A REVISION OF THE EXTENSOR MUSCLES OF THE FOREARM IN TETRAPODS

By R. WHEELER HAINES

Department of Anatomy, St Thomas's Hospital Medical School

INTRODUCTION

It is among the extensor muscles of the forearm that the most dramatic changes of nerve supply are to be found. In some animals, such as turtles, there are four motor nerves to the extensors; in others, such as frogs and crocodiles, there may be but one. But the changes have been little understood, and there is as yet no agreement as to the primitive state from which the modern structures have been derived. In the case of the muscles also, though they are better known than the nerves, the relationships in the various groups of animals are not understood, and the ancestral plan has never been clearly defined. In this paper, from a study of the most primitive types now available, the turtles, *Sphenodon* and the urodele amphibians, the primitive conditions are defined, and illustrated by a reconstruction of an early reptile, and then the arrangements in the more specialized types are considered. The literature, particularly the works of Brooks, Ribbing and Howell, will be considered in the text.

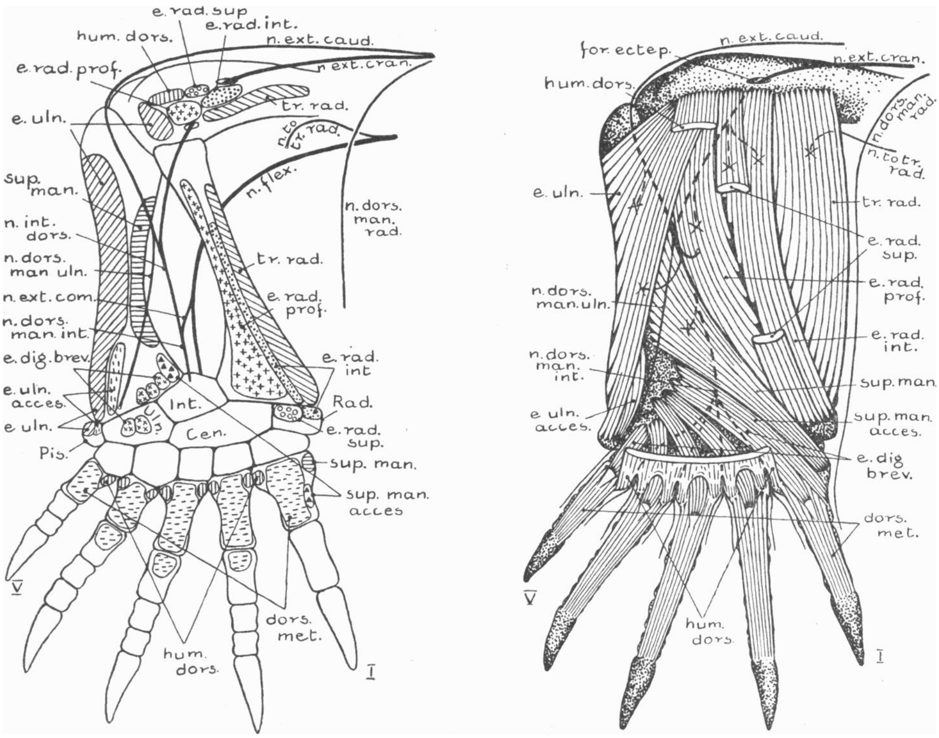
The material contains representatives of all living orders of reptiles and amphibians which possess limbs, with a monotreme and a marsupial to represent the mammals. Classical types have been used in preference to relatively unknown animals except where they appeared too highly specialized. I have to thank the trustees of the Thomas Smythe Hughes Fund for a grant towards the purchase of specimens, and the Conservators of the Museum of the Royal College of Surgeons, Prof. A. B. Appleton, Prof. Gowland and Prof. Watson for special material.

MUSCLES AND NERVES OF PRIMITIVE TYPES

Chelonians. The turtles, in spite of the development of the carapace, seem to have preserved a very primitive type of forelimb. *Emys* is a good type chosen by Ribbing (1907).

Muscles. From the humerus arise three groups of muscles, a humerodorsalis, an ulnar extensor mass, and a radial extensor series including a tractor radii. The humerodorsalis has eight slips of insertion, to the bases of the metacarpals from the ulnar side of I to the radial side of V. The main ulnar extensor passes to the shaft and lower end of the ulna and to the pisiform, and an accessory ulnar extensor, peculiar to *Emys*, passes from the lower end of the ulna to the pisiform.

The four radial muscles are described by Ribbing (1907, extensor antibrachii et carpi radialis *a*, *b*, *c* and *d*), but have not been figured. They will be called here the extensor radialis superficialis, profundus and intermedius, and, to avoid the name extensor for a muscle supplied by a flexor nerve, the



· Fig. 1. *Emys blandingii.*

tractor radii. The superficialis inserts on the radiale, the others on the radius, except for a small slip of the intermedius to the radiale. The three extensors are supplied by the n. extensorius cranialis after it has pierced the ectepicondylar foramen, the tractor by a special flexor nerve which pierces the biceps-brachialis mass.

Of the shorter muscles the supinator manus passes from the shaft of the ulna to the base of metacarpal I, and an accessory supinator inserts on its shaft. The five extensores breves, three of which arise from the ulna, and two from the ulnare, pass between the insertions of the humerodorsalis to the digits, where they blend with the dorsometacarpales. These arise from the metacarpals, and in the middle three digits from the proximal phalanges, and insert on the bases of the distal phalanges.

Nerves. There are four motor nerves in the extensor region, the n. extensorius cranialis (Sieglbauer, 1909) which passes through the ectepicondylar foramen, the n. extensorius caudalis which lies in the groove between the ectepicondyle and the olecranon, the n. extensorius communicans which reaches the extensor region from the flexor nerves by passing through the radio-ulnar interosseous space, and the special nerve to the tractor radii. The cranialis and caudalis join to form the dorsal interosseous nerve, which is joined deep to the supinator manus by the n. communicans.

Of the three cutaneous nerves to the digits, the nn. dorsales manus ulnaris, intermedius and radialis, the ulnaris is formed from the n. extensorius caudalis just as it joins the cranialis, and passes superficial to the supinator manus and then along the groove between the ulnar extensors and the extensor brevis digiti V. The intermedius is the direct continuation of the dorsal interosseous, while the radialis is a special branch from the extensor nerve in the upper arm, and passes down the radial border of the forearm and hand. This account differs from that given by Ribbing (1907) in a few particulars. The radial and ulnar extensors are said to reach the metacarpals, the short extensors to arise from the intermedium, and the dorsometacarpals to reach the carpal bones. The communicating extensor nerve was not seen. The nerve to the tractor radii was first noticed later (1911*a*).

The muscles of other chelonians appear to resemble those of *Emys*, apart from peculiarities such as the accessory ulnar extensor and supinator manus (*Cyclanorbis*, *Chelhydra*, *Hydromedusa*, Sieglbauer, 1909; *Sternothaerus*, Ribbing, 1907; confirmed in *Chelhydra*, *Sternothaerus* and *Testudo*, R. W. H.). In some turtles with specialized swimming paddles (*Thalassochelys*, Sieglbauer, 1909; *Trionyx*, Ogushi, 1913) the muscles are modified, but seem to have been derived from an *Emys*-like state.

Sphenodon. In *Sphenodon* the humerodorsalis has only four insertions instead of eight, for those to the radial sides of the metacarpals have been lost. The extensor ulnaris has become subdivided into an extensor antibrachii ulnaris to the upper half of the ulna, and an extensor carpi ulnaris to the pisiform and base of the fifth metacarpal with an extension to the humerodorsalis. The radial muscles are arranged as in *Emys*, but only the superficialis reaches the radiale. The supinator manus and a small slip of the extensor brevis digiti I arise from the ulna, the rest of the extensores breves from the intermedium and ulnare. The dorsometacarpals are much more complicated than in chelonians. Those for digits II, III and IV arise each by three heads, from their own metacarpals and from those on either side, the first arises from its own metacarpal and from II and the more radial centrale, and the fifth from its own metacarpal only.

