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Evolution Evolving

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By the time he wrote the Origin of Species, Darwin had reached at least four main conclusions from his palaeontological studies:

1. Most fossils represented the hard parts (skeletons) of species that are not now found living – that is, a large number of species had become extinct.
2. Most fossils could be seen to have features in common with species that are still living – for example, skeletons that were obviously similar in many respects to those of modern reptiles could be found extending back in the record for some considerable time.
3. Overall it was possible to recognise a progression of complexity in organisms through geological time.

From these three conclusions, together with observations on living animals, he drew the following inferences: fossils are related to living organisms by descent, or as he says “species have been produced by ordinary generation: old forms having been supplanted by new *and improved* forms of life...” (Darwin, 1859); or elsewhere “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 palaeontologists, that organisation on the whole had progressed” (author’s italics).

He was, however, only too well aware of a fourth point:

4. Although organisms from one period were different from, but related to, organisms from preceding and succeeding periods, it was not possible to find the graded sequences of organisms he had predicted.

From this he concluded something quite different from what might have been expected – *not* that his idea of gradual transitions between species might be incorrect, but rather that the geological record was incomplete. After a long discussion of the matter he concluded “... all these causes taken conjointly, must have tended to make the geological record extremely imperfect, and will to a large extent explain why we do not find interminable varieties, connecting together all the extinct and existing forms of life by the finest graduated steps” (Darwin, 1859).

In other words he accepted that the record overall was good enough to show the main patterns of evolution – that is, it established the fact of morphological change in a number of directions that he would have predicted, such as increasing complexity; but he considered that the record

was not good enough to support the view that change had been as gradual as he thought it should be if his theory of natural selection was correct. This obviously caused him concern because he wrote: “Passing from these difficulties, all the other great leading facts in palaeontology seem to me simply to follow on the theory of descent with modification through natural selection” (Darwin, 1859, p. 343).

It is clear from this and his previous statements that he introduced a serious confusion because he did not distinguish between the concept of evolution as descent with modification on the one hand, and the means by which this modification was thought to have taken place – namely, natural selection on the other. Of course the theory of natural selection was Darwin’s main contribution to evolutionary studies, but the efficacy of natural selection could not be established or confirmed from the fossil record. All that he could have done was to show that (a) morphological change had been gradual; (b) that, by devising suitable measures, successive species had become more efficient; and (c) that these observations were consistent with, but did not establish, the hypothesis of natural selection. Therefore Darwin’s statements left two bad legacies criticism of natural selection was taken by many protagonists as rejection of evolution, and the record was widely accepted to be very inadequate (Fig. 1).

NEO-DARWINISM

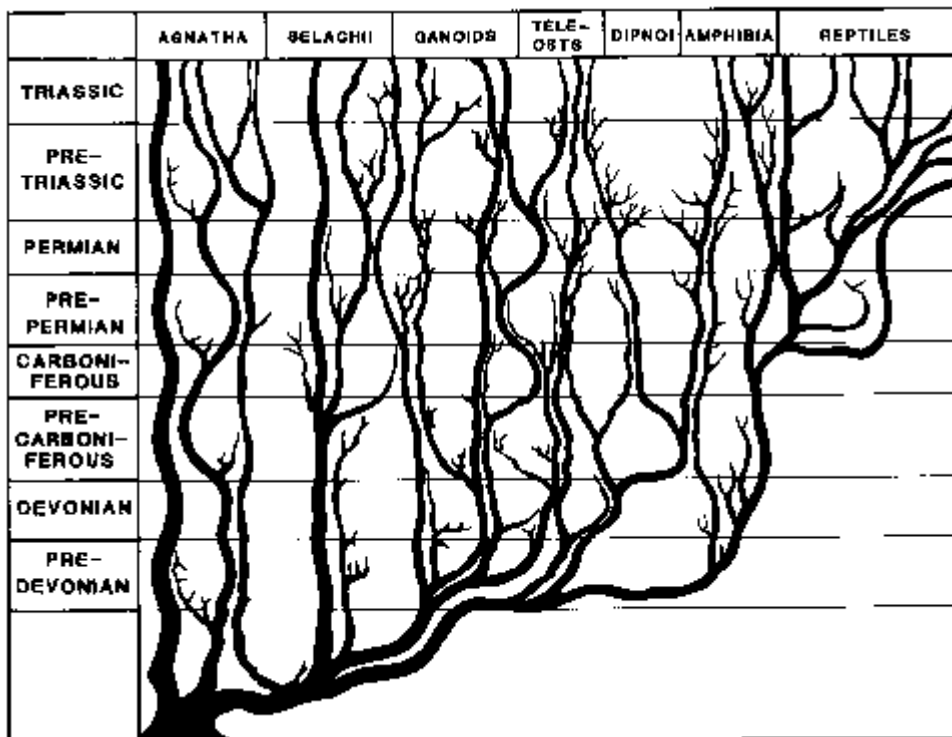


Fig. 1 Part of a figure produced in 1866 by the German biologist Haeckel. It shows his conception of the relationships between jawless fishes (Agnatha), sharks, skates and rays (Selachii), primitive ray-finned fishes (Canoids), advanced ray-finned fishes (Teleosts), lungfishes (Dipnoi), amphibians and reptiles. This diagram illustrates the extent to which major branchings in the tree of life were considered to have taken place in time intervals unrepresented in the fossil record. Not only are the initial branches shown in undifferentiated pre-Devonian time; many of the subsequent ones are in the pre-Carboniferous, pre-Triassic etc., time intervals without rock records.

