Origin of the Tetrapod Limb

Gordon Gunter

Thousands of species of aquatic arthropods, whose ancestors never left the water in all their evolutionary history, have perfectly good walking legs. The legs and mechanics of walking in the land crabs differ in no fundamental aspect from those of their relatives that have never left the sea. Thus, it seems proper to assume that the arthropods did not undergo any extreme modification of their locomotor appendages when they moved into the atmosphere. The situation may have been different with regard to the evolution of the tetrapod limb, but it probably was not as different as current writings imply.

Romer has suggested that the tetrapod limb arose as an adaptive modification that enabled amphibians to migrate from drying water bodies of the Devonian lands to areas of more permanent water (*1*). However, Orton pointed out that modern amphibians concentrate at the dampest spots available and will disperse only to wetter areas (*2*). She advanced the alternative hypothesis that the tetrapod limb was originally an adaptation for digging prior to estivation. Ewer has noted, however, that a normally aquatic South African toad will leave a drying pond and go to a larger body of water, apparently because of population pressure (*3*). He also pointed out that if the tetrapod leg first evolved as a fossorial appendage, we still must discover the selective agency that led to its change of function to terrestrial locomotion. There are other things to be said.

It is difficult to see how discontinuous and somewhat catastrophic events, such as the drying of water bodies, could have led to the formation of limbs strong enough to cope with these events at the very first effort. This would be evolution without selection, and this theory can be accepted only by those who believe that evolutionary processes take place by jumps and bounds. The latter idea has not been entirely ruled out to the satisfaction of all evolutionists, but the weight of evidence seems to be against it, and almost certainly it was not the common process. In any case, a plausible theory of the origin of the tetrapod limb, based on slow and gradual evolution, is available.

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A Gradual Process

Tetrapod limbs are certainly derived from the paired fins of ancient fishes. Thus the ultimate origin of the tetrapod limb goes back to the time when these fins arose, whether from fin folds or the paired appendages of ostracoderms, as is suggested by Gregory and Raven (*4*). But this is the origin of a fin and not of the tetrapod limb. Nevertheless, it is well to hold in mind that the so-called "origin" of the tetrapod limb was the transformation of a fin into a leg. It is highly unlikely, as Westoll (*5*) has stated, that the process occurred suddenly. We would expect that some use of fins as props and supports came first, prior to any attempts at locomotion. Examples of such uses of fins among modern fishes are legion. The next step would be walking and the development of walking fins. There are many such cases among modern fishes. Many triglids walk by means of special rays of the pectorals. The batfishes, Ogcocephalidae, walk well and swim only poorly. Several gobies and blennies walk, and the Antennaridae not only walk but climb with little fins that have a remarkable resemblance to hands. The fact that these fishes are extremely specialized, with fin bones not homologous with those of the tetrapod limb, is beside the point. The point is that several hundred species of modern fishes do walk under the water.

It is quite reasonable, then, to suppose that the famous "bridge that walks" first rested on weak and trembling piers, which, of necessity, arose under water. Such piers were not legs, but fins. Eaton (*6*) has suggested that the "paddles" first served to prop the fish without bearing its weight. Following this, we might suppose some increase and strengthening of these supports as the fishes skittered about and made elementary walking movements in the shallows, probably with their backs out of water part of the time. Anatomical considerations led Eaton to suggest that the essential elements of the amphibian type of locomotion could have arisen before the lobefins emerged from the water. Next would come short invasions of the land and movements along the shore, which would become longer and longer as time went on.

Predators and Food

These developments would have been caused or accelerated by the pressure of predators and the search for food. In the ancient waters, one thing was quite different from what it is today. All enemies came from the water. No birds stood on shore to impale a fish in the shallows or dive at it from above. No mammals lived on land to pounce upon the clumsy water animal that was out of its element. Indeed, there was nothing on shore except a large arthropod fauna, which was largely prey and food. The large predators were all, in the beginning at least, other fishes of larger size that could not travel the shallows. Safety lay in shallows and on the land. Thus the direction of the pressure was all toward the land. It was a much more attractive environment to a weak, amphibious creature than it is today. Enemies were lacking, and there was abundant food. We might surmise that the weak and lowly, in a sense, were being shoved or pushed out of the waters by their stronger relatives.

Today, the situation is greatly changed, and modern fishes are beset by predators from land, water, and air. Even so, modern fishes show various stages of land invasion. Darnell (*7*) has recently called attention to the terrestrial forages of *Gobiomorus dormitor,* a common euryhaline goby of the Gulf of Mexico. He observed it several times at night, 4 or 5 feet from the water, along the Rio Tomesi drainage of Mexico. Apparently it goes ashore for food. The Asiatic goby, *Periophthalmus,* and the climbing perch, *Anabas,* are more advanced cases. *Periophthalmus* runs and skips about quite actively and even climbs low trees in pursuit of insect prey. Donald R. Moore, of our staff, tells me that he has observed Asiatic gobies many times and that they are not particularly wild but are so elusive that he never succeeded in his attempts to catch one with his hands.

