BIOLOGY 524
ADVANCED VERTEBRTE MORPHOLOGY
-OSTEOLOGY-

POSTCRANIAL SKELETON – IV
ANTEBRACHIUM AND MANUS

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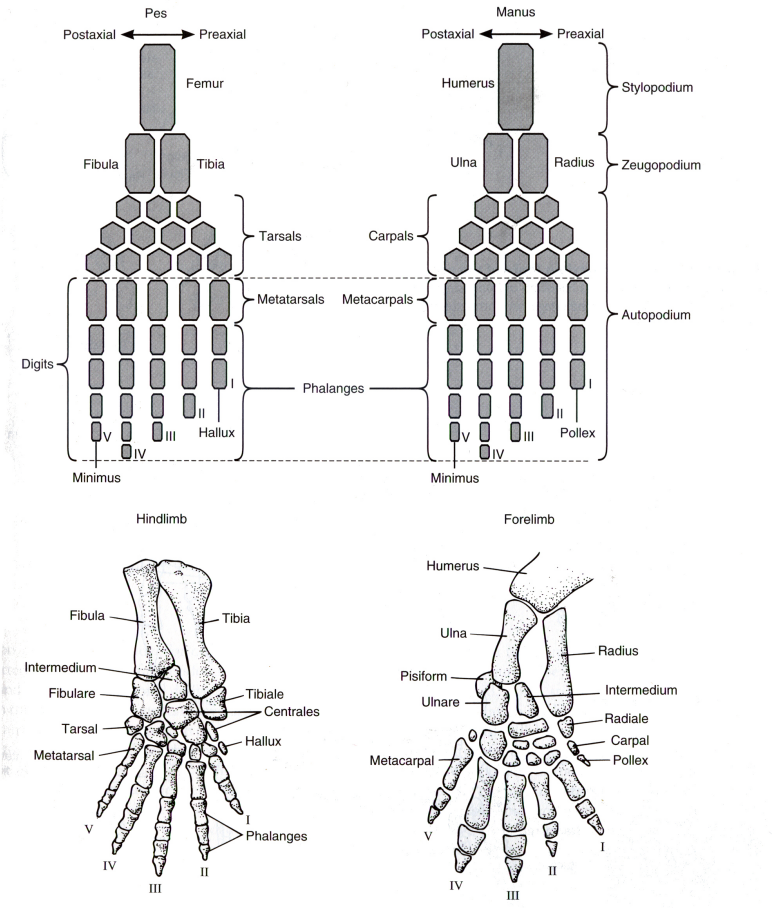
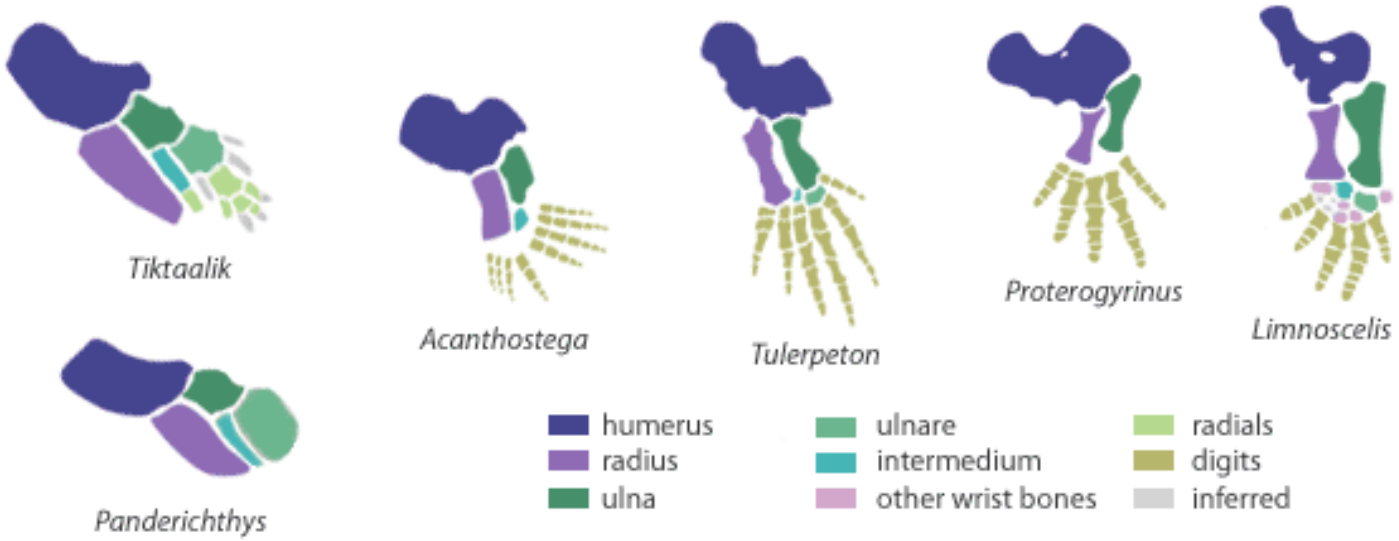
INTRODUCTION

The basic organization of limbs, both forelimb and hindlimb are like that of a pyramid, with a single element proximally (humerus/femur); two more distal elements (radius & ulna / tibia & fibula); then four, the five rows of more distal carpals; then digits composed of multiple phalanges.

