Article VII.—THE PECTORAL LIMB OF ERYOPS AND OTHER PRIMITIVE TETRAPODS

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INTRODUCTION

It is generally agreed that the primitive tetrapod is a direct evolution from an original fishlike ancestor, and there seems no doubt that this primitive tetrapod was an amphibian. The members of this group retain fishlike characters possessed by no other group of tetrapods, and among them are the most generalized four-footed animals.

There is strong evidence that the early Amphibia gave rise to the most primitive reptilian groups, and there seems no serious question, at the present day, that the birds and mammals are offshoots from the reptilian stem. It is even possible to postulate that the origin of the first reptiles may be looked for in the group Stegocephalia among the Amphibia; while the birds unquestionably arose from some swift-moving, light-boned diapsid type, and the paleontological evidence that the cynodont reptiles gave rise to the primitive mammals has been greatly strengthened in recent years. In all these cases there are transitional types which, from the standpoint of paleontology and comparative anatomy, give a reasonable explanation for the origin of many of the most characteristic structures typical of the various tetrapod classes, which in many cases is strengthened by embryological data.

Between the most primitive Amphibia, however, and the original fish ancestor, there is a more serious gap. The fishlike segmentation of the amphibian body musculature, the possession in most forms of functional gills and gill slits at least at some time in the life history, the intermediate condition of the heart and circulatory system in general, the brain, the survival of lateral line organs, the arrangement of the dermal and cartilaginous bones of the skull, the presence of dermal scales, and many other anatomical and physiological features, bespeak a fish ancestry for the group; but the origin of the pentadactyl tetrapod limb is not well known. No transitional types leading to its essential structure exist, and yet no comparative anatomist of today can deny its ultimate origin from the paired fins of fishes. Clear indications of the piscine origin of the early amphibian shoulder girdle are to be seen in such structures as the cleithrum and primitive clavicle of the stegocephalian amphibian; but the limb itself, with its humerus, radius, ulna, carpals, metacarpals and phalanges, may as yet be only categorically referred to their probable origin in a hypertrophy and rearrangement of certain basal fin elements of the crossopterygian ganoid, the fish type which in other respects most nearly suggests an approach to amphibian ancestry.
We have, then, in the primitive amphibian a creature that evolved from a fishlike ancestor, but in the full possession of a typical digitated limb, articulating from a girdle betraying its piscine origin, but separated by a considerable gap from the true fish-fin. On the other hand, we have in the amphibian tetrapod limb the most primitive structure of this kind among the higher animals. Its musculature is fundamental to that of the higher types, and a clear understanding of its structure and arrangement is essential in interpreting the manifold changes which have taken place in the limb muscles of the various tetrapod classes and orders. It will also give the nearest approach to the fundamental musculature of the paired fish-fin. Should fossil transitional forms at some time be found, the relationship between the musculature and skeleton of the amphibian limb would be helpful in interpreting its significance, and, since the earliest stegocephalian amphibian is by far the most primitive tetrapod, it is clear that a knowledge of its musculature, could it be gained, would be of great importance. The remains of the Stegocephalia, though abundant, are naturally skeletal in their nature, and, at first sight, it would seem impossible to arrive at even an approximately accurate idea of their musculature. Nevertheless, we know from the physiological processes of bone formation, that the vertebrate skeleton is deposited in the form of cartilage or carbonate of lime, or both, in the interstices of the connective tissue network which also encloses the contractile muscle cells. It is obvious that these hard, skeletal deposits cannot exist where they would interfere with muscle action, and, conversely, it is evident that they would occur in most highly developed condition where they would assist and strengthen that action. The areas of lost motion between opposing muscle groups would best answer this purpose, and it is in such intermuscular fibrous regions of connective tissues that the fundamental internal bony or cartilaginous skeleton is found. In the course of time, this was combined with bony protective plates on the outer surface of the body, which, through underlying connective tissue strata, are connected with muscle areas, and the two systems of rigid structures were welded into a framework where customary muscle contraction most required it.1

The vertebrate endoskeleton may, therefore, be said to have been extensively molded by muscle activity, and its form to the smallest detail often shows indications of this fundamental influence. If, therefore, the skeleton of vertebrate types is studied in conjunction with the muscular and connective tissue systems and interpreted from this light, much can

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1The skull conspicuously illustrates this principle, for it is composed of a series of arches braced mechanically against the pulls and stresses of vigorous jaw and trunk muscles.
be inferred, conversely, regarding the original musculature of fossil types by an intelligent study of their skeletal remains, especially if careful comparisons are made with the skeletons of the most nearly related living forms.

In this paper an attempt has been made, first, to restore the pectoral girdle and limb of a primitive amphibian tetrapod of the stegocephalian group, and, by a careful comparison of the musculature of a primitive living amphibian with that of a living reptile in relation to the skeletal structure, to infer the typical stegocephalian musculature of this region and interpret it with especial regard to its character as the fundamental anterior limb musculature of the tetrapods as a whole. The species *Eryops megacephalus* Cope has been chosen for restoration: first, because it is one of the most typical of the Stegocephalia; second, because of the abundance of its fossil remains; third, because of its large size and, consequently, the comparative ease with which the characters of the skeleton and the surface indications of the muscle attachments may be made out; fourth, because of the very complete ossification of the skeleton, which makes it unnecessary to restore hypothetically large areas of cartilaginous skeleton, and, to a corresponding degree, renders more certain the size, shape and articulation of the comparatively small cartilages that must be inferred; finally, because it is evident that it has not been greatly specialized either for an aquatic habitat or for any restricted terrestrial habit of life.

Hence, it exhibits a generalized condition of fundamental importance as indicating a center of anatomical radiation for the skeletal and muscular systems of all the later specialized and more closely adapted vertebrate groups. A clear understanding of its structure is thus of the greatest significance in throwing light upon the origin and evolution of the morphology of present-day vertebrates, as contrasted with the former custom of selecting specialized modern types for this purpose.

The pectoral girdle and limb have been chosen for this study, partly because of the necessity for a limit to the inquiry, partly because their evolution is typical of that of the locomotor mechanism as a whole, and partly because of various interesting problems which have arisen in connection with the later history of the limb along both the amphibian and the reptilian lines.

Much has been written regarding a possible "serial homology" between the various bones and muscles of the pectoral and pelvic systems. This question, though interesting, is so complicated, and many of its aspects are so doubtful, that it will not be touched upon in this paper,
other than to record the writer's impression that the many similarities, close as they often appear to be, are probably the result of parallel evolution of two systems of similar origin undergoing progressive adaptive changes, under similar conditions.

This paper, therefore, will be confined entirely to a consideration of the fundamental vertebrate skeleton and musculature of the pectoral girdle and limb and their bearing on the evolution of later types.

The jaw muscles of vertebrates have been treated in a similar way in a valuable paper by L. A. Adams (1919), while W. K. Gregory and C. L. Camp (1918) have shown the value of utilizing primitive types for interpreting the musculature of modern forms by their study of the skeleton and inferred musculature of *Cynognathus*, as a basis for analyzing the evolution of the fundamental mammalian musculature. In this work, however, they adopted the homologies of Fürbringer and Gadow for reptilian and mammalian musculature. A. S. Romer (1922) has carried this work further and has established a more exact basis of homology by comparing modern reptilian and mammalian musculature and skeletal features with the skeletal features of a large series of fossil reptiles, and has succeeded in throwing considerable light on the chief features of mammalian muscle systems as evolved from reptilian prototypes.

The present paper aims to emphasize the splitting of the generalized stegocephalian musculature into that characteristic of the primitive amphibia as distinguished from the musculature of the primitive reptiles, contrasting the basic features of the pectoral limb musculature of each, with especial reference to the evolution of the amphibian type of muscle arrangement as distinguished from that of reptiles.

The method of investigation has been as follows: Because of the established ancestral relationship of the Stegocephalia as a group to both the amphibian and the reptilian stems, (1) the fossil remains of a typical stegocephalian limb skeleton were restored, reassembled and compared with the limb skeletons of the most generalized living reptile and one of the most generalized living amphibians, and the undoubted skeletal homologies noted. (2) The pectoral limb musculature of the two recent types was dissected, and its relations to the respective skeletal features noted. (3) The amphibian musculature was then homologized as far as possible with that of the reptile, using as criteria the location of the basic muscle systems; their relations to each other and to the bones; their position with reference to the chief nerve trunks and blood vessels, and, especially, to the principal intermuscular connective tissue areas; their origins and insertions, and, finally, their innervations. (4) An endeavor
was then made to infer the ancestral stegocephalian musculature, by assuming that homologous muscles in both groups would be represented in their common ancestral stock; that the origins and insertions of this musculature would be largely determined, first, by surface features on the ancestral skeleton homologous to those on the recent amphibian and reptilian girdle and limb bones, and, second, by assembling the fossil skeleton as nearly as possible in its original position; that the chief differences between the recent and fossil skeletons would also give a clue to corresponding differences between recent and stegocephalian musculature; and that the chief differences between recent reptilian and amphibian musculature might be explained by comparing them simultaneously, in connection with the correlated skeletal features with a limb skeleton representative of their common ancestral type and its inferred musculature. (5) These observations were checked by a comparison with other fossil material and modern types, by considering the work of other investigators and by giving due weight to embryological data so far as they are known.

During the course of the work an attempt was made to reassemble the shoulder girdle of Eryops in relation to the axial skeleton, and, by a restoration of the musculature, to arrive at the muscular action of the anterior part of the animal and its probable appearance in life.

An attempt has been made to solve several of the moot questions regarding Eryops, as well as the evolution of certain problematic amphibian features.

The recent types chosen for comparison are Sphenodon punctatus (Gray) of New Zealand, and Megalobatrachus maximus (Schlegel) of Japan. The works of Fürbringer (1900) and Osawa (1898, 1902) have been freely consulted in connection with their dissection, and several differences noted between my own opinions and interpretations and those of these authors. The opportunity has also been utilized to present clearer figures of certain features of dissection than have hitherto been published, and to figure others which have never been illustrated.

As is well known, the genus Sphenodon is a very ancient type, belonging to the group Rhynchocephalia, with fossil representatives reaching back to mid-Triassic times. The only living species possesses, on the whole, the most generalized skeleton and musculature of all known living reptiles, and it is practically a "living fossil."

Megalobatrachus japonicus (Schlegel), until recently grouped with Cryptobranchus alleganiensis (Daudin), is now considered to be generically separate. It is the largest known urodele, and, together with
Cryptobranchus and the primitive hynobiids (Noble, 1922; Dunn, 1922), exhibits what is probably the most primitive musculature of living Amphibia. It shows considerable adaptation to life in the water, but its cenotelic characters are readily detected and have to do mostly with general body form and a greater development of cartilaginous skeleton, or rather, what amounts to the same thing, a very incomplete ossification.

I wish to acknowledge especially the great assistance derived from the various works of Fürbringer (1873-1900) on reptilian and amphibian shoulder musculature, as well as those of Osawa (1898, 1902), Ribbing (1907), Rabl (1901), Siegelbaur (1904-1909), Wilder (1903-1912) and McMurrich (1903-1920). I wish to acknowledge my indebtedness to the paleontological works of Abel (1919), Case (1900-1915), Williston (1910-1920) and Moodie (1909-1916), and to express my admiration for the excellent work of Professor D. M. S. Watson (1917a) on the evolution of the tetrapod shoulder girdle and the classification of primitive tetrapods.

Especial thanks are due to The American Museum of Natural History for the use of the collections; to President Henry Fairfield Osborn, Director F. A. Lucas and Curator W. D. Matthew for many courtesies extended to me; to Dr. A. S. Romer and Dr. G. K. Noble for critical discussions and valuable suggestions during the final revision of the manuscript, and, finally, but particularly, to Dr. W. K. Gregory for the inspiring interest and enthusiastic support he has given me in connection with the whole work and for his invaluable aid and advice during its gradual evolution.
Fig. 1.—Mounted specimen of *Eryops megacephalus* in The American Museum of Natural History, showing right side.

Fig. 2.—Same as figure 1, showing left side.
SECTION I. PECTORAL SKELETON

A. SHOULDER GIRDLE

a. The Shoulder Girdle of Eryops

*General Description of Eryops.*—The chief skeletal remains of *Eryops* have been derived from the Permian deposits of Texas and Oklahoma, where the species *Eryops megacephalus* is abundantly represented. It is also known from the Permian of Kansas and Illinois (Case, 1915, p. 127) and doubtfully from New Mexico. Case has found vertebral remains in the Upper Pennsylvanian of Pittsburgh, Pennsylvania, which he assigns to the genus *Eryops*. Hence the range of the genus may be said to extend from the Upper Carboniferous through the Permian.

The fossils thus far found include practically the entire skeleton, of which a nearly complete specimen is shown restored in the American Museum of Natural History (Figs. 1, 2, 4). Numerous skulls of remarkable completeness are known, and separate limb bones and vertebrae are frequent, of which the richest collections are those of the American Museum of Natural History, the Walker Museum at the University of Chicago, and the Museum of the University of Michigan.

*Eryops* is the largest known Permian amphibian (Case, 1915), reaching more than six feet in length, with massive solid-roofed skull of the stegocephalian type (Fig. 4), elongate powerful jaws, well equipped with conical pleurodont teeth of irregular size, as usual in animals having carnivorous habits of feeding. The eye sockets, set posteriorly and toward the summit of the skull, are in the position characteristic of animals accustomed to a partly submerged habit of life, though the powerfully built limb bones, capable of supporting the weight of the body, betray a capacity for terrestrial locomotion. *Eryops* doubtless lived in comparatively shallow waters on the margin of swamplike lakes and streams, as shown by the geological character of the deposits in the region where it lived and pursued its prey. Coprolites found in the vicinity of its remains, if referable to *Eryops*, would indicate that its food included fish and smaller amphibians (Case, 1915).

The massive pectoral girdle (Figs. 3, 7, 10, 15) consists of paired scapulocoracoids, clavicles and a single median interclavicle. The scapular blade is equipped with a well-developed cleithrum.

The pectoral limb bones (Figs. 7, 18, 21) comprise a short, massive humerus, short radius and ulna, a well-ossified carpus, consisting of eleven carpal bones, four digits and a prepollex, with short metacarpals and phalanges. The latter, though not completely known, probably possessed the formula, 2.2.3.2.
These elements will now be described in detail.

Scapulocoracoid.—The scapulocoracoid (Fig. 3) is a heavy single bone, there being no evidence of a suture separating it into scapular and coracoid elements. The greater portion consists of the elongate scapular blade extending vertically, while the ventral coracoidal portion is a comparatively small region with rounded border. On the anterior border of the scapula there is a moderately well-developed cleithrum, a membrane bone with a slender stem ventrally and an expanded portion dorsally, which overlaps the dorsal end of the scapula and tapers to a curving point at the upper posterior angle.

Fig. 3.—Restoration of the shoulder girdle of Eryops, with elements in their proper relations, but represented as if in one plane.

Note that the clavicles are separated from each other on the median line, and thus do not overlap. The coracoid cartilage (COR. CART.) and sternum (ST) are inferred and separate the scapulocoracoids.

The comparatively small coracoidal portion is mostly anterior to the glenoid cavity, with a much smaller extension posterior and ventral to the glenoid. It is pierced by the supracoracoid and glenoid foramina, just ventrally to the anterior part of the glenoid cavity. It is worthy of note that the greater expanse of the coracoid is situated anterior to the supracoracoid foramen.

The medial margin of the coracoid is marked around the thickness of its edge by a shallow groove that extends from well around the anteromedial border to a point just back of its posterior curve, terminating a short distance below the posterior limit of the glenoid. This marks the articulation with the cartilaginous portion of the coracoid, which is, of course, not preserved in the fossil specimens.
Fig. 4.—Mounted specimen of *Eryops megacephalus* in The American Museum of Natural History. Dorsal view.
The scapulocoracoid is braced on the inner side by the heavily ossified supraglenoid buttress, spanning the oval, tunnel-like supraglenoid foramen at the junction of the scapular and coracoid regions (Figs. 10 and 11). This arch extends upward as a strong buttress on the inner side of the scapular blade, while its lower extremity curves medially and posteriorly to form the posterior border of the coracoid. On the outer face the base of the scapular portion terminates in a boss-shaped process which forms the anterior or scapular limit of the glenoid cavity, the posterior part of which is excavated out of the posterolateral surface of the supraglenoid buttress which embraces it from behind. It is thus framed in between these two features of the bone.

The glenoid cavity is "screw-shaped" and elongate. It runs in an anteroposterior direction. Its form and relations to the scapula and supraglenoid buttress are shown in figures 3, 11 and 15. It will be further described in considering the articulation of the humerus.

Immediately posterior to the glenoid cavity on the hinder edge of the coracoid, is an excavated triangular area (Fig. 11 E), which is in the proper position to serve as the attachment for the coracoid head of the anconeus muscle.

Just below the supraglenoid buttress there is a triangular pit, the subscapular fossa, within which lie the inner openings of the supraglenoid and supracoracoid foramina. At the junction of the supraglenoid buttress with the internal coracoidal surface is the inner aperture of another foramen which opens on the outer surface of the coracoid in a depression posterior to the supracoracoid foramen and below the center of the glenoid cavity. This has been termed the glenoid foramen (Williston, 1909).

Clavicle.—The clavicle (Figs. 3, 15), like the cleithrum, is a membrane bone, as indicated by its sculptured outer surface. Dorsally, it overlaps the anterolateral surface of the ventral stem of the cleithrum, following the lower anterior border of the scapulocoracoid. It is somewhat narrowed dorsally, but it expands ventrally to form a thin tapering plate, strengthened by a rounded ridge along its outer median surface. It tapers to a blunt point at the ventral terminus where its surface is ornamented by low, fluted ridges. Ventromedially, it extends beyond and anterior to the scapulocoracoid, and articulates with the interclavicle in the manner shown in figure 3, as will be explained below. At about two-thirds of its extent, ventrally, it shows a slight bend, forming a low boss at an angle of about 150 degrees. Several clavicles have been found bent at varying angles nearly approaching a right angle, as in the
articulated girdle (No. 4186, A. M. N. H.) described and figured by Cope (1888) and by Case (1911) but these give clear evidences of having been bent and crushed out of shape. A pair of clavicles in the American Museum (No. 4307), although broken, have perfect contact surfaces and are uncrushed. They doubtless show the correct angle and also to a large extent the surface sculpture.

**Interclavicle.**—The interclavicle (Figs. 3, 10, 15) is a median membrane bone, rhomboid, or rather fan-shaped in outline, sculptured on its lower surface, although the girdle figured by Cope, above mentioned, possesses an interclavicle sculptured visibly only at its anteromedian edge, where it shows a number of toothlike projections. These appear to be about seven in number, the median one being the longest.

**Restoration of the Shoulder Girdle** (Figs. 3, 7, 10, 15).—The fossil remains of the shoulder girdle are so complete that the form of the various osseous elements is well known. There is, however, some question as to the details of their articulation and their exact positions with relation to each other. The girdle of Cope, referred to above, was found with its elements in situ, but, as already mentioned, to a certain extent crushed and distorted out of shape. For example, the coracoids have been forced together on the median line, while the clavicles have buckled practically to a right angle and forced the interclavicle posteriorly, till it is overlapped by the coracoids. The clavicles also considerably overlap on the median line. Case considers this the normal position, but the evidence drawn from the uncrushed separate clavicles (A. M. N. H. No. 4307) above mentioned, would of itself necessitate a restoration such as that shown in figures 3, 10, and 15, when they are placed in relation to the scapulocoracoid of the same animal, of which a separate specimen has also been preserved. This is in the collections of the American Museum (A. M. N. H. 4307) and forms the basis of the restorations here figured. The mounted specimen in the American Museum has likewise been restored erroneously for the same reason (Fig. 1; cp. Fig. 7). The clavicles are bent inward until their extremities form a transverse line with each other and overlap, while the interclavicle is thrust backward like that in Cope’s specimen.

This position appears to be quite unnatural and unnecessary. I believe that the conception here outlined (Figs. 3, 7, 10 and 15) presents not only a more natural contour and one that will admit of better muscular insertions and directions, as will be shown in a later section, but is in harmony with the conditions obtaining in *Archegosaurus*, *Mastodonosaurus*, *Lydekkerina* and other Permian amphibians in which
Fig. 5.—Shoulder girdle of *Archegosaurus* from ventral side, after von Meyer.

Note the correspondence with the restoration of the shoulder girdle of *Eryops* (Fig. 3). The clavicles are separated on the median line. In none of von Meyer's figures do they overlap. Note the position and arrangement of the ventral scutes.
these elements have either been preserved in their apparently correct
relations, or show their method of articulation by their surface markings.

I am convinced that the lateral angles of the interclavicle were held
between the ends of the clavicles, ventrally, and the cartilaginous portion
of the coracoid, dorsally, as shown in figure 3, and that there was a
considerable interval between the medial points of the two clavicles, thus
leaving free the median more heavily sculptured ventral face of the inter-
clavicle, together with its toothed anterior border. Indications on the
inner surface of the clavicles seem to confirm this.

The articulation in Archeosaurus is especially well shown by von
Meyer (1858, Pl. ix), from whose work a plate (Fig. 5) has been re-
produced. Sketch figures in Watson's excellent article (1919, Fig. 9,
p. 18, and Fig. 22, p. 37) also show the same conditions in Mastodonos-
saurus and Lydekkerina. All of these stegocephalians are closely related
to Eryops, and show very clearly that the anterior edges of the rhomboid
interclavicle were reserved for articulation with the ends of the clavicles,
while the two posterior surfaces are in position to articulate with an
anterior series of ventral scutes superficial to the cartilaginous border
of the coracoid. In no cases do the clavicles overlap, though in Metopias
(Fraas, 1888, Pl. xv), a relative of Mastodonosaurus, the girdle has been
specialized to form a closely articulated plastronlike structure ventrally,
with the medial edges of the clavicles meeting on the median line for a
considerable distance, and apparently welded together, but nevertheless
without overlapping. The posterior part of the "plastron" is formed by
the interclavicle, the two anterior edges of which firmly interlock with
the posteromedial edges of the clavicles.

In the case of Eryops and Archeosaurus, these elements appear to
have moved freely upon each other within certain limits, but I can see
no indication that they normally overlapped, as shown in the mounted
skeleton in the American Museum. It is also necessary to allow space
for the coracoid cartilages indicated by the marginal grooves on the
bone. They could not have been very wide and doubtless overlapped
anteriorly, like the coracoids in modern urodele amphibians (Megalob-
obotrachus, Fig. 12) and the precoracoids of Sphenodon (Fig. 14)\(^1\). These
cartilages doubtless slid freely one over the other and dorsal to the inter-
clavicle, the lateral corners of which articulated in the notch formed by
the ends of the clavicles and the anterior ends of the cartilaginous cora-
coids (precoracoids).\(^2\) Shallow depressions on the dorsal or inner side of
the fossil clavicles seem to confirm this method of articulation.

\(^1\)After Förbringer (1900).

\(^2\)The term "precoracoid" is taken to signify the anterior median portion of the coracoid cartilage
in both reptiles and amphibians, while the "precoracoid" represents the dilated anterior projection of
the coracoid in urodeles contiguous to the articulation with the scapula (see Figs. 12 and 14).
Fig. 6.—Original type of *Alegeinosaurus aphthitos* Case (A. M. N. H. No. 4756) drawn reversed for comparison with figure 7. See page 165.

Fig. 7.—Restoration of shoulder girdle and pectoral limb of *Eryops*, shown from the right side.

Compare with present mounting of specimen in the American Museum (Fig. 1) and with figures 6 and 10. See pages 159-165.
Figs. 8, 9.—Shoulder girdle and fore limb of *Megalobatrachus maximus* and *Sphenodon punctatus* for comparison with *Eryops* (Fig. 7).
The entire apparatus, articulated in this way, gives greater freedom of motion than in previous restorations and extends the range of the relatively limited backward and forward movement of the humerus, thus making a more efficient locomotor mechanism.

Again, the more anterior projection of the ventral part of the girdle on the median line, as compared with previous restorations, presents a more natural profile, and one more nearly in harmony with the elongate skull. This is evident from figure 7. The position is a more natural one for the attachment of the trapezius and omohyoideus muscles and gives them a more logical direction.

The natural dorsoventral slant of the scapulocoracoid is shown in the figure, and is obtained by this arrangement of the girdle when the ventral profile of the girdle is nearly parallel with the ground, and the dorsal extremity of the scapula with its cleithrum is properly oriented with reference to the spinal column. The suggested transverse slant of the scapulocoracoids is shown in figure 10, which brings the glenoid in the

Fig. 10.—Restoration of shoulder girdle of Eryops, viewed anteriorly.
Note relative positions of clavicles and interclavicle; the slope of the scapula; also the position of the humerus at the end of the stride (a), and at its beginning (b). The coracoid cartilage (COR. CART.) is inferred. See pages 158-159.
best mechanical position with reference to the head of the humerus, where
the supraglenoid buttresses it to the best advantage, and the glenoid
itself partly arches over the condyle in such a manner that the weight
of the animal is planted squarely upon it when the foot rests upon the
ground. The outward swing of the scapula does not extend beyond a
line drawn backward from the angle of the jaw, parallel to the vertebral
column. The anteroposterior position of the scapulocoracoid harmo-
nizes with that of the related form Alegeinosaurus, of which the Museum
possesses a specimen (A. M. N. H. 4756) with the scapulocoracoid
practically in situ (Fig. 6).

The hyoid apparatus, as may be seen by comparison with such a
primitive living amphibian as Megalobatrachus, would fit nicely in the
great triangular space embraced between the rami of the lower jaw and
the anterior part of the shoulder girdle (Figs. 33a and 33c).

Articulation with the Humerus (Figs. 10 and 11).—The glenoid
surface for articulation with the humerus is a "screw shaped" elongate
excavation along an anteroposterior axis on the posterolateral face of the
scapulocoracoid, immediately posterior to and beneath the supraglenoid
buttress, and embraced by the backward extension of the latter and the
"boss" or projecting process at the lower posterior angle of the scapula.
As the shape of this surface can be well understood only by viewing it
from different angles, a series of figures (Fig. 11 A to F) are given here-
with to illustrate it, beginning with a directly lateral view (Fig. 11 A)
and gradually rotating the bone, until it is seen from a directly posterior
position (Fig. 11 F).

The articular surface of the condyle of the humerus is a counterpart
of the glenoid in shape, and exactly fits into it, when the humerus is in
its most posterior position. It is strap-shaped, the anterior half being
situated on the extreme proximal end of the humerus head, and therefore
directed forward when the humerus is in its posterior position and
parallel with the body, as in figures 10 (a) and 15, while the posterior
half of the condyle is mostly on the inner surface of the humerus head,
curving forward spirally to become continuous with the anterior portion.

Thus, in the position above mentioned, the anterior part of the
condyle fits against the portion of the glenoid situated against the back
of the posteroventral process of the scapula (Fig. 11 A–F, x) while the
medial portion of the condyle fits against the posterolateral portion of the
glenoid (Fig. 11 A–F, y). The humerus is in this position when the
animal has finished its stride and is on the point of raising its foot for the
next. In reaching forward, the distal end of the humerus is moved
anteriorly, until the bone is practically at a right angle to the body, in the position shown in figure 10 (b). In this movement, the anterior part of the condyle, on the proximal end of the humerus head, slides backward through the glenoid, until it reaches the laterally directed posterior part (y), which, in the former position of the humerus, is articulated with the posterior part of the condyle. The latter has now slid back posterior to the glenoid.

Fig. 11.—The screw-shaped glenoid cavity of Eryops.

As its peculiar shape can best be understood by viewing it from different angles, it is shown first at A as a directly lateral view. Then it is represented as gradually rotated in the successive views, B, C, D and E, and finally at F in a directly posterior position. When the humerus is in its most posterior position at the end of the stride, the anterior part of the screw-shaped condyle, situated on the proximal end of the humerus head, fits at X, and the posterior part, which winds around to the medial side of the humerus head, snugly fits at Y, the entire condyle thus occupying the glenoid throughout its whole extent. When the humerus is moved forward in its reach at the beginning of the next stride, the condyle slides backward through the glenoid until the part formerly resting on X is half-way toward Y, and the posterior part of the condyle has moved out of the glenoid. Since the end of the humerus head now rests against that part of the glenoid formerly occupied by the side of the humerus head, the humerus has necessarily rotated on its longitudinal axis, in the meantime, through an angle of 90 degrees, as shown in figure 10.

Thus, the proximal end of the humerus head now fits in the part of the glenoid (y) formerly occupied by that part of the condyle which is on the inner side of the humerus head, and by this process the lower surface of the distal end of the humerus is turned upward about ninety degrees so that it now faces forward, at the same time that the limb is brought to a right angle with the body. This results from the screw shape of the
condyle and the fact that the end of the humerus head now fits in a part of the glenoid formerly occupied by the side of the head. In this position the lower limb would be raised and stretched forward. The weight of the body is now shifted over on to this limb, as the foot is brought down to the ground; the coracoid and clavicle together slide forward around the side of the interclavicle, and thus lengthen the forward reach of the limb.

The humerus cannot be thrust forward through more than a right angle without dislocation, but the articulation of the radius on the radial condyle of the humerus is very free, and the play of the scapulocoraco-clavicular apparatus around the anterior border of the interclavicle, as well as the alternate shifting of the animal's weight first upon one side and then upon the other, with the resulting sinuous motion of the spine, produce a stride equivalent to a considerable forward thrust, and would probably enable the creature to bring its foot well under the body at the extreme forward limit of the stride.

Now the body is pulled forward, while the head of the humerus slides anteriorly through the glenoid, until the condyle occupies its first position, and, at the completion of the stride, the limb is again parallel with the body, with the elbow directed posteriorly. Then with a thrust upward on the toes, the weight of the body is thrown over to the opposite side, when the process is repeated.

Watson says (1917a, p. 3) that the screw-shaped glenoid and the articular condyle "wound around the head of the humerus" of Eryops "show that the humerus has its motions very strictly limited; it is incapable of any rotation on its long axis, and that axis must be so placed that it lies nearly parallel to the ground," and that "its only possible motion is such that a point on the distal extremity when viewed directly laterally moves along a small segment of a large circle placed parallel to the animal's sagittal plane, with the chord of the segment placed nearly horizontally; in other words, as the humerus moves forward its outer end is first slightly depressed and then raised again."

However, by means of specimens in the American Museum, I am able to demonstrate the possibility of a motion such as I have just described, and to show that a strap-shaped condyle which winds about the humerus head so as to fit into a screw-shaped glenoid, would necessarily give the humerus a virtual rotation on its long axis, which in this case would amount to about ninety degrees.

It may be objected that this motion would cause the posterior part of the condyle to pass outside the limits of the glenoid posteriorly in the
forward motion of the humerus. The obvious answer is, that this is true of the condyles of modern amphibians, reptiles and mammals to an even greater extent, for the articular surface of the condyle is usually much larger than that of the glenoid, so that portions of its surface are continually passing away from the area of contact with the glenoid, the humerus being held in joint only by the walls of the articular capsule.

Doubtless *Eryops* had such a capsule, and there was sufficient play to allow half the surface of the condyle to pass posteriorly to the glenoid.

The very complete ossification of the appendicular skeleton would show that the cartilaginous caps of the joints were comparatively thin.

b. The Shoulder Girdle of *Megalobatrachus*

*General Description.*—The shoulder girdle of *Megalobatrachus* (Fig. 12) is largely a cartilaginous structure, its only ossified portion being the bony scapula. This is a somewhat flattened cylinder of bone rising vertically at the side of the body, expanding to a moderate degree dorsally to articulate with the cartilaginous suprascapula, and having a larger fan-shaped expansion ventrally which articulates with the extensive coracoid cartilage. By far the greater part of this ventral expansion is directed anteriorly toward the procoracoid, while the smaller posterior portion is included within the anterior part of the glenoid. At about the center of the ventral expansion, the bone is pierced by a foramen (Figs. 13a and 13b, FGL?) which seems to be homologous with the glenoid foramen of *Eryops*. A small blood-vessel, apparently a branch of the A. circumflexa scapulae, passes through this opening and connects on the dorsal side of the coracoid with A. supracoracoidea by means of an anastomosing branch. Dorsolaterally from this foramen is a shallow pit (FSGL?), the cavity of which is directed posteriorly toward the glenoid border of the scapulocoracoid but does not pierce it in the specimen examined. This blind pit is so situated as to suggest that it is the remnant of a former supraglenoid foramen, while the bridge of bone arching its opening posteriorly and forming the posterior border of the scapulocoracoid strongly resembles the supraglenoid buttress of *Eryops*, but in a greatly reduced condition. It leads directly to that portion of the scapulocoracoid which embraces the anterior part of the glenoid cavity, and which is associated with the M. subscapularis, as in *Eryops*.

