PALAEONTOLOGY AND EVOLUTION

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ABSTRACT—The two ideas of fossils (1) as dating their containing rocks and (2) as indications of an evolutionary ramification, are of independent origin. A very variable, but always infinitesimal proportion of the living fauna can be preserved as fossils. The chief controls of this proportion are indicated. The "ladder of life" conception of Bonnet is contrasted with the ramification postulated by Lamarck.

THE ideas of Palaeontology and Evolution are so closely associated today that it seems strange that they should have been so independent in origin. Scientific palaeontology may be said to have started with Leonardo da Vinci (1452–1519) and his Italian engineering contemporaries, the marine shells in whose excavations taught them that there had once been sea where now is land. This was the first step towards geological history, though the belief in a single universal deluge caused some confusion of ideas. The idea that fossils were not sports of nature, but the remains of once living animals spread during the sixteenth and seventeenth centuries, and it was Robert Hooke (1635–1703) who first vaguely suggested that fossils might provide a geological chronology. It was left to William Smith (1769–1839) to establish such a chronology in the Bath district and extend it in a more general way over Britain. Cuvier and Brongniart, and afterwards d'Orbigny did the same for France, as did Quenstedt and Oppel for Germany, and by the middle of the nineteenth century the Jurassic and Cretaceous rocks were divided on a palaeontological basis and the divisions broadly correlated throughout western Europe. The study of the more disturbed older and more scattered newer formations gradually followed.

On the other hand the idea of Evolution, whatever vague form it may previously have taken, acquired definiteness with Lamarck (1744–1829) who had so little idea of palaeontological sequence that he doubted whether there were any extinct species except those exterminated by man. He was of course aware of Cuvier's discoveries in the Paris gypsum beds, but as one of these was an opossum, generically identical with the living American form, it was obviously possible that the associated ungulates, such as *Palaeotherium*, might still be living in unexplored regions. The more sensational discoveries of extinct reptiles—*Pterodactylus* (1809), *Ichthyosaurus* (1814), *Plesiosaurus* (1821), *Iguanodon* (1829) all came after the publication of Lamarck's *Philosophie Zoologique* in 1809.

Lamarck's fore-runner was Bonnet (1720–1793), a very able naturalist, who proclaimed the unity of animal life in the form of a "ladder of beings" (*échelle des êtres*). He was careful to explain that he did not mean that all species formed a single linear series : at each rung of the ladder there was a cluster of species formed by a limited amount of branching. Lamarck modified this conception by greatly increasing the amount of branching. Nevertheless the dead hand of Bonnet long hampered evolutionary doctrine by suggesting the derivation of higher groups from the *highest*, instead of from the *lower* members of lower groups. Thus the notion still lingers that mammals may have evolved from birds, the monotremes being transitional, instead of mammals and birds being derived from quite separate groups of reptiles.

A famous discussion between the evolutionist Etienne Geoffroy St. Hilaire (1772–1844) and the creationist Cuvier (1769–1832) in 1830 illustrates this. St Hilaire claimed close similarity between the highest invertebrates and the fishes, the only differences being that the former had dorsal hearts and ventral nervous systems, the latter *vice versa*. Turn the one upside down and the difference vanishes. Cuvier won the case by showing there were important differences not got rid of by such inversion. He substituted for Bonnet's unity of design four separate designs, and divided the animal kingdom into Vertebrata, Articulata (later called Arthropoda), Mollusca and Radiata—a classification which held the field for over half a century, slowly dissolving as the two last of these sub-kingdoms were split up into many natural divisions. By the middle of the nineteenth century, though actual evolution was believed in by few, the idea of a general advance during geological time in animal structure and behaviour, mainly among Vertebrates, was very generally accepted. Thus Louis Agassiz (1807–1873), the great Swiss naturalist who never accepted the doctrine of Evolution, wrote in 1844 :

> "The successive creations have gone through phases of development analogous to those that the embryo passes through in its growth, and resembling the steps shown by the living creation in the ascending series which it presents in its totality." (Poissons fossiles du Vieux Grès Rouge, Introd., p. XXVI, my translation.)