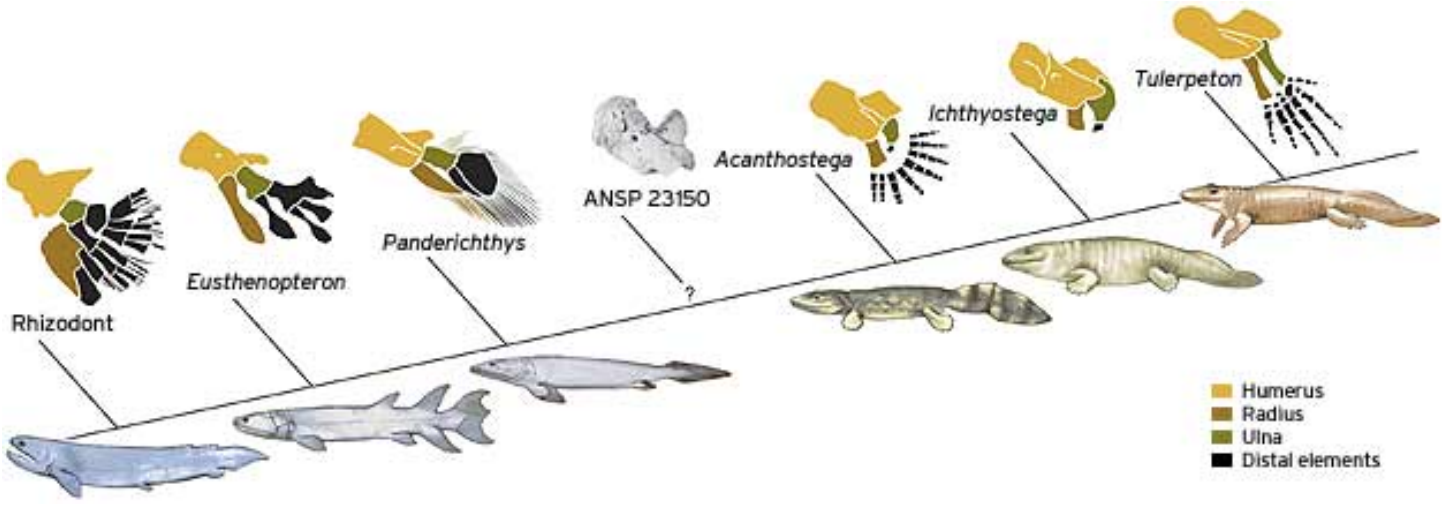


The earliest and most primitive known examples of the tetrapod limb are now known to be pentadactylous; i.e. having more than five digits. It was long thought that five digits was the primitive tetrapod condition, but it is now known that *Acanthostega* had at least eight digits on its manus (hand). *Tulerepeton* had six. It was not until later in tetrapod evolution did the number of digits settled on five.



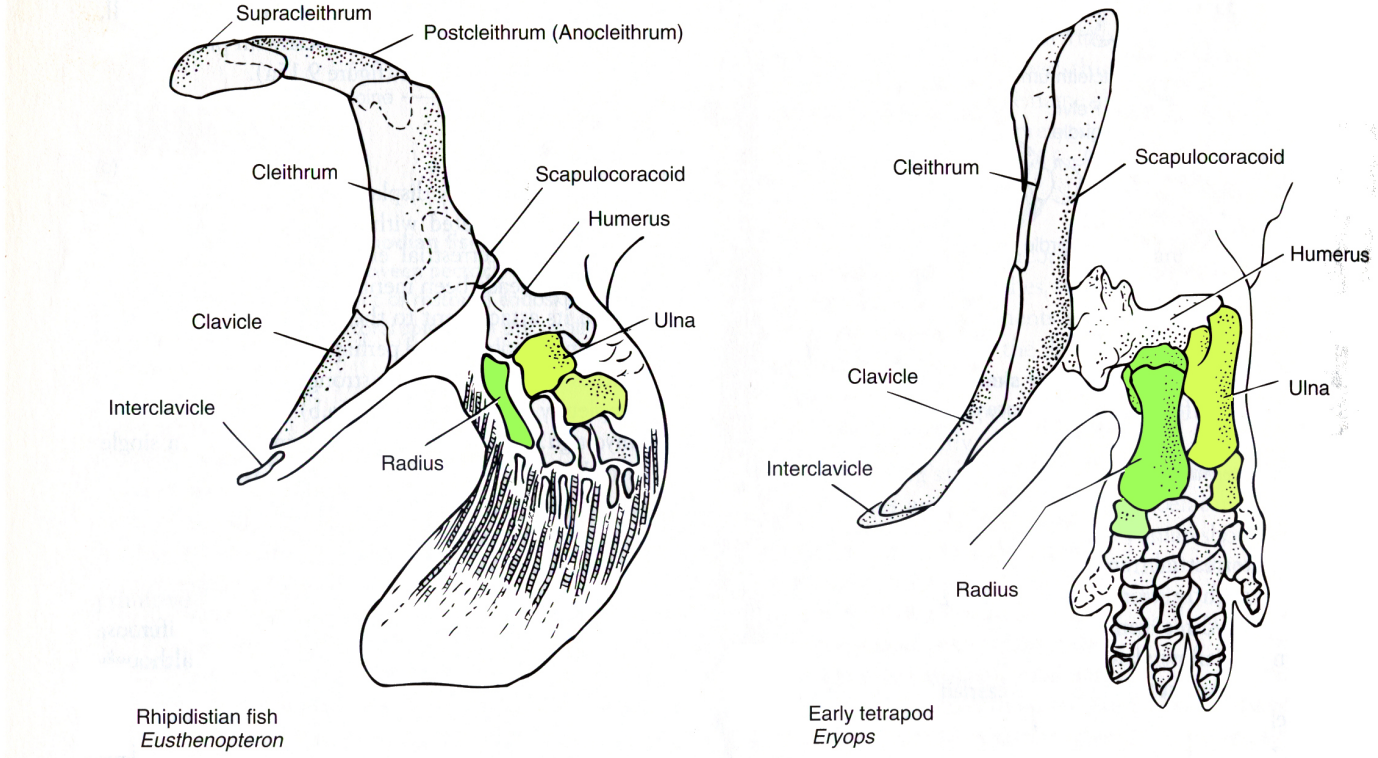
The basic tetrapod antebrachium, or forearm, is composed of two elements, distal to the humerus, the RADIUS on the side of the first digit (thumb), and the ULNA on the side of the fifth digit.

Distal to the ulna is an element known as the ULNARE; between that and the radius is an element known as the INTERMEDIUM.



In the transition to tetrapods, the MANUS (hand) consolidates into a more discrete series of structures:

- The intermedium and ulnare are inherited from crossopterygian fishes.
- The RADIALE is a new element, becoming the third element at the base of the manus.
- Up to four CENTRALIA (singular CENTRALE), numbered 1-4 make up the next row of the manus.
- Five DISTAL CARPALS, numbered 1-5 make up the next row.
- Each digit has a METACARPAL at its base.
- The digits have a variable number of PHALANGEAL ELEMENTS. The PHALANGEAL FORMULA is the number of phalangeal elements in digits 1-5.

