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Article X.—THE CARPUS OF *ERYOPS* AND THE STRUCTURE OF THE PRIMITIVE CHIROPTERYGIUM

By W. K. Gregory, R. W. Miner and G. K. Noble

The recent papers by Steiner (1921, 1922) and by Huene (1922) have raised again the old question of the structure of the primitive chiropterygium. Since this problem was discussed by the senior writer (Gregory, 1915) some evidence has been brought forward to modify or to supplement the conclusions reached at that time. This evidence has been considered by the present writers while undertaking independent lines of investigation. As it was found that our conclusions agreed, it seemed advisable to publish these conclusions in advance of our other work, which only indirectly considers the structure of the primitive chiropterygium.

The problem is immediately concerned with the phylogenetic significance of the prepollex, prehallux, and postminimus. It is not our intention to discuss the numerous arguments which have been brought forth to support various theories in regard to these elements. Some of these theories are most curious, as for example, the one recently offered by Gillies and Hopkins (1922). The following remarks may be taken as a reply to Gillies and Hopkins, and as a supplement to the views expressed by Steiner and by Huene.

Without attempting a historical sketch, it may be briefly stated that it is now fairly well established that the Tetrapoda arose from crossopterygian ancestors and very probably from some generalized rhipidistian. Investigators such as Wintrebert (1922) who have disputed this conclusion have, for the most part, limited their studies to only a few sets of structures and have not considered all of the numerous characters upon which this conclusion is based.

The two best preserved pectoral limbs found among the Rhipidistia are those of *Sauripterus* and *Eusthenopteron*. A complete description of these limbs has been given by Gregory (1915) and by Bryant (1919). In both genera a single proximal element or humerus articulates with a small coraco-scapula attached to a large cleithrum. Distally, two elements, a radius and an ulna, articulate with the humerus. In *Sauripterus* two radials attach to the radius and two to the ulna, while the latter two form the basis for additional radials. In *Eusthenopteron* the radius does not bear radials and the ulnar series of radials is reduced. It should be noted, however, that the radius is perfectly distinct from the ulna and its series of radials.

The homology of the humerus, radius, and ulna of these crossopterygians with elements of the same name in the Tetrapoda is obvious. The development and musculature of the pectoral appendage of *Polypterus* confirms this homology. Much confusion has arisen by the use of the terms preaxial and postaxial in former discussions. The various adaptations of the ichthyopterygium to locomotion have little bearing on the question of homology. The radius of crossopterygian and tetrapod has a preaxial origin, although in later development it may assume a more postaxial position (e.g., in frogs).

The great difficulty has been to homologize the tetrapod carpus with elements in the crossopterygian limb. It will be recognized at once that the homology cannot be a very exact one. Numerous fusions, losses, or even additions, may have taken place within the carpus. Although the modern tendency in palæontology is to consider that most skull elements do not fuse, but become reduced and finally disappear, we know from the development in modern Amphibia that numerous fusions have taken place within the carpus and tarsus. It therefore would not require a great stretch of our imagination to suppose that the number of radials in the pectoral appendages of *Sauripterus* was reduced by fusion, to a condition such as that found in primitive tetrapods (Fig. 3).

In making the comparisons, it would be well to examine first the structure of the more primitive chiropterygium. The oldest known carpus is that of *Eryops megacephalus*, already described many times (see Gregory, 1915, p. 368). In the best preserved specimen of this carpus (Amer. Mus. No. 4186) there is a gap distal to what has been called "carpal 2." It has been assumed that there was originally a digit, which has been lost in preservation, opposite this carpal. The restored manus would thus have five digits, as figured (Gregory, 1915). It was recognized that no other amphibian, fossil or recent, was known to have five digits in the manus, but the structure of the specimen seemed to indicate that there were originally five in *Eryops*. *A priori*, one would assume that the primitive Amphibia must have had five digits, since there is much evidence to believe that reptiles sprang from the Labyrinthodontia.