This provisional interpretation would indicate that the mesocoracoid arch of fishes, which as suggested by Romer (1922) may have given rise to the supraglenoid buttress of stegocephalians and primitive reptiles, and, through the latter, to the ligamentum sternoscapulare internum of
Sphenodon and modern lizards, is also ancestral through the stegocephs on another line of evolution to this buttresslike remnant surviving in *Megalobatrachus*. It would be interesting to note whether this is a unique case, or if a similar structure occurs in other urodeles.

If the above mentioned homologies are correct, the supracoracoid foramen in *Megalobatrachus* has been carried medially and posteriorly, as compared with *Eryops*, in correlation with the expansive evolution of the cartilaginous part of the coracoid.

**Supracapula.**—The supracapula is a thin, disklike expansion of cartilage surmounting the bony scapula. Its anterior edge thins out into a band of connective tissue which embraces and unites with the levator scapulae muscle. Posteriorly, it shades insensibly to a thin band of connective tissue, continuous posterovertrally with the enveloping connective sheath of the body.

**Coracoid.**—The coracoid cartilage comprises two portions, the coracoid proper and the procoracoid.

The coracoid proper is a fan-shaped expansion of cartilage, relatively narrow at its lateral junction with the procoracoid and the scapula and with a broadly rounded margin medially. This medial margin overlaps the coracoid of the other side, the right coracoid being the more ventral one.

**Procoracoid.**—The procoracoid (Fig. 12) is a thin, elongate, spatulate cartilage extending forward from its junction with the coracoid and scapula on the ventrolateral margin of the body, superficial to the trunk musculature. Its anterior limit is an imaginary line drawn between the posterior angles of the jaw. Its medial margin bounds an indentation embraced between it and the coracoid proper, extending almost to the ventral edge of the scapula. This indentation is filled by a thin membrane which is continued anteriorly around the forward end of the procoracoid. Near the junction of the coracoid with the procoracoid, the cartilage is pierced by the supracoracoid foramen.

**Sternum.**—The sternum (Fig. 12) is a single triangular piece of thin cartilage with a shallow posterior median indentation, causing it to appear somewhat heart-shaped. It occupies the median angle formed by the posterointernal margins of the overlapping coracoids, which movably articulate with it by means of pocketlike slots or grooves, situated on the dorsal side of its anterior borders.

**Homologies of the Amphibian Shoulder Girdle.**—The preponderance of cartilage, or rather the failure to ossify, in the greater part of the shoulder girdle of *Megalobatrachus*, while an adaptation to aquatic life,
Fig. 12.—The shoulder girdle of *Megalobatrachus* shown from the ventral side for comparison with figures 3 and 14 (represented in one plane).

Figs. 13a and 13b.—The scapulocoracoid and procoracoid of *Megalobatrachus* from the inner (13a) and outer (13b) side, to show the probable remnant of the supra-glenoid buttress (SPG.B) of stegocephs; the blind pit (FSGL) probably representing the supraglenoid fossa; the homologue (?) of the glenoid foramen (FGL), and the distribution of nerves and blood vessels in this region. In 13b, the relation of the M. scapulohumeralis (sch.) to M. procoracohumeralis (procor. hum.) is also shown.

Fig. 14.—The shoulder girdle of *Sphenodon* shown from the ventral side for comparison with figures 3 and 12 (represented in one plane, adapted from Fürbringer).

The shaded areas in this figure and in Fig. 12 represent areas considered homologous in this paper.
is also an inheritance of great antiquity. The urodeles according to Moodie (1916) probably date back to Carboniferous times, when, this author asserts, they form a direct ancestral connection with the aquatic branchiosaurus, through such forms as *Micrerpeton caudatum* Moodie. The branchiosaur girdle was largely cartilaginous with a single center of ossification, the "coracoid" of authors. This bone, however, is certainly a scapula, or at least a scapulocoracoid, since the element often referred to as the "scapula" has the form and position of the cleithrum, articulating in the conventional way with the clavicles, and situated anterodorsally to the bone in question, which should therefore be termed the scapulocoracoid ossification (See Gegenbaur, 1895). This view is confirmed by the fact that the element is usually associated with the humerus head, as seen in the fossils of *Archegosaurus* where they are preserved nearly in situ (Fig. 5), and apparently first ossified to mechanically reinforce the shoulder joint. It is evident from the relative positions of the bones as preserved in many cases, that the remainder of the girdle was largely of cartilage.

In aquatic groups the ossification area would remain relatively small, while in terrestrial, or heavy-bodied, semiterrestrial forms, like *Eryops*, it would be greatly strengthened, accounting for the very complete ossification of the latter form. Throughout the urodeles, the scapula alone is ossified. Forms like *Proteus, Necturus* and the young axolotl have the narrow scapular stem alone ossified. Others, such as *Megalobatrachus*, show that the bony area invades the anterior border of the glenoid. In *Molge*, it embraces not only a large part of the glenoid, but the proximal part of the procoracoid as well, and also includes a small part of the coracoid, completely surrounding the supracoracoid foramen, all from a single center of ossification. In the adult *Amblystoma*, the single ossification is even more extensive, including the entire glenoid, with a considerable invasion of the coracoid. In all these cases the cartilaginous area is very extensive, but the ossified portion appears to be a true scapulocoracoid bone, like that of *Eryops*, but without such an extensive invasion of the coracoidal area and indicating that this is an amphibian character inherited from the very earliest times, before the origin of the reptilian stock.¹

The fossil remains of the branchiosaurus are comparable to the condition in urodeles, except that the former still possess the dermal cleithrum, clavicle and interclavicle, which have been lost by the latter through a continuance down the ages of the aquatic habit of life. This

¹*Siren*, however, and perhaps others are exceptions to this general rule.
loss seems to be the result of a progressively general failure of the dermal skeleton to develop in the urodele stem, since they have also completely lost the external dermal skeleton of bony scales and scutes characteristic of the branchiosaur. The Carboniferous amphibians, in general, including branchiosaur, microsaur and stegocephalian, were well equipped with dermal armature, at least on the ventral side. In the modern urodeles, the only derm-bones remaining are those of the skull, and even here they are greatly reduced in number. Hence, this reduction of the exoskeleton must be regarded as one of the great features of urodele history from the earliest times, and indicates that long-continued adaptation to aquatic life, in this case, affects first of all the dermal skeleton, the only ossifications remaining in the appendicular apparatus being of cartilaginous origin.

The case is different in the Anura. Here the terrestrial leaping habit has necessitated the retention of a compact, well-strengthened pectoral girdle as well as the pelvic specialization along this line.\textsuperscript{1} Not only the scapula but also the coracoid elements are well ossified, while a dermal clavicle has been retained to overlie and strengthen the “procoracoid.” Even the suprascapula possesses a superficial ossification, and Schmalhausen (1917) has shown, from embryological data, that this is a dermal ossification, corresponding closely in position and development with the dermal cleithrum, and is without doubt a survival of this ancient structure. Otherwise, the dermal skeleton has also been lost in the girdle of the Anura, but these traces seem to speak for an antiquity of the group extending back to a much earlier time than the Jurassic, from which the earliest unquestioned fossils have hitherto been taken, and adding interest to the suggestion (Moodie, 1916, p. 73) that the Carboniferous Pelion lyelli Wyman, with its strong, frog-like characters, may be an anuran or at least transitional to this stock.\textsuperscript{2}

The girdle of Anura articulates with a well-developed and partly ossified cartilaginous sternal apparatus on the median ventral line of the body, which has no trace of dermal elements. The “procoracoid” of authors, an anterior transverse bar of cartilage, underlies and is reinforced by a “clavicle” which appears to be of membrane bone.\textsuperscript{3} The “obturator fossa” separates this from the coracoid proper, and through it passes the supracoracoid nerve. Authors generally have homologized the anterior element with the procoracoid of urodeles, the “obturator

\textsuperscript{1} Though the hind limbs may be the principal factor in the act of leaping (Holmes, 1907, p. 27), the shock of landing is partly absorbed by the fore-limbs and the pectoral girdle with their musculature.

\textsuperscript{2} Gregory (1917) has brought forward good evidence, however, to show that the Anura may have been derived structurally directly from the rhachitomous stegocephalians.

\textsuperscript{3} Gegenbaur, C. 1897. “Clavicula and Cleithrum,” Morphol. Jahrb., XXIII.
fossa” with the coracoprocoracoid fenestra of the latter, and the posterior element as the coracoid in both groups. Anthony and Vallois (1914), however, though they accept the homology of the coracoid, regard the “procoracoid” of Anura as not a true procoracoid, but merely a coracoidal prolongation, and the anuran acromion as homologous with the procoracoid of urodeles. They consider the “obturator fossa,” therefore, as an enlarged space about the supracoracoid nerve, and hence, as it were, a supracoracoid fossa. The homologue of the coracoprocoracoid fenestra of urodeles would then be represented by the shallow indention of the anterior border of the girdle, between the acromion and the “soi-disant procoracoide” of anurans. They base their argument on the following points:

1. The acromion of anurans is directed cranially like the procoracoid of urodeles.

2. The axis of the glenoid is directed toward the coracoprocoracoid fenestra in urodeles and toward the indentation between the acromion and so-called “procoracoid” of anurans.

3. The supracoracoid nerve passes through a supracoracoid foramen in the coracoid cartilage in urodeles and through the “obturator fossa” in anurans.

4. The acromiohumeral muscle of anurans corresponds in form, mode of insertion, function and double innervation (by N. dorsalis scapulae and N. supracoracoideus) to the procoracohumeralis of urodeles.

5. This interpretation simplifies the otherwise puzzling homology of the musculature in general of the pectoral girdle in the two groups.

In my opinion the points of Anthony and Vallois have been, as a whole, well taken. In addition I would call attention to the adaptive changes the various parts of the girdle pass through, while the course of the supracoracoid nerve remains relatively stable with reference to the main topography of the girdle. Even in Anura it remains in a position corresponding to that in urodeles, though the axis of the glenoid has changed in its direction, the procoracoid is reduced to an acromion, and the supracoracoid foramen has enlarged to an “obturator fossa.”

The figures of Anthony and Vallois also illustrate the variability of the ossification of the scapulocoracoid in urodeles. In Siren and Menobranchus (Necturus) the scapular shaft only is ossified; in Cryptobranchus (Megalobatrachus) the ossification has invaded the coracoid and the anterior border of the glenoid; in Triton (Molge) it includes the supracoracoid foramen and the coracoid as far as the coracoprocoracoid fenestra, as well as the greater part of the glenoid. This same process is shown
in the ontogeny of the axolotl larva (*Amblystoma*), in young specimens of which only the shaft of the scapula is ossified, while older examples show that the ossification includes a large portion of the coracoid as well, including the entire glenoid and the supracoracoid foramen.

Through all, the general position of the supracoracoid foramen seems relatively stationary, and would seem to be a landmark of importance, ranking with the acromion in this respect, and aiding in identifying the precoracoidal part of the girdle. The urodele condition corresponds to that in *Eryops*, where the scapulocoracoid bone has grown around the supracoracoid foramen.

This condition is, therefore, another amphibian character of great antiquity. The part of the *Eryops* coracoidal area anterior to the supracoracoid foramen may be conceived as homologous with the proximal part of the precoracoidal area of urodeles. It will be noted that the precoracoidal region of *Eryops* includes the greater part if not all the ossified part of the coracoidal expanse, while the metacoracoid is either very small and not separated by a suture or does not exist in *Eryops*.

c. The Shoulder Girdle of *Sphenodon*

*General Description and Comparison with Megalobatrachus and Sphenodon.*—The girdle is figured for comparison (Fig. 141). The principal differences, as compared with the amphibian girdle, are correlated with a much more efficient adaptation for an active terrestrial life. There is an ossified scapula and suprascapula, and the coracoid is separated from the scapula by a suture on the line of the glenoid and shares the glenoid cavity with it. The bony coracoid is pierced by a supracoracoid foramen, anterior to which the precoracoidal portion is bony proximally, and is continued forward by a cartilaginous precoracoidal area, overlapping that of the other side, just dorsal to the interclavicle and projecting slightly beyond it anteriorly. Posteromedially, the coracoidal cartilage is continuous with the cartilaginous extension of the coracoid proper. There is a dermal clavicle connecting the scapula with the interclavicle, articulating with the former by means of an acromion, and with the latter on the ventral side, a short distance from the median line of the interclavicle. It therefore does not overlap its fellow on the opposite side.

The interclavicle (the episternum of Fürbringer) is T-shaped and widely expanded anteriorly to form a well-braced structure with the clavicles, and extends posteriorly along the median line to unite with the sternum.

1Reproduced from Fürbringer (1900).
Posteromedially the cartilaginous portions of the coracoid articulate movably in a marginal groove with the sternum, which is much stronger and larger, and of more significance to the girdle than in Megalobatrachus. The posterior border articulates with three pairs of sternal ribs.

The whole apparatus forms an efficient structure of support for the internal organs, and for the attachment of the powerful ventral muscles inserting on the proximal part of the limb and supporting the weight of the body.

The following differences, as compared with the pectoral girdle of Megalobatrachus, are especially to be noted:

1. More extensive ossification,
2. Ossification of scapula and coracoid from two centers,
3. Presence of dermal clavicle,
4. Presence of interclavicle,
5. Larger and stronger sternum articulating with ventral ribs.

The principal differences as compared with the girdle of Eryops are:

1. Absence of cleithrum,
2. Ossification of scapula and coracoid, from two centers instead of one,
3. Posterior median extension of interclavicle.

d. General Homologies of the Pectoral Girdle of Eryops, Megalobatrachus and Sphenodon

General Conditions of the Homology.—The position of Eryops, as a member of the ancestral group, Stegocephalia, should render it possible to derive from the elements of its girdle those of the reptiles on the one hand, as typified by the generalized reptile, Sphenodon, and those of the urodele amphibians, on the other, as exemplified by Megalobatrachus; for it is generally admitted that the reptiles are an offshoot of the earliest Stegocephalia through the cotylosaurs, while the urodeles are derived from other stocks of the same basal group. Likewise, a comparison of the skeletons of these two recent forms with those of Permian and Carboniferous times, should help to throw light on the unknown cartilaginous portions of the Eryops skeleton, and of its method of articulation.

It must be borne in mind that the original skeleton of all osseous vertebrates is laid down in cartilage derived from membranous areas of mesenchyme. Therefore the real homologous regions are to be sought in the basic cartilage, ossified to a greater or less degree due to mechanical
Fig. 15.—The shoulder girdle and right humerus of *Eryops*, restored, and shown from the ventral side, in perspective, to illustrate the inferred cartilaginous epicoracoids (COR. CART.), and sternum (ST), and their relations to the underlying abdominal scutes (ABD.S.). Compare with Figs. 16 and 17.

Figs. 16 and 17.—Ventral view of pectoral girdles of *Megalobatrachus* and *Sphenodon* for comparison with Fig. 15.

Note the total lack of dermal elements in *Megalobatrachus* (Fig. 16), and their retention in *Sphenodon* (Fig. 17).
stresses or hereditary tendencies, and to which has been applied a certain number of membrane bones derived originally from dermal scutes of the original superficial bony armature.

The mechanical stresses increase the size of the cartilage bones and preserve the ancestral quota of dermal bones in a more or less expanded condition.

Conversely, aquatic habitat, providing, as it does, an evenly distributed external support for the body, may considerably diminish the mechanical stresses on the skeleton and tend to retard the development of ossified areas and to cause the loss of dermal ossifications.

The ancient branchiosaurus had already started on the road toward the series of aquatic specializations evident in modern urodeles, while Eryops and the related stegocephs had begun the adaptations leading to terrestrial life further evolved successively by Permian cotylosaurs and the other groups of fossil reptiles, and brought down to recent times by the specializations of modern reptiles, birds and mammals, with Sphenodon as a connecting link with the past.

Homology of the Suprascapula.—The cartilaginous suprascapula is obviously homologous in both Sphenodon and Megalobatrachus. It is easily recognizable in all urodeles and reptiles, though in varying degrees of extension. In Anura, the cartilage is more or less covered by a dermal ossification, which (Schmalhausen, 1917) appears in the embryo as a bladelike plate overlying the anterior edge of the suprascapula and, in the adult, extends over the proximal part of that cartilage, retaining, however, a tendency to a greater expansion on the anterior edge. It seems quite clear from the researches of Schmalhausen that this membrane bone is a rudimentary cleithrum. This strengthens the view that the cleithrum in Eryops, and in all primitive tetrapods, capping as it does the dorsal end of the scapular blade, and extending beyond it dorsally and anteriorly, was laid down over a cartilaginous base which was the dorsal unossified end of the scapula, homologous with the later suprascapula. It is also possible that the distal portion of the scapular blade itself extended its ossification somewhat over that part of the general primitive cartilaginous shoulder girdle corresponding to the suprascapula in later amphibians and reptiles.

Homology of the Scapula.—In Eryops and other Carboniferous and Permian Amphibia, the scapular blade, as stated previously, forms but a part of the same ossification that includes the ossified portion of the coracoid, and thus forms with it a single bone, the scapulocoracoid. This ossification may also include, dorsally, the proximal part of the later
cartilaginous suprascapula, as just stated in connection with the discussion of that element. In *Sphenodon*, the term scapula is applied only to the dorsal ossification above the glenoid, which is separated from the coracoid by a suture passing through and anterior to the glenoid cavity itself. In later reptile groups the scapula is similarly limited. Dorsally, it unites with the cartilaginous suprascapula.

Among the urodeles, the scapula of authors should more properly be termed a scapulocoracoid, in so far as it is a single ossification, which includes a varying amount of the proximal part of the coracoidal and procoracoidal surfaces and occasionally surrounds the supracoracoid foramen (page 173). In this group, therefore, it is very nearly homologous with the scapulocoracoid of *Eryops*, while the cartilaginous surface in which the ossification took place is nearly homologous with the cartilage invaded by the double ossification of *Sphenodon* and the Permian reptiles.

The anurans show a condition in which the scapula is nearly homologous with that of reptiles, having an ossification separated by a suture from the coracoid in the region of the glenoid cavity.

**Homology of the Coracoid and Procoracoid.**—The coracoidal portion of the stegocephalian scapulocoracoid, exemplified by *Eryops*, as previously mentioned, possesses a marginal groove on its median edge which betrays the existence of a cartilaginous extension of the girdle, as indicated in figure 15. Its medial extent can only be surmised, but if the two halves of the girdle be articulated as in the figure, and the conditions compared with those in *Archegosaurus* (Fig. 5), it is evident that it must have been relatively narrow, but of wider extent anteriorly, to form a procoracoidal expansion similar to that of *Sphenodon*. Apparently *Sphenodon* is primitive in this respect. Hence in figure 15, the restoration of the cartilage is adapted from that in the latter type. The shoulder girdle of modern urodeles in general is secondarily adapted to aquatic life, both in its failure to ossify in by far its greater expanse and in the fact that a procoracoidal region\(^1\) has become extensively developed

\(^1\)The following table indicates the homologies of the scapula and coracoid here adopted, including those of the procoracoid and procoracoid:

<table>
<thead>
<tr>
<th>AMPHIBIA</th>
<th>ANCESTRAL AMPHIBIA</th>
<th>REPTILIA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suprascapula</td>
<td>Coracocapula (Pelvis internally conneced)</td>
<td>Scapula</td>
</tr>
<tr>
<td>Scapulocoracoid <em>pars</em> (vertical stem)</td>
<td>Coracocapula</td>
<td>Pars suprascapularis</td>
</tr>
<tr>
<td>Pars glenoida</td>
<td>Coracoid</td>
<td>Pars scapularis <em>s.s.</em></td>
</tr>
<tr>
<td>Procoracoid (a distinct process in urodeles) = &quot;aeromion&quot; of Anura</td>
<td>&quot;Procoracoid&quot; of cheloniens and plesiosaurs</td>
<td></td>
</tr>
<tr>
<td>Scapulocoracoid <em>pars</em> (ventral body expansion) + Cartilaginous coracoid</td>
<td>Precoracoid (epicoracoid)</td>
<td>Coracoid (metacoracoid)</td>
</tr>
</tbody>
</table>
Miner, The Pectoral Limb of Eryops and other Primitive Tetrapods

Laterally to lie along the ventrolateral margin of the body in response to the general flattening and broadening of the ventral surface of the body, as an aquatic adaptation. This is well exemplified in *Megalobatrachus* (Fig. 16), where the effect is seen on the anterior border of the ossified scapulocoracoid as well, which is strongly concave where the ossification includes the proximal part of the procoracoidal expansion. A similar condition is evident in *Molge* and the adult *Amblystoma*, but in forms like the young of the latter, where the ossification has not proceeded so far, and in *Proteus, Siren* and *Necturus*, where only the vertical stem is ever ossified and no part of the procoracoid is included, the anterior edge of the scapula is practically straight. In urodeles, the cartilaginous procoracoid is very variable, extending far forward in *Megalobatrachus* and *Necturus*, and remaining comparatively undeveloped in comparison with the coracoid in *Molge* and the larval *Amblystoma*, while in the adult of the latter it becomes entirely united and continuous with the coracoid, except for a small fenestra.

The coracoid proper in modern urodeles is an expanded oval structure of considerable extent, in correlation with the broad, flattened under surface of the body. In some forms, it is entirely cartilaginous; in others, as above stated, it is invaded proximally by the ventral portion of the scapulocoracoid ossification. In general, a broad, thin plate of cartilage is developed in correlation with the expansion of muscular attachments made necessary by the disappearance of dermal clavicle, interclavicle and other advantageously located and braced areas of muscular purchase. As will be shown later, muscles attached to the clavicle and the anterior coracoidal margin in reptiles are attached only to the elongate procoracoid in urodeles, while the more greatly expanded procoracoid in the latter compensates for the loss of the clavicle possessed by the former.

The precoracoid of *Eryops* was doubtless continuous with the coracoid and directed somewhat toward the median line, as in the case of *Sphenodon*, since its girdle with its clavicle and interclavicle is arranged similarly, and it was unaffected by aquatic adaptations, as in urodeles. The position of the girdle as restored would permit an extension of a precoracoid anteriorly somewhat beyond the clavicles, as shown in the figure.

Homology of the Clavicles.—The clavicle in *Eryops* is clearly homologous with that of *Sphenodon*. It articulates with the scapula in a similar way, except that the latter, in reptiles, possesses an acromion. It doubtless formed the attachment for the deltoid posteriorly, and for
the trapezius anteriorly, as in *Sphenodon*. This matter will be discussed later in the section devoted to muscle homologies (p. 232 ff.).

Modern urodèles possess no clavicle, since it has disappeared along with the other dermal elements as an aquatic adaptation. Its function in that group has been taken over by the greatly expanded procoracoid for the deltoid (procoracohumeralis) muscle and by the anterior edge of the scapula for the trapezius muscle. It is retained in the Anura.

**Homology of the Interclavicle.**—This is also lost in urodèles, but occurs in varying form as a median rhomboid, spatulate or T-shaped plate in Stegocephalia and primitive reptiles, as a variously modified or reduced T-shaped plate in most recent reptiles, and as the omosternum in all except some specialized Anura.

**Homology of the Sternum.**—The sternum of *Sphenodon* is a broad, shield-shaped plate, tapering anteriorly to fit the triangular notch formed by the coracoid cartilages, the posteromedial edges of which articulate with the anterior edges of the sternum by means of marginal grooves in the latter. Its rounded posterior edge articulates with three or four pairs of ventral ribs and possesses a posterior median notch. As shown by Hanson (1919a), by his own researches and by bringing together the results of many authors, the sternum of reptiles as well as of mammals, contrary to the hitherto prevalent views based on Ruge (1879), is to be regarded as an independent structure and not as a product of the fused ends of the costal cartilages. He derives it, however, from the coracoidal apparatus, but Camp (1923) regards his evidence as insufficient to support this view. Its independence of the ribs, nevertheless, seems to be clear.

The sternum of *Megalobatrachus* is a triangular cartilaginous plate with a median posterior notch and articulates in a similar way with the posteromedian edges of the overlapping cartilaginous coracoids (epicoracoids) by means of a marginal groove. It is evident that the sternum is homologous with that of *Sphenodon* and must have arisen phylogenetically in a similar way, as clearly pointed out by Ruge for Amphibia in general. Hence this structure is endoskeletal in both forms.

*Eryops* and other stegocephs exhibit no endoskeletal sternum in their fossil remains, for none has been preserved in any known form. As their girdle, however, indicates by its groovelike coracoidal edges the presence of a coracoidal (epicoracoidal) expansion, homologous in every way with that of later forms, it is fair to assume that the median posterior notch formed by the overlapping right and left epicoracoids was likewise filled by a triangular cartilaginous sternum (Fig. 15).
An ossified sternum and series of ossified ventral endoskeletal ribs were doubtless not needed by Eryops and its congeners, partly because of its semiaquatic life, and partly because it had a well-developed external support furnished by a paired, interlocking series of dermal scutes or scales, arranged in forward pointing, chevronlike rows on its ventral surface. This ventral armature, apparently common to all stegocephs, is especially well preserved in Archegosaurus, as shown by von Meyer's plates, one of which is reproduced in this paper (Fig. 5). It finds its homologue in the dermal abdominal ribs of Sphenodon, situated posteriorly to the sternum and overlapping ventrally its posterior median notched surface. These exist in certain other reptiles but less extensively,—another indication of the primitive structure of the Sphenodon skeleton. In Archegosaurus, the ventral armature continues anteriorly to a point somewhat posterior to the tapering, caudal end of the elongate rhomboid interclavicle. From here on, their chevronlike arrangement becomes reversed, so that the points of the chevrons are directed posteriorly, the rows here conforming in their arrangement about the two posterior edges of the interclavicle. An X-shaped pattern is thus formed by the scutes of this region, into the lateral spaces of which some of the forwardly directed scutes are continued, but without meeting medially. Their arrangement is such that the two latter series of scutes must have overlapped ventrally the cartilaginous coracoids, thus strengthening and supporting them, while the triangular area formed by the anterior rows of the converging series of forwardly directed scutes is in a position to have supported the inferred cartilaginous sternal plate as the epicoracoids were supported. This whole arrangement would thus account for the lack of an ossified ventral endoskeleton in the heavier-bodied semi-terrestrial stegocephs. This idea is adopted herewith in the restoration of Eryops (Fig. 15), the ventral scutes of which have been preserved, but not in situ.

In their reptilian descendants, because of their terrestrial habits, this contrivance developed into a complicated, well-braced girdle, while in the urodeles, on the other hand, continued aquatic adaptations involved the loss of all except the cartilaginous sternum.

Wilder has noted (1903) the tendency in Necturus to chondrify the medial parts of three pairs of myosepta in this region, and he regards this as the beginning of the process which in other urodeles evolved the cartilaginous sternum. He interprets it as an evidence of the primitive nature of Necturus (1909). It is obvious that Necturus is not so primitive as the branchiosaur, and both of these are less primitive than the stego-
cephs from which they are descended. There is a progressive loss of the dermal skeleton passing from the stegocephs, to the branchiosaurs on the one hand, and to modern urodeles on the other. *Necturus* has an excessively simplified skeleton and is at the end of a line progressively more and more specialized to aquatic life, with even greater skeletal losses than *Megalobatrachus*, which still possesses a sternum. We must regard the chondrifications in the myosepta of *Necturus* as abortive attempts to produce the ventral dermal ossifications or scutes of the ancestral stegocephs, while the cartilaginous sternum has disappeared.

B. THE PECTORAL LIMB BONES OF *Eryops*, *Sphenodon* AND *Megalobatrachus* COMPARED

Description and Homologies of the Humerus

Figures 18, 19, 20

The humerus of *Eryops* (Fig. 18, A-A") is a short, massive bone consisting of two fan-shaped extremities set with their plane surfaces at right angles to each other on a shaft so short as to be practically negligible and forming a tetrahedral prism. Adopting Case's nomenclature (1911) for the four aspects of the bone, an outer, inner, posterior and anterior side may be designated. The proximal extremity, or head, is flattened on its outer and inner sides and is furnished with a "strap-shaped" condyle, as before mentioned. The distal extremity is flattened anteroposteriorly and spreads out to form strong, entepicondylar and ectepicondylar processes, with an articulation between for the ulna. Below the ectepicondylar process on the anterior side is the prominent, rounded, articular surface for the radius. A strong, flattened, stublike process juts out from the side of the bone, proximal and somewhat anterior to the ectepicondylar process. This may be called the "supinator process," for reasons to be discussed later. The space between the supinator process and the ectepicondylar process forms a notch, which, as may be seen from figure 20 A-F, can be homologous only with the ectepicondylar foramen of reptiles, as mentioned below. As described by Case (1911), four strong ridges bound the four sides of the short shaft, giving it a quadrangular section. In line with the ridges bounding the outer face of the humerus at their junction with the humerus head, there is a strong process above (posterolaterally) and below (ventrally). These may be called, respectively, the "processus latissimi dorsi" and the "deltoid crest." Opposite the latter on the inner side of the humerus is the "pectoral crest."
Fig. 18.—Right humerus of *Eryops* (A-A'''), *Sphenodon* (B-B'''), and *Megalobatrachus* (C-C'''), shown from posterior, anterior, outer and inner sides for comparison of homologous skeletal features.
Fig. 19.—Right humerus of *Eryops* (A–A′′′), *Sphenodon* (B–B′′′), and *Megalobatrachus* (C–C′′′), showing homologous areas of muscle attachment.
That these processes are appropriately so called is readily seen by comparing the drawings of the four sides of the *Eryops* humerus in figures 18 A to A″ with the corresponding figures of the humerus of *Sphenodon* (Figs. 18 B to B″). If the longer shaft of the *Sphenodon* humerus be ignored, the extremities of the two bones closely correspond, the chief differences being those of proportion.

The correspondences include the caput humeri with its condyle; the processus lateralis, with its attachments for the pectoralis and deltoid muscles, ossified into the above-mentioned strong processes in *Eryops*; the eminentia m. latissimi dorsi, corresponding likewise to the processus latissimi dorsi of *Eryops*; the two epicondylar processes, and the articulatory surfaces for the radius and ulna.

The chief differences consist in the respective lengths of the shaft; the saddle-shaped condyle of *Sphenodon*, for articulating with the shoulder girdle as compared with the strap-shaped condyle of *Eryops*; the possession of an entepicondylar foramen by *Sphenodon*, entirely lacking in *Eryops*; and an ectepicondylar foramen in *Sphenodon*, as compared with the ectepicondylar notch of *Eryops* and its accompanying process.

By comparing a series of humeri like those in figure 20 A to F, the homology of this notch with the ectepicondylar foramen is clearly evident. The notch exists in practically all stegocephs, the process standing out abruptly in forms like *Eryops* (A), and *Acheloma* (B), and becoming directed distally and quite parallel with the bone in *Cricotus* (C) and *Dimetrodon* (D). In *Naosaurus claviger* (E), the outer part of the notch is bridged with bone, resulting in a foramen, which assumes its characteristic reptilian condition in such forms as *Sphenodon* (Fig. 18 B) and *Varanus* (Fig. 20 F). In the latter, it is also obvious that the proximal part of the supinator crest corresponds with the process bounding the proximal side of the notch in Permian reptiles and stegocephs, and would therefore be appropriately termed the supinator process. This is further discussed in connection with the muscles.

It is evident, then, that the various parts of the stegocephalian humerus, as exemplified by *Eryops*, are homologous with corresponding parts of the humerus of *Sphenodon*, as typical of the later reptiles. This is confirmed by comparison with many related and intergrading fossil types.

