CHAPTER 1

ETERNAL METAPHORS OF PALAEONTOLOGY

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The Content of Palaeontology

Of eternity

Alexander wept at the height of his triumphs because he had no new worlds to conquer. Whitehead declared that all of philosophy had been a footnote to Plato. The Preacher exclaimed (Ecclesiastes 1:10): "Is there *any* thing whereof it may be said, See, this is new? It hath been already of old time, which was before us."

The essential questions of a discipline are usually specified by the first competent thinkers to enter it. The intense professional activity of later centuries can often be identified as so many variations on a set of themes. The arrow of history specifies a sequence of changing contexts within which the same old questions are endlessly debated — "The thing that hath been, it is that which shall be; and that which is done is that which shall be done" (Ecclesiastes 1:9).

In this paper, I wish to propose that (1) the basic questions palaeontologists have asked about the history of life are three in number; (2) the formulation of these questions preceded evolutionary thought and found no resolution within the Darwinian paradigm; (3) the major contemporary issues in palaeobiology represent the latest reclothing of these ancient questions. Although fencesitting, waffling, and middle-of-the-roadism have a pedigree as long as the three questions themselves, palaeontologists have generally come down clearly on one side or the other of each issue. The issues are so pervasive and general that chosen opinions reflect social and cultural climates as well as a supposedly "objective" reading of the fossil record. There are strong correlations among the issues, but all eight possible combinations (for two opinions on each of three questions) can and have been maintained by palaeontologists. Adherence to one or the other side of each issue has usually been expressed in metaphor — hence the somewhat cryptic title of this chapter.

Three antitheses as the subject of palaeontology

I do not contend that these three questions inform all the work that palaeontologists have done. They are issues for the major features of life's history. One can spend a lifetime taxonomizing local faunas and correlating sections within a basin and never encounter them in any serious way. I identify the three questions and their polar opinions as the following:

(1) Does the history of life have definite directions; does time have an arrow

specified by some vectorial property of the organic world (increasing complexity of structure, or numbers of species, e.g.). No question received more discussion during the establishment of modern palaeontology in the early to mid-nineteenth century. Despite the misunderstanding of most modern geological textbooks, it was the central issue in the debate between "uniformitarianism" and "catastrophism". The catastrophists were, for the most part, progressionists who viewed each new episode of life as a distinct improvement leading inexorably towards the modern creation dominated by *Homo sapiens.* Lyell, on the other hand, had a vision metaphorically linked to the Newtonian timelessness of endlessly revolving planets. Species came and went; land rose and fell; seas went in and out — but the world was ever the same. During the late nineteenth century, the battle raged again in an evolutionary context, with vitalists and finalists speaking of inevitable direction (e.g., Osborn's "aristogenesis"), and some strict Darwinians maintaining that evolution means nothing more than successive adaptation to changing local environments. In contemporary palaeobiology, we find the neo-Lyellian metaphor in the stochastic, equilibrium models of Raup et al. (1973), while Huxley's notion of anagenesis and successive grades (1958) upholds the idea of direction. I will refer to the vectorial view as *directionalist* (rather than progressionist, because the direction might be down), and the Lyellian vision as *steady-statist.*

(2) What is the motor of organic change? More specifically, how are life and the earth related? Does the external environment and its alterations set the course of change, or does change arise from some independent and internal dynamic within organisms themselves? In pre-evolutionary times, debate raged on the importance to life of geological change. The opposing sides included some strange bedfellows — or so we judge it, wearing the anachronistic spectacles of later categorizations. (In fact, our reluctance to see Buckland and Lyell as joint protagonists, for example, leads directly to our total blindness towards this major debate during the early nineteenth century.) Buckland and Lyell believed that alterations in the physical environment provided the primary impetus for organic change (for Buckland, the earth changed in a directional fashion; for Lyell it did not — hence their differences on the question of directionalism—steady-statism. They were united on the issue of physical control). Agassiz, on the other hand (though conventionally a "catastrophist" like Buckland), argued vigorously that life changed by a dynamic of its own, quite unrelated to modification of the physical environment. Direct control by the physical world, Agassiz claimed, would be a crassly vulgar way for the creator to pursue his evident design for the history of life. In a later evolutionary context, various orthogenetic trend theories upheld Agassiz's position, while the most Darwinian of palaeontologists — Dollo and Matthew in particular — argued that evolution proceeded when changes in the physical environment established selective pressures for new adaptation. Today, the Buckland—Lyell thesis reemerges in Valentine's vision (1973) of the external environment as a motor for all major evolutionary change, while claims for an internal dynamic can be seen in Stanley's invocation of the cropping principle to explain the Cambrian explosion (1973) and Flessa and Levinton's

belief (1975) that the potential for finer niche partitioning may be virtually limitless. I will refer to the belief in external control as *environmentalist* and to claims for an inherent cause of change as *internalist.*

(3) What is the tempo of organic change? Does it proceed gradually in a continuous and stately fashion, or is it episodic? In pre-evolutionary times, Lyell was a dogmatic gradualist in arguing for continual exercise of the creative power at about the same rate through time (with consequently constant rates of extinction). The more colourful catastrophists, with their claims of nearly complete destruction followed by wholesale creation of new faunas, occupied the other pole. With the guidance of evolution, Darwin followed the Lyellian metaphor of gradualism, while D'Arcy Thompson invoked the spirit of Pythagoras to support macromutational steps between idealized forms (Gould, 1971). The current debate between Eldredge and Gould's notion of "punctuated equilibria" (1972) and Gingerich's defense of phyletic gradualism (1976) merely replays an old tale. I will label stately, Lyellian change as *gradualist*, and episodic views as *punctuational.* I recognize — and this will be important for the concluding section — that scaling has its usual effect and that one can be a gradualist at one level (the origin of species, for example) and a punctuationist at another (by asserting the importance of mass extinctions as a general control of diversity).

Apologia

I was assigned to write a general history of palaeontological attitudes towards evolution. Instead, I am denying that evolution had any influence in shaping the major questions of palaeontology (though it changed completely and permanently the context in which they are debated). I am also writing a most peculiarly anhistorical history — no chronologies, no sequential accounts of the worthy bricklayers who built our modern edifice. It might even seem to verge on a structuralist denial of history, by asserting the timelessness of central themes (to which the true history of changing contexts is merely so much superficial recasting). So be it. I would only say that the changing contexts *are* the subject matter of palaeontology, and that I do not view their historical sequence as superficial in any respect. I also regard this theme of "eternal questions" as a legitimate way to present a coherent, conceptual account of palaeontological history in the allotted space.

Some will be offended at what might seem to be a claim of patrimony. A modern directionalist may well reject an "ancestor" like Buckland, claiming with invincible logic either that he never heard of the man, or that he chooses not to be ranked with the author of "Geology and mineralogy considered with reference to natural theology" (Buckland, 1836). But I am not making a claim of homology via chains of physical descent like pedigrees of kinship. Pedigrees of ideas can be "homologous" — indoctrination of child by parent, or student by teacher, for example. But the chains of which I speak are forged of analogous links only. Basic ideas, like idealized geometric figures, are few in number. They are eternally available for consumption, and the sequential list of their consumers is no pedigree, but the convergence of independent minds to one of a very limited set of basic attitudes. They are, of course, consumed in very different contexts: Buckland's benevolent God and Valentine's drifting continents are phenomena of such a different order that it becomes difficult to see how they function for both men in a similar way — as the "motor" for changes in the physical world that control patterns of organic form and diversity. I am even tempted to claim that the task of history is to explain the contexts so clearly that they can be separated and subtracted, thus permitting us to see the unchanging themes.