Recently, Huene (1922, Fig. 44) has produced a sketch of this same carpus which he states he made over ten years ago from the original. Huene, influenced by the recent work of Steiner, has attempted to make a reconstruction of this carpus, on the assumption that some of the elements in the specimen were pushed out of place before preservation. The reconstruction which Huene has produced did not impress the present

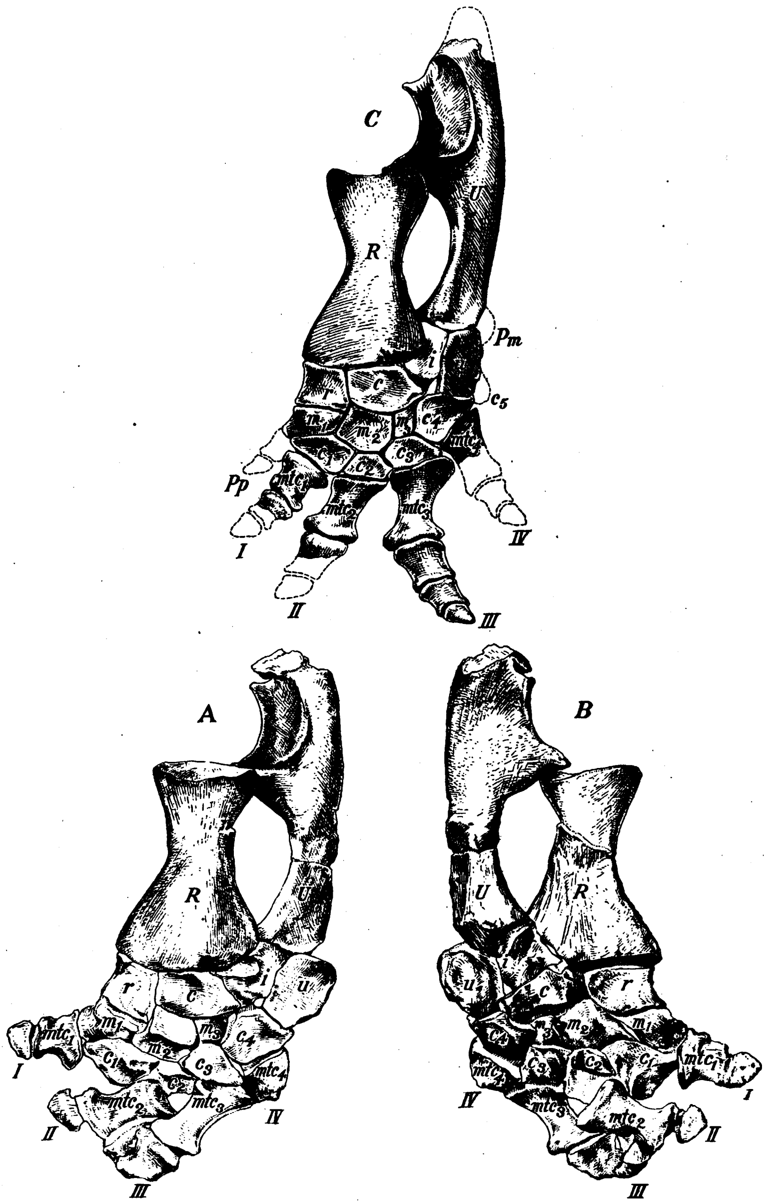


Fig. 1. *A*, Lower arm, carpus and manus of *Eryops megacephalus*, extensor side (drawn from original specimen, Amer. Mus. No. 4186, one-third natural size).

B, Same, flexor side.

C, Restoration of lower arm, carpus and manus of *Eryops*, based on above specimen (drawn in perspective, one-third natural size).

writers as a very "workable" one. Careful examination of the original carpus has convinced us that Huene is mistaken as to displacement of some of the elements. It has also convinced us that the old reconstruction adopted in the literature is incorrect in several particulars. A correct understanding of these details is necessary before proceeding further with our problem.

It is apparent from the figure of the specimen under discussion (Fig. 1, *A* and *B*) that the carpus as a whole must have withstood a force which dislocated most of the elements slightly toward the radial side. An examination of the articular surfaces of the various carpal elements shows that this dislocation was not great. The large element indicated by Huene as "Ce+5" could not have been originally in the position which Huene indicates in his reconstruction. Its articular surfaces, together with a slight notch on its preaxial side, shows that this element is an ulnare resting in approximately its original position (Fig. 1 *A*, *B*,), and not overlapping the intermedium as stated by him (Huene, 1922, p. 455).

