LAND-DWELLING VERTEBRATES AND THE ORIGIN OF THE TETRAPOD LIMB*

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> "Most students become acquainted with many of the current concepts in biology whilst still in school and at an age when most people are, on the whole, uncritical. Then when they come to study the subject in more detail, they have in their minds several half truths and misconceptions which tend to prevent them from coming to a fresh appraisal of the situation. In addition, with a uniform pattern of education most students tend to have the same sort of educational background and so in conversation and discussion they accept common fallacies and agree on matters based on these fallacies.
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> "The answer (to the quest for the origin of higher categories of organisms) will be found by future experimental work and not by dogmatic assertions that the general theory of evolution must be correct because there is nothing else that will satisfactorily take its place."
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> Kerkut[6], 1960

Terrestrial and amphibious tetrapods generally locomote with the aid of distinctive paired appendages which we refer to as "limbs," "arms" or "legs." Since the structure of the arm and the leg is basically similar, this discussion will treat them as if they were equivalent.

Fish, on the other hand, employ a fundamentally different form of locomotion. (This is true even when they are locomoting on land, as in the case of the nocturnal excursions of eels or the normal life of the mudskipper, *Periopthalmus* or the African *Clarius lazera* which actually steals millet out of gardens.) The locomotion of the fish is accomplished by serial contractions of the segmentally arranged *myotomal* musculature, producing a resultant force which tends to propel the fish forward by reaction when in water, or by contact when on land. Some fish are able to utilize their limbs, or projections from the opercula of the gills, or other devices to secure a hold on the substrate when not actually swimming. However, such appendages never contain the intrinsic musculature which would enable true walking to be accomplished. Generally they serve as stabilizers or as a point of contact to minimize lateral slippage while wriggling.

In contrast to this, most tetrapods rely little upon the segmental musculature in locomotion. Instead, in order to drag their bodies over obstacles in the terrestrial habitat, they utilize the muscles in the *limbs themselves* or in direct association with them *(par ex:* the *gluteus maximus* of man). The basic source of power in these animals is not the *trunk* but the *appendicular musculature.* Obvious exceptions to this rule are salamanders, which seem to combine the two modes of locomotion, and snakes which are confirmed wrigglers. In both of these forms and in similar forms the limbs are reduced or entirely absent.

Additionally the tetrapod limb functions to support the body at a distance from the ground. We may compare the typical land vertebrate to a bridge supported by two pairs of trusses. If the trusses are near to the center of the main axis of the bridge they will support it much more effectively than if they are arranged at either side. Similarly, tetrapods which have their limbs joined directly below the body axis do not need to employ great effort to stand up; their construction is essentially stable. On the other hand, those tetrapods whose legs are placed more laterally than ventrally must employ much effort and considerable musculature on the distal surface of the limbs just to lift their bellies off the ground. Most, but not all, of the latter are extinct at the present time.

(The reader is advised at this time to refresh his memory on anatomical terminology which has necessarily been employed in the following section. Any standard textbook of comparative anatomy may be consulted.)

As a generalization, the tetrapod limb is divided into three segments, the *stylopodium,* the *zeugopodium* and the *autopodium.* Their composition is as follows :

Segment	*Anterior limb*	*Posterior limb*
Stylopodium	Humerus (upper arm)	Femur (thigh)
Zeugopodium	Radius Ulna (forearm)	Tibia Fibula (shank)
Autopodium	Carpus (wrist)	tarsus (ankle)
	Metacarpus (hand)	metatarsus (foot)
	Phalanges (fingers)	Phalanges (toes)

Please note that this division is not based upon evolutionary presuppositions. It is purely functional. If these functional divisions are the basis for one's thought regarding the comparative anatomy of the limb, it is especially difficult to derive the limb of the tetrapod from the limb of the presumed fish ancestors of the tetrapods. Such divisions are never found in fish fins, ancient or modern, so far as is known. Thus, if one is committed to the thesis that land dwelling tetrapods are derived from a fishlike

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*Illustrations to accompany and clarify this discussion may be obtained upon request from the author at Shelton College, Cape May, New Jersey.

ancestry, one is faced with the problem of stating the *way* in which the transition from an aquatic to a terrestrial animal was accomplished. The ancient Rhipidistian crossopterygian, or lobe-finned fish, appeals to the evolutionists as the most likely ancestor for the terrestrial vertebrates.