Thus the road was cleared for the triumphant march of Evolution after the publication of Darwin's "Origin of Species" in 1859. The enormous increase in palaeontological discoveries within the last hundred years has placed evolution on a firm basis of fact, at least so far as Vertebrates are concerned. In regard to Invertebrates the results are more fragmentary. In a few cases, as with Graptolites, good genealogies have been or are being worked out. In other cases, as with Echinoids, broad lines of advance can be traced. In no case is there any approach to the detailed genealogies now established for Vertebrates. This is mainly due to the fact that the skeletal structures of Invertebrates are less closely related to the basic functions of life.

A side-issue may be considered here, though not directly bearing on palaeontology: the belief in spontaneous generation, which persisted for many centuries. Lucretius (first half of first century B.C.) had no doubt on the subject :

> "Even now multitudes of animals are formed out of the earth with the aid of showers and the sun's genial warmth. So it is not surprising if more and bigger ones took shape and developed in those days, when earth and ether were young." (On the Nature of the Universe, Bk. V, c. 1. 800, transl. R. E. Latham, Penguin books.)

If we may trust Shakespeare (Ant. & Cleop., II, 7.) the less philosophical contemporaries of Lucretius believed serpents and crocodiles to be bred of Nile mud by the sun's warmth. As late as the mid-seventeenth century Izaak Walton added to this traditional legend a belief in the spontaneous generation of eels ("Compleat Angler", ch. xiii and xix). In view of these beliefs, which do not appear to have been condemned as irreligious, we may doubt whether some sayings that have been held as asserting a belief in evolution may not simply record a belief in spontaneous generation, or in transformations as sudden as those of caterpillar into butterfly or tadpole into frog. The Linnaean name of the acorn barnacle, *Lepas anatifera*, perpetuates the belief that the fixed marine animal might give rise to a goose.

When, therefore, we are told that St. Augustine of Hippo (354—430) may be counted as an early evolutionist, because he insisted that God created organic forms by "conferring on the material world the power to evolve them under suitable conditions", we may well doubt whether he had anything other than spontaneous generation in mind. (*Vide* St. G. Mivart, Genesis of Species, 2nd Edn. (1871), pp. 302–305).

The Italian naturalist Redi (1626–1698) disproved the spontaneous generation of maggots in decaying meat, by excluding flies from it. Gradually this belief became restricted to lower and lower forms of animal life, but it was not finally demolished until the decade 1870–80, when Pasteur and Tyndall proved experimentally that even bacteria cannot arise spontaneously.

To return to Palaeontology—the fossil fauna or flora of any bed is determined by a number of factors :

1. The actual faunal or floral community that was living in the immediate area of deposition of the sediment now constituting that bed. This in turn depends upon—

(a) the state of evolution of the animal and vegetable world at the time ;

(b) the geographical barriers to dispersal which isolate provinces, and, when they cease to exist, allow of sudden and rapid migration ;

(c) the controlling conditions determining what forms of life could and could not live in any area.

2. The facilities for transport of dead organisms to areas where they were not found living.

3. The local conditions which allow of or prevent the preservation of dead organisms.

Let us consider these in order.

1 (a). That fossil animals and plants, viewed broadly, show a general progression from the earliest fossiliferous rocks onwards to the present, was recognized long before Darwin's theory of evolution was propounded, and by palaeontologists like Agassiz who rejected that theory. But the dating of strata by fossils is mainly empirical. No one can say why trilobites are confined to the Palaeozoic rocks : they were not ancestral to any later forms. With Cephalopods the case is better, for Goniatites are less evolved than the Ammonites which succeeded them. It is among the Vertebrates, and especially the Mammalia, that the stage of evolution can be most safely used as a time-marker.