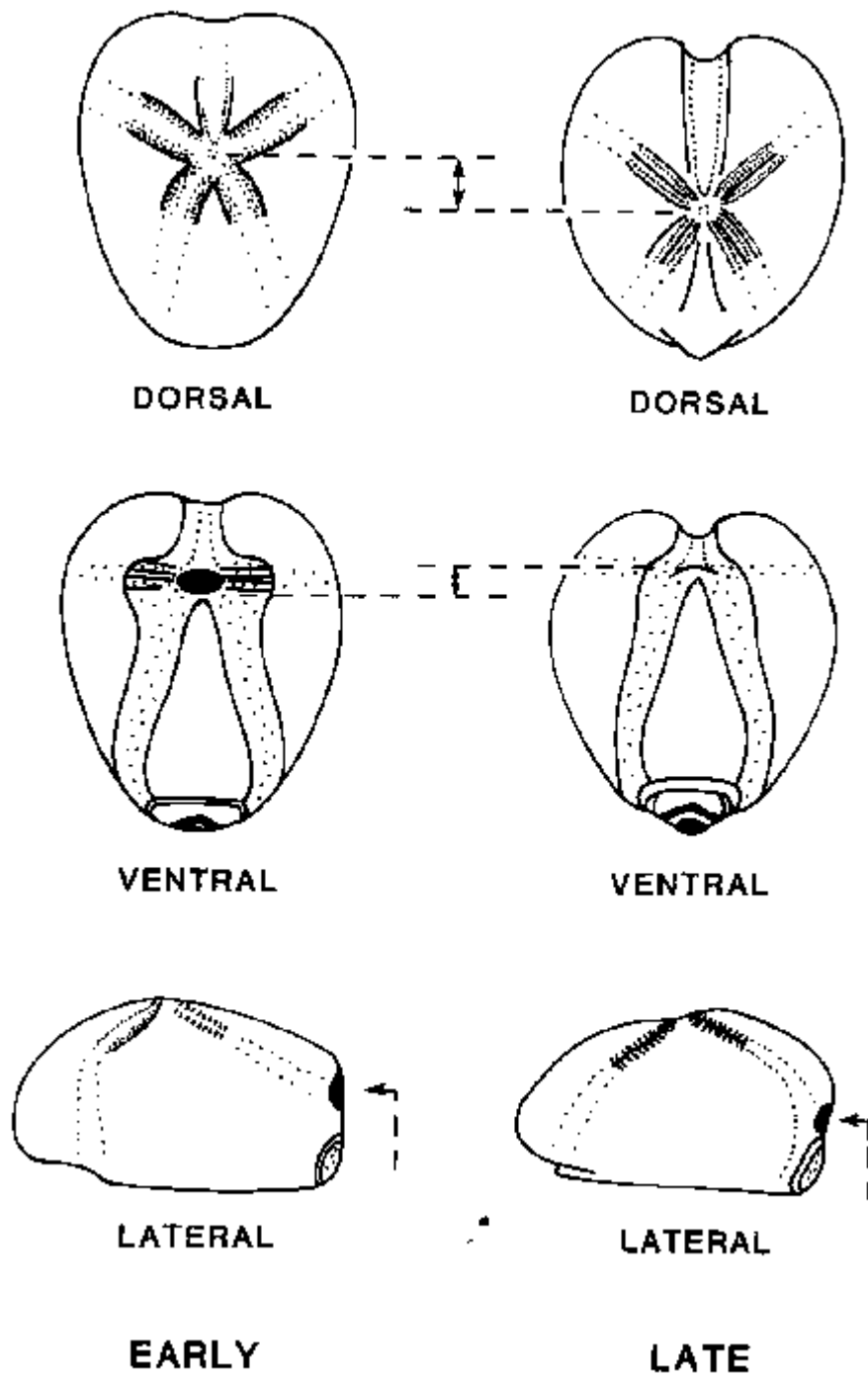


Fig. 2 Early and late representatives of the sea-urchin *Micraster* from the Chalk of England. They are separated by about 8 million years. During this time the conditions of sedimentation over the chalk basin remained relatively constant, and the genus was probably able to inhabit some part of the basin during that entire period. The main changes that took place involve proportions of the whole skeleton, the shapes of furrows and ridges, the position and shape of the mouth and its lip, the shape and division of the food-gathering (ambulacral) areas, and the general granulation of the whole surface. Several

species have been recognised over the time interval; these have been arbitrarily defined because successive populations show intergradation.

For the next forty years or so there was little effort on the part of palaeontologists to follow up this problem of continuously evolving sequences. This seems to have been the result of two factors: geologists were convinced that the record was so bad that such changes could not be found and it was useless searching for them; and many palaeontologists, while accepting that evolution had occurred, could not accept the idea that natural selection *by itself* could produce the changes observed. There were a few examples of gradual change forthcoming, such as *Micraster* in the Cretaceous chalk (Fig. 2) and *Zaphrentis* in the Carboniferous shales, but these were exceptional. Note that this is not to say that sequences could not be found, but rather that species transitions appeared at that time to be rare.

The rediscovery of Mendel's genetics, and the great expansion of evolutionary thinking in the first thirty years of this century produced little impact on palaeontology, but during this period the concepts took shape that have dominated evolutionary thinking almost up till the present. These are known collectively as Neo-Darwinism or the Synthetic Theory. The essential tenets of this theory are:

1. Change took place by small steps.
2. Mutation is the raw material of evolution.
3. Mutation is not directed but occurs in a 'random' fashion.
4. Direction and rate of change were imposed by the environment.
5. Rapid evolution took place in isolated populations of moderate size.
6. Rapid evolution took place in areas of geographic differentiation.
7. Evolutionary trends resulted from uni-directional selection.