The four motor nerves described in chelonians are found again in *Sphenodon*, but the n. dorsalis manus ulnaris now arises on the flexor surface and winds round the ulnar border of the hand to the ulnar side of the fifth digit.

The muscles and nerves of *Sphenodon* have been described by Brooks (1889), Osawa (1898), Ribbing (1911) and Miner (1925). The account given here agrees best with Ribbing's text, Miner's figures of the muscles, and Brooks's of the nerves.

Salamandra. Salamandra has been chosen as a type of the Amphibia, rather than the better known *Megalobatrachus* or *Necturus*, as its muscles seem on the whole more primitive. The muscles have been well illustrated by Perrin

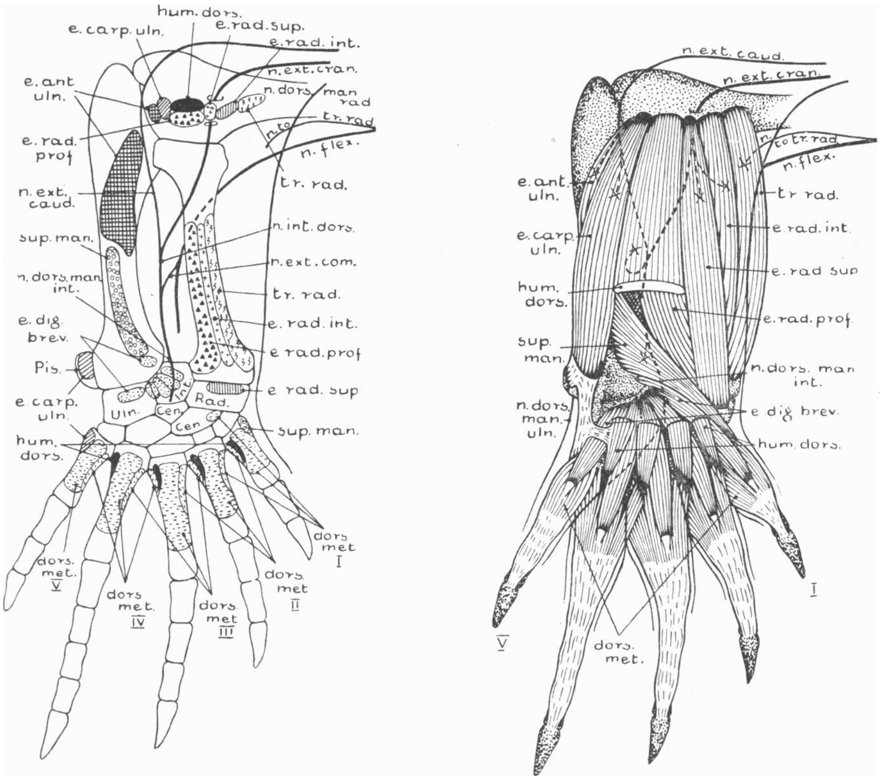


Fig. 2. *Sphenodon punctatum.* Skeleton from Miner (1925).

(1899), with their bony attachments, and Sieglbauer's (1904) illustrations of the nerves are excellent. For this paper the arrangements have been checked by a complete serial section through the forearm and hand.

The humerodorsalis is inserted as in chelonians by two slips to the base of each metacarpal, but that to the first is usually missing, and on the ulnar side the fifth digit has been lost (Gregory *et al.* 1923) and with it the attachment to the metacarpal, so that only six slips remain. The extensor carpi ulnaris, with the loss of the pisiform, inserts on the intermedio-ulnare, and a powerful extensor antibrachii ulnaris passes to the ulna.

There are only three muscles in the radial group, all supplied by extensor nerves, two by twigs which spring from the n. dorsalis manus radialis before it pierces the most radial of the muscles. The identification of the extensor radialis superficialis and profundus is clear, both from their attachments and relations, and from the courses of the nerves, for the supply of the superficialis reaches it by passing on the radial side of the profundus, so separating it from the rest of the musculature. The most radial muscle is probably the intermedius, the tractor radii having disappeared together with its nerve supply. It might on the other hand be a fused intermedius and tractor supplied only by an extensor nerve, but this is less probable. Since there must be some un-

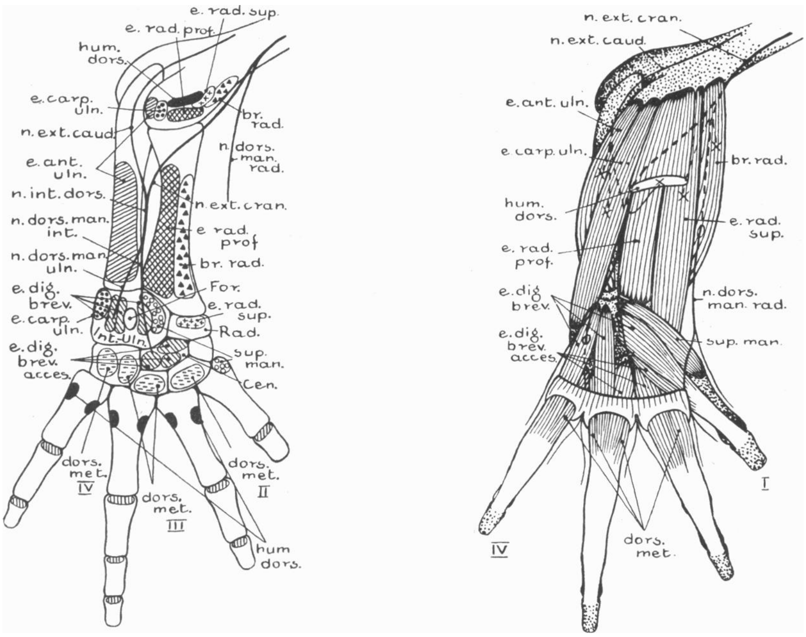


Fig. 3. *Salamandra maculosa.* Skeleton from Perrin (1899), muscles partly from Perrin, nerves partly from Sieglbauer (1904), checked by a complete serial section.

certainty, and since the matter has never before been discussed in the light of the four reptilian muscles and their nerve supplies, it is convenient to call the muscle the brachioradialis, as all authors are agreed that it corresponds to that muscle in mammals.

The supinator manus is peculiar in its origin from the carpus only. Ribbing (1907), supposing that the first digit of urodeles was equivalent to the second of reptiles, could not consider the supinator manus homologous in the two groups. He postulated an ancestral form in which all the short muscles inserted on the terminal phalanges, and later an independent transference of the supinator to the marginal metacarpals, a hypothesis which is no longer necessary. The short extensors to digits I, II and IV take origin from the intermedio-ulnare, and in the specimens figured by Perrin and Sieglbauer a slip also passed to digit II. A second group of origins, probably migrated parts of the short extensors, arise from the centrale. The dorsometacarpals pass from the carpals to digits II, III and IV.

The cranial extensor nerve pierces the profundus, instead of passing deep to it. The communicating extensor nerve is absent in *Salamandra*, but is found in several urodeles. The n. dorsalis manus ulnaris is, as in *Emys*, derived from the extensor nerves, and supplies the third cleft as well as the ulnar border of the hand, and the n. dorsalis manus radialis, after piercing the brachioradialis, supplies the first cleft.