A Taxonomic Interlude

Before I proceed in more conventional, chronological fashion, I would like to defend my categories by demonstrating that all eight combinations of the three antitheses have been upheld by famous students of the history of life. I will defend my assignments in later sections and confine myself here to thumbnail sketches drawn from different periods of time. (The accompanying diagram, Table I, is set up as a contingency table, not a flow chart. I do not believe that the structure of the three basic questions is hierarchical.)

(1) SEP (steady-statist—environmentalist—punctuational). D'Arcy Thompson (1917, 1942) believed that physical forces shaped organisms directly — a radical environmentalism (see Gould, 1971). No viable intermediate forms exist between many basic designs (*Baupläne*), just as many geometrical figures can-

TABLE I

Classification of early palaeontologists' evolutionary beliefs

Direction of change	Mode of change	Tempo of change	Code	Name and school	Frequency
steady state (S)	environmentalist (E)	punctuational (P)	SEP	D'Arcy Thompson	rare
		gradualist (G)	SEG	early Lyell, part of Darwin, "strict uniformitarianism"	fairly common
	internalist (I)	punctuational (P)	SIP	late Agassiz	very rare
		gradualist (G)	SIG	Lamarck	very rare
directional (D)	environmentalist (E)	punctuational (P)	DEP	Buckland "catastrophism"	common
		gradualist (G)	DEG	late Lyell, part of Darwin	common
	internalist (I)	punctuational (P)	DIP	early Agassiz, Oken, most of "Naturphilosophie"	moderately common
		gradualist (G)	DIG	Osborn "orthogenesis"	common

not be smoothly transformed one into the other; transitions must be by macromutation — punctuationism. Since physical forces shape organisms and have not varied through time, life has no direction — steady-statism.

(2) SEG. Lyell's school of strict uniformitarianism. The mean complexity and diversity of life does not vary through time (S); geological changes regulate the extinction and origination of new taxa (E); rates of origination and extinction are slow and fairly constant through time (G). Lyell never abandoned E and G, but accumulating evidence for direction in the history of vertebrates led him to surrender S when he converted to evolutionism (Wilson, 1970; Gould, 1970). Darwin also never wavered on E and G, but had an ambiguous attitude toward directionalism—steady-statism. He argued vigorously that nothing in his theory of natural selection itself permitted any belief in inherent progress or direction, for natural selection refers only to adaptation in local environments. But natural selection did not forbid progress as an empirical result if local adaptation led occasionally to general improvement in structural design.

(3) SIP. Agassiz held firm to his belief in punctuations (glaciers as "God's great plough," for example), and in the independence of newly created forms from physical control (P and I). For most of his career, Agassiz was a firm progressionist as well (D). But after Darwin's *Origin of Species* (1859) he began to see progressionism as an argument for the dreaded notion of evolution, and he turned against it to favour the idea that mean complexity of life had not changed since the Cambrian explosion (S).

(4) SIG. Few will dispute a characterization of Lamarck's evolutionary theory as gradualist and internalist (progress by the "sentiment intérieur" — the "force which tends incessantly to complicate organization"). But how, given all his talk of progress up the ladder of life, can he be called a steady-statist. In a brilliant essay, Simpson (1961) has shown that Lamarck's more global view is non-directional. An individual lineage exhibits undisputed progress from amoeba towards man. But the highest forms of organization are inevitably degraded to their basic constituents, and must start the upward trek anew by spontaneous generation at the bottom. Upward motion is just one phase of an endlessly repeating cosmic cycle of advance and degradation.

(5) DEP. This is a characteristic combination of early nineteenth century catastrophism, as found, for example, in William Buckland. Each new creation, following a mass extinction (P), is an improvement on the previous inhabitants (D). The improvements place the new inhabitants into harmony with an altered earth (E).

(6) DEG. Lyell reluctantly submitted to the empirical evidence for progressionism (D), but held firm to his uniformitarian beliefs in gradual change (G) for the physical environments that set the course of organic evolution (E).

(7) DIP. Another group of catastrophists shared Buckland's convictions about progressive and discontinuous change (P and D). But they saw no relationship between this advance and any change in the earth's physical appearance. The creator, according to Agassiz, had his own plans for displaying the order and progress of his thoughts; he would not resort to so vulgar a device as simply fitting life to its external situations (I). L. Oken, a prominent German

Naturphilosoph, spoke of drastic reformulation of each higher stage (P) from the primal zero (D) as spirit strove ever upward in its inherent attempt to become man (I).

(8) DIG. Most "orthogenetic" beliefs of the late nineteenth century viewed straight-line evolution as an upwardly mobile affair, proceeding gradually through time without reference to any environmental control exerted by such unimportant factors as natural selection.

Finally, I emphasize that the filling of all eight categories does not deny that attitudes are strongly correlated from one question to the next. The guestimated column on frequencies reflects these correlations. Directionalism and internalism form the strongest link (DI). Very few internalists lack a belief in progress — why postulate an inherent mechanism for change unless it is leading somewhere?

Pre-evolutionary Establishment of the Three Questions

Introduction

The "eternity" of my title is prospective only. Philosophy needed its Plato to write the documents for later annotation. Palaeontology could not pose its three basic questions until it had resolved two prior issues in favour of the beliefs that established its modern character. The likes of Steno and Hooke, Smith and Cuvier deserve all the usual accolades for the resolution. But their story is not the tale I have chosen for this work; need I say more in their honour than that eternity begins with them?

(1) The organic nature of fossils had to be established. This debate, largely over by the mid-eighteenth century, had consumed much attention during the early years of the Royal Society (late seventeenth century). We praise Steno for the meticulous arguments of his *Prodromus* and *Canis carchariae dissectum caput* (1667, reprinted 1958, with its appendix on the organic nature of fossil shark's teeth), especially his proofs that sedimentary rocks are the historical products of deposition. But we should recognize that the opposing views of Lister, Lhwyd and Plot were reasonable in the context of their times (Rudwick, 1972), and that the cause of poor Beringer's undoing was vanity rather than stupidity (Jahn and Woolf, 1963; Beringer considered the possibility that his figured stones were hoaxes, but finally concluded that the Lord in his wisdom had salted the mountain with these wondrous objects for him, i.e., Beringer, to find).

(2) Fossils had to be recognized as the sequential products of an extended history. Organic status was not enough; fossils had to be imbued with a history, i.e., their potential use for establishing a time scale had to be recognized. Many palaeontologists are not aware that the question of extinction was not settled until Cuvier's time, and that Thomas Jefferson himself had argued in the opening years of the nineteenth century that no animals could disappear from the earth. If fossils only record a single creation (one still with us), then none of

the three questions can be posed at all. Even a two-stage classification of pre and post Noah will not suffice. Fossils must record a long and varied history of organic change before any rocks can be correlated and any of the three questions asked.

The modern character of palaeontology begins not with the acceptance of evolutionary theory in the mid nineteenth century, but with the establishment of a methodology for temporal ordering by Smith and Cuvier during the earliest years of the nineteenth century. By Lyell's time, the three questions had been posed and debated extensively. Since then, we have not stopped — and I doubt that we ever will.

Progression vs. steady state as the essence of the uniformitarian catastrophist debate

Contrary to popular belief, no serious nineteenth century scientist — not even the most theological catastrophist — argued for the direct intervention of God in the earth's affairs. All accepted the constancy of natural law. God had ordained unchanging principles when he wound up the universal clock; he did not need to meddle by miracle with the subsequent history of the earth. None-the-less, God was scarcely banished from the thoughts of leading palaeontologists; for opinion in the debate of steady-statists and directionalists reflected one of two basic positions on the nature of divine benevolence . Either God ordained his laws so that the earth's history would be a steady march from simple beginnings towards divine glory; or, like a timeless presence, he had set the original world as he wanted it for all time — earth "history" would be as anhistorical as the endless cycling of Newton's planets.