Note that this is a theory of evolutionary *mechanisms*. Clearly it will have implications for the course of evolution, and hence should be consistent with the fossil record. For example, it should be possible in many instances to correlate changes in structure with changes in environment. It is true that some structures will presumably be selected for in a constant environment, simply because they enable the organisms bearing them to perform functions more efficiently. However, other structures will change because they are required to perform more efficiently in changing environments. The classic fossil example is the evolution of the horse which shows a number of 'trends' all of which are consistent with a change from soft to hard ground, a change from soft nutritious food to hard less nutritious food, and a change from slow to fast movement, all at a time when the central North American region, where the horses were evolving, was changing from wet forest to dry prairie (Stahl, 1974). Although it played some part in the formulation of the synthetic theory, palaeontology was essentially reduced to providing possible examples of the theory of natural selection in action.

SOME DISSENTERS

Now this synthetic theory or Neo-Darwinism, was generally accepted by biologists, and it is still accepted by the majority today. However, in the 30's and 40's there were two groups who were uneasy about it.

The first group was typified by one of the most influential evolutionary thinkers of this century – George Gaylord Simpson, an American. He wrote a book entitled "Tempo and Mode in Evolution" in 1944, and a revised and expanded book "The Major Features of Evolution" in 1953. He was not worried about the basics of the synthetic theory - in fact he was one of its

main supporters; in particular he was convinced that natural selection was the directing force in evolution – His main reservation was that the theory did not explain all the observed phenomena. Though in his view the synthetic theory could explain gradual change from species to species, he doubted whether it could explain the evolution of groups such as families or even higher taxa, which often appear in the fossil record abruptly. Is it reasonable, he was asking, to expect that very rapid small-scale evolution could and did produce the large-scale abrupt effects that we observe? He concluded that such an explanation was not acceptable. Instead he decided that evolution had several modes. These came to be known by a variety of names, but we can consider them here as microevolution, macroevolution and megaevolution. Subsequently he retracted the term megaevolution.

Microevolution was the kind of evolution that resulted in gradual transition between species, produced by a gradual spread of new genes through a population. *Micraster* provides a good example from the fossil record. Macroevolution on the other hand, was the kind of evolution that produced higher taxa. He considered that the observed gaps between these taxa were not due to gaps in the record, but real evolutionary phenomena requiring a special explanation. This explanation involved especially high rates of evolution – not just rates at the upper end of the microevolution range, but a special class of rates. However, the ‘determinants’, as he called them, were the same. They just came together in unusual ways at various times to produce high rates. Simpson still wanted external controls on tempo and mode of evolution in the usual manner of the Neo-Darwinians.

The second group of dissenters had no one scientist to act as a focus. Nor did they have a thought-out, unified, position to advocate. Among them were numbered the German palaeontologist Schindewolf, the French zoologist Grasse, the American geneticist Goldschmidt, and the English biologist L.L. Whyte. What enables us to consider these people as a group is the fact that they considered external factors to be inadequate to explain tempo and mode, and that therefore some factor internal to the organism (preferably some genetic factor) played a major role, particularly in introducing evolutionary novelty in an irregular fashion. Unfortunately for them, they were never able to put their fingers on this elusive factor. As a result it became fashionable to pour scorn on them especially in the English-speaking world. In any historical science an hypothesis without a mechanism has traditionally been an object of pity, as witness the fate of Wegener’s hypothesis of continental drift until the mechanisms of plate tectonics were discovered.

So by the mid-1950’s there were three groups of evolutionists differing in their views of the course of evolution and the mechanisms that controlled it:

1. Neo-Darwinists who thought that change was gradual, perhaps a little faster here and a little slower there; that the apparent jumps between major groups were the result of imperfections in the fossil record; and that direction and rate were the result of natural selection, acting on phenotypes that differed slightly as the result of small mutations.
2. Simpsonians who were essentially Neo-Darwinists but who considered that not all change was gradual – some was very rapid and took place under special environmental conditions.
3. Internalists who thought that change was very variable; that the jumps between major groups were real; and that direction and rate were at least in part the result of some internal factor as yet undiscovered.

The conflict between these three groups remains to be resolved, and it is interesting to note a rough correlation between adherents of each of the groups, and areas of scientific endeavour.

For example, population geneticists tend to belong to the first group; palaeontologists are over represented in the second group; and molecular biologists of various persuasions are main contributors to the third group. This in itself should alert us to the possibility that evolution is not a uniform process, and that scientists working in different fields tend to emphasise different aspects of the process. We should not conclude, as some non-scientists do, that this disagreement casts doubt on the whole concept of 'evolution'. To do so is an elementary mistake in logic.

Numerous contributions to the resolution of the conflict have been made, and obviously they come from a variety of quarters. The subsequent papers in this symposium deal with biological contributions, and I will now discuss three quite different palaeontological approaches, all of which relate to metazoan organisms.

THREE PALAEOONTOLOGICAL ARGUMENTS

First Argument

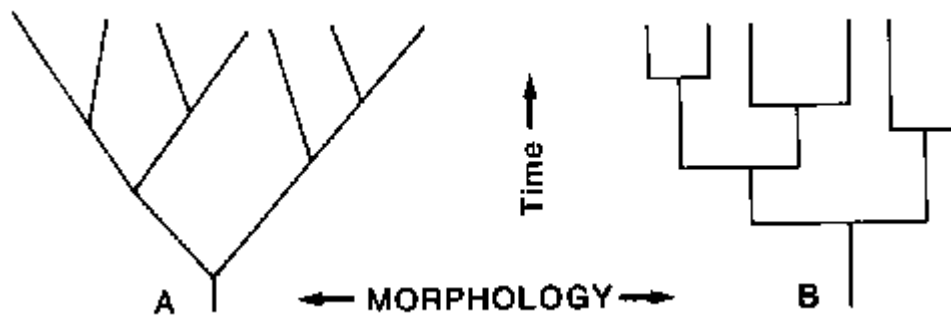


Fig. 3 Diagrammatic representation of the Neo-Darwinian (A) and the Simpsonian (B) models of morphological change involved in the production of taxa at suprageneric levels.

