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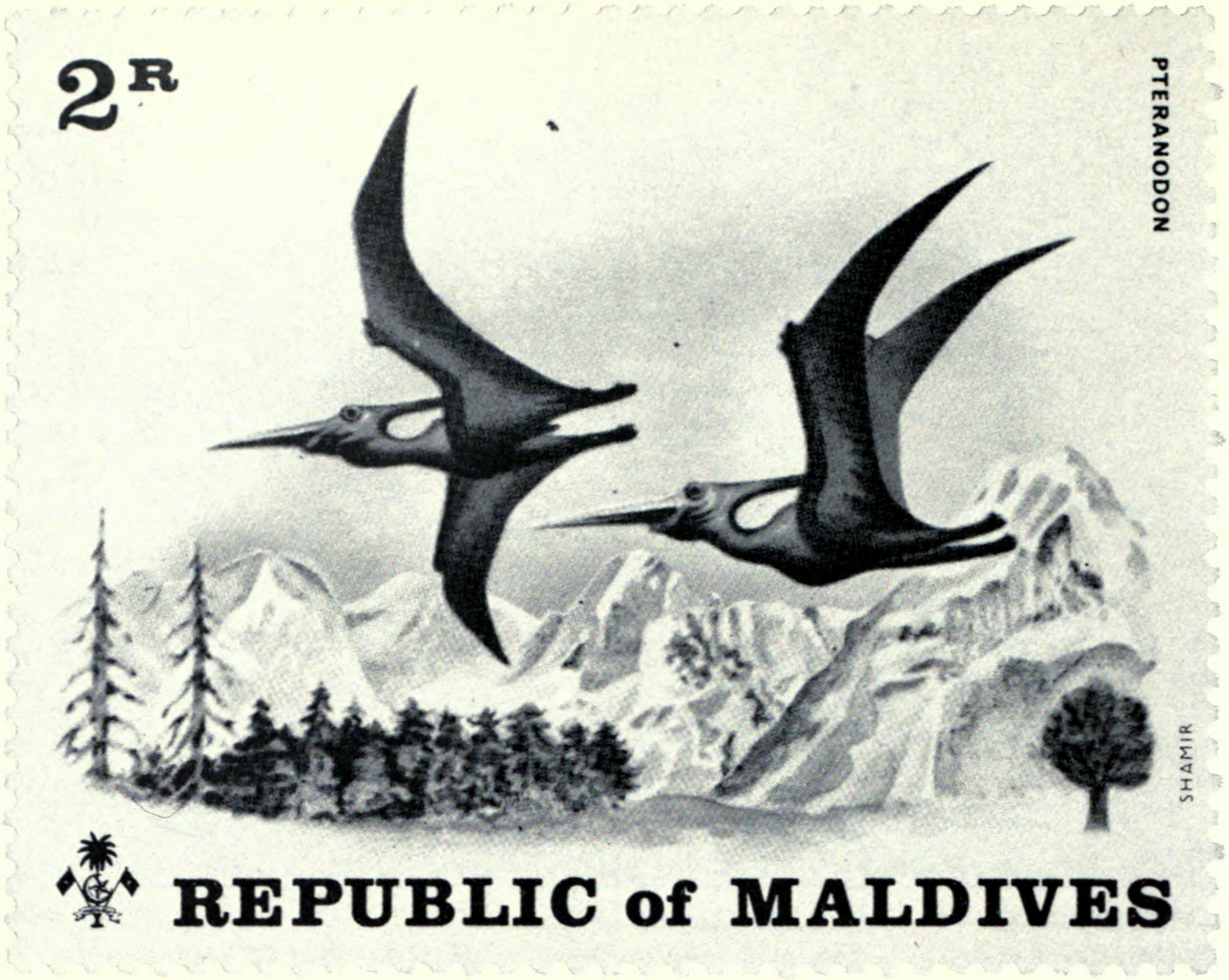
CONFLICTS BETWEEN DARWIN AND PALEONTOLOGY



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Part of our conventional wisdom about evolution is that the fossil record of past life is an important cornerstone of evolutionary theory. In some ways, this is true — but the situation is much more complicated. I will explore here a few of the complex interrelationships between fossils and darwinian theory, but let me first set the stage by commenting about the geologic record itself.

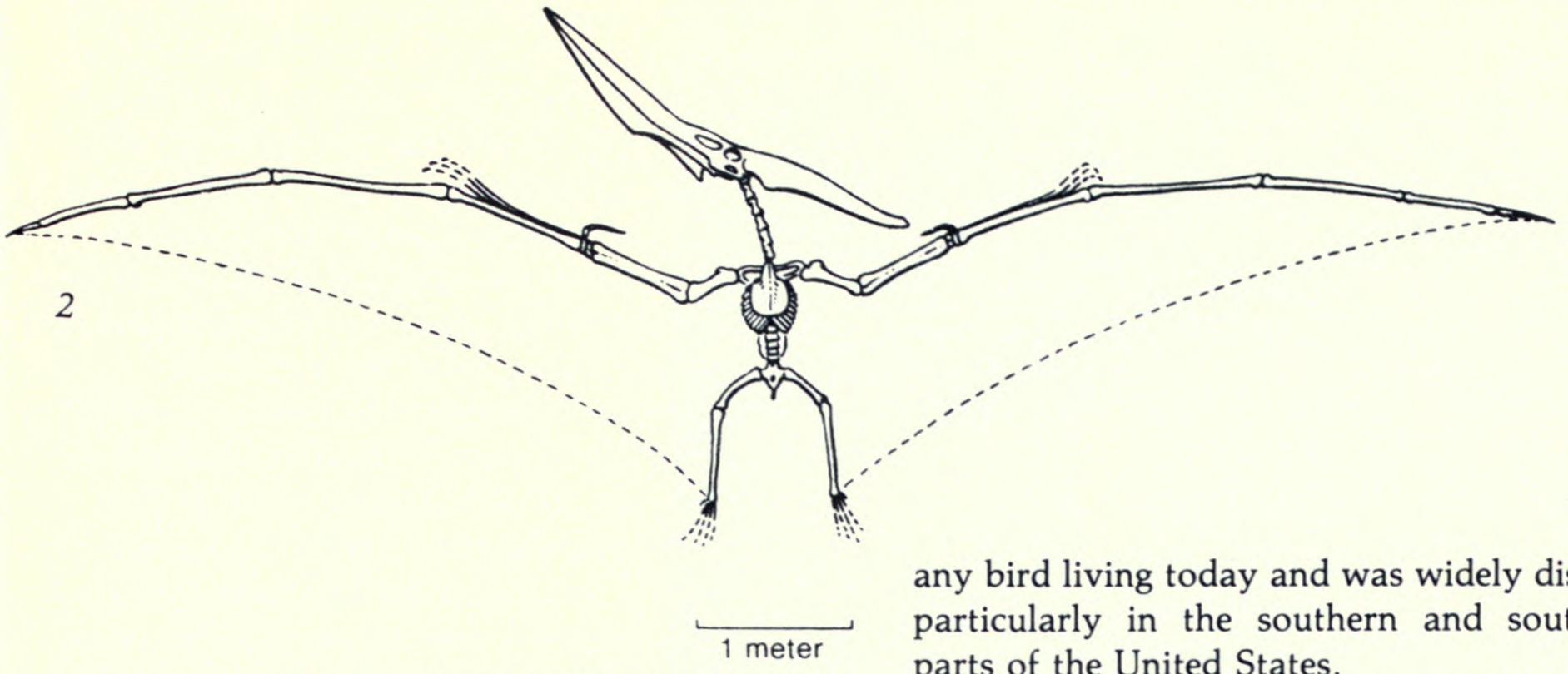
There are about 250,000 different species of fossil plants and animals known. These have been named and described and specimens have been deposited in museums throughout the world. Field Museum has in its collections representatives of perhaps 20 percent of these known species. In combination with other museums, we thus have an enormous amount of statistical information on changes in the biological world that have occurred since the origin of life on Earth. In spite of this large quantity of information, it is but a tiny fraction of the diversity that actually lived in the past. There are well over a million species living today and known rates of evolutionary turnover make it possible to predict how many species *ought* to be in our fossil record. That number is at least 100 times the number we have found. It is clear that fossilization is a very chancy process and that the vast majority of plants and animals of the past have left no record at all.