Empirically, the fossil record as known to Cuvier and his contemporaries — and it is not much different now — displayed a sequence of faunas, each separated from the one below by a major break both in organic form and geological environment. Moreover, as more and more fossil vertebrates were described, their sequence seemed to mirror the conventional ladder of advance among the classes — fish first of all, followed by amphibians and reptiles, then by mammals and finally by man (whose fossil remains had yet to be found at all).

Cuvier, again contrary to his popular image as an overt, theological apologist, was a rigid empiricist who proffered no opinion on the largely metaphysical question of organic progress. But most of his catastrophist colleagues did not feel so constrained. Rudwick (1972) has shown convincingly that the progressionist world view had become a coherent, recognized and well articulated geological paradigm during the years preceding Lyell's *Principles.*

William Buckland, Dean of Oxford Cathedral and first Reader of Geology at the University, stated "that the more perfect forms of animals become gradually more abundant, as we advance from the older into the newer series of depositions" (1836, p. 115). (He hastened to add that "imperfect" did not mean ill-adapted, but only simpler in structure. All God's creatures are ideally fit for their appointed stations — 1836, pp. 107—108.)

Louis Agassiz articulated a well-developed theory of progress with his "threefold parallelism" between the stages of ontogeny, the sequences of comparative anatomy and the successive introduction of higher types into the fossil record (Gould, 1977). Of vertebrate history, he writes (1857, in 1962, p. 108): "Through all these intricate relations there runs an evident tendency towards the production of higher and higher types, until at last Man crowns the whole series".

James Hutton had rather little to say about life, but his "world machine" of endlessly cycling erosion, consolidation and uplift provided a timeless, non-directional stage for Lyell's steady state of geological and biological history. In asserting that the mean diversity and complexity of life had not changed through time, Lyell encountered the empirical dilemma of an apparently progressive vertebrate history. Lyell's response was typical of his methodology — he argued that prior theory had to be imposed upon an imperfect record to establish the plausibility of his view in the face of opposing documents. Some may brand this as dogmatism; I regard it as sound and imaginative science, for it transfers the argument to the prior theory itself (which must be falsifiable to be scientific). (And Lyell was surely no uncompromising dogmatist, for he abandoned his steady state by the 1850s when predicted evidence against progression did not develop.) Lyell presents three main arguments for not accepting the empirical evidence of progression.

(1) The fossil record is notoriously imperfect. Fossil mammals will eventually be found in all Palaeozoic periods; the rocks investigated so far would not preserve their remains:

> "We must not, however, too hastily infer from the absence of fossil bones of mammalia in the older rocks, that the highest class of vertebrated animals did not exist in remoter ages. There are regions at present, in the Indian and Pacific oceans, co-extensive in area with the continents of Europe and North America [domain of virtually all Palaeozoic rocks studied by Lyell's time], where we might dredge the bottom and draw up thousands of shells and corals, without obtaining one bone of a land quadruped" (1842, p. 231 — these quotations, from the widely read 6th edition of the *Principles*, differ in no substantive way from the 1st edition of 1830).

Lyell (1842, pp. 238—239) took great comfort from the recent discovery of a single mammalian fauna in Jurassic beds of the Stonesfield Slate. If the Mesozoic had fallen, the Palaeozoic could not be far behind. Moreover, he saw no evidence for improvement in the Tertiary, where the record was at least adequate, if not good:

> "In this succession of quadrupeds, we cannot detect any signs of a progressive development of organization, — any clear indication that the Eocene fauna was less perfect than the Miocene, or the Miocene than that of the Older or Newer Pliocene periods" (1842, p. 249).

(2) Lyell offered another potential answer to the directionalist claim that the earth's temperature had been decreasing as a result of cooling from the primal nebula (and that this cooling had inspired such progressive adaptations as the creation of warm-blooded mammals). Lyell admitted the potential decrease

through time, but disputed the inherent and irreversible directional mechanism. He argued instead that cooling had been a contingent and reversible result of the distribution of land. The Northern Hemisphere had been largely oceanic during the warm Carboniferous, and had become progressively continental since then. Climates followed continents, and continental disposition varied cyclically or stochastically through time. The cooling had occurred, but it had been part of a grand cycle, not the first stages of an ineluctable trend (Ospovat, 1975). We are now, he stated, in "the winter of the 'great year,' or geological cycle". Warmer times will come again, and when they do, Lyell states in what must be the most striking passage of the entire *Principles*:

> "Then might those genera of animals return, of which the memorials are preserved in the ancient rocks of our continents. The huge iguanodon might reappear in the woods, and the ichthyosaur in the sea, while the pterodactyle [*sic*] might flit again through the umbrageous groves of tree-ferns" (1842, p. 193).

I shall have more to say later of the ichthyosaur's return.

(3) But what of Man? No human fossils had been found, and Lyell was not about to deny our superiority. In a resolution, uncomfortable even in his own context, Lyell argued that the introduction of Man marked a discontinuity to which his system did not apply — an imposition of a new moral order upon the steady state of the material world. As an event within the moral sphere, it did not come under his purview. The Lord had ordained consciousness so that the steady state external to it might be appreciated as a sign of divine order.

> "To pretend that such a step, or rather leap, can be part of a regular series of changes in the animal world, is to strain analogy beyond all reasonable bounds" (1842, p. 252).

Our own arrival has not interrupted the steady state of geological and biological change:

> "And so the earth might be conceived to have become, at a certain period, a place of moral discipline, and intellectual improvement to man, without the slightest derangement of a previously existing order of change in its animate and inanimate productions" (1842, p. 258).

The motor of change and the nature of creative power: internal and environmental theories

For a brief period during the early nineteenth century, geology was the queen of the sciences. The greatest minds of Europe flocked to it, and even became palaeontologists. The relationship between geological and biological change became a major subject and source of contention. The world reflected a divine order, to be sure, but how did it do so? A school of "environmental determinists" (Ospovat, 1975) saw greatest evidence of design in the perfect fitting of each organism to its appointed station in the environment. The geological alteration of environments became the primary cause of organic change

— an unavoidable conclusion if newly created forms are constrained to fit new environments perfectly. But other palaeontologists rejected this link between a material earth and the history of life. Their vision of organic order required an independent dynamic — a separation of life from the earth and an affirmation of self-directed, organic uniqueness. The extreme versions are visions, not empirical readings of the fossil record. Some men are attracted to the idea of harmonious interaction and oneness, others to a separate and irreducible status for life.

William Buckland took the environmentalist position; life progressed because it had to fit an improving physical world:

> "We may collect an infinity of arguments, to show that the creatures from which all these fossils are derived were constructed with a view to the varying conditions of the surface of the earth, and to its gradually increasing capabilities of sustaining more complex forms of organic life, advancing through successive stages of perfection" (1836, p. 107).

Lyell agreed with Buckland's tie of life to the earth. But since his earth did not progress, neither did his history of life. And so we return to the importance of what must strike most modern readers as Lyell's utterly absurd statement about returning ichthyosaurs. (Indeed, it also struck some of his contemporaries as absurd — witness Henry de la Beche's cartoon of the future Professor *Ichthyosaurus* lecturing to his students about a fossil human skull, Fig. 1.) What could this founder of geology, this great and sober uniformitarian, have meant by such nonsense. In an 1830 letter to Gideon Mantell (quoted in Ospovat, 1975), he was even more explicit and definite:

> "I will not tell you how, till the book is out — but without help from a comet, or any astronomical change, or any cooling down of the original red-hot nucleus, or any change of inclination of axis or central heat, or volcanic hot vapours and waters and other nostrums, but all easily and naturally. I will give you a recipe for growing tree ferns at the pole, or if it suits me, pines at the equator; walruses under the line, and crocodiles in the arctic circle. And now, as I shall say no more, I am sure you will keep the secret. All these changes are to happen in future again, and iguanodons and their congeners must as assuredly live again in the latitude of Cuckfield as they have done so."