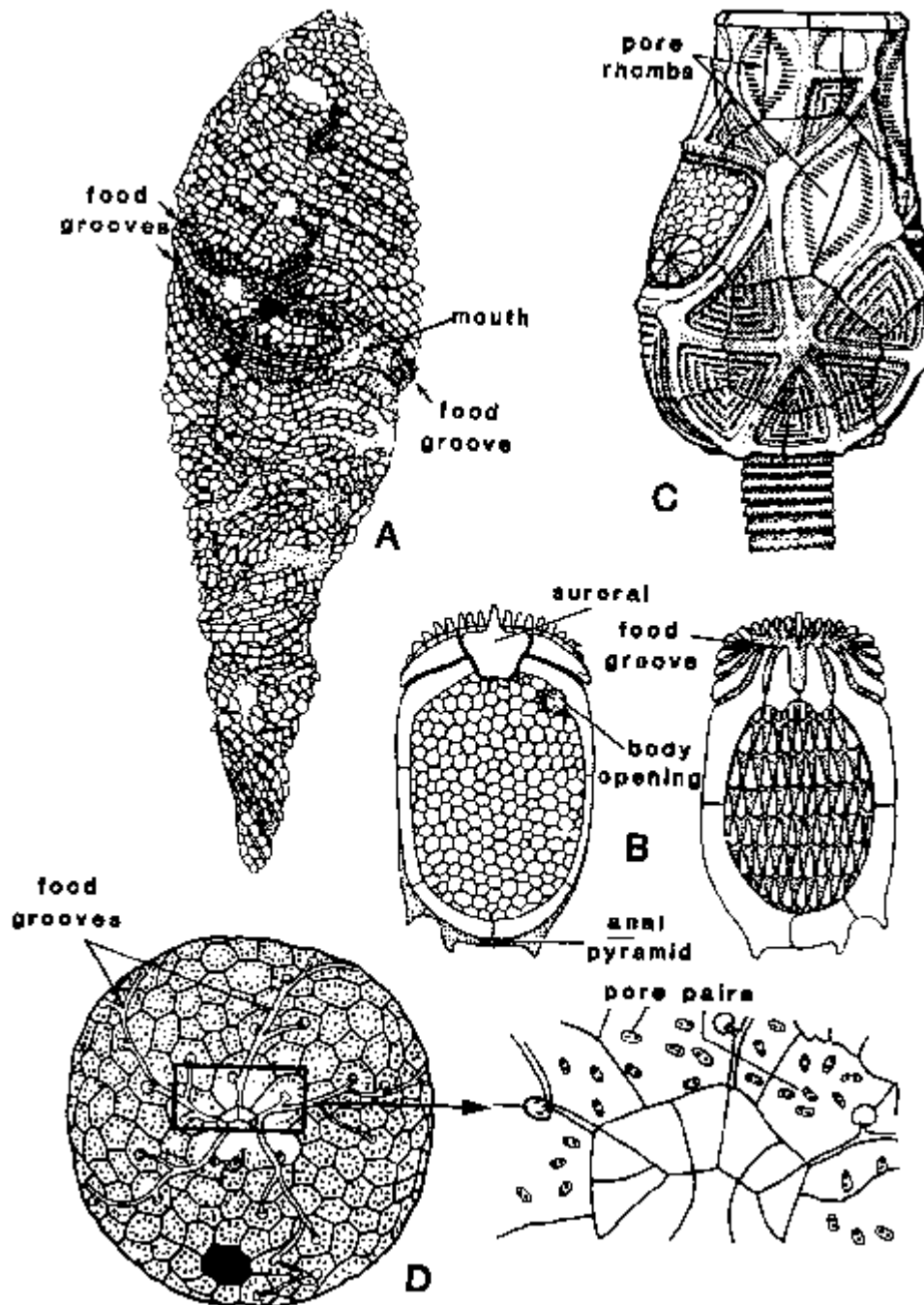


Fig. 4 Examples of different types of echinoderm respiration

- A. *Helicoplacus* from the Early Cambrian; a form with a flexible skeleton made of overlapping plates, and three spiral ambulacral areas with pores for tube feet in the sutures between the ambulacral plates.
- B. A primitive carpoid *Ctenocystis*. This is not an Early Cambrian representative, but one from the Middle Cambrian. There is no evidence of pores for tube feet, and no clear evidence of any means for coelomic respiration. It is possible that the whole skeleton was sufficiently flexible for water to be drawn in through the mouth and oxygen to be exchanged across membranes similar to those in the modern holothurians (sea cucumbers). However, it is most probable that the whole surface

of the organism was respiratory because most modern echinoderms function in that way.

- C. The Early Ordovician diploporitan *Gleptosphaerites* showing the pairs of pores in the skeletal plates through which coelomic fluids passed into thin membranous tubes, allowing oxygen exchange to take place.
- D. The Middle Ordovician rhombiferan *Homocystites* showing the rhomb-shaped groups of slits that permitted sea water to pass deeply into the coelomic cavity and allow oxygen exchange across thin layers of tissue.

(A is modified from Paul & Smith, 1984; B from Robison & Sprinkle, 1969; C & D from Kesling, 1967)

The first approach is to examine the fossil record to see if major groups of animals converged towards their times of origin. This has been important because the Neo-Darwinian model would have produced patterns as in Figure 3A whereas the Simpsonian model would have resulted in patterns as in Figure.3B.

The results of this kind of work have been ambiguous. Analysis of the various classes of molluscs shows that when the critical changes took place the animals concerned were small and were very similar to one another in all the observable characters (Runnegar, 1987). The echinoderms on the other hand seem to show that most of the classes are distinct from the time they appear in the record, and they are not represented by unusually small species. One thing the two groups have in common is the fact that most of the classes were established very early in the Palaeozoic – that is by about 470 million years ago. Also several of the classes survived for relatively short periods of time (Campbell & Marshall, 1987).