In the case of modern urodeles, adaptation to aquatic life has resulted in a lack of ossification of the condylar portions of the humerus, as shown by *Megalobatrachus* (Figs. 18 C-C″″). There is also a general
smoothness of the bone and a lack of the processes and rugosities which render homologizing easier in *Sphenodon* and *Eryops*. It is evident, however, that the bone presents the primitive "twisted humerus" type, characteristic of stegocephs, since the two extremities of the bone are at right angles. They are also of the primitive fan shape, and the ectepicondylar and entepicondylar processes are present, as well as the processus lateralis. The characteristic articular surfaces for the radius and
ulna are shown in the distal cartilage, and the shaft of the humerus is almost of stegocephalian shortness, though the proportions of the whole are more slender.

The proximal condyle, however, is unlike that of both Eryops and Sphenodon in being ball-shaped and tilted inward to articulate in a cup-shaped glenoid. As the cartilaginous extremities have not been correctly figured hitherto, so far as I can ascertain, careful drawings are shown herewith, from a large specimen preserved in alcohol. Their peculiar shape need not be described, as it is well shown in the figures (Figs. 18 A-A‴).

While a number of landmarks do not appear in the Megalobatrachus humerus, nevertheless the different areas of the bone are readily homologized with those of Sphenodon and Eryops, and this comparison is considerably aided by a comparison of the muscles with those of Sphenodon, as shown later, and their areas of origin and insertion (Fig. 19). It should be mentioned here, however, that neither of the epicondylar foramina is present in Megalobatrachus, and there is no process or rugosity for the m. latissimus dorsi, as the latter inserts on the surface of m. anconeus scapularis in this genus.

Description and Homologies of the Radius and Ulna

The radius and ulna of Eryops (Figs. 7, 21) are proportionately short and stout, as compared with Sphenodon (Figs. 9, 17) and later reptiles on the one hand, and Megalobatrachus (Figs. 8, 16) and recent Amphibia, on the other. The radius is somewhat flattened and has wide extremities. The ulna articulates with radius and humerus in the usual manner. Both are well ossified, and there was probably little cartilage capping the joints, comparing well with Sphenodon in this respect. Megalobatrachus, on the other hand, has an entirely cartilaginous olecranon projecting well above the distal end of the humerus. The cartilage capping the radius, however, is comparatively thin. The homologies of these bones in all three forms are self-evident.

Description and Homologies of the Carpus

The carpus of Eryops (Figs. 7, 21) contains eleven bones, that of Sphenodon, ten (Figs. 9, 17); while there are but seven unossified elements composing the wrist of Megalobatrachus (Fig. 8). Radiale, ulnare and intermedium are obviously homologous in the three animals. There are five distal carpalia in Sphenodon, one for each of the five digits. These have been reduced to three in Megalobatrachus, one having been lost with
the fifth digit, and that for the first having probably fused with the second carpal, as both share in its articulation. As shown by Gregory, Miner and Noble (1923), Eryops also possessed but four true distal carpals, the fifth having been lost with the fifth digit, or reduced to a sesamoid cartilage, for which a facet shows on the ulnar-distal corner of the ulnare, though the cartilage has not been preserved.

The Eryops carpus has a large centrale articulating with the radius between the radiale and the intermedium, thus leaving three medial carpals, forming a row from the radial side of the carpus, between the distal carpalia distally and the radiale and centrale proximally. These are termed medialia 1, 2, and 3, by Gregory, Miner and Noble, following Schmalhausen (1917) for the tarsus of Ranodon sibericus.

The Sphenodon carpus (Figs. 9, 17) has two centralia, which may either be homologous with the three medialia of Eryops, through the fusion of two, while the true centrale fused with the intermedium; or the more ulnar of these may be the true centrale, crowded out of place by the ulnare and intermedium, while the more proximal represents the three medialia fused; or the other two may have been lost.

Megalobatrachus (Fig. 8) has a single centrale, all the medialia having been fused with other elements, or lost, the latter being more likely because of the general reduction of the skeleton.

Description and Homologies of the Manus

Sphenodon (Figs. 9, 17) has five digits, the typical number for the tetrapod limb. All the known Amphibia (Fig. 8) have but four, but embryological investigations show (see Steiner, 1921, 1922) that in this group the embryonic blastoderm starts the development of a fifth finger which soon disappears. Since this occurs in both Anura and Urodela, the pentadactyl hand like the pentadactyl foot is a fundamental feature of the entire group and was inherited from the common ancestor of the amphibians and reptiles, somewhere among the embolomeric Stegocephalia. Until recently, it was supposed that Eryops represented this pentadactyl ancestor. This idea was based on a specimen of the carpus in the American Museum of Natural History (A. M. N. H. No. 4186), which is the best preserved known, in which a digit is shown associated with distal carpalia 1, 3, 4 and 5, as they have been considered until recently, when von Huene (1922) suggested that the first digit had been displaced in fossilization. Examination of the specimen showed that this was correct, and Gregory, Miner and Noble have collaborated in a paper (1923), in which the matter is discussed in detail, a new reconstruc-
Fig. 21.—Restoration of left antebrachium and manus of *Eryops*, drawn in perspective from a study of the original specimen, A. M. N. H. No. 4186. See text for description.
tion made of the skeleton (Fig. 21), and its significance correlated with the recent embryological work of various investigators. I was able to test this further in connection with the restoration of the muscles of the carpus of *Eryops*, with confirmatory results, as will be shown later in this paper (pp. 258, 266, 273, 274, 278, 290, 291). A summary of the conclusions reached by the collaborators is all that need be given here. They are as follows.

(1) The first digit was found to fit on the second distal carpal, while the first was too small for articulating a functional digit. Hence the number of digits in *Eryops* was demonstrated to be four instead of five, as in all known Amphibia.

(2) There is, nevertheless, a distinct but small articulation on the first distal carpal, which can have been associated only with a prepollex, thus confirming the view of Gregory (1915) that all true digits are associated with the ulnar pyramid of carpals. This is further confirmed by the investigation of the musculature in this paper.

(3) Embryological and paleontological evidence favor the view that the most primitive stegocephalian Amphibia had five digits and a post-minimus in the hand, which points to a six-rayed primitive pectoral tetrapod limb.

(4) There is no reason in the fossil material to assign a greater phalangeal formula to the *Eryops* manus than 2-2-3-2, the typical urodele arrangement.

The accompanying figure (Fig. 21) shows the reconstruction of the *Eryops* antebrachium, as thus worked out. It will be noted that for the first time, through a proper arching of the carpus, the carpal bones have been made to fit; that the notch of the intermedium articulates with the ulnar-distal angle of the radius on its ventral side; and that there is a foramen surrounded by the intermedium, ulnare, carpal 5 and the centrale. The articulation on the mediale is the evidence for a prepollex, which may have had but one joint, but which is here tentatively assigned two on the ground that the articulation indicates that it was partly functional and may have even reached the ground.

A terminal phalanx must be assigned to digit I, since the fragment preserved is clearly not a terminal one. It is too small to make more than that likely. The same argument applies to digit II.

Digit III is preserved complete with three phalanges. Metacarpal IV is represented only by the stump of a metacarpal, which is sufficiently large to assign it two phalanges by comparison with digit II.
Articulatory surfaces make it necessary to postulate a vestige of digit V, and a pisiform, which is assignable to an original digit VI or postminimus.

The only possible method of articulating the phalanges indicates that I and II were directed radially, while III and IV were directed ulnarward, diverging strongly from I and II. The carpus was doubtless partly supported by a pad ventrally.

The arch of the carpus is indicated by the articulatory surfaces of the carpal bones, which converge ventrally, so that the flexor surface of each is smaller than the dorsal surface, with the exception of the radiale and mediale. In fossilization, the carpus was flattened so that the articular surfaces were mostly separated ventrally, though the bones remained in contact dorsally.

The metacarpals are much shorter in Eryops than in either Sphenodon or Megalobatrachus. This is true of the phalangeal elements as a whole and is a primitive feature.

The phalangeal formulae are as follows.

- *Eryops*: 2-2-3-2
- *Megalobatrachus*: 2-2-3-2
- *Sphenodon*: 2-3-4-5-3

By a comparison of these, it is evident that in both urodeles and reptiles the outer side of the hand is more important functionally. Apparently, the greatest muscular energy is directed to the outer side of the foot in both lines of descent. This is correlated with the arrangement of the carpal elements, of which the greater number form a pyramid of support for the base of the ulna as indicated above. It is also evident, from a comparison of the number of phalanges, that terrestrial reptiles have practically preserved the primitive phalangeal formula. In the earliest reptiles, such as Eosauravus and Limnoscelis, the formula is 2-3-4-5-4. In modern terrestrial reptiles all are retained, except for the dropping of a single phalanx in digit V. In the most primitive amphibian, on the other hand, as well as in those of recent times, we have the formula 2-2-3-2 in the manus. This may be due to the beginning of aquatic specialization shown in skeletal reduction of the foot, and is a part of the same process which caused the total loss of digit V throughout the group.
SECTION II. MUSCULATURE
A. MUSCLES FROM BODY TO SHOULDER GIRDLE
Trapezius and Sternocleidomastoideus
Figures 22 to 27

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>a. As single muscle</td>
<td>a. As more or less double muscle</td>
</tr>
<tr>
<td>b. Posterior part of skull (medial part of squamosal bone)</td>
<td>b. Posterior part of skull (squamosal, parietal and supraoccipital bones). —[The smaller, anterior portion (sternocleidomastoideus)]</td>
</tr>
<tr>
<td>c. Dorsal fascia</td>
<td>c. Mostly from neck fascia from skull to 8th or 9th vertebral segment.— [The larger posterior portion (trapezius proper)]</td>
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<table>
<thead>
<tr>
<th><strong>Insertion</strong></th>
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</thead>
<tbody>
<tr>
<td>Narrow, but including whole anterior border of bony scapula as far as junction with cartilaginous procoracoid</td>
<td>a. Sternocleidomastoideus. Lateral two-thirds of clavicle</td>
</tr>
<tr>
<td></td>
<td>b. Trapezius—Narrow insertion on acromion</td>
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<table>
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<tr>
<th><strong>Innervation</strong></th>
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<tr>
<td>Branch from ramus intestinalis of vagus</td>
<td>a. N. Vagoaccessorius</td>
</tr>
<tr>
<td></td>
<td>b. 4th, 5th and 6th spinal nerves</td>
</tr>
</tbody>
</table>

From the above comparison it is clear

(1) That in both *Megalobatrachus* and *Sphenodon* a muscle suspends the anterior border of the pectoral girdle from the posterior region of the skull and the anterodorsal fascia of the back.

(2) That in both these cases there is an innervation from the vagoaccessorius nerve belonging to the visceral system.

(3) That, while in *Megalobatrachus* (Fig. 25) this muscle is single, and is innervated solely by the vagoaccessorius nerve, in *Sphenodon* (Figs. 24, 26) it is more or less split into two muscles, and, in addition to an anterior visceral innervation, receives a considerable posterior innervation from spinal nerves of the somatic series, i.e., the ventral rami of the 4th, 5th and 6th spinal nerves.

Fürbringer has shown (1900, p. 400) that, in recent Lacertilia, the trapezius and cleidomastoideus, in the simplest condition, form a single
Fig. 22.—Dissection of the superficial dorsal musculature of shoulder girdle and upper arm of Megalobatrachus maximus.

Fig. 23.—Dissection of the superficial dorsal musculature of shoulder girdle and upper arm of Sphenodon punctatus.
muscle mass. From this state of affairs, there is a continuous series of examples in the various genera of the group showing a gradual separation into two distinct muscles culminating in *Phrynosoma* as the most extreme type. In all cases, the anterior slip (cleidomastoideus) originates as in *Sphenodon* from the rear of the skull, while the insertion tends to include not only the clavicle but the transverse projections of the episternum as well. In every case also, the innervation of this muscle is largely visceral, but with some spinal somatic fibres included. The trapezius proper throughout is innervated by spinal somatic nerves from a varying number of segments, corresponding to the number of muscle somites included in its backward extent. It is evident, therefore, first, that the incompletely separated condition of the muscle mass in *Sphenodon* is a primitive character as compared with the other modern reptilian groups, and, secondly, that its complex innervation is typical of the modern reptiles as a whole.

![Diagram showing muscle mass and innervation](image)
In the urodele Amphibia, on the other hand, the muscle is single, comparatively narrow, and is innervated entirely by the vagoaccessorius nerve and hence belongs to the visceral series. In *Megalobatrachus* and the most typical modern urodeles, the most important and most fleshy part of the origin is from the skull, though in branchiact forms more specialized for aquatic life, like *Necturus* (Wilder, 1912, p. 389), the attachment to the skull has been secondarily lost, while the visceral innervation remains. The condition in *Megalobatrachus* is doubtless primitive, since it is correlated with the anterior position of the girdle and short neck, as in the Stegocephalia. Among the reptiles, with the advent of terrestrial life, the disappearance of the gills, the consolidation of the former gill arches into the hyoid apparatus and the lengthening of the limbs, the neck became more important functionally. This resulted in a retreat of the anlagen of the pectoral limbs and, hence, the inclusion of a greater number of vertebrae in the neck, while the greater demands made upon the limb muscles by the progressively more active terrestrial life caused in the case of trapezius a posterior expansion of the muscle mass, by the inclusion of contributions from the myotomes of the neck, together with their somatic innervation. Hence the only part of this muscle complex that can be considered homologous to the trapezius of *Megalobatrachus* is that portion of the cleidomastoideus innervated by the vagoaccessorius nerve (Fürbringer, 1900).

The simple trapezius of *Megalobatrachus*, with its visceral innervation, is directly comparable to a similar muscle in *Acipenser* (except *Acipenser sturio*, where it is secondarily absent—Meissner, 1908), *Polypterus*, the Elasmobranchii, Holocephali and Teleostii generally (Shann, 1921), where it arises from the rear of the skull and inserts into the anterior border of the scapula and, in bony fishes, on the cleithrum as well. It is innervated by the intestinal branch of the vagoaccessorius.

The trapezius in *Megalobatrachus* shows an intermediate condition between the fishes and the reptiles and, hence, may be held to more nearly represent the status of this muscle in *Eryops* and the stegocephs generally (Fig. 27). Here it must have been a narrow muscle because of the anterior position of the girdle, and the weight of the body must have necessitated a posterior expansion of the muscle so far as the girdle allowed, as well as a strong suspension from the squamosal and the posterior part of the skull generally. Its insertion seems to have been on the ventral part of the cleithrum, the clavicle and lower anterior border of the scapula. The innervation was doubtless through the vagoaccessorius nerve, as in fishes and amphibians generally.
Figs. 25, 26, 27.—Comparison of the trapeziusleidomastoideus musculature in *Megalobatrachus* and *Sphenodon*, and the homologous musculature as inferred for *Eryops*. 

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The exceptional character of the trapezius muscle in being the only visceral muscle attached to the shoulder girdle, throughout the vertebrate groups, has always been perplexing. Johnston (1906, p. 203) adduces it as ground for supporting Gegenbaur’s theory of the origin of the girdle from a branchial arch, though he apparently applies this only to the girdle itself and not to the limb, and of course makes no attempt to extend the application to include the pelvic arch, which has no such innervation. The evidence adduced by the majority of modern writers in supporting the fin-fold theory has effectually disposed of the possibility of the gill-arch theory but has not, so far as the writer is aware, explained the innervation of the trapezius. The following considerations are therefore offered as throwing some light on this difficult subject.

(1) In Megalobatrachus the trapezius is located posteriorly and medially to the series of branchial muscles comprising in order the levatores arcuum II, III, IV, hyotraealis, dorsotraealis and dorso-laryngeus, and is so placed as to form the last and innermost of the series.

(2) All these muscles are innervated from the intestinal branch of the vagus.

(3) Hence all, including the trapezius, should be included in the same group.

(4) The origin of the scapulocoracoid from the outer mesenchyme of the body (Osburn, 1907, p. 431) precludes its being grouped with the visceral arches which arise from the splanchnic mesenchyme.

(5) Hence we are led to the inference that the trapezius is derived from the musculature of a vanished gill arch, formerly existing posterior to the fifth gill arch of most modern elasmobranchs and fishes in general.

(6) The possibility of additional gill arches in primitive elasmobranch types is evidenced by the survival of such forms as Hexanchus and Heptanchus, and, if it be objected that their supernumerary arches are secondarily acquired and that one of the most ancient fossil sharks known, Acanthodes, from the Coal Measures, had but five gill slits, it may be noted that this shark was regarded by Smith Woodward as a member of a highly specialized Paleozoic group, while Cladoselache, from the Lower Carboniferous, had at least seven, and probably nine gill slits, according to Dean (1895), and is regarded by him as probably ancestral to such forms as Acanthodes (Dean, 1895, pp. 78 to 81).

(7) This view is also borne out by embryological evidence. Miss Hawkes (1905) found vestiges of a sixth branchial arch in two recent species (Gyropleuroodus francesci Girard and Heterodontus phillipi Blainville) of the family Heterodontidae, which was abundant in Paleo-
zoic seas. Thus there is clear evidence for previously existing visceral arches to which the trapezius muscle could have been attached.

(8) Osburn has observed (1907, p. 429) that "the pectoral girdle of Cestacion [one of the genera investigated by Miss Hawkes] as it develops moves toward the gill-region. When it first appears, the scapular portion of the girdle is separated from the last gill arch by a considerable space, but as development proceeds the girdle and the arch approach each other until the intervening space is eliminated. At first this space is fully twice as great as that between the gill arches; . . . . at 60 mm. the arch and girdle are practically in contact. In the adult they overlap slightly."

This observation is highly significant, though used by Osburn in a different connection. It is what one would expect as an ontogenetic record of the migration forward of the pectoral arch to occupy the place of a disappearing gill arch.

(9) On these grounds it is possible to suggest that the ancestral elasmobranchs possessed more than five gill arches; that, through the well-known tendency toward consolidation in the direction of the head-region (evidenced among other phenomena by the gathering together of posterior nerve roots to form the vagoaccessorius nerve trunk), the pectoral girdle migrated forward, interfered with the sixth gill opening, and crowded it and its arch until they degenerated and disappeared in situ. In this process the insertion of the levator arcus VI musculature and perhaps other slips were taken over by the anterior border of the girdle, together with its post-trematic visceral nerve supply, to form the trapezius branch of the intestinal ramus of the vagoaccessorius nerve.

Levator Scapulae
Figures 28 to 30

The similar origin, insertion and innervation by the spinal nerves show that these muscles in Amphibia and Reptilia are generally homologous. The similar location with reference to other muscles is an argument in the same direction.

The principal differences are as follows.

(1) The origin in Megalobatrachus (Fig. 28) is from the pharynx wall, while in Sphenodon (Fig. 29) it is from transverse vertebral processes.

(2) In Megalobatrachus the muscle is single; in Sphenodon it is double.

(3) In Megalobatrachus the ventral three-fourths becomes apo-neurotic before insertion, only the dorsal fibres continuing to their attachment on the suprascapula (Figs. 28, 53).

(4) The innervation in Megalobatrachus includes visceral nerves from the vagus nerve trunk, while that in Sphenodon is wholly somatic.
MEGALOBATRACHUS

Origin
From connective tissue of pharynx wall near the base of the skull as a ribonlike band. A single muscle

Insertion
Dorsal portion as a narrow strand on the outer surface of the vertebral border of the suprascapula; the ventral three-fourths becomes aponeurotic and inserts on the anterior border of the suprascapula as a membranous continuation of the dorsal portion

Innervation
Small nerves from Ramus intestinalis vagi, hypoglossus (N. spinalis I), and N. spinalis II.

SPHENODON

Origin
Transverse processes of 1st and 2d vertebrae. A single origin immediately dividing into two slips

Insertion
a. Superior. Anterodorsal part of outer surface of suprascapula
b. Inferior. Anterior edge of bony scapula near the acromion and the most dorsal part of the clavicle

Innervation
Nn. spinales IV, V (VI)

Each of these points, when examined, is significant. They will therefore be taken up in order.

(1) The origin of the muscle in the neighborhood of the fascia of the pharynx brings this part of the muscle into intimate relation with the muscles of the pharyngeal system. This suggests a comparison with the visceral muscle system.

(2) The single condition of the muscle in *Megalobatrachus* is primitive as compared with the differentiation into two slips in *Sphenodon* (Fig. 29).

(3) The tendency to become aponeurotic toward the insertion seems to be correlated with the lessened stress on the girdle in an aquatic animal and may be looked upon as an aquatic adaptation.

(4) A comparison of the innervations indicates that the history of the levator scapula is similar to that of the trapezius. The suggestion is offered that it represents the deeper portion of the "trapezius" muscle, described by Shann and Vetter (Shann, 1919, p. 550) for Holocephali, and by Shann and earlier writers as one of the deeper portions of the trapezius of selachians. It is described as innervated by the vagus nerve. In fishes generally there is a great development of the anterior protractor and levator pectoralis systems, extending from the cleithrum and scapula to the base of the skull, and more deeply from the posterior...
Figs. 28, 29, 30.—Comparison of the levator scapulae, omohyoides, and serratus systems in *Megalobatrachus* and *Sphenodon*, and their restoration as inferred for *Eryops*. The serratus profundus system of *Sphenodon* is shown in figure 32.
branchial arches. The trapezius and levator scapulae are interpreted by me as representing the remainder of this system in urodeles as exemplified by *Megalobatrachus*, and that, as in the case of trapezius among reptiles, there has begun a taking over of this muscle by the somatic system, through a posterior addition of spinally innervated muscle elements from the anterior trunk myotomes. This is carried further in reptiles as represented by *Sphenodon*, where the visceral portion of the muscle has been entirely lost in correlation with the posterior “migration” of the pectoral girdle, and the muscle is innervated solely by the 4th, 5th and 6th spinal nerves.

As shown in the discussion of the trapezius muscle, the latter, in *Sphenodon*, is in the stage of evolution of the levator scapulae in *Megalobatrachus*, so far as innervation and composition of the muscle are concerned.

Earlier writers, for example, Osawa (1902, p. 270) and Humphry (1872, p. 31), mention the levator scapulae of *Megalobatrachus* as a narrow strandlike muscle inserting on the vertebral border of the suprascapula. My dissections show, however, that the muscle is quite fleshy and broad (8 mm. in the specimen examined) during the greater part of its course, but the change to an aponeurotic condition of the ventral portion as it nears its insertion causes it to appear quite narrow upon superficial examination.

As the stegocephalian group is ancestral to both Amphibia and Reptilia and is intermediate between the fishes and the higher vertebrates, the condition of this muscle in *Eryops* (Fig. 30) should involve the features common to *Megalobatrachus* and *Sphenodon*, and where they differ should incline toward the more primitive side, to which it should be more directly prophetic. Due allowance should be made for the secondarily aquatic features and for the retention of the dermal girdle in *Eryops*, including the piscine cleithrum.

The inferences are as follows.

(1) The muscle was single in *Eryops*, as representing the deeper trapezius layer of fishes, on the one hand, and the single condition of the muscle in urodeles, on the other.

(2) It was inserted in the cleithrum as in fishes.

(3) It is represented as originating from the transverse process of the anterior vertebrae, as well as from the pharynx wall, because it would seem that greater ossification of the heavy skeleton of *Eryops* and the weight of its body would require a firm attachment like that found in *Sphenodon*, while partially retaining the close association with the visceral musculature inherited from the fishes and perpetuated in the urodeles.
(4) It did not extend far down on to the clavicle, thus agreeing with Sphenodon, in which the attachments of both slips are practically dorsal to that feature and occupy the position of a cleithrum, which has disappeared. In this connection, it may be remarked that the specialization of the levator scapulae into two slips in Sphenodon may be correlated with both the differentiation of the scapular blade into the bony scapula proper and the cartilaginous suprascapula, as well as the tendency of the dorsal portion (pars superior) to insert on the lateral face of the girdle, and of the ventral portion (pars inferior) to insert on the medial face.

(5) There was no tendency to become aponeurotic as in Megalobatrachus, since this is a secondary aquatic feature. As shown in the first section of this paper (page 169 ff.), the secondarily aquatic modifications of the urodeles involved the entire loss of the dermal skeleton, so far as the girdle is concerned. In the case of the superficial muscles attached to the suprascapula, the tendency to become membranous seems to be associated with this loss and is a further step in the same direction. (See discussion of serratus superficialis below.) As stated before, the skeleton of Sphenodon is more primitive, generally speaking, than that of Meagalobatrachus, but the opposite of this is at times true regarding the musculature, which is often more generalized in Megalobatrachus than in Sphenodon, so far as the differentiation of the muscle masses is concerned, while the general status of their origin and insertion would tend to follow the trend of the skeleton, and would thus be nearer to the ancestral condition in Sphenodon. For example, the existence of a dermal clavicle in the latter is a survival from the stegocephalian condition. Hence the muscles attaching to it would necessarily show more primitive relations to the skeleton than in the case of the urodeles where the clavicle is lost and the musculature must find a secondary attachment on the underlying primary girdle elements.

In the restoration of the Eryops musculature, the levator scapulæ, therefore, is shown (Fig. 30) as a single muscle mass originating on the side of the pharynx and from the transverse processes of the anterior vertebrae, and as inserting along the anterior surface of the cleithrum as far as its junction with the clavicle. The Eryops scapula shows good opportunity for this insertion. The innervation may be assumed to be from the vagoaccessory nerve and from as many spinal nerves as would correspond with the number of transverse processes which may have shared in its origin.
Serratus Superficialis
Figures 29, 30

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>The only apparent homologue in this form is a tendinous sheet which arises from the superficial fascia of the lateral surface of the body wall posterior to the pectoral girdle</td>
<td>As two fleshy slips from the distal ends of the last cervical and the first sternal rib (vertebral segments 8 and 9). These slips soon unite</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>By an insensible gradation into the cartilage of the posterior part of the suprascapula</td>
<td>As a single broad muscle on the medial surface of the posterodorsal margin of the suprascapula and of the posterodorsal corner of the bony scapula</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nn. thoracici superiores of the 8th spinal nerve and to a certain extent of the 7th and 9th spinal nerves</td>
</tr>
</tbody>
</table>

As above indicated, this muscle does not appear as a separately differentiated muscle in *Megalobatrachus*, as it does in *Sphenodon* (Fig. 29). In reptiles generally, the serratus superficialis is that muscle of the serratus system which originates on the ends of the last cervical and first thoracic ribs and inserts on the medial surface of the posterior border of the suprascapula and to a slight extent on the bony scapula. It is composed of more superficial fibres than the serratus profundus and inserts posteriorly to it. The serratus muscles of urodèles, as will be shown in the discussion of the serratus profundus, are more nearly comparable to the latter. In *Megalobatrachus* the posterior border of the suprascapula gradually attenuates into a connective tissue sheath occupying the superficial position of the serratus superficialis of *Sphenodon* and extending in the direction of the thoracic ribs beneath the latissimus dorsi. This may well represent a vestige of the serratus superficialis, common to the ancestors of reptiles and urodèles, which has disappeared as the result of lessened stress on the girdles due to aquatic adaptation.

It should, however, be considered an integral part of the general serratus system, which comprises superficially the fibres of the serratus superficialis, and more deeply the deeper fibres of the serratus profundus. This will be further discussed below.
As *Eryops* was a partially terrestrial animal, the stresses on the girdle, necessitated by dragging its considerable weight over the ground, would necessitate a well-developed serratus system, including a powerful serratus superficialis. As a variable origin of the two slips in *Sphenodon* is recorded (Führinger, 1900, p. 466, last cervical and first thoracic; Newman, 1877, p. 238, last two cervicals; Osawa, 1898, p. 553, first two thoracic ribs), it is apparent that they arise from the ribs most favorably situated with reference to the position of the suprascapula. In *Eryops* two ribs would be in this position. Hence it is probable that there were at least two slips for this muscle, inserting together into the posterior border of the heavy scapula as indicated in the inferred restoration (Fig. 30).

**Serratus Profundus**

**Megalobatrachus**

<table>
<thead>
<tr>
<th>Origin</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superficial layer—</td>
<td>Superficial layer—</td>
</tr>
<tr>
<td>Extremity of third rib</td>
<td>Extremities of third and fourth ribs</td>
</tr>
<tr>
<td>Deeper layer—</td>
<td>Deeper layer—</td>
</tr>
<tr>
<td>Extremities of second and third ribs; in latter case, immediately beneath origin of superficial layer</td>
<td>First to fifth ribs, i.e., all the cervical ribs, from above their extremities, the last from the region of the uncinate process</td>
</tr>
</tbody>
</table>

**Insertion**

<table>
<thead>
<tr>
<th>Superficial layer—</th>
<th>Deeper layer—</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anteroventral border of suprascapula on medial side near junction with bony scapula as a single straight ribbonlike muscle</td>
<td>The various slips partially unite to insert contiguously in a line along the dorsomedial border of the suprascapula throughout its whole extent. Anteriorly, the insertion is above that of the two slips of the superficial layer</td>
</tr>
<tr>
<td>Deeper layer—</td>
<td></td>
</tr>
<tr>
<td>The slip from the third rib as a single tapering muscle with a narrow insertion on the medial surface of the suprascapula near its posterodorsal border. The slip from the second rib is broad and separates to three equal parts, inserting near the anterior and anterodorsal border of the suprascapula on the medial surface</td>
<td></td>
</tr>
</tbody>
</table>

**Innervation**

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. spinalis III</td>
<td>Nn. spinales IV to VIII</td>
</tr>
</tbody>
</table>
This is variously named by Fürbringer, in the case of *Sphenodon*, levator scapulae et serratus profundus and the collothoraciscapularis profundus, while Osawa makes the superficial and deeper layers two separate muscles under the names of serratus profundus and colloscapularis respectively. I agree with Fürbringer in considering them two layers of the same muscle, but both his names seem to me an unnecessary complication, as the various slips form the profound layer of the serratus system as compared with the serratus superficialis, and they are, therefore, more appropriately and more simply to be termed the serratus profundus, thus including under this name both the serratus profundus and colloscapularis of Osawa.

In *Megalobatrachus*, Osawa gives but one serratus muscle under the name of thoraciscapularis as equivalent to the serratus magnus of Humphry and Hoffman. This is evidently homologous to the serratus profundus of *Sphenodon* and not to the serratus superficialis, since the insertions of all the slips are on the dorso-anterior border of the supra-scapula and not on the posterior border as in the case of the latter muscle.

Osawa mentions but one muscle here, originating from the point of the third rib as a single bundle and dividing to insert as three slips. My dissections (figures 28 and 31) show an origin from both the second and third ribs. The slip from the second rib divides into three slips as in the case of Osawa’s muscle, only differing from it in the rib of origin. In addition, I find two other muscles arising from the third rib, overlapping at their origin. The inner muscle passes anterodorsally and parallel to the triple muscle from the second rib and inserts posteriorly to its most dorsal slip by means of a tapering point, as shown in the figure. The more superficially originating muscle passes straight anteriorly as a long band, and, crossing all three slips from the second rib on their superficial side, inserts ventrally to them on the lower anterior medial surface of the suprascapula, just above its junction with the bony scapula. This latter slip, as it is located more superficially than the others, appears to be homologous with the superficial part of the serratus profundus in *Sphenodon* (Fig. 32), while the remaining deeper slips are equivalent to the deeper layer in *Sphenodon*.

It might be suggested, in passing, that the single muscle arising from a rib and then separating into three slips may indicate three fused segments and also the phylogenetic dropping out of vertebrae. In *Sphenodon*, which in this respect may represent more nearly the ancestral condition, each slip of the same layer arises from a separate vertebral segment.
Fig. 31.—Dissection of the serratus profundus musculature of *Megalobatrachus*. Fig. 32.—The serratus profundus system of *Sphenodon*, after Fürbringer.
As Osawa's observations on the specimens examined by him are without doubt accurate, there is apparently a considerable variation possible in this muscle. This also occurs in *Sphenodon* in the case of the serratus superficialis. While Fürbringer records it as arising from the fifth and sixth ribs, Newman records it from the fourth and fifth ribs, and Osawa from the sixth and seventh. Likewise, Fürbringer records the serratus profundus (my nomenclature) as arising in its superficial layers from the third and fourth, or second, third and fourth ribs, while Osawa records it from the fourth, fifth and sixth ribs. In the deeper layer there is a similar variation, while the innervation varies to correspond.