Huene, nevertheless, is correct in assuming that the first digit has been displaced. Its articular surface fits exactly on "carpal 2" (c_1 in Fig. 1). Shifting digit I to this position reduces the number of digits by one, and gives *Eryops* only four digits in the manus, similar to all other known Amphibia.

Further examination discloses that the carpus before us has not only undergone a slight preaxial dislocation, but has also been decidedly flattened before fossilization. The articular surfaces of the various carpal elements clearly indicate that the carpus was originally arched—convex above. In the flattening process the articular surfaces of the carpal elements were sprung, and the ulna pushed the intermedium out of place. The intermedium bears a distinct notch (poorly indicated by Huene) which must have received the postaxial, distal corner of the radius on its flexor side.

When the carpal elements are pushed back into position in such a way that their articular surfaces make contact, a compact carpus results, one very similar to the carpus of primitive urodeles. It differs from the urodele carpus in having more elements and in forming a shallow arch.

Restoring the first digit of the manus of *Eryops* before us to its original place exposes a small but undoubted articular surface on the end of the most distal carpal of the first preaxial series. This is too small to have carried the displaced digit found in partial contact with it, and must have originally carried a distal element much smaller than any digit. Comparison of the carpus with that of several of the more generalized salamanders (hynobiids), or even with the carpus of some advanced types (*Ambystoma opacum*, Fig. 2 *A*), has led us to believe that this element must have been a prepollex.

There can be no doubt that the prepollex is a primitive structure. Its presence in the most generalized urodeles and its almost universal occurrence in the Salientia confirms this opinion.

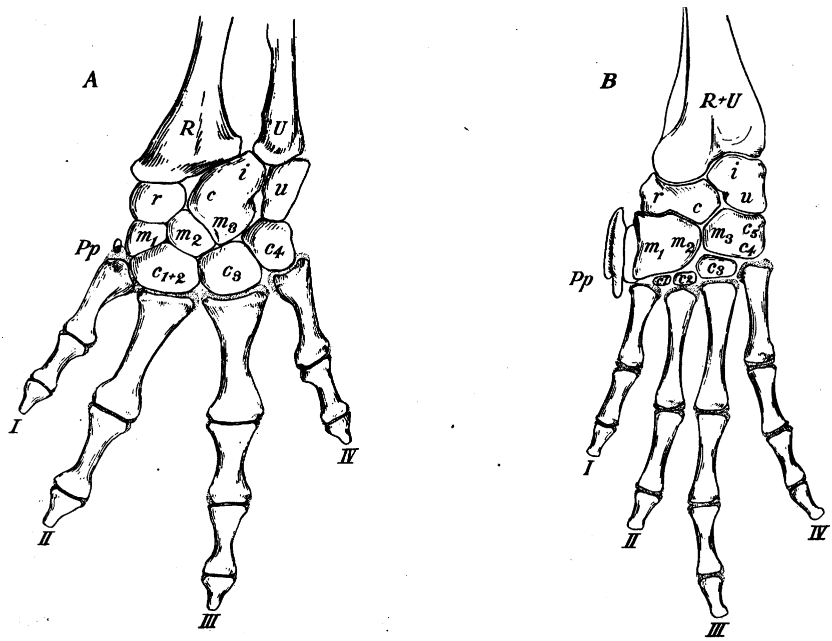


Fig. 2. Carpus of modern Amphibia.
A, *Ambystoma opacum* (Gravenhorst).
B, *Ascaphus truei* Stejneger.

The carpus of *Eryops*, then, consisted of a radial series (Fig. 3), ending in a prepollex, and an ulnar series carrying the four digits. This distinction between the radial and ulnar series, although emphasized long ago (Emery, 1894, 1898), has been often confused since, and we are largely indebted to Steiner (1921, 1922) for the clear way in which he has reviewed the whole subject, and pointed out this distinction.