There are, however, a number of cases in which slow, short-range evolution may be of stratigraphical value. Such are the lineages in Lower Carboniferous corals, the gradual changes in detailed structures of *Micraster* during the deposition of the White Chalk, and those in certain long-range Foraminifera which are proving of value to oil-geologists. These are characteristic of periods and areas where external conditions remained fairly constant, or changed fairly steadily in one direction, so that evolution (far slower than the average) took place without the disturbance of faunal migration.

In general, as we descend from Vertebrates to Invertebrates, and from eras and periods to the finer time-divisions, the direct applicability of evolutionary grade to age diminishes, owing to the increasing importance of other factors, namely :

(i) *Persistence of Type*. There are certain forms of life which endure for long periods with no significant change. The classical example is the brachiopod *Lingula* ranging from Ordovician to Recent. This genus is the only burrowing brachiopod, and this habitat seems to have offered it freedom from the risk of extermination. It has been suggested that the successive species of *Lingula* are not directly affiliated, but that each represents the end-form of a separate lineage (as is the case with the series of Jurassic oysters which have been lumped under the generic name *Gryphaea*); but this is improbable, since we have no repeated series of non-burrowing brachiopods from which successive species of *Lingula* might be derived. The primitive lamellibranch *Nucula* (or nearly allied forms) ranges from Palaeozoic to Recent, as does the primitive gastropod *Patella*. *Nautilus* extends from Triassic to Recent. Even among the rapidly-evolving Mammalia, the opossum *Didelphys* already existed in Eocene time. The surroundings to which those genera were adapted must have had long continuity.

A side-issue of this persistence is the deceptive age-value of some species. There are certain oysters which are taken as horizon-markers because they flare up in profusion in certain beds, but which did not then become extinct. Solitary specimens may therefore be untrustworthy guides to age, e.g. *O. gryphoides*, accepted as distinctively Miocene, but still surviving in small numbers in the Bay of Bengal. Again, the graptolite *Dictyonema* occurs in great profusion at the base of the Tremadoc beds (basal Ordovician) but there seem to be two such horizons in North Wales.

(ii) *Repetition and Convergence of Types*. Among Mollusca, especially Lamellibranchs, the possible variety of shell-form and ornament is so limited that it is not surprising that similar-looking forms should re-appear at different horizons. Thus some Tertiary Pectens have been mistaken for Jurassic species. When the shape is an adaptation to special surroundings there may be *convergence* between widely separated groups, as in the boring bivalves *Teredo*, *Clavagella* etc. Occasionally there is accidental convergence, as in the case of *Petricola* and *Pholas*, very similar externally, but easily distinguished by internal characters of the shell.

(iii) *Deceptive Evolutionary Series.* Among Ammonites, Hyatt, Buckman and others have tried to establish certain principles of evolution in shell-form, but they are so subject to exceptions that their application to novel cases is dangerous. Thus, in the Lower Lias the very characteristic square-whorled *Asteroceras* is followed by the stream-lined *Oxynoticeras;* but in the Middle Lias the stream-lined *Amaltheus* precedes the square-whorled *Pleuroceras*.

1 (b). *Facies.* This term denotes the totality of characters, physical and palaeontological, other than those under 1 (a), which give a formation its individuality. Thus there are only a limited number of facies, repeated again and again with time-variations. The biggest distinction of facies is between marine, freshwater and subaerial. Marine facies are dependent partly on depth, partly on the lithic character of the deposit —muddy, sandy, pebbly, neritic, etc. On the present sea-bottom there live a number of *communities*, each with its own series of *stations*, the totality of stations forming the *province* of which the totality of communities forms the *fauna*.

1 (c). It is a familiar fact that the native animals and plants of one continent are very different from those of another, and the same is true of the oceans. This is only partly a matter of climate, since artificially introduced species often thrive as well as the natives. It indicates past isolation of regions or provinces, so that floras and faunas have evolved independently. That similar provinces have existed in the past, and that from time to time the breaching of the barriers between them has led to extensive migrations, has been amply proved. One result of this is that newly arriving genera may serve as excellent dating fossils in their new habitat, but may be misleading in their old home. Thus Old-World palaeontologists established a simple sequence for the Orbitoids—*Orbitoides*, Cretaceous; *Discocyclina*, Eocene ; *Lepidocyclina*, Oligocene and Miocene. This sequence partly broke down when applied to the New World.

