'égard des nouveau-nés; et en particulier sur ces glandes chez les cétacés," Gazette Médicale de Paris, s.2, II (1834) pp. 9-10.

85 Geoffroy, "Mémoire sur les glandes mamellaires . .," pp. 186-187.

86 Etienne Geoffroy Saint-Hilaire, "Mémoire sur les glandes destinées a la nourriture des petits, et spécialement sur leur forme et leur position dans un foetus de baleine," Gazette Médicale de Paris, s. 2, II (1834) p. 25.

87 Richard Owen, "Response to Etienne Geoffroy Saint-Hilaire, Memoir on the abdominal glands of the Ornithorhynchus," Zoological Society of London. Proceedings I (1833) p. 30.

88 Geoffroy, "New Observations on the nature of the abdominal glands," p. 95.

89 Owen, "On the young of the Ornithorhynchus . .," p. 223.

90 Owen, "Response to 'New observations . .,'" p. 95.

91 Owen, "On the young of the Ornithorhynchus . .," p. 226.

92 Geoffroy, "Mémoire sur les glandes mamellaires," p. 188.

[93]Henri Ducrotay de Blainville, "Sur la génération de l'Ornithorhynque," *Société Philomathique de Paris. Bulletin*, s.4 (1833) p. 48.

[94]Owen, "Observations sur les jeunes de l'Ornithorhynque," p. 306.

[95]Richard Owen, "On the ova of the *Ornithorhynchus paradoxus*," *Royal Society of London. Philosophical Transactions* CXXIV (1834) p. 564.

[96]*Ibid*., p. 555.

[97]Richard Owen, "On the generation of the marsupial animals, with a description of the impregnated uterus of the kangaroo," *Royal Society of London. Philosophical Transactions* CXXIV (1834) p. 356.

[98]In 1834, while Owen argued that Blainville's subclass of "didelphs" is characterized by a single mode of generation, Blainville divided the marsupials and monotremes into two separate subclasses. This division is reflected in modern taxonomic systems which divide mammals into two subclasses Prototheria (egg-laying mammals) and Theria, which includes the infraclasses Metatheria (marsupials) and Eutheria (placentals). See Gregory, "The orders of mammals," p. 82.

[99]Richard Owen, "On the mammary gland of the *Echidna hystrix*, Cuv.," *Zoological Society of London. Proceedings* II (1832) p. 180.

[100]Owen, "On the ova of the *Ornithorhynchus* . . .," p. 563.

[101]Owen, "On the mammary glands of the *Ornithorhynchus* . . .," p. 526.

[102]Owen, "On the ova of the *Ornithorhynchus* . . .," pp. 563-564.

[103]R. P. Lesson, "Observations générales d'histoire naturelle, faites pendant un voyage dans les Montagnes-Bleues de la Nouvelles-Galles du Sud," *Annales des Sciences Naturelles* VI (1825) p. 249.

[104] Geoffroy, "Sur les glandes abdominales . . . faussement présumées mammaires," p. 79.

[105] Geoffroy, "Considerations sur des oeufs," pp. 162-163.

[106] Harry Burrell, The platypus (Sydney: Angus & Robertson Limited, 1927) p. 38.

[107] Maule, ["Habits and oeconomy of the Ornithorhynchi,"] p. 145.

[108] Owen, "On the mammary glands of the Ornithorhynchus .," p. 534.

[109] Geoffroy, "New Observations on the nature of the abdominal glands," p. 93.

[110] George Bennett, "Notes on the natural history and habits of the Ornithorhynchus paradoxus, Blum.," Zoological Society of London. Transactions (1835) pp. 240, 244.

[111] Owen, "Observations sur les jeunes de l'Ornithorhynque," p. 308.

[112] Owen, "On the young of the Ornithorhynchus," p. 223.

[113] Etienne Geoffroy Saint-Hilaire, "Nouvelle révélation d'oviparité dans les Monotrêmes," Institut II (1834) p. 339.

[114] Owen, On the ova of the Ornithorhynchus . .," p. 536.

[115] Owen, On the mammary gland of the Echidna . .," p. 180.

[116] Geoffroy, "Sur les glandes abdominales . . faussement présumées mammaires," p. 157.

