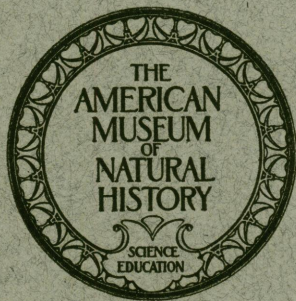


THE MORPHOLOGICAL AND FUNCTIONAL EVOLUTION OF THE TARSUS IN AMPHIBIANS AND REPTILES

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Article VI.—THE MORPHOLOGICAL AND FUNCTIONAL EVOLUTION OF THE TARSUS IN AMPHIBIANS AND REPTILES

BY BOBB SCHAEFFER¹

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INTRODUCTION

The possibility of tracing satisfactorily the phylogeny of any part of the vertebrate skeleton is naturally limited by the fortuitous discovery of the proper material that will enable one to define the critical stages in the transition from a more primitive morphological type to a more advanced. Although the true nature of the tarsus of many extinct tetrapod groups is either unknown or at best but poorly known, either due to lack of ossification or preservation, there has become available within recent years a wealth of material which makes it practicable to follow the general evolution of this region in considerable detail.

The purpose of this paper is to describe the morphological and the functional evolution of the tarsus in the amphibians and reptiles, and to present a synthetic picture of the steps leading to the various definitive types of tarsal structure. While the morphological discussion is based as much as possible on actual material, it has been necessary to resort to the literature for several important structural stages that are only represented by material in collections in Europe and South Africa. Although conclusions drawn from published descriptions and diagrams may not be as accurate as those based on actual specimens, it is felt that constant cross-checking through papers on the same subject but by different authors has reduced to a minimum most of the inaccuracies and misconceptions.

The functional aspects have been treated in considerable detail for the primitive tetrapod tarsus and many of the types derived from it. Some of the functional interpretation is admittedly more or less superficial, as it has not been possible with the time and the material available to treat each important functional change with the same degree of thoroughness. In studying the functioning of the tarsus and its relation to the movements of the hind-limb and body as a whole, it is highly desirable to have experimental data on the angulation and movement of the various limb segments and on the method of loco-

motion in recent types in the form of motion pictures, together with experiments on the action of individual muscles and groups of muscles that tend to act together. Such information is of great value in interpreting and supplementing the conclusions drawn from the fossil material. Whereas such data have been determined for the caudate amphibian and the alligator, it is realized that comparable data should also be gathered for a typical lizard, a bird, and a primitive mammal in connection with further studies on this general topic.

The evolution of the tarsus and its effect on the method of locomotion are obviously intimately associated with the evolution of the crus, the femur, and the pelvis. Although it has not been possible within the space of this paper to integrate all of this information, the more important changes in the crus, the femur, and the knee-joint are briefly considered.

As might be suspected, the literature relating to the tetrapod tarsus (excluding the mammalian) is very large. Most of the accounts are purely descriptive, some comparative, while very few make any attempt at discussing the functional implications. In the descriptive category, the work of Boonstra, Broom, Gregory, Houghton, Holmgren, von Huene, Rabl, Romer, Schmalhausen, Sewertzoff, and Watson is of the greatest importance. From the functional point of view, the contributions of Elftman, Gray, Gregory, Hirsh, von Huene, Houghton and Boonstra, Morton, Nauck, and Romer are the most illuminating of the very few ventures into this field. The study of the mechanics of locomotion in the lower tetrapods has been sadly neglected and any information in this field is very desirable.

The writer wishes to acknowledge his deep gratitude to Professor W. K. Gregory for suggesting the problem and for his constant interest and guidance throughout the investigation. The writer is also indebted to Mr. H. C. Raven and to Professor A. S. Romer for helpful suggestions, and to Mr. Howard Pearson for lending his knowl-

edge of mechanics to many discussions on locomotion. He also wishes to thank Curators Barnum Brown and Walter Granger for permission to use the vertebrate paleontological collections in the American Museum, and Dr. A. J. Ramsay for assist-

ance in making the motion pictures. The drawings have been made by Mrs. Helen Ziska with her usual skill, and the writer wishes to thank her for her cooperation and patience.

THE AMPHIBIAN TARSUS

THE TARSAL PATTERN OF THE PRIMITIVE TETRAPODS—LABYRINTHODONTES

The tetrapod tarsus may be defined as that portion of the posterior appendage that lies between the tibia and fibula on the one hand and the metatarsals on the other. It is a region that has always been associated with the flexion and extension of the pes on the lower leg and is clearly constructed for such movements. Due to this function and because of its position relative to the body, the tarsus has been constantly subjected to varying tension and compression forces throughout its history. These forces, the result of the effect of gravity and of locomotion, are intimately associated with the modifications that have occurred throughout its evolution.

Although the oldest known amphibian tarsus already possessed the basic tetrapod pattern, it is quite evident that it retained the fundamental features of the rhipidistian pelvic fin. The convergence of all the tarsal elements toward the fibula, except those in line with and more distal to the tibia, is without question a heritage character of great significance, derived from a similar convergence of all the radials, except the first preaxial one, toward the second mesomere (Gregory and Raven, 1941).

A consideration of the primitive amphibian tarsus is a necessary prerequisite for the interpretation of this region in all higher tetrapods. Although the earliest known tarsus is that of the embolomere *Pholidogaster* (Watson, 1926b) from the Lower Carboniferous of Scotland, it is by no means completely preserved and for that reason will be discussed later. At present, the only completely known Paleozoic amphibian tarsus is that of the rhachitome *Trematops*.

Through the kindness of Dr. E. C. Ol-

son, it is here possible to describe a recently collected and very complete lower leg and tarsus of *Trematops milleri* (Fig. 1). The phalanges are unfortunately missing. The bones were preserved in their natural positions with the exception of the third centrale which was slightly crowded under the medial border of the fourth tarsale.

Because of the completeness of this specimen a revision of Williston's description (1909) is warranted. His figures are somewhat diagrammatic owing to the fact that the borders of the bones of his specimen were not well preserved and, also, because the tarsus is lying across several of the vertebrae, somewhat distorting the natural position of the elements. Some of the corrections appear significant when the functioning of the foot is considered.

The fibulare is proximodistally elongated with its greatest transverse width at the level of the articulation between the intermedium and the fourth centrale. It is narrowest at the point of articulation with the fibula. The distal border is somewhat v-shaped, forming separate facets for contact with the fourth and fifth tarsalia. The medial and lateral borders are thickened and rounded.

The intermedium, also, has its greatest length proximodistally rather than the reverse as indicated in Williston's figures (1909, 1913). The central portion of the dorsal surface is depressed. The distal half of the medial border is elevated above the rest of the bone and is rounded, giving every indication of having made a ligamentous attachment with the lower end of the tibia. The proximal half of this border is free and rounded and is not in contact with the tibia. (Williston considered the

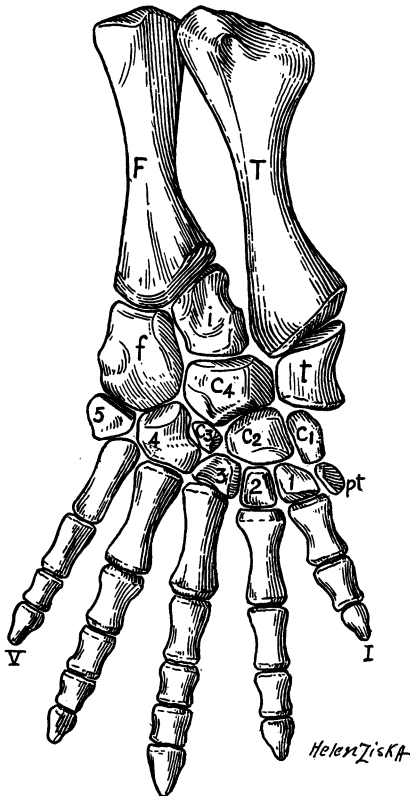


Fig. 1.—The tibia, fibula, and pes of *Trematops milleri* Williston (Phalanges restored after Williston).

- | | |
|---------------------------------|-------------------------------|
| T, tibia | c ₂ , centrale two |
| F, fibula | c ₁ , centrale one |
| t, tibiale | 1, tarsale one |
| i, intermedium | 2, tarsale two |
| f, fibulare | 3, tarsale three |
| c ₄ , centrale four | 4, tarsale four |
| c ₃ , centrale three | 5, tarsale five |
| | pt, pretarsale |

intermedium to be entirely free of the tibia which is definitely not the case.) The articulation between the intermedium and the fourth centrale appears to have been intimate. The lateral border of the intermedium is not notched in the specimen studied and there is no indication of a foramen between the intermedium and fibulare for the perforating artery, although it must have been present.

The tibiale has an internal border that is decidedly concave and about twice as long as the external. Proximally, it articulates

only with the tibia, and distally, with the first centrale and possibly the proximo-medial corner of the second centrale.

The fourth centrale (proximal centrale of Schmalhausen and others) is, as Williston points out, one of the largest bones in the tarsus. It is transversely widened and not rectangular as previously figured. The proximal border is very slightly concave for articulation with the intermedium. The proximomedial corner is rounded, and probably it contacted the tibia. Laterally, centrale four articulates with the fibulare, and medially, with the tibiale. The distal edge of the bone is decidedly v-shaped, dividing this articular surface into two distinct parts. The lateral surface articulates both with the centrale three and a corner of tarsale four, while the medial surface articulates with the third centrale and appears to be slightly concave.

The first centrale, at least so far as its ossified portion is concerned, is elongated proximodistally and is of constantly narrow width transversely. There is no indication that it has been broken, but rather that there was a cartilaginous portion extending medially from the ossified part. It was presumably widest proximally to increase the surface articulating with the tibiale. The second centrale is the second largest in the centrale series. Proximally, it has a convex border for articulation with centrale four. Distally, it articulates with tarsalia one and two. The lateral border contacts the third centrale and the third tarsale, while the medial border articulates with the first centrale throughout the length of the latter.

The third centrale is by far the smallest of the centrale series. It is wedged between the second centrale and the fourth tarsale, being somewhat triangular in shape.

A tarsale is present at the proximal end of each of the five metatarsals. The first, second, and third approximate a keystone in shape. The fourth element is the largest of the tarsalia series, with seven contacts, as follows: with the fourth metatarsal, the fifth metatarsal, the fifth tarsale, the fibulare, the fourth centrale, the third centrale, and finally the third tar-

sale. The fifth tarsale is rather triangular with its lateral border as the base. It articulates with the fibulare proximally and with the fourth tarsale medially. There is no evidence that the fifth digit was divergent as Williston postulated.

There is a small nodule of bone, apparently not broken off from any of the neighboring elements, that is situated just mesiad to the first tarsale. It is also present in the specimen described by Williston, although Olson (personal communication) is quite certain that it represents an independent and hitherto undescribed ossification. Its significance can only be conjectured, but it is undoubtedly a pretarsale.

The metatarsals as well as the phalanges are oval and dorsoventrally compressed in cross-section, and the heads and bases are characteristically expanded. The first metatarsal is shorter and broader than the other four, and as Williston pointed out, resembles a proximal phalanx. The second, third, and fourth are very much alike, the third and fourth being of almost equal length and the longest of the series. The fifth metatarsal has a more slender shaft and less expanded ends than the other metatarsals.

The phalangeal formula in all probability is 2-3-4-4-2(3?). Williston's first figure of the foot (1909) included only three phalanges in the third digit, while his later figure (1913) included four, which is without question correct. In the type, the only specimen in which the digits are at least partly preserved, the middle phalanx of the third digit appears to be 21 mm. long. Olson has recently examined this bone and is convinced, as finally was Williston, that this actually consists of two phalanges that are not quite distinguishable from each other; otherwise this bone would be much too long to be a single phalanx in this position. Furthermore, in a third but incomplete specimen of a *Trematops* tarsus in the Walker Museum, the second phalanx on this toe is well preserved and of the proper length. The other features of the digits are discussed in detail by Williston (1909).

One of the most striking characteristics of the *Trematops* tarsus is the presence of

three transverse rows of bones on the tibial side and but two on the fibular side. The relatively great proximodistal length of the fibulare makes up for the lack of the extra row on the fibular side. This condition exists in the *Archegosaurus* foot, to be described later, and persists to the caudate amphibian tarsus.

With regard to the planes of flexure, it appears that there were two major ones. In a foot of this sort, in which the tarsus is composed of a number of small units that articulate with one another by simple, plane surfaces, there is a certain amount of movement between each element and all of its neighbors. The summation of movement, however, produces the gradually curved tarsal region during locomotion, so characteristic of the amphibian foot (Fig. 21,A).

It is also clear that the very arrangement and relative size of certain of these elements results in considerably restricted movement at definite points. It would appear that there was some movement between the fibula and the fibulare and the intermedium on the one hand and the tibia and the tibiale on the other. Since the fibula, however, is much shorter than the tibia, the added length of the latter would certainly interfere with transverse tarsal flexure at the level of the fibulo-tarsal joint. The difference in the relative length of the tibia and fibula was carried over into the pelycosaurs, but several modifications, to be discussed later, permitted a functional joint to develop between the crus and tarsus.

A similar situation exists at the level of the distal end of the tibia. The joint plane between the tibia and the tibiale is carried at the same level across the foot between the intermedium and the fourth centrale. Beyond this point, however, this plane is broken by the presence of the elongated fibulare which is continuous across it. From this, it is evident that the proximal and more distal joint planes do not extend across the entire width of the tarsus and for that reason must have been of very minor importance in dorsiflexion or plantar flexion.

It must be stressed, however, that the

labyrinthodont tarsus was undoubtedly quite supple. As in the caudate tarsus, the degree of suppleness or bending between elements depends mainly on their dorsoventral thickness and the binding force of the interosseous ligaments. Assuming maximum flexibility, the tarsal mosaic will permit moderate warping and bending in several directions. Bending about the longitudinal axis of the foot is of importance in adapting the foot to uneven terrain, and also in connection with the necessary adjustments which must be made in the tarsal region during propulsion, to be discussed later.

There must have been a moderate degree of folding between the preaxial series (tibia, tibiale, centrale one, and pretarsale) and the elements radiating from the fibula, resulting in an arching effect across the midtarsal region. Movement also must have occurred between the various tarsalia, permitting an undulation of the distal border, or an arching of the entire border, also in response to an uneven terrain or during swimming.

Unquestionably the most important planes of flexion are the true transverse tarsal joints that are present between the fibulare, the fourth centrale, and the tibiale on the one hand and the remaining centralia and the fourth and fifth tarsalia on the other; also, the joints between the tarsalia and the metatarsals. Both these joints extend across the entire tarsal region. Tornier (1927) has pointed out that in the Caudata the tarsus is functionally part of the leg, the "foot" beginning with the metatarsals. A model of the *Trematops* foot, with the various elements loosely united with latex, indicates that the greatest amount of flexion does occur between the tarsalia and the metatarsals (Fig. 21, A).

The first three centralia form a wedge between these two joints, the proximal border of this wedge forming part of the upper transverse tarsal joint, and the distal border, a supplementary joint with the tarsalia; that in turn becomes continuous with the proximal joint plane laterally.

But one other truly primitive amphibian tarsus is well enough preserved to warrant

consideration, that of the rhachitome *Archegosaurus*. A single specimen, in Tübingen University Museum, has been described by Quenstedt (1861), Baur (1886), Emery (1898), Zwick (1898), and Jaekel (1909). Since the pes of *Trematops* was unknown during this period a reconsideration in the light of this subsequent information may prove profitable.

Von Meyer's (1858) lengthy treatise on *Archegosaurus* includes figures of specimens of all ages, but it is not possible to work out the ontogeny of the tarsus. The younger specimens without exception have an unossified tarsus. The pes of an older individual is figured (Pl. XIX, fig. 8) in which there is an uninterpretable bony mass in the position of the intermedium, centrale four, and the tibiale. These may be the first elements that were ossified during development. That this tract of ossification should run from the proximo-fibular side to the distal tibial side of the foot may be significant. It may represent ossification in response to mechanical stress. As will be discussed later, there is reason to believe that considerable pressure against the ground is exerted along this diagonal line during locomotion.