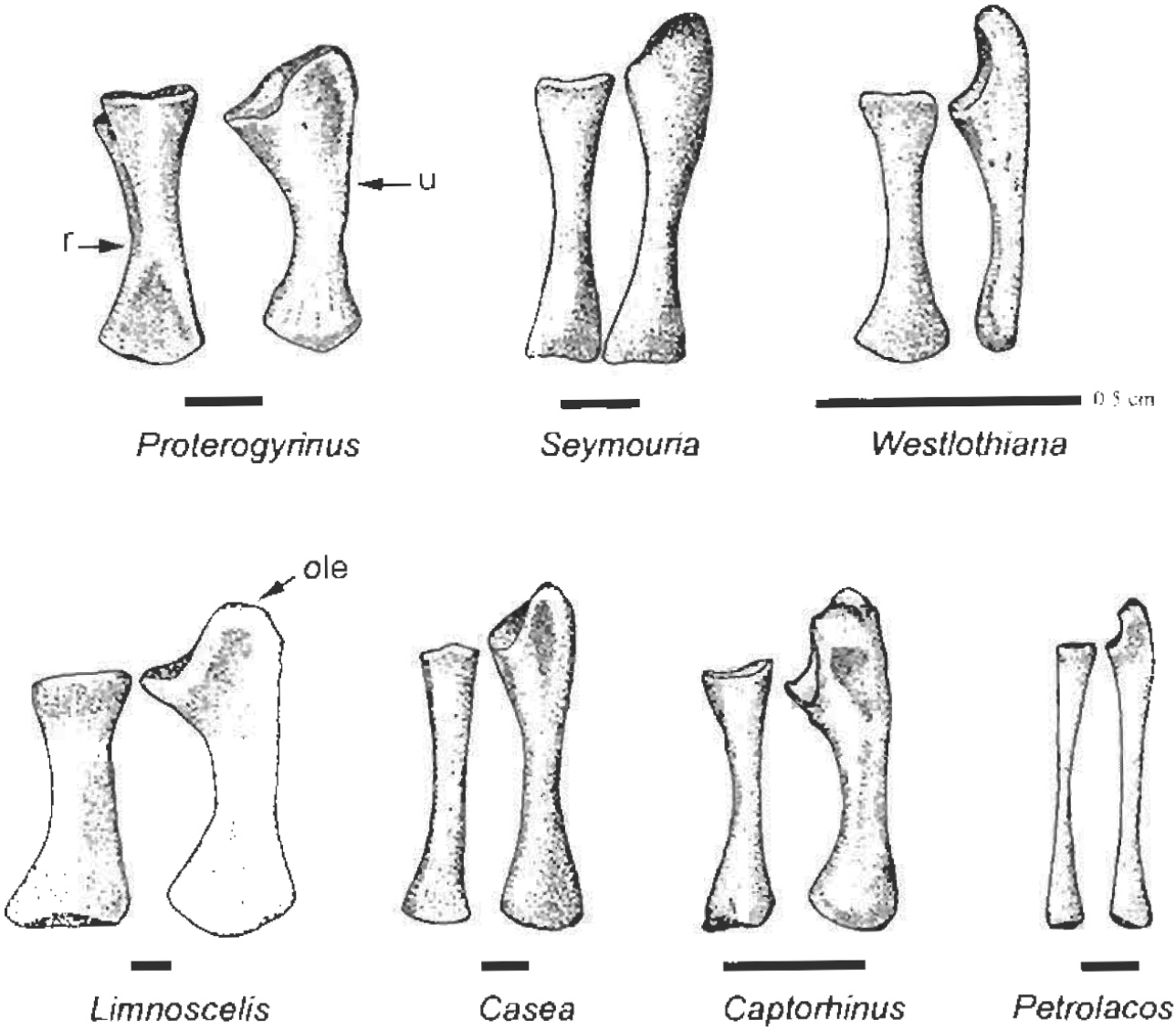


ANTEBRACHIUM

The ulna is easily recognizable due to the conspicuous presence of the OLECRANON PROCESS for insertion of the extensors of the antebrachium, the triceps musculature.

In tetrapods with a sprawling posture, both the radius and ulna are quite robust, as the weight of the entire fore-trunk is suspended between them on either forelimb.

In the survey of tetrapod antebrachii following, note that the olecranon process is recognizable throughout.

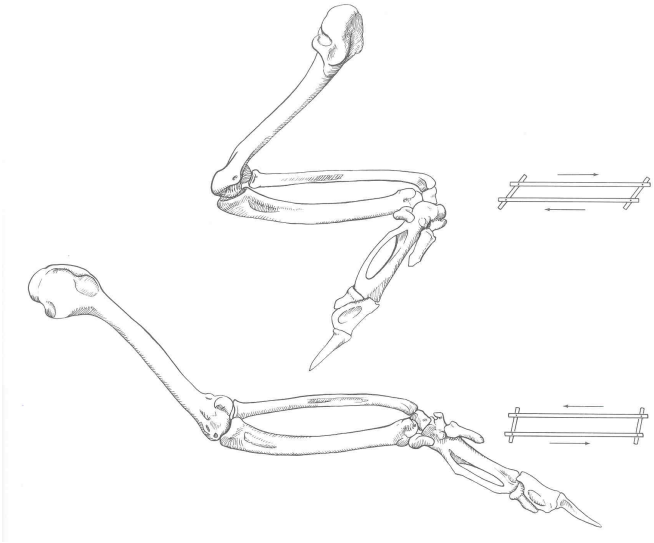


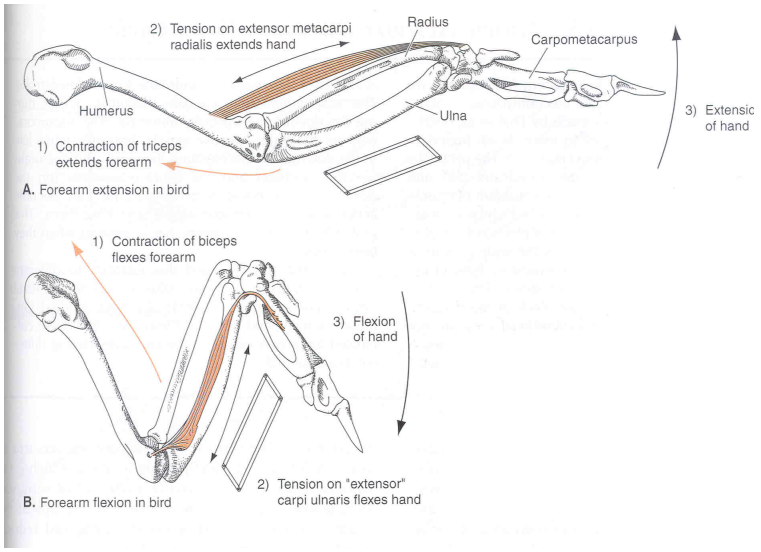
DINOSAURIA AND AVES:

In some derived theropod dinosaurs, the radius and ulna (and manus) can become comically reduced in size. However, they remain well-developed in those maniraptoran theropods that gave rise to birds.

In birds, the radius and ulna remain well developed, and the ulna is element along which secondary flight feathers attach directly to the bone. Notably, the radius and ulna of birds form the long sides of a parallelogram, the shorter sides being the wrist and base of the humerus. This essentially constrains flexion at the wrist and elbow such that the hand elements and humerus will always remain parallel.

The hand has been reduced to digits 1-3.