[117] "D'abord si c'est un fait incompris, au même titre, par exemple, que la chute des pierres venant du ciel, c'est à accepter avec soumission; les explications d'ailleurs viendront après, et peut-être point du tout; mais quel motif

viendrait justifier notre incrédulité? y a-t-il une raison valable a prodruire pour faire croire à l'oviparité comme une chose nécessairement différente de la lactation? J'avoue que je n'en connais d'autre que celle-ci: cette association ne s'est jamais rencontrée. . . ." Geoffroy, "Nouvelle révélation d'oviparité," p. 339.

[118] *Ibid.*, p. 340.

[119] Etienne Geoffroy Saint-Hilaire, "Mémoire sur les Monothrèmes," *Annales des Sciences Naturelles* (*Zool.*) s.2 II (1834) pp. 310-311.

[120] [Robert Chambers], *Vestiges of the natural history of creation* (New York: Humanities Press, 1969 [reprint of first edition, 1844]) p. 219.

[121] [Adam Sedgwick], "Review of *Vestiges of the natural history of creation*," *The Edinburgh Review* LXXXII (1845) p. 73.

[122] Jules Verreaux, "Observations sur l'*Ornithorhynque*," *Revue zoologique* XI (1848) p. 130.

[123] Richard Owen, "Remarks on the 'Observations sur l'*Ornithorhynque*' par M. Jules Verreaux," *Annals and Magazine of Natural History*, s.2, II (1848) pp. 318-319.

[124] Richard Owen, "On the marsupial pouches, mammary glands, and mammary foetus in the *Echidna hystrix*," *Royal Society of London. Philosophical Transactions* CLIX (1865) p. 673.

[125] *Ibid.*, p. 678.

[126] *Ibid.*, p. 684.

[127] W. H. Caldwell, "The embryology of Monotremata and Marsupialia. Part I," *Royal Society of London. Philosophical Transactions*, Series B, CLXXIX (1887) p. 464.

[128] W. Haacke, "On the marsupial ovum, the mammary pouch, and the male milk glands of *Echidna hystrix*," *Royal Society of London. Proceedings* XXXVIII (1885) p. 72.

[129]Richard Owen, "Description of an impregnated uterus and of the uterine ova of *Echidna hystrix*," *Annals and Magazine of Natural History*, s.5, XIV (1884) p. 376.

CONCLUSION

Pre-Darwinian biologists encountered considerable difficulty in understanding the marsupials and monotremes because contemporary theoretical explanations had developed largely without reference to these peculiar creatures. Attempts to accommodate these animals within the existing theoretical framework strained accepted explanatory theories. The failure of accepted theory to provide adequate explanations pointed to the limitations of those theories and thus contributed to the development of a radically new structure--Darwinian theory.

The marsupials and monotremes presented biologists with peculiarities of anatomy, classification, geographic distribution, and fossil history which could not easily be explained within the traditional frame of reference. These same general issues were central to the theoretical debates which led to the development of the Darwinian theory of evolution. Thus marsupials and monotremes provided empirical evidence with which to test new theoretical principles. In some instances (the Wellington Caves, for example) the evidence directly suggested an evolutionary approach. In others (e.g., platypus eggs), new, unexpected evidence was easily accommodated within an already fully formulated evolutionary framework.

Before the discovery of marsupials and monotremes, biologists assumed that all mammalian reproduction conformed to the placental pattern. By expanding their conceptual framework to include mammals that laid eggs and mammals that did not nourish their developing young by means of a typical placenta, biologists were able to construct a transitional series leading from reptiles to monotremes to marsupials to placentals. By using these reproductive differences as criteria in distinguishing the major mammalian taxonomic divisions, biologists were able to arrange the mammals in a progressive series, thus suggesting an evolutionary model of mammalian development. The fact that modern paleontologists no longer accept this hypothetical phylogeny does not detract from its importance in the development of nineteenth-century evolutionary concepts.

Paleontological discoveries of marsupials (or animals identified as marsupials) were also significant. The identification of marsupials as primitive mammals, coupled with the identification of the earliest mammals as marsupials, contributed to the concept of a gradual increase in organic complexity through time. Organic progression, as revealed in the fossil record, provided a major argument in favor of evolutionary development. The discovery of the giant, extinct marsupials of the Wellington Caves directly contributed to Darwin's formulation of the law of succession. This law, which states that the animals now living in any given geographic area bear a close resemblance to the extinct animals of the recent geological past, provided the continuity between past and present which was a prerequisite for a theory of gradual evolution.