To return to the Tübingen specimen (Fig. 2), there is little question that the proximal bony mass includes the fibulare, intermedium, and tibiale. Apparently, because of poor preservation, it is not possible to be confident of the exact size and shape of the tibiale. There is a small medial projection from the tibiale region called "b" by Baur, and considered to be part of, or the entire tibiale, by Emery, Zwick, and Jaekel.

In the middle of this mass there is a poorly preserved region labelled "x" by Baur, considered to be a paracentrale by Emery, the first centrale by Jaekel, and finally, simply part of the tibiale by Zwick. Comparison with *Trematops* definitely indicates that it is a separate element with ill-defined boundaries, the centrale four of Williston. Sewertzoff (1908) considers the tibiale and the fourth centrale to be fused, which is possible but not probable.

What may be considered as the first centrale has a prominent medial projection

that is probably not a separate bone, and certainly not the remains of a prehallux as Emery believed. The second centrale is a separate and well-defined element. The element on the fibular side of the second centrale is generally considered to be a tarsale. Zwick, followed by Emery, believed that a "stony" porous elevation just distal to the second centrale is a portion of the fourth tarsale. Strangely, neither Baur, Jaekel, nor Quenstedt mentions or figures this elevation. In the light of the condition in *Trematops* it has no significance, making the size of the fourth tarsale more in agreement with that of the other members of the series.

Zwick and Jaekel believe that digits 2, 3, 4, and 5 have been preserved, while the others are of the opinion that they are 1, 2, 3, and 4. Zwick supports his opinion by the presence of two slivers of bone (?) along the tibial border of the foot, which he believes represent the remains of the first metatarsal. The proximodistal row on the tibial side is continuous, however, and there is no space for the missing tarsale one. On the other hand, the fifth tarsale could fit very well into the space on the fibular side of the foot. The presence of five digits is demonstrated, according to Baur, by another specimen in the Strassburg Museum.

As determined by a study of all the available illustrations of the Tübingen specimen, there are eleven elements in the tarsus of *Archegosaurus*, in contrast to the thirteen present in *Trematops*. The former presumably lacks centrale three and the pre-tarsale. Assuming the relative sizes of the tarsal bones as preserved to be correct, the restored pes has the same general configuration as that of *Trematops*, with a three-rowed tibial border, and a two-rowed fibular border. Watson (1913) also considers this type to be the most primitive. Hence, the foot of *Archegosaurus* is rather important in that it affords a second example of the primitive tarsal pattern found in *Trematops*.

The tarsus is known to be at least partially ossified in several other rhachitomes. It is more or less completely so in *Micropholis* (Broili and Schröder, 1937). The

centrale region is poorly preserved, however, and its structure cannot be definitely determined. The same holds for the tarsus of *Sparagmites* (Fritsch, 1889), which is unfortunately completely dissociated and not favorable for restoration. Both *Chelydosaurus* (Fritsch, 1889) and *Uranocentrodon* (Broom, 1921) had a partially ossified tarsus, with a possible reduction in the total number of tarsal elements present.

That there is definite evidence of ossification in the tarsus of at least one member of the Embolomeri, indicates that it was not completely cartilaginous as is generally supposed. The apparent exception to the rule is found in *Pholidogaster* (Watson, 1926). Although the tarsus is again incompletely ossified, at least four of the elements are bone. As Watson points out, however, it is not well enough preserved to be interpreted with certainty.

The nature of the tarsus in the Stereospondyli is not known (Fraas, 1889). It has been restored in *Metoposaurus* (Abel, 1919) as consisting simply of four round, bony nodules and being otherwise cartilaginous. So far as can be determined, there is no basis for this conclusion.

Romer (1939) has cited much evidence indicating that many of the Phyllospondyli are actually larval embolomeres and rhachitomes, accounting for the cartilaginous or poorly ossified tarsus. The possibility that some of the branchiosaurs are neotenuous rather than simply larval stages of the above mentioned orders should be considered.

Although the phylogenetic relationships and hence the classification of the Amphibia are in a state of flux at the present time, Gregory, Romer, and others are of the opinion that the Amphibia may be divided into two principal groups, the Labyrinthodontia, from which the anurans and reptiles are descended, and the Lepospondyli, from which the coecilians and the caudates are derived through the microsaurians. Since the labyrinthodont tarsus is considered to be at least structurally ancestral to all the other types, it has been placed at the base of the chart on the phylogeny of the amphibian tarsus

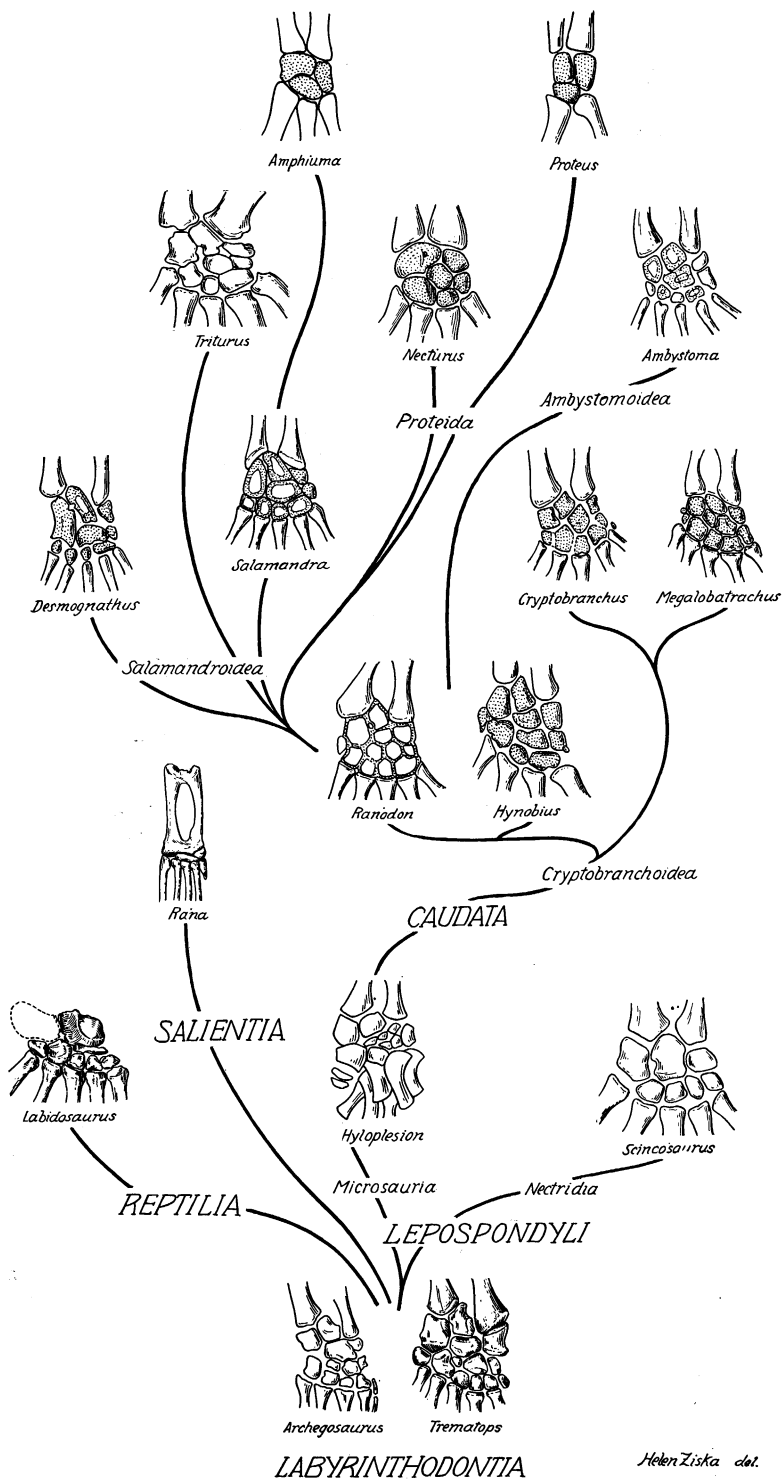


Fig. 2.—The phylogeny of the amphibian tarsus. Stippled areas, cartilage; unstippled areas, bone.

(Fig. 2). The chart is otherwise constructed according to the views of Noble (1931),

Boyden and Noble (1933), and Romer (1939).

THE TARSUS OF THE LEPOSPONDYLS

The Lepospondyli seemingly may be, at present, divided into three suborders (Romer, 1940): the Nectridea, Microsauria, and Aistopoda, the latter lacking limbs completely. But one nectridian tarsus is known, that of *Scincosaurus* (Jaekel, 1909). It is completely ossified. The fibulare and the intermedium are about the same size and are the largest bones in the tarsus. The tibiale has apparently suffered a relative decrease in size. The centrale series has presumably completely disappeared, as has the fifth tarsale.

Broom is of the opinion (1921) that the foot of *Scincosaurus* (Fig. 2) is structurally ancestral to the primitive reptilian foot. There is, however, very little evidence to support this conclusion, particularly since the nectridians are apparently aberrant and not ancestral to any later group. Broom believes that the mammalian navicular has developed from a displaced tibiale, and he constructs a series to show the supposed progressive reduction in the

size of the tibiale and its gradual migration to a position directly under the reptilian astragalus. There is no real evidence, however, either embryological or paleontological, that any of the bones of the tarsus have migrated to new positions, the one exception to this possibly being the raising of the astragalus onto the calcaneum. Furthermore, there is every reason to believe that the navicular is composed of one or more centralia, and as a corollary the latter could not be absent in the reptilian ancestor.

A single ossified microsaurian tarsus is known, that of *HylopleSION* (Steen, 1938). It is not possible, from the published figures of the specimen, to make a restoration (Fig. 2). It is obvious, however, that the foot bears a close resemblance to the primitive pattern, including the presence of centralia. It might very well be ancestral, therefore, to the caudate amphibian tarsus, which in turn, as will be seen, is very similar to that found in *Trematops*.

THE TARSUS OF THE CAUDATE AMPHIBIANS COMPARISON WITH THE PRIMITIVE TETRAPOD PATTERN

On the whole the caudate amphibian tarsus has changed but little from the primitive ground pattern. In some forms there has been a considerable degree of fusion between the various tarsal elements, but in most cases the embryology reveals the distinct origin of the parts concerned. Much work has been done on the caudate foot, and the following papers appear most significant in this connection.

Gegenbaur (1864, 1876) believed that the primitive tetrapod tarsus contained one or two centralia, basing his conclusion on a study of recent caudate amphibians only. He pointed out for the first time the tendency of all the tarsal elements, except those running out from the tibia to the first digit, to converge toward the fibula.

Baur (1885, 1886, 1888) studied the elements of the caudate tarsus in great detail, including the few fossil forms known at the time. Some attention is paid to variation. He first recognized the presence of four centralia (1886) as the primitive number.

Emery (1898) discussed the morphology of the carpus and tarsus at great length. He realized the significance of the *Archeogosaurus* foot in interpreting that of the caudate amphibia. Emery believed that the prehallux (or prepollex) is homologous in the Amphibia, Reptilia, and Mammalia. He made a distinction between the propodium, made up of elements in line with, and distal to the tibia, and the mesopodium, consisting of the elements converging on the fibula.

Zwick's (1898) thorough work includes comparative and embryological studies. *Archegosaurus* is reconsidered, but not too successfully, since *Trematops* was then unknown. In the discussion on the centrale complex, it is pointed out that there is no paleontological evidence of more than two centralia (except abnormally). Unfortunately, the Hynobiidae were not investigated.

Sewertzoff (1908) made a very comprehensive investigation and survey of the literature on the carpus and tarsus of both recent and fossil amphibians and reptiles. He pointed out the individual variation that occurs in the centrale region of the caudate tarsus and of the resemblance of this type to the tarsus of *Archegosaurus*.

Rabl's (1910) lengthy treatise, so far as the amphibian foot is concerned, is simply a review of previous work. The reptilian tarsus is covered in greater detail. He maintains his previous conclusion (1901) that the *Proteus* tarsus, consisting of three elements, is the ancestral type. This is, of course, now entirely rejected since the degenerate tarsi of *Proteus* and of *Amphiuma* are obviously associated with the degenerated condition of the limbs in these exclusively aquatic types and since their derivation from more normal salamanders is now generally accepted.

Schmalhausen's study (1910, 1917) of the development of the tarsus of a primitive member of the Caudata (*Hynobius*), together with a study of the adult tarsus of *Ranodon* in the light of the *Trematops* foot indicates, without doubt, that the latter is at least structurally ancestral to the caudate tarsus.

Tornier (1927) is one of the few to attempt a functional explanation of the evolution of the foot. He points out that the main functional tarsal joint in the Amphibia lies between the metatarsals and tarsalia, and that most of the tarsus is functionally part of the lower leg. He considers fusion of the centralia to be a characteristic terrestrial modification, constant in higher terrestrial animals. Tornier sees in certain fusions in the recent urodele foot the origin of several of the elements in the mammalian tarsus; the

fourth and the fifth tarsalia uniting to form the cuboid and the two centralia forming the head of the astragalus, the body of the latter being composed of the intermedium and the tibiale. Although such conclusions may ultimately prove to be correct, Tornier, by ignoring the paleontological evidence as to the ancestral and the intermediate stages between the primitive and the more advanced types, lacks perspective with regard to which elements were fused, when and under what conditions they fused, and which elements were lost.

Steiner's first work (1921) is a lengthy discussion of the phalangeal formulae of various recent Amphibians, some of which are incorrect (Gregory, Miner, and Noble, 1923). But little attention, however, is paid to the tarsus itself. The fact that variation in the phalangeal formula is recognized is an important contribution. In his 1934 paper, Steiner compares one of the variants of the *Cryptobranchus* tarsus, having four centralia, with that of *Trematops*. As pointed out before, such comparisons, while suggestive, are not valid.

Dollo (1929) discussed the forms having various numbers of centralia and reached the conclusion that four is the primitive number. He claimed that if the primitive pentadactyl tetrapod limb is considered in the light of a numerical progression, the presence of four centralia is inevitable. This is also the case when the segments of the limb are considered as alternating. There is no rational basis for applying such a mathematical analysis to the hind limb. The arrangement of the tarsal elements in the primitive tetrapod is obviously not in accordance with such a plan because they are not arranged in transverse rows as the theory requires but, excepting the tibiale, the first centrale, and the pretarsale, all the elements converge toward the fibula.

Howell (1935b) points out the very significant fact that there is, up to the present time, no proof that the prepollex and postminimus of the manus ever occurred as true digits. The same holds for the prehallux and postminimus of the pes. He makes the excellent suggestion that these terms are misleading and that pre-carpale and post-carpale (pretarsale and

post-tarsale) are much more accurate, that is, the pretarsale of *Trematops*.

Holmgren's work (1935, 1939) is important mainly in that it supports the theory of the dual origin of the Amphibia, a thorough discussion of which is beyond the scope of this paper (see p. 408). Of more pertinent value here is his emphasis on the fact that the caudate amphibian tarsus is subject to considerable variation and that many separate rudiments are concerned in the ontogeny of the tetrapod tarsus.

The sporadic occurrence of ossification in the amphibian tarsus is of great interest. But few of the well-known tarsi, fossil or recent, are completely ossified in the adult stage, in most cases being partly or completely cartilaginous. There is no reason for believing that the amount of ossification is related to the aquatic or the terrestrial habits of the animal or to its size or weight, but rather that it is entirely genetic. This problem is worthy of further investigation with regard to the variation in the amount of tarsal ossification within a species, the constancy of ossification of the same tarsal elements within a species, and finally the possibility of experimentally altering the extent or degree of tarsal ossification.

The tarsus of the more primitive of the caudate amphibian families (Hynobiidae and Cryptobranchidae), as well as of some of the members of the more specialized Salamandroidea and Ambystomoidea, resembles the rhachitome tarsus in having the fibulare and intermedium articulate along their proximal borders only with the fibula, which, in turn, is much shorter than the tibia. The shorter fibula is, as was previously pointed out, a primitive character.