Loss of Fin Rays

It is not necessary to suppose that the first vertebrate to walk on land was a member of the Amphibia. More than

likely it was a fish, still with fin supports. It doubtless had fin bones homologous with those of the modern tetrapod limb, such as those of the rhipidistian crossopterygians. These fins would have become "tetrapod limbs," albeit weak ones, by the simple transformation of losing their fin rays and increasing the size of the fleshy base. Thus, the so-called "origin" of the tetrapod limb, as differentiated from a fin, was simply the loss of fin rays. There is no other place to draw the line. Eaton (*6*) has pointed out, in this connection, reasons why the first land invader was probably a "fish," as he called it, rather than an amphibian. He said that the only way an adaptive premium could be placed on reduction of the fin membrane was for the "fish" to spend part of the time out of water "to escape predators or for other reasons." Presumably, while these processes were going on, the lungs were increasing and other characteristics of the Amphibia were evolving, so that the original land-invading fish became a sort of amphibiopiscine, later a piscioamphibian, and then finally a true amphibian, by a process so gradual that even if we had the actual specimens it would be difficult to place them all in the separate major categories.

The limbs and girdles of present-day caudate Amphibia are small and weak—similar, we may postulate, to the weak limbs of an animal that has recently come from the water to shuffle clumsily about on dry land. Few of the caudate Amphibia of today are given to extensive excursions across really dry land, for which they are not fitted because of their weak limbs and moist, living skins; the early amphibians of Devonian swamps must have had similar limitations, at least with regard to weak legs. A situation involving fairly long journeys overland could be met by the Amphibia only after considerable evolution of the legs had taken place, and it is reasonable to suppose that this situation may have led to perfection of the limbs, by selection against the weak, long after the limbs arose. Thus, the suggestion of Romer (*1*) fits very well into the picture when it is considered as operative at a much later stage in the evolution of the tetrapod limb than the "origin."

Summary

The paired fins of fishes were first used as props and supports for resting on the bottom; these were later used in a clumsy, walking manner, and this behavior perforce began first in the water, because the weak props could not support the animals without the water bouyancy; increased perfection of the mechanics of walking took place in the shallows, which was a refuge from the chief predators; the land was also attractive as a haven and as a source of food; the first vertebrate invaders of land probably had fins, and these became legs by enlargement of the fin base and loss of fin rays; these original limbs and girdles were weak and probably underwent a considerable period of evolution in swampy country; later they were perfected by further selection when it became necessary for early amphibians to move across dry land because of a failing local water supply.

This syllogism conforms to the known behavior and capabilities of fishes and amphibians and to the general facts of zoology and paleontology. It suggests that common, continuous activities and stresses—escape from enemies and food getting—led to the origin of the tetrapod limb. This obviates the necessity for explaining how discontinuous and somewhat catastrophic events, such as the drying up of water bodies, could have led to the origin of limbs, which at the very outset had to be fairly strong.

The general theory stated here is fairly clearly implied by Berry (*8*), who said, "Those fishy pioneers with air-bladders —and paired fins—which, after ages of using their fins for pushing and paddling themselves over mud flats, gradually ventured onto drier and drier ground—where they avoided the competition for food—and the dangers of swarming hordes of ganoid pirates of the waters, were the ancestors of the amphibians."

References

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C. R. Moore, Zoologist and Contributor to Medicine

The morning was clear and cold, and the autumn leaves had covered the ground with colors of red, brown, and yellow. The family and a small party of friends had come to the summer home of Carl R. Moore in northern Michigan to scatter his ashes in a grove of white pine trees. Dr. Moore had planted these trees in front of the north window of a little study some 200 yards back of the main cottage. In the quiet of this retreat in the woods, he spent many hours over his microscope and with his manuscripts. Here he did much of the work that gained him fame as a zoologist and as an endocrinologist who made a major contribution to medicine. The summer home was also a place of relaxation and enjoyment for Dr. Moore.

Thirty years earlier a small group of faculty friends had established a summer colony that came to occupy an important place in the lives and affections of its members. Carl Moore loved the open country. He was an ardent and indefatigable fisherman, and he loved to work in the woods, to plant trees, and to engage in the many tasks of country life.

He was born 5 December 1892, on a farm in Green County, Missouri, and spent his early years there. Although he loved his home and associations in the colony in northern Michigan, he never forgot the scenes of his boyhood and looked forward to spending years of retirement on some little farm in the Ozarks, a dream that he never realized. After preliminary education in the schools of Springfield, he entered Drury College in 1909, coming under the in-