To many people, the most interesting fossils are the oldest ones and the youngest ones. The oldest ones (up to 3,500 million years old) give us information about the origin and early evolution of life — at a time when physical and chemical environments were very different from those that prevail today. The youngest rocks, on the other hand, are of interest because they include fossils of early man. These, of course, have been worked on with particular success by the Leakeys in East Africa.

But these extremes account for only a small part of the quarter of a million fossil species — and for one interested in the broad range of evolutionary change, the extremes do not contribute much. In between is a long geologic interval which contains the basic record of the evolution of all major groups of plants and animals. Time control and quality of preservation are excellent compared with the rather thin record of the oldest or youngest fossils. (I might point out here that the East African material the Leakeys have worked on is relatively poor, there are only a couple hundred specimens, and age-dating is very uncertain.)

Darwin's theory of natural selection has always been closely linked to evidence from fossils, and probably most people assume that fossils provide a very important part of the general argument that is made in favor of darwinian interpretations of the history of life. Unfortunately, this is not strictly true. We must distinguish between the *fact* of evolution — defined as change in organisms over time — and the *explanation* of this change. Darwin's contribution, through his theory of natural selection, was to suggest *how* the evolutionary change took place. The evidence we find in the geologic record is not nearly as compatible with darwinian natural selection as we would like it to be. Darwin was completely aware of this. He

By David M. Raup, curator of geology



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1 meter

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was embarrassed by the fossil record because it didn't look the way he predicted it would and, as a result, he devoted a long section of his *Origin of Species* to an attempt to explain and rationalize the differences. There were several problems, but the principal one was that the geologic record did not then and still does not yield a finely graduated chain of slow and progressive evolution. In other words, there are not enough intermediates. There are very few cases where one can find a gradual transition from one species to another and very few cases where one can look at a part of the fossil record and actually see that organisms were improving in the sense of becoming better adapted. To emphasize this let me cite a couple of statements Darwin made in his *Origin of Species*: At one point he observed, "innumerable transitional forms must have existed but why do we not find them embedded in countless numbers in the crust of the earth?"; in another place he said, "why is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain, and this perhaps is the greatest objection which can be urged against my theory."

Instead of finding the gradual unfolding of life, what geologists of Darwin's time, and geologists of the present day actually find is a highly uneven or jerky record; that is, species appear in the sequence very suddenly, show little or no change during their existence in the record, then abruptly go out of the record. And it is not always clear, in fact it's rarely clear, that the descendants were actually better adapted than their predecessors. In other words, biological improvement is hard to find. Let me give an example: During the interval from about 65 to 200 million years ago there were a lot of flying reptiles known as pterosaurs (see "Pterosaur," by John Bolt, in the May, 1976, *Bulletin*). Their fossil record is quite good in spite of the fact that the skeleton of these animals is difficult to preserve. The giant *Pteranodon* was particularly spectacular. It was much larger than any bird living today and was widely distributed, particularly in the southern and southwestern parts of the United States.

Figure 1 shows a reconstruction of *Pteranodon* as it probably looked. The mountains in the background are not there by accident: it is felt by some people that these reptiles could become airborne only by climbing up on cliffs and jumping. *Figure 2* shows the skeleton. Wings were formed by greatly extending the bones of one finger on each hand and filling in with skin the area enclosed by the dotted line. This is basically the device used also by some modern bats. There is little question that this animal was capable of flight — a conclusion based on sophisticated engineering studies involving extensive analysis of weight, lift, drag, and other aerodynamically important factors — along with wind tunnel experiments with scaled models.