The articulation of the intermedium with the tibiale is primitively weak or non-existent, as in *Trematops*. Among the caudate amphibia, this articulation becomes much stronger, as in *Cryptobranchus* or *Salamandra*. In some cases, however, there is a relative increase in the size of the tibiale accompanied by a loss of all but one member of the centrale series. This results in the leveling off of the joint between the lower leg and the tarsus, as in *Triturus*. The same condition also exists

in those forms in which there has been fusion in the proximal tarsal row, that is, in *Necturus*, *Ambystoma*, *Proteus*, and *Amphiura*.

These changes, however, are not necessarily significant, for they do not alter the structure of the tarsus so profoundly that it suffers any change in function. They are simply genetic differences which are actually subject to much specific variation. The extensive fusion in the tarsus of *Proteus* and *Amphiura* is most probably associated with the reduction in the number of the digits. Terrestrial locomotion in these exclusively aquatic forms consists mainly of lateral undulations of the body, the legs being relatively too small to be effective propellers.

The phylogeny of the amphibian tarsus demonstrates very well that the primitive pattern has been retained among the caudate amphibia with but little modification. This, together with the fact that the pattern is similarly modified in distantly related forms, for instance, *Proteus* and *Amphiura*, demonstrates that it would be impossible to build up a phylogeny of the Amphibia on the basis of the tarsus alone. Noble (1931, p. 466) has pointed out that a common mode of generic evolution in the Amphibia may be associated with the development of parallel modifications in the derived genera of a widely dispersed stock. This hypothesis is certainly supported by the modifications in the tarsus. Of course, the anuran tarsus is strikingly different, while the reduced tarsi of *Necturus* and *Amphiura* are clearly derivatives of the *Trematops* pattern. On the other hand, the tarsus of such forms as *Triturus* and *Ambystoma*, even allowing for variation, are closely similar to the Permian amphibian pattern.

As pointed out before, the proximal and distal regions of the tarsus are the most constant. The tibiale, intermedium, and fibulare are always present, the intermedium fusing with the fibulare in some forms, such as *Amphiura* and *Necturus*. While the intermedium, as will be discussed later, gives every evidence of having fused with a centrale and possibly the tibiale in the reptiles, it never does so in the caudate amphibia.

THE CENTRALE COMPLEX

There has been much speculation as to the exact number of centralia in the primitive tetrapod tarsus. As far as urodeles are concerned, Zwick, Rabl, and Holmgren are of the opinion that two is the basic number. The latter claims, on embryological evidence, that in all cases never more than two rudiments develop and that extra centralia merely represent buds from these rudiments.

Not only is there variation in the number of tarsal elements present in the feet of the different caudate amphibian suborders and families, but there is a significant amount of variation in a number of different species. This variation is particularly common in the centrale region, as Holmgren (1939) has pointed out, and there may be as few as one or as many as four or six centralia in certain species; specifically, *Ambystoma* sp.? (*Siredon pisciformis*), *Ambystoma opacum*, *Hynobius kayserlingii*, *Cryptobranchus alleganiensis*, and *Megalobatrachus japonicus*.

Steiner, as pointed out elsewhere, considers the supernumerary centralia to be of phylogenetic importance, since in cases where they are present the foot resembles that of the labyrinthodonts. Holmgren, on the other hand, claims that this similarity exists in only a few cases and hence is of no atavistic significance. He agrees with Schmalhausen that the supernumerary centralia are separated rather late in embryonic development from normal rudiments, and always on the fibular side (Fig. 12,A). Holmgren further believes that the primitive condition for urodeles is that in which there are two centralia (in some cases fused into one).

The principal criticism of Holmgren's work, and for that matter Steiner's, is the great emphasis placed on structural detail in comparing the caudate and labyrinthodont tarsus. A more valid comparison would seem to be centered about the deep-seated resemblances in the tarsal pattern in the Caudata and the Labyrinthodontia, regardless of whether one or four centralia are present. The two most striking characters are the constant articulation of the

fibula with the fibulare and the intermedium, and the convergence of the tarsal elements toward the fibula. Since the number of centralia present in a given tarsus has no apparent effect on the locomotion, it would appear that there has been no selection toward a constant number. Whether this variation also existed in the lepospondyl or rhachitome tarsus is, of course, unknown, but it may have been more extensive than we now have reason to believe.

All available evidence indicates that the Hynobiidae are the most primitive of the caudate amphibians. One member of this family, *Ranodon*, has, in the adult, three and sometimes four centralia that apparently have independent rudiments in the embryo (Schmalhausen, 1917). Holmgren attributes these "extra" centralia to a larval adaptation for broadening the foot, and, as in the other cases, fails to see any atavistic tendencies. He does not take into account, however, the phylogenetic position of the Hynobiidae.

There can be little question that the tarsus of *Ranodon* is very close to that found in *Trematops*. The element labelled "m" by Schmalhausen, "y" by most workers, and by some the prehallux or pretarsale, is clearly homologous with the so-called first centrale as labelled by Williston for *Trematops*, and is possibly present as a small nodule in *Archegosaurus*. Although the third centrale and fourth tarsale are usually fused, individuals are known in which they are separate, resulting in four centralia, just as in *Trematops*. A specialization independently acquired in the Hynobiidae is the fusion of the first and second tarsalia.

The fact that only two centrale rudiments appear in the tarsus of most urodeles is no indication that there has been a secondary segmentation of the centralia in the individuals having a greater number. It is just as reasonable to suppose that *Trematops* had two rudiments from which the "supernumerary" centralia budded. In other words, throughout the Amphibia but two primary centrale rudiments may appear, and in those forms which always or occasionally have more

than two, the condition may be brought about by budding. The only reasonable alternative is that certain centralia have indistinguishably fused with each other or with other tarsal elements, a condition existing in the earliest embryological stages.

The development of a two-rowed tarsus on the medial side of the foot in certain caudates and lepospondyls is quite possibly associated with the position assumed by the foot during propulsion. Through the action of certain muscles at the beginning of propulsion, the long axis of the foot approximately parallels the long axis of the body. This position tends to cause the tarsal elements on the medial side to be crowded together and those on the lateral to be separated (Fig. 3). Such crowding would produce strain on the medial side, tending to favor both the elimination of the first centrale and possibly the other modifications in the centrale region.

COMPARISON OF THE CAUDATE AND ANURAN TARSUS

The embryology of the anuran foot has been investigated by Tschernoff (1907), Schmalhausen (1908a), Steiner (1921), and Holmgren (1933). All agree that there is no sign of the intermedium, although the latter suggests that it may be present as a bridge between the proximal ends of the tibiale and fibulare. With regard to the centralia, Holmgren makes what would appear to be some questionable homologies between the fore- and hind-limb. In the manus of *Pelobates* the first centrale anlage has attached to it two streams of prochondral cells in which the second and third centralia develop, respectively. In the pes (Fig. 12,B) similar streams arise from the distal end of the tibiale, also giving rise to the second and third centralia. Holmgren argues that these streams could not arise from the first centrale in the hand and from the tibiale in the foot, and, therefore, that the tibiale must really include the first centrale. In fact he considers this element to be mostly the first centrale.

Needless to say, the remarkable parallelism in development and adult morphology between the manus and pes has given rise

to many false conclusions and worthless attempts to homologize the bones and muscles of the hind- and fore-limbs. There is no reason to suppose that a first centrale must be present in the tarsus in order to permit the development of the second and third centralia, or that these streams of prochondral cells "issue" from the first centrale. They simply represent concentrations of cells that develop *in situ* in a manner resembling their development in the manus. The element called the first centrale by Holmgren, the fourth centrale by Williston, may still be regarded as principally the tibiale. There is no convincing evidence of the presence of the first centrale. Schmalhausen and Holmgren agree that the fourth tarsale and the first centrale (C_4 of Williston?) fuse with the fibulare. In *Rana*, according to Holmgren, there is a fifth tarsale that also fuses with the fibulare. A centrale apparently fuses with the third tarsale, while the first and second tarsalia ossify separately. With the y-element of Holmgren and others equal to Williston's first centrale, there are, according to this author, five centralia in Anura and certain of the higher forms. The interpretation and identification of the anlagen in the anuran embryonic tarsus are very difficult in view of the obvious specialization from the very moment at which the rudiments are laid down.

This discussion suggests that all the tarsal elements may be accounted for in the Anura, except the intermedium, Steiner being the only one possibly demonstrating its presence (1921). The early indistinguishable fusion of this element with others must represent a profound and ancient modification since its persistence along with the tibiale and fibulare is so characteristic of all the other amphibian orders. The Lower Triassic preanuran *Protobatrachus* (Piveteau, 1937) unfortunately sheds no light on the subject. Two elements, which are very presumably the tibiale and fibulare, are somewhat elongated, foreshadowing the anuran condition, but there is no indication that they were united, although they may have been through proximal and distal cartilages.

There are two small ossicles between the crus and the elongated elements that are thought to be sesamoids by Piveteau. The possibility must also be considered that they are the last remnants of the intermedium and proximal centrale.

Without going into the matter in greater detail, there is little question that the *Trematops* pes is very unfit for jumping and that much consolidation must have occurred during the evolution of the anuran tarsus to create a lever arm that could act as a single unbending unit. The loss of an independent intermedium and the losses and fusions of the centralia and tarsalia are further expressions of this consolidation. It would appear that they are of no functional importance, except possibly as "bearings" in the tarsometatarsal joint. Noble (1931, p. 243) considers the reduction in the distal elements of the tarsus a consequence of the elongation of the tibiale and fibulare. The persistence of these free elements on the tibial side and their fusion on the fibular may be simply an expression of their mechanical importance on the medial side.

The anuran tarsus is a striking example of uniformity in development brought about as a result of localized function at the tarsometatarsal joint. While the tarsus has been greatly modified and reduced, there is very little variation in the elements present. In other words, the anuran tarsus is a region of great movability with each element serving a definite mechanical need. As a result, there tends to be a lack of great structural variation. This is the situation in most reptiles and all mammals and for the same reason, the normal variation being of little functional significance.

The resemblance between the early embryonic stages of the anuran and caudate foot is very striking. In both cases the tibiale and prehallucial elements arise together in a separate ray. In any case, if the anuran tarsus appears to be derived from the labyrinthodont type, as many now believe, there is certainly more evidence for believing the same for the caudate amphibian tarsus.

THE RELATION OF THE TARSUS TO THE ORIGIN OF THE AMPHIBIA

The comparison between the caudate and the anuran tarsus quite naturally leads to the question of the diphyletic origin of the Amphibia. Considerable evidence has been amassed (Graham-Kerr, 1907, 1932; Säve-Söderbergh, 1934; Kindahl, 1938; and Wintrebert, 1910, 1922), which has been interpreted as indicating that the Caudata are closely related to the Dipnoi, while the Anura and the extinct amphibian orders are separately derived from the Crossopterygii. If this be true, the *Trematops* type of tarsus cannot be considered as ancestral to that of the urodeles, but only to that of the Anura and Reptilia. The plan of the tarsus is so very similar in the labyrinthodonts and the Caudata, particularly the Hynobiidae, that the possibility of this resemblance being due to parallelism is very difficult to visualize. If this is so, it is even more remarkable than the parallelism between the manus and the pes.

Holmgren (1939, p. 120) lists nine "most striking" differences between the urodele and the anuran hand and foot. It is practically impossible to evaluate these so-called differences, first, because there are so many gaps in the evolutionary record of the foot, and secondly, because of the lack of certain experimental evidence. How significant, for example, are heterochronic differences in the development of the manus and pes as a whole, or in the order of development of the fingers. Such differences are to be expected in groups so far apart as subclasses, and in view of the specialization of the Anura it would appear precarious to consider these differences of such great basic importance. This sort of reasoning also holds true when considering the fact that the urodeles always have four digits in the manus instead of five.

The ontogeny of both the urodele and the anuran tarsus definitely foreshadows the adult condition. The modification of the anuran tarsus for a leaping habitus is clearly seen early in ontogeny; for instance, the two proximal tarsal elements are elongated when they first appear and

very possibly the more ancestral-like stages, which might have appeared during development, have been greatly condensed or even eliminated. That the ontogeny of the anuran tarsus could be so modified is very probable when the hundreds of millions of years at the disposal of the group for its evolution are considered.

It appears quite evident that the diphyletic origin of the Amphibia will have to be

demonstrated on other grounds and, if generally accepted, will of course modify the theories on the origin and the evolution of the tetrapod limb. Romer (1940) has stated the more reasonable view that the Caudata are descended from the Lepospondyli, more specifically from the gymnarthrids. He considers the great number of characters common to all Amphibia as ample proof of their common origin.

AMPHIBIAN LOCOMOTION

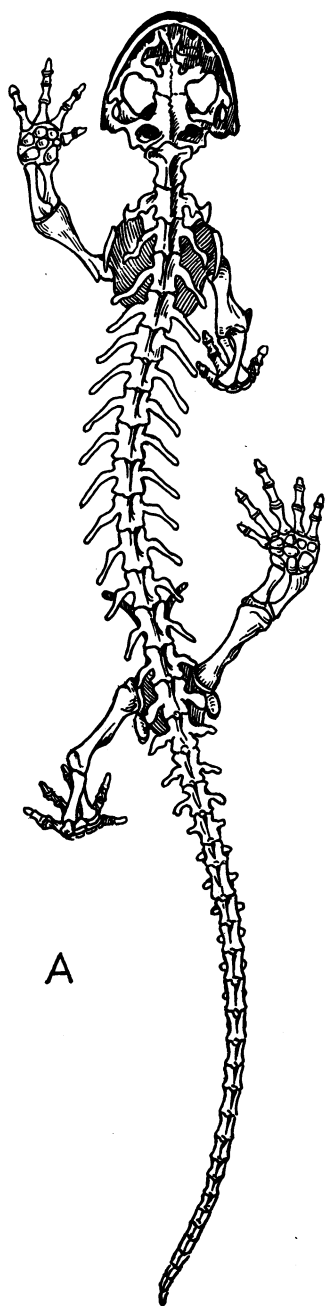
Neither a study of the osteology nor of the myology of the amphibian hind-limb will suffice to describe exactly how the limbs are used during progression, or set the stage properly for evaluating the changes that took place during the origin and evolution of the reptilian foot. Romer (1931, 1940) has made the observation that the oldest known tetrapod footprints point forward, as they do in all modern Amphibia, during locomotion (Fig. 7). This important point has not been generally realized, as most mounts of Permian-Carboniferous tetrapods will testify. The error is readily understood as there is nothing in the bony construction of the leg or particularly in the foot which would indicate such a position.

