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Article XXVII.— ON THE ORIGIN OF THE CHEIROPTERYGIUM.

By R. Broom, D. Sc.

Numerous attempts have been made from time to time to trace the origin of the Tetrapod limb from the fin of one or other of the fishes. There can be little doubt that the toed limb has been so derived, but opinions have differed greatly as to what type of fin has been the origin of the limb and also as to how the change might have come about. In recent times only four theories may be said to hold the field; (1) that advocated by Wiedersheim and others that the digits represent some of the posterior rays of the Elasmobranch fin; (2) that held by Klaatsch and others that the tetrapod limb is derived from a fin of the type seen in the pectoral fin of *Polypterus;* (3) the view held by Braus and others that the cheiropterygium is derived by reduction from the type of fin preserved in *Ceratodus;* and (4) the view held by Watson and one or two others that the tetrapod limb has been evolved from a reduced archipterygium such as occurs in the Osteolepidotous Crossopterygians such as *Eusthenopteron.*

Apart from the fact that the Amphibia have not sprung directly from Elasmobranch ancestors the theory as presented by Wiedersheim must be rejected as it entails the homology of the posterior or metapterygial border of the shark's fin with the anterior or radial border of the tetrapod limb.

The theory worked out by Klaatsch with so much ingenuity seems to me impossible from its converting the posterior border of the fin into the radial border of the limb and the dorsal surface of the fin into the palmar of the hand. We have no evidence from comparative anatomy or embryology of such changes having ever taken place.

The other two theories are really modifications of one and the same. They involve no changing of borders or surfaces, and show us elements which when no longer required to support the fin rays might have developed into digits.

The test that must be applied to all theories of this sort is — how did the intermediate stage work?

Let us consider the view as presented by Watson in the Anatom. Anz. a few weeks ago. He derives the tetrapod limb from a reduced archipterygium such as found in *Eusthenopteron.* The extremely interesting type of fin found in this remarkable fish has been studied by Whiteaves, Smith Woodward, Goodrich, Patten, Hussakof and Watson, and as there are some few differences in interpretation a further figure may be excused. My restoration is founded on the two excellent specimens in the British Museum. All that is represented in line is I think undoubted. In all essentials my figure agrees with that of Goodrich. There is I think no doubt that the processes on the postaxial side of the limb are not distinct elements. The endoskeleton supports all round, except at the base, a large fin.

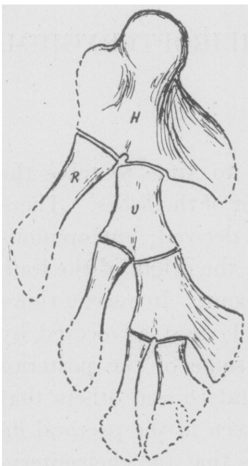


Fig. 1. Pectoral limb of *Eusthenopteron.* H, Humerus; R, Radius; U, Ulna.

If such a fin became converted into the tetrapod limb, were the fin rays completely lost before the digits developed? Evolution moves very slowly. Must we assume that through thousands of generations the fin rays became steadily reduced till the fin was practically useless for swimming, and that though the fin rays became aborted the endoskeleton still remained powerful, and after many more thousands of years, developed into a useful limb? It seems impossible to believe that fishes evolved through countless generations with appendages which were practically useless either as fins or as limbs.

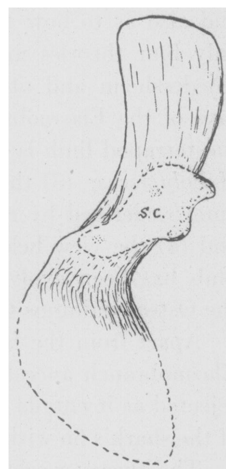
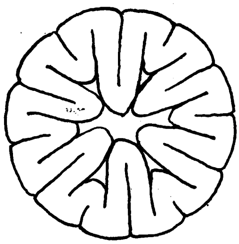


Fig. 2. The scapulo-coracoid and cleithrum of *Sauripteris taylori.* ½ nat. size. The specimen is viewed from the inside. The extent of the scapulo-coracoid is doubtful. The two small dotted areas are believed to be portions of the element and give some indication of its shape and size.

If however a modification of the theory be accepted all difficulty disappears in imagining the intermediate stages. Instead of having a stage when there was neither a good fin nor a good limb, I believe in the intermediate period the appendage was both a good fin and a good limb.

From theoretical reasons alone I have long held, and taught to my students that whether the tetrapod limb be derived from an ichthyopterygium like that of the shark, or an archipterygium like that of *Ceratodus,* or a reduced archipterygium like that of *Eusthenopteron* it could only have evolved by the development of the skeletal elements on the preaxial side of the fin, and that there was no reason why the main axis might not have continued to support a functional fin while a cheiropterygium was developing on the front.