Steiner, however, has not given a complete account and, both for reasons of priority and for simplicity, we have adopted names other than those employed by him for the medium transverse series of carpal elements. Schmalhausen (1917) has compared this median series with

Evolution of the Carpus

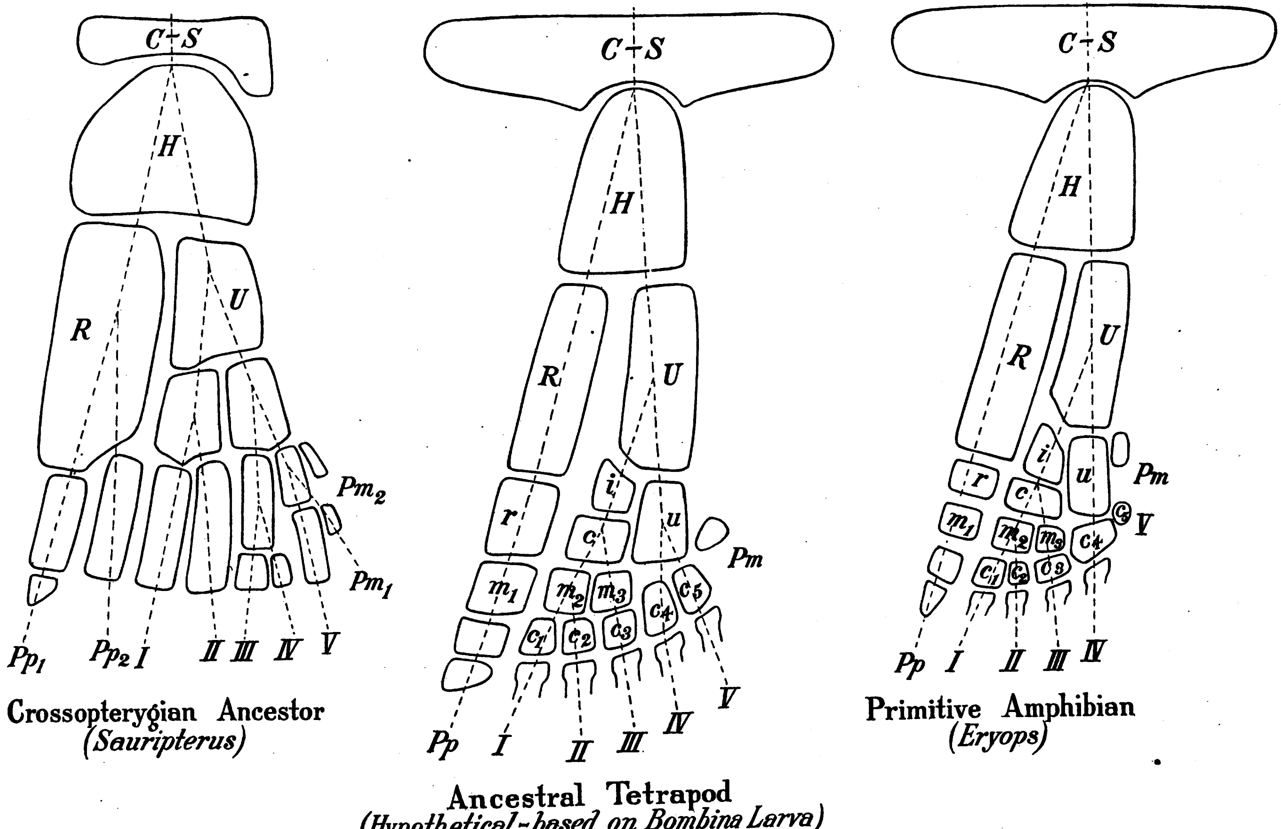


Fig. 3.