With the evidence of the footprints demonstrating beyond doubt that the labyrinthodont feet, like those of the caudates, were pointed forward during locomotion, the disposition of the crural and tarsal elements during propulsion becomes of interest as the true solution to the problem, particularly since it is very evident that, because of its terminal head, the femur can only move in a horizontal plane. By manipulating the limbs of cleared and stained specimens of, for instance, the caudate *Triturus*, such observation is possible. The diagram (Fig. 3) represents an attempt at a comparison of the skeletons of a typical caudate and *Trematops* posed as if in motion. The posture of the limbs of *Trematops* is based on casts of the fore- and hind-limb elements and girdles of *Eryops*, which were posed, without difficulty or violation to the articular surfaces, in the same positions

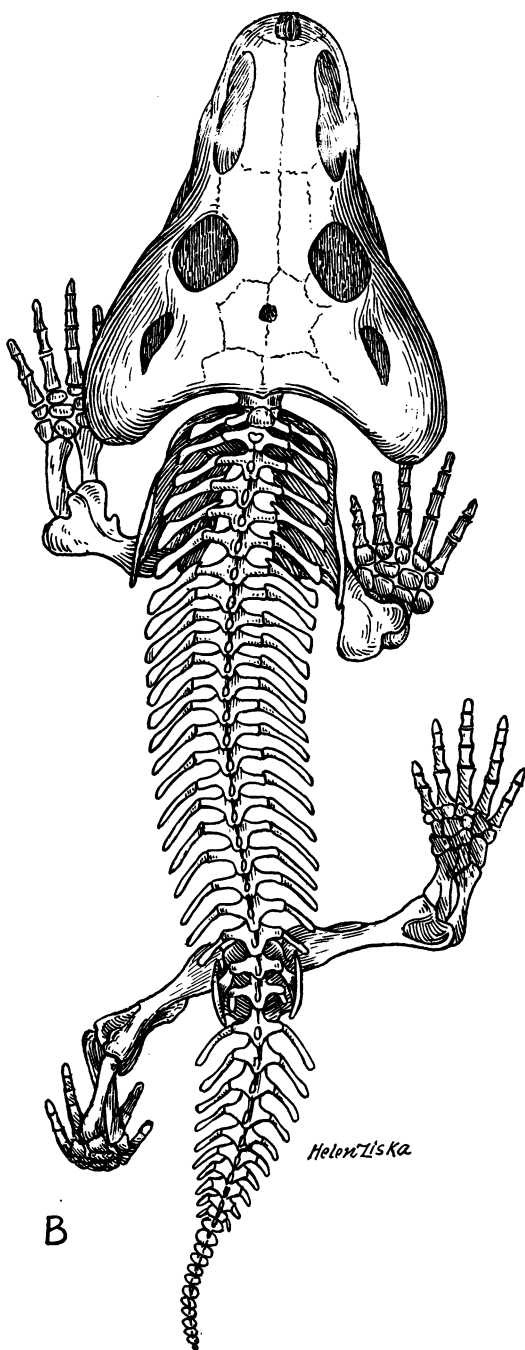
assumed by the *Triturus* limbs during locomotion. A model of the pes of *Trematops* has also been made with the bones loosely joined together with rubber cement and latex to simulate the binding action of the ligaments and muscles. By these means, it can be demonstrated with a reasonable degree of certainty exactly how the recent caudate amphibia and the labyrinthodonts operated the entire hind-limb.

The extrinsic flexor muscles of the foot arise, with minor exceptions, from the fibular shaft and insert in the tarsal region on the tibial side. Their action is not only to flex the tarsus, but to turn the foot forward (adduct) to a slight extent just before it is placed on the ground at the end of the recovery phase and to maintain it in this position throughout the propulsion phase. At the beginning of propulsion, however, the forward position of the crus automatically places the foot in a forwardly directed position. This is a function of the muscles operating on the crus rather than on the foot. Hence it would appear that the extrinsic foot flexors, as will be pointed out, are more concerned with maintaining this position during propulsion than in actually initiating it.

In order that the foot may remain in this position while the femur is moving backward, the tibia is forced to move around the fibula in such a manner that it crosses diagonally in front of the fibula (cf. relations of tibia and fibula in Watson's restoration of *Diplovertebron*, 1926a, Fig. 31). The obvious result of this action is to shorten the distance from the knee to the foot on the tibial side by throwing, so to speak, the tibia out of line, into a diagonal



A



B

Fig. 3.—A comparison of a typical caudate and a labyrinthodont (*Trematops*), showing the positions of the limbs during locomotion. The left fore-limb and the contralateral hind-limb are at the beginning of the propulsive phase, the other two about ready to enter the recovery phase.

instead of a vertical position, permitting, in turn, the foot to remain forwardly directed. There is also some separation of the tarsal elements on the fibular side and a close approximation of the elements on the tibial side and also some folding of the preaxial tarsal series laterally (cf. discussion of flexion in *Trematops* tarsus).

The position assumed by the tibia produces considerable torsion on the medial side of the foot, particularly at the place where it articulates with the tarsus. As the femur moves backward, it attempts to

This forward position serves an important purpose in that it orients the long axis of the foot so that it is parallel to the long axis of the body and hence to the direction of movement, thus allowing the muscles of the lower leg and foot to operate under the greatest possible mechanical advantage. Only with the foot in this position can the muscles impart power to the propulsive stroke.

Morton (1926), from his study of the footprint of *Thinopus*, believed that the hind-foot of a primitive tetrapod was di-

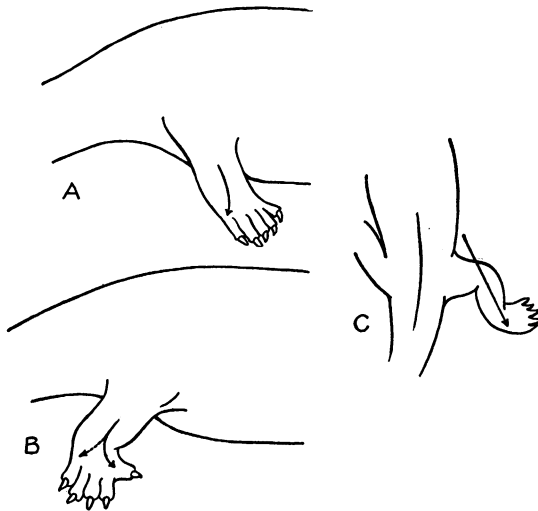


Fig. 4.—Diagrams (after Morton, A, B, 1935; C, 1926) showing the supposed distribution of stresses in the primitive tetrapod tarsus if the long axis of the foot is at right angles to the long axis of the body. There is a shift from the postaxial border (A) at the beginning of propulsion to the preaxial border (B) at the end. In C the stress is considered to be localized along the postaxial border throughout propulsion.

rotate the tibia counter-clockwise in the case of the left limb. This action is opposed, on the other hand, by the action of the extrinsic flexors and the weight of the body bearing down on the foot, both of which tend to maintain the forwardly directed position of the foot.

In some of the cleared specimens of *Triturus* it is apparent that the torsion is so great in the proximomedial region of the tarsus that the first tarsale has been forced plantarward, out of the plane of the other tarsal elements, thus narrowing the medial border of the tarsus.

rected outward during the greater portion of the propulsive stroke (Fig. 4). The chief evidence, however, for this assumption is possibly the footprint of *Thinopus* itself. Morton believed that the footprint belonged to a pentadactyl form which maintained its hind-limb in the above position during locomotion. The resultant pressure on the fibular side, he believed, forced the second and third digits into an elevated position so that they would not make prints. This ingenious explanation is, however, only based on one footprint. That this footprint is exceptional is indi-

cated by the presence of hundreds of early tetrapod footprints (although from a later horizon) of normal tetrapod type. In a more recent publication, Morton (1935) is of the opinion that the primitive position of the foot during propulsion caused the functional stresses to be concentrated at first along the postaxial border and then toward the end of this phase to be transferred transversely across the tarsus to the preaxial border.

The propulsion and recovery movements of the lower leg and foot have been carefully investigated for this study in several salamanders by means of motion pictures. *Ambystoma maculatum*, a relatively terrestrial salamander, and *Triturus pyrogaster*, almost exclusively aquatic, were used as subjects for the motion pictures. It was found that there is no major difference in the locomotion of the two, even as far as the details of limb movement are concerned, the only noticeable difference being the greater lateral undulation of the body in *Ambystoma* because of its relatively greater length. Noble (1931, p. 92) has observed that there are no functional changes in the locomotion of salamanders which have lost the outer digit of the hind-foot.

The pictures were made at 64 f.p.s. with the subjects walking over a thin sheet of plate glass. A mirror was set up at an angle of 45 degrees to the glass so that the animal could be photographed simultaneously from two aspects. This arrangement made it possible to study the positions of the limbs in detail at any stage during the locomotor cycle both with regard to the range of lateral and of vertical movements.

The series of diagrams (Fig. 5) has been carefully drawn from one of the films by projection. It represents selected stages during one-half of a normal locomotor cycle for *Triturus*. A complete cycle would show the propulsion and recovery phases for each limb.

The pattern of movement here illustrated is found in most tetrapods (Gray, 1939). When the right fore-foot is forward the left hind-foot is also in that position, and vice versa, when the left fore-foot is forward the right hind-foot is also in this position; in other words, the se-

quence of limb movement is right fore-limb, left hind-limb, left fore-limb, and right hind-limb. Gray states that during rapid locomotion the protractor and retractor phases take about the same period of time, but that in slow progression the time required for the retractor phase is relatively increased.

The movement of the left hind-limb may now be described in detail. The retraction or propulsion phase begins immediately on the contact of the plantar surface of the foot with the ground. As will be explained later, the flexor musculature pushes the foot against the ground, thus making of the crus and pes a kind of stationary pivot on which the femur rotates, and the net result of hind-limb movement is to move the body forward. The body is always more or less concave on the side on which the hind-limb is just beginning the propulsive phase. This curvature actually decreases the length of the body on that side and, hence, increases the length of the stride of the hind-limb (see Watson, 1926a, p. 202).

As the body moves forward, the leg, relatively speaking, moves backward, principally through the action of the coccygeo-femoralis complex. As this occurs, the foot itself gradually rolls off the ground, flexure occurring at each one of the joint planes mentioned earlier. The foot remains in contact with the ground until the last phalanx of the longest digit has been turned plantar-side up, thus producing the greatest possible propulsive effort. Once the tarsal region is off the ground, the dorsal surface of the foot begins to turn laterally until, by the time all the digits are free, the foot is in a vertical position.

The recovery phase of the limb is comparatively complicated, as the limb not only has to sweep through almost 180 degrees but must also bring the foot itself into the proper position to meet the ground for the next propulsive stroke. The thigh musculature, in particular the pubo-ischio-femoralis internus, is concerned with the forward movement of the entire limb. The crural and intrinsic foot musculature brings the foot itself into position. The upper and lower portions of the leg are brought

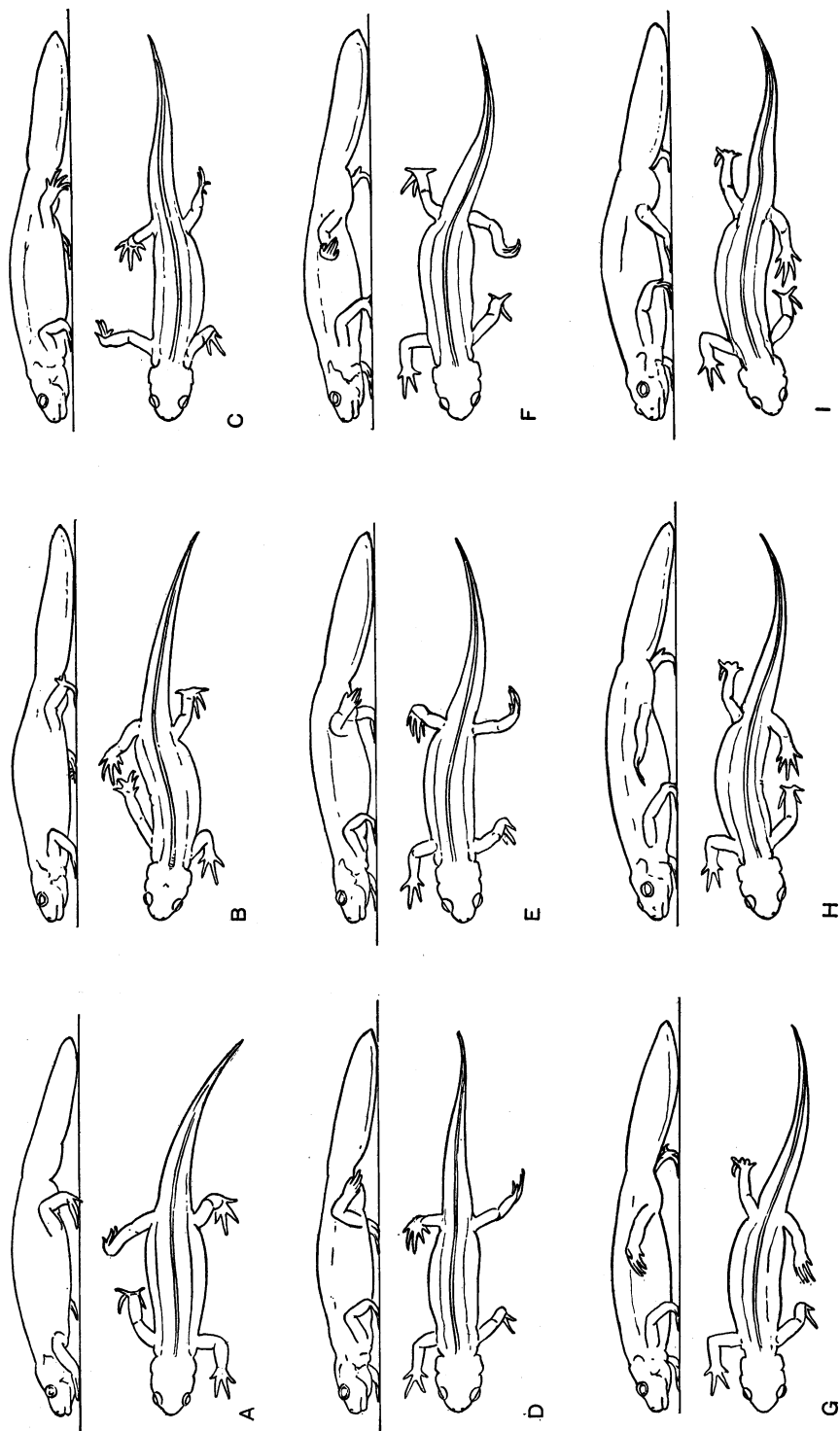


Fig. 5.—Series of diagrams showing the positions assumed by the limbs during the locomotion of *Triturus pyrogastrus*. Made from motion picture by projection.

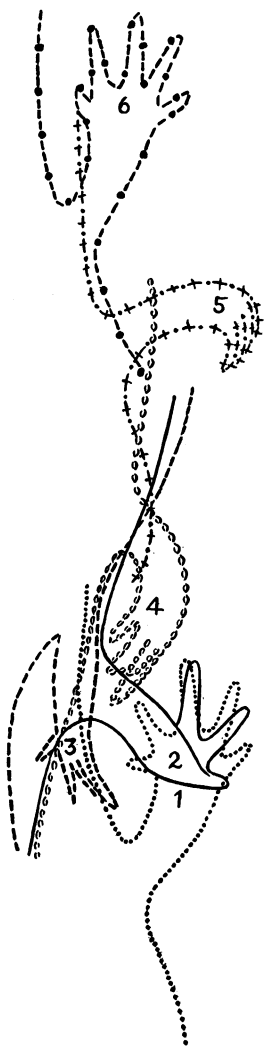


Fig. 6.—The movement of the hind-limb of a caudate amphibian during propulsion (1-2) and recovery (3-6).

forward as a unit until they are just beyond a position at right angles to the body. At about this position there is flexion at the knee.

Up to this point, the foot has remained directed backward since there has been no active participation on the part of the extensors. The digits are adducted as soon as the foot leaves the ground and remain so until just before the beginning of protraction. With the continued forward move-

ment of the upper leg, plus the flexure of the crural portion, the limb is very rapidly brought into the forward position by a sort of crawl-stroke movement (Fig. 6). At about the stage when the knee is flexed, the foot extensors begin to operate and the foot is unrolled. Other muscles, which will be discussed shortly, act on the pes, bringing it into a position parallel with the body. With the foot brought forward, the digits are abducted and the foot is very rapidly lowered to the ground. Throughout the protraction and retraction phases, the extreme suppleness of the foot is very noticeable. This allows for some variation in the placing of the foot during the cycle, particularly when the animal is moving slowly.

Gregory and Camp (1918) have pointed out that the Permian reptiles had permanently crooked knee-joints. This also appears to have been true for the labyrinthodonts (Fig. 3). The distal articular surface of the femur of *Eryops*, for instance, is more ventral than terminal. In fact this surface is so located that it was impossible to extend the lower leg beyond making an angle of about 135 degrees with the femur. This condition of permanent flexure must have been maintained by the flexor muscles of the crus inserting on the tibia and fibula, namely, the pubo-tibialis, the pubo-ischio-tibialis, the flexor tibialis internus and externus, and the ilio-fibularis.