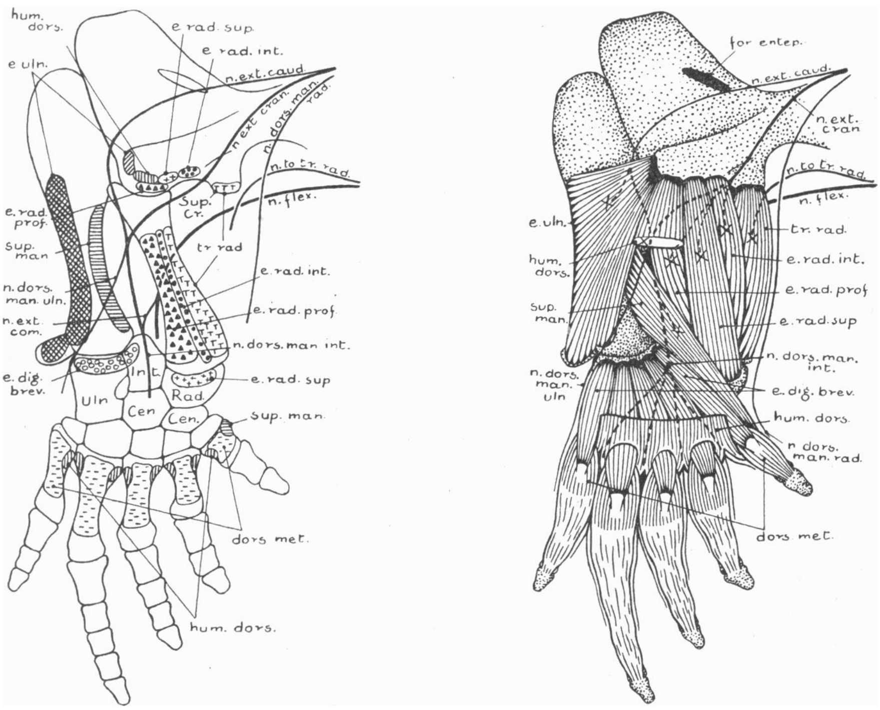


Fig. 4. *Ophiacodon mirus*, a Permian reptile. Skeleton from Williston & Case (1913).

This description agrees with those of Eisler (1895), Perrin (1899) and Sieglbauer (1904) except in some unimportant details. Other unspecialized urodeles agree in general plan (*Triton*, *Necturus*, *Ambystoma*, Sieglbauer and Ribbing; *Necturus*, Wilder, 1912). In *Necturus* all the short extensors seem to have disappeared, leaving only the dorsometacarpals on the back of the manus. The extensor ulnaris is usually undivided, *Salamandra* and *Triton* having probably developed the division into an antibrachial and a carpal part independently of the reptiles such as *Sphenodon*.

Ophiacodon. The primitive form of tetrapod limb can now be defined in some detail, and can be reconstructed in *Ophiacodon*, an early reptile described by Williston & Case (1913), though the individual peculiarities cannot of course be deduced. The humerodorsalis arises from the ectepicondyle, and is inserted by eight slips to the bases of the metacarpals as in *Emys*. A single undivided extensor ulnaris passes as in *Emys* from the distal end of the ectepicondyle to the shaft and lower end of the ulna and to the pisiform, but probably not to the fifth metacarpal. The four radial muscles are all perfectly distinct, the extensor radialis superficialis passing as usual to the radiale, and the profundus and tractor radii to the radius. Probably the intermedius also is confined to the radius, as the extension below the wrist in *Emys* is unusual in reptiles. The origins of this group are more difficult to define.

As noted by Ribbing (1911 *a*), those living animals which have an ectepicondylar foramen have also a special motor nerve from the flexor region, the nerve to the tractor radii, while the animals which have no foramen (amphibians, crocodiles and mammals) have no such nerve (exception in tejid lizards, R. W. H.). If the nerve, as suggested here, always supplies the tractor radii and no other muscle, it may be taken that the presence of an ectepicondylar foramen is associated with an arrangement of the radial muscles similar to that in *Emys* and *Sphenodon*. Now though the foramen is found in several fossil groups, it is primitively absent in both reptiles and amphibians (Romer, 1922), its place being taken by a deep groove between the ectepicondyle and the "supinator crest". So the cranial extensor nerve lying in the groove runs between the musculature arising from the two bony processes. In later reptiles in which these two processes have become fused to close over the foramen, the origins of the musculatures are contiguous, so that it is no longer possible to say with certainty which muscles arose from the one process and which from the other. Since, however, the tractor is separated from the other muscles by its nerve supply it seems probable that it alone arose from the crest, and the rest from the epicondyle as shown in the reconstruction. Again the early amphibians possessed a crest similar to that of *Ophiacodon*, and the tractor was presumably well developed. There is no evidence that the crest ever joined the epicondyle as in reptiles; it seems rather to have disappeared together with the muscle and its nerve supply, leaving the cranial extensor nerve proximal to the remaining muscles, as would be expected if they arose originally from the epicondyle.

The supinator manus and short extensors are always closely related in both reptiles and amphibians, and in *Ophiacodon* probably stretched from the ulna to the intermedium and ulnare, for the arrangement in *Salamandra*, where they are confined to the hand, is peculiar. The dorsometacarpals are more difficult to reconstruct as they differ widely in *Emys*, *Sphenodon* and *Salamandra*. It seems perhaps most probable that the single metacarpal origin in *Emys* is primitive, and that in *Sphenodon* and lizards, and to a lesser degree in anurans, they have spread on to the neighbouring metacarpals, while in urodeles they have moved proximally on to the carpal bones.

The motor nerves of primitive tetrapods probably resembled those of *Sphenodon*, with all four possible routes developed, and it seems safe to attempt their reconstruction, although in other regions it has been usual to show the muscles only in reconstructions. The three digital nerves are arranged on the chelonian plan, with the n. dorsalis manus ulnaris springing from the extensor nerves and not from a flexor nerve as in *Sphenodon.* The only doubtful point is the presence of a communicating extensor nerve. This is found in most urodeles, in chelonians and in *Sphenodon* and lizards, and if not ancestral, must have been developed independently in these three lines. It seems more probable that it has been lost in a few urodeles, and in anurans, crocodiles and mammals, all relatively specialized animals.

The structure of the primitive forearm has not been precisely defined by other workers, so that no exact comparisons are possible. Ribbing (1907) and Miner (1925) consider the metacarpal insertion of the humerodorsalis secondary and its insertion on the terminal phalanges primitive, but in all reptiles and most urodeles the insertions are on the metacarpals, and Howell (1936*a*) considers these primitive. The four radial muscles are recognized by Ribbing (1907 *Emys,* 1911 *Sphenodon*), but not the constant relations to their nerve supplies, nor the loss of the tractor in urodeles, nor is the primitive condition defined. Howell, working on *Necturus* in which the tractor is missing, and the lizard Iguana in which the superficialis is missing, and not recognizing the double nerve supply, describes only two muscles, an extensor carpi radialis longus and brevis. The interpretation of the nerves agrees in the main with Ribbing (1908) but other authors have been inclined to regard the communicating nerve as an anomalous structure rather than an ancestral heritage, for its wide distribution in reptiles and amphibians has not been appreciated.

The morphology of the tractor radii is doubtful, for its nerve supply suggests that it is a flexor though associated with extensor muscles. There is no absolute objection to the origin of a flexor muscle from the radial side of the humerus. In the hind limb the tibial head of the gastrocnemius arises on the tibial side of the main mass of the flexor musculature.

It can now be seen that the turtles come very near to the primitive type, the chief differences being those leading to the formation of an ectepicondylar foramen. *Sphenodon* is specialized in the splitting of the extensor ulnaris and its extension to the fifth metacarpal, the reduction of the insertions of the humerodorsalis, and the new origin of the n. manus ulnaris, while all urodeles have lost the bones and muscles of the ulnar border of the hand, and also the tractor radii with its nerve supply.

AMPHIBIAN TYPES

Megalobatrachus. Megalobatrachus and the related *Cryptobranchus* are specialized, secondarily aquatic forms, but have unfortunately been chosen for intensive study by several anatomists (Humphrey, 1872; Osawa, 1898; Miner, 1925, etc.), probably on account of their large size, and have had a profound effect on myological theory. The extensor ulnaris is undivided. The three radial extensors are arranged as in *Salamandra,* the tractor radii being lost as in all other urodeles. The supinator manus takes origin from the ulna instead of being confined to the hand. The n. dorsalis manus ulnaris has encroached on the intermedius as in *Salamandra*, but not the radialis. The communicating extensor nerve is well developed.