Since we may consider the reduced condition in *Megalobatrachus* as secondary, the serratus profundus of *Eryops* was nearer to the more typical arrangement seen in *Sphenodon*, though doubtless still more primitive in its segmental separation. The variation in the number of slips recorded within the same species, as exemplified in both *Sphenodon punctatus* and *Megalobatrachus japonicus*, on both the amphibian and reptilian lines, shows that this was always characteristic of the muscle and that it probably depends on the number of segments attracted into the anlage of the pectoral limb during the ontogeny of the individual, and their adaptive location with reference to the position of the scapular blade. In *Eryops*, four slips are shown in figure 30 posterior to the shoulder girdle, and doubtless a slip arose from each cervical rib as well.

The insertions of the serratus profundus in both *Sphenodon* and *Megalobatrachus* seem to follow the line on the under surface of the suprascapula of the primordial cleithrum, i.e., along the dorsal and anterior border. This may account for the presence of dermal cleithral-like bones in Anura, as shown by Schmalhausen (1917). Shann (1919, p. 536), has shown that in selachians the serratus muscle (retractor lateroventralis pectoralis) inserts as to its superficial fibres on the posterior border of the scapula, while a few deeper fibres insert on its inner surface. The former may be regarded as more or less equivalent to the serratus superficialis of reptiles and the latter to the serratus profundus. In Holocephali, he has shown (*loc. cit.*, p. 548) that this mass has separated into two distinct muscles, one of which inserts on the outer surface of the scapula and the other on the inner surface. In Chondrostei he finds (p. 556) that the entire muscle inserts on the inner side of the scapula, but that it does not reach the cleithrum, while, in the majority of the Teleostei (p. 560), it is attached to the upper portion of the cleithrum. In *Lophius*, however, the muscle is highly developed in correlation
with the mobility of the pectoral fin and is differentiated into five distinct slips, all of which insert at intervals along the inner side of the cleithrum. From the above facts and from the condition of the insertion in amphibians and reptiles, it may be inferred

(1) That the serratus, both superficialis and profundus, originated as a series of segmental muscles arising from the septa and the ribs, strengthening them and inserting on the posterior and inner surface of the cartilaginous scapular bar of early sharks and ganoids;

(2) That, in the bony fishes, as the cartilaginous scapula became reduced and functionally replaced by the cleithrum, the serratus became attached to the cleithrum or lost;

(3) That, in the Stegocephalia and in the transitional types that led to them, there was a tendency for this muscle to divide into a more superficially located serratus superficialis, inserting on the posterior border of the scapula, and a deeper-lying serratus profundus, the fibres of which, in segmental bundles from the respective ribs, inserted on the upper and anterior part of the inner surface of the scapula where it was braced by the cleithrum. This is the condition adopted in the restoration of *Eryops*;

(4) That, in the reptiles, the cleithrum soon disappeared leaving the serratus profundus insertions to mark its former position, while the serratus superficialis was retained;

(5) That, in urodeles, the latter muscle disappeared as a result of aquatic life, leaving only a membranous fascia to mark its former position, while the former was retained as in reptiles, but with a lessened number of slips. In Anura, the same was true with regard to the serratus profundus, but the homologue of the serratus superficialis is, apparently, present and the cleithrum is often retained.
Omobyoideus and Sternohyoideus (anterior part)

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>As omohyoideus it arises from the anterior border of the bony scapula at junction with procoracoid</td>
<td>Anterior border and inner face of the bony scapula and from the ligamentum sternoscapulare internum</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Joins sternohyoideus as two slips, at first and second inscriptions tendinei anterior to the heart. After this junction, the sternohyoideus runs anteriorly to insert on the ventral surface of the oesophagus and then on the copula and medial ends of the two branchial arches</td>
<td>On hyoid bone and its posterior process and on the second branchial arch</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Sternohyoideus</td>
<td>N. hypoglossus</td>
</tr>
<tr>
<td>N. hypoglossus</td>
<td>Ramus ventralis of N. cervicalis I</td>
</tr>
<tr>
<td>N. sternohyoidei</td>
<td>N. sternohyoideus</td>
</tr>
<tr>
<td>Omohyoideus</td>
<td>N. supraclavicularis</td>
</tr>
</tbody>
</table>

As seen above, the omohyoideus of *Sphenodon* is homologous with the omohyoideus of *Megalobatrachus* plus the anterior part of the sternohyoideus. This is evident for the following reasons.

1. Similar origin on the anterior border of the bony scapula. (But note the additional origin from the ligamentum sternoscapulare internum in *Sphenodon.*)

2. Insertion on the two hyoid arches of the combined muscles in *Megalobatrachus*, which together have the same relations as the so-called omohyoideus of *Sphenodon*.

3. Almost identical innervation in both cases, the hypoglossal nerve and the most anterior spinal nerves functioning in a similar way in both types. This innervation clearly interprets the muscle homology as above stated.

It is thus apparent that the omohyoideus may be regarded as the lateral slip of an original single anterior ventral muscle which arises from...
the shoulder girdle, and, as will be shown below, from the sternum as well, and inserts typically on the hyoid arches. This lateral slip is thus separated only at its origin in *Megalobatrachus*, and throughout its entire extent in *Sphenodon*. It should be regarded as an integral part of a general ventral muscle system including also those treated immediately below.

Sternohyoideus  
(posterior part)

Sternocoracoidei and Costosternocoracoideus

<table>
<thead>
<tr>
<th><strong>MEGALOBATRACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
</tbody>
</table>
| Posterior border of sternum just anterior to insertion of M. abdominis rectus | Sternocoracoideus superficialis  
Inner surface of sternum following the labium internum sulci coracoidei and from first sternocostale |
| **Insertion**        | **Insertion** |
| Joins omohyoideus and with it inserts on the two gill arches | Sternocoracoideus superficialis  
Inner surface of coracoid toward medial part |
| **Innervation**      | **Innervation** |
| N. sternohyoideus    | Sternocoracoidei  
Both from Nn. spinales VII, VIII and IX, but especially from VIII |
| N. rectus abdominis  | Costosternocoracoideus  
Nn. spinales VIII and IX |
| both from N. spinalis II |               |

Figure 33

The sternocoracoidei and costosternocoracoideus muscles of *Sphenodon* (Fig. 33b) can best be explained as the remnants of a former
Fig. 33.—The ventral girdle musculature of *Megalobatrachus* (33a), *Sphenodon* (33b), compared, and the homologous musculature as inferred for *Eryops* (33c). Note also the restoration of the cartilaginous epicoracoids, sternum, and the arrangement of the abdominal scutes in *Eryops*. The shoulder girdle in each case is shown as if transparent.
sternohyoideus muscle as seen in its more primitive condition in Megalobatrachus (Fig. 33a). This view is strengthened by the following points.

(1) In both forms, these muscles arise wholly or in part from the interior surface of the sternum especially toward its posterior border.

(2) In Megalobatrachus, the sternohyoideus' unites with the omohyoideus and, with it, inserts on the hyoid skeleton, while, during its course, it is crossed by a number of inscriptiones tendinei, thus attesting its segmental nature. In Sphenodon, the outer slip, the costosternocoracoideus muscle, inserts on the posterior side of the ligamentum sternoscapulare internum, from the anterior side of which arises a part of the omohyoideus muscle which finally inserts on the hyoid skeleton. Both these muscles as part of the ventral system were originally segmental muscles, and the ligament above mentioned may be interpreted as equivalent to a fusion of tendinous myocommata of the original segments. As shown by Romer (1922, p. 547), in the fishes and lower vertebrates this was expressed by the mesocoracoid arch (supraglenoid buttress). In Sphenodon and lizards generally, this became reduced to a ligament, while, under the view here presented, in the aquatic urodeles, as represented by Megalobatrachus, it became still further reduced as an aquatic adaptation along with many other features of the skeleton. In Megalobatrachus, as shown on page 168 and in figure 13a of this paper, there is a structure which may be a reduced supraglenoid buttress, but in most urodeles there is apparently no indication of it, except in so far as the tendinea scripta of the muscle may be regarded as homologous in part.

(3) The fact that the sternocoracoidei in Sphenodon have short courses and insert on the coracoid may be explained by regarding them as segmental units of a former sternohyoideus, the anterior segments of which are represented by the episternohyoideus.

(4) The posterior relations of the origin of the sternocoracoidei to the abdominis rectus parallel the similar relations in Megalobatrachus of the origin of the sternohyoideus to the insertion of the abdominis rectus in that form. It is evident from the innervation and these relations that the whole anterior ventral system is a continuation of the general rectus abdominis musculature in both Sphenodon and Megalobatrachus. As applied to Eryops (Fig. 33c), the inference would be that the abdominis rectus inserted on the posterior border of a cartilaginous sternum. From this point forward, it was in practical continuation with a sternohyoid segment which in turn passed anteriorly internal to the median cartilaginous extensions of the coracoids to insert on the inner face of the interclavicle which interrupted its continuity with the
episternohyoid. The latter in turn inserted on cartilaginous hyoid arches similar to those of *Megalobatrachus*. The lateral portions of this anterior muscle mass arose from the M. abdominis rectus laterally, or from the first sternocostal cartilages, and passed forward with the sterno-hyoid to insert on the posterior edge of the mesocoracoid (supraglenoid) buttress, while from the anterior edge of the latter, and from the inner face and lower anterior angle of the scapular border, the omohyoid passed forward laterally to the sterno- and episternohyoid to insert also on the hyoid apparatus. It is suggested that this whole muscle mass was crossed at intervals by myocommata, and formed a unified system. The ventral scutes were arranged along the myocommata ventral to the ribs and with them converged to support the sternal apparatus ventrally, just as they overlap the posterior part of it in *Sphenodon*.

While much of this arrangement is necessarily conjectural because of the extent of the cartilaginous restoration, there are many indications that suggest its accuracy along broad lines.

The weight of the internal organs would require the efficient support of a cartilaginous ventral skeleton, which could have been formed only on the suggested lines, while the efficient bracing of the heavy, bony scapulocoracoid would require a powerful opposing pull on opposite sides of the mesocoracoid buttress.

B. Ventral Musculature from Shoulder Girdle to Arm, and on Upper Arm

**Pectoralis**

<table>
<thead>
<tr>
<th>MEGALOBATRACHUS</th>
<th>SPHENODON</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Outer surface of the sternum and 2d and 3d myocommata of the rectus abdominis</td>
<td>Outer surface of clavicle, episternum, sternum and ends of ventral ribs</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Converges to processus ventralis humeri just posterior to M. supracoracoideus</td>
<td>Converges to processus ventralis humeri posterior to M. supracoracoideus</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>N. pectoralis from N. brachialis longus inferior</td>
<td>N. pectoralis from N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

The pectoralis is the most superficial portion of the ventral or flexor system of muscles which arises on the chest region and typically
inserts on the upper arm. Its superficial character is indicated not only by its position with reference to the other muscles of the system, but also by its origin from the dermal bone elements of the ventral part of the girdle, and by its insertion on the most superficial part of the most prominent and most proximally situated bony protuberance of the forearm, the processus ventralis humeri, or deltopectoral crest.

In both reptiles and urodeles, this muscle is seen to vary with the ventral dermal elements of the girdles with whose fortunes its history is
linked. This is clearly brought out by a comparison of the conditions in *Megalobatrachus* and *Sphenodon* as typical of these two groups.

In *Sphenodon* (Figs. 35, 37), where the ventral dermal elements are particularly complete, the main divisions of the muscle arise respectively from the clavicle, interclavicle, episternum, sternum and ends of the abdominal or ventral ribs, all of which parts, except the sternum, are dermal bones. In *Megalobatrachus* (Figs. 34, 36), on the other hand, in which the clavicle and interclavicle are wholly lacking, the origin of the pectoralis is confined to the sternum, represented only by a cartilaginous plate and the first two myocommata of the rectus abdominis, as indicating vestigially the course along which the ventral scutes were arranged in the stegocephalian ancestors.

But *Eryops* had bony ventral scutes of dermal origin which were arranged in parallel rows much as in *Archegosaurus* (Fig. 5), its near relative. These must have supported the sternal plate ventrally, overlapping it as in the homologous dermal ventral ribs of *Sphenodon*, but to a much greater extent (Figs. 15, 38). When the dermal skeleton disappeared in the ancestral urodeles as an aquatic adaptation, the cartilaginous sternum was left behind, while the only representatives of the dermal ventral ribs and the cartilaginous pectoral ribs are the membranous myocommata. Hence, the pectoralis abdominalis of urodeles arises from the latter and the pectoralis sternalis from the former. There are no interclavicular or clavicular pectoral slips present, partly because of the total disappearance of these parts of the dermal girdle, partly because of the lack of underlying cartilaginous parts to take their place, and partly because of the great expansion of the supracoracoideus muscle which functionally has taken the place of the anterior slips of the pectoralis in the urodele group.

As will be obvious from the above, *Eryops* would more nearly resemble *Sphenodon* in respect to the pectoralis musculature, because of the presence of the primitive dermal skeleton. The weight of the animal also presupposes a powerful pectoral system. Hence, as shown in figure 38, all four slips of this muscle are inferred arising respectively from the clavicle, interclavicle, the interclavicular and sternal ventral scutes (inferred from the conditions in *Archegosaurus*), and from the abdominal armature of dermal scutes of which there are abundant remains in the fossil skeleton.
Figs. 36, 37, 38.—Comparison of the pectoral muscle in *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops.*
Supracoracoideus
Figures 19, 34, 39 to 43

<table>
<thead>
<tr>
<th>MEGALOBATRACHUS</th>
<th>SPHENODON</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Outer surface of coracoid leaving its border free. Also slips arise from medial border of procoracoid and from membrane between it and coracoid. The most lateral of these slips, however, arising from center of procoracoid not homologous with supracoracoid of <em>Sphenodon</em>. (See scapulohumeralis)</td>
<td>Anterior half of outer surface of coracoid except part bordering on scapula</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>Processus ventralis humeri between procoracohumeralis and pectoralis and part of humerus head anterior to it as well as part of capsule</td>
<td>Processus lateralis humeri between deltoide clavicularis and pectoralis</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>N. supracoracoideus from first spinal nerve entering plexus</td>
<td>N. supracoracoideus from first spinal nerve entering plexus</td>
</tr>
</tbody>
</table>

In *Megalobatrachus* (Figs. 34, 39, 41), this muscle covers the entire coracoid except its extreme border. It also has anterolateral slips arising from the membrane between the coracoid and procoracoid and from the medial border of the procoracoid. Another slip, however, arising from the center of the procoracoid underneath the M. procoracohumeralis, appears to be a deeper layer of the latter muscle, for both have an axillary innervation. It appears, therefore (Fig. 58), to be homologous to the scapulohumeralis muscle of *Sphenodon* and to the axillary innervated part of the acromiohumeralis of Anura, while the slip of the supracoracoideus arising from the medial border of the procoracoid corresponds to that part of the acromiohumeralis having a supracoracoid innervation (Cf. Anthony and Vallois, 1914, p. 251).

In *Sphenodon* (Figs. 40, 42), the supracoracoideus arises from the anterior half only, excluding also the part bordering on the scapula, from which originates the M. scapulohumeralis anterior. The latter occupies the same position and has the innervation of the lateralmost slip in *Megalobatrachus* as mentioned above and is therefore to be considered homologous with it.
Fig. 39.—Dissection of the supracoracoid and neighboring musculature of *Megalobatrachus*.

Fig. 40.—Dissection of the supracoracoid and neighboring musculature of *Sphenodon*.
The supracoracoid proper is clearly homologous with the main portion of that muscle in *Megalobatrachus*, though it is confined to the anterior half of the coracoid by the encroachment of the coracobrachialis system on the caudal part of the latter. In *Megalobatrachus*, the M. coracobrachialis brevis arises from the caudal part but is overlapped by the posterior part of the supracoracoid-coracoradialis mass, while the coracobrachialis longus is confined to the posterior border of the coracoid.

That the supracoracoid is not related to the pectoralis system, or to the coracobrachialis, as Romer suggests (1922, p. 533), is shown by the remoteness of their respective innervations, the former arising from the anterior border of the plexus, in fact hardly uniting with it, while the latter is from N. brachialis longus inferior. The supracoracoid nerve as judged by its anterior situation and interzonal course, together with its muscle, probably represents an anterior myotomic segment, while the pectoralis muscle with its nerve represents a following segment or perhaps more than one. Both the supracoracoid and pectoralis nerves are ventral and follow approximately parallel courses, except that the former passes through the girdle and the latter behind it. Again, the supracoracoid and pectoralis muscles follow each other in segmental fashion on the ventral side of the girdle, though the former overlaps the latter anteriorly. Again, the former inserts on the anterior side of the processus lateralis humeri and the latter on the lateral and posterior surface.

As the supracoracoideus exists in both amphibians and reptiles, it must have existed in the Stegocephalia, and is represented in the restoration of *Eryops* (Fig. 43) as arising from the cartilaginous part of the coracoid portion of the girdle throughout practically its whole extent.

### Coracoradialis Proprius

**Figures 39, 44, 46**

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>In common with and as a deeper layer of M. supracoracoideus, separate in its posterior two-thirds</td>
<td>Not present as a separate muscle. The deeper fibers of the supracoracoideus are probably homologous with it</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Converges to a long tendon which gives off a slip to the processus ventralis humeri and inserts principally on head of radius above M. brachialis inferior</td>
<td>No tendon present as such, but this may be partly homologous to tendinous part of biceps brachii in <em>Sphenodon</em> (q.v.)</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>N. supracoracoideus</td>
<td></td>
</tr>
</tbody>
</table>
Figs. 41, 42, 43.—Comparison of the supra-coracoideus and scapulohumeralis anterior musculature of *Megalobatrachus* and *Sphenodon* and their inferred restoration in *Eryops*. 
This muscle is characteristic of Amphibia generally but is not found in reptiles, where it is functionally replaced by the M. biceps brachii. The innervation is from a branch of the N. supracoracoideus and is formed as a deeper layer of that muscle, being separated from it only caudally (Figs. 44, 46). It converges rapidly to a tendon on which it inserts, and through which it attains an insertion on the proximal part of the radius just beneath its head. This tendon apparently is derived from the membrana intermuscularis and separated off from it through the mechanical pull of the muscular mass of the coracobrachialis proper.

Fig. 44.—Dissection of the ventral upper arm musculature of *Megalobatrachus* with especial reference to the relations of the coracobrachialis proprius to the surrounding muscles.

Fig. 45.—Dissection of the ventral arm musculature of *Sphenodon* with especial reference to the biceps muscle.
While there is nothing equivalent to this as an independent muscle in *Sphenodon*, the deeper part of the supracoracoid in the latter may be taken as homologous with the muscular portion of the coracoradialis proprius of Amphibia.

This muscle probably did not exist in *Eryops* (Fig. 48), since it seems to be a secondary feature brought about by the attenuation of a primitive stegocephalian biceps, as explained under the discussion of that muscle (page 225).

### Coracobrachialis Brevis

**Figures 19, 40, 44 to 48**

<table>
<thead>
<tr>
<th><strong>MEGALOBATRACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Outer surface of caudal part of coracoid near posterior border beneath M. coracoradialis proprius</td>
<td>Outer surface of posterior half of coracoid anterior to origin of M. coracobrachialis longus and lateral to that of M. biceps</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>On proximal end of humerus on medial side of processus ventralis humeri and by several strands on proximal part of tendon of coracoradialis proprius</td>
<td>Flexor surface of humerus between processus lateralis and medialis</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>N. coracobrachialis as for M. coracobrachialis longus</td>
<td>N. coracobrachialis as for M. coracobrachialis longus</td>
</tr>
</tbody>
</table>

This muscle should be considered as the deeper portion of the pectoralis system because of its closely related innervation, because of the general position of its origin caudal to the supracoracoideus system and because of the insertion of its main mass practically beneath that of the pectoralis insertion. In *Megalobatrachus* certain posterior fibres insert on the tendon of M. coracoradialis proprius. Their bearing on the homologies of the M. biceps brachii is discussed below under the heading of that muscle. In this same connection the contiguity of its origin in *Sphenodon* to that of M. biceps brachii should be noted.

The muscle is clearly recognizable in both reptiles and urodeles as homologous. It is evident that it occupied a similar position in *Eryops*. 
Coracobrachialis Longus

Figures 19, 34, 35, 39, 40, 44 to 48

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Caudal border of coracoid medial to origin of M. anconæus coracoideus</td>
<td>Posterior corner of coracoid medial to origin of M. anconæus coracoideus</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Main mass of muscle splits to insert along the distal half of the antero-medial surface of the humerus by two fleshy bundles. Some fibres insert on the tendon of M. coracoradialis proprius</td>
<td>Distal part of medial surface of the humerus</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>N. coracobrachialis arising in common with N. pectoralis from N. brachialis longus inferior by three separate branchlets</td>
<td>N. coracobrachialis plus biceps arising in common with N. pectoralis from N. brachialis longus inferior, together with a series of more distal branches from the lateral branch of the latter</td>
</tr>
</tbody>
</table>

The fibres of this muscle arise in continuity with those of the preceding muscle from the posterior border of the coracoid in *Megalobatrachus* (Figs. 44, 46), and from the posterior surface of that region in *Sphenodon* (Figs. 45, 47), practically forming its most posterior mass.

It is much longer than M. coracobrachialis brevis, however, and inserts along the flexor surface of the humerus, a few fibres uniting with the posterior part of the tendon of the M. coracoradialis proprius in *Megalobatrachus*. The significance of these is discussed in connection with the discussion of the M. biceps brachii.

The innervation is the same as that of M. coracobrachialis brevis, together with which it forms a part of the pectoralis system.

It bears practically the same relations in *Megalobatrachus* and *Sphenodon* and the homology is clear. In *Eryops* (Fig. 48) it was present under practically the same circumstances, but, owing to the shortness of the humerus shaft, was probably scarcely to be separated from the mass of coracobrachialis brevis. It arose from the posterior part of the coracoid and inserted on the anterior margin of the broadly expanded entepicondyle.
Biceps Brachii (Coracoantibrachialis)

Figure 19, 35, 40, 45, 47, 48

<table>
<thead>
<tr>
<th>MEGALOBATRACHUS</th>
<th>SPHENODON</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Non-existent as biceps brachii, but perhaps equivalent at its origin to strands of M. coracobrachialis brevis which insert on tendon of M. coracoradialis proprius</td>
<td>Medial border of coracoid caudal to M. supracoracoideus and medial to coracobrachialis brevis. The proximal portion passing from a fleshy muscular belly to a flat tendinous portion over the capsule of the joint. The latter is perhaps homologous in part to the tendon of the amphibian M. coracoradialis proprius</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>The posterior part of M. coracobrachialis longus splits off several strands that insert on the distal part of the tendon of M. coracoradialis proprius, which then inserts on the proximal end of the radius in close proximity to the insertion of M. brachialis inferior, which latter also inserts by a tendinous slip on the proximal part of the ulna. This arrangement is generally similar to that of the distal belly and insertion of M. biceps brachii in <em>Sphenodon</em></td>
<td>The above tendon becomes a distal fleshy tendon occupying the distal part of the flexor surface of the humerus symmetrically placed beside the M. brachialis inferior, with which it unites distally to insert by a double tendon on the proximal end of the radius and ulna and on the elbow capsule</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Both muscles are innervated by Nn. coracobrachiales from the trunk of N. pectoralis and finer branchlets from N. brachialis longus inferior</td>
<td>Proximal belly innervated by N. coracobrachialis plus biceps from main trunk of N. brachialis longus inferior in close proximity to N. pectoralis. Distal belly innervated by Nn. coracobrachiales plus biceps from N. brachialis longus inferior lateralis which is the lateral continuation of the above trunk</td>
</tr>
</tbody>
</table>

The M. biceps brachii does not properly exist in amphibians, its place being taken functionally by the M. coracoradialis proprius. It is represented in a generalized condition in *Sphenodon*, where it is typical
Figs. 46, 47, 48.—Comparison of the humeroflexor musculature of *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*. 

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of the same muscle in reptiles and mammals. There are, however, certain homologies in *Megalobatrachus* which throw light on its origin and relations to other muscles.

In *Sphenodon* (Figs. 45, 47) it has two muscular regions, consisting of a proximal and a distal belly connected in the neighborhood of the processus lateralis humeri by a broad tendinous band. The proximal belly arises from the posterior part of the coracoid medial to, and in close proximity with the origin of the M. coracobrachialis brevis with which it shares the innervation, and with which it must be regarded as genetically connected. It inserts, as above mentioned, on a broad tendon which pulls freely over the joint of the humerus and in turn forms the origin of the posterior belly, innervated by the same nerve as the M. coracobrachialis longus but from more distally situated branches than those supplying brevis and the proximal belly of the biceps. It is also situated parallel to coracobrachialis longus throughout its course, the latter bounding it on the ulnar side. This distal belly, in turn, unites finally with the terminal portion of the M. brachialis inferior which bounds it radially and, together with it, inserts by means of a double tendon on the proximal part of the radius and ulna. It seems likely that this distal belly of the biceps has been formed by the union of fibres from both Mm. brachialis inferior and coracobrachialis longus.

In *Megalobatrachus* (Fig. 46) corresponding features are represented, but in rudimentary condition. Slips from the posterior part of the M. coracobrachialis brevis insert on a tendon, that with which the coracobrachialis proprius unites, while distal slips from the M. coracobrachialis longus join the distal portion of the same tendon. I would suggest therefore that the tendinous portion of the biceps in *Sphenodon* and the tendon of coracobrachialis proprius in *Megalobatrachus* are generically homologous, in so far as they both represent portions of the membranous septum intermuscularis which continues the medial angle of the humerus. These portions respectively have received the insertions of the proximal portion of the biceps (*Sphenodon*) and the muscular part of the coracobrachialis proprius (*Megalobatrachus*), and by the mechanical pull of the distal belly of the biceps and its radio-ulnar insertion, in the one case, and the radial insertion of the tendon in the other, have been separated off from the general mass of the intermuscularis connective tissue to become tendinous areas for the respective muscles. The slips in *Megalobatrachus* from the two coracobrackiales show the tendency of these muscles to unite with this tendon in the urodeles, and, as they are similar in situation, derivation and innervation to the two bellies of the
biceps muscle in *Sphenodon*, they may well be regarded as generally homologous to them except for that part of the posterior belly derived from M. brachialis inferior. They are perhaps remnants of a former stegocephalian biceps which has practically disappeared in urodeles to be superseded by the coracoradialis apparatus, conceivably as part and parcel of the general aquatic adaptation which took place in that group. If so, the distal union with M. brachialis inferior has been lost, though its close proximity in *Megalobatrachus* is to be noted, as well as its insertion on both radius and ulna, and the nearness of the radial insertion to that of the tendon of M. coracoradialis proprius. As will be seen, the innervation of M. brachialis inferior is similar to but more distal than that of Mm. coracobrachialis longus and biceps. Therefore all the flexor muscles which enter the upper arm, including the tendons, form a closely related whole in both types, but the muscular part of the coracoradialis proprius is excluded from this relationship, as it possesses the supracoracoid innervation and is, properly speaking, a strictly coracoid muscle which does not enter the upper arm, but merely seizes hold of a tendon that does so.

In *Eryops* (Fig. 48) the tendinous connective tissue region represented as the membrana intermuscularis was doubtless particularly prominent as extending the strong ridge which crosses the humerus diagonally on the posteromedial surface from the pectoral crest to the proximal part of the ectepicondylar expansion. It would thus come into close relation with both coracobrachialis and brachialis inferior, and perhaps could be reached by the most distal part of the supracoracoid mass, thus giving opportunity for the derivation of a biceps through the adherence of radial fibres of the coracobrachialis both distally and proximally, as well as a brachialis inferior union distally, to form an insertion on the lower arm through the intermediary of tendons separated from the connective tissue of the joint. This would give rise to the condition in *Sphenodon*. By the attenuation of the biceps muscle, on the other hand, and by the invasion of the deeper layer of the supracoracoideus, the formation of the coracoradialis proprius of urodeles could be brought about, as the upper limb flexors became less important than chest musculature when terrestrial locomotion with its stresses on the limb flexors gave way to aquatic progression by a swimming movement of the entire limb, more particularly adapted to the evolution of chest and shoulder-girdle musculature.
Brachialis Inferior (Brachialis Anticus)

Figures 19, 44 to 52

<table>
<thead>
<tr>
<th><strong>MEGALOBATRACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Lateral surface of humerus beneath insertion of Mm. dorsalis scapula and procoracohumeralis</td>
<td>From whole lateral and lateroventral surface of the humerus from the processus lateralis humeri to beginning of elbow joint</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Proximal end of radius below insertion of tendon of M. coracoradialis proprius, where it is bounded on either side by Mm. extensor and flexor carpi radialis Also inserts on flexor side of ulna by means of slip from medial side of muscle</td>
<td>Unites with M. biceps brachii on medial side of elbow joint and inserts in common with it by a double tendon on proximal part of radius and ulna</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>N. brachialis inferior from trunk of N. brachialis longus inferior lateralis just distal to the nerve supply of the distal portion of Mm. coracobrachialis longus and biceps brachii</td>
<td>N. brachialis inferior from lateral branch of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

That this muscle should be grouped with the system including Mm. coracobrachiales brevis and longus as well as biceps brachii (in reptiles) is shown

1. by the related innervation
2. by the common insertion with biceps in reptiles, which in turn is largely derived from the coracobrachialis system.

That it is homologous in reptiles and urodeles is shown

1. by the homologous innervation
2. by the similar origin and insertion
3. by the identical position on the ventral side of the forearm
4. by the similar location with reference to surrounding muscles, membranes, nerves and blood vessels, provided due allowance is made for the absence of M. biceps brachii in urodeles.

The flexor system of the upper arm in reptiles as exemplified by *Sphenodon* appears to be the generalized arrangement for primitive forms adapted to terrestrial locomotion, while the condition in urodeles as
exemplified by *Megalobatrachus* bears the marks of aquatic adaptation as explained above (page 225). The presence of M. biceps is thus interpreted as a terrestrial feature, as compared with its practical disappearance and the substitution of the M. coracoradialis in urodèles as aquatic features. Hence we may look for various persisting remains of the typical
condition in the latter group. One of these seems to be the insertion of a slip from the distal end of the M. brachialis inferior on the ulna as well as its proper radial insertion. In Sphenodon, the biceps-coracobrachialis complex is the radial flexor of the upper arm, while the brachialis is the ulnar flexor. Both these sets join distally and their insertion by a double tendon on the radius and ulna respectively may possibly be interpreted as an indication of a primitive separate condition in the earliest tetrapod, in which each was the appropriate flexor of the radius and ulna respectively. They also point back to a possible original coalescence of separate radials to form the humerus in a primitive fish ancestor. This is also suggested by the double proximal crests of the humerus and the enlarged duplicate condyles of the distal end, associated with the radius and ulna respectively. Under this conception, the flexor musculature of the upper arm shows a stage of coalescence from a double into a single system, corresponding to that of the anconæus muscle elements on the extensor side. The latter muscle, however, shows a more advanced stage, correlated with its insertion on the dorsally projecting olecranon of the ulna. Both these systems originate partly on the shoulder girdle and partly on the upper arm, but they show a clear convergence from a multiple origin, apparently from separate myotomes, to a more concentrated insertion on the proximal ends of the bones of the lower arm. The flexor series inserts on both lower-arm bones, which can be readily reached by it on this side, and the extensor series inserts only on the ulna, since the position of the radius excludes it from approach by the anconæus series.