Pines at the equator, crocodiles in the arctic and iguanodons again in England. Each environment has its characteristic forms of life. Organisms will follow the migrations of their environments over the earth; they will even reappear — at least at the generic level of basic design — when their environment, now present nowhere on earth, forms again during the returning phase of the great cycle.

"Catastrophism" was not a monolithic dogma. We find Buckland united with the uniformitarian Lyell in support of environmentalism. Louis Agassiz, America's greatest catastrophist, argued vehemently for an intrinsic and independent control of life's direction. The history of life displays the thoughts of the Creator in their most sublime embodiment; life does not merely map a sequence of environments. Physical history is catastrophic, but it has no direction; organic history, on the other hand, is inherently progressive:

Fig. 1. Professor *Ichthyosaurus*, at some future time after his triumphant return, lecturing to his students on the fossil skull of a peculiar Quaternary mammal. Satirical figure by de la Beche, commenting on Lyell's strict environmentalism and non-progressionism (from Buckland, 1890).

"While the material world is ever the same through all ages in all its combinations, as far back as direct investigations can trace its existence, organized beings, on the contrary, transform these same materials into ever new forms and new combinations. . . This identity of the products of physical agents in all ages totally disproves any influence on their part in the production of these ever changing beings which constitute the organic world, and which exhibits, as a whole, such striking evidence of connected thoughts" (1857, 1962 ed., pp. 97—99).

The tempo of organic change

Cuvier hestitated to write about what he could not see. He carefully avoided the issue of directionalism, but hesitated not at all in expressing his belief in the episodic nature of both geological and organic change. The literal record of the rocks required it. "The surface of the earth", he wrote (1817, p. 7), "has been much convulsed by successive revolutions and various catastrophes." The fossil record of life is equally episodic: "If the species have changed by degrees. . . we ought to find traces of this gradual modification. . . We should be able to discover some intermediate forms; and yet no such discovery has ever been made" (1817, p. 115). Its episodes, unsurprisingly, match the physical revolutions, as waves of extinction prepare an earth to receive new forms. (Cuvier did not believe that physical revolutions wiped out all of life; some new forms of a subsequent fauna may have migrated into an area from a pool of survivors elsewhere):

> "Numberless living beings have been the victims of these catastrophes; some have been destroyed by sudden inundations, others have been laid dry in consequence of the bottom of the seas being instantaneously elevated. Their races even have become extinct, and have left no memorial of them except some fragment which the naturalist can scarcely recognize" (1817, pp. 16—17).

How could Lyell assert his gradualist notions of slow and constant tempos for extinction and creation against the weight of Cuvier's evidence? Lyell defended gradualism by invoking his distinctive principle of scientific methodology (as he did in arguing for a steady state of life against the evidence of vertebrate progression). When evidence is imperfect, a scientist must probe behind appearance. He must establish and defend a general theory, predicting from it the expectations of evidence. When empirical evidence does not meet these expectations, a scientist must decide whether the evidence is illusory or the theory false. Disconfirming, but inconclusive, evidence should be reinterpreted in the light of theory; as long as the reinterpretation works, the theory should be maintained. In this case, Lyell stuck with his uniformitarianism by invoking the incontestable incompleteness of the geological record — the preservation of a few words per page of the earth's book, our prejudices as inhabitants of dry land where sedimentation is so sporadic, etc. In a remarkable passage, Lyell defends his method. At first reading, it seems riddled with the folly of dogmatism; but the message grows on you. And when we recognize that no observations are independent of theory — that, in fact, theory is a proper guide to observation — it begins to make sense. The antidote to dogmatism is a willingness (that Lyell had) to abandon theory, not an assertion of the primacy of unbiased observation:

> "It is only by becoming sensible of our natural disadvantages that we shall be roused to exertion, and prompted to seek out opportunities of discovering such of the operations now in progress, as do not present themselves readily to view. We are called upon, in our researches into the state of the earth, as in our endeavors to comprehend the mechanism of the heavens, to invent means for overcoming the limited range of our vision. We are perpetually required to bring, as far as possible, within the sphere of observation, things to which the eye, unassisted by art, could never obtain access" (1842, p. 121).

The Altered Context of Evolutionary Theory

For palaeontology, evolutionary theory was not the watershed that later reconstructions usually proclaim. It did enlighten some issues — gradualism at the lowest level of the species became possible for the first time (even Lyell's extreme gradualism at higher levels had required the immediate creation of each new species). But it provoked virtually no change in taxonomic or stratigraphic practice — the backbone of our day-to-day activity. The fossil record, with its literal evidence of catastrophe and sudden faunal transition, proved more of a problem for Darwin than a benefit. His chapter bore no such triumphant title as "proof of evolution from the recorded history of life", but rather the apologetic: "on the imperfection of the geological record."

Evolutionary theory swept through palaeontology as rapidly as it triumphed in other disciplines. A few, like Agassiz, took their creationism to the grave, but the battle was over within a decade after 1859. However, by accepting the fact of evolution, none of the three great issues was resolved. I cannot even say that the relative frequency of belief changed markedly for any of the three sets of alternative positions. Directionalism or steady-statism, internalism or environmentalism, gradualism or punctuationism — all could be easily encompassed within evolutionary theory.

Darwin convinced his colleagues about the fact of evolution. If his theory of natural selection had found equal favour, palaeontology might have reached a consensus on at least two of its three great issues. In a famous statement, Darwin said that he felt as if his books had come half out of Lyell's brain. The extensive accuracy of this statement has rarely been appreciated, and many commentators have read it as just one more exercise in sham, Victorian modesty. Darwin's position on the three central issues was that of Lyell, updated for an evolutionary context. He was a convinced gradualist at all levels, and this is the only opinion on the three issues that most nineteenth century evolutionary palaeontologists shared with him. He, like Lyell, was an environmentalist. Internal forces do little more than provide a spectrum of random variability for the creative agent of natural selection. Local environments determine the direction of selection.

On the third issue of steady state vs. direction, Darwin experienced Lyell's ambiguity; but whereas Lyell espoused the two positions sequentially, Darwin managed to hold them simultaneously. By the mid 1850s, Lyell was ready to bow to the evidence for progression in the phyletic history of vertebrates. It is widely believed that he converted to evolution about the same time because Darwin had convinced him. I maintain that he accepted evolution as a "minimum retreat" from his former set of beliefs, once he had been forced to accept the fact of progression (Gould, 1970). Progressionistic theories of life had been the property of catastrophists who, to a man, were strongly committed to the punctuationist theory of paroxysms — catastrophes removed much of life, and new, higher creations repopulated the void. For Lyell, evolution provided a way to accept progressionism without abandoning either the gradualism or environmentalism so vital to his "uniformitarianism."

Ironically, progression was not an important argument for Darwin's personal belief in evolution. In fact, I maintain that an explicit denial of innate progression is the most characteristic feature separating Darwin's theory of natural selection from other nineteenth century evolutionary theories. Natural selection speaks only of adaptation to local environments, not of directed trends or inherent improvement. Darwin wrestled with the issue of progression and finally concluded that his theory provided no rationale for a belief in evolutionary directions — adaptation to local environments meant just that and nothing more. He wrote to the American directionalist Alpheus Hyatt: "After long reflection I cannot avoid the conviction that no innate tendency to progressive development exists" (quoted in F. Darwin, 1903, p. 344).