So far *Megalobatrachus*, where it differs from *Salamandra*, is the more primitive, but the muscles to the digits are profoundly modified. Apart from a single insertion into the base of the fourth metacarpal the humerodorsalis joins the short extensors and reaches the terminal phalanges. The dorsometacarpals have disappeared completely, the supposed remnant described by Miner being

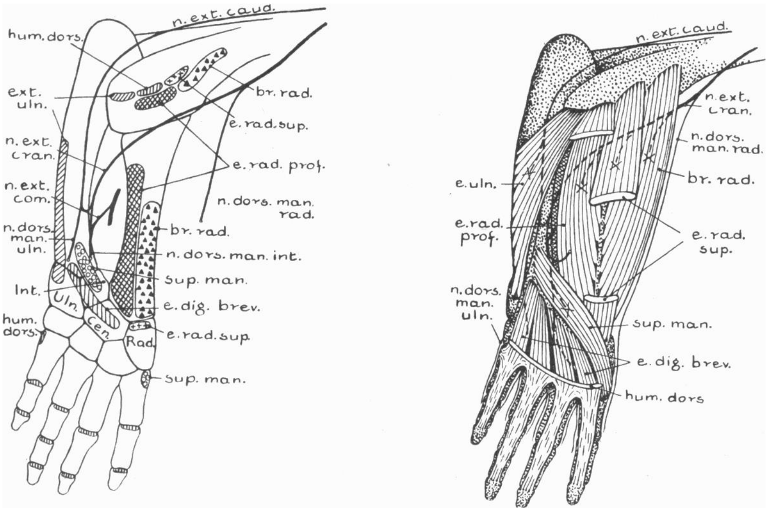


Fig. 5. *Megalobatrachus japonicus*. Skeleton from Miner (1925).

a flexor muscle supplied by a flexor nerve. It is clear then that this arrangement cannot be considered primitive. Other supposed extensions of the humerodorsalis beyond the metacarpals seem to be erroneous (Brooks (1889) in *Necturus*, corrected by Wilder (1912) and Howell (1936*a*), Ribbing (1907) in *Ambystoma*, absent according to Sieglbauer (1904), confirmed R. W. H.; Eisler (1895) in *Salamandra*, corrected by Perrin (1899)).

Eryops. The muscles of *Eryops*, a large land-living Permian form, have been carefully reconstructed by Miner (1925), and this is the only detailed reconstruction of the forearm and hand so far attempted in any animal. It is now possible to correct this work in several details, and to add the courses of the nerve trunks.

The humerodorsalis is shown inserted on the bases of the metacarpals, not on the phalanges as in *Megalobatrachus*, which was one of Miner's types. The extensor ulnaris is shown single, and inserted below the wrist only on the pisiform and ulnare, below which it does not extend in urodeles and chelonians, not inserted more distally as in *Sphenodon*, Miner's other type. The similarity of the lower end of the humerus to that of *Ophiacodon* justifies the reconstruction of four muscles as in reptiles, not three as in modern urodeles, and apart from the superficialis all are inserted on the radius. Miner figures these muscles correctly in *Megalobatrachus* and *Sphenodon* apart from the separation of the tractor and intermedius, but in his description of *Sphenodon* and his reconstruction of *Eryops* the profundus is supposed to insert below the wrist. The nerves are shown as similar to those of *Ophiacodon*.

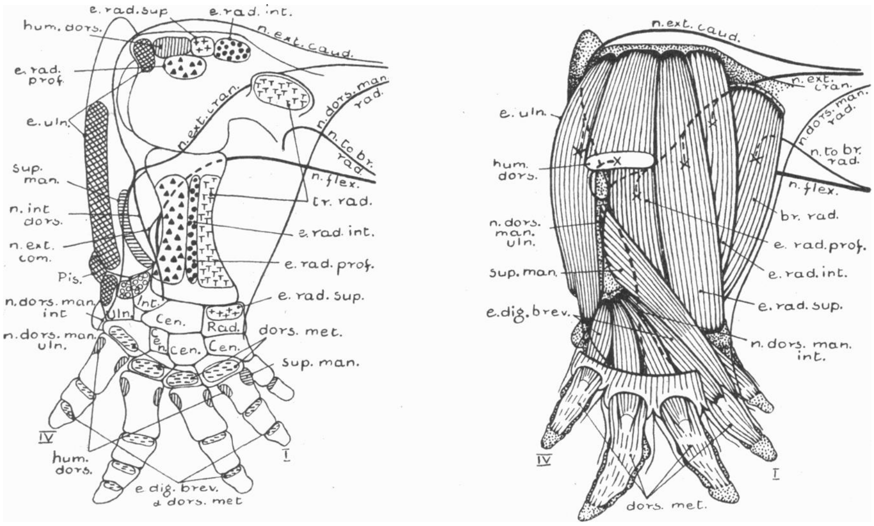


Fig. 6. *Eryops megacephalus*. Skeleton from Gregory *et al.* (1923).

Rana. In anuran amphibians the musculature is very highly specialized. In *Rana catesbiana*, the giant American bullfrog, the extensores carpi and antibrachii ulnaris are separate, and the humerodorsalis reaches the terminal phalanges of digits II, III and IV, with a small insertion on metacarpal IV. The extensor radialis profundus (Gaupp, 1896, "Flexor antibrachii lateralis profundus") is arranged as usual. The brachioradialis (Gaupp, "F. antib. lat. superficialis, cap. inferius") can be recognized by its position, although its relation to the cranial extensor nerve has changed. The extensor radialis superficialis (Gaupp, "E. carpi radialis, cap. inferius") also has the usual relations to the nerves, but is inserted on the peculiar ligamentous arch which stretches from the radio-ulna to the intermedius. Two small accessory slips (Gaupp, "e. carpi radialis, cap. superius and flexor ant. lat. superfic., cap. superius"), probably migrated parts of the extensor radialis superficialis or intermedius, or both, take origin above the nerve, and are inserted the one with the extensor radialis superficialis and the other directly on the radio-ulna. This group of muscles, which varies in development in the two sexes (Gaupp, 1896; Howell, 1935), needs further study.

The supinator manus is large, and has an unusual origin from the humerus besides its origin in the forearm. Between the two heads passes the nerve to the humerodorsalis and the n. dorsalis manus ulnaris, and these nerves must have been crossed by the humeral head of origin in its migration to the humerus. Ribbing (1907) thought that this head was a part of the humerodorsalis which joined the supinator, but this seems improbable on account of its insertion on the radial side of metacarpal I, and on account of its deep position. The short extensors again are specialized. One group, the extensores breves superficiales,