The flexor muscles pull in opposition to the anconæus muscles on the principle of a lever of the first order. To offset this pull, when the foot is on the ground and the leg is supporting the body weight, the greater stress must pass through the extensor series over the outer angle of the elbow. Hence the greater consolidation of the anconæus insertion may be correlated with the fact that the ulnar musculature of the lower arm supplies all the fingers of the hand, while the radial musculature is more typically associated with the medial side of the wrist. It may also be correlated with the further fact, as shown by Gregory (1915, pp. 363–4), that the phalanges are the termini of a series of rays which radiate from the distal end of the ulna and bear its weight. The radius and radiale, on the contrary, together with their musculature, are practically excluded from this complex, and, as will be shown later, are dwindling remnants of an ancestral radial system with the prepollex as a terminus (see pp. 266, 290).
The M. brachialis in *Eryops* (Fig. 48) is therefore represented as a muscle inserting on the radius, partly united distally with M. biceps, which in turn is represented as closely associated with the M. coracobrachialis longus as explained above (p. 224), and inserts on the ulna. The distal union of the two muscles is represented as not so complete as in *Sphenodon*.
The location of these muscles is clearly indicated on the bones of *Eryops*, except for M. biceps, which from the nature of the case must be inferred.

C. DORSAL MUSCULATURE FROM SHOULDER GIRDLE TO ARM, AND ON UPPER ARM

Procoracohumeralis

(Dorsal part)

Deltoides Clavicularis

(Superficial part)

Figures 19, 49 to 57

<table>
<thead>
<tr>
<th>MEGALOBATRACHUS</th>
<th>SPHENODON</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Outer surface of anterior end of procoracoid</td>
<td>Outer surface of distal part of clavicular and from episternum</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Processus ventralis humeri above supracoracoideus muscle</td>
<td>Dorsolateral part of processus lateralis humeri, above supracoracoideus muscle</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>N. procoracohumeralis from axillary part of plexus, from same root as N. dorsalis scapulae</td>
<td>N. deltoideus clavicularis from axillary part of plexus in close association with N. dorsalis scapulae</td>
</tr>
</tbody>
</table>

This muscle belongs to the group innervated by the "dorsal" part of the brachial plexus and therefore to the "retractor" or adductor series, speaking in terms of the ancestral fish musculature.1 As to whether the elements of this group act with the retractor or protractor series in tetrapods depends on the position of their origin and the direction of their fibres with reference to their insertion on the head of the humerus. This varies in different types. In general, however, the muscles of this series pull forward or dorsally, or both, while the muscles of the ventral side, innervated by the ventral nerves of the plexus, pull caudally or ventrally or both.

The most anterior muscles of the dorsal series, e.g., the deltoideus clavicularis, the scapulohumeralis anterior and the humeroradialis externus, are contiguous to the supracoracoideus and the pectoralis episternalis, which are the most anterior muscles of the ventral series,

1Since this paper was sent to press, a very interesting article by A. S. Romer has appeared (1924), in which he divides the main muscle masses of the tetrapod limb into a dorsomedial and ventrolateral group, as derived from the adductor and abductor muscle masses of the fish fin respectively. He includes the deltoide (axillary) series with the latter, thus differing from my interpretation. This view demands careful consideration, and will be dealt with in a supplementary paper.
Fig. 53.—Dissection of deeper muscles of the upper arm and shoulder girdle of *Megalobatrachus*, showing origins and insertions.

Fig. 54.—Dissection of the deeper muscles of the shoulder region of *Sphenodon*, with especial reference to the ligamentum scapulohumerale laterale (lig. sch.)
though the former, with its separate and anterior innervation, scarcely included in the brachial plexus, really occupies a somewhat anomalous position, neither dorsal nor ventral. The scapulohumeralis anterior and supracoracoideus muscles, as Romer has pointed out (1922, p. 533), blend into each other, and because of this he is led to group them together. I cannot agree with this because of the separate innervation, which Romer mentions but fails to emphasize in its true significance. It is certain that innervation, wherever recognizable, is a criterion which must throw light on the history of the muscle or part of the muscle concerned, as has been pointed out by many authors (Fürbringer, Johnston, Kingsley, etc.) hitherto. It is also certain that mere contiguity, or even blending of muscles and the consequent "double innervation," cannot be taken seriously as an indication of a common origin. Double or multiple innervations indicate derivation from separate muscle units which have become blended into an apparently "single" muscle mass. This same argument applies to Romer's contention (loc. cit.) that "separation (of the supracoracoid) from the coracobrachialis is an entirely artificial one."

These are clearly muscles of very diverse relationship, as shown above, though they happen to be situated so as to practically blend into each other on their contiguous borders. This matter will be further dealt with in connection with the discussion of the Mm. scapulohumerales.

I agree with both Watson (1917a, p. 4) and Romer (1922, p. 529) in connecting the history of the two deltoide muscles with the fate of the dermal girdle. In Sphenodon (Fig. 56), the M. deltoideus clavicularis arises from the dermal clavicle. This is true in all forms in which the clavicle remains. In Megalobatrachus (Fig. 55) the clavicle has disappeared along with the rest of the dermal limb skeleton, depositing the origin of the deltoideus clavicularis muscle bodily on the underlying and greatly elongated procoracoid, thus transforming the muscle into a procoracohumeralis. The insertion of course remains the same, being located on the deltoit crest posterodorsal to that of deltoide scapularis (dorsalis scapulae), and above that of M. suprascapularis. Both muscles are innervated similarly by a nerve that arises in close association with the N. dorsalis scapulae. The homologies are therefore clear.

As Eryops (Fig. 57) possessed a well-developed dermal clavicle, and a conspicuous deltoit crest on the humerus head, the restoration of a deltoideus clavicularis is a simple matter. Its relation to the M. dorsalis scapulae is discussed below.
Dorsalis Scapulae (Deltoides Scapularis)

Figures 19, 49 to 57

<table>
<thead>
<tr>
<th><strong>MEGALOBatrACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Kidney-shaped area occupying center of cartilaginous suprascapula, leaving borders free</td>
<td>Anterior three-fourths of ventral part of suprascapula and dorsal corner of bony scapula</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>Lateral surface of processus ventralis humeri, anterodorsal to M. procoracoohumeralis and close to M. supracoracoideus</td>
<td>Dorsally on processus lateralis humeri, anterodorsal to M. deltoideus clavicularis and dorsal to M. supracoracoideus</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>N. dorsalis scapulae from axillary stem</td>
<td>Nn. dorsales scapulae from axillary stem and from N. supraclavicularis</td>
</tr>
</tbody>
</table>

As shown above, the origin, insertion and innervation of this muscle are similar in *Sphenodon* and *Megalobatrachus*. They may therefore be considered homologous. This is also confirmed by the similar relations to the neighboring muscles. There are, however, certain differences correlated with the divergent evolution of the skeleton in the two groups to which the types belong. Thus in *Sphenodon* (Fig. 56), the M. dorsalis scapulae is closely associated along its anterioventral border with the dorsal border of M. deltoideus clavicularis, while in *Megalobatrachus* (Fig. 55) the muscles are widely separated except at their insertion, by the wide divergence of the procoracoid from the scapula and its prolongation forward. It is evident from the innervation of the two muscles and their contiguous insertion, that they are genetically related, while their superficial position and the association of the deltoideus clavicularis with the dermal girdle suggest that both were originally associated with dermal portions of the skeleton. In *Eryops* and all known stegocephs, as well as in the primitive reptiles, the cleithrum is the dermal element associated with the scapula in the same way that the clavicle is associated with the procoracoid. In *Eryops*, the dorsalis scapulae would inevitably find its origin on the cleithrum and the portion of the scapular blade immediately posterior to it, just as the deltoideus clavicularis would arise from the clavicle and the procoracoidal region adjacent. The clavicle and cleithrum, however, form with the interclavicle a continuous collar of bone on the anterior border of the girdle, thus suggesting the continuity
Figs. 55, 56, 57.—Comparison of the latissimus dorsi and deltoid muscle system of *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.

Figs. 58, 59, 60.—Comparison of the scapulohumerales and subscapularis of *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.
of the origins of the two muscles. This and their community of innervation in later forms justify the inference of their origin from a single muscle mass in Stegocephalia, and they are so indicated in their restoration in *Eryops* (Fig. 57).

It seems evident that their divergence into two muscles in later forms is correlated with the dwindling of the cleithrum, as pointed out by Romer (1922, p. 529), the origin of the dorsal portion following the degenerating cleithrum up into the suprascapula (which is a cartilaginous expanse functionally replacing the dermal cleithrum in all later vertebrates, as the procoracoid replaced the clavicle in urodeles), while the ventral portion of the muscle mass was retained in its ancestral relation to the clavicle, the acromion being left to mark the original point at which the two portions were originally joined in the stegoceph ancestor, i.e., the junction of the primordial cleithrum and clavicle.

Schmalhausen (1917) has shown that in various genera of Anura (*Pelobates, Hyla, Pipa, Xenopus, Bombinator* and *Alytes*) a dermal ossification appears in the anterior border of the suprascapula, in the position of the stegocephalian cleithrum, with which he finds good reason to homologize it. This later becomes the suprascapular bone and is associated with the deltoïdes clavicularis. It seems clear that in the Amphibia the original single deltid muscle divided as the cleithrum dwindled, and that this dwindling took place upward, separating the two dermal elements and carrying the dorsalis scapulæ part of the deltid muscle with it.

The fact that so many important muscles find their origin or insertion in *Sphenodon*, on both the outer and the inner side of the cleithral region of the suprascapula, i.e., on the anterior and dorsal surface, strengthens the view that the cleithrum formerly occupied this region as a strengthening element. As it disappeared in both reptiles and urodeles, a wide cartilaginous expansion took its place to replace a strong and localized area of origin, stressed by a short and somewhat perpendicular pull in short-limbed forms like *Eryops*, with a wide cartilaginous area from which the proportionately longer muscles of later types pulled in a more parallel direction.

In small forms like *Sphenodon* and the smaller lizards, this cartilaginous expansion distributes the pull over a large surface, counteracted by the similar pull of muscles on the opposite face of the suprascapula, and further supported by the closeness with which the suprascapula is bound to the side of the body by the more superficial musculature, acting like a series of bandages over its outer surface. In larger reptiles like the croco-
dile, this is not sufficient, and here we find a proportionately small supra-
scapula well ossified, and a much larger and longer bony scapula resem-
bling that of *Eryops*, in which the mechanical conditions were similar.
The urodèles went much further in the cartilagizing of the skeleton. Here most of the group are aquatic forms and the stress on the skeleton is still less, while the cartilaginous expansions of suprascapula, coracoid and procoracoid are much greater, with the muscle origins on these elements proportionately expanded. In the more terrestrial anurans, however, we again find a dwindling of cartilage and a strengthening of the bony girdle in proportion, with a corresponding narrowing of the muscle origins. Here also the dermal skeletal elements are more largely retained.

These adaptive features must be taken into consideration in any attempt to homologize the muscles and skeleton of the respective types.

### Scapulohumeralis Anterior

**Figures 19, 53, 54, 58, 59, 60**

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td>Ventral part of outer surface of the bony scapula and dorsal anterior part of coracoid, ventral to tendinous origin of M. anconeus scapularis and origin of M. scapulohumeralis posterior</td>
</tr>
<tr>
<td>Represented by two slips arising on the procoracoid beneath and resembling deeper slips of the M. procoraco-humeralis</td>
<td></td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td>Extensor surface of humerus head immediately dorsal to insertion of Mm. latissimus dorsi, dorsalis scapula and deltoide clavicularis</td>
</tr>
<tr>
<td>Outer surface of humerus immediately anterior to insertions of Mm. pro-coraco-humeralis and dorsalis scapulae</td>
<td></td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td>N. scapulohumeralis from the axillary bundle</td>
</tr>
<tr>
<td>Axillary innervation</td>
<td></td>
</tr>
</tbody>
</table>

This muscle is evidently a deeper portion of the deltoid muscle system as shown by the following points.

(1) In *Sphenodon* (Figs. 54, 59), it lies directly beneath the deltoide clavicularis, with its origin beneath and directly posterior to that of the latter muscle, and its fibres follow the same course.
(2) The insertion is on the head of the humerus on an area contiguous to that of the deltid, which being superficial inserts on the high deltoid crest while the scapulohumeralis inserts dorsally but beneath it.

(3) The innervation is axillary in intimate association with that of the Mm. deltoides clavicularis and dorsalis scapulae.

It is not related to the supracoracoideus, as described by Romer (1922, p. 533), if we follow the criterion of innervation which is here widely separated in its origin from that of the supracoracoideus. The blending of the muscles on their contiguous margins gives an impression of a single muscle system with a "double" innervation, but this is not a tenable conception, if muscles are to be genetically associated with the nerves that supply them. In urodeles, as Romer states, the procoraco-humeralis appears to have a double innervation, but it is evident from the conditions in *Megalobatrachus*, as shown below, that there is an invasion of the procoracoidal region by supracoracoideus fibres and a tendency to weld with some of the deeper fibres of the procoraco-humeralis. In this connection, see the preceding discussion of the supracoracoideus muscle.

This muscle hitherto has been considered absent from urodeles. My dissections of *Megalobatrachus* (Figs. 39, 41), however, show two irregular slips arising from the outer surface of the procoracoid beneath the procoraco-humeralis and proximal to its origin, which insert dorsal to and beneath the deltid crest and the insertion of the procoraco-humeralis and occupy the same position that the scapulohumeralis anterior occupies in *Sphenodon* (Figs. 54, 59) with reference to the deltoides clavicularis, which as we have seen must be regarded as homologous to procoraco-humeralis.

These slips are also innervated by branches of the axillary nerve, and hence are apparently homologous to M. scapulohumeralis anterior of *Sphenodon*.

Again there is a tendency in *Megalobatrachus* for a migration of the supracoracoideus elements toward the procoracoid, for an inner slip in my dissection has apparently separated from the lateral edge of the supracoracoid mass and invaded the membranous area, bridging the gap between the coracoid and the procoracoid. This slip possesses a supracoracoid innervation.

Anthony and Vallois (1914, pp. 251–271) have shown in Anura that portions of the procoraco-humeralis and supracoracoid have fused, carrying their respective innervations with them, and forming a so-called acromiohumeralis with a double innervation. They regard these fused halves, however, as derived from the supracoracoid and axillary systems respectively.
As above mentioned, we have here an instance of the close approach of the dorsally innervated and ventrally innervated muscle systems of the arm in the anterior part of the limb anlage where the two rotate anteriorly about the shoulder girdle until they meet and fuse their fibres.

In *Eryops* (Fig. 60), as an ancestral and primitive form, I regard this muscle as a deeper portion of the deltoideus, arising on the scapulocoracoid just posterior to the origin of the deltoid, and inserting on the head of the humerus in the position indicated in both *Sphenodon* and *Megalobatrachus*.

**Scapulohumeralis Posterior**

*Figures 19, 53, 54, 58, 59, 60*

<table>
<thead>
<tr>
<th><strong>MEGALOBATRACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Same as M. scapulohumeralis anterior</td>
<td>From bony scapula dorsal to origin of Mm. anconeus scapularis and scapulohumeralis anterior</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>Same as M. scapulohumeralis anterior</td>
<td>Extensor surface of humerus head on distal end of tuberculum mediale dorsal to insertion of M. scapulohumeralis anterior</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>Axillary innervation</td>
<td>N. scapulohumeralis from the axillary bundle</td>
</tr>
</tbody>
</table>

There is no muscle slip to correspond to this in urodèles. Its characteristic feature appears to be that it arises from the scapula on the area posterior to the acromion and inserts on the head of the humerus just dorsal to the insertion of the scapulohumeralis anterior, separating it from the insertion of the M. subcoracoscapularis.

Romer (1922, pp. 530-533) regards it as an offshoot of the latter and unrelated to the M. scapulohumeralis anterior, basing his view on the fact that the tendinous origin of the M. anconeus scapularis arises between the two muscles and "sets them off clearly" from each other. I am unable to agree with this view, firstly, because the two Mm. scapulohumerales are innervated by branches of the same nerve, which arises from the axillary stem in much closer relationship to the deltoid innervation than to that of the M. subcoracoscapularis, and, secondly,
because Fürbringer (1900, Pl. xv) in an admirable series of comparative figures has shown (though in another connection) that in various reptilian types the place of origin of the tendon of M. anconæus scapularis is extremely variable in various genera. I am strongly inclined to the view that it is a greater forcing of the issue in homologizing muscles to disregard such a fundamental matter as related innervation in favor of variable tendinous origin than to take the opposite ground.

Again, the occurrence of a separate scapulohumeralis posterior is rare in reptiles. While, as Fürbringer has shown (1900, p. 489), both muscles are preserved in Sphenodon, only scapulohumeralis anterior occurs in the majority of lizards, and only the posterior muscle in the crocodile. Both muscles also occur in birds. This seems to indicate considerable variability in the area of an original scapulohumeralis mass, which, like the deltoid, was doubtless originally single, but early divided into two slips as seen in Sphenodon, and as inherited by birds from their primitive diapsid stock, while, as Fürbringer states, the anterior muscle degenerated in crocodiles and the posterior muscle in the majority of modern lizards. It is easy to comprehend how le shifted variability in both the scapulohumeralis muscle and the place of origin of the tendon of anconæus scapularis would make it possible first for the latter to shift to its position as in Sphenodon, and then for a posterior slip to split off from the scapulohumeralis mass and grow dorsally to the tendon. The shifting powers of the M. scapulohumeralis are well shown in Fürbringer's figures. The innervation therefore remains the most constant criterion and definitely relates the two slips of this muscle to each other.

In Eryops (Fig. 60), the M. scapulohumeralis is inferred as a single mass arising from the outer surface of the scapulocoracoid as a deeper layer of the deltoid and inserting on the head of the humerus between the processus lateralis and medialis.
Latissimus Dorsi
Figures 19, 22, 23, 49 to 57, 61

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Dorsal fascia opposite vertebrae by four slips</td>
<td>Dorsal aponeurosis extending from vertebrae 6-17</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Most anterior slip on a tendinous arch extending from posterior border of bony scapula to the tendinous investiture of the joint capsule</td>
<td>Proximal outer surface of humerus head ventral to insertion of M. scapulo-humeralis anterior and anterodorsal to anterior part of origin of M. anconaeus lateralis and posterodorsal to the insertion of M. deltoideus clavicularis</td>
</tr>
<tr>
<td>Three posterior slips on upper side of tendinous portion of anconaeus scapularis which terminates as the tendon of origin of that muscle</td>
<td></td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>N. latissimus dorsi from N. brachialis longus superior in association with base of axillary bundle</td>
<td>Nn. latissimi dorsi from N. brachialis longus superior in association with origin of axillary bundle</td>
</tr>
</tbody>
</table>

This muscle is clearly identified in all reptiles and urodeles. It arises in varying extent from the dorsal fascia of the back, spreading over several segments. Through the influence of the segmented connective tissue over which its origin has spread, it gives a superficial impression of being a segmental muscle. That it belongs properly, however, to the arm is shown, firstly, by its ontogenetic origin from the blastema of the arm muscles; secondly, by its insertion on the humerus or fascia of the humerus musculature, and not on the girdle as in the case of the true segmental muscles; thirdly, by its innervation, which arises in close association with the origin of the axillary nerve trunk from the plexus, thus relating it in general to the deltoid group of muscles; fourthly, the insertion in *Sphenodon* is on the head of the humerus at its junction with the shaft between the origins of Mm. anconaeus lateralis and medialis, and in close association with the insertions of Mm. deltoideus clavicularis and scapulo-humeralis posterior. This association of axillary insertions with the insertion of M. latissimus dorsi is a further confirmation of its affinities with the deltoid group. It will be noted that this muscle corresponds to the pectoral muscle on the ventral side and opposes it in the elevation and depression of the limb as a whole.
In *Megalobatrachus*, there is a similar origin. The insertion, however, does not reach the humerus, but the posterior three-fourths of the muscle inserts on the upper side of a tendinous band which runs forward obliquely to the posterior angle of the scapula to become the tendon of origin for the M. anconeus scapularis. This muscle unites with the under side of the tendinous band directly opposite the insertion of M. latissimus dorsi. The anterior one-fourth of the latissimus inserts on a tendinous arch which extends from the fascia of the joint capsule to the posterior border of the scapula, and it is continuous with the connective tissue in which the brachial plexus is imbedded. This difference as compared with *Sphenodon* is doubtless due to the comparatively incomplete ossification of the humerus in urodèles. The bone barely reaches the head of the humerus, which is entirely cartilaginous, and is contained in a capacious membranous capsule imbedded in much connective tissue. The anconeus scapularis and the latissimus have apparently formed their common tendon by inserting their fibres in this connective tissue, from which an outer strip continuous with the scapula separated through their common pull. In *Sphenodon*, as well, there is much connective tissue in this region, and the insertion of the latissimus is on a part of the humerus head that is cartilaginous in *Megalobatrachus*. The condition in the latter form is, without doubt, a simplification due indirectly to aquatic adaptation.

In *Eryops* (Figs. 18, 19, 57), the completely ossified humerus head exhibits a bony protuberance on its anterodorsal border which corresponds in position with the rugosity on which the muscle inserts in *Sphenodon*, and which is clearly intended for the latissimus dorsi. The anteroposterior expansion of the muscle origin can be inferred only from the position of the scapula which doubtless marked its anterior border, and from the weight of the body which must have necessitated a considerable posterior development.
Subcoracoscapularis
Figures 19, 58 to 61

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
</tbody>
</table>
| From the posterior margin of the lower third of the bony scapula, and the adjacent margin of the coracoid as far as the origin of M. anconaeus coracoideus | By two heads
|                     | (a) Very well developed. From whole dorsal surface of the coracoid except the medial and caudal borders
|                     | (b) Caudal rim of bony scapula, somewhat ventral from insertion of M. serratus superficialis |
| **Insertion**       | **Insertion** |
| Proximal half of the medial angle of the humerus | Both parts unite and converge strongly as they pass over the shoulder joint and insert on the processus medialis by means of a powerful tendon |
| **Innervation**     | **Innervation** |
| N. subcoracoscapularis from N. radialis superior | N. subcoracoscapularis arising near root of N. axillaris from N. radialis superior |

This muscle is very powerful in *Sphenodon*, rising from a greater part of the inner surface of the coracoid, as well as from the posterior edge of the scapula. It converges to the processus medialis to insert in a small area by a strong tendon.

In *Megalobatrachus* (Fig. 61), its area of origin is much more contracted, being localized on the posterior edge of the scapula and coracoid through about one-third the extent of each. It is nevertheless a strong muscle, the extent of its insertion compensating for the comparatively reduced origin as compared with *Sphenodon*, for it attaches along fully one-half the length of the humerus.

The innervation indicates that it should be grouped with the axillary muscles that insert on the humerus head. Osawa (1898, p. 558) assigns it a second innervation from the N. coracobrachialis, but this is denied by Fürbringer (1900, p. 440), and I can see no evidence of it in my dissections. He also gives a double innervation to the muscle in *Megalobatrachus* (*Cryptobranchus*), from Nn. radialis superior and pectoralis, but I cannot confirm the latter. Such an innervation would be surprising in either case, and unless definite evidence to the contrary should materialize, these muscles should be regarded as related to the axillary system.
As Romer has pointed out (1922, pp. 530–531), it is difficult to believe that in the primitive reptile this muscle had an extensive coracoideal origin. In *Eryops*, this part of the muscle probably arose from the posterior edge of the supraglenoid buttress, and the scapular portion from the normal region on the posteromedial surface of the scapular blade, where the modeling of this surface presents a convenient area of attachment. The processus medialis is directed toward both of these areas.

We thus have a series of fan-shaped muscles related to the deltoid group inserting around the head of the humerus and arising from the girdle, the superficial fascia of the back and the superficial fascia or dermal skeleton of the chest. The dorsally located muscles are all innervated from the axillary nerve or from nerves arising in association with it, while the ventrally situated pectoral muscle with its widely divergent subdivisions is innervated by the pectoral nerve, which branches from the ventral side of the plexus in association with the root of the N. brachialis longus inferior, in a similar and somewhat symmetrical manner to that by which the axillary nerve and its associates arise from the dorsal side of the plexus in association with the root of the N. brachialis longus superior.

The supracoracoideus muscle, on the other hand, is the most anteriorly placed of the series of muscles that pass from the girdle to the head of the humerus. It is placed like a keystone between the dorsal and ventral
musculature, and is correspondingly innervated by the most anteriorly situated nerve of the plexus, the supracoracoid nerve, which can hardly be reckoned as belonging to either the dorsal or ventral side of the plexus, with which it barely connects and then shunts off. It occupies a similar relation in all tetrapods. Thus, muscles arising on the girdle or on the body fascia and inserting on the outer side of the humerus head may be divided into three classes, as follows:

1.—The Dorsal Muscles (axillary and associated innervation)
   (a) Latissimus dorsi
   (b) Dorsalis scapulae
   (c) Deltoides clavicularis
   (d) Scapulohumerales anterior and posterior
   (e) Subcoracoscapularis

2.—The Anteromedian Muscles (supracoracoid innervation)
   (a) Supracoacoides
   (b) Coracoradialis proprius (inserts on a tendon in the neighborhood of the humerus head)

3.—The Ventral Muscles (pectoral innervation)
   (a) Pectoralis
### Anconæus (Triceps)

Figures 19, 22, 23, 49 to 54, 61 to 67

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>(1) Scapulo</td>
<td>humeral part</td>
</tr>
<tr>
<td>humerus scapularis</td>
<td></td>
</tr>
<tr>
<td>Anconæus</td>
<td></td>
</tr>
<tr>
<td>By means of a tendon arising from the posterior border of the scapula close to the glenoid and also from the joint capsule passing upward between the M. latissimus dorsi and the muscular part of A. scapularis to form the insertion of the former and the origin of the latter</td>
<td>By means of a tendon arising from the lateral surface of the scapula between the origins of Mm. scapulohumerales anterior and posterior</td>
</tr>
<tr>
<td>(b) Anconæus</td>
<td>humeralis lateralis</td>
</tr>
<tr>
<td>Proximal one-fourth of anterolateral surface of humerus shaft along its superior angle</td>
<td>Entire anterolateral surface of the humerus shaft</td>
</tr>
<tr>
<td>(2) Coraco</td>
<td>humeral part</td>
</tr>
<tr>
<td>humerus coracoideus</td>
<td></td>
</tr>
<tr>
<td>Anconæus</td>
<td></td>
</tr>
<tr>
<td>Narrow muscular origin from posterior angle of coracoid between origin of M. subcoracoescapularis and M. coracobrachialis longus</td>
<td>Tendinous band arising from posterior angle of coracoid between origin of M. subcoracoescapularis and M. coracobrachialis longus</td>
</tr>
<tr>
<td>(b) Anconæus</td>
<td>humeralis medialis</td>
</tr>
<tr>
<td>Dorsomedial surface of humerus including distal part of processus medialis and extending along proximal half of shaft</td>
<td>Dorsomedial surface of humerus including distal part of processus medialis and extending along proximal half of shaft</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>(1) (a) unites with (1) (b)</td>
<td>(1) (a) unites with (1) (b)</td>
</tr>
<tr>
<td>(2) (a) unites with (2) (b) and the joined slips unite to insert as one muscle around the tendinous capsule of the olecranon of the ulna</td>
<td>(2) (a) unites with (2) (b) and (1) (b) then all converge as one muscle to unite around the proximal end of the ulna in a semicircular insertion</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Nn. anconæi from Nn. radiales inferior and superior</td>
<td>Nn. anconæi from N. brachialis longus superior</td>
</tr>
</tbody>
</table>
Figs. 62, 63, 64.—Comparison of the anconeus musculature of *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*, as seen from the outer side of the arm.

Figs. 65, 66, 67.—Same as seen from the inner side of the arm.
There is no doubt as to the general homology between the anconeus of reptiles and that of urodeles. As shown in both Sphenodon and Megalobatrachus, it is the general extensor muscle of the upper arm. It corresponds to, and acts in opposition to the coracobrachialis, biceps-brachialis mass of the ventral surface of the humerus. The homologies of the slips which compose it, however, have certain difficulties. It may be well, therefore, to consider them successively.

The four slips composing the anconeus may be divided vertically, as shown in the table, into two main groups, each composed of a head originating on the girdle and a head arising from the humerus; or they may be grouped horizontally into a superficial set composed of the two zonal heads, anconeus scapularis and anconeus coracoideus, and a deeper set composed of the two humeral heads, anconeus humeralis lateralis and anconeus humeralis medialis. Originally, they may have formed one mass, which occupied the two dorsal faces of the humerus, shown very effectively, as Romer has pointed out (1922, pp. 555–556), by Acheloma and by Eryops, to consist of the two upper faces of the primitive tetrahedral humerus, with its mutually alternating triangular surfaces. It is likely that the ridge connecting the humerus head with the supinator crest, which is very prominent in these two types and sets the two surfaces off at right angles with each other, is correlated with the division of the deeper anconeus layer into two slips diverging proximally. Along this ridge the insertion of the latissimus dorsi thrusts itself still further, separating these two anconeus heads. In later reptiles, the latissimus dorsi inserts between the origins of the muscle slips in question. The two superficial slips, anconeus scapularis and anconeus coracoideus, are likewise separated by this muscle, hence it becomes natural to group them with the respective deeper portions. As a rule, each deeper slip tends to unite with the superficial slip above it before all join to insert on the ulna. Hence the classification shown in the table becomes a natural one. In later Amphibia, the latissimus dorsi either does not reach the humerus or inserts so far proximally as not to divide the anconeal mass.

(a) Anconeus Scapularis (Figs. 62 to 67). Primitively, this slip originated from the dorsal part of the fibrous connective tissue enwrapping the joint capsule, as is still the case in Necturus (Wilder, 1912, p. 393). This portion separated to form a tendon closely associated with the capsule, and clinging to it at its junction with the base of the scapula, as in Megalobatrachus (Figs. 53, 62, 65), and in Salamandra (Perrin, 1899, p. 255). This is the general condition in urodeles and anurans. In reptiles there is considerable specialization. For example, in Sphenodon
(Fig. 54), where the most extreme condition is reached, the anconeus scapularis arises from the outer surface of the bony scapula at about the middle point, between the origins of the two Mm. scapulohumerales. On this account Romer regards this as the morphological posterior border of the scapula (1922, p. 531). However, because of the notorious variability both of this tendon and of the origin of M. scapulohumeralis (p. 239), especially as shown by Fürbringer's excellent figures (1900, Pl. xv, Fig. 142), I believe that the position of the tendon in Sphenodon is secondary, having been shifted anteriorly in correlation with the strong development of the scapulohumeralis muscles which are both present in this form, arising in an anterior position on the girdle. In changing its position it carried with it a portion of the connective tissue of the capsule as a vertical slip to form the ligamentum scapulohumerale laterale. Fürbringer's figures (1900, Pl. xv) show all degrees of transition in various genera of lizards between this extreme condition and that in Chameleo and Brookia, in which anconeus scapularis inserts on the posterior border of the scapula as in urodeles, while the scapulohumeralis arises from the posterior part of the girdle below it, just in front of the joint capsule, and the ligamentum also occupies a posterior position, acting as a second humeral ligamentous origin of anconeus scapularis.

Variations in the insertions, origins and muscular connections of ligaments and tendons is not surprising when one remembers that the skeleton is first laid down in connective tissue as localized in areas first of cartilage, then of bone. Thus in the humerus the shaft first forms in cartilage in a humeral tract preformed in mesenchyme, and in which the connective tissue areas are retained at the joints, to be finally invaded by cartilage, except where they articulate and except for the connective tissue which surrounds the joint and later becomes the capsule. Meanwhile bone replaces the cartilage of the shaft, but the latter is retained at the articulating surfaces, and the connective tissue remains as the membranae intermusculares, the periosteum and the perimysium. All these connective tissue tracts offer opportunities both ontogenetically and phylogenetically for the developing muscles to seize as areas of origin and insertion, as well as aponeurotic connections. These areas are often specialized into ligaments and tendons, their points of attachment varying according to the mechanical necessities of the case, and occasionally forming bridges like the ligamentum scapulohumerale externum, to span invading muscles like the scapulohumerales. Probably if a careful comparative study of connective tissue areas were carried on in a series of types, correlated with a study of the musculature and skeleton, many of the puzzling problems of unusual muscle attachments could be solved.
(b) *Anconæus Humeralis Lateralis* (Figs. 19, 62, 63). This slip seems to be fairly constant in all types and there are no essential differences found in the comparison of *Megalobatrachus* and *Sphenodon*. Its lesser extent in the former is probably the result of aquatic habits.