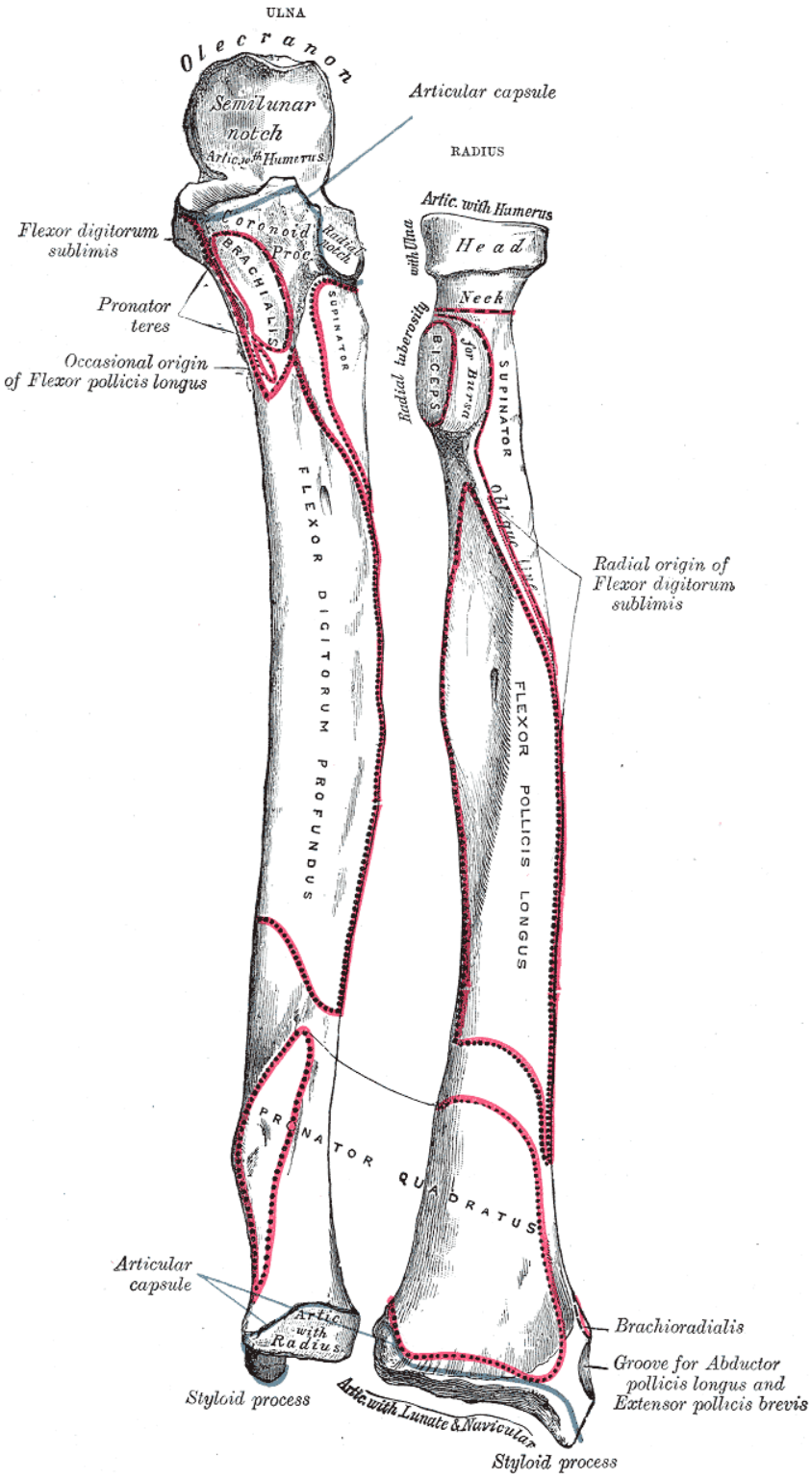




Note the attachment of the flight feathers to the ulna in the radiograph of a peregrine falcon below.

MAMMALIA

In the illustration following, a human demonstrates the major features of the mammalian ulna and radius.



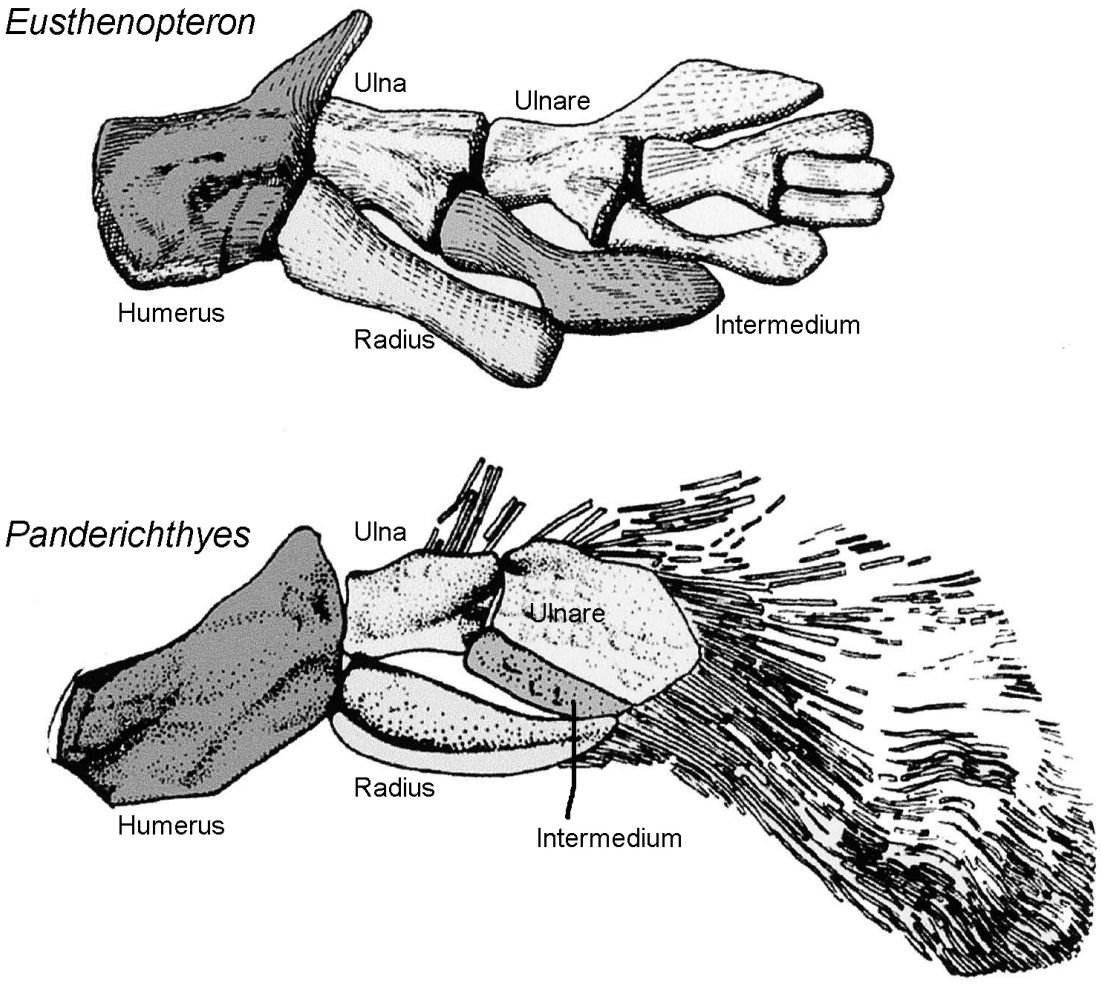
MANUS

The tetrapod MANUS is composed of the palm of the hand, or CARPUS which is a flexible mosaic of carpal bones and five metacarpals; and the DIGITS, each with varying numbers of phalangeal elements. Differing groups of tetrapods are often characterized by the number of phalangeal elements each as a PHALANGEAL FORMULA (for instance, that of humans is 2,3,3,3,3).