Another way of looking at this same problem would be to take some function of a whole phylum, such as the echinoderms, and see how long it took for all the known structures that serve that function to evolve. Take respiration, for example. This was achieved by four basic means, all of which had been evolved by the Early Ordovician (Campbell & Marshall, 1987). These involve oxygen exchange between sea water and the fluids of either the water vascular system or the coelomic cavity. Exchange with the water vascular system involved the use of tube feet with their thin membranous walls and internally circulating fluids. Tube feet evolved very early in echinoderm history, being known in the *Hellcoplacoldea* from the Early Cambrian (Fig. 4A). With coelomic fluid exchange there seems to be only three possibilities (see Fig. 4B-D):

- i. across an unmodified body wall, an arrangement that seems to have been present in at least some of the ‘carpoids’ of the Early Cambrian;
- ii. across membranes within the coelomic cavity, the sea water being pumped in through slits or pores in the wall, an arrangement found in Early Ordovician rhombiferans;
- iii. across membranes external to the main body wall, the coelomic fluids being pumped out through pores in the wall, an arrangement found in the Late Cambrian diploporitan cystoids.

The examples quoted are only the earliest known representatives of the three modes, and modes (ii) and (iii) seem to have been evolved subsequently several times. However, the point is well made that all the possible major styles of respiration had appeared by about 500 million years ago. The basic plans were established early in evolution, and subsequently only modifications or eliminations of these plans occurred. This suggests a pattern of the Figure 3B type. Much more work of this kind on a variety of organisms is required to provide an adequate data base from which secure conclusions may be drawn.

Second Argument

The second approach is an attempt to find unusual faunas in the early Palaeozoic with a view to filling some of the gaps between classes. This step is a response to the suggestion that if the Neo-Darwinian model is correct, we may find some evidence of intermediate animals among soft bodied faunas that are normally not preserved. An excellent example is the Middle Cambrian Burgess Shale fauna which has been studied in great detail by Whittington and his students at Cambridge (Conway Morris & Whittington, 1985). The organisms were marine and were preserved by clouds of muddy sediment that descended from the adjacent shallow water shelf. Whole biota were engulfed, and were preserved *in toto*. Because of the mode of entombment and the reducing environment within the mud cloud, little decay of the biological soft tissues took place. Thus it has been possible to extract specimens that show details of fine soft supporting tissues such as arthropod appendages and even parts of the alimentary tracts. Reconstructions of two of these animals are given in Figure 5. As might have been expected, some of the fauna had hard skeletons, and these turned out to be normal trilobites, brachiopods, sponges, etc. However, the part of the fauna without mineralised skeletons produced some unexpected results. Details are shown on Figure 6. Not only are 17% of the genera unassignable to any previously known phylum, a high percentage of those that can be so assigned (e.g. to the Arthropoda) cannot be assigned to a previously known class. What is more, no gaps between known phyla or known classes have been diminished; rather, more problems have been created. These early faunas are much more divergent and show more body plans than anybody would have predicted on the basis of the hypothesis that major taxa should converge morphologically towards their times of origin. Serious work on the implications of such faunas for the understanding of evolutionary theory is just beginning (Gould, 1985).