Figure 3 shows what *Pteranodon* probably looked like at rest and when flying. The most striking aspect of *Pteranodon* is its size, demonstrated

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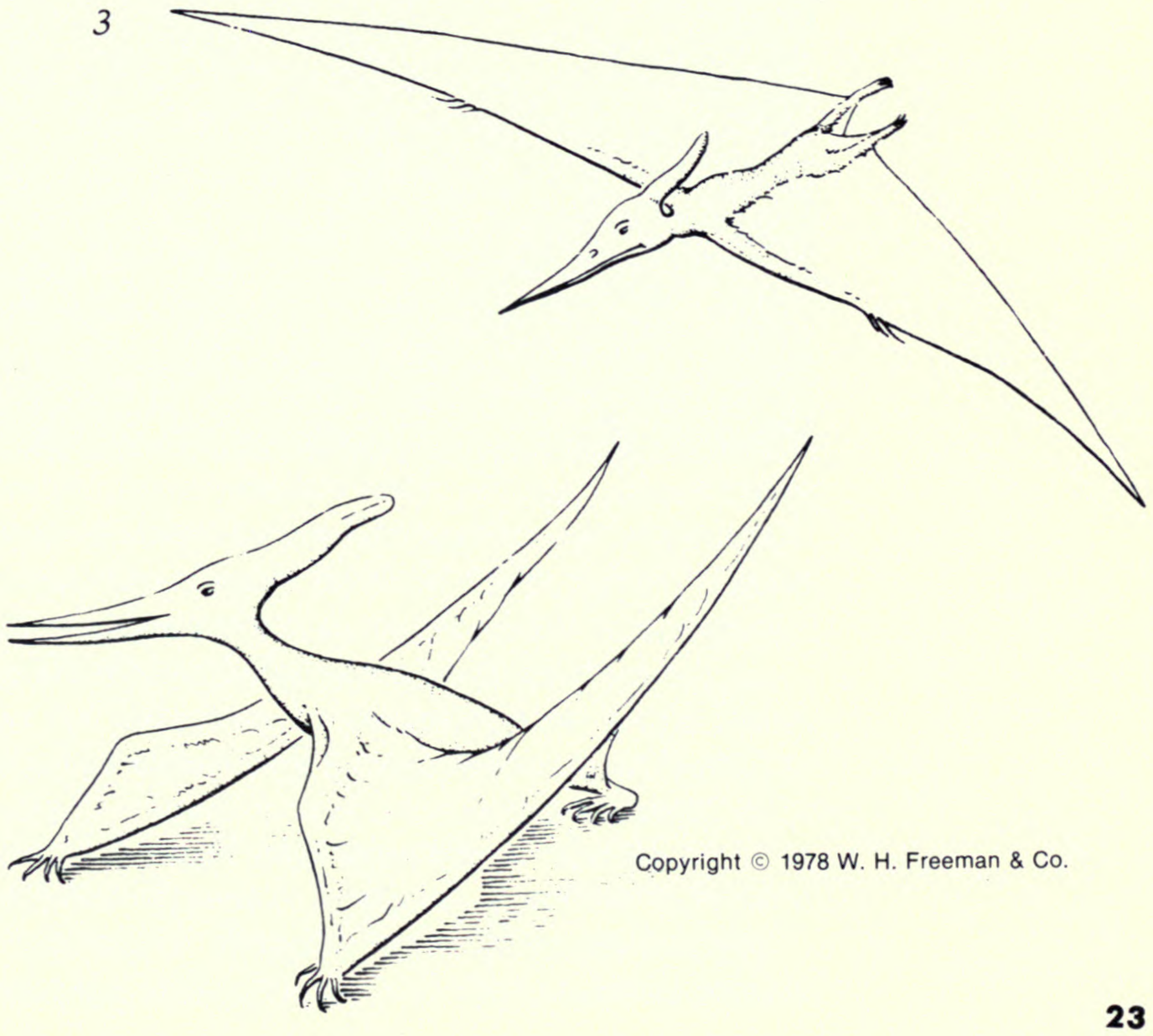

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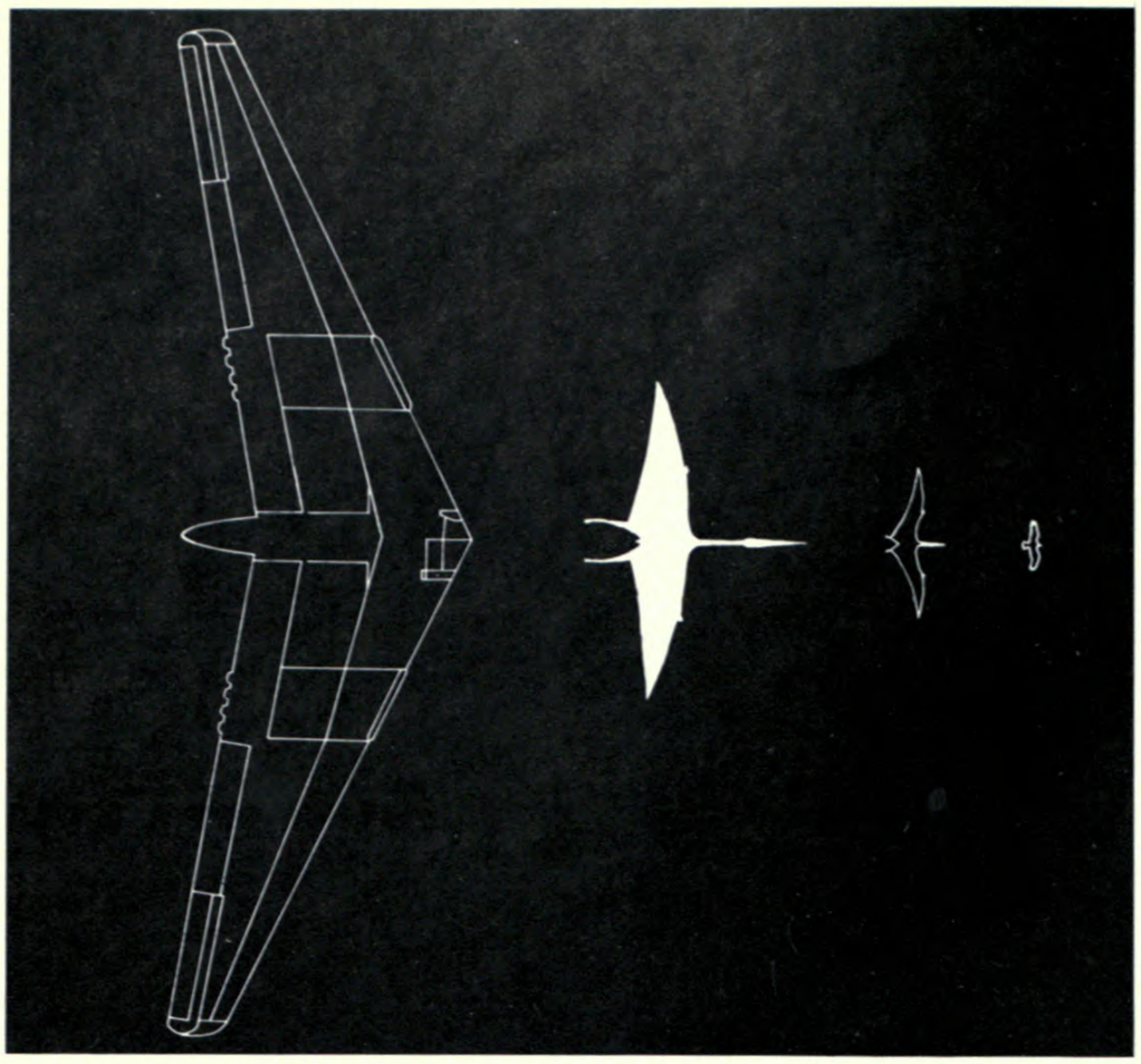