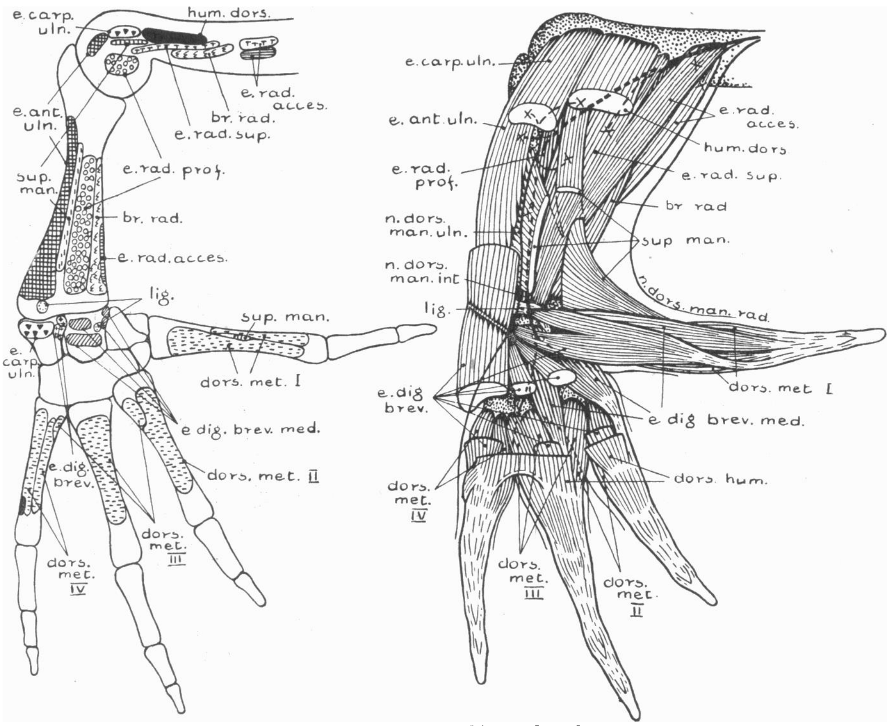


Fig. 7. *Rana catesbiana*, female.

has a slip to I from the tendinous arch and ulnare, to II and III from the ulnare, and IV from the extensor carpi ulnaris insertion, while a deeper group, the extensores breves medii to I, II and III, arises from the radiale, that to II by two heads which embrace the attachment of the tendinous arch. The dorsometacarpales are highly developed, that to III arising from metacarpals II, III and IV, as the corresponding muscle in *Sphenodon*.

This description agrees with those of Gaupp (1896, *Rana esculenta*) and others. Other anurans seem similar (Ribbing, 1907, 1911*b*, literature), though the lack of adequate illustrations makes comparisons difficult. It is clear that all frogs are highly specialized when compared with other groups, and that even if some of the muscles have been identified wrongly, there must have been some changes in the relations of the muscles to the nerves.

SPECIALIZED REPTILIAN TYPES

Varanus. The most satisfactory type of lizard known is *Varanus*, for though highly specialized in other regions of its body, its forearm is relatively primitive, and at the same time is large enough to allow accurate dissection. It is best to compare the lizards, not directly with the primitive reptiles, but with *Sphenodon*, for the specializations found in *Sphenodon* reappear in the lizards, together with several specializations of their own. It is highly probable

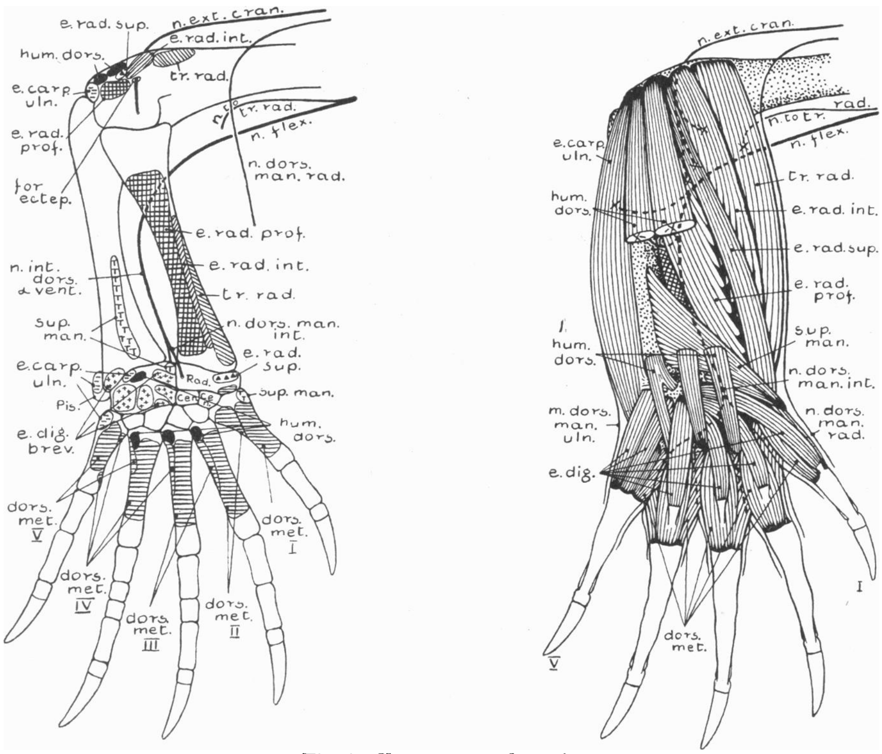


Fig. 8. *Varanus exanthematicus.*

that the two lines are closely related (Broom, 1925), and certainly the ancestors of the lizards must have resembled *Sphenodon* very closely as regards their limbs.

The humerodorsalis has two parts, one to metacarpals II and III, the other to IV and the ulnare. The slip to I has been lost. The extensor carpi ulnaris reaches metacarpal V as in *Sphenodon*, with slips to the pisiform and ulnare. The extensor antibrachii ulnaris, already reduced in *Sphenodon*, has been lost. The radial group is said by Ribbing (1907) to consist of two muscles only, the superficialis and a combined mass representing the rest. In *Varanus exanthematicus*, *griseus* and *niloticus* however, all the muscles described in *Sphenodon* are perfectly distinct. The supinator manus arises from the ulna with a small slip from the ulnare, and the short extensors from the ulnare except an extra slip to V from the lower end of the ulna. The dorsometacarpals are arranged as in *Sphenodon*, but the ulnar slips of digits I, II and III have been lost, while that to IV retains its slip from metacarpal IV, but this now arises indirectly from a tendinous arch.

The nerves are highly specialized in lizards. The tractor radii is served as usual by a special nerve, and the three radial extensors by the n. extensorius cranialis, which however ends in these muscles. The n. extensorius caudalis is

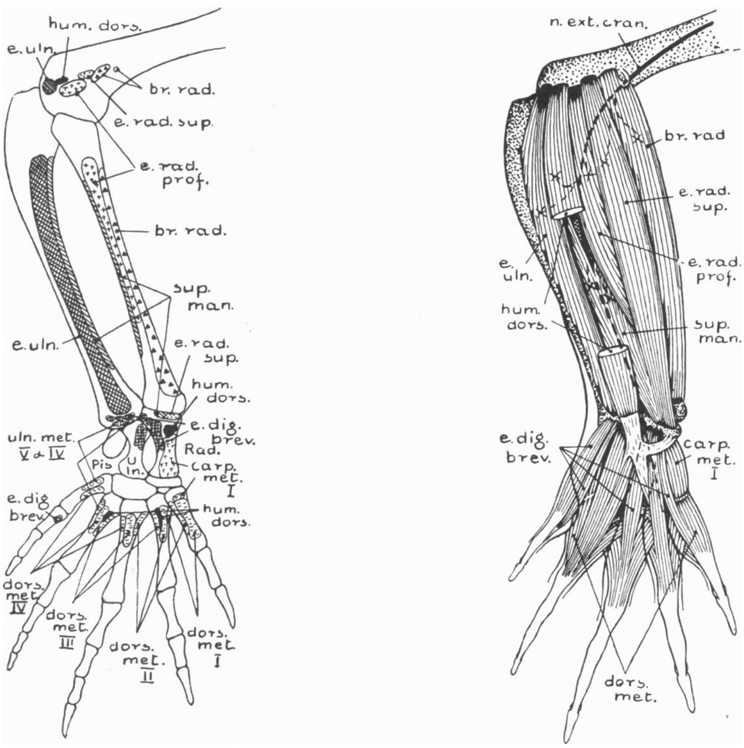


Fig. 9. *Alligator mississipiensis.*

absent, and all the rest of the muscles are supplied by a greatly enlarged communicating nerve, which also forms the sole source of the dorsal interosseous nerve and the n. dorsalis manus intermedius.