The law of succession also suggested that the same laws which now regulate current geographic distribution operated in the past as well.

The Darwinian explanation of the Australian environment provided an ideal example of the capacity of evolutionary theory to explain current geographic distribution. Darwinists explained the peculiar features of the Australian flora and fauna as a result of isolation and divergence. Thus, by referring to a single explanatory model, Darwinists could account for the isolation of marsupials in Australia, their "primitive" nature, and their failure to compete successfully with placentals.

The importance of the evidence from marsupials and monotremes in formulating a new theoretical framework for nineteenth-century biology has not been generally recognized. In part, this is due to the way scholars have examined the history of evolutionary theory. Most historians have concentrated on the work of a particular individual (e.g., Darwin, Wallace, Lyell) or on a particular scientific concept (e.g., evolution, progression, uniformitarianism). This dissertation approaches the subject somewhat differently. An examination of the way opposing theorists confronted a particular scientific problem provides a different perspective on the way scientific theories develop.

As biologists struggled to develop an explanatory system, they imposed their theoretical principles upon the facts, rearranging and reinterpreting those which did not fit their theories. Theorists were often led into error in attempting to develop a self-consistent system which would account for all of the empirical evidence. In proposing new explanations, they were often limited by the research methodologies available to them, the conceptual categories which shaped their thinking, and the theoretical principles which they espoused. In the process of scientific conflict, advocacy often interfered with objectivity.

The geographic isolation of marsupials and monotremes severely limited European experience with these animals. Most trained scientists could only examine preserved specimens in the laboratory, and field observers lacked the necessary training to interpret their experiences in the light of accepted scientific theory. The conflict between those who believed that marsupial young originated in the pouch and those who believed that marsupials followed the normal placental pattern of development can thus be seen as a conflict between two different research methodologies. This conflict is equally apparent in the European rejection of Australian reports of platypus eggs.

Often biologists failed to find the correct solution to the problem because their conceptual categories limited their imagination. The prevailing theoretical framework restricted the kinds of questions which could be asked and the kinds of answers which would be accepted. Thus, biologists who believed that there was only one kind of mammalian reproduction (placental) were reluctant to accept evidence of a second kind (marsupial). Later evidence of a third kind (monotrematic) was met with even greater resistance. Biologists refused to believe that the platypus was oviparous because they could not accept the possibility of an egg-laying, milk-giving mammal. The Stonesfield mammals were identified as marsupials because taxonomists believed that all mammals must be either monotremes, marsupials, or placentals. The modern concept (that the Stonesfield fossils are primitive mammals, combining features of marsupials and placentals) could not be developed until the branching model of evolutionary development provided an appropriate category to account for this fact.

Theorists emphasized the evidence which was consistent with their theoretical principles, discounting the importance of data which appeared to contradict their position. Thus, evolutionists seized on the paleontological evidence in favor of continuous organic progression. Anti-evolutionists, on the other hand, pointed to the discontinuities within the fossil record in order to discredit the evolutionary position. Anti-evolutionists wished to make the platypus a mammal just like other mammals because this interpretation reinforced taxonomic discontinuities and thus challenged evolutionary theory. Evolutionists, in contrast, denied that monotremes were mammals at all, making them into a special transitional class linking the mammals to the lower vertebrates.

Theoretical conflicts rigidified and polarized scientific opinion. Once committed to a theoretical position, biologists were reluctant to admit to error. A strong personal commitment to a theory often prevented a scientist from recognizing the significance of new data. Richard Owen, for example, was so convinced of monotreme viviparity that he failed to recognize the true function of the egg tooth and denied the value of eye-witness descriptions of platypus eggs.

Theorists were influenced not only by the evidence and the logical requirements of their own theoretical systems but also by the arguments of their opponents. For example, special creationists developed an explanation of the "ancient" appearance of the Australian flora and fauna which was specifically designed to counteract Chambers' interpretation. Chambers, in turn, severed the connection between environmental progression and organic progression in order to discredit special creationist explanations based on adaptation.

These considerations serve as a reminder that, while science is a very special and powerful branch of human knowledge, it is also a human endeavor. As a human construction, the development of science is subject to all the human failings of other branches of thought, and analyses of scientific development must take into account these psychological factors.

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