But we cannot label Darwin as a pure steady-statist; for, while he denied progress as an intrinsic ingredient of evolutionary mechanisms, he did not deny the possibility of direction as an outcome of the operation of natural selection. Evolution is adaptation to local environments, but one pathway to adaptation lies in structural "improvement" conferring a more general success upon its bearer:

> "The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life, and are, in so far, higher in the scale of nature; and this may account for that vague yet ill-defined sentiment, felt by many paleontologists, that organization on the whole has progressed" (1859, p. 345).

A few palaeontologists accepted Darwin's theory of natural selection — some of the German ammonite workers and a few functional morphologists, Kovalevsky and Dollo, in particular. But it was as much a minority view among students of fossils as it was in the community of evolutionists at large. The standard reasons given for its disfavour cite strictly scientific difficulties — particularly, Darwin's inability to explain the genetic nature of variation. I do not deny the importance of these arguments; nonetheless, I believe that natural selection was rejected during the nineteenth century primarily because it was philosophically too radical (Gould, 1974a) and that this radicalism is primarily expressed in Darwin's position on the three issues. Comfortable Victorians had no quarrel with gradualism; if things had to change, they might as well do it in a slow and orderly manner. But with his environmentalism and his partial steady-statism, most of Darwin's colleagues could muster no agreement. They deplored the coarsely materialistic nature of natural selection, a theory that granted no special uniqueness to living material and that identified the agent of change not within organisms themselves, but in a fluctuating external environment. They were not willing to view organisms as being directed nowhere and buffeted continually by external forces not under their control. If Darwin had removed a benevolent God from the domain of life, then purpose and uniqueness would have to be sought in the very nature of life itself.

Thus, the common thread of anti-Darwinian evolutionary theories during the late nineteenth and early twentieth centuries is their "DI bias"; i.e., they proclaim an intrinsic direction for evolution and they locate the directional force within organisms themselves. Evolution can be rescued from Darwin's materialism; life can remain separate and inviolate.

It has often been said — and truly — that Darwin's main competition within palaeontology came from orthogenetic, vitalistic and finalistic theories of life (Simpson, 1949, for example). It has rarely been noted that the common denominator of these theories is their DI bias. We may specify three "levels" of anti-Darwinian DI theories.

(1) Claims for universal direction. Henry Fairfield Osborn spent a lifetime trying to induce the laws of evolution from the history of fossil vertebrates. Most of his conclusions were negative. He flirted with Lamarckism as a young man, but rejected it when no mechanism could be found for the inheritance of acquired characters. He saw a role for natural selection in eliminating the unfit, but did not understand how it could create the fit. The fossil record did teach him that change was slow and continuous, and that it seemed to lead in definite directions — larger titanotheres, with bigger horns, for example.

> "It has taken me thirty-three years of uninterrupted observation in many groups of mammals and reptiles to reach the conclusion that the origin of new characters is invariably orthogenetic" (Osborn, 1922, p. 135).

Osborn developed a finalistic theory of "aristogenesis" to explain the direction of life. Since evolution is slow and gradual, structures useful only at large size must go through a long prior history of gradual and non-adaptive increase. (Titanothere horns must begin as tiny, useless nubbins and increase directionally through a long non-adaptive phase towards the rather large size of their incipient utility.) "Aristogenes" — little more than a name for ignorance — control the origin and direction of traits with only distantly prospective value. Moreover, Osborn drew his phylogenies to support his DI theory. Osbornian phylogeny is always highly polyphyletic — a bush with numerous independent branches joining only at the base (Fig. 2). Traits marking the predetermined paths of evolution can arise independently and progress directionally in any number of lineages. Though environments can enhance or eliminate, they do not direct the trend.

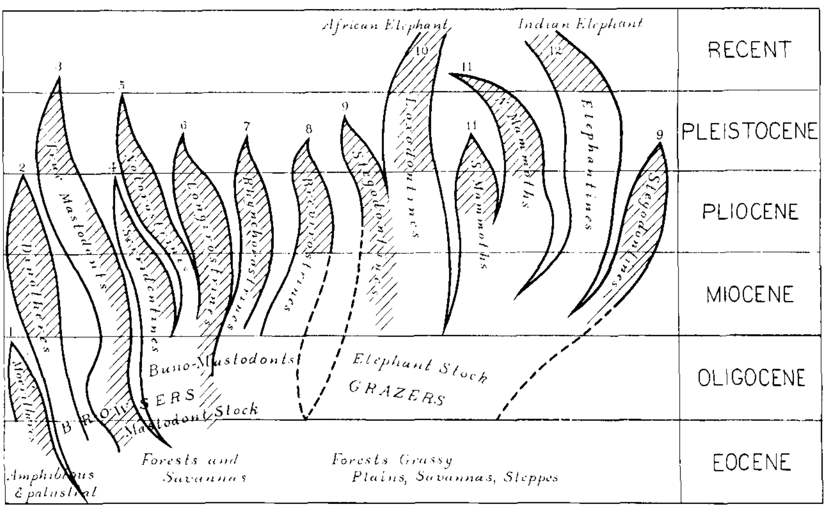

Fig. 2. Osborn's phylogeny of elephants (from Osborn, 1921). Independent, largely pre-programmed trends characterize the phylogeny of each lineage. Similar characters do not, therefore, reflect common descent and nearly every lineage springs independently from the basal stock.

Finalism — the control of evolution by preset goals — is not entirely dead. The omega-point of the Jesuit palaeontologist Teilhard de Chardin reflects its most recent popularity, while the finalistic gospel of human evolution according to Clarke—Kubrick formed a major theme of the story and film *2001*.

(2) The theory of racial life cycles. Alpheus Hyatt believed that lineages, as individuals, had appointed cycles of birth, youthful vigour, confident maturity, eventual decline and final death. His "old age theory", as he fondly called it, located the preset and inevitable history of lineages in the inherent properties of what later generations would call "germ plasm". Hyatt argued explicitly against any environmental control of these programmed trends. In his monograph on the Tertiary species of *Planorbis* at Steinheim (1880), for example, he thought he could discern five independent lineages living sympatrically through an identical sequence of environments. But three of these lineages displayed "progressive" tendencies: they increase in size, strength of ornament and degree of regular, helical coiling. The two other lineages regress: they become smaller, thinner and begin to coil so irregularly that they seem to reflect the agonies of impending phyletic death. How could the same environments permit such different trends in related lineages? Hyatt answers that the environment exerts no control over an internally directed evolution; it may eliminate the inadaptive by selection, but it plays no role in initiating any phyletic change. Very simple, the three progressive lineages were in vigorous phyletic youth and could meet and overcome any environmental challenge; the regressive lineages were in phyletic senility.

Of the internal mechanism of phyletic change, Hyatt claimed to understand very little. But the inductive study of phylogeny provided one important hint: acceleration in development is a universal feature of life. Adult traits of ancestors appear earlier and earlier on the ontogeny of descendants, leaving "room" at the end of ontogeny for the addition of new features. Early in the history of a lineage, these added features exhibit the vigour of youth; later on, the senile traits of impending extinction join the treadmill. Phylogeny is a programmed ontogeny (see more detailed analysis of Hyatt's schema in Gould, 1977). Darwin stated his belief in "no innate tendency to progressive development" during a long exchange with Hyatt about the principle of acceleration.