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in *Figure 4*, where it is shown in comparison with other flying objects. On the left is a modern tailless aircraft — the Northrop YB-49 — with a wingspan of about 170 feet. Next to it is the largest known pterosaur, which had a wingspan of about 50 feet. Next is a smaller pterosaur. The drawing on the far right shows one of the largest living birds — a condor with a wingspan of about nine feet. Thus, some pterosaurs were larger than all flying birds and even many small airplanes. They achieved this size and were still able to fly because their design was nearly optimal.

So here we have an adaptation which was apparently successful for many millions of years but which is now extinct and has not been repeated. That this animal went extinct implies some sort of failure. At least that is the conventional wisdom. *Pteranodon,* along with most other large reptiles, was replaced by mammals and birds. Mammals and birds were already around, but in small numbers. We assume in darwinian fashion that the big reptiles went extinct because there was something wrong with them; that is, they either couldn't compete with new forms that had evolved, or there was some change in environment that they couldn't adapt to fast enough to survive. As we will see, this interpretation may not be correct. We don't have any real evidence that there was anything wrong with the flying reptiles—in fact, they lived on the earth for a much longer time than humans have been around. During their tenure on earth the flying reptiles diversified into several quite distinct species but it is very difficult to put these species into any sort of series of improvement.

Here is another example: Figure 5 shows a fossil trilobite—a member of an extensive but now extinct group of arthropods. Figure 6 is a closeup of one eye of a trilobite. The eyes were generally large and quite similar to the eyes of modern insects, crabs, and other arthropods. But if we look at the individual elements of the trilobite eye, we find that the lens systems were very different from what we now have. Riccardo Levi-Setti (a Field Museum research associate in geology and professor of physics at the University of Chicago) has recently done some spectacular work on the optics of these lens systems. *Figure 7* shows sketches of a common type of trilobite lens. Each lens is a doublet (that is, made up of two lenses). The lower lens is shaded in these sketches and the upper one is blank. The shape of the boundary between the two lenses is unlike any now in use — either by humans or animals. But the shape is nearly identical to designs published independently by Descartes and Huygens in the seventeenth century.

The Descartes and Huygens designs had the purpose of avoiding spherical aberration and were what is known as aplanatic lenses. The only significant difference between them and the trilobite lens is that the Descartes and Huygens lenses were not doublets — that is, they did not have the lower lens. But, as Levi-Setti has shown, for these designs to work underwater where the trilobites lived, the lower lens was necessary. Thus, the trilobites 450 million years ago used an optimal design which would require a well trained and imaginative optical engineer to develop today — or one who was familiar with the seventeenth century optical literature.

Most fossils are not as easily understood as this. We have no idea why most structures in extinct organisms look the way they do. And, as I have already noted, different species usually appear and disappear from the record without showing the transitions that Darwin postulated.

Darwin's general solution to the incompati-

bility of fossil evidence and his theory was to say that the fossil record is a very incomplete one — that it is full of gaps, and that we have much to learn. In effect, he was saying that if the record were complete and if we had better knowledge of it, we would see the finely graduated chain that he predicted. And this was his main argument for downgrading the evidence from the fossil record.

Well, we are now about 120 years after Darwin and the knowledge of the fossil record has been greatly expanded. We now have a quarter of a million fossil species but the situation hasn't changed much. The record of evolution is still surprisingly jerky and, ironically, we have even fewer examples of evolutionary transition than we had in Darwin's time. By this I mean that some of the classic cases of darwinian change in the fossil record, such as the evolution of the horse in North America, have had to be discarded or modified as a result of more detailed information — what appeared to be a nice simple progression when relatively few data were available now appears to be much more complex and much less gradualistic. So Darwin's problem has not been alleviated in the last 120 years and we still have a record which *does* show change but one that can hardly be looked upon as the most reasonable consequence of natural selection. Also the major extinctions such as those of the dinosaurs and trilobites are still very puzzling.

Now let me step back from the problem and very generally discuss natural selection and what we know about it. I think it is safe to say that we know for sure that natural selection, as a process, does work. There is a mountain of experimental and observational evidence, much of it predating genetics, which shows that natural selection as a biological process works. Darwin's strongest evidence for selection actually came from the experience of plant and animal breeders who were employing artificial selection to produce evolution by breeding. And selection, be it natural or artificial, can clearly lead to better adapted types through a series of generations and through gradual transformation of a population.

So natural selection as a process is okay. We are also pretty sure that it goes on in nature although good examples are surprisingly rare. The best evidence comes from the many cases where it can be shown that biological structures have been optimized — that is, structures that represent optimal engineering solutions to the problems that an