Manus: Fishes to Tetrapods

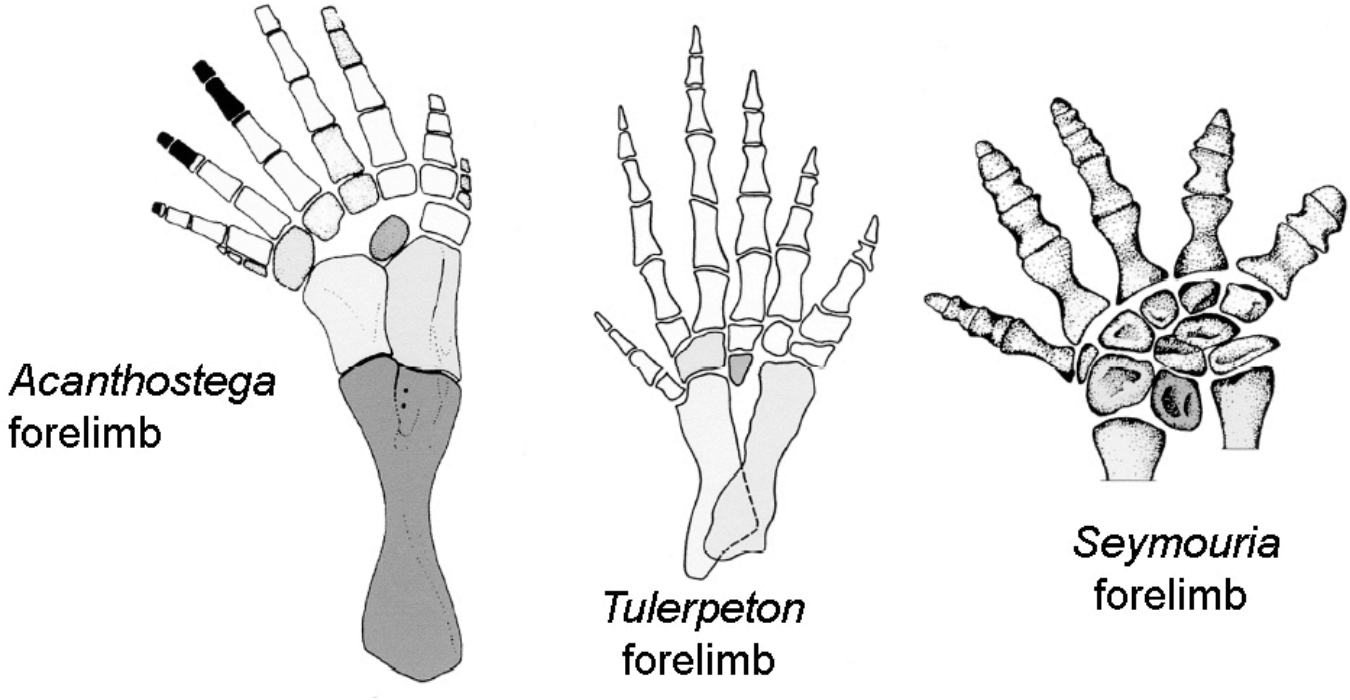
Amongst crossopterygian fishes, none has a true hand. However, the very advanced crossopterygian fish *Tiktaalik* appears to have developed a genuine WRIST JOINT, which would indicate that more distal elements acted functionally as a manus.

Crossopterygian fishes have an ulnare distal to the ulna and an intermedium distal to the radus, but do not yet have a true radiale.



Manus: Basal Tetrapods

As fishes transitioned to basal tetrapods, there was a reduction from the polydactylous condition to five digits.



Within the manus, distal to the two elements of the antebrachium there are three successive rows of carpals (review first image of this presentation):

THREE PROXIMAL CARPALS
(from digit I /thumb side)