(c) *Anconæus Humeralis Medialis* (Figs. 19, 65, 66). This slip also is clear in its homologies. It is the muscle of the dorsomedial surface and characteristically arises on an area extending from the joint capsule to a varying degree along the humerus, joining the common insertion from beneath. It is proportionally more extensively developed in *Sphenodon* than in *Megalobatrachus* for reasons similar to those in the case of the preceding slip.

(d) *Anconæus Coracoideus* (Figs. 65, 66). The homologies here are more puzzling than in any of the other slips, because of the position of the muscle with reference to inferior trunks from the brachial plexus. In *Sphenodon*, the entire N. brachialis inferior with its branches lies outside of and posterior to this slip, and thus to the entire anconæus muscle. In *Megalobatrachus*, the case is different. Though anconæus coracoideus arises from the posterior coracoidal angle, between the origins of Mm. subcoracoideus and coracobrachialis longus as in *Sphenodon* (Figs. 61, 65, 66), and inserts as the posterior division of the anconæus and in common with it on the proximal end of the ulna, it is nevertheless situated entirely outside the N. brachialis inferior, which passes between it and the other slips of the anconæus muscle. It also appears to be innervated near its origin by a small branch of the coracobrachialis nerve. This innervation and the fact that its fibres adjoin at their origin and are practically continuous with those of M. coracobrachialis longus, would indicate that in *Megalobatrachus* this slip is not homologous with the anconæus coracoideus of *Sphenodon*, but is rather a derivative of the M. coracobrachialis longus, to which it appears to be allied in innervation as well as in position. Its insertion, however, is clearly on the ulna in common with the anconæus, though at the most posterior part of the capsule not far from the distal fibres of the coracobrachialis longus insertion. If this diagnosis should prove to be correct, the anomalous insertion may be explained by a comparison with the condition in *Sphenodon*. Here the anconæus coracoideus has been reduced to a narrow strandlike tendon from the coracoidal origin throughout the greater part of its course. Near the insertion into the capsule, however, it expands into a thin fan-shaped muscular slip, which almost immediately enters the common insertion on the posterior part of the capsule, rising here above the level of the nerve complex. I would suggest that the tendinous part of this slip is derived from the connective tissue associated
with the immediately posteriorly situated nerve complex and with the posterior membrana intermuscularis; that the muscular slip has dwindled to its present distal position, but keeping its connection with the connective tissue, a portion of which became specialized as the tendon; that the muscular part is homologous only with the most distal fibres of the so-called anconeus coracoideus of *Megalobatrachus*, where they have been picked up by the proximal portion derived from the M. coracobrachialis longus, which thus constitutes by far the greater part of the slip. A muscle band is thus formed, occupying the position of a true anconeus coracoideus, so far as origin and insertion are concerned, but lying posterior to the N. brachialis inferior, and composed of a greater proximal coracohumeral portion and a much smaller distal anconal portion with an anconal insertion.

This view needs further verification, but it is the only one which will explain the varying relationship to the N. brachialis inferior.

The condition in *Sphenodon* probably represents the ancestral condition, except that the slip was probably muscular throughout its whole extent. It is manifest that a slender tendinous band would not be as mechanically efficient for an animal the size of the larger stegocephs. In the restoration the anconal coracoideus is therefore represented as a somewhat narrow muscular band forming a fourth slip of the anconal mass.

**Humeroradialis (Humeroantibrachialis Lateralis)**

Figures 35, 40, 50, 52, 54, 70, 71

<table>
<thead>
<tr>
<th><em>Megalobatrachus</em></th>
<th><em>Sphenodon</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>There is no muscle corresponding to that of <em>Sphenodon</em>. The ligamentum intermusculare, however, is here very strong and occupies the position of the M. humeroradialis of <em>Sphenodon</em>. It arises from the processus ventralis in close association with the deltoides system</td>
<td>Ligamentum scapulohumerale laterale and from its tendinous continuation to the processus lateralis humeri. These origins are therefore associated with the processus lateralis and with the Mm. supracoracoideus and deltoideus</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>The ligamentum intermusculare forms part of the origin of the M. supinator longus and is distally in continuity with the ectepicondyle</td>
<td>Superficially on the proximal part of the M. supinator longus and on the forearm fascia in close association with the ectepicondyle</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>No innervation, but the ligament connects an axillaris innervated muscle and a supinator innervated muscle</td>
<td>Proximally by a branch of the deltoides system; distally by a branch of the N. radialis lateralis (N. supinator)</td>
</tr>
</tbody>
</table>
This muscle is peculiar to *Sphenodon*. According to Fürbringer it does not exist in other lizards, but has a partial homologue in the crocodile and in birds. It is entirely lacking in Amphibia. As Fürbringer has pointed out (1900, pp. 496–497), it is in reality a compound muscle having a double innervation. The smaller proximal portion is a derivative of the deltoides clavicularis, as it is innervated by a branch of the same nerve. The greater distal portion is an offshoot of the M. supinator longus of the lower arm, innervated by a branch of the supinator nerve. The two portions are not visibly differentiated from each other, but together form a single long flat muscle band, arising partly from the ligamentum scapulohumerale laterale just distal to an insertion of the M. supracoracoideus on the more anterior part of the same ligament, partly from a tendinous continuation of the ligament which receives on its anterior side a part of the insertion of M. deltoides clavicularis (Fig. 54). It inserts on the proximal part of the M. supinator longus on its anterior edge.

In *Megalobatrachus*, and in urodeles generally, there is no muscle homologous with the humeroradialis as such, but, as indicated in the above table, the strong membrana intermuscularis of the anterior side of the limb runs along the same course from the deltoid region on the head of the humerus to the ectepicondyle, where it forms a large part of the origin of the most proximal slip of the extensor carpi radialis mass, shown below to be homologous with the M. supinator longus of reptiles. This would signify that on the reptilian branch the Mm. supinator longus and deltoide clavicularis extended their respective muscle areas along this membrane until they met to form the compound M. humeroradialis, in response to the greater demands of terrestrial life on the muscular apparatus of the limb, while on the amphibian side this did not take place. This is dealt with further in connection with the M. supinator longus.

The probable situation in *Eryops* can also be best understood after that muscle is discussed.
D. DORSAL MUSCULATURE OF LOWER ARM AND HAND

Supinator Longus

Figures 19, 51, 52, 68 to 71, 74, 77, 80

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Distal part of humerus on lateral angle, from ligamentum intermusculare and lateral surface of ectepicondyle</td>
<td>Ectepicondyle and elbow-joint capsule beginning proximally to other extensor muscles</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>Radial side of radius near distal end</td>
<td>Radial side of radius near distal end</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>Branch of ramus radialis medialis of N. brachialis longus superior</td>
<td>Branch of ramus medialis of N. brachialis longus superior</td>
</tr>
</tbody>
</table>

The salient ectepicondyle of the humerus is the place of origin for the extensor muscles of the lower arm, the most proximal of which in *Sphenodon* is the M. supinator longus. This arises both on the condyle itself and on the connective tissue adjacent to it, extending proximally for some distance along the supinator crest, which is quite prominent in *Sphenodon* (Figs. 18, 19, 20 F), as in reptiles generally. This origin is entirely lateral and proximal to the ectepicondylar foramen. It inserts on the radial side of the distal end of the radius.

In *Megalobatrachus*, Osawa (1902, pp. 280–281) considers the general extensor carpi radialis to be a single muscle, and does not differentiate a supinator. Humphry (1872, pp. 40–41) regards this mass as homologous to extensor carpi radialis brevis (superficialis), extensor carpi radialis longus (profundus), and supinator longus of reptiles. My dissection of *Megalobatrachus* (Figs. 44, 68, 69, 74) clearly shows a deeper proximal layer of this mass which is exactly in the position of M. supinator longus, arising from the ectepicondyle and especially from the ligamentum intermusculare, and which can be taken only as a supinator. It is innervated by a branch which may therefore be called the supinator nerve.

As stated in the section on the skeleton (p. 185), *Megalobatrachus* has no foramen through the ectepicondyle as in *Sphenodon*. In the latter animal, the ramus radialis medialis of the N. brachialis longus superior passes through this foramen. In *Megalobatrachus*, however, this nerve passes through the ligamentum intermusculare in just the position that
Fig. 68.—Dissection of the superficial extensor musculature of the forearm of *Megalobatrachus*.

Fig. 69.—Dissection of the deeper extensor musculature of the forearm of *Megalobatrachus*.

Fig. 70.—Dissection of the superficial extensor musculature of the forearm of *Sphenodon*.

Fig. 71.—Dissection of the deeper extensor musculature of the forearm of *Sphenodon*.
would be assumed by an ectepicondylar foramen, if the condyle had ossified out into the membrane to form a supinator crest including this part of the ligamentum. As the bone and cartilage are merely the ossified or chondrified portion of the original connective tissue membrane, the ligamentum intermusculare must be interpreted as that part of the original connective tissue which failed to ossify, and the part surrounding the medialis nerve is therefore an unossified supinator crest with its appropriate nerve penetration, and homologous to the ectepicondyle in Sphenodon with its foramen.

In Eryops (Fig. 20A), as shown on page 183, this foramen is incomplete, being indicated by a notch bounded by a prominent bony protuberance just proximal to the condyle. As already shown, this notch is also found in cotylosaur reptiles, and a series of fossil forms exhibits its gradual enclosure by an approximation of the projecting outer bone to the condyle until its distal end connects with the latter to form an ectepicondylar foramen (Fig. 20 A-E). It is evident that this enclosure took place around the medialis nerve and thus brought about the condition in modern reptiles (Fig. 20 F). In Megalobatrachus and the urodeles, on the other hand, the failure of complete ossification, due to aquatic specialization, left this foramen with its nerve but in the unossified membrane, with the result that the foramen is not found on the urodele humerus, and the nerve merely crosses the end of the bone without penetrating it. The condition in Eryops and the cotylosaurs is intermediate and ancestral to both extremes, with the notch functioning as an ectepicondylar foramen. The bony protuberance arose as a strong point of origin for the outer portion of the powerful extensor radialis muscle system necessary to lift the heavy body of Eryops, as the foot was planted on the ground. This outwardly projecting peg tended to separate the outer muscle slip to form a separate true supinator longus and apparently also acted as a point of insertion for part of the deltoid muscle or a prolongation from it, thus forming another fulcrum for the extensor system acting in connection with the deltoid. This extension of the latter muscle to this point was possible because of the short humerus and the consequent proximity of the deltoid crest. In fact, it is probable that a strong ligamentum intermusculare extended from this supinator crest to the neighboring deltoid crest, as in later forms. The configuration of the Eryops humerus shows a ridge (Fig. 20) connecting the two crests in exactly the position to be continued by a ligamentum intermusculare, as in later forms. In this case, it would be easy for the deltoid muscle to invade the dorsal surface of this ligament as a part of its inser-
tion. This process would bring it immediately into contact with the supinator crest, thus forming a M. humeroradialis inserting on the bony crest or protuberance. As this crest gradually swung parallel to the condyle in enclosing the foramen, as in the reptile stem, it would be drawn away from the primitive humeroradialis, leaving it to insert on the membrane near the M. supinator longus and finally on the muscle itself, as in Sphenodon. In the urodeles, on the other hand, there was a failure of ossification as an effect of aquatic habits, the "peg" deteriorated, the humerus elongated, the musculature became weaker, the supinator was left originating only from the distal end of the ligamentum intermusculare, while the weakening deltoid retreated to insert only on the processus ventralis, and, with the failure of the dermal cleithrum and clavicle and the resulting expansion of the cartilaginous procoracoid and supracoracoid expansions, divided to form the dorsalis scapulæ and procoracohumeralis muscles. Thus the ligamentum alone was left lying between the Mm. brachialis inferior and anconeus lateralis to connect the insertion of the deltoides system with the origin of the supinator, as in Megalobatrachus.

The restoration of the Eryops musculature thus requires a M. supinator longus arising from the projecting supinator crest, and a M. humeroradialis inserting on this same crest and on the ligamentum intermusculare connecting the two crests (Figs. 80, 103).

<table>
<thead>
<tr>
<th align="left">Extensor Carpi Radialis Superficialis (Brevis)</th>
<th align="left"></th>
</tr>
</thead>
<tbody>
<tr>
<td align="left">Figures 19, 69 to 71, 74, 77, 80</td>
<td align="left"></td>
</tr>
<tr>
<td align="left"><strong>Megalobatrachus</strong></td>
<td align="left"><strong>Sphenodon</strong></td>
</tr>
<tr>
<td align="left"><strong>Origin</strong></td>
<td align="left"><strong>Origin</strong></td>
</tr>
<tr>
<td align="left">Distal part of ligamentum intermusculare laterale humeri and from lateral surface of the ectepicondyle</td>
<td align="left">From the lateral side of the ectepicondyle and from the elbow-joint capsule distal to origin of M. supinator longus</td>
</tr>
<tr>
<td align="left"><strong>Insertion</strong></td>
<td align="left"><strong>Insertion</strong></td>
</tr>
<tr>
<td align="left">Radiale and radial part of centrale</td>
<td align="left">On distal end of radius close to that of M. supinator</td>
</tr>
<tr>
<td align="left"><strong>Innervation</strong></td>
<td align="left"><strong>Innervation</strong></td>
</tr>
<tr>
<td align="left">Branch of ramus radialis medialis from N. brachialis longus superior</td>
<td align="left">Branch of ramus radialis medialis of N. brachialis longus superior</td>
</tr>
</tbody>
</table>
This muscle, the extensor carpi radialis brevis of Osawa, is more appropriately to be termed the extensor carpi radialis superficialis, both because of its more superficial position with respect to the other radialis muscles and because it is longer than the “longus” (page 257).

In *Sphenodon* (Figs. 19, 70, 71, 77), it arises from the ectepicondyle just distal to the supinator longus and inserts on the distal end of the radius also in close proximity to that muscle.

In *Megalobatrachus* (Figs. 19, 69, 74), a similar muscle is clearly homologous, though it inserts on the radiale and centrale. However, the insertion in *Sphenodon* in my dissection is so near the radiale that it may well be a variable matter. Osawa says (1898, p. 562) that in *Sphenodon* it unites with an aponeurosis which inserts on the proximal end of metacarpus I. This is not the case in my dissection.

In *Eryops* (Fig. 80), because of the strong ectepicondyle, this muscle must have been comparatively powerful and inserted on the large radiale and perhaps also on the expanded distal end of the radius.

### Extensor Carpi Radialis Profundus (Longus)

**Figures 19, 69, 71, 74, 77, 80**

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Distal part of ectepicondyle adjoining origin of M. extensor carpi radialis superficialis</td>
<td>Distal part of ectepicondyle and from elbow joint distal to origin of M. extensor carpi radialis superficialis</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>Almost the entire length of the radius, the membrana interossea and on the intermedium</td>
<td>Distal half of the radius and on mem- brane inserting on radiale and mem- brane of wrist</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>By short nerve from plexus antibrachialis, i.e., from both rami radiales medialis and lateralis of N. brachialis longus superior</td>
<td>By branches from both rami radiales medialis and lateralis of N. brachialis longus superior</td>
</tr>
</tbody>
</table>

This muscle as shown above is quite clear in both *Sphenodon* and *Megalobatrachus*. The origin is similar, and, while the insertion varies somewhat in the two forms, it is largely associated with membranous tracts, which, as we have seen, are notoriously variable.
The innervation is exactly homologous, though in *Megalobatrachus* the two nerves unite in an antibrachial plexus before entering the muscle, while in *Sphenodon* they enter it without forming a plexus.

This was doubtless a very important muscle mass in *Eryops* (Fig. 80), the large overhanging surface of the ectepicondyle giving it a strong attachment, while the widely expanding distal end of the radius furnished it with a large triangular facet for insertion, with a very direct pull. The intermedium is also in an excellent position to receive a part of the insertion, which also, perhaps, invaded the centrale. The small interval between the radius and ulna speaks for a small attachment on an interosseous membrane, and, therefore, together with the wide bony area for insertion, implies that the muscle was exceptionally powerful.

As this muscle is comparatively short, Osawa's term "longus" is scarcely descriptive. As it is situated more deeply than the preceding muscle, I have thought it well to give it the name "profundus."

**Extensor Carpi Ulnaris**

**Figures 19, 68 to 72, 75, 78**

<table>
<thead>
<tr>
<th><strong>MEGALOBATRACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>With Mm. extensores carpi radialis and digitorum longus from point of the ectepicondyle and the fascia between it and the M. extensor digitorum longus</td>
<td>From surface of ectepicondyle in common with the other extensors</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Ulnar border of ulna, and slightly on ulnar side of ulnare</td>
<td>Distal end of ulna, on pisiform, and on ulnar side of metacarpus V, near joint with phalanx</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Ramus radialis lateralis from N. brachialis longus superior</td>
<td>Ramus radialis lateralis from N. brachialis longus superior</td>
</tr>
</tbody>
</table>

The origin, insertion and innervation of this muscle in *Megalobatrachus* and *Sphenodon* sufficiently attest its homology in both urodele and reptile branches. It is interesting to note that, in reptiles, its insertion generally extends not only to the distal end of the ulna, but also to the pisiform and to metacarpus V. In urodeles, however, in correlation with the loss of digit V, its insertion is more proximal, and on
the ulna only or at most slightly on the ulnar side of the ulnare. The fibres also insert more obliquely toward the outer edge of the ulna in urodeles than in reptiles where the course of the muscle is more parallel with the ulna. In other words, in reptiles the muscle is associated with the fifth digit in its insertion, while in urodeles it tends in a sense to run off the arm before it reaches the hand, as if directed toward the vanished fifth digit.

The “anconeus quartus,” or more properly “quintus” (Osawa) (Figs. 19, 70, 71, 75), is a small slip from this muscle arising from the end of the ectepicondyle in common with it and inserting on the ulnar border proximal to the insertion of the main muscle. In *Megalobatrachus*, there is but a single muscle mass, homologous to both slips.

In *Megalobatrachus* (Fig. 72), also, the muscle arises from the fascia between it and the M. extensor digitorum longus. In fact, all the extensor muscles arising from the ectepicondyle tend to be more unified into a single mass at their origin in urodeles than in reptiles.

In *Eryops* (Fig. 78), the extensor carpi ulnaris was doubtless a single muscle. Because of the four-fingered condition of the *Eryops* hand, it is represented as inserting on the outer border of the ulna, on the ulnare, and the pisiform, extending down to the rudimentary cartilage at the outer distal end of the ulnare, the existence of which is indicated by a facet at that point, as shown in figures 21, 78 to 80.

### Extensor Digitorum Longus

**Figures 19, 68 to 71, 73, 76, 79**

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Ectepicondyle and the fascia between it and the M. extensor carpi ulnaris</td>
<td>Ectepicondyle and the elbow-joint capsule in common with the other extensors</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>Divides into four tendinous slips which insert on the dorsal aponeuroses of the respective fingers</td>
<td>Splits on back of hand into four muscular slips which insert on ulnar side of bases of metacarpales I–IV</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>Short rami musculares from the plexus antibrachialis and thus from both rami radiales lateralis and medialis from N. brachialis longus superior</td>
<td>Rami lateralis and medialis of the radialis system from N. brachialis longus superior</td>
</tr>
</tbody>
</table>
In *Sphenodon* (Figs. 19, 70, 71, 76), this muscle arises as a powerful extensor from the ectepicondyle between the Mm. extensores carpi radialis and ulnaris. It soon divides into three slips which insert on the ulnar side of metacarpales II, III, IV. A slip for the ulnar side of metacarpale I arises from the distal part of that inserting on II. Each insertion is by a delicate tendon alternating with the five slips of M. extensor digitorum communis brevis, the origin of which is covered by this muscle.

In *Megalobatrachus* (Figs. 19, 68, 69, 73), the origin is broader and thinner than in *Sphenodon*, in fact almost aponeurotic. This muscle passes as a single layer distally to the region of the carpus. Here it becomes aponeurotic and divides to form four flat tendinous slips, each of which passes dorsally over its appropriate digit to insert at the base of a terminal phalanx. On the under side of each slip at its base, there is an insertion of one of the four muscular slips of extensor digitorum communis brevis.

It is evident that the two sets of muscles form homologous systems in the two animals. The muscular slips of extensor digitorum communis brevis in *Sphenodon* end in tendons which insert on the terminal phalanges. The homologous slips in *Megalobatrachus* are continuous, from beneath, with the four tendinous slips into which the M. extensor digitorum longus is described as dividing. As a matter of fact, the latter muscle merely extends to the wrist and then inserts on the surface of the brevis at the beginning of its tendons, instead of remaining separate and inserting on the metacarpals between them as in *Sphenodon*. Hence, so far as the M. extensor digitorum longus is concerned, its special homology merely extends to that part of the musculature extending from the origin on the ectepicondyle to the wrist.

It appears to have been originally the superficial portion of the distal part of the general extensor muscle mass which inserted on the outer connective tissue membranes of the wrist, and thus belongs particularly to the lower arm musculature, as distinguished from the muscles of the hand. In *Sphenodon*, it continues to hold its original relations, but has specialized, having evolved four slips and four tendinous insertions on the bases of the metacarpals. This is a terrestrial specialization.

In *Megalobatrachus*, the main muscle mass, as in the majority of urodeles, inserts on the wrist aponeurosis, which in turn receives from beneath the insertions of the four slips of the underlying brevis muscle.

Though *Megalobatrachus* is specialized for aquatic life, I believe this insertion on the dorsal aponeurosis to be more primitive than the condi-
tion in Sphenodon. As the primitive muscle mass penetrated the hand and the fingers, the superficial layers apparently first inserted on the superficial connective tissue, from which they appropriated strips in the direction of the pull to become separated out as tendons. The inferior layers and the origins, on the other hand, became connected with the bone through the intermediary of the perimysium, the periosteum and the intervening connective tissue. As the muscle invaded the finger elements, the lower surface found an attachment on the phalanges, and the upper surface on the under side of the tendinous strips. The mechanical pull would naturally cause these to be situated obliquely with regard to one another, so that the skeletal connection would be situated proximally in the hand and distally in the fingers with reference to the respective connections with the tendons.

In Eryops (Fig. 79), therefore, I am inclined to assign to this muscle a condition more nearly resembling that of Megalobatrachus, but with stronger tendons, as indicated by the heavy ulnar prolongations of the proximal ends of the metacarpals (Fig. 21) and by the more or less terrestrial habits of the animal.

Supinator Manus (Abductor et Extensor Pollicis Longus)

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Distal end of ulna on its radial border and from intermedium</td>
<td>Outer side of distal part of ulna and from the ligamentum intermusculare</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>After a diagonal course across the wrist it inserts on the fascia of the radial border of the wrist and on the base of metacarpal I on its dorsal side</td>
<td>After a diagonal course across the wrist it inserts on the radial border of the wrist and on the dorsal aponeurosis of digit I</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Ramus dorsalis manus intermedius from plexus radialis antibrachii, which is formed by rami radiales lateralis and medialis from N. brachialis longus superior</td>
<td>Nn. radiales medialis and lateralis from N. brachialis longus superior</td>
</tr>
</tbody>
</table>

Figs. 72, 75, 78.—Comparison of M. extensor carpi ulnaris in Megalobatrachus and Sphenodon, and its inferred restoration in Eryops.

Figs. 73, 76, 79.—Comparison of Mm. extensor digitorum longus and extensor digitorum communis brevis in Megalobatrachus and Sphenodon, and their inferred restoration in Eryops.

Figs. 74, 77, 80.—Comparison of the radioextensor muscle system in Megalobatrachus and Sphenodon, and its inferred restoration in Eryops.
In *Sphenodon* (Fig. 71), this muscle has a widespread origin on the distal half of the ulna and from the membranous area between it and the radius.

In *Megalobatrachus* (Fig. 69), the origin is much more compressed, arising merely from the radiodistal end of the ulna and from the intermedium. It is to be noticed, however, that the origin is generally ulnar in character and is closely associated with the common origin of the M. extensor digitorum communis brevis, together with which it combines in a fan-shaped system to the hand.

In both animals, it takes a diagonal course across the carpus and inserts on the radial side of the wrist-capsule. In both cases, it pulls on the radial side of the base of the first metacarpal and hence has an influence on the first digit, for which it thus acts as an extensor as well as for a general abductor for the carpus. The point to bear in mind is that it has a general ulnar origin and yet an insertion on the radial side of the carpus. This is to be considered in connection with the following muscle.

The innervation in both forms is homologous. As the homologies are so clear, this muscle must have been well defined in the Stegocephalia, and hence is represented in *Eryops* as a part of the fundamental hand musculature.

The abductor et extensor pollicis longus is termed the abductor digiti secundi in *Megalobatrachus* by Osawa (1902, p. 283), on the theory that the first digit has disappeared in urodeles. As it has been clearly demonstrated by recent workers that the fifth digit has disappeared and that the first is still present in these forms, Osawa's terminology is faulty in this respect, and the muscle should have the same name as its homologue in *Sphenodon*. 
Extensor Digitorum Communis Brevis
Figures 69, 71, 73, 76, 79

<table>
<thead>
<tr>
<th>MEALOBATRACHUS</th>
<th>SPHENODON</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Radial part of ulnare and from intermedium</td>
<td>Distal radial corner of ulnare and from intermedium</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Ventral side of aponeurotic slips of M. extensor digitorum longus, where they enter the digits I, II, III and IV</td>
<td>Immediately forms five slips to fingers I to V, respectively, where they terminate as tendons inserting on the bases of the terminal phalanges</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Rami dorsales manus intermedium and ulnaris as well as ramus dorsalis manus radialis, the two former from plexus antibrachii formed by Nn. radiales lateralis and mediales, and the latter from N. radialis superficialis, all from N. brachialis longus superior</td>
<td>Ramus medialis of N. radialis from N. brachialis longus superior</td>
</tr>
</tbody>
</table>

Osawa (1902, p. 284) states that the origin of this muscle in *Megalobatrachus* includes the radiale, ulnare and three radial carpalia. In my dissection (Fig. 69), the origin is shown clearly as the radial part of the ulnare and the intermedium. After careful examination, I could find no trace of origins from either radiale or carpalia. As this corresponds exactly with the condition in *Sphenodon*, I feel certain that Osawa is mistaken. Again, Osawa (1898, p. 566) mentions only four slips as belonging to this muscle in *Sphenodon*, inserting on digits II to IV respectively. In my dissection, a fifth slip similar to the other four goes quite conspicuously to end as a tendon on the terminal phalanx of digit I, arising in common with the other four, as shown in figure 71.

In *Megalobatrachus* (Figs. 69, 73), the terminal tendons of these muscles unite with the aponeurosis of M. extensor digitorum longus to insert on the terminal phalanges, while, in *Sphenodon*, this does not take place, since the slips of the latter muscle, as mentioned above (page 259), insert on the ulnar side of the bases of metacarpales I to IV (Figs. 70, 71). This condition in *Sphenodon* is a terrestrial adaptation which apparently arose in the following way.
M. extensor digitorum longus is a muscle belonging to the lower arm rather than to the hand. This is shown by the fact that its muscular mass is situated entirely in that region and inserts into the aponeurosis of the wrist. M. extensor digitorum communis brevis is a carpal muscle, arising from carpal bones only, and inserting into the dorsal aponeuroses of the phalanges. The former mass, therefore, derived its tendinous termination from the wrist, while the latter derived its five tendons from the fingers. The muscular action of the fingers in terrestrial locomotion would naturally tend to keep them independent of the arm muscle in action, while its primitively single sheetlike tendon would eventually split through the action of the contracting finger muscles, remaining attached only between the slips. In Megalobatrachus, however, because of its swimming method of progression, the limb would move as a whole and the fingers would not be subject to independent stress and action; hence their musculature would become relatively unimportant, while the pressure of the paddlelike action would affect the hand and arm as a unit. In this case the broad aponeurotic insertion of the extensor digitorum longus would act most effectively in connection with the hand as a whole, while the brevis connection would be weakened and subordinated to it. This condition is realized in the Megalobatrachus hand, the paddle-like action of which is further assisted by the broad skin flanges on the sides of the flat fingers.

Interossei et Abductor Pollicis Brevis (Dorsometacarpales and Extensor Digiti Quartii)

<table>
<thead>
<tr>
<th>MEGALOBATRACHUS</th>
<th>SPHENODON</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>The only representative of this series is apparently the M. extensor digit quarti (&quot;quinti&quot; of Osawa), which arises on the distal end of the ulna, and runs down the ulnar side of the fourth metacarpal (considered the fifth by Osawa)</td>
<td>Including the abductor pollicis brevis, these are ten little muscles, which, excepting the above, rise from the bases of the respective metacarpals, in pairs, on either side the digit. The abductor pollicis brevis arises from the radiale. Otherwise it corresponds to interosseus on the ulnar side of the thumb</td>
</tr>
<tr>
<td>No muscles on I to III</td>
<td></td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Dorsal aponeurosis of fourth or ulnar-most finger</td>
<td>Basal phalanx of each finger in pairs on radial and ulnar sides respectively, then fusing with dorsal aponeurosis</td>
</tr>
<tr>
<td>No muscles on I to III</td>
<td></td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>As in preceding muscle</td>
<td>As in preceding muscle</td>
</tr>
</tbody>
</table>
These muscles should be treated as a unit, and as a whole might better be called in *Sphenodon* the "dorsometacarpales," as they lie along the dorsal side of the metacarpal bones. They have the same innervation as the extensor digitorum communis brevis and are evidently the deeper slips of the same muscle system. The radial muscle of digit I has extended its origin to the radiale. As it is on the outside of the digit, this results in its acting as an abductor. There is also a tendency for the ulnar slip of digit V to encroach proximally to derive its origin from the carpus. The development of these slips is correlated with terrestrial habits.

In *Megalobatrachus*, on the other hand, there exists the usual lack of development to be expected in an aquatic animal. There being no independent stress on the digits, no deeper muscles of this series appear except on the ulnar side of digit IV, where a well-developed slip arises from the ulna, called by Osawa the "extensor digitii quinti proprius." As, however, there is no fifth digit, it should rather be known as the "extensor digitii quarti proprius" (Fig. 69). The innervation is the same as in M. extensor digitorum communis brevis, and should be classed as a deeper element of that system, like the corresponding muscle in *Sphenodon*.

As *Eryops* had a powerful and well-developed carpus and more or less terrestrial habits, a system of metacarpal muscles somewhat like those of *Sphenodon* would be necessary, as a part of the dorsal extensor system of the hand.

E. The Extensor Arm Muscles in General

The extensor system of the upper arm consists of the four anconeus muscles which unite in a single insertion on the proximal end of the ulna, thus transmitting all extensor pulls and stresses to that element of the skeleton. This extensor muscle group is continued to the lower arm by the series of extensors arising from the ectepicondyle of the humerus, which is therefore the extensor condyle. This series acts as a brake on the flexor system in lowering the hand to the ground. The muscles arising from the distal part of the condyle insert on the ulna and on practically the entire carpus. These are the extensor carpi ulnaris and the extensor communis digitorum longus, and are continued into the hand by the supinator manus, the extensor digitorum communis brévis, and the dorsal finger muscles generally. On the contrary, the muscles arising from the proximal part of the ectepicondyle and inserting on the radius, together with the similar set on the flexor side and the anconeus system
of the upper arm, are those most effective in lifting the hand from the
ground from its backward position, preparatory for the forward reach.
They are the extensores radiales superficialis and profundus and the
supinator longus.

Thus it will be seen that the muscle arrangement corresponds with
the bones of the lower arm and the hand. All the digits radiate from a
pyramid of carpal bones including all but the radiale as shown by Gregory
(1915, pp. 363–364). The apex of this pyramid is formed by the inter-
medium and ulnare, which together support the ulna. Thus the most
powerful extensor muscles converge on the ulna from the upper arm,
while, in the manus, it is evident from figure 71 that practically all the
extensor muscles of the hand and fingers diverge from the ulna and the
ulnar pyramid of carpal bones. The proximal muscles, on the other
hand, converge from the supinator crest and the proximal part of the
condyle to the radius and radiale and seem to run off the hand on the
radial border. As shown by Gregory, Miner and Noble (1923), the com-
parative anatomy of the reptile and amphibian skeleton, supported by
embryological indications, clearly proves the former existence of a pre-
pollex in the ancestors of these groups, articulating from the radial series
of bones, namely, the radius, radiale and mediale. The latter element
may have disappeared in the adult modern form, but was clearly evident
in the _Eryops_ carpus (Fig. 21).