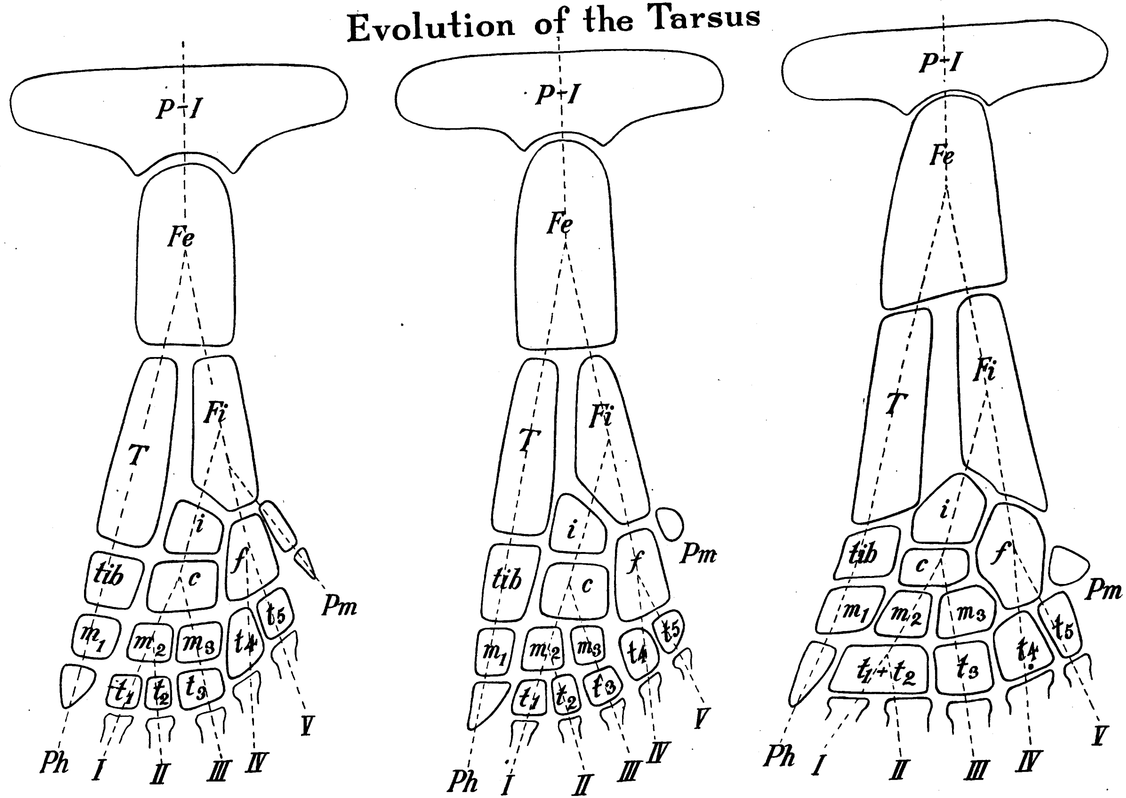
the median elements in the tarsus of *Ranodon sibericus,* and his term, "mediale," for the elements of this series, seems appropriate. The term mediale is merely indicative of position. As shown in Fig. 3, m_1 belongs to the radial series, m_2 and m_3 to the ulnar group.

It will be noted that our reconstruction of the manus of *Eryops* (Fig. 1C) is practically identical with the primordial chiropterygium postulated by Steiner (1922, Fig. 13), except for the absence of the fifth digit and its carpal. This primitive chiropterygium possessed a prepollex at the termination of a radial series, and five digits terminating the ulnar series. There was also some indication of a postminimus or sixth digit. The primitive tetrapod carpus exhibited three medialia and one centrale in addition to the proximal r, i and u, and the distal c_1–c_5. The carpus of all Amphibia, fossil or recent, has become specialized in the loss of the fifth digit (or its reduction to a small cartilage) and in the loss of the postminimus or the sixth digit.

What evidence is there that the Amphibia ever possessed a fifth finger? The evidence is chiefly embryological and as that has been fully discussed by Steiner (1921, 1922), it need not be repeated here. In the embryos of both urodeles and frogs the fifth finger is clearly marked out in blastoderm but never differentiates. The primitive reptiles need not have developed their pentadactyl fore limb from a typical amphibian limb by addition—say by mutation—of a fifth finger, but both reptiles and amphibians probably evolved from pentadactyl ancestors. These ancestors were, of course, Amphibia and probably Embolomeri. Very early in their phylogeny the Amphibia lost the outer finger and its carpal. The foot (Fig. 4), however, being more conservative, retained its original form in some of the Rhachitomi (*Trematops*) and underwent only very few fusions in the more primitive urodeles (Schmalhausen, 1917; Steiner, 1921). The carpus of recent Amphibia has specialized by additional fusions. In the Salientia, because of the narrow and twisted wrist, this specialization is extreme. The embryo and even the adult carpus of such a primitive form as *Ascaphus* (Fig. 2 *B*) suggests where these fusions have occurred.