- Radiale
- Intermedium
- Ulnare

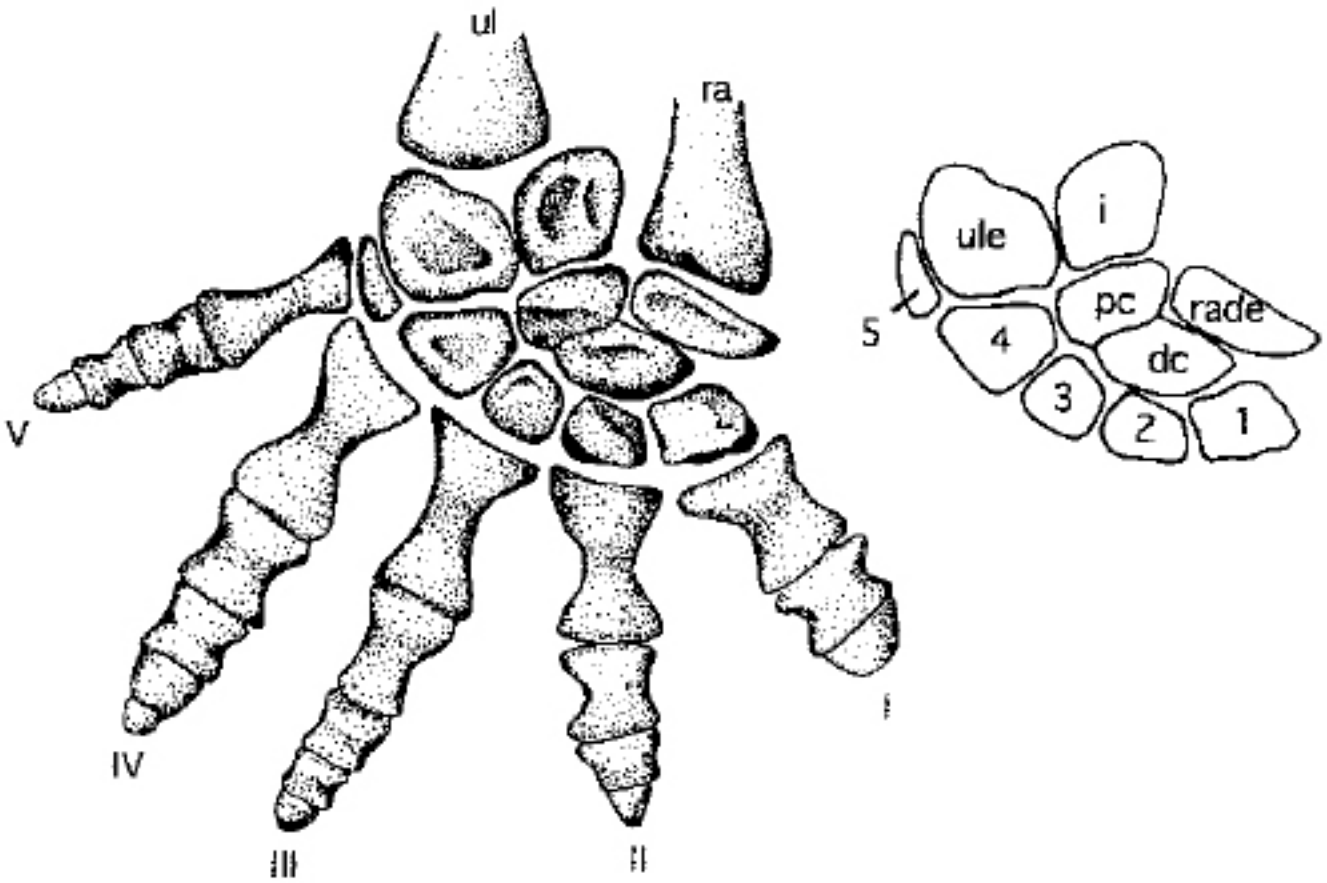
(As many as) FOUR MIDDLE CARPALS

- Centrale 1
- Centrale 2
- Centrale 3
- Centrale 4

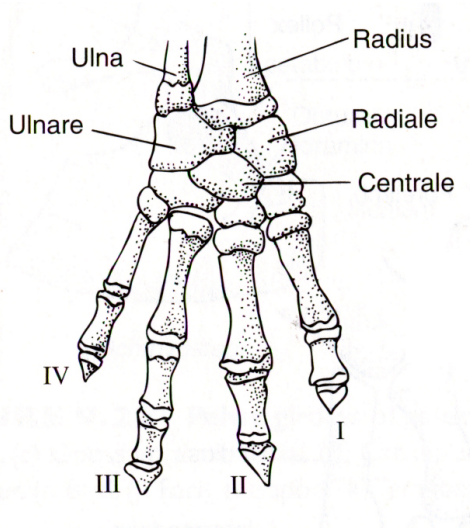
FIVE DISTAL CARPALS

- Distal Carpal 1
- Distal Carpal 2
- Distal Carpal 3
- Distal Carpal 4
- Distal Carpal 5

Following is the condition in the highly terrestrial, Early Permian amphibian *Seymouria*. Note that *Seymouria* has already reduced the number of Centralia to two, in this case a proximal central (pc) and distal central (dc).



Manus: Living Amhibians



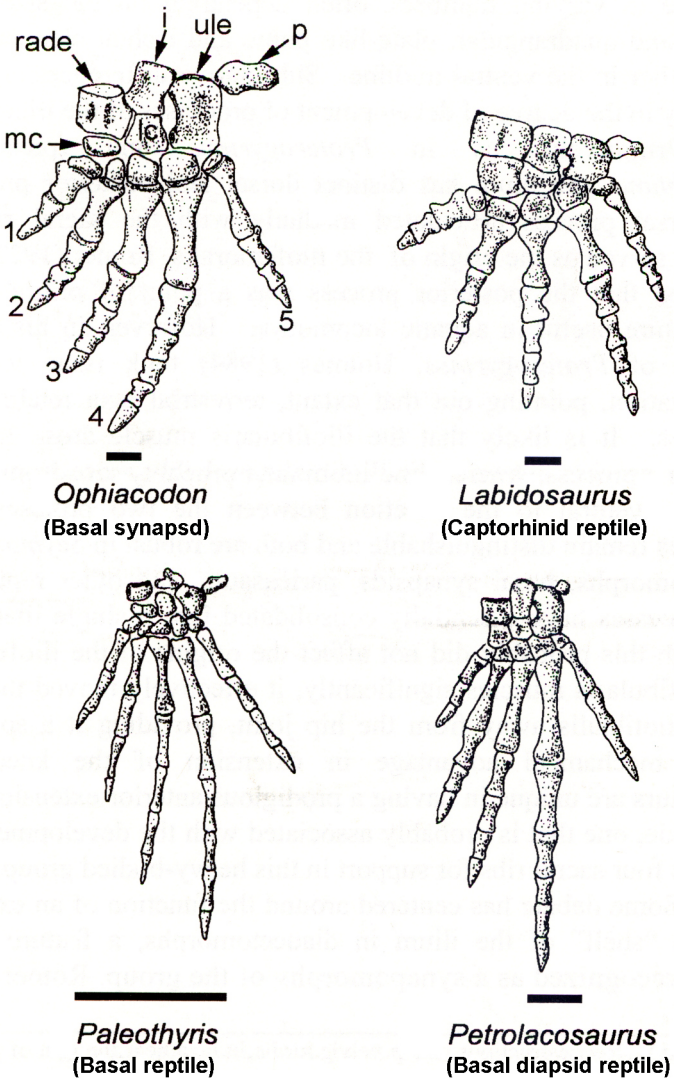
Living amphibians have:

- Reduced the number of digits to four. It is generally thought they have lost the fifth digit.
- Lost the intermedium.
- Retain only one central
- Lost distal carpal 4; or it has fused to 3.
- Lost distal carpal 5.

Manus: Basal Amniota

Within amniotes:

- A neomoprh (new element) is added to the three proximal carpals (radiale, intermedium, and ulnare) – the PISIFORM. It is on the ulnar side of the carpus.
- Centralia are generally limited to two, usually referred to by position as the LATERAL CENTRALE and MEDIAL CENTRALE.
- Five distal carpals remain.
- The phalangeal formula of the hand is usually: 2-3-4-5-3.



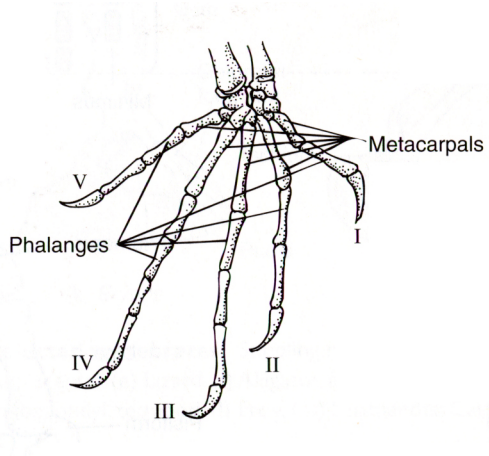
Ophiacodon
(Basal synapsd)

Labidosaurus
(Captorhinid reptile)

Paleothyris
(Basal reptile)

Petrolacosaurus
(Basal diapsid reptile)

Manus: Extant Reptiles



Living lizards have a phalangeal formula of 2-3-4-5-3.