The course of the radial musculature in _Megalobatrachus_ inserts on
this series. This consideration, and the fact that it does not enter into
the musculature of any of the five surviving digits where they exist, are
strong evidence that these muscles are the survival of a prepollical mus-
culature. In the reconstruction of _Eryops_ they are made to converge to
that element. The evidence of the musculature thus supports, as well,
the thesis of Gregory and others regarding the ulnar pyramid and the
arrangement of the primordial rays of the hand. Likewise, the insertion
in _Sphenodon_ of the M. extensor carpi ulnaris on the pisiform, and its
ulnaroblique course and insertion on the ulna itself, suggest the former
existence of a postminimus element, of which it appears to be vestigially
the former musculature. It thus confirms, from the point of view of
musculature, the proofs from embryology along the same line (see
Gregory, Miner and Noble (1923).

It is also noteworthy, in _Megalobatrachus_, and other urodeles which
have lost both digit V and the postminimus, that the M. extensor carpi
ulnaris inserts on the ulna in a more proximal position than in five-
fingered forms like _Sphenodon_, and is directed toward the ulnar border by
a wider angle, as would be expected if its course were aimed at two lost digits instead of one.

F. Ventral Musculature of Lower Arm and Hand

Palmaris Communis Superficialis

Figures 19, 81 to 84, 86, 89, 92

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Entepicondyle of the humerus in common with Mm. flexores carpi radialis and ulnaris</td>
<td>Entepicondyle of the humerus and elbow-joint capsule in common with Mm. flexores carpi radialis and ulnaris</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Forms broad aponeurosis at wrist into which the M. palmaris profundus inserts from dorsal side and which then divides into five tendinous slips, one of which inserts on the radial side of metacarpal I, and the rest insert on the bases of the terminal phalanges of digits I to IV</td>
<td>Forms broad aponeurosis at wrist, which is joined dorsally by M. palmaris profundus and then splits into five tendons which insert on the terminal phalanges</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Ramus superficialis medialis of N. brachialis longus inferior</td>
<td>Ramus superficialis medialis of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

While the homologies of this muscle are clear, as the origins, insertions and innervations correspond in urodeles and reptiles, nevertheless its relations to the Mm. flexores breves sublimes have been complicated by the fact that in the hand region its aponeurosis in reptiles is spanned on the ventral side by the aponeurosis of the latter muscles, while in urodeles it lies superficially. This particular feature will be dealt with under the heading of the Mm. flexores breves sublimes (p. 281 ff).

The palmaris communis superficialis [palmaris superficialis, Mc-Murrich, Wilder; flexor digitorum communis profundus of Sphenodon, Osawa; flexor digitorum longus sublimis of Megalobatrachus (Cryptobranchus), Osawa; flexor sublimis digitorum, Humphry; epitrochleoulno-digitalis, Fürbringer; flexor digitorum profundus, Günther; flexor primordialis communis, Ribbing] occupies the greater part of the superficial palmar aspect of the hand. It always arises from the entepicondyle as a muscular sheet which inserts into the palmar aponeurosis, which in
Fig. 81.—Dissection of the superficial flexor musculature of the forearm of *Megalobatrachus*.

Fig. 82.—Dissection of middle layer of flexor muscles in the forearm of *Megalobatrachus*.

Fig. 83.—Dissection of the superficial flexor musculature of the forearm of *Sphenodon*.

Fig. 84.—Dissection of the middle layer of flexor muscles in the forearm of *Sphenodon*.
turn splits into tendinous bands inserting on the terminal phalanges. It thus corresponds to the extensor digitorum longus of the dorsal side of the hand.

In *Megalobatrachus* (Figs. 81, 82, 86), as there are but four digits, there are four slips extending along the phalanges. A fifth slip is also present, inserting on the radial margin of the first metacarpal, perhaps a rudiment of a former connective tissue slip to the vanished prepollex.

In *Sphenodon* (Figs. 83, 84, 89), the muscular portion is more powerful and fleshy than in *Megalobatrachus*, as would be expected in view of its terrestrial habits.

The innervation is by the medial branch of the ramus superficialis of the brachialis inferior, the same ramus that innervates all the more ulnar muscles.

In *Eryops* (Fig. 92), a muscle of the same general type, common to both forms, is to be inferred, but inclined to the more powerful type characteristic of *Sphenodon* and the lizards generally. There would be four well-developed tendons, as in urodèles, and perhaps a small tendon to the prepollex, indicated by the rudimentary fifth slip of *Megalobatrachus*. It is possible, however, that this rudiment is merely a fascial carpal support to strengthen the wrist, since the prepollex doubtless had its own independent radial musculature.

### Palmaris Communis Profundus

**Figures 19, 82, 84, 86, 89, 92**

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>(a) Ventral head</td>
<td>(a) Distal head</td>
</tr>
<tr>
<td>From ulnar border of ulna near distal end</td>
<td>From distal three-fourths of ulna</td>
</tr>
<tr>
<td>(b) Dorsal head</td>
<td>(b) Proximal head</td>
</tr>
<tr>
<td>From radial part of the distal half of ulna, separated from above by M. ulnocarpale</td>
<td>From proximal surface of ulna just beneath the joint capsule, and under the origin of M. palmaris communis superficialis</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Both heads insert on the dorsal side of the aponeurosis of M. palmaris communis superficialis, (a) being situated to the ulnar side of (b), which inserts between it and the insertion of M. palmaris profundus dorsalis</td>
<td>Both heads insert in common into the proximal end of the palmar aponeurosis immediately beneath the junction of M. palmaris communis superficialis with it</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Ramus superficialis medialis of N. brachialis longus inferior</td>
<td>Ramus superficialis medialis of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>
In both *Megalobatrachus* and *Sphenodon*, three deep muscle heads arise from the ulna and insert on the dorsal side of the palmar aponeurosis of the palmaris communis superficialis. Two of these are innervated by the same nerve as that muscle, the ramus superficialis medialis, while the third is innervated by a different nerve, the ramus profundus. The latter head, the palmaris profundus dorsalis, will be treated later (page 279), as it belongs to a different series. The two former heads, grouped together as the palmaris communis profundus, because of their innervation, must also be related to the superficial muscle, of which in reality they form the deeper layer.

In *Megalobatrachus* (Figs. 82, 86), the two heads are separated by the M. ulnocarpalis, which passes between their ulnar portions. The course of these muscles is diagonal and parallel, one being located ventral to the other, as shown in the above table. Both insert on the dorsal side of the palmar aponeurosis, the dorsal head having an insertion radial to the ventral head.

The relations in *Sphenodon* (Figs. 84, 89) are similar, except that no M. ulnocarpalis is present; the two heads arise from the ulna, one from a greater distal origin, and the other from a lesser proximal origin; their course is at the same depth, and their fibres join before insertion. The insertion also appears to enter the proximal end of the aponeurosis rather than its dorsal side, sharing this feature with the muscular fibres of the M. palmaris communis superficialis which enter immediately ventral to the insertion of the former.

A similar condition must have existed in *Eryops* (Fig. 92), as these muscles are found in both lines of descent from the common stegocephalian ancestry. There was probably a closer resemblance to the urodele condition, hence a M. ulnocarpalis is postulated.

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td>Entepicondyle of the humerus, beneath and radial to the origin of M. palmaris communis superficialis</td>
</tr>
<tr>
<td>No muscle of this name, but the deeper radial fibres of M. palmaris communis superficialis are homologous with it</td>
<td></td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td>Lower part of the radial side of the radius</td>
</tr>
<tr>
<td>None</td>
<td></td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td>Ramus superficialis medialis of the N. brachialis longus inferior</td>
</tr>
<tr>
<td>None</td>
<td></td>
</tr>
</tbody>
</table>
In *Sphenodon*, there is another deep muscle head of the same series as the preceding, as shown by the innervation, the M. pronator teres. It arises in common with the proximal head of the M. palmaris communis profundus, but from the lower and under part of the entepicondyle. It diverges from the palmaris, however, and inserts on the distal part of the radius.

In *Megalobatrachus*, there is no muscle of this nature, and this probably represents the more primitive condition, since the pronator is obviously a radial derivative of the deeper palmaris musculature.

In *Eryops*, we must postulate the more primitive condition, hence no separate M. pronator radii teres is inferred.

**Flexor Carpi Ulnaris**

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td>From entepicondyle of the humerus distal to M. palmaris superficialis and proximal to M. epitrochleoanconaeus</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td>On flexor and ulnar surfaces of ulnare and on tendinous arch which gives rise to carpometacarpales</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td>Ramus superficialis ulnaris of N. brachialis longus inferior</td>
</tr>
<tr>
<td><strong>Origin</strong></td>
<td>From entepicondyle of the humerus between Mm. palmaris superficialis and epitrochleoanconaeus</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td>On flexor surface of pisiform</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td>Ramus superficialis ulnaris of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

This muscle and the Mm. epitrochleoanconaeus and ulno-carpalis also form a related series, as shown by their common innervation by the ramus superficialis ulnaris of the N. brachialis longus inferior. The first two are found in both urodeles and reptiles, but the latter only in urodeles.

The flexor carpi ulnaris arises in both *Megalobatrachus* and *Sphenodon* from the distal end of the entepicondyle, adjacent to the M. palmaris communis superficialis, and between it and the M. epitrochleoanconaeus.

In *Megalobatrachus* (Fig. 87), it inserts on the ulnar part of the ulnare as well as on the tendons of the wrist. In *Sphenodon* (Figs. 84, 90), it inserts on the pisiform alone. As it seems to be clear that the latter
Eryops

Figs. 85 to 93

272
element is the base of a vanished sixth digit, the ulnaris may possibly have been part of the musculature of that digit.

Epitrochleoanconæus

Figures 19, 84, 87, 90, 93

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Distal end of entepicondyle and capsule of elbow joint</td>
<td>Distal end of entepicondyle and capsule of elbow joint</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>Median one-third to one-half of ulnar border of ulna</td>
<td>Distal end of ulna on ulnar border</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>Ramus superficialis ulnaris of N. brachialis longus inferior</td>
<td>Ramus superficialis ulnaris of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

This is really a more distal portion of the preceding muscle, but is nevertheless separate in both urodeles and reptiles. It arises in both *Megalobatrachus* and *Sphenodon* from the most distal portion of the entepicondyle, distal to the origin of M. flexor carpi ulnaris, and inserts on the ulnar border of the ulna. In *Megalobatrachus* (Fig. 87), this insertion is on the middle part of the ulna, while in *Sphenodon* (Fig. 90) it is on the distal part. As on the extensor side (page 266), this may be significant, as in the urodeles two digits are lost, the minimus and postminimus, while in reptiles the postminimus only is lacking. On both sides of the carpus, therefore, the ulnar musculature "runs off" the arm at a higher point in urodeles than in lizards.

As both ulnar muscles are present in both groups, they are presented as separate muscles with similar relations in *Eryops* (Fig. 93). As seen in the discussion of the manus of *Eryops* (page 188), there are clear indica-

Figs. 85, 88, 91.—Comparison of M. flexor carpi radialis in *Megalobatrachus* and *Sphenodon*, and its inferred restoration in *Eryops*.

Figs. 86, 89, 92.—Comparison of Mm. palmaris communis superficialis, palmaris communis profundus and ulnocarpalis, in *Megalobatrachus* and *Sphenodon*, with especial reference to their relations to the aponeurosis palmaris superficialis, and their inferred restoration in *Eryops*.

Figs. 87, 90, 93.—Comparison of the Mm. flexor carpi ulnaris and epitrochleoanconæus in *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*. 
tions on the ulnar side of the fossil carpus of articular surfaces for both minimus (digit V) and pisiform (digit VI), to which this musculature is directed.

\[
\text{Ulnocarpalis} \\
\text{Figures 82, 86, 92, 94, 100}
\]

<table>
<thead>
<tr>
<th><strong>MEGALOBATRACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Proximal half of radial surface of ulna</td>
<td>None</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Delicate tendon inserts on tendinous bridge which forms origin of contrahentes digitorum</td>
<td>None</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Ramus superficialis ulnaris of N. brachialis longus inferior</td>
<td>None</td>
</tr>
</tbody>
</table>

This purely urodele muscle is present in its typical condition in *Megalobatrachus* (Fig. 94). It arises on the proximal half of the ulna and inserts by means of a much attenuated tendon on a delicate and very deeply situated palmar bridge connecting the most ulnar elements of the deep finger musculature with the most radial elements of the same series. It is said by McMurrich (1903, p. 179) to insert on the distal carpal bones in *Amblystoma* and *Plethodon*. Wilder (1912, p. 402) gives its insertion in *Necturus* as carpalia 4 and 5. Osawa\(^1\) (1902, p. 279) states for *Megalobatrachus* (*Cryptobranchus*) that it inserts partly on the base of metacarpale V, and partly as a tendinous band as far as the base of metacarpale II. Ribbing’s investigation agrees most nearly with mine, although he is not explicit. He says (1907, pp. 624-625) that this muscle distally fastens itself with a fan-shaped spreadout tendon to some of the carpal pieces. From this tendon, as well as from the same carpal pieces, arise the Mm. flexores digitorum. The union between these flexors and the M. ulnocarpalis, he says, is most intimate in *Siredon* and *Amblystoma*, and least intimate in *Menopoma*. I have made a most careful dissection of this muscle, shown in figure 100, and I have found that the “tendinous bridge” wraps itself around the ulnar side of carpale IV and gives off a muscle slip to the ulnar border of metacarpale IV.

\(^1\)Osawa calls this muscle the “flexor profundus longus.”
Figs. 94, 95, 96, 97.—Dissection and comparison of the deepest layer of forearm muscles and the Mm. contrahentes digitorum of *Megalobatrachus* and *Sphenodon*, and their inferred restoration in *Eryops*.
It then passes transversely across the hand to terminate in one of the Mm. contrahentes digitorum, which inserts on the radial border of metacarpale I. During its course, it receives the insertion of M. ulnocarpalis at the junction of carpale IV with the centrale, but arching freely over both. The tendon of M. ulnocarpalis seems to be practically continuous (through the membrane of the bridge at its junction with it) with the origin of a muscle slip of the contrahentes system inserting on the radial side of metacarpale IV. I agree with Ribbing’s suggestion that the M. ulnocarpalis was formerly continuous with the deeper finger flexors, and formed one muscle with them in ancestral types, thus making the deepest layer of the general ulnar muscle complex, as distinguished from the purely radial musculature of the ancestral prepollex, now remaining as the musculature of the radius and radiale.

In *Eryops* (Fig. 92), this musculature was doubtless more important, since it is in a degenerate condition in modern urodèles, and to this primitive condition *Megalobatrachus* gives an intermediate clew. Hence in the restoration of *Eryops* with its heavier demands on all elements of the limb muscles, we may picture an ulnocarpalis arising from the whole radial surface of the ulna, passing straight down into the deeper hand-layer and then radiating out to supply all digits except the prepollex.

**Flexor Carpi Radialis**

*Figures 19, 81 to 85, 88, 91, 98*

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td>From the entepicondyle of the humerus and from the capsule of the elbow joint</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td>Entire radial border of radius, on radial side of radiale, and on radial side of wrist capsule</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td>Ramus profundus of N. brachialis longus inferior</td>
</tr>
<tr>
<td></td>
<td>Ramus profundus of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

In both *Megalobatrachus* and *Sphenodon* this muscle takes its origin from the entepicondyle in close juxtaposition to the insertion of the M. coracobrachialis longus and from the radial part of the joint capsule. In
Megalobatrachus (Figs. 81, 82, 85), it forms a single mass which inserts on the distal end of the radius and on the radiale. In Sphenodon (Figs. 83, 84, 88, 98), it arises by two heads, one from the entepicondyle and the other from the entepicondyle and the joint capsule. The first and most radial of these inserts along the whole radial border of the radius, forming a broad, thin muscle which inserts along its inner edge, while the outer edge is free. The second and ulnar slip is narrower and inserts on the radiale.

As the double muscle of Sphenodon is obviously a more specialized condition, the flexor carpi radialis in Eryops (Fig. 91) was doubtless a single mass more like that of Megalobatrachus, but very powerful like all the flexors, as shown by the greatly developed entepicondyle. There is a conspicuous ridge on the proximal part of the entepicondyle on its lower border and just at the angle posterior to the insertion surface of the M. coracobrachialis. This is in the proper position for the origin of this muscle. There is a clearly marked facet on the distal half of the radius on the radial side which can be nothing but its radial insertion, while its most medial fibres found their insertion on the radiale as in both Megalobatrachus and Sphenodon. It was thus the chief flexor muscle of the proximal part of the radial series of elements as distinguished from the ulnar muscles occupying the greater part of the hand and lower arm.

### Pronator Quadratus

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td>Origin</td>
</tr>
<tr>
<td>Entire radial side of the ulna</td>
<td>Nearly the entire radial side of the ulna</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td>Insertion</td>
</tr>
<tr>
<td>Fibres run obliquely to the radial border of the radius, the whole flexor surface of the radiale, and the flexor surface of carpale I</td>
<td>Distal half of radius and ulnar corner of radiale</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td>Innervation</td>
</tr>
<tr>
<td>Ramus profundus of N. brachialis longus inferior</td>
<td>Ramus profundus of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

This is the deepest muscle of the lower arm. It arises from almost the entire radial border of the ulna, crosses obliquely the membrana intermuscularis connecting the ulna and radius, immediately ventral to the
ramus profundus of the N. brachialis longus inferior, which innervates it, and inserts on the ulnar border of the radius. The fibres in *Megalobatrachus* (Figs. 94, 95) are approximately parallel in their course, thus forming a quadrate muscle with an insertion about equal in extent to its origin. In *Sphenodon* (Figs. 96, 98), the fibres converge and insert on the distal half of the radius, thus forming a more triangular muscle with a strong proximodistal pull.

In *Megalobatrachus*, the distal half of this muscle continues in its more superficial fibres, as a flat, fleshy band, over the distal face of the ulna, to insert strongly on the whole flexor surface of the radiale and on carpale I. Osawa does not mention the latter insertion, but it is very clear in my dissection. This part of the muscle thus forms a powerful pronator carpi. It is not found in *Sphenodon*.

The strong development of this slip, its extreme radial insertion on both the radial elements of the carpus, to which it is limited, and the innervation from the ramus profundus suggest that this is the more distal part of that series of radial muscles which I conceive as having been originally the musculature of the prepollex of *Eryops*. That *Eryops* had a well-developed prepollex is shown in the discussion of the skeleton of the manus (page 188 and Fig. 21). The articulation of this element is so clear that it must have been a movable feature and thus must have required a musculature. The radial musculature herewith described, together with that on the extensor surface, is in the exact position demanded by such an element, and upon its disappearance the distal fibres because of their oblique position were taken over as a supinator and pronator of the hand.

The pronator quadratus was present in *Eryops*, as shown not only by its presence in both urodèles and reptiles, but also by the opposing ridges on the inner edges of radius and ulna, while the proximal position of the ulna with reference to the radius (figure 21) postulates a proximodistal direction of its oblique fibres in a line with the prepollex. Likewise, on the lower radial edge of the ulna there is a broadening of the ridge suggesting the origin of a powerful muscle band like that in *Megalobatrachus*, which is thus indicated as the “flexor prepollicis” in the restoration of *Eryops* (figure 97).
Palmaris Profundus Dorsalis  
Figures 82, 86, 98

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>Deeper and dorsal to the heads of M. palmaris communis profundus. Arises from nearly the whole radial angle of the ulna</td>
<td>With oblique fibres from the ventral surface of the ulnar side of the distal end of the ulna</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Dorsal side of wrist aponeurosis radial to insertion of ventral head of M. palmaris communis profundus</td>
<td>Dorsal side of palmar aponeurosis</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Ramus profundus of N. brachialis longus inferior</td>
<td>Ramus profundus of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

This is a deep muscle overlying the preceding, arising like a more superficial layer of it and with oblique fibres inserting radially on the dorsal side of the aponeurosis of the M. palmaris communis superficialis, deeper than the other deep heads of that system. At first sight, it seems associated with these elements, which, as already shown (page 270), are grouped as the M. palmaris communis profundus. The innervation from the ramus profundus, however, marks it as a part of the radial system which has become connected with the palmar aponeurosis.

In *Megalobatrachus* (Figs. 82, 86), it arises from nearly the entire radial border of the ulna, and is a well-developed muscle, but in *Sphenodon* (Fig. 98), it is reduced to a mere vestige, arising from the ventral side of the distal end of the ulna and with but a slight insertion on the aponeurosis.

The relations of the whole series of forearm flexors correspond closely with those of *Amblystoma*, *Plethodon* and various reptiles described by McMurrich in his admirable paper on “The Phylogeny of the Forearm Flexors” (1903), and they may therefore be considered as typical of both amphibians and reptiles.

In *Eryops*, there is a facet on the radial face of the distal third of the ulna, which may have belonged to this muscle, though it is possible that in stegocephs it may not have separated definitely from the ventral surface of the pronator quadratus, of which it may have been the superficial portion in especial association with the “flexor prepollicis.”
Fig. 98.—Dissection of the forearm of *Sphenodon* to show Mm. pronator quadratus, pronator radii teres, and palmaris profundus dorsalis.
### Megalobatrachus

**Origin**
As a series of slips in three layers from the dorsal side of the palmar aponeurosis of M. palmaris communis superficialis, where it divides into four slips for the ventral side of each finger. Figs. 101 A and B, flex. br. subl. (a), (b), (c)

**Insertion**
All three layers of slips pass distally and insert, after uniting, on the metacarpophalangeal capsule

**Innervation**
Branches from loop formed by union of rami superficiales medialis and ulnaris of N. brachialis longus inferior

### Sphenodon

**Origin**
As a series of slips in three layers:
(a) *Superficial layer*—from an aponeurosis formed by the conjoined proximal ends of the slips, situated in the palm of the hand, overlapping superficially the palmar aponeurosis of the M. palmaris communis superficialis and its attached muscles. Fig. 101 C, flex. br. subl. (a)
(b) *Middle layer*—arising from the ventral surface of the palmar aponeurosis (of M. palmaris communis superficialis) just proximal to its subdivision into the phalangeal tendons. Fig. 101 C, flex. br. subl. (b)
(c) *Deep layer*—arising from the dorsal surface of the palmar aponeurosis of M. palmaris communis superficialis. Fig. 101 C, flex. br. subl. (c)

**Insertion**
(a) *Superficial layer*—divides into five pairs of slips, one pair for each phalanx, which reunite to terminate in a trough-shaped tendon, which inserts, after traversing the basal phalanx, on the basal joint of the succeeding phalanx
(b) *Middle layer*—In pairs (typically) on the metacarpophalangeal joints of digits II–IV
(c) *Deep layer*—beneath the above on digits II–IV

**Innervation**
Rami superficiales medialis and ulnaris of N. brachialis longus inferior
The homology of these muscles in urodeles and reptiles has been a stumbling-block to many comparative anatomists, because of their differing relations to the aponeurosis and tendons of M. palmaris communis superficialis in the two groups.

Osawa and Günther have interpreted the muscle here described for Sphenodon as the homologue of M. palmaris communis superficialis in urodeles under the name of flexor communis digitorum sublimis, though it arises only in the hand, and call the flexor which arises from the ent-

epicondyle of the humerus and inserts at the terminal phalanges, the flexor communis digitorum profundus. (Osawa, 1898, pp. 560, 564; Günther, 1867, p. 614.)

This is because the M. flexor brevis (superficial layer) is situated superficially to the long flexor in reptiles (Fig. 83), while in urodeles the latter is the most superficial muscle (Figs. 81, 82). McMurrich (1903, p. 206) explains the difficulty by assuming that the superficial aponeurosis of the long flexor of urodeles has disappeared in reptiles, leaving the flexores breves exposed as the superficial layer. Ribbing, however (1907, pp. 598–599), has shown that Emys (flexores breves superficiales)
presents a transitional condition which clarifies the situation, and after carefully dissecting and comparing the palmar musculature in *Megalobatrachus* and *Sphenodon*, I have come to agree with the interpretation suggested by him. Figures 101 A-C in connection with the following considerations will make this clear.

In *Megalobatrachus*, as above stated, the M. palmaris communis superficialis, the long common flexor of the fingers, arises from the entepicondyle and, with its deeper heads, is the principal muscle of the ventral side of the lower arm. It is fleshy until it reaches the wrist, when it terminates in the tough connective tissue of the palmar aponeurosis. This latter feature covers the entire palmar musculature superficially, and splits into four tendons for the ventral side of the four digits. These terminate at bases of the end phalanges. The dorsal side of this aponeurosis gives rise to three layers of phalangeal muscles, shown in their most typical condition in digit II (figures 99, 101 A, B). The most distal and superficial of these muscles originates as a single slip which immediately splits into three portions, one median and two lateral, which unite at their edges distally and insert side by side on the metacarpophalangeal capsule and the base of the proximal phalanx.

The second layer likewise arises as a single muscle, proximal to the above, and likewise divides into three slips, which unite with the first set and insert immediately beneath it. The third layer arises from the dorsal side of the palmar aponeurosis, and after dividing into three slips like the other two layers, inserts in common with them.

In *Sphenodon* (Figs. 83, 84, 89), the palmaris communis of the lower arm has a similar origin and insertion to that in urodèles, as shown in the discussion of that muscle (page 267). Two of the three layers of flexores breves, however, have come to lie ventrally and superficially to it, in the following manner.

The superficial layer of flexores breves (Fig. 83) arises as a single, thin, nearly aponeurotic layer in the palm of the hand, spanning the underlying musculature, and anchored on the ulnar side by a strong connection with the pisiform, and on the radial side by a ligament binding it to the radial border of the wrist. This common origin quickly splits into five portions, one for each of the five digits. Each of these again subdivides and passes around the respective tendons of the M. palmaris communis superficialis, uniting to form an arch or ring (Fig. 101 C). Each pair then terminates in a trough-shaped tendon, which passes distally beneath the palmaris tendon the distance of one phalanx to insert on the base of the succeeding phalanx. (See also Figs. 84, 89,
flex. br. subl. a.) Owing to the phalangeal formula of *Sphenodon*, this results as follows:

<table>
<thead>
<tr>
<th>Digit</th>
<th>Tendon inserts on base of phalanx</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>II</td>
<td>III</td>
</tr>
<tr>
<td>III</td>
<td>IV</td>
</tr>
<tr>
<td>IV</td>
<td>V</td>
</tr>
</tbody>
</table>

The middle layer of flexores breves arises from the superficial side of the palmar aponeurosis of *M. palmaris communis superficialis*, just distal to the junction of the main muscle mass with it (Figs. 84, 89, 101 C), and immediately divides into four fleshy slips (Figs. 84, 89, flex. br. subl. b.), of which the most radial passes to the radial side of phalanx II, and inserts on the proximal end of its basal phalanx; the second slip passes between metacarpalia II and III, to insert on the radial side of basal phalanx III; the third also divides and inserts on the ulnar side of basal phalanx III and the radial side of basal phalanx IV, while the fourth splits in like manner to insert on the ulnar side of basal phalanx IV and the radial side of basal phalanx V.

The deep layer of flexores breves (Fig. 101 C, flex. br. subl. c) arises from the dorsal side of the palmar aponeurosis immediately opposite to the middle layer, and divides into four slips which insert on the basal phalanges of digits II, III and IV immediately beneath and in a similar manner to the corresponding slips of the middle layer, except that there is no slip to digit V.

Thus it is evident that, in *Megalobatrachus* and *Sphenodon*, the arrangement of the layers of these muscles compare, as follows:

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Palmar aponeurosis</td>
<td>Superficial layer</td>
</tr>
<tr>
<td>2. Superficial layer</td>
<td>Middle layer</td>
</tr>
<tr>
<td>3. Middle layer</td>
<td>Palmar aponeurosis</td>
</tr>
<tr>
<td>4. Deep layer</td>
<td>Deep layer</td>
</tr>
</tbody>
</table>

In *Megalobatrachus* (Fig. 101 A, B), the palmar aponeurosis is superficial to all three muscle layers, while in *Sphenodon* (Fig. 101 C), two layers of muscles are superficial to the aponeurosis.

The most satisfactory explanation is as follows: In *Megalobatrachus* we have the more primitive condition, which in the case of terrestrial reptiles, in order to strengthen the muscular action of the toes, was followed by a gradual growth upward of the lateral muscle slips seen in figure 101 C, until their proximal portions invaded the surface of the
palmar aponeurosis, while the median portion gave way to a median tendon which formed the insertion of the lateral slips. This produced the superficial layer. A further development of the proximal ends of these slips and a further encroachment caused them to coalesce above to

form a thin muscular sheet, which appropriated enough of the superficial connective tissue beneath the skin to form a semitendinous expanse. This finally found an attachment on the pisiform and the capsule of the wrist.

The middle layer followed the example of the superficial layer and came to lie just dorsal to it, attaching itself to the superficial surface of
the palmar aponeurosis of the palmaris communis. This layer continued to retain its old insertions on the basal phalanges, but without forming tendons, while its median slips disappeared or united with the lateral slips. The deep layer remained in its original position which corresponds in the two forms.

Ribbing (1907, pp. 598–599), as above mentioned, shows that Emys presents a stage in which the dorsal slips have begun to invade the ventral side of the aponeurosis.

Various reptiles carry this specialization further. In Lacerta and Teius, the superficial layer has seized hold of the ulnar part of the M. palmaris communis and has separated it from the radial part to form a continuous muscle terminating in the flexores breves without the intermediary of the pisiform.

In Eryops (Fig. 92), the more primitive condition naturally prevailed, as the reptilian condition is seen to be secondary, and a specialized advancement. In the restoration of the Eryops musculature, therefore, the M. palmaris communis superficialis is shown in its original superficial position.

Contrahentes Digitorum

<table>
<thead>
<tr>
<th><strong>Megalobatrachus</strong></th>
<th><strong>Sphenodon</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>As six slips from tendon and tendinous carpal arch into which inserts M. ulnocarpalis</td>
<td>As two slips arising from carpalia 2, 3, 4 and the ulnare (Adductores pollicis and digiti minimi, Osawa)</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>(a) Digit I—2 slips, one to radial side of metacarpophalangeal capsule; the other to whole radial side of first metacarpal</td>
<td>(a) Ulnar side of metacarpophalangeal joint of digit I</td>
</tr>
<tr>
<td>(b) Digit II—slip to metacarpophalangeal joint</td>
<td>(b) Radial side of metacarpophalangeal joint of digit V</td>
</tr>
<tr>
<td>(c) Digit III—slip to flexor brevis muscle mass inserting on metacarpophalangeal capsule</td>
<td></td>
</tr>
<tr>
<td>(d) Digit IV—2 slips, one to radial side of metacarpophalangeal joint; the other to extreme ulnar side of the same joint and of metacarpus IV</td>
<td></td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Rami superficiales medialis and ulnaris of N. brachialis longus inferior</td>
<td>(a) Ramus superficialis medialis of N. brachialis longus inferior</td>
</tr>
<tr>
<td></td>
<td>(b) Ramus superficialis ulnaris of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>
In *Megalobatrachus* (Figs. 94, 100), the six slips comprising these muscles are continuations of the M. ulnocarpalis through the intermediary of the deep carpal tendinous arch. The different muscle elements are so blended with this delicate arch that they appear, as Ribbing suggests (1907, pp. 624–625), to be the remnant of a former much stronger deep common flexor continuous with that muscle. In Anura this is carried a step further, where the contrahententes originate from the carpus but radiate from the same ulnar location. In reptiles (e.g., *Sphenodon*, Fig. 96), they appear to be reduced simply to the muscles known to authors as Mm. adductores pollicis and digiti minimi. This is borne out by the innervation, by the place of origin on the carpus, and by the fact that a muscle to digit I, in *Megalobatrachus*, corresponds in origin, shape, course, insertion and mechanical action with M. adductor-pollicis (auct.) in reptiles, while the slip to the ulnar border of digit IV arises from a position on the superficial side of the arch corresponding to that of the muscle just mentioned, and is in a position suggestive of a slip to the vanished digit V of urodeles. The phylogeny of the prominent oblique muscles, known as the adductors of the first and fifth digits, receives a satisfactory explanation only in this way. The slips to the three middle digits have disappeared, superseded mechanically by the increased development of the Mm. flexores breves profundi.