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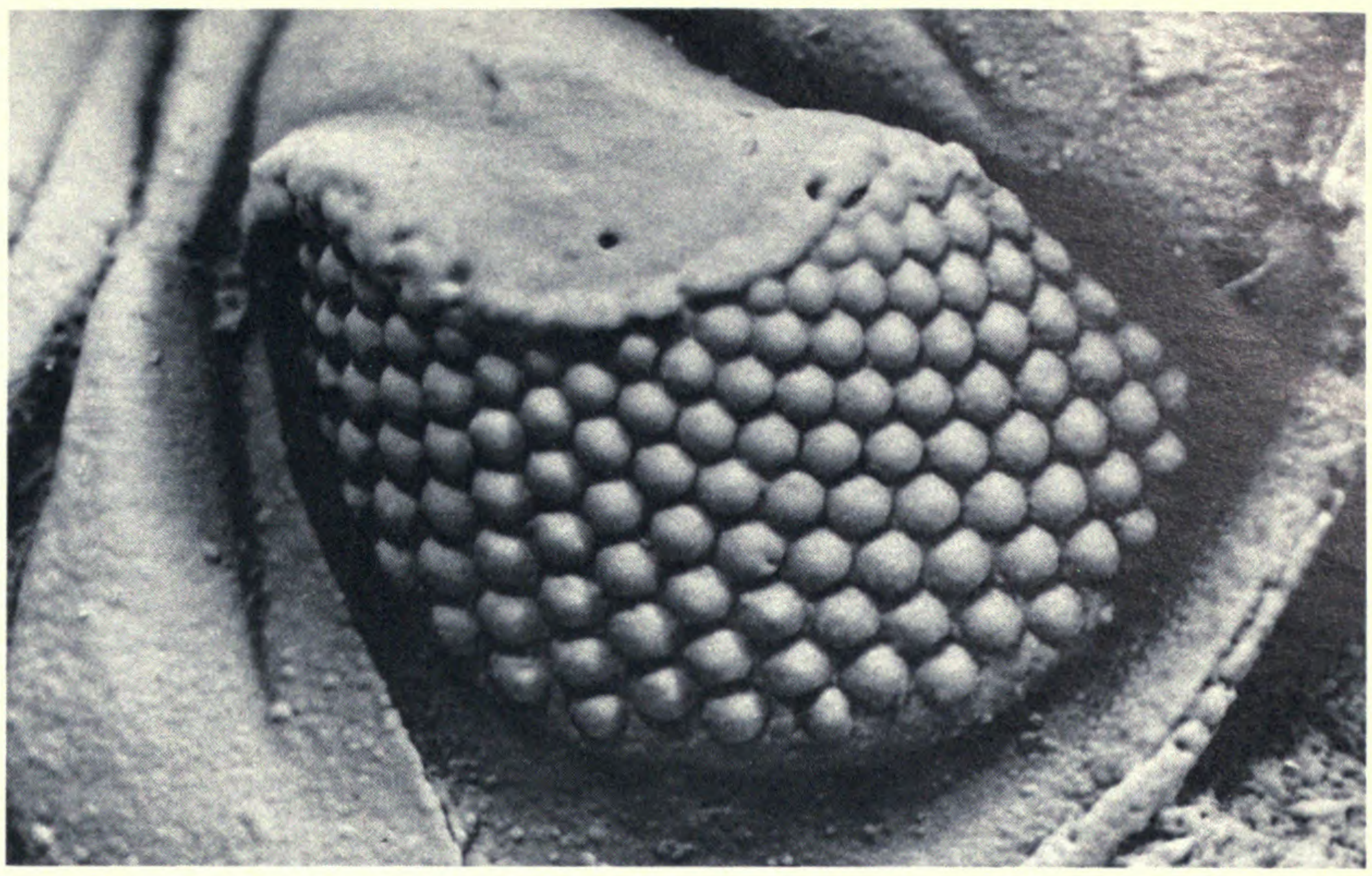

R. Levi-Setti

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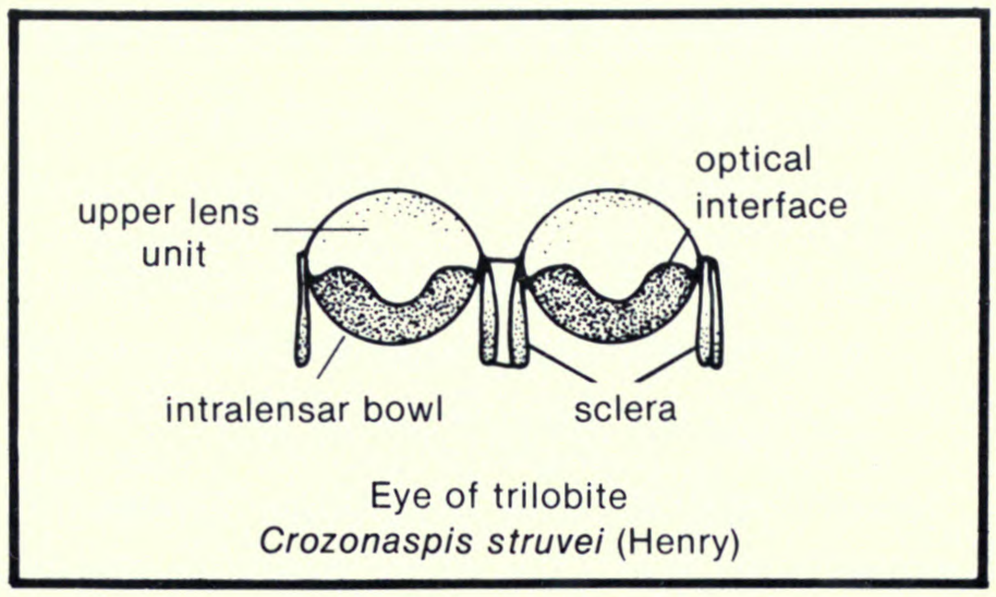

Eye of trilobite
Crozonaspis struvei (Henry)