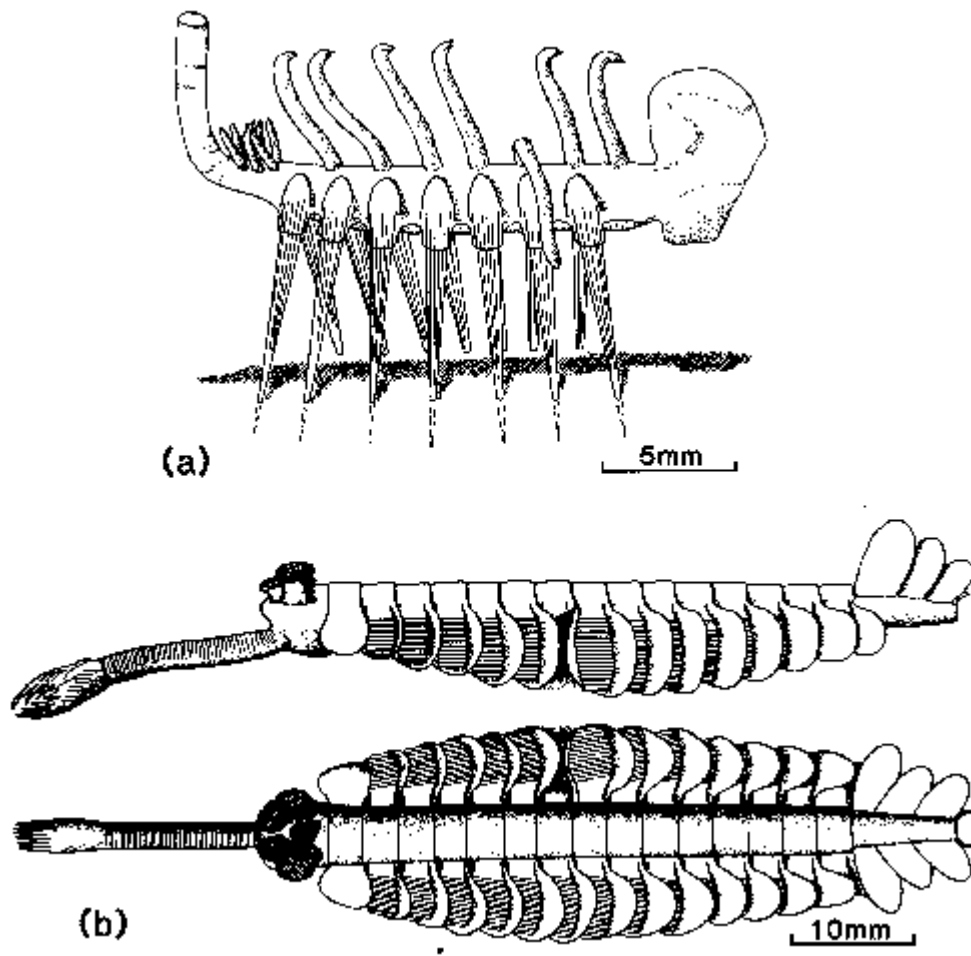


Fig. 5 Two unusual genera from the Burgess Shale, Middle Cambrian, British Columbia. (a) *Hallucigenia sparsa* (Walcott) see Conway Morris (1977). It is difficult to orient this organism. The finger-like extensions on the dorsal surface seem to connect with the alimentary canal. The appendages were apparently stiff and moved as units activated by a number of muscles that have left traces on the fossils. (b) *Opabinia regalis* (Walcott). This is a segmented animal with lateral flaps of soft tissue on each segment. Between the flaps, layers of lamellate tissue, thought to be gills, were regularly arranged. Two pairs of compound eyes and a median eye were developed on the ill-defined head. No jointed appendages were present. Dorsal and lateral views are shown. (Modified from Conway Morris, 1977, and Whittington, 1975).

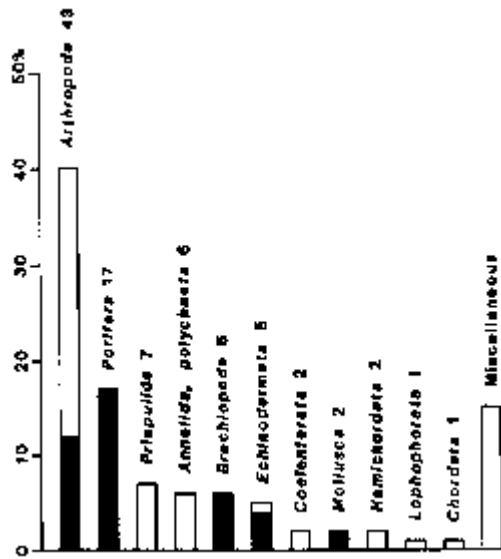


Fig. 6 The taxonomic distribution of organisms from the Burgess Shale. The percentage scale indicates the percentage of the total fauna represented by each phylum; the number at the end of each bar indicates the number of species from each phylum represented in the fauna. (After Conway Morris & Whittington, 1985).