The permanent flexure would modify the movement of the limbs during locomotion somewhat from the above description. The length of the stride would not be as great and the limb as a whole could not reach as far forward relatively at the end of the recovery phase. The length of the propulsion phase would also be shorter because the leg could not straighten out toward the end of the phase. Lastly, the arc described by the leg during protraction would be much closer to the body and, of course, much closer to the ground instead of rising above the acetabulum, as in the Caudata. The pes itself must have moved in much the same manner as in the foregoing description. In a heavy animal such as *Eryops*, however, the tarsal ele-

ments are much more cuboidal than in *Trematops*. This would indicate a more extensive articulation between the bones and consequently a reduction in the flexibility of the foot. Thus, it follows that the lighter labyrinthodonts were able to move their limbs, especially the pes, very much as do the Caudata, while the heavier types had restricted movement with less effective propulsion. It is interesting to note in this connection, however, that the intermedium of *Eryops* has a rounded tibia facet (Romer, personal communication), thus increasing the flexibility and foreshadowing the condition in the cotylosaurs.

Although the femur of the primitive tetrapods undoubtedly had a greater degree of freedom than the humerus, it is doubtful that it was directed relatively further forward than the humerus at the beginning of propulsion. During retraction, in order to maintain the body on an even keel, the humerus and femur must move through essentially the same distance or, in other words, swing more or less in phase with each other. Hence, although the right hind-limb in the *Trematops* restoration (Fig. 3) could be extended further forward without dislocation, it has been placed in a position more in agreement with the contralateral forelimb.

Carman (1927) has estimated that in the case of *Baropus hainesi* and *Ancylopus ortoni* the length of the stride and the size of the tracks indicate an animal weighing close to 400 pounds and measuring six to eight feet in length. In spite of the weight and size, there is absolutely no indication that the body was dragged along the

ground. This is also true of the material from the Grand Canyon (Gilmore, 1926, 1927, 1928), with the exception of *Batrachichnus obscurus* (idem, 1927, p. 41, Fig. 17). In this case there is a distinct path, representing the drag of the body, between the prints of the right and the left limbs. Nevertheless, there is distinct evidence that most of the heavy forms must have been able not only to overcome the inertia of the body with the limbs, but also to overcome gravity to the extent of actually raising the body away from the ground during locomotion as in the Caudata. The body-dragging stage, if it ever existed, must represent a part of the lost record between crossstep and true amphibian.

Gray (1939, Pl. iv) has demonstrated by placing anurans, in which the spinal cord was cut just behind the brain, in contact with a slowly revolving kymograph drum, that they exhibit the same sort of ambulatory movement as the caudates, apparently showing no inclination to leap. This has also been observed by the writer in slowly moving normal toads. It is now becoming evident that the coordinated movements of locomotion, while they are under the control of the central nervous system, are initiated by peripheral stimulation. It is rather tempting to assume in this case, but open to criticism, that the nervous mechanism inducing the primitive tetrapod locomotor pattern has not been completely dominated or obliterated by that producing the leaping mode. The mechanics of the leaping method of locomotion in the Anura have been thoroughly investigated by Hirsh (1931).

PRESSURE DISTRIBUTION IN THE UNSPECIALIZED AMPHIBIAN FOOT AND AN ANALYSIS OF THE FORCES ACTING ON THE LIMBS DURING LOCOMOTION

A knowledge of the distribution of pressure or weight in the amphibian foot is of value in interpreting more exactly the nature of the locomotor process. It also gives some clue as to the functioning of the various elements of the foot and finally is helpful in working out the functional changes.

Most caudate amphibia weigh so little that the most delicate apparatus would be required to measure the weight distribution of the hind-foot. In view of this difficulty, an investigation of fossil tetrapod footprints has been made. Through the kindness of Mr. C. W. Gilmore casts have been obtained of the better preserved

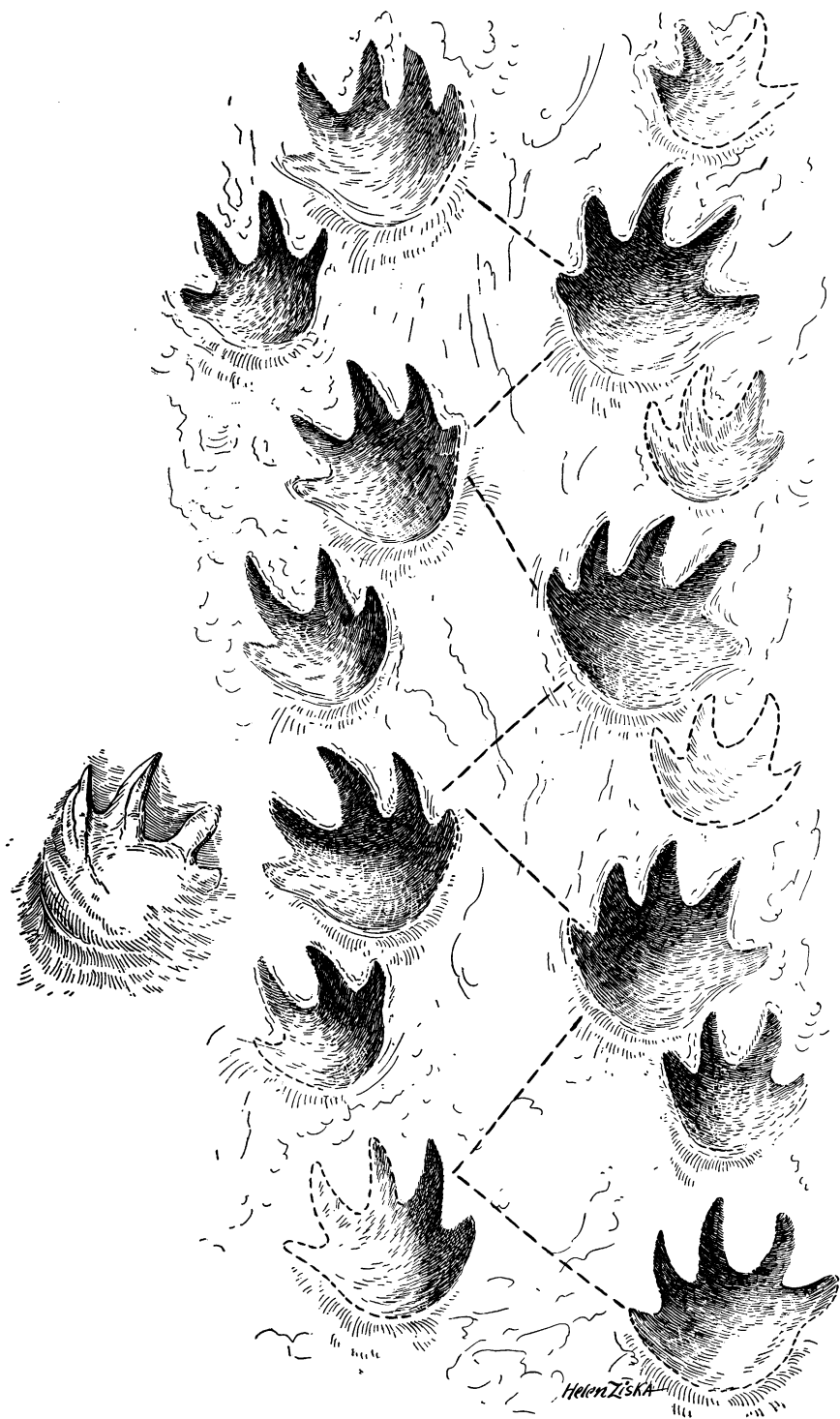


Fig. 7.—The footprints of *Ammobatrachus turbatans* (Supai formation, Pennsylvanian, Grand Canyon) drawn from positive and negative casts of the original tracks. They are consistently deeper on the inner side, particularly in the vicinity of the first three toes. The length of the stride, about 3.25 inches, was relatively shorter than that of *Trematops*. The dotted line connects the hind-foot prints.

footprints found in the Carboniferous and Permian formations in the Grand Canyon (Fig. 7).

Elftman (1934) has criticized the use of footprints made in any soft, yielding material because under such conditions they are a record of the shape of the foot rather than of the pressure distribution. This is to a large extent true, particularly when very accurate results are desired. It is also true, however, that if the foot itself is relatively expansive and supple at least a rough indication of the weight distribution should be indicated by the footprint. That this is so is demonstrated by the fact that different parts of all the well-preserved footprints show variations in their relative depth and that these variations are present in a definite sort of pattern. It has been argued that the variations are due partly to the presence of plantar pads. While this may be true, it would appear significant that the pads all show the same sort of arrangement, indicating a response to pressure.

It is of course impossible to ascertain with certainty which footprints are amphibian and which are reptilian. In either case the great similarity between all of them indicates that the type of locomotion was essentially the same. The deepest part of the print is usually at the base of the first two digits, extending and becoming progressively shallower for a short way along the inner border of the foot. This depression then continues to the posterior portion.

At the beginning of the propulsive phase the entire foot is placed upon the ground at the same time, that is, from the tips of the toes to the tarsal flexure. As mentioned earlier, the gradual sloping of the posterior part of the print is due to the wide curvature of the tarsal region. At no time during this phase is any pressure transmitted through the proximal tarsal elements directly to the substratum. As the body moves forward and the foot relatively backward, the pressure increases, reaching a maximum in the region of the first, second, and third metatarsals and corresponding digits and decreasing laterally toward the fifth metatarsal. The

footprints of the front feet have a path running in a similar direction, essentially from the posterior to the anterior inner border. When the foot is applied to the ground at the beginning of propulsion, the weight of the body proportioned to it is distributed throughout the foot to its maximum extent. As the foot is rolled off the ground, the area supporting this weight is decreased and consequently, with the weight remaining constant (it may actually vary slightly), there is an increase in weight per unit area of foot still in contact with the ground. As a result, the print is deepest in the vicinity of the first three toes of a pentadactyl foot, which is the last part to be raised from the ground. Although it is not possible by this means to determine the path of the resultant of pressure as Elftman and Manter have done for the human and chimpanzee foot (1935b), it is possible to trace the path of relatively greatest pressure or weight distribution in the above manner and to derive some conclusions therefrom.

Nauck has analyzed (1924) the forces acting on the amphibian hind-limb when the body is at rest and in motion. He has postulated, in the resting position (Fig. 8,A), the presence of a raising component in each hind-limb b and b' , and also the components c and c' that draw the limbs toward the midline. The latter counteract, along with friction, the forces w and w' (gravitational effect) which cause the foot to slip sideward. The resultant forces of the two sets of components, bb' and cc' , he designates as a and a' . They cause the body to be raised, counteracting the downward effect of gravity.

During locomotion one hind leg is always in some stage of the recovery phase and the other in some stage of the propulsion phase. The recovering leg is not in contact with the ground and hence only c (or c') is acting, causing the body to move toward the c' (or c side). Under these conditions Nauck claims the propulsive leg will have a forward component, so he calls forth a new force m (Fig. 8,A') that equals c plus a forward component. Since the propulsive leg only is responsible

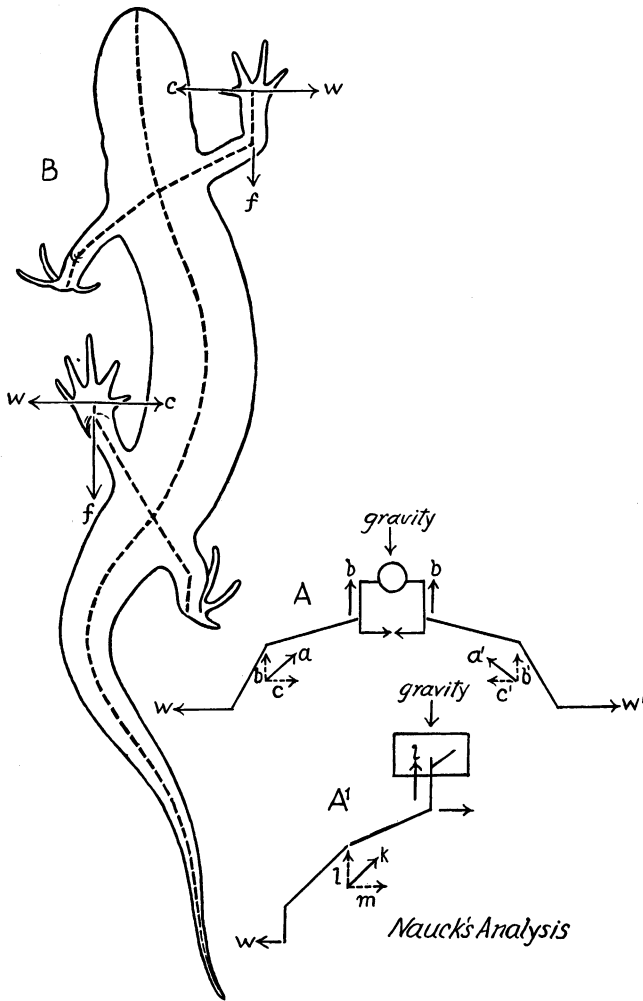


Fig. 8.—The forces acting on the limbs during locomotion.

A. Nauck's analysis of the forces acting on the hind limb at rest (A) and in motion (A').

B. Diagram of forces acting on the fore- and hind-limbs during locomotion, as interpreted here.

for raising the posterior part of the body, the recovering leg being off the ground, there is another component l that equals b plus b' . Nauck concludes that the resultant of these components is a force k that moves the body forward and also sideward. The contralateral fore-limb has a resultant moving the body sideward in the opposite direction, with the result that the animal moves only forward. Nauck errs in assuming that the hind-limbs and particularly the feet are directed at right

angles to the body during locomotion. Since this is not the case, a partial revision of his analysis is in order (Fig. 8,B).

Regardless of the number of limbs on the ground at any one time (two, three, or four) either at rest or during movement, the raising force exerted by the limbs must be greater than the force of gravity, if the body is to be raised from the ground at all. The morphological basis for Nauck's components b and b' , which are supposed to raise the body off the ground in the resting

position, has not been determined. Romer (1922, p. 568) has pointed out that in the primitive tetrapods the ventral musculature of the femur, mainly the pubo-ischio-femoralis externus arising from the pubis and ischium, was responsible for actually raising the pelvic girdle. The downward pull exerted by this muscle mass on the femur was translated into a force raising the pelvis, as the movement of the femur in this direction was limited by the crus. Hence, b and b' might be considered as the effect of a system of forces operating around the pelvis. As pointed out previously, even the very heavy labyrinthodonts were apparently able to raise the body off the ground.

As already noted, the long axis of the front- and hind-feet is parallel to the path of progression during the entire propulsive phase. The forward force exerted on the ground through the movement of the humerus and the femur is the sum of the forward force f_1 exerted by the fore-limb plus the forward force f_2 exerted by the contralateral hind-limb, which, in turn, would be equal to m minus c in the case of Nauck's analysis. Again, it should be stressed that the active participation of the foot in the propulsive effort is practically nonexistent in the primitive tetrapods. The main function of the pes is to increase the area through which the tractive effort of the femur and its associated muscles is applied to the ground. The crus, on the other hand, acts as a sort of pivot with an expanded base, the foot, on which the femur swings in propelling the body forward. The extrinsic and intrinsic flexors of the foot are principally concerned with orienting and maintaining the most advantageous position of the foot during propulsion, as well as with giving it rigidity.

It would appear that Nauck is correct in stating that the forces w and w' are largely counteracted or balanced by the friction that exists to a greater or lesser degree between the sole of the foot and the ground, but more importantly by the extrinsic flexors of the crus, which, through their action, create the forces c and c' .

The relationship between these forces and the structure of the crus and foot remains to be considered. The tibia makes the most extensive articulation with the femur and is certainly the weight bearing axis of the upper portion of the crus. At the crurotarsal joint, however, the fibula is the weight bearing axis, as it, rather than the tibia, is in a position to distribute the weight to the tarsal elements and the digits. It appears evident, therefore, that there must be a weight transfer from the tibia to the fibula. This transfer is accomplished by certain muscles, particularly the pronator profundus and the interosseus cruris. This situation resembles the manner in which forces are transmitted along the human forearm when it is supporting part of the body weight. The forces are transmitted from the hand mostly to the radius and then across the interosseus membrane to the ulna and hence to the humerus (Grant, 1940, p. 74).