It should also be pointed out that Haughton has recently found in *Rhinesuchus,* a close relative of *Eryops,* that there were only four digits in the manus. Unfortunately, the carpus of Haughton's specimen was not well preserved and our knowledge of the carpus of these primitive Rhachitomi rests chiefly upon the evidence furnished by the well-preserved manus of *Eryops* described above.

Evolution of the Tarsus



Ancestral Tetrapod
(Hypothetical-based on Ambystoma Larva)

Primitive Amphibian
(Trematops)

Recent Urodele
(Primitive Hynobiid-Ambystomid type)

Fig. 4.

The modifications of the carpus and tarsus throughout the vertebrate series have recently been reviewed by Steiner (1921, 1922) and need not be entered into here. It may be mentioned that the distinction between radial carpus and ulnar carpus is an important one; and, while the prepollex is sometimes lost, the distinction is still clear. This is especially noticeable in the musculature of this region. The definitive musculature of the digits converges to the ulna, while the radial musculature is primarily associated with the radial series of carpal elements. As these features will be discussed in a later paper by one of us, they need not be further mentioned here.

It may be pointed out, however, that some of the details of Steiner's work cannot be accepted. Thus, the phalangeal formula of 2–2–3–4–2 is not characteristic of the tarsus of *Ambystoma*, but of only a small group of species of that genus. The Hynobiidæ are certainly more primitive than the Ambystomidæ and may be ancestral to them. Further, all hynobiids and many ambystomids, possessing five toes, have a phalangeal formula of 2–2–3–3–2. Thus, it would seem that the extra phalanx in the fourth toe of the *tigrinum* group of ambystomas may be either a progressive (as in the first finger of some gekkos), or possibly an atavistic mutation (since most branchiosaurs possess a phalangeal formula of 2–2–3–4–3).

The phalangeal formula in the manus of *Eryops* could not have been as high as that usually given in the literature. A careful examination of the original specimen shows that there is no evidence of there being more than 2–2–3–2 phalanges. It is this number which we have indicated in our reconstruction (Fig. 1 *C*). It will be noted that this formula is the same as that found in primitive salamanders. Frogs and some branchiosaurs have one more phalanx in the fourth digit.

Summary

(1) *Eryops* had only four digits in the manus.

(2) *Eryops* possessed a well-developed prepollex.

(3) The carpus (as well as the tarsus) consists of two moieties; the radius (tibia) moiety, embracing the prepollex (prehallux) and carpal elements, forming the first preaxial ray, and the ulna (fibula) moiety, including the digits and their carpals, converging toward the ulna (fibula). The distinctness of these two moieties is further demonstrated by the subdivisions of the carpal (or tarsal) musculature.

(4) The pectoral appendage of *Eryops* is readily comparable with the pectoral fin of the rhipidistian crossopterygians. The distinctness of the two primary series of carpal elements even in these forms is obvious.

(5) All known Amphibia, recent and fossil, possess only four digits in the manus, but embryological and indirect palæontological evidence allows us to infer that the most primitive Amphibia had a prepollex, five digits, and a postminimus in the hand; a prehallux, five digits, and a postminimus in the foot.

(6) The primitive chiropterygium was therefore at least seven-rayed in both the manus and pes, but with a tendency toward a reduction in the two marginal rays, which has proceeded furthest in the last postaxial ray.

(7) The carpus of *Eryops* and the primitive chiropterygium possessed three medialia and one centrale, as well as the radiale, intermedium, ulnare and carpalia.

(8) The phalangeal formula of *Eryops* was only 2–2–3–2 in the manus.

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