The muscles of *Iguana*, the type chosen by Rabl (1916) and Howell (1936*a*) to represent the reptilian structure, are similar to those of *Varanus*, except for the loss of the superficialis, which often occurs in lizards (Ribbing, 1907). The tejid lizards are of interest as they have lost the ectepicondylar foramen, so that the n. extensorius cranialis has to pass among the origins of the muscles instead of through the bone. In *Ameiva* the extensor radialis superficialis has been lost, so that, as in *Iguana*, the nerve supplies only two muscles, the intermedius and profundus. Now if the reconstruction of *Ophiacodon* is correct, the nerve when set free of the bone, if it lay in its old position, would be expected to reach the profundus by passing between the tractor and the intermedius. This is in fact the case, giving strong confirmation for the reconstruction. In other animals the loss of the foramen combined with the retention of the tractor is unknown.

Crocodilians. The crocodiles and alligators are a highly specialized group. In the alligator the humerodorsalis is inserted chiefly into metacarpal II with extensions to IV and the radiale, in Ribbing's *Crocodilus* into II and III. The extensor ulnaris is confined to the ulna. The three radial muscles are probably equivalent to those of urodeles, the tractor radii having been lost. The brachioradialis arises partly from the humerus, and partly from a fibro-tendinous arch over part of the flexor musculature of the upper arm. The supinator manus is enormously developed, and its origin has spread from the ulna on to the radius, an extension found elsewhere only in mammals. Its insertion on the first metacarpal has been lost, and a new one formed on the radiale in common with the extensor radialis superficialis. Probably the radiale metacarpale I is a distal fragment of this muscle. These changes are associated with a great mobility of the wrist joint, and the use of the elongated carpus as an extra limb segment. The short extensors and dorsometacarpals are arranged as in *Sphenodon.*

The crocodiles and anurans are the only animals known to have retained but one motor extensor nerve, a n. extensorius cranialis. The n. dorsalis manus ulnaris arises as in lizards and *Sphenodon* from the flexor nerves, but here has spread to supply the fourth cleft as well as the ulnar border of the hand, as in mammals.

MAMMALIAN TYPES

Monotremes. The muscles of mammals are difficult to interpret in reptilian terms, but the monotremes, though they have many specializations of their own, appear to be relatively primitive in the extensor region of the forearm.

In *Echidna* the humerodorsalis has become the extensor digitorum communis by changing its insertion from the metacarpals to the terminal phalanges, with a slip to the basal phalanx of the pollex. This has probably occurred as in frogs and cryptobranchs by a secondary fusion with the tendons of the short extensors. Howell (1936) suggested that the tendons loosed themselves from the metacarpals and laid hold of the neighbouring fascia so as to modify it into a series of tendons, but it seems doubtful whether new tendons are ever formed in this way. It is more likely that a single embryonic matrix is fully subdivided in reptiles forming the humerodorsalis and short extensors, and that in mammals its remains undivided distally, so that both muscles are continued to the digits.

The extensor carpi ulnaris has, besides its old origin from the humerus, a new one from the ulna, and its insertion reaches the terminal phalanx, a monotreme specialization. The extensor digitorum ulnaris lies between it and the humerodorsalis. It has no clear homologue in reptiles, but seems to be derived from a radial migration of a part of the extensor carpi ulnaris. Ribbing (1907) and Howell (1936) mention this derivation, but set it aside in favour of an origin from the communis, Ribbing on the grounds that in *Echidna* it has blended with this muscle in the forearm, a condition not seen in the specimen figured. In fact in *Echidna*, where the three digital extensors co-exist, the ulnaris is the deepest of all, separated from the communis by the pro-

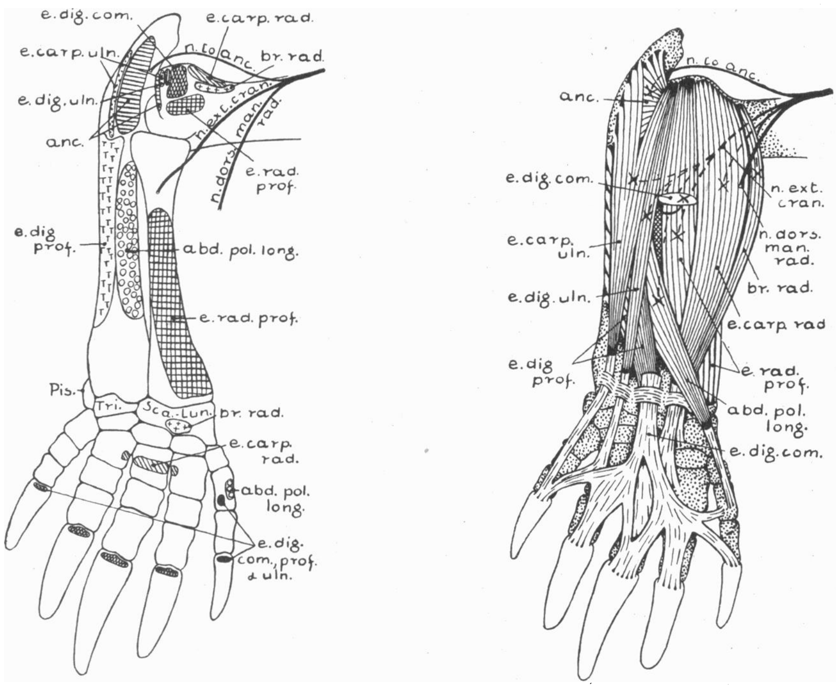


Fig. 10. *Echidna* sp.

fundus, and it is difficult to imagine the migration of the ulnaris through or round the border of this muscle. Brooks (1889) and Eisler (1895) consider the ulnaris a part of the reptilian extensores digitorum breves which has migrated from the ulna to the humerus, but this is improbable, for if any fibres should migrate they would be the uppermost, that is the fibres of the radial digits, not the ulnar ones. The question is discussed in detail by Straus (1938), with whose opinions the present author is in agreement. The extensor digitorum profundus, formed from the coalescence of the originally separate bellies of the extensores breves of reptiles, though blended with the communis, can still be traced to all digits.

The anconeus, well developed in monotremes, has usually been considered as part of the triceps which has migrated distally carrying its nerve supply with it, partly on account of its origin, which may be from the shaft of the humerus in some animals, and partly on account of its peculiar nerve supply, which reaches it by passing between the epicondyle and the olecranon. Brooks (1889) however, from a comparison with the conditions in *Sphenodon*, identified the muscle as an extensor antibrachii ulnaris, and the nerve as a n. extensorius caudalis, and this was accepted by Ribbing (1907), but rejected by Howell (1936*a*) on account of the nerve supply. Conditions in *Echidna* support Brooks's theory, though the reduction from the primitively wide ulnar insertion of the extensor ulnaris must have occurred independently in *Sphenodon* and in mammals.

Of the four radial muscles the tractor has disappeared, though it is just possible that it is represented by Westling's (1889) "brachioradialis" which is supplied by a flexor nerve. The extensor carpi radialis is the old superficialis which has migrated to the metacarpals. The profundus has become the supinator, which in monotremes retains its old origin from the humerus and wide insertion on the radius, as well as its position superficial to the cranial extensor nerve, and between the nerves to the extensor carpi radialis and extensor digitorum communis. Some such derivation has been accepted by all authors except Howell (1936*a*), who thought it might be a part of the supinator manus. This, however, would involve changes in its origin, its insertion and its relation to the nerve to the humerodorsalis, besides the suppression of the profundus, and appears unlikely. The brachioradialis is inserted on the scapho-lunar, a monotreme specialization, also found in marsupials, and as in urodeles appears to be an intermedius. Ribbing derived the brachioradialis as well as the extensor carpi radialis from the superficialis of reptiles, chiefly on account of its insertion below the wrist. But the radial insertion appears primitive in mammals. The supinator manus or abductor pollicis is arranged as in reptiles. The extensor digitorum profundus, formed from the short extensors, arises as a single mass entirely from the ulna, instead of partly or wholly from the carpus as in reptiles, and after fusion with the extensor communis appears to be distributed to all five digits. Dorsometacarpals are not developed.