(3) Orthogenesis within individual lineages. A lineage evolving in a definite and inadaptive direction furnishes the best inductive argument for DI theories against the SE aspect of Darwinian natural selection. (Adaptive orthogenesis can be controlled by selection; but directed evolution towards doom cannot be Darwinian.) Thus, the "overcoiling" of *Gryphaea*, and the hypertely of antlers in Irish Elks, canines in saber-toothed cats, and tusks in mammoths became the standard palaeontological examples of internally directed, non-Darwinian evolution. I have restudied the two most famous cases and, unsurprisingly, have found nothing to support the DI claim. *Gryphaea* did not evolve towards greater coiling at all, and the antlers of the Irish Elk were adaptive in intraspecific competition among males (Hallam, 1968; Gould, 1972, 1974b; Hallam and Gould, 1975). The British orthogeneticist W.D. Lang argued that overcoiling in *Gryphaea* clearly precluded any control by external environments.

> "These trends. . . are soon out of the environment's control; they are lapses which may overtake *Ostrea* [*Gryphaea*'s ancestor in Lang's view] at any moment of its evolution — trends which having once started continue inevitably to the point when their exaggeration puts the organism so much out of harmony with its environment as to cause its extinction" (Lang, 1923, p. 11).

As his major achievement in drawing palaeontology under the umbrella of the modern synthesis, Simpson (1944, 1953) discredited the idea that macro-evolution required laws of its own, separate from those regulating change in gene frequencies within local populations. Thus, he synthesized the vastness of Phanerozoic history with selection experiments in *Drosophila* bottles. All could be encompassed within Darwin's basic theory, and with Darwin's own positions on the three issues — ambiguity on directionalism vs. steady-statism (see Simpson, 1974, on evolutionary "progress"), environmental control by natural selection, and gradualism (but see 1944, pp. 206—207 on "quantum evolution" for relatively rapid transitions across adaptive zones). I would epitomize Simpson's achievement by stating that he invalidated the "classical" DI arguments for the independence of macro-evolution. I say "classical" because I believe that macro-evolution has a legitimate independence from the laws of gene substitution in natural populations, but that its independence is not anti-Darwinian, and not tied to DI arguments.

Contemporary Palaeobiology Recycles the Ancient Issues

The hottest modern debates in palaeobiology are, as they almost have to be, extended discussions of the three great issues in new contexts. Since my assignment specified history, I will not analyse my contemporaries in detail; still, two recent examples should exemplify my contention:

(1) Valentine on diversity and drifting continents: a radical environmentalism.

Valentine (1973, and nearly a score of recent papers) believes that worldwide continental configurations hold the key to the history of diversity, primarily through their influence upon the relative stability of trophic resource regimes. When continents are fragmented and widely separated, world-wide diversity increases by pronounced endemism, and increased predictability of trophic resources resulting from climatic stabilization. When continents coalesce, climatic instability leads to unpredictable trophic resource regimes; previously endemic faunas merge and decimate each other in competitive interaction, and the area of shallow seas is reduced by suturing and eustatic regression.

> "The biotic revolutions in past oceans are related to environmental restructuring and ecological repatterning. The most likely source for such changes lies in the changing geographic patterns of continental dispersion, fragmentation, assembly, submergence and emergence, and oceanic fragmentation and interconnection" (Valentine, 1973, p. 462).

Valentine views the empirical curve of taxonomic diversity through time

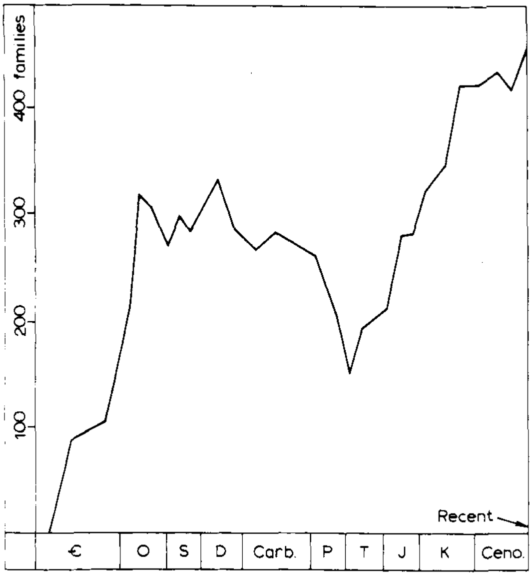

Fig. 3. Valentine's empirical curve of familial diversity among Phanerozoic marine invertebrates. This curve is a "map" of continental positions through time.

(Fig. 3) as, almost literally, a "map" of continental positions (see Raup, 1972, for an alternative interpretation based on biases of preservation). Following the early Phanerozoic rise (for which Valentine also proposes an environmentalist rationale — see below), modest mid Palaeozoic diversity reflects moderately separated continents; late Palaeozoic decline mirrors the suturing of continents with the latest Permian debacle as a sign of the final coalescence into Pangaea; steadily rising diversity since the Triassic records the break-up of Pangaea and the ever widening dispersal of its fragments.

But Valentine's boldest argument by far concerns the origin of the coelom and the basic ground plans of invertebrate design — I'll bet ten to one that he's wrong, but I admire both the daring, and the consistency it imparts to his entire system. If any subject had seemed to lie safely in the domain of classical morphology, and free from an environmentalist interpretation, this was surely it. But Valentine argues that the coelom is an adaptation for burrowing (fair enough so far — see Clark, 1964), and that its origin in the late Proterozoic must record a destabilization in trophic resource regimes — forcing soft, epibenthic creatures into the more stable substrate to lead new lives as burrowing, detritus feeders. Likewise, the Cambrian explosion must represent a skeletonization following the re-invasion of epibenthic sites when trophic resources restabilized. Since Valentine has identified continental assembly and fragmentation as a primary cause of fluctuation in trophic resource regimes, he is led to postulate (with no direct evidence) an assembly of a late Proterozoic supercontinent and its subsequent break-up near the Cambrian boundary (1973, p. 454).

(2) The Lyellian steady state rides again.

Raup et al. (1973) have provided the latest explicit defense of Lyell's steady state, at least as applied to the history of diversity (see also May, 1973 for ecological support). Raup et al. construct a model to simulate evolutionary trees by treating all times and taxa alike, and by setting a constant value for equilibrial diversity within time units. They study the waxing and waning of diversity in major groups (clades) and find remarkable similarities between these stochastic patterns and the fluctuations in real clades that have inspired so many causal hypotheses. Of course, Raup et al. do not claim that total diversity has undergone no real fluctuation through time. They do maintain — and this is the central element of Lyell's steady state — that there are no intrinsic trends towards increasing (or decreasing) diversity. Ecological roles are, in a sense, "preset" by the nature of environments and the topological limits to species packing; they are filled soon after the Cambrian explosion. Thereafter, inhabitants change continually, but the roles remain. Fluctuations are not intrinsic, but a result of externally imposed configurations. If shallow seas disappear, a large number of roles are temporarily eliminated and a mass extinction ensues.

The critics of Raup et al. have reasserted a DI hypothesis to counter the notion of equilibrium. Flessa and Levinton (1975) propose a "continuous diversification" model in which potentials for "speciation and niche division are limitless" (1975, p. 245). This is an intriguing type of *ceteris paribus* (all other things being equal) argument, in which intrinsic direction asserts itself only in constant conditions; i.e. Flessa and Levinton do not maintain that diversity has really increased steadily, but only that it would do so in constant environments. In the real world, major and periodic environmental "zaps" — like the coalescence of Pangaea — disrupt the trend and keep total diversity in check. (Obviously, as one of the *et alii* in Raup's paper, I favour the equilibrium.)