R. Levi-Setti

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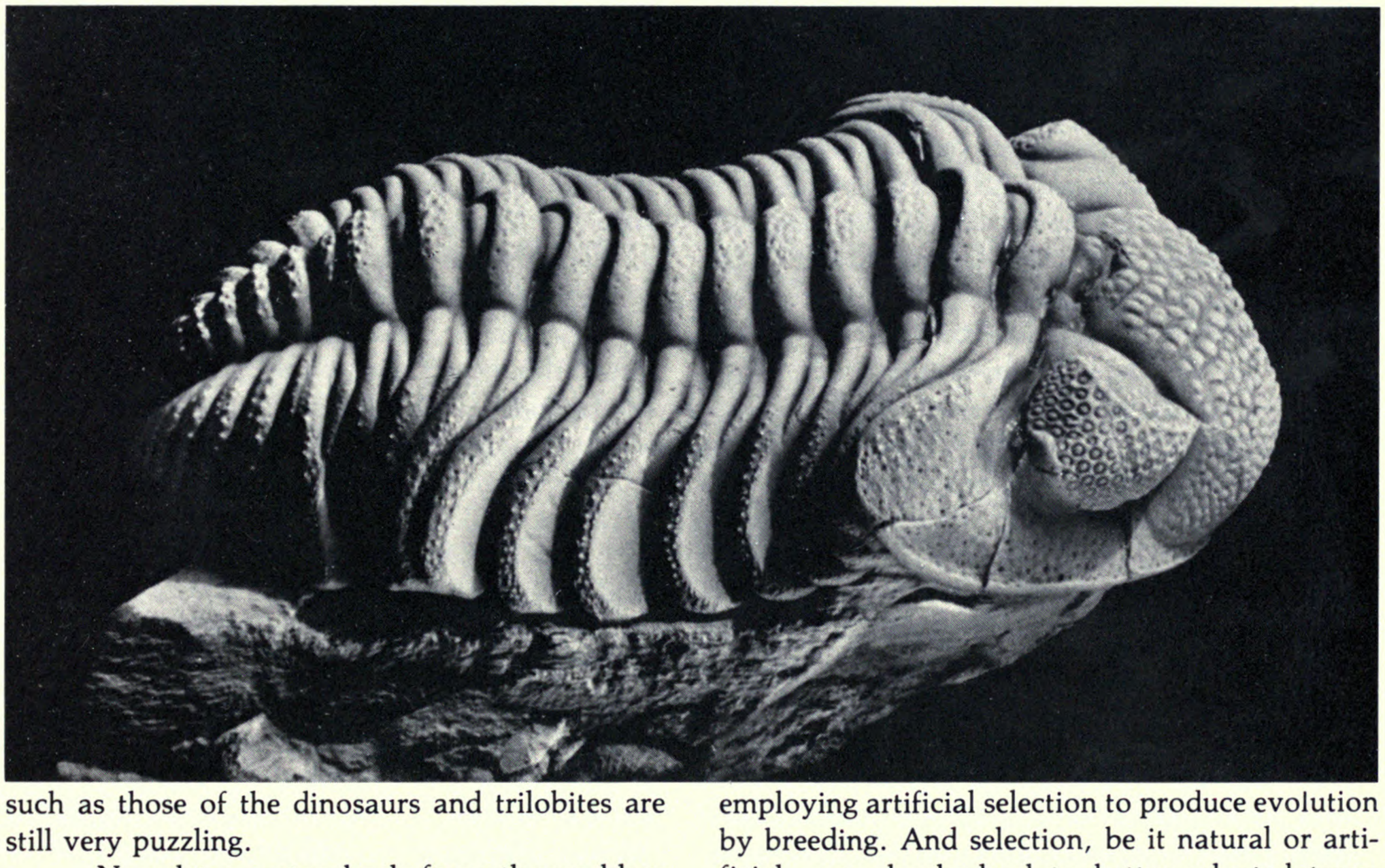

R. Levi-Setti. Copyright © 1975 The University of Chicago

animal has of feeding or escaping predators or generally functioning in its environment. The superb designs of flying reptiles and of trilobite eyes are examples. The presence of these optimal structures does not, of course, prove that they developed through natural selection but it does provide strong circumstantial argument.

Now with regard to the fossil record, we certainly see change. If any of us were to be put down in the Cretaceous landscape we would immediately recognize the differences. Some of the plants and animals would be familiar but most would have changed and some of the types would be totally different from those living today. The average duration of a species on the earth is less than 10 million years. And the record of really abundant life goes back at least 600 million years, so there has been complete turnover in the biological world many times. This record of change pretty clearly demonstrates that evolution has occurred if we define evolution simply as change; but it does not tell us how this change took place, and that's really the question. If we allow that natural selection works, as we almost have to do, the fossil record doesn't tell us whether it was responsible for 90 percent of the change we see, or 9 percent, or .9 percent.

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The very obvious question at this point is: what alternative mechanisms do we have to explain the changes that we observe? A great many alternatives have been suggested both before and after Darwin. Some of the evolutionary theories that have been proposed belong to the lunatic fringe, but others are serious propositions by competent scholars. A currently important alternative to natural selection has to do with the effects of pure chance. It has been suggested that there are traits which are not important enough to the organism to be "seen" by natural selection, and that a purely random system of evolution could work for these traits. Let me give an example which may be important in the fossil record: Many organisms have shells which are coiled in a spiral fashion, such as snails, the pearly nautilus, and a great many other fossil and living organisms. Sometimes the spiral is left-handed, sometimes it's right-handed. One is just the mirror image of the other. In most cases, whole species of snails are either exclusively left-handed or exclusively right-handed. In a few cases, both left-handed and right-handed forms occur within the same species. And it is pretty clear that this is a hereditary trait — although the genetic mechanism is often complex.

In most cases, it's difficult to find an advantage the left-handed form would have over the right-handed form, or vice-versa. In such cases, the coiling direction that dominates the species may just be a matter of chance; that is, the one that got there first, or happened by chance to have more offspring gradually came to dominate the population. This is the sort of trait that might be subject to random evolution — a clear difference between animals but one not seen by natural selection because it does not affect the general life and hard times of the organism. I should add that in some snails it has been shown that this situation is a little bit more complicated because copulatory behavior is affected by coiling direction; specifically, the left-handed ones get along better with other left-handed ones than with shells of opposite coiling direction. This gives a selective advantage to homogeneity in a population without giving preference to left or right. So a left-handed strain that got started might be aided by natural selection even though its origin was a matter of chance. In the general case, however, the symmetry difference is probably neutral.

It would seem that if evolution of shape and form in animals were a random affair, the result would be one of chaos. This, of course, is one of the major counter-arguments to the idea of random evolution (or random walk evolution as it is sometimes called). It is certainly true that one would be most unlikely to develop a functioning flying insect, reptile, or bird by a chance collection of changes. Some sort of guidance is necessary. And in these cases, of course, natural selection is the only mechanism we know of to produce a workable combination of characteristics. On the other hand, it may be that a great many of the differences that we observe within major animal groups are differences which do not have much effect on fitness. We are thus talking about the survival of the lucky as well as the survival of the fittest.

A large number of evolutionary biologists these days are studying the question that I've just considered — it's called neutral or nondarwinian evolution. Much of this research is concentrated in the Chicago area. Most of the work so far has been done with proteins of relatively minor importance in the biological scheme where the case for selective neutrality can be made much more easily. Paleontologists have to work with obvious traits,

and therefore, traits which are more likely to be seen by natural selection, so paleontologists are working at a scale different from that used by biologists. The whole problem of neutral evolution represents a very exciting area and is one of the most hotly debated topics in evolutionary biology today.

I would like now to concentrate on just one aspect of the problem. This has to do with the extinction of large groups such as the dinosaurs, the trilobites, and also somewhat smaller groups such as the flying reptiles that I have already discussed.