Of the four motor nerves only two remain in mammals, the n. to anconeus or n. extensorius caudalis, and the motor part of the radial n. or n. extensorius cranialis which supplies all the other muscles. The n. dorsalis manus radialis has become peculiarly enlarged in monotremes and supplies all the digits (Westling, 1889).

Ornithorhynchus is similar in structure (Howell, 1936*b*, literature). The extensor digitorum ulnaris is not so differentiated from the extensor carpi ulnaris as in *Echidna*, and still occupies the same osseo-fibrous tunnel on the back of the ulna. Howell states that the anconeus is innervated in common with the extensor carpi ulnaris. His "extensor carpi radialis longus" is the extensor carpi radialis, undivided in *Ornithorhynchus* as in *Echidna* (Eisler, 1895), his "e.c.r. brevis" is the brachioradialis, and his "brachioradialis" the supinator, and all are arranged as in *Echidna*.

Didelphys. In *Didelphys*, the type chosen by Romer (1922) and others, the extensor digitorum communis is inserted into only four digits, so emancipating the first for special movements, and the tendons are connected with each other by expansions over the metacarpals. The extensor carpi ulnaris has the normal mammalian insertion on the fifth metacarpal as in lizards, and the anconeus is arranged as in *Echidna*. The extensor digitorum ulnaris splits into two tendons, one to digit V only, the other to III, IV and V. The extensor

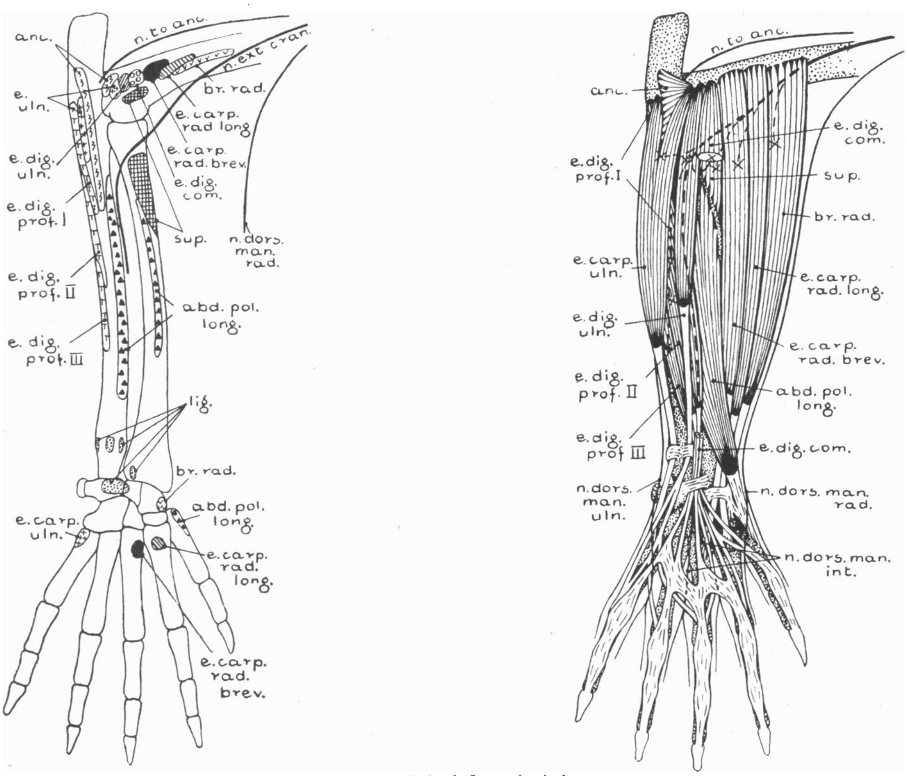


Fig. 11. *Didelphys virginiana.*

carpi radialis is now split as in most mammals into a longus and brevis, passing to metacarpals II and III. The brachioradialis has a peculiar insertion, chiefly into the scaphoid, with a radial expansion to the abductor pollicis longus and an ulnar to the lunate and triquetrum. The supinator is now reduced as in most mammals, so as to reach only the upper end of the radius. The abductor pollicis is large and now arises from both radius and ulna. The three bellies of the deep extensor are inserted into digits I, I and II, and III, the last joining the tendon of the extensor ulnaris to III, but these insertions are variable in *Didelphys* (Coues, 1872; Straus, 1938).

There is no mammal now living that shows the primitive state of the short extensors, but in the common ancestors of the monotremes and other mammals they must have been similar to those of reptiles, with five separate slips to the digits. For in *Echidna* the common belly supplies all the digits, and in other mammals, though the number of slips has been reduced to four as in *Tarsius* (Ribbing, 1907), three as in *Didelphys*, or two as in man, those that remain are separate bellies. Brooks (1889) has described clearly the proximal migration of the short extensors of reptiles on to the forearm of mammals, and this has been accepted by later authors. Ribbing (1907), however, believed that they were primitively a single muscle mass as in monotremes, and that when, in typical mammals, they became independent, they inserted only on digits I and II. This however is not in agreement with the state of the muscles in reptiles, or with their insertion into five digits in monotremes, and three or four digits in most primitive mammals.

The motor nerves are arranged as in *Echidna*, but the cutaneous nerves are more primitive, though variable (Straus, 1938), the three nn. dorsale manus being all well developed.

This account agrees well with that of Coues (1872) and *Didelphys* appears a good type of the mammals, though it may not be primitive in the insertion of the brachioradialis or the splitting of the extensor carpi radialis, very variable features (MacCormick, 1886; Ribbing, 1907, literature). The changes found in other mammals and in primates in particular are discussed fully by Straus (1938).

DISCUSSION OF SPECIAL POINTS

Nerves. The muscles of the radial group are quite constant in their innervation, the tractor radii by a special nerve, and the rest by the n. extensorius cranialis. All the other muscles are variable, for all may be supplied by the n. extensorius cranialis (frogs, crocodiles), or by the n. extensorius communicans (lizards), or they may be supplied by a combination of these and the n. extensorius caudalis (the primitive tetrapod condition), or by the cranialis and caudalis alone (*Salamandra*, mammals). The caudalis when present may supply only the extensor antibrachii ulnaris (mammals), or the whole of the ulnaris and part of the humerodorsalis (primitive state). Clearly in this region little reliance could be placed on the nerve supplies if the homologies of the muscles were doubtful.

On the other hand though in other regions the courses of the motor nerve trunks are known to change (Haines, 1935), in the forearm they are remarkably constant. The n. extensorius cranialis always passes between the tractor and intermedius, and then deep to the intermedius and superficialis and deep to or through profundus. The n. to superficialis always separates the intermedius and profundus, and the n. to humerodorsalis the profundus and extensor ulnaris, whether it comes from the cranial extensor n. or the communicating n.

Again the n. extensorius caudalis always passes deep to the extensor ulnaris or its derivatives and the dorsal interosseous deep to the supinator manus. Only in anurans are any variations found.

The cutaneous trunks are less constant, and in the hand they vary in their relations to the short extensors and dorsometacarpals. The n. dorsalis manus radialis may pass superficial to the brachioradialis (its primitive position), or through it (*Salamandra*), or deep to it (man).

Muscle functions. The functions of the muscles and the mechanical effects of their migrations cannot yet be determined in detail, for the movements of the joints are not sufficiently understood. Watson (1917) has shown however that in early tetrapods the movements of the humerus at the shoulder joint were limited to an antero-posterior swing of the horizontally placed humerus through a short arc, with little dorso-ventral movement and no rotation. The forearm, set at about a right angle on the distal end of the humerus (semiflexion in human terminology), passed downwards and forwards to meet the ground at an angle of 30–40°. Now a mammal in this position would, if it raised its hand from the ground, either raise the humerus at the shoulder joint, or rotate it so as to lift the forearm into a more horizontal position, but both these movements were impossible in early tetrapods. So the forearm at the elbow joint, besides flexion and extension, was capable of a considerable degree of elevation and depression in the sagittal plane. Pronation and supination were, if present, very limited, but the same effective movement was allowed by independent elevation and depression of the radius and ulna, and by movements of the wrist and carpo-metacarpal joints.