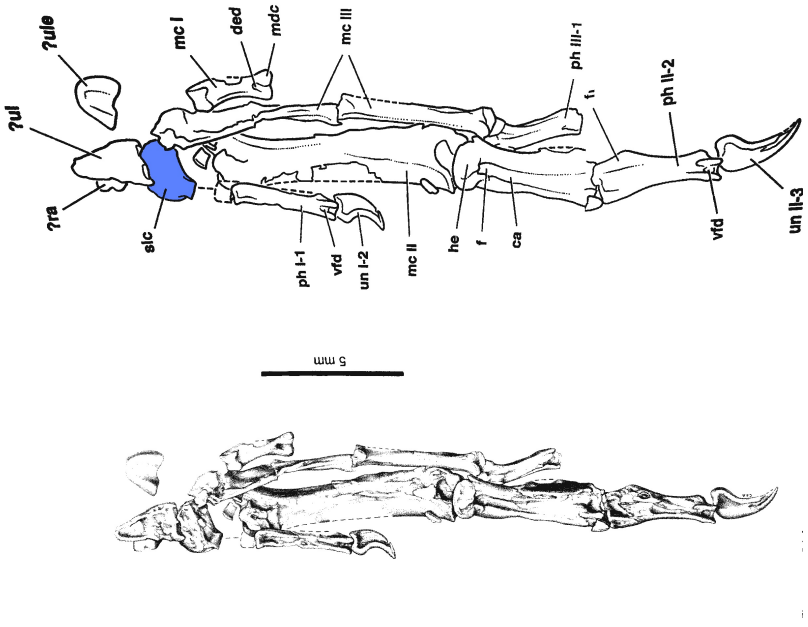
The fourth digit is often particularly elongate.

This is thought by some to aid in pushoff of the hand. (The condition is even more pronounced in the foot.)

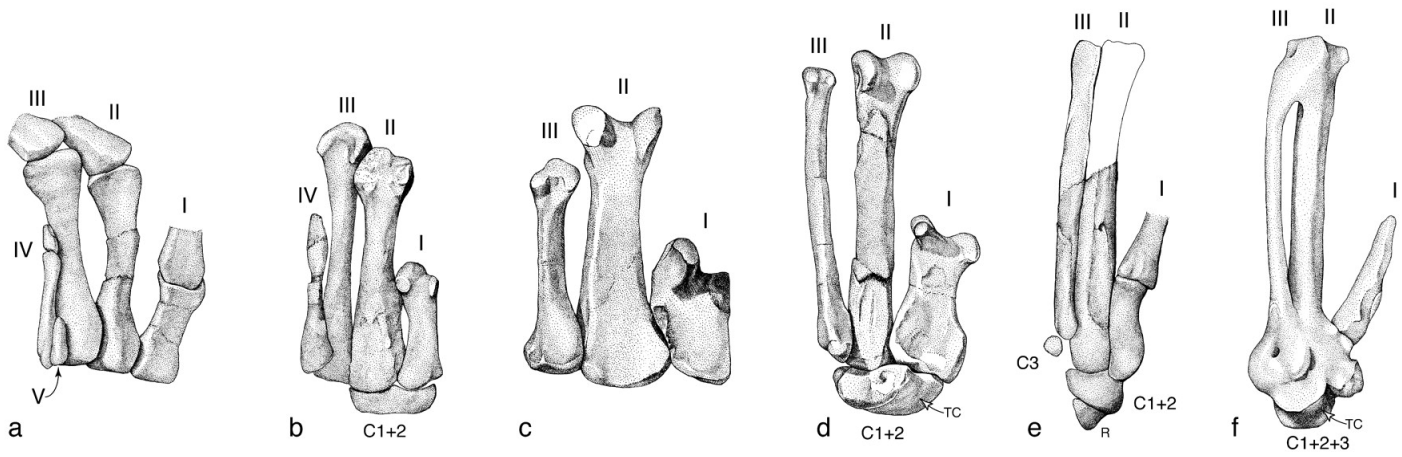
Manus: Dinosaurs to Birds

Maniraptorans are united by the possession of modified elements in the wrist; the SEMILUNATE CARPAL – a fusion of distal carpals 1 and 2, is a bone unique to this group — along with other modifications of the forelimb, it makes the *flight stroke* in birds possible, and was probably *co-opted* by birds for flight from a grasping function.

Following is an illustration of the maniraptoran dinosaur *Velociraptor* with the seilunate carpal shown in blue.



The following progression shows the carpus in a morphological series from primitive theropod dinosaurs to birds. Note the semilunate carpal in *Deinonychus, Archaeopteryx*, and birds.



Herrarasaurus *Coelophysis* *Allosaurus* *Deinonychus* *Archaeopteryx* Bird

Manus: Mammals

At first glance, the mammalian condition appears to be significantly different fro that of all other tetrapods. However, if considered systematically, the homologies between the basal terapod, basal amniote, and mammalian carpus may be determined.

As with basal amniotes, with the addition of the pisiform, there are now four proximal carpals. [HOWEVER!] they are only partialy homologous to the four proximal carpals of the basal amniote carpus:

PROXIMAL ROW OF CARPALS

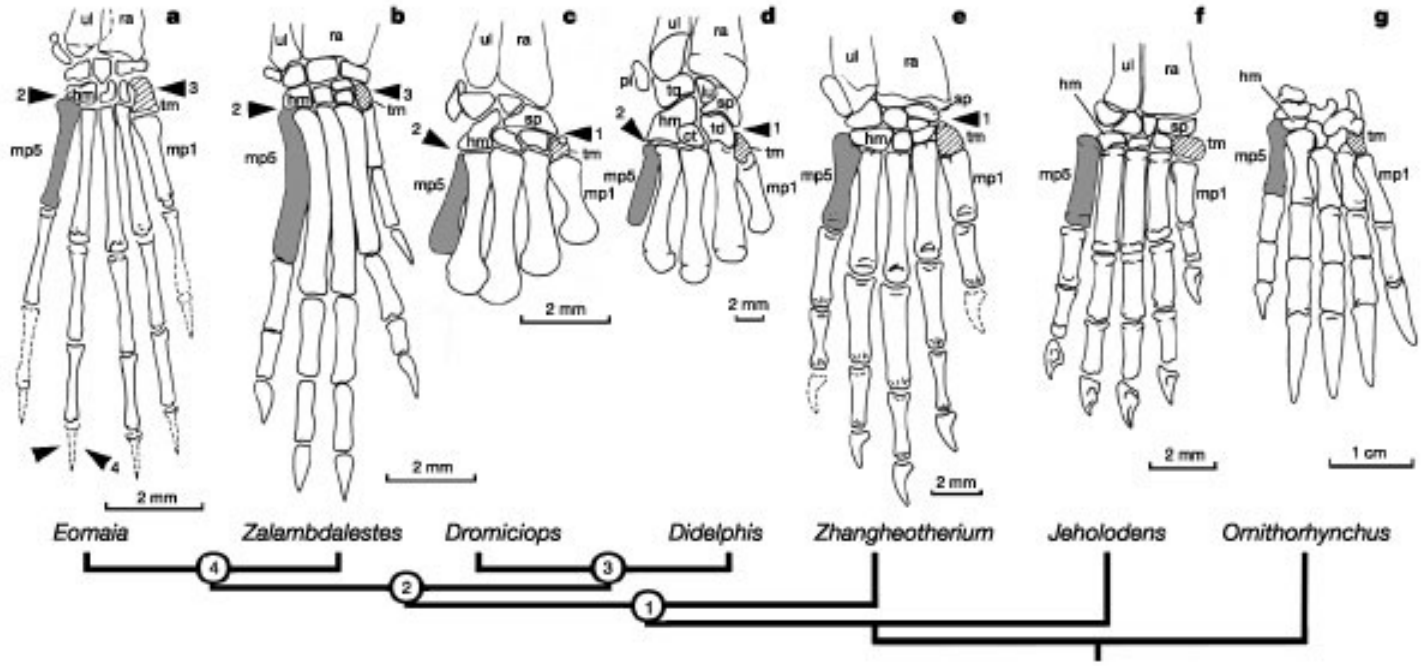
- The PISIFORM is the pisiform.
- The ulnare becomes the TRIQUETRUM. (Note how the triquetrum is located immediately distal to the ulna.)
- The intermedium becomes the LUNATE.
- [You would think then that the radiale becomes the scaphoid – but it does not. The radiale fuses to the distal end of the radius to become the STYLOID PROCESS OF THE RADIUS.
- The two remaining centalia fuse to become the SCAPHOID.

