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The Skeleton of the Arm of *Necturus*

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Wilder's (1903) description of the skeleton of *Necturus* is the only one, to date, that is anywhere near complete. Other authors (Mivart, 1869; Ribbing, 1906-07; Howell, 1936; Straus, 1942) have noted portions of the arm-skeleton incidentally to describing various muscles. Chen (1935) described the embryonic development of the pectoral limb. All of these notes generally agree, except in a few details. Francis (1934) described the skeleton of *Salamandra*. For reasons to appear later, I adopt the terminology of Francis for the skeletal elements of the arm of *Necturus*.

The Humerus

The humerus, like the other shaft bones of the arm, is made up of a partially ossified diaphysis capped by cartilaginous epiphyses. The diaphysis is perichondrially ossified. Hence, the shaft has thicker ossification at the center of its length, and thinner ossification toward its ends. The shaft is nearly cylindrical at its middle, but both ends are flattened.

The proximal epiphysis of the humerus is flattened antero-posteriorly, and bears a rounded head which fits into the glenoid fossa of the pectoral girdle. Also on the proximal end of the humerus, ventral surface, is a large crista ventralis (crista deltoideus) which extends about one-third the length of the humerus. The crista dorsalis described by Francis for *Salamandra* is not present in *Necturus*. The distal end of the humerus is flattened dorsoventrally. Lateral (radial) and medial (ulnar) epicondyles are separated by a shallow trochlear groove (intercondyloid fossa). The lateral epicondyle is nearly spherical, and fits into the concavity of the radius. The median epicondyle is somewhat elliptical in shape. The trochlear groove articulates with the sigmoid notch of the ulna. On the dorsum of the humerus the trochlear groove becomes enlarged slightly as the olecranon fossa. Wilder described a cubital fossa in ventral position on the humerus, but if it is present, it is exceedingly shallow.

The Forearm

The radius and ulna of *Necturus* are completely separate. The radius is preaxial in position in the forearm. The proximal epiphysis of the radius has a shallow concavity to receive the lateral epicondyle of the humerus. The distal epiphysis of the radius articulates with the carpal radiale and with the intermedium of the fused ulnare-intermedium of the wrist. The distal epiphysis therefore appears roughly triangular in shape when viewed from either the flexor or extensor surface of the arm. The diaphysis is oval in cross section, and tapers very slightly toward its middle where it has the smallest cross section. The distal end of the radius is slightly larger than the proximal end.

The ulna is postaxial in position in the forearm. The proximal epiphysis of the ulna is enlarged and elongated to form a definite olecranon process. On the olecranon process is a shallow sigmoid notch with which articulate the median epicondyle and trochlear groove of the humerus. The distal epiphysis of the ulna is smaller, and articulates with the ulnare of the fused ulnare-intermedium of the wrist. The diaphysis of the ulna is oval in cross section, and like the radius, tapers toward its middle where it is smallest in cross section. Ulna is longer than radius, due to the elongation of the olecranon process.

The Carpus

The wrist is usually composed of six carpal cartilages, although seven or rarely eight separate elements may be present. The cartilages of the wrist have reasonably consistent shapes when comparisons are made between individual specimens. In all specimens they are gently-rounded cartilages that superficially have little to distinguish them save their positions in the wrist.

Distal to the ulna is the largest of the carpals, the ulnare-intermedium. This cartilage is formed by fusion of a post-axial ulnare with a medial intermedium (Chen, 1935). A foramen (f. perforans carpi) for the passage of an artery marks the line of separation between the two elements. Sometimes ulnare and intermedium persist as separate cartilages.

Distal to the radius is the radiale. This carpal cartilage is approximately half as large as the ulnare-intermedium.

Centrally placed in the wrist is the nearly-spherical centrale. This cartilage touches all of the other cartilages of the wrist except the ulnare.

Three cartilages form a distal row of carpals. On the preaxial side is a small prepollex, usually somewhat triangular in shape when viewed from the dorsal surface. In most previous accounts this cartilage has been named as carpale 1. Posterior to the prepollex is a small cartilage which is here interpreted as a fusion of carpale 1 and carpale 2. Posterior to carpale 1-2 is carpale 3-4 (Chen, 1935).