Now flexion and extension were chiefly carried out by the muscles of the upper arm, helped by those of the forearm which crossed the elbow joint, particularly flexion, used for dragging the animal forward, by the tractor radii. The other muscles inserting on the forearm, including on the extensor surface the major part of the ulnaris, and the radialis profundus and intermedius, were concerned in controlling elevation and depression, and the large epicondyles of early tetrapods were developed in association with these movements. The chelonians, having preserved a relatively primitive type of gait, in spite of the more anterior position of the elbow enforced by the carapace (Watson, 1914), still possess a very primitive musculature.

In *Sphenodon* and lizards, Fürbringer (1886) mentions besides flexion and extension only movements of the radius and ulna relative to one another. But here again elevation and depression appear important movements, although the shoulder joint is less rigid than in early reptiles. One of the muscles previously concerned mainly with elevation, the extensor ulnaris, is now partly or wholly concerned in wrist movements, while the others remain as before. Howell (1936*a*) after examination of *Necturus* and *Iguana* came to the conclusion that the muscles passing from the lower end of the humerus to the radius and ulna could do nothing but fix the elbow joint. But the muscles are well developed and fleshy, whereas if they could never contract they would be ligamentous, and it seems more likely that they are active in the special movements discussed.

In mammals elevation and depression of the forearm have been lost, and pronation and supination acquired. The anconeus, a remnant of the ulnar part of the extensor ulnaris, is now small and acts as an extensor only, while the remainder of the muscle acts on the hand. The profundus in eutherian mammals is reduced, and specialized for its new function of supination. The tractor radii has gone, while the intermedius, though retaining its insertion on the radius, has changed its function, migrating up the shaft of the humerus and becoming a flexor, the brachioradialis. In monotremes, where as shown by Howell (1937) the bones at the elbow joint form a modified ball and socket articulation allowing flexion, elevation and rotation of the forearm, the profundus retains the reptilian type of insertion.

Too little is known of movements at the wrist for profitable discussion, and the reasons for the extension of the humerodorsalis to the terminal phalanges are not understood.

Table of homologies

Primitive tetrapods and turtles	*Sphenodon*	*Urodeles*	*Didelphys*
Humerodorsalis	Humerodorsalis	Humerodorsalis	Extensor digitorum communis
Extensor ulnaris	Extensor carpi ulnaris Extensor antibrachii ulnaris	Extensor ulnaris	Extensor carpi ulnaris Extensor digitorum ulnaris Anconeus
Tractor radii	Tractor radii	—	—
Extensor radialis superficialis	Extensor radialis superficialis	Extensor radialis superficialis	Extensor carpi radialis longus and brevis
Extensor radialis intermedius	Extensor radialis intermedius	Brachioradialis	Brachioradialis
Extensor radialis profundus	Extensor radialis profundus	Extensor radialis profundus	Supinator
Supinator manus	Supinator manus	Supinator manus	Abductor pollicis longus
Extensores digitorum breves	Extensores digitorum breves	Extensores digitorum breves	Extensor digitorum profundus
Dorsometacarpales	Dorsometacarpales	Dorsometacarpales	—

SUMMARY

1. The muscles of examples of all orders of reptiles and amphibians with limbs are described with their bony attachments, nerve supplies and relations to nerve trunks.

2. In primitive tetrapods the muscles consisted of an extensor ulnaris to the ulna and pisiform, a humerodorsalis to the metacarpals, a tractor radii and extensores radiales superficialis, profundus and intermedius, a supinator manus, extensores digitorum breves and dorsometacarpales. The tractor was supplied by a special nerve from the flexor region, the rest by the n. extensorius cranialis and caudalis, and the n. extensorius communicans passing through the radio-ulnar space. The muscles inserted on the forearm were associated

chiefly with movements of elevation and depression of the forearm at the elbow joint.

3. The less specialized chelonians have preserved the primitive gait, musculature and innervations, but the ectepicondylar foramen, primitively an open groove, has closed.

4. The urodeles have lost the tractor radii, and the ulnaris has moved to the ulnare. In *Necturus* the short extensors have been lost, in cryptobranchs the humerodorsalis has reached the phalanges and the dorsometacarpales have been lost.

5. The early amphibians, such as *Eryops*, still retained the tractor radii.

6. In anurans the ulnaris is split, the humerodorsalis reaches the phalanges, the radial group is highly specialized, the supinator manus reaches the humerus, and the motor nerves are reduced.

7. In *Sphenodon* the humerodorsalis insertions are reduced and the ulnaris is split into antibrachial and carpal parts, and reaches metacarpal V.

8. In lacertilians the humerodorsalis insertions are further reduced, and the extensor antibrachii ulnaris lost. The n. extensorius communicans supplies most of the muscles.

9. In crocodiles the extensor ulnaris is confined to the ulna, the humerodorsalis insertions reduced, the retractor lost, and the hand muscles specialized. All are supplied by the n. extensorius cranialis.

10. In mammals elevation and depression at the elbow joint have been lost. The tractor is missing, and the other radial muscles are specialized. The humerodorsalis extends to the phalanges and the ulnaris to metacarpal V, with an antibrachial part forming the anconeus. The n. extensorius cranialis becomes the motor part of the radial and the caudalis the n. to anconeus.

11. Though the nerve supplies to all muscles except those of the radial group are variable, the courses of the nerve trunks are constant except in anurans.

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KEY TO LETTERING

abd. pol. long.	abductor pollicis longus
anc.	anconeus
br. rad.	brachioradialis
carp. met.	carpometacarpalis
Cen.	centrale
dors. met.	dorsometacarpalis
e. ant. uln.	extensor antibrachii ulnaris
e. carp. rad.	extensor carpi radialis
e. carp. rad. brev.	extensor carpi radialis brevis
e. carp. rad. long.	extensor carpi radialis longus
e. carp. uln.	extensor carpi ulnaris
e. dig. brev.	extensores digitorum breves
e. dig. brev. acces.	extensor s digitorum breves accessorii
e. dig. brev. med.	extensores digitorum breves medii
e. dig. com.	extensor digitorum communis
e. dig. prof.	extensor digitorum profundus
e. dig. uln.	extensor digitorum ulnaris
e. rad. int.	extensor radialis intermedius
e. rad. prof.	extensor radialis profundus
e. rad. sup.	extensor radialis superficialis
e. uln.	extensor ulnaris
e. uln. acces.	extensor ulnaris accessorius
For.	foramen
for. ectep.	ectepicondylar foramen
hum. dors.	humero-dorsalis
Int.	intermedium

Int.-uln.	intermedio-ulnare	*n. to tr. rad.*	n. to tractor radii
lig.	ligament	*Pis.*	pisiform
n. dors. man. int.	n. dorsalis manus intermedius	*Rad.*	radiale
n. dors. man. rad.	n. dorsalis manus radialis	*Sca.-lun.*	scapho-lunar
n. dors. man. uln.	n. dorsalis manus ulnaris	*sup.*	supinator
n. ext. caud.	n. extensorius caudalis	*Sup. cr.*	supinator crest
n. ext. com.	n. extensorius communicans	*sup. man.*	supinator manus
n. ext. cran.	n. extensorius cranialis	*sup. man. acces.*	supinator manus accessorius
n. flex.	n. flexorius	*Tri.*	triquetrum
n. int. dors.	n. interosseus dorsalis	*tr. rad.*	tractor radii
n. int. vent.	in. interosseus ventralis	*Uln.*	ulnare
n. to anc.	n. to anconeus	*uln. met.*	ulno-metacarpalis