These fish had a number of characteristics which might have suited them for the role. Some of them had nostrils communicating with the mouth cavity (which is not the case among sharks and teleosts), and some had ventral air bladders which might have been serviceable as lungs. Most important perhaps is the fact that with sufficient imagination one can present a reasonably plausible scheme for the derivation of the tetrapod limb from their fins. The structure of the fins of all other fish is so remote from that of the tetrapod limb no one has yet appeared with a sufficiently good imagination to make it look plausible.

There is a fundamental difference between the walking and the stabilization functions of the fins. Either the fin is held like a rudder and serves that purpose, or else (rarely) the fin is used as an oar or as a support. The pattern of tetrapod locomotion differs-from this, involving an overhand motion with flexion at the wrist and" elbow. In order to accomplish such a motion, the crossopterygian would-have to bend its fin in a most peculiar and unnatural fashion for a fish. However such a position would be necessitated, since an attempt to preserve the "rowing" motion on land would bring the delicate edge of the fin into contact with the ground, and would probably damage it or wear it away. The natural consequences of this are that the tip of the fin would have to be directed anteriorly, but in such a way that the "flat" of the fin was flat upon the ground. This situation would result in a double flexion of the limb corresponding to the joints of the wrist and elbow, with a corresponding change in the orientation of the bones. Specifically, the elements of the fin which were previously *anterior* (that is, preaxial) now tend to become medial, and those previously *posterior* (postaxial), now tend to become distal.

It is characteristic of the crossopterygian fin that the radial rods of the fin are prsent only on the anterior side. Hence, these preaxial radii would become medial.

By the above hypothesis, one ray would elongate to form the radius of the limb. Such an intermediate stage is purely hypothetical. No such fossil has ever in fact been found. Other elements are also supposed to elongate and/or change. A point to be emphasized and re-emphasized is that no form intermediate between a rhipidistian crossopterygian and a labyrinthodont, primitive amphibian has ever been found. The closest known example[1] is not very close*

There is another point to be made in this connection, and that involves fossilized amphibian trackways. Only a very few of these are known, and it might well be argued that tracks left by limbs of an intermediate form might well have remained undiscovered, as have the limbs themselves. However, even the tracks of fairly advanced labyrinthodonts could be expected to show certain characteristics if they were originally derived from fish. As a matter of fact, the labyrinthodont tracks which *have* been discovered cast considerable doubt upon the above evolutionary theory of tetrapod limb derivation.

In the earlier stages of limb development the leg musculature could not have been very well developed. It is reasonable to suppose that if the above hypothesis were correct, that the animal possessing a moderately well-developed limb would still be relying heavily on the segmental muscles of the trunk for its locomotion. In support of this contention it may be argued as follows: If the evolutionists are correct in their supposition that modern amphibians are derived from labyrinthodont ancestors such as the ones under discussion, then salamanders must be considerably closer to the ancestral form than, for example, the more highly modified frog. The salamander has for the most part well developed leg musculature, although the legs themselves are diminutive. Hence, the salamander is a *more* advanced tetrapod than any really early labyrinthodont is likely to have been, and it *still* relies on trunk-wriggling for the bulk of its locomotion. Therefore, it is reasonable to suppose that its ancestors relied on the trunk at least as much as does the salamander of today.