Again, in Europe the beginning of the Ordovician period is marked by the appearance of new families of Trilobites, but their ancestral forms are known in the Cambrian of North America.

2. Fossil faunas rarely correspond to pure living communities : there is more or less mixture after death. The surface *nekton* and *plankton* sink to mix with the bottom *benthos*. Currents sweep dead shells away from their living home, as modern dredgings show. Still more is this the case with easily floated shells, such as the chambered cephalopods : the empty shells of *Nautilus* are found over a wider area of the Indo-Pacific than the living animal. In the Inferior Oolite of Dorset the perfect preservation of ammonites indicates that they lived on the spot, whereas in the contemporaneous strata of the Cotswolds their shells occur in a broken condition as the result of post-mortem transport.

The tendency to mixture of different communities in fossil faunules adds to the difficulties of the palaeoecologist in interpreting the ecology of ancient oceans, but may be very useful to the stratigrapher. For instance, in the Ordovician and Silurian rocks there are two sharply-distinct facies— "shelly" and "graptolitic"—the correlation of which stage by stage would be difficult, but for their occasional interdigitation or the occasional drifting of graptolities into the shelly area.

Even terrestrial and marine deposits may be correlated if land-animals are drowned and drifted out to sea to be buried in a marine deposit. There is only one known pre-Pliocene Australasian marsupial, *Wynyardia*, and this was found in the marine Miocene of Tasmania. The discovery of the three-toed horse, *Merychippus*, in the marine Upper Temblor formation of California made possible the correlation of that formation with an inland freshwater deposit of the Rocky Mountain region.

3. Everyone is justifiably astonished when soft-bodied jellyfish are found in special deposits such as the Mount Stephen shale (Middle Cambrian) or the Solenhofen lithographic limestone (Upper Jurassic); but no surprise is felt when hard calcareous or phosphatic shells are preserved as fossils. Yet those preserved must be an infinitesimal percentage of those which had been living on the same site.

The destructive agencies acting on dead organisms on the sea-bottom are universal. Perhaps the bivalve molluscs are those which withstand these agencies best, for they are found in nearly all sediments which contain any fossils at all. Yet their greatest abundance is trivial in comparison with their living numbers : thus the Ministry of Agriculture and Fisheries estimates that 4,500,000,000,000 individuals of the bivalve *Spisula* occupy one patch of the North Sea, and this number must be multiplied by the million years or more than the species has persisted there. Other marine animals suffer much greater destruction. The trawl brings up from the bottom waters of the English Channel a great abundance of Fishes, but the dredge brings up sediment in which the only traces of fish are their otoliths (which are pure calcium carbonate, not phosphatic like their bones). Among the stratified rocks fish-skeletons most usually occur in fishbeds in which whole shoals are preserved as a result of some sudden event which inhibited the normal decomposition agents. Intense cold is one possibility : it is only after severe frosts that dead fish are dredged in the Channel. Poisonous gases may be another. One of the most striking examples of such a shoal occurs in the Lower Old Red Sandstone of Achanarras, where in one quarry only are numerous specimens of *Palaeospondylus*, a little lamprey-like fish otherwise quite unknown.

Present-day muddy sea-bottoms are in places crowded with brittle-stars (ophiurids), and in the Devonian black-shales of the Rhineland similar fossils are found at certain levels, while the intervening shales are barren. It seems clear that these (and other) starfish-beds owe their existence to temporary circumstances which inhibited the normal chemical conditions that led to the destruction of these dead organisms.

The rarity of the cases in which beds are found with an abundance and variety of fossils in any way comparable with an actual living fauna must impress on us the serious imperfections of the palaeontological record.