We know that the dinosaurs went extinct about 65 million years ago and we know they went extinct rather suddenly. Now, when we say the dinosaurs went extinct we are saying that a couple of prominent reptilian orders died out at about the same time. It is important to remember that what taxonomists call a class or an order does not exist as such. It's an abstraction denoting a collection of species descended from a common ancestor. It is an abstraction just as a family name in a human community is an abstraction. Therefore, when we say the dinosaurs went extinct what we are actually saying is that the dinosaur species living at a certain time didn't leave any descendants which we would call dinosaurs. The conventional wisdom is that the dinosaurs must have had traits in common or requirements in common such that they couldn't cope with changes in environment. And paleontologists have gone to great lengths to try to find out what happened.

Conventionally, the approach is a completely darwinian one based on the faith or belief that extinction can only be explained by finding some sort of Achilles heel shared by all members of the group. Along with this is the strong implication that the successor group — mammals in the dinosaur case — was somehow better than the dinosaurs, and this implies that if both were living today, the dinosaurs would again lose out to the mammals. This scenario may be true, but it is a very difficult one to prove. We don't have any convincing arguments for why the dinosaurs died out. It has even been suggested that we have a tendency to make what can only be called a *moral judgement* in cases of extinction. If a group went extinct, it must have been bad. The good prosper, the bad die.

What I would like to develop is an idea based on chance or randomness which may lead to the conclusion that the dinosaurs were simply unlucky. One way to approach this is to look at a completely different but analogous situation: one having to do with the evolution of surnames in human families. We know that family names die out. Surnames disappear from our communities. And the same question could be asked of them that is asked of the dinosaurs — does a human surname die out because its members are weak, or do something wrong, or does the family just have bad luck?

> *"It was clever of the pterodactyls to think of flying, but that's all you can say for them. They were doomed from the start because they had no feathers and no wishbone, or furcula, as flying vertebrates should have. They didn't belong in the picture and public opinion was against them. The Archaeopteryx was not much of a bird, but at least it had feathers. As for the pterodactyls, the best thing to do is just forget them. Bats are going to flop, too, and everybody knows it except the bats themselves."* — How to Become Extinct, *by Will Cuppy (1941)*

One reason to turn to the evolution of surnames for help is that the subject has been worked on extensively for about 150 years and several effective mathematical techniques have been developed for working with the problem.

One of the first references to extinction of family names is found, of all places, in Malthus — in his famous *Essay on Population*. We normally associate Malthus with birth and population growth rather than death and extinction. But he mentioned in passing some data on the extinction of families in the town of Berne, Switzerland. He noted that over the 200-year period from 1583 to 1783, fully three-quarters of the prominent families that were present at the start of the period went extinct before the end of the 200 years. This was a startling figure. The same phenomenon was found later in other situations — including the English peerage and various European royal families. Wherever information was available, it showed that the average life expectancy of a family name is surprisingly short. This was intuitively unreasonable. Because all the data came from the upper classes of society, it was assumed that there was something debilitating or weakening about membership in the upper classes — and this gave rise to all sorts of sociological theory and speculation. But these speculations could not be checked because information was not available for the lower classes of society.

It turned out, after some now classic mathematical analysis by Galton and Watson* that what Malthus and others had observed was exactly what should be expected by chance alone, and the social class had nothing to do with it! This was later confirmed by studies of whole communities.

What this means is that families are inher-

**F. Galton and H. W. Watson, 1875, "On the Probability of the Extinction of Families," in the* Journal of the Anthropological Society of London, *Vol. IV, pp. 138-44.*

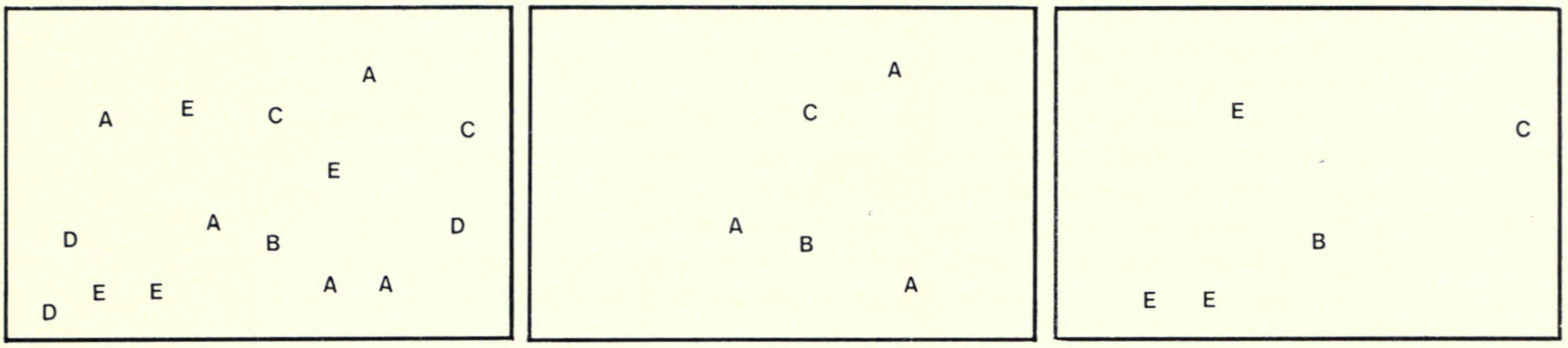
ently prone to extinction even though the population as a whole is stable — or even growing. Now this is still counter-intuitive and hard to accept. We all know of families that are enormous and which have long histories. The biography shelves of any library are full of examples. But the fact is that the ultimate extinction of any family name is statistically inevitable. The only uncertainty is *when*. It is perhaps best understood by noting that a family has about an equal chance of increasing or decreasing in size during a single generation. This is because the chances are about 50-50 of any marriage producing a male heir unless, of course, the couple keeps having children for the express purpose of having a male heir. I must apologize for my emphasis on the male line but since it is the name-bearing line, it is easier to work with. The same results can be gotten with the female lines but it is less convenient to analyze. Anyway, the number of males in a family fluctuates up and down as a random walk. If the number happens to drop to zero, the family is, so to speak, out of the game. The surname is extinct and cannot recover. But there is no such limit on the high side. That is, success cannot guarantee immunity to extinction to the degree that extinction guarantees immunity from success. Thus, ultimate extinction is inevitable and the smaller a family, the greater the chances of its becoming extinct in the next generation. Most families die out quickly because they generally start out small and thus are dangerously close to extinction at the beginning. Most published family histories are written about those families which do survive to become large. And most family histories are written by family members and thus are about families that have not yet become extinct. The biography shelves of a library thus contain a most unrepresentative sample of families. And even these families are doomed in the long run by the random walk nature of family evolution.