When one leg of such a wriggling animal is off the ground, the others form a most unstable tripod until the one off the ground has been advanced by a wriggling motion of the body. The other feet (especially the contralateral foot to the one that is off the ground) will tend to rotate, and on a slippery surface would tend to slip rotationally, forming a track in which soft earth or mud would be pushed up in a ridge at the *lateral* edge of the foot.

Now this, or something even more exaggerated, is the kind of track that the labyrinthodont amphibians could be expected to make if they are indeed derived from crossopterygian ancestors in the way which has been discussed. In actual trackways of such labyrinthodonts, however, there is no evidence whatever for rotational slippage. Slippage exists, but it is antero-posterior; that is, it is simply the result of trying to run across a slippery substrate and would appear today in our tracks under similar circumstances. The posterior position of the mud ridge indicates that these animals relied completely upon the musculature of their limbs for locomotion. In summary, there is no fossil

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*The hypothesis here advanced was first Presented by T. S. Weston[10] and is discussed in somewhat more detail in the appendix to this paper. The interested reader is referred to Weston's original paper, listed in the bibliography.

evidence for the existence of forms intermediate between crossopterygians and amphibians. Not only this, but what little pertinent fossil evidence exists is inconsistent with such intermediate forms. In view of these facts, the very existence, not to say credence of such an inherently improbable idea is puzzling.

There is certainly no unanimity regarding the evolutionary "motivation" behind this change. The investigator is confronted with a cloud-cuckoo land of fantasy when he begins his inquiry into this area of thought. The writer was impressed forcefully at that time by the fact that this kind of thinking requires great faith — that is, faith that the evolutionary process actually took place. The frame of mind seems to be: "Evolution took place. That is our postulate. Therefore, intermediate forms *must* have existed whether they are known or not and there must have been a reason to produce these intermediate forms." This is an example of blind faith raised to the second power of fantasy. That such forms existed is in the first place a fideistic statement. A discussion of the conditions which may have produced such speculative forms seems to be at the same level of significance as the more futile scholastic debates of the middle ages.

Limitations of space prohibit a full discussion of this controversy, so a brief summation must suffice. The controversy began, for the purposes of our discussion, with Romer, the noted paleontologist. He argued that at the time the transition from aquatic to terrestrial life was taking place, intermittent droughts made it necessary for crossopterygians to leave drying fresh water pools, stopping along the way perhaps to snack upon a cockroach or other insect. The availability of such food supply eventually gave the fish which spent the most time out of water an adaptive advantage, so that the best walkers among them would come to predominate in the population, and so on. Doubt was cast upon the Romer hypothesis by the seeming discovery that the era in question was not necessarily drought-ridden, but that the geological formations characteristic of it were more likely to have been laid down in a rain forest.

In the following summary I have presented the name of the author, his main arguments and my comments.

Author	*Thesis*	*Comment*
Orton,[7] 1954	Land locomotion does not require limbs. A drought is a hostile environment. You could not expect a fish to expose itself to dedication by overland journeying. Modern lungfish *burrow* in drought. The tetrapod limb was originally a burrowing device.	Modern lungfish burrow *without* legs. This theory would in any case account only for the front legs. The early amphibians and crossopterygians were also probably too large for effective burrowing.
Ewer,[2] 1955	Why should a structure be evolved for burrowing and then changed so as to be suitable for walking? What caused this *further* change? (Ockham's razor). Even amphibians at present, which burrow, migrate in response to *population pressure.*	By itself, this tells us nothing about what might have brought the limbs about in the first place.
Gunter,[4] 1956	In order for limbs to be effective at all in migration, they have to be strong *before* migration becomes necessary. He thinks the fin became a sort of leg to support the fish halfway out of the water in order to exploit the food value of the shallows and to escape large predators.	Crossopterygians were large, very carnivorous fish with little to fear from predators. They were obviously moderately deep-water fish, and the insects, etc. of the margin would not be enough to support them. Limbs would be a handicap in a generalized ecological niche in competition with fish.
Goin & [3] Goin, 1956	Population pressure was the stimulus for migration. Rainfall and humid conditions occasionally permitted it. Fish could begin to exploit the land environment *once the legs were developed.*	Why did the legs develop? They are simply not needed for migration under humid conditions! (cf. eels)
Inger,[5] 1957	Modern air breathing fish do not migrate to avoid drought or stagnation.	Again, how can a limb be of aid in migration unless it has already