The forward force f_{1+2} is therefore transferred from the femur mainly to the tibia, then across to the fibula and from the fibula it is distributed to all parts of the tarsal region and the digits. A greater proportion of the weight appears to be thrown on the inner side of the foot, as is demonstrated by the footprints and also by the fact that during propulsion the lateral toes are raised first.

THE EXTRINSIC AND INTRINSIC MUSCULATURE OF THE AMPHIBIAN
HIND-FOOT AND ITS RELATION TO LOCOMOTION

The well-differentiated musculature of the lower leg and foot of the amphibian when compared with the relatively undifferentiated musculature that must have existed in the crossopt pelvic fin (Gregory and Raven, 1941) is an indication of a profound change and increase in complexity of function. The range of movement of the amphibian hind-limb has been described and it is now necessary to determine the role of specific muscles in producing the movements.

Muscular differentiation, whatever its cause, is simply an indication of an increasingly complicated range of movement of the part concerned. Le Gros Clark (1939) has pointed out that muscles are capable of progressive variation. That this progressive variation or, in other words, differentiation, is associated with the origin of specific and more localized movements is well brought out by the example cited by Clark. In man the flexor longus pollicis is separated from the common flexor of the fingers and there is a partial separation of the flexor of the index finger. This differentiation can only be associated with the functional importance of these two digits in man in contrast to the other primates.

Very few attempts have been made to assign definite actions to the leg muscles of the caudate amphibians, the most recent designations being those of Francis (1934). These are in most cases correct but frequently the action of a muscle is much more complicated than he describes. The characteristic locomotor movements described above are produced by the cooperation of muscles and for this reason simple statements of their action are not always correct.

The details of movement during propulsion and recovery form a basis for a discussion of the details of the musculature. There is considerable variation in the subdivision of the larger muscles among the various caudate families. This variation, however, is of no functional importance and hence will not be discussed, nor will

all the details of origin and insertion be described, as there are numerous papers on this subject (Eisler, 1895; Osawa, 1902; Wilder, 1912; Francis, 1934).

Dissections were made of the lower leg and foot of *Batrachuperus*, a hynobiid, *Cryptobranchus*, *Necturus*, and *Triturus*. The diagrams show (Fig. 9) the generalized condition of the musculature of a typical caudate. Howell's contention (1935a) that it is not possible to restore accurately the musculature of an extinct form is valid in certain cases, specifically where there are no tuberosities or other indications on the bones for the origin and insertion of the muscles in question. In this case, it should be noted that the structure of the skeleton of such forms as *Trematops* indicates that the mode of locomotion must have been essentially the same as in the Caudata. Hence, it follows that the arrangement and subdivision of the musculature must have been very nearly the same in labyrinthodonts and caudates.

Extensor Series

The origin of all the extrinsic extensors from the lateral condyle of the femur is probably a primitive feature, still persistent in the Caudata. In *Eryops* the lateral condyle is exceedingly well developed as is also the case in *Trematops*. The proximal portion of the lateral border of the tibia is depressed and somewhat convex, making a channel for the extensor mass to reach the lower portion of the crus. The origin on the femur causes these muscles to extend the two lower segments of the leg instead of just the foot alone.

Another important feature of the extrinsic extensors is that their tendons of insertion do not run to the digits. The tibial and fibular extensors insert on the shafts of their related bones and on the tarsus, while the medial digital extensor inserts by a number of tendons on the bases of the metatarsals. Mechanically, such an arrangement produces rapid extension but is not very efficient. The short digital ex-

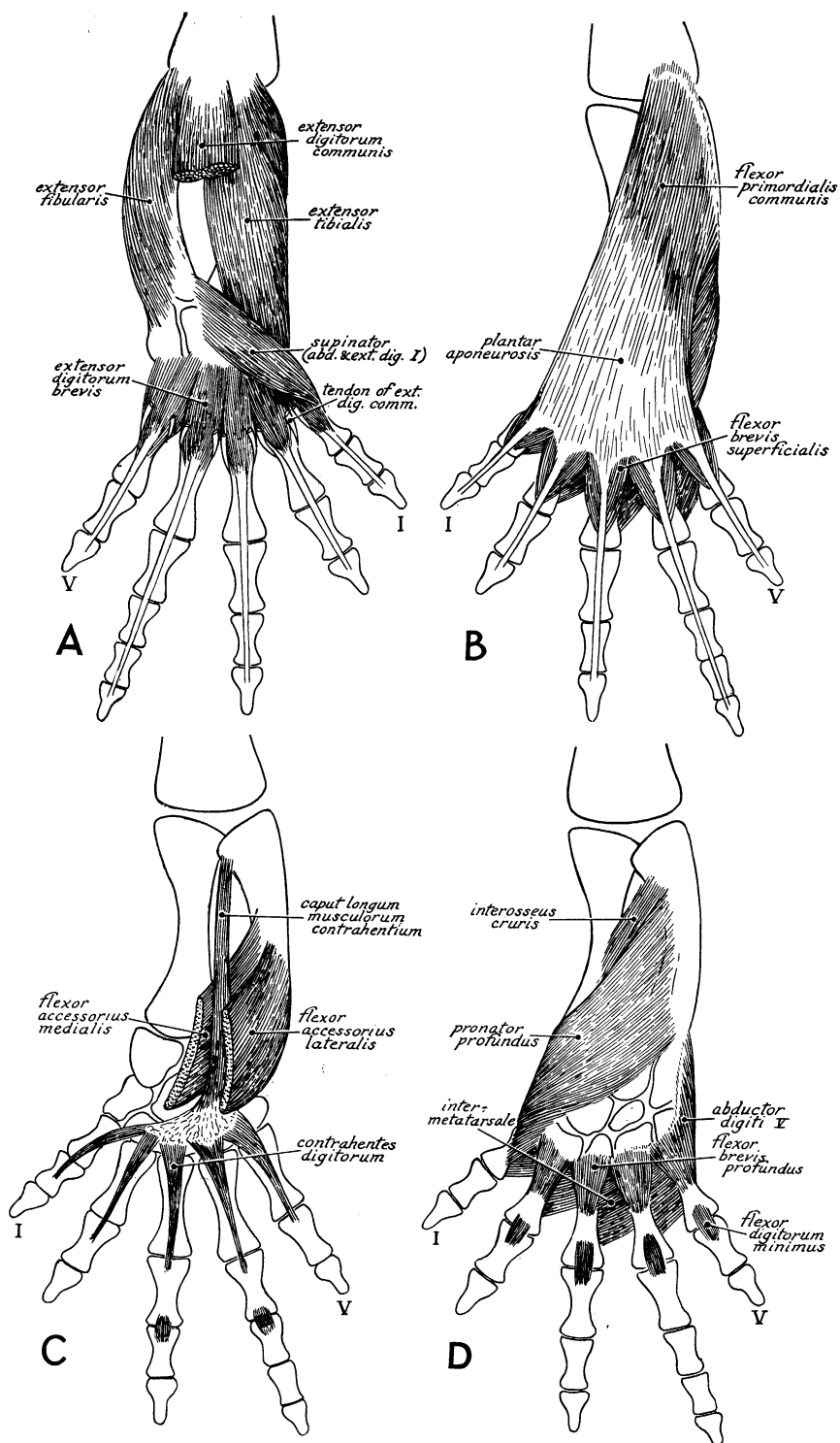


Fig. 9.—The cruro-pedal and pedal musculature of a typical caudate amphibian, based on dissections of *Batrachuperus*, *Cryptobranchus*, *Necturus*, *Triturus*. A, extensor musculature; B, C, D, successively deeper layers of flexor musculature.

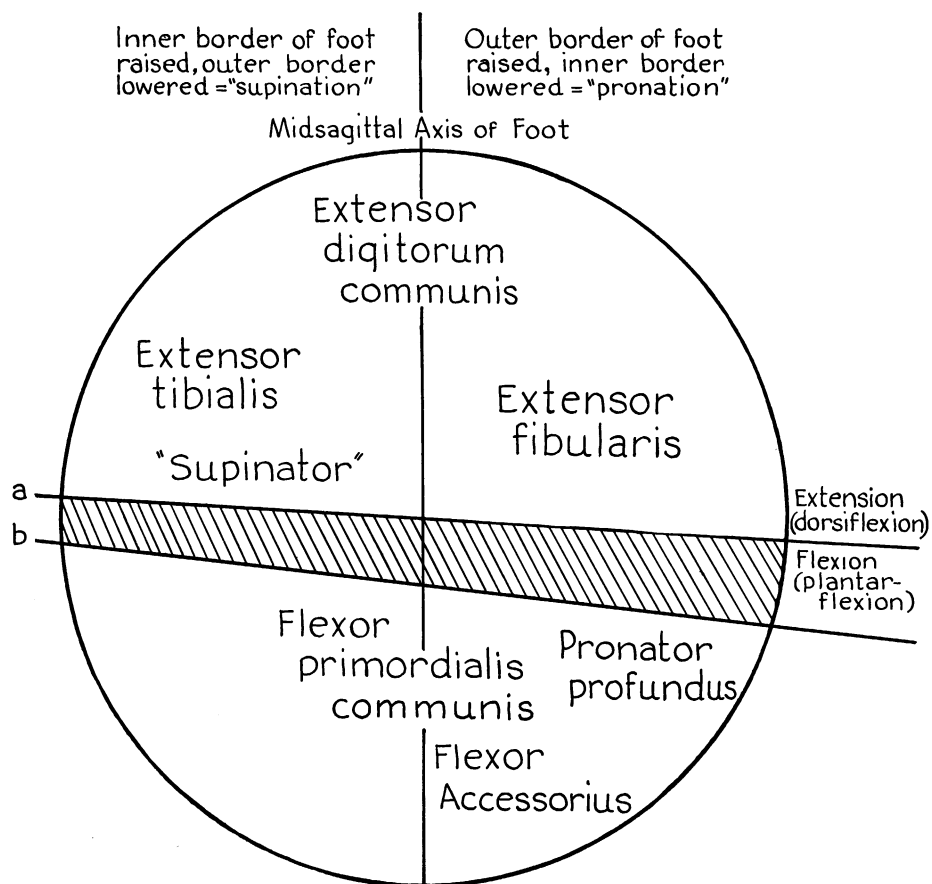


Fig. 10.—A diagrammatic representation of the action of the extrinsic pedal musculature of the caudate amphibian. The shaded area represents the tarsus as a whole in which there is a slight amount of movement between elements. a, axis of tarsometatarsal joint; b, non-functional joint between the crus and the tarsus.

tensors, of course, do have tendinous insertions on the distal phalanges.

All the caudate amphibia have a large combined abductor and extensor digiti I, the part acting as an abductor being called by some, for instance, Wilder, the supinator pedis. It has a diagonal course across the tarsus, arising from the head of the fibula, the intermedium, and a part of the centrale complex and inserting on the base of the first metatarsal. The role of this muscle has not been generally realized. The larger abductor portion is first of all concerned with the slight "supination" of the foot at the end of the propulsive phase, thus bringing it into the position it assumes for the greater part of the recovery phase. Sec-

ondly, it cooperates to some extent with the flexor accessorius and pronator profundus in aiding to maintain the forwardly directed position of the foot during the propulsive phase. Both of these actions are peculiar to the amphibian type of locomotion. Needless to say, these muscles must have been present in the labyrinthodonts to maintain the same positional effect.

Flexor Series

The plantar aponeurosis developed as an extensive tendinous sheet for the common insertion and origin of both intrinsic and extrinsic flexors. Its relatively great size in the primitive tetrapods is undoubtedly

associated with the fact that the posterior border of the plantar surface of the foot is not sharply defined by the presence of an ankle-joint.

The origin of the flexor primordialis communis is subject to variation. In *Necturus* it arises entirely from the lateral condyle of the femur; in *Salamandra*, from the fibular shaft; and in *Cryptobranchus*, from both. This difference in origin causes some slight variation in action. In *Necturus* it is only a flexor of the foot, while in *Salamandra*, because of the extensive fibular origin, it also adducts the foot toward the midline. As Francis points out, this is due to the inequality of the fibers on the tibial and the fibular sides of the muscle. It is impossible to determine which of these conditions is the more primitive. In the more terrestrial Caudata, this muscle undoubtedly assists in the adduction of the foot. Since this movement probably existed in the Permian types, at least a partial origin on the fibula seems probable. Romer (1922) believes that it arose from the femur, and the roughened ventral surface of the lateral condyle of *Eryops* indicates that it at least partly did so. The role of the flexor primordialis communis in locomotion is discussed elsewhere (pp. 419 and 462).

The caput longum musculorum contrahentium is the only crural flexor in which the fibers run in a proximodistal direction only. It functions as a flexor of the tarsus and is a narrow, comparatively weak muscle in the Caudata. There is no basis for determining whether or not this muscle was present in the labyrinthodonts. It appears to have split off from the common flexor mass as a separate muscle with only flexor action, possibly during the stage in which the flexor primordialis communis was developing an extensive fibular origin. It might be reasoned from this that it must have been present in the primitive types. This muscle may represent a case in which the insertion has shifted toward the postaxial side of the foot. It does arise from the fibula, in common with the other flexors. The ligamentous band on which it inserts, along with the origins of the contrahentes digitorum, might as-

sist in such a migration in that an entirely new attachment with the bone would not have to develop during the shift.

The plantaris profundus of Wilder or the flexor accessorius of Francis presents some difficulty. Francis divides it into a lateralis and a medialis on the basis of innervation, with the contrahentium longum running between the two divisions. Wilder states that it is divided into two masses by the latter muscle but does not give them separate names. In any case, both parts of the muscle have a similar action, that is, slight flexion of the tarsus. When the foot is in contact with the ground during propulsion these muscles then act as adductors, moving the foot toward the midline of the body. Both parts arise from the fibular shaft and lateral tarsals, inserting on the plantar aponeurosis.

The pronator profundus varies but little in its origin and insertion, running from the shaft of the fibula to the head of the tibia and the tibiale. Its fibers run in the same direction as those of the plantaris, both muscles having the same action.

The role of the flexor accessorius and of the pronator can be demonstrated in a negative fashion by transecting these muscles in the living animal. When this is done, the animal is no longer able to adduct the foot, making the retraction of this limb very ineffective. The flexors cannot operate properly as the propulsive stroke is now a sort of abduction rather than flexion. This would indicate the necessity of joint action on the part of the extensors and flexors located along the lateral border of the entire leg in a fashion which Morton believes is indicated by the *Thinopus* footprint. It appears evident that the arrangement of the musculature of the entire leg does not favor the view that the hind leg was at any time sprawled out at right angles to the body during locomotion.

It is obvious that the primitive tetrapod tarsus does not allow pronation, or for that matter supination, of the foot on the lower leg. In fact, as will be pointed out later, so-called pronation and supination can only occur in the mammalian foot. To name the above muscles pronators and

supinators by no means sets forth their true function.

That the interosseus cruris simply acts as an elastic ligament, as Francis believes, is rather doubtful. The fact that it is a muscle rather than a ligament indicates a more active role. Its function may be that of approximating the tibia and fibula, which undoubtedly have a tendency to separate during the propulsive stroke, because of the relative positions they are forced to assume. The interosseus cruris is also of importance in the weight transfer between the tibia and fibula in that it binds these bones together as a functional unit. The fibers run in the same direction as those of the flexor accessorius and pronator.

In *Necturus* there is a muscle named by Wilder the "flexor tibialis." It arises from the lateral condyle of the femur and inserts on the tibia and tibiale. It is not present in the other Caudata investigated and may simply represent a deep portion of the pronator that has separated as a distinct muscle. Morton (1935) has postulated the presence of a tibial and a fibular flexor as the primitive tetrapod condition. Unless these names are substituted for certain other differently named muscles, that is, flexor primordialialis communis, flexor accessorius, and caput longum contrahentium, it is not possible to confirm his conclusion after carefully examining the extrinsic flexors of the foot in the caudates in which this region was dissected, nor can any record be found in the literature of the presence of tibial and fibular flexors (properly so-called) in any caudate amphibian.