Third Argument

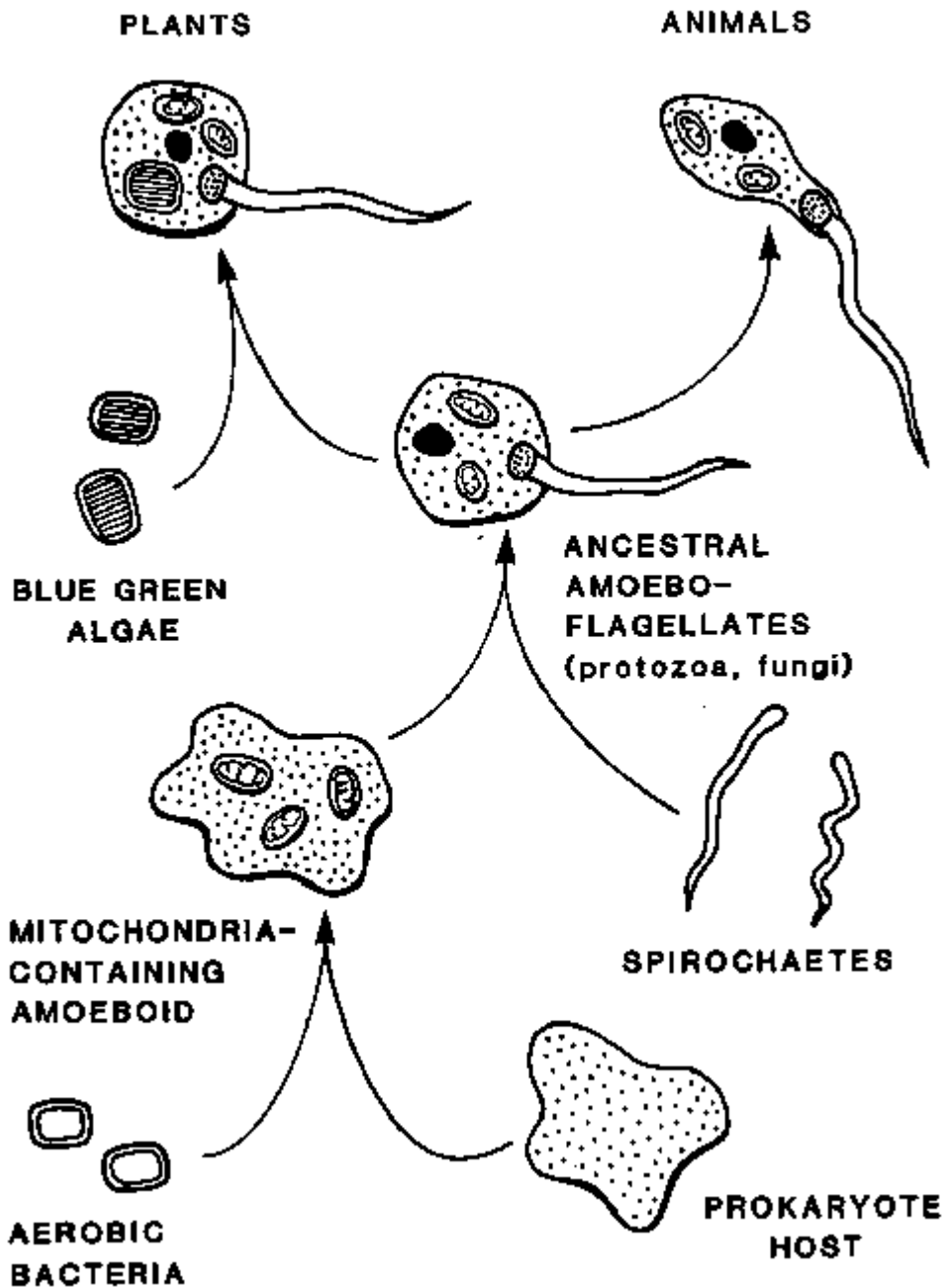


Fig. 7 Diagrammatic representation of the symbiotic origin of eukaryotic cells from prokaryotic cells. (Modified after Margulis, 1970)

A third approach is represented by the work done on periodic extinctions, and results from an examination of the time ranges of organisms in the fossil record (Raup & Sepkoski, 1984). These authors concluded that there have been catastrophic extinctions approximately every 26 million years (Fig. 7). Some of these have been more extensive than others. The cause or causes of these extinctions are irrelevant for present purposes. The important point is that organisms seem to have been wiped out willy-nilly. That is, at many times in the past organisms have disappeared not by natural selection of the fittest, but by elimination of the fit as well as the unfit. Obviously this introduces another important factor into the evolutionary process because after such an extinction event evolution has had to make do with what is available in the way of genetic

material, and selection pressures would have changed drastically. In other words, the evolutionary clock has been reset periodically through geological time.

A WIDER PERSPECTIVE

At this point we should note that most of the work on which all the above views were based was done on metazoan animals or, in rare instances, on vascular plants. But a great deal of evolution, perhaps the main part, had taken place before such higher organisms appeared. Hence it is worth asking if the broad sweep of the fossil record in association with what is known of recent organisms, rather than an examination of the detail of its later parts, provides any reason for us to conclude that the mechanisms of evolution may have changed through geological time. To do this we would have to establish that the modes of transmission of genetic information, or the nature of biological processes changed in kind at one or more times during the earth's history. An investigation along these lines would have to take into account a mass of evidence from the Precambrian, most of which has become available only in the last twenty years (for summaries see Schopf, Hayes and Waiter, 1983; Glaessner, 1984). For example, the oldest known fossil organisms were prokaryotes that appeared in the record some 3.5 Ga. ago. The genetic material of living prokaryotes is carried in strands of DNA which are not organised into chromosomes; DNA is synthesised and passed to descendant cells without complex processes such as mitosis or meiosis. Organisation of the genetic material into a nucleus with a membrane and the advent of mitosis must surely have introduced new factors into the evolutionary process when the first eukaryotes appeared about 1.5 Ga. ago. Similarly, sexual reproduction, which on palaeontological evidence is unlikely to have occurred before about 1.0 Ga. ago, provided another kind of process involving the redistribution of genetic novelty through populations. Not only were genetic factors affected at that time; sexual reproduction is vital to the process of speciation which is central to Neo-Darwinian evolutionary theory. Associated with these biological changes were environmental changes that expanded or contracted the opportunities for organisms, and some of these produced revolutions in the biota. For example, the earliest prokaryotes were probably anaerobic chemoheterotrophs, and a series of stages must have been passed through before aerobic photoautotrophs could survive in the available water on the earth's surface. With the advent of the various levels of metabolism and the necessary environmental changes, new worlds became available to conquer in new ways (Schopf, Hayes & Walter, 1983).

In the light of this discussion we might have expected the processes of evolution to have changed character through geological time. However, at all stages it would have been necessary to have means for introducing heritable novelties, be they biochemical or morphological, and these novelties would have been accepted or rejected by the prevailing environments. In this sense 'mutation' and 'selection' would always have had a vital role in any evolutionary process; on the other hand the kinds of mutations, the kinds of biological processes and the kinds of selection would have changed through time.

These considerations, which depend primarily on studies of prokaryotic structure and molecular genetics, lead us to different types of approach to the study of evolutionary mechanisms. And as so often happens in science some of them were developed by people who were attempting to solve problems outside the immediate field of evolutionary studies. I will mention just three of these as examples.