	They breathe air so as to be able to *stay* in stagnant water. They migrate to find food and uncrowded habitats. A continuously humid climate would favor invasion of the land.	come into existence from some other cause?
Romer,[8] 1958	Limbs were developed prior to terrestrialism. Few insects were originally found on land, but some must have inhabited shallow water. Limbs enabled fish to exploit this environment as in Gunter's 1956 theory. In subsequent geological time, drought conditions forced migration with development of insectivorous habits. (Insects were by now abundant.)	See criticism of Gunter's 1956 theory. It is controversial that subsequent (Devonian) time was arid. Inger's 1957 argument still refutes Romer's major thesis.
Warburton[9] & Denman, 1961	If the crossopterygian *larvae* could exist in the shallows, predators could not get to them. When the pools began to dry up, the larvae might be isolated in mud puddles. In that case, limbs would enable them to walk back to the main body of the pool. These limbs would also enable adults to seek out mud puddles in the first place, which were initially isolated and free from the competition of other fish larvae.	What could the larvae eat in the puddles? Would not limbs initially *handicap* the adults while they were still competing with fish? Since returning larvae would have to be big enough to compete with adults, the puddle they just left would have to be sizeable indeed!

In summary, we may tabulate these theories as follows:

Larva		Warburton & Denman		
Adult	Romer	Goin & Goin Ewer Inger	Gunter Romer	Orton
Ecological motivation	Migration-drought	Migration—Population pressure	Exploitation of margin	Burrowing

Obviously there are a number of as yet unused combinations, combinations of combinations, or even new ideas. For instance, by combining the two concepts of exploitation of the margin, and larval adaptation we have a most attractive theory which states that the larva exploited the marginal food supply and also thereby avoided the larger predators. Legs would give it an advantage over the ordinary minnow, and the loss of these legs as an adult would remove the handicap of their presence. The larvae might take to spending more and more time on or near land, and eventually get to the point where they become capable of reproduction while retaining their larval form (Paedogenesis). Perhaps one might even propose a *burrowing* larva. It is an entertaining game, and any number, it seems, can play.

In the opinion of this writer, an attempt to press evolutionary thought to its logical conclusion is in reality a *reductio ad absurdum* and cannot result in anything other than paradoxes, riddles and enigmas. When we survey the wonderful and variegated patterns of living creation, we behold an almost unlimited display of great virtuosity expressed in a great number of variations on a limited number of basic themes. This view of the living universe is more consistent with the facts than the views of the evolutionist.

APPENDIX

The Weston Hypothesis

The basic argument of Weston is as follows: Inasmuch as Rhipidistia primitively possess only pre-axial radii (later, postaxial radii are thought to be geomorphic), and the pre-axial aspect of the fin is directed ventrally in them, an inward turning of the entire limb towards the body axis would cause several of these radii to roughly parallel the median elements. Weston feels that:

A. The most proximal radius became the radius of tetrapods.

B. In its consequent enlargement it interfered with, and suppressed in a manner of speaking, the second radial element.

To shorten an otherwise involved discussion, Westoll believes that he can homologize the structures of the labyrinthodont forelimb with the above considered rhipidistian structures as presented below in the following table:

Rhipidistian fin

1. Median elements
2. "Postaxial processes" of median elements
3. Radial elements
4. No equivalent

Labyrinthodont limb

1. Ulna, intermedium, distal and proximal axial centralia
2. Ulecranon, postocentralia
3. Radius, Precentrale, radiale
4. Supposedly geomorphic phalangeal structures (formed as heterotopic bones in the fin membrane?)

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