The Metacarpals and Phalanges

The metacarpals and phalanges are all similar in appearance. Except for the distal phalanges, each unit is dumb-bell-shaped, with cartilaginous epiphyses capping a slightly ossified diaphysis. Each unit is slightly larger at its proximal end than at the distal end. The terminal phalanges are approximately triangular in outline, and lack distal epiphyses. The fifth finger is considered here to be the missing one. Digit three has 3 phalanges, the other fingers normally having only two phalanges each. Occasionally, digit 1 has only one phalanx, and digit 2 may have three phalanges. Adams (1926) is apparently in error in listing the digital formula as "3-3-4-3", although he may have had an exceptional specimen.

It should be added that not one of the skeletal elements of the arm of *Necturus* ossifies completely. At all times the arm skeleton is flexible, due to the abundance of cartilage.

Discussion

Francis (1934) made a thorough comparison of the fore- and hindlegs of *Salamandra*. In this genus the hindleg has five toes, and the foreleg has four fingers; the prepollex is practically free of muscle attachments, and the digital muscles for the first two digits attach to the fused carpale 1-2. Francis observed that in *Salamandra* the preaxial borders of the foreleg and hindleg are practically identical, and so concluded that the reduction in number of digits in the foreleg must have occurred on the postaxial border. Francis refers to Perrin (1893) and Sieglbauer (1904) who reached the same conclusion regarding *Salamandra*; and to Steiner (1921) who reached the same conclusion regarding the missing finger in *Triton* and *Diemyctalus*. Incidentally, Wilder (1908) has pointed out the close homologies of the distal portions of the arm and leg in *Necturus*. It can be stated here that the foreleg of *Necturus* very closely resembles that of *Salamandra*.

Wherever reference has been made to the fingers of *Necturus*, it has been assumed that the first finger or thumb is missing, apparently by analogy with the pattern of reduction in mammals, etc. (Mivart, 1869; Wilder, 1903, 1912; Ribbing, 1906-07; Kingsley, 1907; Adams, 1926; Chen, 1935; Senning, 1937; Gray, 1938; Breland, 1943; Atwood, 1949, and others.) It seems to me that *Necturus* follows the pattern of reduction of digits as it is thought to have occurred in *Salamandra*. Some substantiating evidence is presented below.

Carpale 1-2 in *Necturus* is round or oval when viewed from above. On the ventral surface it is raised into a gently-curving transverse ridge, that continues on to carpale 3-4. This forms a crescent-shaped ridge across the wrist near the bases of the metacarpals. I have seen one specimen of *Necturus* in which this usually single element was doubled. Also, some skeletal preparations stained with alizarin red or toluidin blue give evidence of two centers of ossification, though most of such preparations show no differentiation. The most conclusive evidence for the double nature of this

cartilage is that offered by the pattern of attachment of the muscles to the wrist cartilages.

Practically no muscle fibers attach to the prepollex. Instead, the flexor- and extensor muscles for the more preaxial finger attach to the fore part of carpale 1-2, while muscles of the second digit present, attach to the posterior part of the same carpale. Origins and insertions of the muscles will be described in a later note. Specimens macerated in KOH solution can be used for additional proof. A needle pushed against the ventral ridge on carpale 1-2 causes movement in the two preaxial fingers. Similar treatment of the prepollex causes little or no movement of the fingers. Significantly, the prepollex has no ridge on the ventral surface to offer muscle attachments, and as described for carpale 1-2 and carpale 3-4.

Chen (1935) studied serial sections of *Necturus* larvae, and definitely established the double nature of carpale 3-4 in this genus. Skeletal preparations which I have stained with alizarin red or toluidin blue give evidence of the two centers of chondrification in carpale 3-4, though most such preparations show no differentiation. On the ventral surface carpale 3-4 is raised into a transverse ridge, as described above. A needle pushed against this ridge causes movement in the two post-axial fingers.

It therefore seems that in *Necturus* the pattern of reduction of digits in the foreleg is such that the missing digit is the fifth finger, not the thumb as is generally accepted.

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