DISTAL ROW OF CARPALS

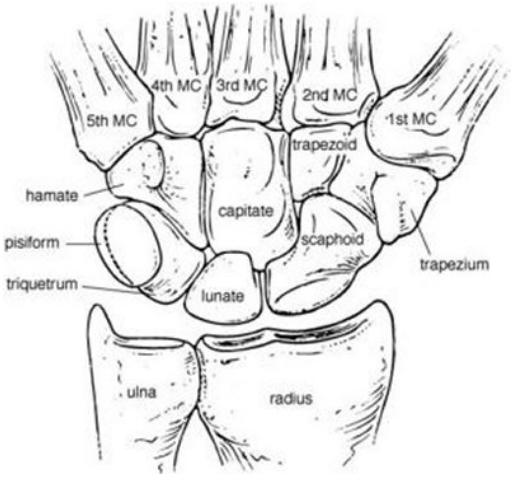
- Distal carpal 1 becomes the TRAPEZIUM.
- Distal carpal 2 becomes the TRAPEZOID.
- Distal carpal 3 becomes the CAPITATE.

- Distal carpal 4 becomes the HAMATE.
- Distal carpal 5 is lost.

The following illustration shows the arrangement of the carpal elements in a variety of basal mammals:



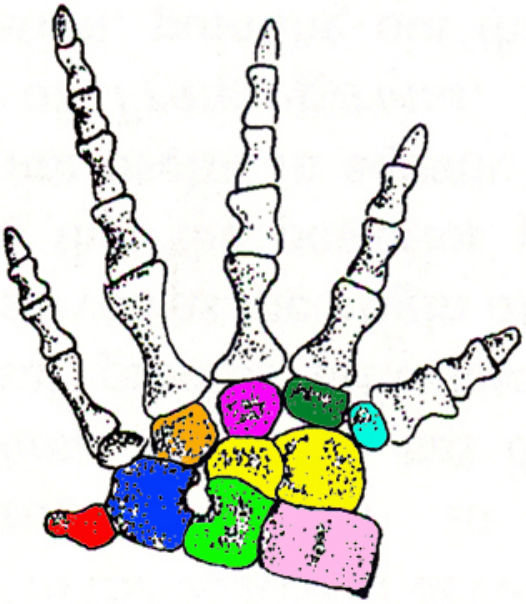
Although the proportions of some of the carpals of the human hand ar slightly different from other mammals, they are in essentially the standard positions relative to one another:



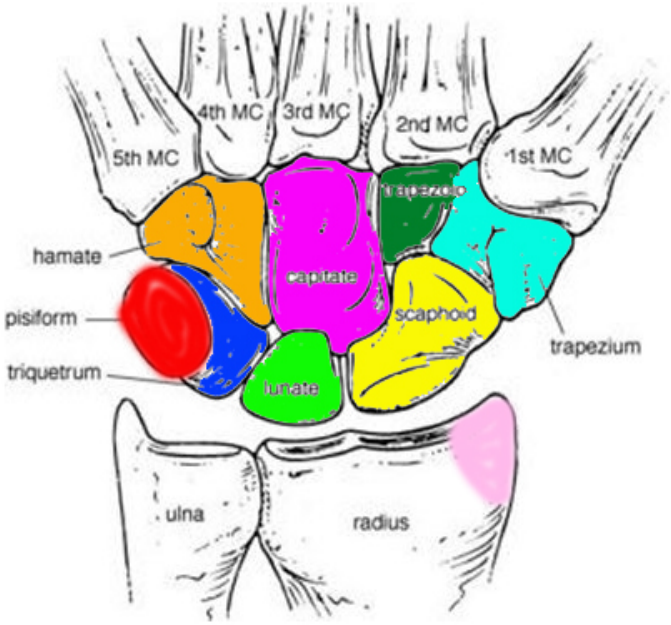
HOMOLOGIES OF MANUS ELEMENTS BETWEEN BASAL TETRAPODS AND MAMMALS

	NON-MAMMALIAN TETRAPOD	BASAL AMNIOTE	MAMMAL
ANTEBRACHIUM	Radius	Radius	Radius
	Ulna	Ulna	Ulna
CARPALS	Radiale	Radiale	Styloid process of radius
	Intermedium	Intermedium	Lunate
	Ulnare	Ulnare	Triquitrum
		Pisiform (neomorph)	Pisiform
	Centrale 1	Centrale 1	Scaphoid (part)
	Centrale 2	Centrale 2	Scaphoid (part)
	Centrale 3	(lost)	
	Centrale 4	(lost)	
	Distal Carpal 1	Distal Carpal 1	Trapezium
	Distal Carpal 2	Distal Carpal 2	Trpezoid
	Distal Carpal 3	Distal Carpal 3	Capitate
	Distal Carpal 4	Distal Carpal 4	Hamate
	Distal Carpal 5	Distal Carpal 5	(lost)
METACARPALS	Metacarpals 1-5	Metacarpals 1-5	Metacarpals 1-5
PHALANGES	Phalanges	Phalanges (2,3,4,5,3)	Phalanges (2,3,3,3,3)

Following is a color-coded comparison of elements of the carpus in a basal amniote and a mammal (Human):



Labidosaurus
(Basal reptile)



Homo
(Human)