Being keenly interested in the question one of the first objects I made enquiry for on my visit to the American Museum was any specimen likely to throw light on the problem, and Dr. Hussakof at once called my attention to the specimen of *Sauripteris taylori* first described and figured by J. Hall in 1843. Hall's description occupies only a few lines, and his figure for morphological purposes is quite worthless. The specimen has been reexamined by Newberry and Smith Woodward, but by neither of these authors has it been refigured or redescribed, Newberry in fact saying it is "too imperfect for satisfactory study." Hussakof published a photograph of the fin and of the vertebrae in his Catalogue of American Fossil Fishes and Dr. W. K. Gregory has used the type to illustrate his lectures at Columbia University on the development of limbs. In Smith's paper on the Development of *Cryptobranchus* a figure of the specimen by Hussakof is used for comparison but no description is given, nor has any discussion been published so far as I am aware on the evidence afforded by the specimen as to the mode of origin of the Cheiropterygium.



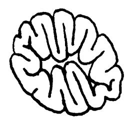


Fig. 3. Section of large mandibular tooth of *Sauripteris taylori*. × 6. The upper half is from the specimen, the lower half is restored.

Fig. 4. Section of one of the small maxillary teeth of *Sauripteris taylori*. × 6.

Sauripteris is only known by fragments of the head, a series of crushed vertebræ, a large number of scales and the beautifully preserved right pectoral fin with most of the cleithrum and part of the supraclavicle. The large comparatively thin scales resemble those of *Rhizodopsis* and the cleithrum closely resembles that of *Rhizodus*. The vertebral centra are formed by rings of bone. Owing to the crushed condition of the vertebræ it is impossible to be quite sure whether the ring is entire or made up of four parts. There is certainly a well ossified neural arch and above this in some of the vertebræ at least a well developed flattened neural spine.

The teeth have the enamel deeply folded at the bases as seen in the figures given.

The scapulo-coracoid is probably fairly large. Only the glenoid part is well preserved but two fragments still adhering to the inner side of the cleithrum give some indication of the size.

The humerus has a rounded head which fits into the glenoid cavity. Its preaxial border is greatly developed into a scoop-like plate which curves towards the palmar surface. The dorsal side of this scoop-like development is protected by a series of greatly thickened bony scales. The distal end of the humerus gives articulation to two bones which may safely be determined to be the radius and ulna.

Fig. 5. Pectoral limb of *Sauripteris taylori* Hall. $\frac{3}{7}$ nat. size. SC, Fragment of Scapulo-coracoid; H, Humerus; R, Radius; U, Ulna.

The radius is the largest bone of the limb. It has a short articulation with the humerus and its whole preaxial side is developed like that of the humerus into a curved scoop-like organ. Distally it gives articulation to two bones the relations of which will best be understood by the figure. The anterior of the two bones is much the shorter and itself gives articulation to a triangular flat element. The posterior of the pair of bones supported by the radius is long and slender and apparently had a pair of distal elements, but these probably remained cartilaginous.

The ulna is a short broad bone. Distally it gives articulation to two bones which are not improbably the homologues of the ulnare and pisiform. The supposed ulnare gives articulation to two distal elements and the supposed pisiform to three. The figure gives as much as can be made out of the different elements in the specimen. The parts in line are seen in the specimen; the parts dotted are probable restorations. The only fin rays preserved in the specimen are a considerable series closely attached to the elements distal to the supposed pisiform, and one ray opposite the posterior of the two elements distal to the supposed ulnare. There are certainly no fin rays on the preaxial side of the fin at least as far as the distal end of the radius nor probably on any part. Most probably the fin rays were confined to the distal end of the fin and the greater part of the posterior border. The anterior border of the fin was probably covered with scaleless skin in front and was used for digging in the sand.

Though the fin is too specialised to have been the ancestor of the tetrapod limb it is probably nearly identical with the ancestral type as regards

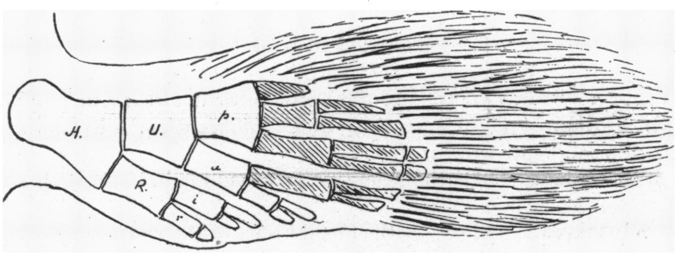


Fig. 6. A fin representing the supposed pre-Sauripteris stage. The elements are as in *Sauripteris* without the specialisation. The elements shaded are those that will be lost when the appendage ceases to be a fin. H, Humerus; R, Radius; U, Ulna; i, Intermedium; p, Pisiform; r, Radiale; u, Ulnare.

the elements, and is particularly interesting as showing a fin that was partly used as a limb.

In Fig. 6 I have represented what was probably the pre-Sauripteris condition. The elements in number and arrangement are exactly as in *Sauripteris* except that the peculiar specialisation of the humerus and radius are not developed. It was probably from such a fin that the Tetrapod limb developed. As the front part gradually developed the hind or fin part would gradually become lost, and the elements shaded would disappear. Of the postaxial elements beyond the ulna only the pisiform is retained on account of its importance as a muscular attachment.

It is unnecessary to speculate further as to how the various carpal, metacarpal, and phalangeal elements were evolved. But the figure shows how it is that five digits were formed. Had six or seven been retained for a time, they would have been found too feeble to usefully reach the preaxial border. Even as it is the aquatic Amphibia found the fifth useless and it was lost. The progressive increase in the number of phalanges was determined by the distal elements proliferating till the toes came into line.

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