For the reader who is still skeptical, I recommend any of the published catalogs of the English peerage. The English peerage provides a particularly clear-cut situation. When a single individual is declared to be a peer of England, with the title to be inherited through the male line, we have the start of what is, in effect, a new family with a single founder. Some lines last a long time but most disappear in the first one, two, or three generations.

A good example of such disappearance is that of the earldom of Rochester. Henry Wilmot was declared the First Earl of Rochester in 1652 but died seven years later leaving one son, John, who became the Second Earl. John died 21 years after that and *his* only son died as a child and the title became extinct. Now all three earls died of specific causes — John died of syphilis for example. One can say that John was unlucky, but the extinction of the line cannot be said to have happened without cause. *But* if we look at a whole group of such families, their histories are indistinguishable from a system controlled only by chance. By assuming a system of chance, we can accurately predict the approximate number of families that will be short-lived — even though we cannot predict in advance which families will be short-lived.

Now, suppose we have an imaginary human community which has a variety of surnames. Most of the families will be small — either because they just started or because they are on the verge of extinction. Only a few families will be large. This imaginary community would have a telephone book much like that of Chicago in the sense that a few names are very abundant but most are not. Now suppose that the population were suddenly reduced by epidemic disease. And suppose that family affiliation was not a factor in the reduction: that is, assume that Smiths were not more susceptible to disease than Browns. If this were to happen, there would be simultaneous extinction of many families. Most of the disappearing families would be the small ones but some large ones would be included. If someone were to look at family records later, it might *appear* that the reduction in population size was due to extinction of families — rather than the other way around — and one might be tempted to search for common denominators of failure among the families that died out in order to find out *why* they died out. But this would be entirely wrong because surname extinction was the effect rather than the cause of the population drop.

I can illustrate the general principle by a hypothetical example. The left side of *Figure 8*, above, shows a random array of 15 letters —ranging from *A* to *E*. Each letter may be thought of as representing a different surname; *A* is the most common and *B* the least common. Now, if we remove letters randomly, we may get something



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like the middle of *Figure 8*. Ten letters were selected for removal by using a table of random numbers. The letter *A* survived which is not surprising because it was the most common to begin with. But *B* also survived — by good luck. *D* and *E* went extinct. The right side of *Figure 8* shows another try with the same original pattern. This time, *A* and *D* went extinct and *B*, *C*, and *E* survived. *B* was lucky both times.

Let me return now to the fossil record of evolution. The dinosaurs died out at the end of the Cretaceous period (about 65 million years ago). Several other important animal groups also died out at about the same time. The groups seem to have little in common. Some lived on land, others in the sea. Some were large animals, some were small. And so on. (There is nothing surprising, by the way, in the fact that all these groups died out near the boundary two periods in the geologic time scale because the boundary itself is defined on the basis of the extinctions.) Many paleontologists have spent years trying to figure out what failing was shared by such different animal groups. Some explanations have been suggested but none of them is really convincing (to me, at least). The only thing we know for sure is that a lot of groups died out at about the same time. The fact of the extinctions is not geologically unusual — only the number of extinctions in a short time.

The business about extinction of human surnames may provide a solution. We may postulate that the end of the Cretaceous period was a time when an unusually large number of species died out. This could have resulted from some sort of epidemic, or a worldwide change in climate, or from a rare astronomical event. If a lot of separate species died out, some families and orders would inevitably also die out, as we have seen through the surname analogy. Some species would survive by luck and some would survive because they were fit. But these differences in fitness need not have anything to do with membership in a group such as reptiles and mammals.

Thanks to the mathematical techniques developed by people working with surnames, it is possible to test the geologic case against the proposition that species extinctions are not biased by the group to which the species belongs. It turns out that tests of several mass extinctions in the fossil record show that group membership (family name, if you will) is not statistically correlated with the extinctions. The dinosaur extinctions have not been fully tested yet. But experience with other extinction events leads one to look at the dinosaur extinctions as a possible chance phenomenon. It may be that the mammals were not better than the dinosaurs but just luckier at a time when an unusually large number of species were dying. This leads to the rather disquieting conclusion that if the Cretaceous extinctions were to be reenacted, a different suite of groups might have survived and this suite might not include our ancestors.

The ideas I have discussed here are rather new and have not been completely tested. No matter how they come out, however, they are having a ventilating effect on thinking in evolution and the conventional dogma is being challenged. If the ideas turn out to be valid, it will mean that Darwin was correct in what he said but that he was explaining only a part of the total evolutionary picture. The part he missed was the simple element of chance!

BORDEN EXPEDITION

Continued from p. 8

The Museum's *Annual Report* for 1927 carried this description of the zoological specimens collected:

". . . The zoological results of this expedition include a . . . group of Peninsula Brown Bears (*Ursus dalli gyas*) which are the largest carnivorous animals now living, rivalling in size the Cave Bear of Pleistocene times. Of the four specimens selected for a group, two were shot by Mrs. John Borden, one by Miss Frances Ames, and the fourth, . . . by Mrs. R. B. Slaughter. The expedition also obtained . . . Polar Bears and the complete skin and skull of a large male Pacific Walrus, . . ."

Five of the eight Sea Scouts survive today: Andrews, Purcell, Carstenson, Ram and McClelland. Andrews, who became an engineer, and Carstenson, who became a tool and die maker, are living in Florida. Ram, the only scout to become a professional mariner, is with the merchant marine. Purcell, a Jesuit priest, is a research professor at Georgetown University and a distinguished industrial labor relations authority. McClelland, a Chicago resident, is a retired physics teacher. Shortly after the expedition, McClelland made a name for himself by skippering the winning schooner, *Blue Moon*, in the 1929 Chicago-Mackinac yacht race.

Frances Ames, who collected botanical specimens on the expedition, is now Mrs. Douglas Wolseley, of Santa Barbara, CA. Mrs. Charles B. Goodspeed, widowed and remarried, is now Mrs. Gilbert W. Chapman, of New York. Mrs. John Borden (née Courtney Letts), subsequently wife of the Argentine ambassador to the United States (1931-43), Felipe Espil (deceased), is now Mrs. Foster Adams, of New York. Mrs. Adams will be at Field Museum on Saturday, February 3, to introduce the film "The Cruise of the Northern Light," which will be shown in James Simpson Theatre. □