Even Valentine, for all his talk of environmental control, accepts a DI argument for both increasing complexity and diversity through time. He believes that the primary control by continental fragmentation and assembly is so strong that we don't see the "vector" of increasing niche partitioning in Phanerozoic diversity curves (except, perhaps, as a co-contributor with increasing endemism for the post-Permian rise). Valentine considers the ancient subject of direction as sufficiently important to set the final lines of his book (in which he argues that a "standardized" environment through time would display increased diversity and morphological complexity of its species):

> "A sort of moving picture of the biological world with its selective processes that favor increasing fitness and that lead to "biological improvement" is projected upon an environmental background that itself fluctuates. . . The resulting ecological images expand and contract, but, when measured at some standardized configuration, have a gradually rising average complexity and exhibit a gradually expanding ecospace."

I hope that readers will now appreciate why I chose to designate positions on the three issues as eternal "metaphors".

An Editorial Comment in Conclusion

I hope that no one reading this account has been inspired to ask: "Well, which set of positions is right after all?" — because the cryptic answer can only be: "either none of them, or all of them". They all capture a part of complex reality; if they did not, they would not have been vying for our attention and support for so long.

But I am urging neither a council of despair, nor a cynical claim that science cannot solve any deep problems. I only state that the world is too complex to permit the total triumph in all situations of any extreme position on such fundamental questions. Thus we have the ancient wisdom of Aristotle's *aurea mediocritas* — the golden mean. None the less, I believe (with all scientists) that any specific claim for one position or another, stated in the context of verifiable hypotheses, has a potentially definite resolution. Thus, it either is or is not true that the evolution of the coelom is correlated with a destabilization of trophic resource regimes produced by continental coalescence.

The psychological issue of why and how scientists choose their basic attitudes and metaphors is another matter, and one for which I claim very little insight. The historical choices of major palaeontologists have been the theme of this paper. I would only reiterate my claim that attitudes are largely set by *a priori* predispositions, and that these predilections, in turn, are strongly influenced by cultural belief and social position. I think I understand why theistically inclined, nineteenth century, socially comfortable evolutionists reacted against the materialism of natural selection by asserting a DI theory of macro-evolution. In any case, we all have our biases. (I confess to a general SEP bias for micro-evolution, with a dose of DIP for an important aspect of macro-evolution — see below.)

Resolvable arguments about the three issues arise when proponents of one or another position extend their favourite metaphors beyond the domain of evident utility into the large middle ground of unresolved arguments or into the realm of the other camp itself. Intersections between attitudes occur at *domains* and *levels*. By domains, I refer to the competition between attitudes for an explanation of specific issues at a level. By levels, I refer to the more interesting situation in which one alternative is appropriate at one level (of a hierarchical system, for example) and another for what seems to be the same question at a higher level. I believe, for example, that the independence of macro- from micro-evolution resides in the propriety of DI thinking for a process that is invisible in ecological time (where the SE metaphor is appropriate). But the process is thoroughly Darwinian, and the error of most nineteenth century evolutionary palaeontology lay not in identifying the DI component in macro-evolution, but in thinking that it had no Darwinian basis.

I conclude, therefore, by illustrating the conflict of domains for the gradualist—punctuationist and internalist—environmentalist debates, and the interaction of levels for steady-statism and directionalism.

(1) G vs. P. I take it that no one would now deny the importance of rapid and major faunal crises in the history of life. The great Permian extinction has

been copiously documented (e.g., Newell, 1973), and we now have explanations that invoke sound ecological theory and the latest in plate-tectonic reconstruction (Schopf, 1974). On the other hand, no one would quarrel with the claim that our view of speciation in ecological time is more gradual than that proposed by such discredited theories as creationism and de Vriesian macromutationism.

There is, however, a vast territory between these two phenomena — the patterns of organic change in "normal" geological times, in particular. Traditional palaeontology accepted Darwin's view of phyletic gradualism — change accumulates by slow and steady transformation of entire lineages, or by slow separation, at about the same rate, of descendant species from their persisting ancestors. Eldredge and Gould (1972), however, have proposed the alternative of "punctuated equilibria." Species do not generally change after their successful origin. In geological terms, they arise very rapidly from very small populations peripherally isolated from the parental range (the model works equally well for sympatric or parapatric speciation, as long as diverging populations remain small and speciate rapidly). The geological record of descent in a local section should record the "sudden" replacement of ancestors by their fully formed descendants (the event actually recorded is the migration of the established descendant into the ancestral range, and the replacement of the ancestor by competition or emigration).

If Eldredge and I are generally right, then gradualism can only be important in ecological and micro-evolutionary time. The entire range of palaeontological or macro-evolutionary time (not just the rare event of mass extinction) falls into the domain of punctuation.

Gingerich (1976) has defended phyletic gradualism for the evolution of mammalian tooth size in Eocene sections of the Bighorn Basin; I believe that his data fit the model of punctuated equilibria equally well (Gould and Eldredge, in press).

(2) E vs. I. Environmental control for certain events would be denied by no one. We may be sure that Bermuda's endemic pulmonate land snail would no longer grace this earth if the island had ever been completely submerged during Pleistocene fluctuations in sea level. But physical scientists are forever trying to extend their "billiard ball" models to major events in the history of life. (By "billiard ball model", I refer to a habit of explanation that treats organisms as inert substances, buffeted by an external environment and reacting immediately to physical stress without any counteracting, intrinsic control or even temporary resistance.) Thus, in the Berkner—Marshall hypothesis (Berkner and Marshall, 1965), the Cambrian explosion merely represents the point at which atmospheric oxygen reached a sufficient level to provide ozone screening and effective respiration. No lag times, no recognition that metazoan *Baupläne* do not arise automatically from a procaryotic level just because external conditions now favour them. Likewise, four physical scientists (Reid et al., 1976) would tie mass extinctions to decay of the geomagnetic field during reversals — to "catastrophic depletions of stratospheric ozone caused by solar-proton irradiation over a reduced geomagnetic field" (Reid et al., 1976, p. 177). I have

labelled as "physicalist" these purely environmental explanations, based upon billiard ball models; i.e., stimulus leads to immediate and passive response (Gould, 1974c).

For all my general support of environmental control, I applaud the attempt of several palaeobiologists to counteract these physicalist explanations by asserting the independence and internal dynamic of biological processes in complex systems, particularly of ecological interaction and the genetic and morphological prerequisites of complexity. It is hard, for example, to see how the Cambrian "explosion" could have occurred before the eucaryotic cell evolved with its potential for enhanced genetic variability in sexual reproduction. And I doubt that any crude physicalism will explain the origin of the eucaryotic cell. Environmentalism will have to be tempered with a strong dose of internalism to explain these major events. I am, for this reason, strongly attracted to Stanley's (1973, 1976) ingenious ecological (and internalist) explanation of the Cambrian explosion. He argues that the Precambrian flora formed a stromatolitic "monoculture," with low diversity characteristic of uncropped ecosystems. The Cambrian explosion was the final result of a biogenic process mediated by positive feedbacks accompanying a single, key biological event — the evolution of a cropping herbivore (almost surely a protist). This cropper freed space for a rapid diversification among primary producers. These, in turn, provided a diversity of habitats for other herbivores and, eventually, carnivores. The ecological pyramid expanded rapidly in both directions.

(3) S vs. D. Directionalists of the last century did not assert their claims with the blindness of *a priori* social prejudice alone. They had quite a few facts going for them, especially the appearance of "progress" in vertebrate history, the body of data that eventually converted Lyell to progressionism. Yet Darwin's theory speaks, just as clearly, of adaptation to local environments alone. Since local environments fluctuate stochastically, with no directional trend through time, the basic Darwinian mechanism would seem to offer no rationale for a belief in progress. This apparent dilemma led most nineteenth century evolutionary palaeontologists to believe their own data and reject Darwin for a DI theory of evolution.