On the radial side of metacarpal I, the tendinous arch terminates in a broad muscular sheet partly overlapped distally by the oblique slip to the digit. This helps to strengthen the arch and with the other slip acts as a strong adductor for this digit. Its position, as in the case of the corresponding slip of the superficial palmar aponeurosis, suggests that it may have been originally the adductor of the former prepollex.

The ulnar slip to the first digit and its relation to the musculature, strongly confirms the view that this digit in urodeles is homologous with digit I of reptiles, and not digit II, as was formerly supposed by many authors, since it forms a typical pollical musculature.

The slips to digits II and III and the radial side of IV arise from the deeper side of the tendinous arch, while both of those to digit I and the slip to ulnar side of digit IV arise from its superficial side.

Since the condition in urodeles is clearly the more primitive, we may assume that it more nearly resembled the stegocephalian musculature, and hence that of *Eryops* (Fig. 97), with an adductor to the prepollex added. The theory is advanced that, as the marginal digits disappeared in the evolution of the tetrapod hand, their basic musculature was added to the outer margins of the carpus and metacarpus to form supinators and adductors, thus strengthening and perfecting the action of that organ.
Flexores Breves Profundi

Figure 100

<table>
<thead>
<tr>
<th><strong>MEGALOBATRACHUS</strong></th>
<th><strong>SPHENODON</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Origin</strong></td>
</tr>
<tr>
<td>From the carpals of the distal row,--four small muscles</td>
<td>Four muscles from metacarpals II to V, and to a certain extent from the adjacent carpalia</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td><strong>Insertion</strong></td>
</tr>
<tr>
<td>Each slip inserts on its appropriate metacarpal along its ventral face beneath the more superficial flexores breves</td>
<td>Each muscle divides, sending a radial slip to metacarpals I to IV respectively, inserting on their ulnar sides, and the other to the distal part of the metacarpal from which it arises</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td><strong>Innervation</strong></td>
</tr>
<tr>
<td>Branches from rami superficiales medialis and ulnaris of N. brachialis longus inferior</td>
<td>Rami superficiales medialis and ulnaris of N. brachialis longus inferior</td>
</tr>
</tbody>
</table>

Except for the Mm. interossei, these are the deepest flexors, and, as McMurrich (1903) has pointed out, are situated dorsally to the nerves above mentioned, while the more superficial flexores breves and the contrahentes digitorum are situated ventrally to them.

In the urodèles (Fig. 100), they arise from the distal carpalia and insert on the respective metacarpals, while in reptiles they are more differentiated, as is sufficiently shown in the above table.

In *Eryops*, the large size of the distal condyles of the metacarpals indicates a considerable muscular insertion. Hence we may assume that these deeper muscles, as well as the more superficial digital musculature, found their attachment there. For the origins we are justified in inferring the more primitive condition shown by urodèles, as arising from the distal carpalia.
Interossei

<table>
<thead>
<tr>
<th>Megalobatrachus</th>
<th>Sphenodon</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td></td>
</tr>
<tr>
<td>Three little muscles between the digits. They arise from the radial side of metacarpals II, III and IV</td>
<td>Four tendinous bands which arise from metacarpals I, II, III and V, from the ulnar side of the first three and from the radial side of the last</td>
</tr>
<tr>
<td><strong>Insertion</strong></td>
<td></td>
</tr>
<tr>
<td>On the ulnar side of metacarpals I, II and III</td>
<td>On the radial side of metacarpals II, III and IV, and on the ulnar side of IV</td>
</tr>
<tr>
<td><strong>Innervation</strong></td>
<td></td>
</tr>
<tr>
<td>Branches from rami superficiales medialis and ulnaris of N. brachialis longus inferior</td>
<td>None</td>
</tr>
</tbody>
</table>

These deepest muscles occur generally in urodeles. In reptiles, however, they are reduced to tendinous bands. As the fleshy condition is the more primitive, we may assume for Eryops their presence as in Megalobatrachus. It is worthy of note that in Sphenodon, digit IV receives two insertions and gives rise to no origins.

Since the insertions are at the distal ends of the metacarpals, while the origins are more proximal, the result would be a more efficient support for digit IV, a fact that may be correlated with its greater length.

Like the Mm. flexores breves profundi, the Mm. interossei are situated dorsal to the innervation, and hence may be grouped as offshoots of the profundi series.

G. The Flexor Arm Muscles in General

The flexor arm muscles on the ventral side of the upper arm, which correspond to the anconeus extensor system on the dorsal side, consist of the Mm. coracobrachialis proprius, coracobrachialis longus and brachialis inferior in urodeles; and Mm. coracobrachialis longus, biceps brachii and brachialis inferior in lizards. These arise like the anconeus either from the shoulder girdle or the humerus, and insert on the proximal part of the radius, or on the humerus in close connection with the ventral side of the elbow joint, as the anconeus inserts on the proximal part of the ulna on the dorsal side. Thus, as the ulna is the bone of the lower arm associated with the converging upper arm extensors, so the radius is the bone of the lower arm associated with the converging upper arm flexors.
Mm. supracoracoideus and coracobrachialis brevis should also be included, at least indirectly, with this part of the flexor system, since M. coracobrachialis proprius is an offshoot of the former, and there is good reason to believe that M. biceps brachii is derived from the latter in its proximal region, as well as from M. coracobrachialis longus in its distal region, thus accounting for its double innervation (page 224). In this connection, it is worthy of note that this method of accounting phylogenetically for the doubly innervated M. biceps brachii of the flexor system in Sphenodon, helps to make understandable the theory advanced (page 249) regarding the origin of the apparently doubly innervated and anomalously placed muscle of the extensor system of Megalobatrachus, known as the M. anconaeus coracoides.

This flexor system of the upper arm, again paralleling the extensors, is continued to the lower arm by the series of flexors arising from the entepicondyle of the humerus, which is therefore the flexor condyle.

Again, as in the case of the extensors, the muscles arising from the distal part of the condyle insert on the ulna and practically the entire carpus. These are the Mm. flexor carpi ulnaris, epitrocleoanconeus, ulnocarpalis, palmaris communis superficialis, and palmaris communis profundus (both heads). The M. pronator radii teres is an exception in its insertion on the radius, but since it is evident (page 270) from its innervation and origin that it is an offshoot of the M. palmaris communis profundus, it is equally clear that it belongs to the ulnar series.

Again closely paralleling the extensor side, this system is continued into the hand by the intrinsic flexor hand muscles, most of which originate from the ulnar side of the carpus and radiate into the fingers from that location.

On the contrary, and also in close parallel with the extensor condition, the lower arm muscles which arise from the proximal part of the condyle, namely, the two slips of the flexor carpi radialis, insert respectively on the radius and the radiale, and thus belong to the radial ray of the carpus, which we have seen (page 266) originally terminated in the prepollex.

Here again the arrangement of the musculature corresponds with the arrangement of the bones of the lower arm and the hand in such a way as to confirm the argument (Gregory 1915, pp. 363–364), based on the skeleton, that the present manus and carpus of tetrapods form an ulnar pyramid, which primitively arose from rays articulating from the ulnar element of the lower arm, while the prepollex was the termination of the radial element.
In the manus, the special musculature of the thumb in reptiles is exactly paralleled in its essentials in urodeles, thus confirming the view that the radial digit of urodeles is homologous with that of reptiles and is therefore actually digit I, and not digit II, as assumed by many authors, while the ulnar muscles of the lower arm, as shown on pages 266, 273 indicate a more extensive loss of primitive digital rays on that side than on the radial border of the manus where the prepollex is the only element known to have disappeared.

SECTION III. SUMMARY AND CONCLUSIONS

A. Skeleton

The Shoulder Girdle

1. In Eryops, the coracoidal portion of the scapulocoracoid is continued medially by a cartilaginous expansion, as shown by articulating grooves on the border of the fossil skeleton. These probably overlapped on the median line as in urodeles.

2. The clavicles of Eryops did not overlap on the median line as maintained by Case.

3. There was a short cartilaginous precoracoidal region like that of Sphenodon, extending forward beyond the clavicle.

4. The anteroventral skeleton is a freely articulating complex, in which the lateral angles of the interclavicle are embraced by the cartilaginous expansions of the coracoid dorsally, and the median ends of the clavicles ventrally, thus extending the freedom of movement of the humerus by moving the scapulocoracoid back and forth with it.

5. Contrary to Watson's view that the head of the humerus had a very limited motion in the glenoid, of a rocking character, it is shown that the strap-shaped condyle sliding forward and backward through the screw-shaped glenoid turned through an arc of about ninety degrees. This motion was extended by the free play of the clavicular-interclavicular-coracoid complex, by the rocking motion of the entire body and the play of the spine.

6. The bony portion of the Megalobatrachus girdle is a scapulocoracoid like that of Eryops.

7. The supracoracoid foramen marks the precoracoidal region and is a landmark of importance.

8. When derm bones of the girdle have disappeared in phylogeny, the underlying cartilaginous elements often become greatly expanded to compensate for the loss of the concentrated and strong dermal units, and to these their muscle attachments are transferred.
9. *Eryops* had cartilaginous ventral ribs, which probably coalesced in a sternal apparatus, as shown by the terminal articular surfaces of the bony ribs. These in turn may have articulated with a cartilaginous sternum.

10. The dermal scutes of *Eryops* overlapped the cartilaginous sternum, as the abdominal ribs of *Sphenodon* overlap its sternum, but to a greater extent.

11. The ventral segmental chondrifications, supposed by Wilder to represent the first stages of an evolving sternum, probably indicate abortive attempts to reproduce the ventral dermal armature of stegocephs.

The Limb Bones

1. The humerus of *Eryops* forms a tetrahedral prism. It closely corresponds with that of *Sphenodon*, but with much-shortened shaft.

2. It has clear evidences of the origin and insertion of muscles homologous with most of the muscles of *Sphenodon* and *Megalobatrachus* attached to it.

3. It has an ectepicondylar notch homologous with the ectepicondylar foramen of reptiles, bounded anteriorly by a projecting process for the supinator muscle, to which the name "supinator process" is here given.

4. There is no entepicondylar foramen.

5. The humerus of *Megalobatrachus* is adequately described and figured for the first time.

6. The humerus of both urodeles and reptiles is readily derived from the humerus of *Eryops*; that of *Sphenodon* by lengthening the shaft, the addition of epicondylar foramina, and the shortening and straightening of the proximal condyle; that of *Megalobatrachus* by the loss of all processes and failure of ossification in the region of the extremities, and only a slight lengthening of the shaft.

7. In addition to the points made by Gregory, Miner and Noble regarding the carpus of *Eryops*, it may be stated that the notch in the intermedium articulates with the ulnاردistal angle of the radius on its distal side, as a result of arching the carpus so that the wristbones properly fit; that there is a foramen surrounded by the intermedium, ulnare, carpale 5 and the centrale (radiale). It is also suggested that the articulation of the prepollex is sufficiently important to show that it was a small jointed phalanxlike structure which may have been functional, as is later confirmed through an analysis of the lower tetrapod musculature.

8. The short metacarpals of *Eryops* are a primitive feature.
9. The phalangeal formula of lower tetrapods emphasizes the greater importance of the outside of the hand. This is correlated with the greater muscular development of the ulnar side, and the arrangement of the carpal bones to form an ulnar pyramid.

General Conclusions Regarding the Pectoral Skeleton

1. The pectoral skeleton of *Eryops* is homologous in all its essential elements with the pectoral skeleton of reptiles and urodeles, and its component parts can be homologized in detail to a great extent.

2. The pectoral skeleton of *Eryops* is more primitive than that of either urodeles or reptiles and therefore stands nearer the original tetrapod stock.

3. A musculature homologous to that of the later reptiles and urodeles is indicated for *Eryops* by the skeletal evidence as developed in the text, but of a somewhat more generalized character, and without the secondary adaptive characters evolved by many members of these groups.

4. The pectoral skeleton of *Eryops* bears evidences of attachment corresponding to the following reptilian and urodele muscles:

<table>
<thead>
<tr>
<th>Muscles</th>
<th>Muscles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trapezius</td>
<td>Supinator longus</td>
</tr>
<tr>
<td>Serratus</td>
<td>Extensor carpi radialis</td>
</tr>
<tr>
<td>Pectoralis</td>
<td>Extensor carpi profundus</td>
</tr>
<tr>
<td>Supracoracoideus</td>
<td>Extensor carpi ulnaris</td>
</tr>
<tr>
<td>Coracobrachialis longus</td>
<td>Extensor digitorum longus</td>
</tr>
<tr>
<td>Brachialis inferior</td>
<td>Dorsometacarpales</td>
</tr>
<tr>
<td>Deltoides clavicularis</td>
<td>Palmaris communis longus</td>
</tr>
<tr>
<td>Deltoides scapularis</td>
<td>Palmaris communis profundus</td>
</tr>
<tr>
<td>Scapulohumeralis</td>
<td>Flexor carpi ulnaris</td>
</tr>
<tr>
<td>Latissimus dorsi</td>
<td>Epitrochleoaconaeus</td>
</tr>
<tr>
<td>Anconaeus lateralis</td>
<td>Small flexors of hand</td>
</tr>
<tr>
<td>Anconaeus medialis</td>
<td></td>
</tr>
<tr>
<td>Anconaeus scapularis</td>
<td></td>
</tr>
<tr>
<td>Anconaeus coracoideus</td>
<td></td>
</tr>
</tbody>
</table>

Other muscles, as shown in the following section, are inferred from necessary relations to neighboring muscles, and by their presence in both the lines of reptilian and urodele descent.

B. Musculature

1. The attempt to restore the musculature of *Eryops* from the evidence of detailed muscle homologies between two lines descended
from the stegocephs, namely, the urodeles and reptiles, as exemplified by *Megalobatrachus* and *Sphenodon*, has resulted in a complete confirmation of the evidence from the skeleton, and the addition of muscle elements not indicated directly by the bones, but inferred by their occurrence in both modern types and by the necessary relations to other muscles.

2. It would be difficult to summarize the specific conclusions regarding these muscle homologies and their application to *Eryops*, in this part of the paper, without defeating its purpose as a summary. Special summaries of the homologies are given in the tables preceding the treatment of the individual muscles, while their applications to *Eryops* are given at the close of each muscle discussion.

3. From a reexamination of the muscle homologies, and from the restoration of the musculature of *Eryops*, several new points have been brought to light, and additional evidence has been secured confirming or modifying the conclusions of other investigators. Some of these are outlined in the following paragraphs.

4. The visceral innervation of the M. sternocleidomastoideus is explained by interpreting this muscle as originally derived from a vanished sixth gill arch like that of primitive sharks and ganoids, which became secondarily attached to the anterior border of the shoulder girdle as its advance crowded out the sixth gill arch.

5. The levator scapulae of *Megalobatrachus* represents an intermediate condition between the viscerally innervated levator scapulae of fishes and the somatically innervated muscle of the same name in reptiles.

6. The serratus profundus of *Megalobatrachus* originates from two ribs instead of one, as stated by Osawa. These divide into five slips arranged in two layers homologous with the superficial and deep layers of serratus profundus of *Sphenodon*.

7. The omohyoideus and sternohyoideus in *Megalobatrachus* are homologous with the ventral system in *Sphenodon*, formed by the sternocoracoidei, costosternocoracoideus and episternohyoideus. They are anterior continuations of the rectus abdominis musculature. In *Sphenodon*, the lateral slips brace the ligamentum sternoscapulare internum anteriorly and posteriorly as the omohyoideus and costosternocoracoideus muscles.

8. The supracoracoideus muscle is not genetically connected with the pectoralis system, or with the coracobrachialis, as Romer suggests, but forms a separate anterior muscle mass, as shown by its innervation, and is secondarily fused with the pectoralis along the adjacent edges.
Fig. 102.—Inferred restoration of the superficial musculature of the pectoral limb and girdle of *Eryops megacephalus*. Lateral view.
9. The biceps brachii of reptiles was originated by elements belonging to the coracobrachialis longus and brevis respectively, in fusion with a portion of the anterior membrana intermuscularis in the region of the shoulder joint and fibres from M. brachialis inferior.

10. The coracoradialis proprius was evolved in amphibians by the reduction of the primitive biceps brachii fibres, while a deeper layer of the supracoracoideus became attached proximally to the region of the membrana intermuscularis, on which the biceps fibres were inserted, and replaced them functionally.

11. The conditions in the *Eryops* humerus would lead equally to the evolution of either a biceps brachii or a coracoradialis proprius muscle system.

12. The muscles inserting on the caputhumeri form a fan-shaped series consisting of three systems, identified by their position and innervation. They are (a) a dorsal system with an intrazonal innervation, consisting of the latissimus dorsi, deltoides scapularis, deltoides clavicularis, scapulohumerales anterior and posterior and subcoracoscapularis muscles; (b) an anteromedian system with interzonal innervation, consisting of the supracoracoideus and coracoradialis proprius muscles; and (c) a ventral system with pectoral innervation, consisting of the pectoral muscle.

13. It is more reasonable to regard the scapulohumeralis posterior as an offshoot of the scapulohumeralis anterior than, as Romer suggests, as intimately connected with the subcoracoscapularis.

14. The anconæus muscle is divided naturally into an anterior and a posterior set consisting of two heads each, indicated by the primitive dorsal ridge of the *Eryops* humerus and the proximal separation of the two sets by the typical insertion of the latissimus dorsi muscle.

15. The tendinous origin of the anconæus scapularis on the lateral surface of the scapula in *Sphenodon*, does not mark the posterior border of the bony scapula as, Romer claims, but the tendon has shifted anteriorly from the primitive posterior position, carrying with it the connective tissue elements that form the ligamentum scapulohumerale laterale.

16. It is doubtful whether the anconæus coracoideus of *Megalobatrachus* is homologous with the anconæus coracoideus of *Sphenodon*. The former is apparently related to the M. coracobrachialis longus, and has become welded with the anconæus mass distally; the latter is a purely anconæal muscle attached proximally to a connective tissue ligament.

17. The humeroradialis of *Sphenodon* is explained as the result of the fusion of supinator longus elements with deltoid elements on opposite
sides of the supinator process, and the membrana intermuscularis. When the process receded to form the supinator crest, these elements were left attached to each other.

18. The supinator process of Eryops was the area of origin for the supinator longus muscle.

19. The distal part of the ligamentum intermusculare in Megalobatrachus is homologous with that part of the supinator crest in Sphenodon which is external to the ectepicondylar foramen, and with the supinator process of Eryops.

20. The insertion of the extensor carpi ulnaris in reptiles is associated with the fifth digit. In urodeles, it is directed toward the vanished fifth digit. Its position also indicates the original existence of a sixth digit.

21. The arrangement of the extensor digitorum longus in Megalobatrachus is more primitive than that in Sphenodon. The proximal muscle mass is homologous in both types. The extensor digitorum communis brevis plus the distal tendinous slips of extensor digitorum longus of Megalobatrachus are together homologous to the extensor digitorum communis brevis with its distal slips as they are seen in Sphenodon. It is inferred that in Eryops the condition was more like that in Sphenodon.

22. The extensor digitorum communis brevis arises from the ulnare and the intermedium alone, and not from the radiale and carpalia, as stated by Osawa, and thus corresponds with the condition in Sphenodon. There are five slips instead of four, as also stated by Osawa.

23. The muscle arrangement on the extensor side of the lower arm and hand corresponds with the arrangement of the bones in such a way as to confirm the theory of an ulnar pyramid. The muscles of the hand of reptiles and urodeles are an ulnar complex, while the radial muscles of the lower arm converge from the supinator crest to the radius and radiale and are the survival of a prepollical musculature.

24. As Eryops had a prepollex, it is inferred that the radial musculature was directed to its base, and was taken over by the radial border of the lower arm and hand in later forms.

25. The muscle arrangement on the flexor side of the lower arm and hand also confirms the above view, as it is parallel to the arrangement of the extensor muscles, and also indicates the presence of a former prepollex.

26. The relations of the flexor carpi ulnaris and epitrochleoanconaeus confirm the view indicated by the corresponding extensor muscles that there were originally a fifth and sixth digit on the ancestral tetrapod hand.
Fig. 103.—Inferred restoration of the superficial musculature of the pectoral limb and girdle of *Eryops*. Anterior view.

Fig. 104. Same. Posterior view.
27. The relations of the ulnocarpalis to the contrahentes digitorum in *Megalobatrachus* are demonstrated by dissection, and are shown to be rather in harmony with the observations of Ribbing than with those of McMurrich, Wilder and Osawa. The ulnocarpalis inserts by a tendon into a tendinous bridge, from which in turn arise the six slips of the contrahentes digitorum, which thus form a continuous series with it.

28. A portion of the pronator quadratus is differentiated as a pronator carpi in *Megalobatrachus*. This muscle has not been recorded before and is a clear indication of a former prepollex. It is therefore inferred for *Eryops* as a *M. flexor prepollicis*.

29. The palmar aponeurosis of the palmaris communis superficialis is situated superficially in *Megalobatrachus*, with three layers of flexores breves subtending arising from its dorsal surface. In *Sphenodon*, two of these layers are superficial to the palmar aponeurosis, while only one layer arises from its dorsal surface. This puzzling difference is explained by McMurrich by assuming that the superficial aponeurosis has disappeared in reptiles, exposing the first two layers of breves lying on a subsidiary aponeurosis. Ribbing suggests that the condition in reptiles results from an upgrowth of the proximal ends of these slips to lie superficially. The present investigation confirms the suggestion of Ribbing, since the analysis of the muscle shows its greater reasonableness. This is discussed in detail on pages 281 to 286 of the present paper.

30. The outer slips of the contrahentes digitorum of *Megalobatrachus* are homologous with *Mm. adductores pollicis et digiti minimi* of *Sphenodon*. In the case of the former slip, the homology greatly strengthens the view that the radial digit of urodeles is homologous with the pollex of reptiles.

31. The theory is advanced that, as the marginal digits of the primitive tetrapod hand disappeared in the evolution toward that of modern types, their basic musculature was added to the outer margin of the carpus and metacarpus to form supinators and adductors, thus strengthening and perfecting that organ.

32. The large size of the distal metacarpal condyles of *Eryops* indicates a well-developed carpal and metacarpal musculature in that form.

33. The general conclusions regarding the extensor and flexor arm muscles as a whole are given on pp. 265 to 267, and on pp. 289 to 291.

34. It is evident that the essential musculature of modern reptiles and urodeles had already differentiated in *Eryops*, and hence within the group Stegocephalia, but correlated with more primitive skeletal features.
Hence the homologies here given for the combined amphibian-reptile stems are a key to the fundamental tetrapod musculature, and may be taken as a starting point for interpreting that of higher forms.

C. A Classification of Lower Tetrapod Musculature

The muscles are most naturally classified according to the chief criteria by means of which they were homologized, as follows:

Torsozonal Musculature
(Muscles from body to shoulder girdle)

**Anterodorsal Series**
(Typically wholly or partly innervated by visceral nerves and anterior spinal somatic nerves)
1Sternocleidomastoideus
Trapezius
1Levator scapulae

**Dorsomedial Series**
(Innervated by spinal nerves, muscles typically segmental, inserting principally on inner side of suprascapula)
1Serratus superficialis
1Serratus profundus

**Ventral Series**
(Segmentally innervated, typically with inscriptiones tendineae, derived from ventral longitudinal musculature)
1Omohyoideus
1Sternohyoideus (urodeles)
Sternocoracoidei (reptiles)
Costosternocoracoideus (reptiles)
1Episternohyoideus (reptiles)
1Rectus abdominis

Zonocaputhumeri Musculature
(Muscles typically from shoulder girdle or body fascia—perhaps originally dermal scutes—to head of humerus)

**Dorsal Series**
(Innervated by axillary and related nerves)
1Deltoides clavicularis (reptiles)
Procoracohumeralis (urodeles)
1Deltoides scapularis (Dorsalis scapulae)
1Scapulohumeralis, anterior
Scapulohumeralis posterior
1Latissimus dorsi
1Subcoracoscapularis

**Anteromedian Series**
(Innervated by supracoracoideus nerve)

1Inferred for Eryops.
Miner, *The Pectoral Limb of Eryops and other Primitive Tetrapods* 301

1 Supracoracoideus
1 Coracoradialis proprius (amphibians)

**Ventral Series**
(Innervated by pectoral nerve)

1 Pectoralis

**Humeroextensor Musculature**
(Extensor muscles lying on the upper arm, innervated by N. brachialis longus superior)

1 Anconeus
1 Humeroradialis (*Sphenodon*) (also axillary innervation)

**Humeroflexor Musculature**
(Flexor muscles on the ventral side of the upper arm, innervated by N. brachialis longus inferior)

1 Coracobrachialis brevis
1 Coracobrachialis longus
1 Biceps brachii (reptiles)
1 Brachialis inferior

**Ulnoextensor Musculature**
(Extensor muscles of the lower arm and hand innervated largely by ulnar branches of N. brachialis longus superior)

1 Extensor carpi ulnaris
1 Extensor digitorum longus
1 Supinator manus
1 Extensor digitorum communis brevis
1 Dorsometacarpales

**Radioextensor Musculature**
(Extensor muscles of the lower arm and radial border of carpus innervated by radial branch of N. brachialis longus superior)

1 Supinator longus
1 Extensor carpi radialis superficialis
1 Extensor carpi radialis profundus

**Ulnoflexor Musculature**
(Flexor muscles of lower arm and hand innervated largely by ulnar—superficial—branches of N. brachialis longus inferior)

1 Epitrochleoanconeus
1 Flexor carpi ulnaris
1 Palmaris communis superficialis
1 Palmaris communis profundus
1 Pronator radii teres
1 Ulnocarpalis

*Inferred for Eryops.*
1Palmaris profundus dorsalis
1Flexores breves sublimes
1Contrahentes digitorum

Radioflexor Musculature
(Flexor muscles of the lower arm, radial border of carpus and deeper part of hand, innervated by radial—deep—branch of N. brachialis longus inferior)
1Flexor carpi radialis
1Pronator quadratus
1Flexores breves profundi
1Interossei (Intermetacarpales)

1Inferred for Eryops.
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LIST OF ABBREVIATIONS

ABD. R. abdominal ribs
ABD. S. abdominal scutes
ACR acromion
anc M. anconeus
anc. cor. M. anconeus coracoideus
anc. lat. M. anconeus lateralis
anc. med. M. anconeus medialis
anc. qu. M. anconeus quartus
anc. scap. M. anconeus scapularis
apo. flex. br. subl. (a) aponeurosis M. flexoris brevis sublimis (superficial layer)

apo. palm. sup. aponeurosis M. palmaris communis superficialis
bi M. biceps brachii
bi\textsuperscript{i} M. biceps brachii (proximal belly)
bi\textsuperscript{ii} M. biceps brachii (distal belly)
BR\textsubscript{1}, BR\textsubscript{2} first and second branchial arches
bri M. brachialis inferior
c centrale
c\textsubscript{o}, c\textsubscript{o}, c\textsubscript{4}, c\textsubscript{s} carpalia 1, 2, 3, 4, 5.
caps. j. capsule of the shoulder joint
cbb M. coracobrachialis brevis
cbl M. coracobrachialis longus
CL clavicle
chm M. cleidomastoideus
contr. dig. MM. contrahentes digitorum
COR coracid
COR. CART. coracoid cartilage
cor. rad. prop. M. coracoradialis proprius
cost. cor. M. costocoracoides
CRD deltoid crest
CRDP deltopectoral crest
CRP pectoral crest
cste M. costosternocoracoideus
CTH cleithrum
dcl or delt. cl. M. deltoideus clavicularis
delt. sc. or delt. scap. M. deltoideus scapularis
depr. mand. M. depressor mandibuli
DERM. SC. dermal scutes
dors. met. MM. dorsometacarpales
D. PR. deltoid process
dsc. M. dorsalis scapulae
ECTC ectepicondyle
ECT. N. ectepicondylar notch
ENTC entepicondyle
episthy M. episternohyoideus
epitr. ane.  M. epitrochleoanconaeus
ext. carp. rad.  M. extensor carpi radialis
ext. carp. rad. prof.  M. extensor carpi radialis profundus
ext. carp. rad. sup.  M. extensor carpi radialis superficialis
ext. carp. uln.  M. extensor carpi ulnaris
ext. dig. comm. br.  M. extensor digitorum communis brevis
ext. dig. long.  M. extensor digitorum longus
ext. dig. quarti  M. extensor digitii quarti
FECT  ectepicondylar foramen
FENT  entepicondylar foramen
glenoid foramen
FGL
flex. br. pro.  MM. flexores breves profundi
flex. br. subl.  MM. flexores breves sublimes
flex. br. subl. (a)  MM. flexores breves sublimes (superficial layer)
flex. br. subl. (b)  MM. flexores breves sublimes (middle layer)
flex. br. subl. (c)  MM. flexores breves sublimes (deep layer)
flex. carp. rad.  M. flexor carpi radialis
flex. carp. uln.  M. flexor carpi ulnaris
flex. prepoll.  M. flexor prepollicis of Eryops
FSGL  supragnoid foramen
FSPC  supracoracoid foramen
glenoid cavity
GLEN
HUM  humerus
HUMC  condyle of humerus
hum. rad.  M. humeroradialis
HY  hyoid arch
i  intermedium
ic  MM. intercostales
ICL  interclavicle
ld  M. latissimus dorsi
LD. PR.  processus latissimi dorsi
lev. scap.  M. levator scapulae
lev. scap. inf.  M. levator scapulae inferior
lev. scap. sup.  M. levator scapulae superior
lig. sch.  ligamentum scapulohumeralis
lig. stsc.  ligamentum sternocapulare internum
m₁, m₂, m₃  media 1, 2, 3
mem  membrane
mem. st.-est.  membrana sternoeipisternalis
mtc₁, mtc₂, mtc₃, mtc₄  metacarpalia 1, 2, 3, 4
N. brach. long. sup.  Nervus brachialis longus superior
N. dors. scap.  Nervus dorsalis scapulae
N. procor. hum.  Nervus procoracoohumeralis
N. spc.  Nervus supracoracoideus
ohy  M. omohyoideus
ohy₁  M. omohyoideus (lateral slip)
ohy₂  M. omohyoideus (medial slip)
p. int.  M. pectoralis interclavicularis
M. pectoralis
M. pectoralis abdominals
M. palmaris communis profundus
M. palmaris communis profundus (dorsal head)
M. palmaris communis profundus (ventral head)
M. palmaris profundus dorsalis
M. pectoralis clavicularis
precoracoid
M. pectoralis episternalis
postminimus
prepollex
procoracoid
M. procoracohumeralis
M. pronator quadratus
M. pronator radii teres
M. pectoralis sternalis
radiale
second, third, fourth, fifth and sixth ribs
radius
M. rectus abdominals
condyle of radius
M. radialis superficialis
M. subcoracoscapularis
M. subscapularis
scapula
scapulocoracoid
M. scapulohumeralis
M. scapulohumeralis anterior
M. scapulohumeralis posterior
M. serratus
M. serratus profundus
M. serratus profundus (superficial layer)
M. serratus profundus (deeper layer)
M. serratus superficialis
M. supracoracoideus
supraglenoid buttress
M. sternocoracoidei
M. sternocoracoideus profundus
M. sternocoracoideus superficialis
M. sternohyoideus
sternal ribs
supinator crest
M. supinator longus
M. supinator manus
supinator process
suprascapula
t. bi. or ten. bi. tendon of M. biceps
t. cor. rad. prop. tendon of M. coracoradialis proprius
td₁, td₂, td₃, td₄, td₅ first, second, third, fourth and fifth inscripiones
tendineae of M. sternohyoideus
t. flex. br. subl. (a) tendons of MM. flexores breves sublimes (superficial layer)
t. palm. comm. sup. tendon of M. palmaris communis superficialis
trap M. trapezius
u ulnare
UL ulna
uln. carp. M. ulnocarpalis