It appears more likely that the most primitive condition was a single, large flexor mass, the fibers of which arose mainly from the lateral condyle of the femur and inserted on the head of the tibia and the tarsus at various points, including the bases of the digits. Such a muscle-mass

would have had an extensive tendinous insertion. As this mass subdivided, the tendinous sheet seemingly became the plantar aponeurosis. This conclusion is supported by the common direction of the fibers of all the crural muscles except the contrahentium caput longum.

The Plantar Musculature

The intrinsic musculature of the pes is concerned with various movements of the toes. The flexores breves superficiales are subdivided into a number of slips for each toe. They arise from the plantar aponeurosis and insert on the metatarsals and proximal phalanges. The propulsion phase is carried out until all the toes have their dorsal surfaces turned plantarward in the order of their length. When the third and fourth toes, and finally the fourth alone, are the only portions of the foot in contact with the ground, the added length of the tendons of insertion (to the second most distal phalanges), plus the action of the interphalangeal muscles of these digits give the digits rigidity.

The contrahentes digitorum all arise from a ligamentous band in the region of tarsalia three and four. Hence, as Francis points out, the slips to the first and fifth digits act primarily as adductors, secondarily as flexors, while those of digits two, three, and four act as flexors only. They all insert on the heads of the proximal phalanges.

The flexores digitorum breves profundi are also flexors except for those on digit one and digit five where they are also adductors. That on digit five may be strongly developed with some fibers arising from the distal end of the fibula.

The intermetatarsales, arising and inserting on adjacent metatarsals at different levels, act as adductors of the digits. They function mainly during the recovery phase when the digits are drawn close together.

THE REPTILIAN TARSUS

The reptilian tarsus, in contrast to the amphibian, has evolved into many distinct morphological and functional types (Fig. 11). For the sake of more complete

integration, the locomotor methods of each group will be discussed along with the particular type of tarsus, as well as in the section on reptilian foot musculature.

THE ORIGIN OF THE PRIMITIVE REPTILIAN TARSUS

The primitive reptilian tarsus contained eight or nine bones. There are but two in the proximal row, the astragalus and the calcaneum, and they are relatively larger than any of the elements in the proximal row of the primitive amphibian tarsus. The origin of the astragalus has caused much speculation. Gegenbaur and Williston believed that it consists of a fused tibiale and intermedium, while Baur, Broom, Jaekel, Romer, Watson, and most other paleontologists are of the opinion that the astragalus is made up of the intermedium only. Schmalhausen (1908b) was one of the first to consider the astragalus as consisting of the intermedium and the fourth centrale. Dollo (1929) carried this point of view further by including the tibiale.

Recently Holmgren (1933) has reinvestigated the entire problem and has confirmed quite convincingly the belief that the astragalus of reptiles and mammals is the product of fusion of at least two and possibly three anlagen. If the ontogeny of the reptilian tarsus is considered in the light of de Beer's restatement of the Biogenetic Law (1940), the problem can be considered more intelligently in its proper perspective. According to this interpretation, ontogenetic events of the ancestor may be repeated in the descendant, but embryonic characters of the descendant do not represent those characters of the adult ancestor. The degree of resemblance between the embryonic tarsi of amphibians and reptiles and mammals is great enough to permit identification of homologous elements. While these anlagen remain separate in the adult amphibian, there is, of course, considerable fusion (and elimination) before the adult reptilian (and mammalian) stage is reached.

In connection with the present investigation it has not been considered necessary

to reinvestigate the ontogeny of the reptilian tarsus, since a survey of a fairly extensive literature shows that there is more or less general agreement as to the identification and disposition of the anlagen present, except in the case of the tibiale, the presence of which is still open to question.

As in the embryonic amphibian tarsus (Fig. 12,A), the anlagen of all the tarsals converge toward the fibula, with the intermedium and the fibulare making up the proximal row. In most cases the tibiale is conspicuous by its absence (Fig. 12,C,E), although Howes and Swinnerton (1901) and Rabl (1910) claim that there is a separate tibiale in *Sphenodon* (Fig. 12,D) as a very small concentration of cells at the base of the tibia that fuses very early with the centrale. The evidence, as presented, is not conclusive, although, in its favor, the centrale does extend under the tibia, suggesting the fusion of the tibiale and the centrale. The other case of a supposed separate tibiale is in the crocodilian foot (Fig. 12,F). Although the anlage identified by Rabl as the tibiale is in the position of the centrale, both Steiner (1934) and Holmgren (1933) present more convincing evidence of its presence. In all cases, the very close proximity of this element to the distal end of the tibia makes its existence open to question.

The intermedium is conspicuously present and is always located between the tibia and the fibula. Its relatively large size has suggested that the tibiale may be indistinguishably fused with it (Sewertzoff, 1908) for which there is apparently no real evidence pro or con. It is evident, however, that the centrale (there is a single centrale rudiment in most cases) fuses with the intermedium during ontogeny. Hence, it may be stated with con-

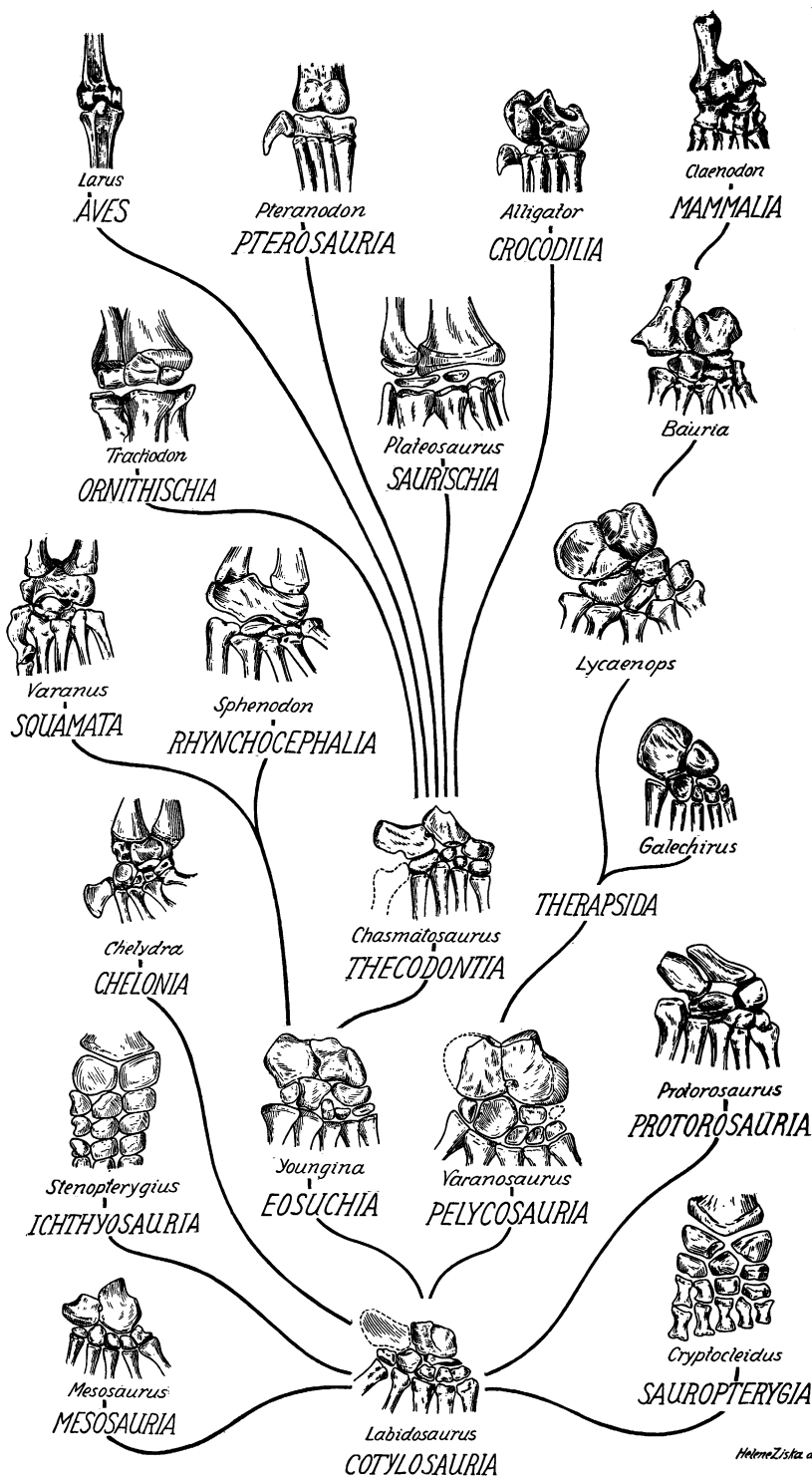


Fig. 11.—The phylogeny of the reptilian tarsus. Original drawings of specimens, with the exception of *Youngina* and *Chasmatosaurus* (modified after Broom), *Protorosaurus* (after Peyer), and *Pteranodon* (after Eaton and Williston).

siderable assurance that the astragalus is composed of the intermedium and one member of the centrale complex of Amphibia.

Sjögren (1940), investigating the development of the tarsus of *Chamaeleon*, has arrived at a novel conclusion. He found no evidence of the intermedium, but considered an anlage that formed near the distal end of the tibia to be the tibiale. This anlage then migrated into the position of the intermedium at a later stage. He

mammal *Claenodon*, Matthew (1937) has described the presence of a small, laterally compressed bone which he suggests may be the remains of the tibiale (Fig. 11), the astragalus being made up of the intermedium only. That this bone and the "accessorium" are the same thing must be considered as a distinct possibility.

There is no real indication of the loss of the tibiale in the labyrinthodonts. Broom's arrangement of types (1921) to support his theory, as pointed out earlier,

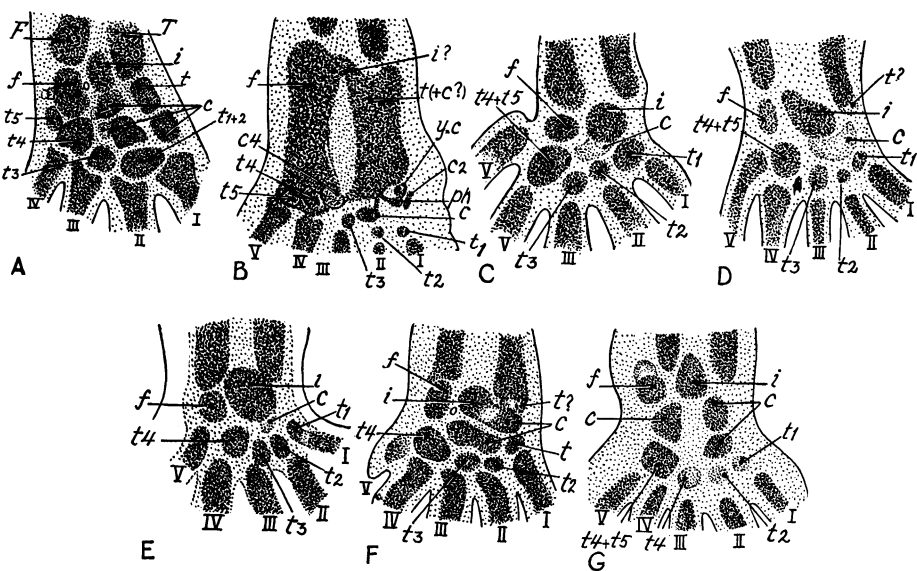


Fig. 12.—Embryonic stages of the tetrapod tarsus. The stage selected in each case shows the greatest number of anlagen present at any one time during ontogeny. A, *Hynobius* (after Schmalhausen); B, *Pelobates* (after Schmalhausen, Holmgren); C, *Chelonia* (after Rabl); D, *Sphenodon* (after Howes and Swinnerton, Rabl); E, *Tarentola* (*Ascalabotes*) (after Sewertzoff); F, *Crocodilus* (after Holmgren, Rabl, Steiner); G, *Mus* (after Schmalhausen, Holmgren).

also found that the fibulare and centrale fused at an early stage. Needless to say, it is very difficult to reconcile these conclusions with the other results.

Both Schmalhausen (1908b) and Holmgren (1933) are agreed that the mammalian astragalus (*Mus*) is made up of the intermedium and the centrale (Fig. 12,G). They consider a condensation at the distal end of the tibia to be a tibiale and that it forms the "accessorium" to which the prehallux is attached. In the Paleocene

would appear to be an illogical assemblage, although it supposedly demonstrates a progressive reduction in the size of this bone and a shift in its position, making it homologous with the mammalian navicular. As far as paleontological evidence is concerned, it must be concluded that the tibiale simply disappears in the Reptilia. Hartmann-Weinberg's attempt (1929) to distinguish all the primitive tarsal components except the tarsalia in the single pareiasaurian proximal tarsal element, according to the arrange-

ment of the spongiosa and compacta, is not convincing. Haughton and Boonstra (1930) also made sections of this element, but were unable to determine by this means which elements are included. The presence of three proximal tarsal elements in the cotylosaurs *Seymouria* (Fig. 13,A) and *Limnoscelis* may be explained by the fact that, in these forms, the tarsus is still on the way toward becoming truly reptilian. Its presence, or supposed presence, in a number of the secondarily aquatic reptiles may be considered as due to a secondary fragmentation of this region, or to a neotenic condition.

The position here taken is that the astragalus of reptiles and mammals is really

a compound bone phylogenetically, composed of the intermedium, a proximal centrale, and possibly the tibiale. This is based mainly on embryological evidence and on the lack of any really contradictory paleontological evidence. The constant position of the foramen for the perforating artery between the fibulare and the intermedium in the amphibians, and between the calcaneum and the astragalus in the reptiles, does represent paleontological evidence that the fibulare and the intermedium are present as the calcaneum and part of the astragalus, respectively. It is not evidence, however, in the case of the astragalus, that only the intermedium is present.

THE COTYLOSAURIAN TARSUS AND ITS FUNCTION

The cotylosaurian tarsus evolved in the Permian into a number of distinct types (Fig. 13). In fact, the extent of the alteration from the primitive condition found in *Seymouria* is probably the most extreme to be found in any single reptilian order.

THE SEYMOURIAMORPH TARSUS

In *Seymouria* (Fig. 13,A), a member of the most primitive cotylosaurian suborder, the Seymouriamorpha, the tarsus still possesses three proximal elements, an obvious holdover from the primitive tetrapod condition. These are the fibulare, intermedium, and tibiale (Watson, 1918; White, 1939). The tibiale is not reduced in size, nor does it show any tendency to migrate into the position of the navicular. On the other hand, there is a mesial centrale lying just distal to the tibiale, which is certainly homologous with the navicular of *Labidosaurus*. This is further evidence against Broom's theory (1921) that the navicular is simply the tibiale that has migrated distally. The exact number and the disposition of the unossified elements cannot be safely determined. It would appear reasonable to assume that more than the one centrale was present, particularly if the thesis that the astragalus is always composed of a centrale and the intermedium is believed correct.

The tibia and the fibula of *Seymouria* are of about the same length and their distal ends must have been extensively capped with cartilage in life. The three proximal tarsal elements are hence all on the same transverse level; with the intermedium articulating about equally with the tibia and fibula. According to White (*op. cit.*, p. 384) the proximomedial corner of the tibiale is relatively thickened dorsoventrally, foreshadowing the rounded tibial facet on the astragalus of pelycosaurs. This may be true, if it be admitted that the tibiale is included in the astragalus.

For the first time in tetrapod evolution, there may have been definite flexure between the crus and the tarsus, but the articular surfaces give no evidence of it, as they were finished in cartilage. The greatest flexure must still have been between the tarsalia and the metatarsals, and the mechanics of locomotion hence essentially the same as in the labyrinthodonts. The distal articular surface of the femur faces ventrally, indicating a permanently flexed knee-joint, while the proximal articular surface is terminal, allowing only horizontal movement.