I believe that the concept of independent levels provides a resolution. Natural selection is undeniably steady-statist and environmentalist in ecological time. But once we discard the shackles of phyletic gradualism as an explanation for "trends", we see that the operation of natural selection in evolutionary time can yield direction. Sewell Wright (1967, p. 120) proposed a profound analogy: just as mutations are random with respect to the direction of selection in ecological time, so might speciation itself be random with respect to the direction of trends in evolutionary time. The primary events of speciation yield no direction, for they only adapt populations to local environments. But all speciations do not have an equal phyletic longevity or an equal opportunity for further speciation. Trends represent the differential success of subsets from a random spectrum of speciations (Fig. 4). Improved biomechanical efficiency, for example, represents one pathway to adaptation in local environments. The species that follow this path — rather than the acquisition of a limiting, mor-

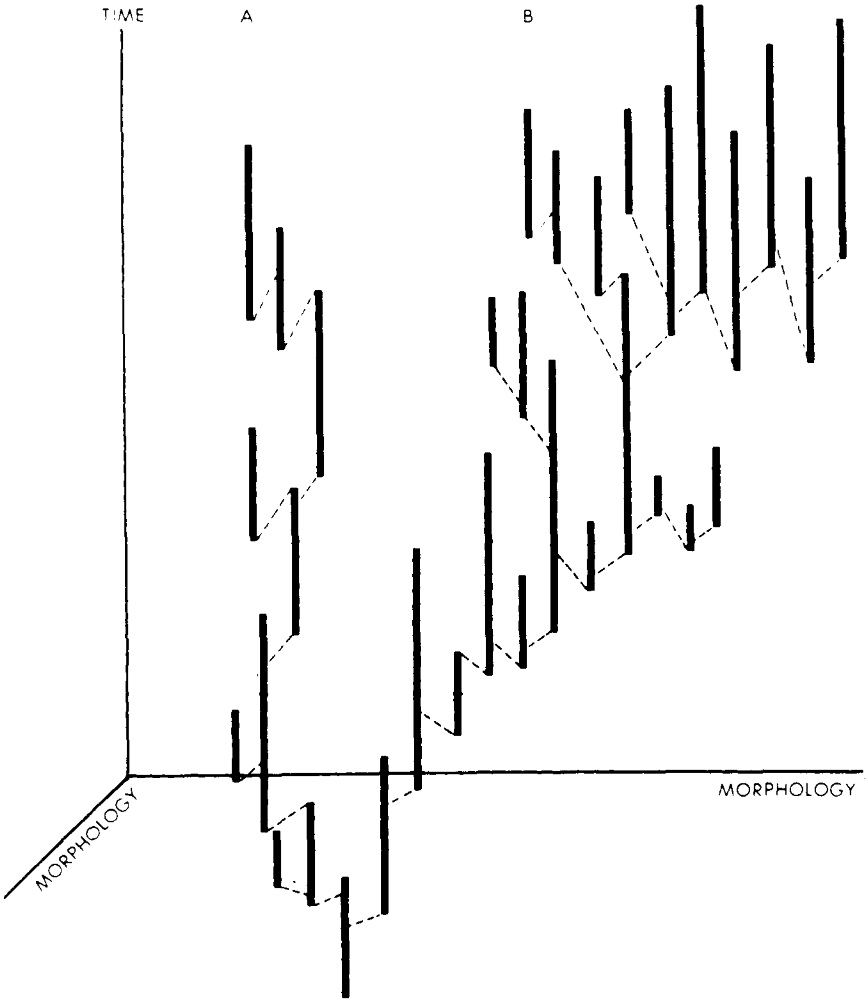

Fig. 4. An evolutionary trend in clade B according to Wright's rule (from Eldredge and Gould, 1972). There is no preferred direction of speciation, merely the differential success of those species defining the "trend". Note also the P feature of this "punctuated equilibrium" model — evolutionary change occurs during very rapid events of speciation.

phological specialization — might form the subset of a directional trend. (I would also regard such a trend as "internal" because an engineer might predict its path on structural principles alone.) Eldredge and Gould (1972, p. 112) write:

"A reconciliation of allopatric speciation with long-term trends can be formulated along the following lines: we envision multiple 'explorations' or 'experimentations' (see Schaeffer, 1965) — i.e., invasions, on a stochastic basis, of new environments by peripheral isolates. There is nothing inherently directional about these invasions. However, a subset of these new environments might, in the context of inherited genetic constitution in the ancestral components of a lineage, lead to new and improved efficiency. Improvement would be consistently greater within this hypothetical subset of local conditions that a population might invade. The overall effect would then be one of net, apparently directional change: but, as in the case of selection upon mutations, the initial variations would be stochastic with respect to this change. We postulate no 'new' type of selection."

Stanley (1975) has given a name to the phenomenon that Eldredge and I chose explicitly not to christen. He calls it "species selection", with a strong hint of its fundamentally non-Darwinian nature. But surely, the differential success of species is as Darwinian a process as their origin; there is nothing non-Darwinian about the extinction and expansion of species. The issue is not the scope of Darwinism, but the results of Darwinism at different levels — SE effects in the origin of each species as an adaptation to local environments, and potential DI effects in the differential success of species within larger clades through time. ("Species selection" furnishes an appropriate description, but it carries the unfortunate implication of a "new", non-Darwinian mechanism. If a key aspect of the phenomenon must have a name, I would prefer "Wright's rule of differential success", or — of this be judged too cumbersome — just "Wright's Rule", which is no vaguer than "Cope's Rule" or "Dollo's Law", and at least has the virtue of pleasant alliteration. Its précis need be no longer than: "Speciation is stochastic with respect to the direction of evolutionary trends". The rest follows from basic assumptions of the "punctuated equilibrium" model.)

In any case, Stanley (1975) correctly argues that Wright's rule "decouples" micro-evolution from macro-evolution, thus affirming the independence of palaeontology as an evolutionary subdiscipline. (Under phyletic gradualism, trends are merely extensions of directional selection within local populations, and macro-evolution has no separate status.) There can scarcely be a more important task for palaeontologists than defining the ways in which macro-evolution depends upon processes not observed in ecological time. In uniting palaeontology with neo-Darwinism, Simpson (1944, 1953) argued that macro-evolution had no such independence. This was an appropriate (and necessary) argument while palaeontology stood its distance from modern evolutionary theory by asserting principles that genetics could not support. Yet the greatest testimony I can offer to Simpson's success is my claim that the time has come to affirm the independence of macro-evolution by recognizing that Darwinian processes work in different ways at different levels. If Simpson had not buried so thoroughly the ghosts of vitalism and orthogenesis, I would be fearing their unintended resurrection in asserting such a claim.

I began this paper with a lament that all great thoughts had been developed in days of old. By now, I hope I have demonstrated that their modern contexts are not without interest (even fascination). I must also confess that I cheated a bit on the first quotation. Alexander's statement is usually cited as I gave it — as a lament for a world with no new directions (as by Wordsworth in his Supplementary Essay of 1815). But the first classical reference I can find cites it in an opposing context (from Plutarch's Morals):

"Alexander wept when he heard from Anaxarchus that there was an infinite number of worlds. . . 'Do you not think it a matter worthy of lamentation that when there is such a vast multitude of them, we have not yet conquered one?' "

A better statement, to be sure. Our ignorance is in no danger of ceding its general domination to our understanding.

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