First Example

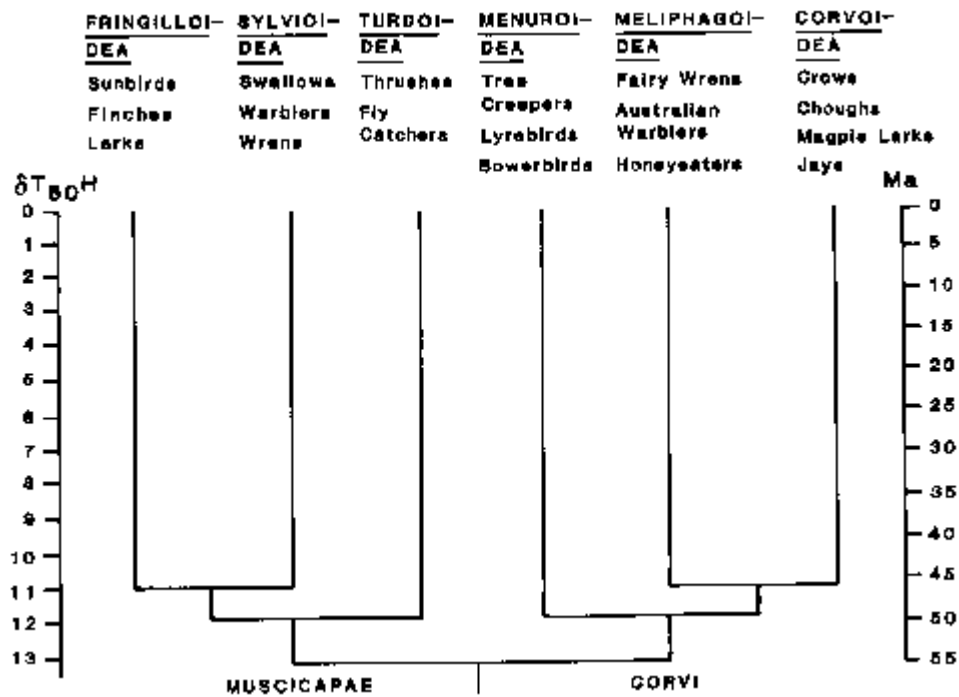


Fig. 8 Representation of the relationships between several superfamilies of the Corvoidea that have apparently differentiated in the Australian region, and the Muscicapae that differentiated possibly in Africa and Europe. On the left is the measured value of Delta TP, the temperature at which 50% of the hybrid DNA of representatives of component genera becomes dissociated. On the right is the geological time scale in millions of years. For details of the method refer to Sibley & Ahlquist (1985) from whose work the above diagram has been modified by removing all the generic and family taxa. The whole group as shown is considered to have separated earlier than 55 million years ago from the Old World groups that include morphologically similar taxa such as honeyeaters, warblers, larks, etc.

First is the suggestion by Lyn Margulis (1970) that the change from cells without a nucleus (prokaryotes) to cells with a nucleus (eukaryotes) probably took place, not by a series of small, imperceptible steps, but rather by a series of symbioses (Fig. 8).

In brief, she suggested that the initial step took place when a very primitive prokaryote, capable of anaerobic metabolism, symbiotically acquired another aerobic prokaryote. Associations of this kind exist today and so there is nothing unusual about this hypothesis. What is unusual is the suggestion that the association became permanent, the anaerobe providing the ground nucleus and cytoplasm within which the aerobes were able to oxidise carbohydrates; this would be the expected function of protomitochondria. The next step is thought to have involved a symbiosis between this new type of amoeba-like structure with a spirochaete-like prokaryote which formed a flagellum. This suggestion is based largely on the observation that spirochaetes and flagellae have longitudinal protein threads arranged in a characteristic 9+2 pattern. This symbiotic structure was ancestral to all subsequent mitotic eukaryotes. The plants gained their photosynthetic capacities by symbiosis with prokaryotes such as blue-green algae which already possessed that capacity.

Although this hypothesis has not gained universal support for all its details, there is sufficient confirmation from the work of other scientists for it to be accepted in its essentials. Here then is an example, albeit at a lowly level of biological organisation, of rapid changes without transitions.

Nobody has suggested that this type of mechanism would be valid for organisms at a higher level of organisation, but it is now possible to say that at least one major evolutionary change may have been different in kind from what we could have expected according to the synthetic theory. Thus, a possible mechanism to support the proposal has been produced.

Second Example

Second, it has been found that by measuring the genetic distance between living organisms it is possible to determine a sequence of points marking their relative times of divergence. If this pattern of divergences can be calibrated against two of three points on a time scale by reference to the fossil record, it should be possible to calculate the times of divergence of the other groups of organisms in the system. This has been done now for many groups. A good example is the bird study by Sibley and Ahlquist (1985) (Fig. 9 [*Not included in the original paper*]) which I use not because it confirms some palaeontological hypothesis, but because it uses Australian material to great effect. The above authors have shown by the method known as DNA/DNA hybridisation that most Australian passerine birds are more closely related to one another than to their European look-alikes. By this means it may be possible to estimate the divergence times of major groups that have living representatives and check these against the divergence time estimated from the fossil record. Of even greater importance is the prospect of determining the divergence times of organisms that have left little in the way of fossil record. In this way it will be possible to augment currently available information on phylogenetic patterns.

Third Example

A third advance has come from a study of the great variety of new ways of introducing new genetic features into an organism. This will be discussed to some extent by the later contributors to the symposium, but I must mention one example – that of multigene families. These are sets of identical, or almost identical, homologous genes that vary in number from two to thousands. They have many properties that single genes lack. They can vary without affecting the phenotype; genetic variation may accumulate without the influence of external selection, and this variation may subsequently be expressed phenotypically; elements of a family may combine to produce new hybrid genes; they can code not only for one protein, but a collection of closely related proteins, that may have different properties. It is now apparent that with increasing complexity, the number of possible novelties increases dramatically. As John Campbell (1983) says “We are discovering that the complex phenotype is the creation of very different sorts of determinants. These complex, individualistic, active, profane, internally organised, and self-governed genes are ‘smart’ machines in the current vernacular sense. Smart genes suggest smart cells and smart evolution.” Direction and rate of evolution may be more under internal control than the Neo-Darwinians thought.

CONCLUSION

New advances in all these areas suggest that evolution is likely to have been episodic rather than uniform, and that while the synthetic theory may remain unchallenged as an explanation of part of the evolutionary story (microevolution), it is unlikely to be the explanation of the whole. The genetic determinant must have been changing through geological time, and occasional events, such as symbioses, may have played vital roles in addition to mutation. External selection may not have been the sole determinant of direction and rate of evolution – internal direction may be an important control on both at some levels. And finally, selection of the fittest may have been based on remnants left after episodes of major extinction that took little account of the fittest. The modes of evolution have not been constant over time but themselves have been changing.

The mechanisms of evolution as they have changed at all levels of the evolutionary scale, from the earliest phases when emphasis must have been on the biochemical organisation of genetic material to the phases of metazoan evolution when emphasis must have been on modification of established genetic patterns and on phenotypes. Evolution, in this sense, has been evolving.

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