THE CAPTORHINOMORPH TARSUS

Although the Captorhinomorpha are considered to be advanced cotylosaurs in several characters, the limbs are quite

primitive. The tarsus of *Limnoscelis* (Williston, 1911a) is almost identical with that of *Seymouria*, in that there are three separate proximal elements. The fibulare and the intermedium are, incidentally, the only ossified elements. As in *Seymouria*, the intermedium articulates about equally with the tibia and fibula, the latter two bones being of the same length. With the tibia extensively articulating with the intermedium, it was in a position to support a large share of the body weight directly, thus removing the necessity of a weight transference from the tibia to the fibula as

plete specimens by Case (1899, 1911) and Williston (1908). Complete preparation of Case's material (A.M.N.H. No. 4883) for the present study has resulted in a tarsus that does not resemble very closely any of the previous restorations. The fibula was mistaken for the tibia, thus giving the restorations a rather strange appearance. The fibula always articulates with both the astragalus and the calcaneum, but never with the tibia, as was supposed in this case.

The astragalus is well preserved and can be compared in some detail with the pely-

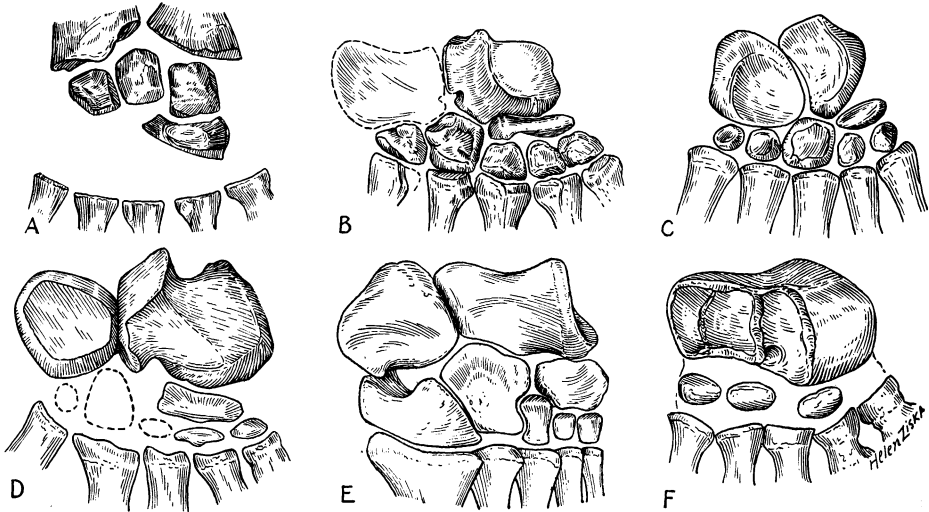


Fig. 13.—The cotylosaurian tarsus.

A, *Seymouria* (after White and specimen); B, *Labidosaurus* (from specimen); C, *Tuditanus* (from photographs); D, *Diadectes* (after Romer and specimen); E, *Nyctiphruretus*, plantar view (after Efremov); F, *Scutosaurus* (after specimen).

in *Trematops*. In support of this conclusion, the distal end of the tibia is relatively more expanded than in the labyrinthodonts.

The tarsus of the captorhinomorph *Labidosaurus* (Fig. 13,B) is the only cotylosaur tarsus known that might be considered as representative of the primitive definitive reptilian type, in which there are two distinct proximal elements, an astragalus, and a calcaneum. The diadectomorph tarsus, as will be pointed out, is clearly specialized. The tarsus of *Labidosaurus* has been described from two incom-

plete specimens by Case (1899, 1911) and Williston (1908). Complete preparation of Case's material (A.M.N.H. No. 4883) for the present study has resulted in a tarsus that does not resemble very closely any of the previous restorations. The fibula was mistaken for the tibia, thus giving the restorations a rather strange appearance. The fibula always articulates with both the astragalus and the calcaneum, but never with the tibia, as was supposed in this case.

The astragalus is well preserved and can be compared in some detail with the pely-

cosaur astragalus. It belongs without question to the left foot rather than to the right, as figured by Case (1911). This is undoubtedly the most primitive astragalus known and it is, therefore, of great interest. It has the L-shaped appearance of the pelycosaur astragalus, although the vertical arm, in particular, is relatively very much shorter than in the typical pelycosaurs. The tibial facet on the horizontal arm is not rounded as in the pelycosaurs, and it is located more on the lateral than the dorsal surface. The fibular facet is simply the proximal sur-

face of the vertical arm, that in turn is dorsoventrally compressed, in contrast to the condition in pelycosaurs in which the vertical arm is more oval in cross section. There is a decided notch on the medial border for the passage of the perforating artery.

The calcaneum is not preserved in this specimen, and is only represented by a fragment in Williston's specimen. From this, and the shape of the space it occupied, it seems evident that it must have resembled that of the pelycosaurs or eosuchians rather closely.

There is but a single centrale or navicular that is very much compressed proximodistally. Its proximal surface is slightly convex and fits into the slightly concave distal surface of the astragalus. The fragment considered by Case and Williston to be the centrale gives every appearance of being the distomedial corner of a part of the astragalus that broke off during preservation. There is apparently no sign of the navicular in Williston's specimen, unless it was not separated from the astragalus during preparation.

Tarsale four is the largest of the tarsalia and has a very characteristic square shape resembling that found in the pelycosaurs and the eosuchians. There are four other tarsalia, subequal in size.

The tarsus of *Labidosaurus* is ideally suited to be the ancestor of that found in either the pelycosaurs or the eosuchians or the more aberrant types. In the pelycosaurs the L-shaped astragalus was favored, while in the other groups it was suppressed. The only feature which might be considered as specialized, or rather pointing more in the direction of the pelycosaurs than the other groups, is the location of the tibial facet. Being slightly distal to the fibular facet, it automatically directed the foot forward as in the pelycosaurs. (Cf. Fig. 21, B.) There is no indication, however, that the ankle-joint was crurotarsal in *Labidosaurus* as in the pelycosaurs. The tibial facet being essentially a plane surface, although directed dorsomedially as well as proximally, it allowed very little movement between the tibia and the astragalus. Hence, there is reason to be-

lieve that the functional ankle-joint was still in its old location between the tarsalia and the metatarsals.

The affinities of *Tuditanus* Cope (*Eosaurus* Williston) have long been a difficult problem (Romer, 1930). Romer (1925) has pointed out the reasons for considering it a lepospondyl, although later (1933) he concluded it was a cotylosaur. Although reptiles are known having three proximal tarsal elements, no primitive amphibians are known with but two. Furthermore, *Tuditanus* has the typical reptilian phalangeal formula. The tarsus is not distinctive enough to be definitely cotylosaurian (Fig. 13, C), although it does definitely suggest one of the primitive reptilian orders. There are six distal tarsal elements, with two situated at the base of the fifth metatarsal in the fossil. The tarsus has been restored with a single element at the head of each metatarsal, and an elongated bone, as the navicular, which was displaced in the original specimen. No known reptile, fossil or recent, has two tarsalia at the head of any of the metatarsals, excluding a pretarsale. On the other hand, the largest tarsale is usually the fourth, here it is considered as the third, and, furthermore, the navicular as restored, only lies proximal to the inner two tarsalia. That the tarsus of *Tuditanus* belongs to a primitive reptile there is little question, more than that is not known.

THE DIADECTOMORPH TARSUS

The tarsus of the Diadectomorpha is specialized for supporting a fairly large and heavy-bodied animal, and it is distinctive for each of the three families in this suborder.

The diadectid tarsus (Fig. 13, D) has been described fully by Romer and Byrne (1931) for *Diadectes* and for both *Diadectes* and *Diasparactus* on incomplete material by Case (1911) and by Williston (1913). The two proximal elements are relatively much larger than those of *Labidosaurus* and are considerably thickened dorsoventrally. All the articular surfaces were finished in cartilage and it is not possible to determine their exact extent, or shape.

The astragalus at hand is the same speci-

men described by Case, although, as Romer and Byrne have pointed out, it belongs to the left rather than the right side. The fibular facet is a plane surface facing proximally and somewhat dorsally. The tibial facet, which is separated by a notch from the fibular, is quite convex and faces more medially than dorsally or proximally. The orientation of these facets indicates, as Romer and Byrne have stated, that the astragalus was set at an angle to the plane of the crus, although by no means approaching a right angle.

The calcaneum is a circular nodule of bone, and the fibular and astragalar articular surfaces are not distinct and must have been finished in cartilage. According to Romer and Byrne, there are three ossified distal tarsal elements, the navicular and the first and second tarsalia. It may be supposed that there were three more cartilaginous tarsalia.

The astragalus and calcaneum completely dominate the tarsus, both structurally and functionally. Romer and Byrne are of the opinion that the astragalus and calcaneum were set at an angle of about 45 degrees with the crus, which would appear to be correct. Furthermore, they are of the opinion that a considerable amount of movement was possible between the crus and tarsus and that the rounded tibial facet on the astragalus was of importance in permitting the tibia to rotate on the astragalus as propulsion progressed.

Although it must be admitted that the rounded tibial facet is undoubtedly associated with the torsion and resultant stress produced on the inner side of the foot, and that some movement of the tibia on the astragalus occurred, there is no indication from this material that the crurotarsal joint was the main functional ankle-joint. The possibility must also be considered that there was a considerable degree of flexure between the proximal and more distal tarsal elements, forming a mesotarsal joint as in the pareiasaurs. This view is supported by the extensive rounded articular surface on the distal border of the astragalus and also on the calcaneum. These surfaces might very well have fitted into a transversely elongated socket

formed largely by ligaments and connective tissue, after the manner of the mesotarsal joint in the typical lizards.

With the proximal tarsals making an angle of 45 degrees with the crus, the plantar pad, which was undoubtedly present, may not have covered these elements completely proximally, thus giving them a certain amount of independence over the remainder of the tarsus. Hence, the flexure of the crus on the foot may have been distributed between the crurotarsal and the intertarsal joints, with the greater amount of movement at the latter. It seems quite impossible, from the nature of the articular surfaces, that all the movement could have occurred at the crurotarsal joint.

Romer and Byrne have further pointed out that the forwardly directed position of the foot on the leg caused a shortening of the preaxial border of the tarsus, mainly by the loss or shifting of the tibiale and a raising of the postaxial border from the ground, or, in other words, a tilting of the tarsus from the outer to the inner side. As pointed out in the discussion of the *Seymouria* tarsus, it seems more likely that the first step in the shortening of the tarsus occurred with the fibulare, intermedium, and tibiale taking up positions on the same transverse level, and the fibula becoming the same length as the tibia. This was probably initiated through a change in the centrale region, specifically through a reduction in size of the proximal centrale or a fusion of some or all of the other centralia to form the navicular. A comparison of the *Seymouria* and *Labidosaurus* tarsi would seem to indicate that there has been no shortening of the inner border of the tarsus through the loss of the tibiale, as the astragalus of *Labidosaurus* takes up relatively about the same amount of space as the intermedium and tibiale of *Seymouria*. The shortening effect was produced in the crus by the rotating and tilting of the tibia in the primitive tetrapods. The necessity for this effect was eliminated by the various groups of reptiles in different ways, as will be pointed out; in the case of pelycosaurs, for instance, by the rounded tibial facet on the

astragalus and the more distal articulation of the tibia than the fibula with the crus.

THE PROCOLOPHONID TARSUS

The complete procolophonid tarsus is known for the genera *Nyctiphruretus* (Efremov, 1940), *Procolophon* (Broom, 1903, 1921; Watson, 1920), and imperfectly for *Telerpeton* (von Huene, 1920a) and *Anomiodon* (von Huene, 1939).

In the case of *Nyctiphruretus* (Fig. 13,E) the tarsus is very similar to that of *Labidosaurus*, with one important exception, namely, that although only the plantar surface of the foot is figured, it appears quite certain that the tibial facet is restricted to the proximal border of the rectangular astragalus. The calcaneum is more or less round and probably dorsoventrally compressed. The navicular lies proximal to the first and second tarsalia and contacts the proximomedial portion of the third tarsale, suggesting the condition in the restored tarsus of *Tuditanus*. The fourth tarsale is, as usual, the largest of this series and, as in *Labidosaurus*, articulates both with the astragalus and calcaneum. The fifth tarsale is relatively larger than in *Labidosaurus*.

It is evident that there was no appreciable movement at the crurotarsal joint, and Efremov has stated that the functional tarsal joint was mesotarsal. He considered the reductions in the size of the first three tarsalia and the "beginning of growth" of the fourth and fifth tarsalia as evidence of increased flexibility within the tarsus and the first step toward the formation of a mesotarsal joint. In every case, however, the development of the mesotarsal joint, as will be pointed out, was associated with a reduction in the size and number of the tarsal elements distal to the astragalus and the calcaneum and a functional union of these elements with the metatarsals. There is no appreciable modification of this region from the condition found in *Labidosaurus*, and hence it would appear more logical to consider the functional joint as tarsometatarsal, although there undoubtedly was some movement at the mesotarsal joint and possibly some at the crurotarsal. If this were the

case, and the tibial and fibular facets on the astragalus and calcaneum were on the same level, the foot could only be forwardly directed through a rotation of the tibia in front of the fibula as the femur moved backward. The shaft of the femur is twisted somewhat as in the lizards, indicating that the knee was held fairly close to the ground. The position of the foot throughout propulsion cannot be accurately determined; it may have been twisted laterally to some extent.

It is not possible to make out the detailed morphology of the *Procolophon* tarsus from the illustrations of Broom and Watson, particularly with regard to the articular facets on the astragalus and calcaneum. The astragalus has a rather distinctive shape, which might have been derived from the type found in *Diadectes*. It is dorsoventrally compressed and somewhat constricted transversely in the region of the notch for the perforating artery. The tibial articular surface was apparently restricted to the proximal border with no extension on to the dorsal surface. The fibular facet is of the same nature and is not tilted forward as in *Diadectes*. The calcaneum is also dorsoventrally flattened and, according to Watson, articulates directly with the fifth metatarsal and the entire lateral border of the fourth tarsale, the fifth tarsale being absent. Watson considers the loss of the navicular to be an advance in the structure of *Procolophon*. It might better be considered as a specialization, as both the eosuchian and pelycosaurian tarsi possess this element.

According to von Huene, the astragalus and the calcaneum of *Telerpeton* are fused. This element bears a marked resemblance to the transversely elongated astragalus of *Procolophon* and, since it is the only preserved element in the tarsus, as figured, the possibility of a separate calcaneum must be considered.

The articulation between the crus and the tarsus must have been a simple hinge-joint capable of only a limited range of movement. It would appear that the principal plane of flexure was at the primitive location between the tarsalia and the metatarsals. With the lack of a rounded

tibial facet on the astragalus, the method of locomotion must have been very much as in the primitive tetrapods, with the tibia forced into a diagonal position as propulsion progressed. The head of the femur is terminal and the distal articular surface is directed downward, inferring a permanently flexed knee-joint.

THE PAREIASAURIAN TARSUS

The structure and function of the pareiasaurian tarsus (Fig. 13,F) has been studied in detail by Haughton and Boonstra (1930). It is the most specialized of the cotylosaurian tarsi, having the astragalus and calcaneum fused into a single, massive element and the more distal tarsals reduced to from three to five poorly ossified nodules. The tarsi of the Russian form *Scutosaurus* (A.M.N.H. No. 5148) and the South African *Embrithosaurus* (A.M.N.H. No. 2450) have been available for this study.

The astragalocalcaneum is essentially the same in both the South African and the Russian pareiasaurs. Viewed from in front, it is a rectangular mass of bone with the lateral half of the dorsal face flattened. The tibial facet is but poorly ossified in the South African forms and must have been capped with a rather thick layer of cartilage to articulate with the tibia at a reasonable angle. In *Scutosaurus*, however, this articular surface is better ossified and is convex. In both, it extends on to the dorsal surface, implying a considerable range of movement. The fibular facet is restricted to the proximal surface and is slightly concave. Haughton and Boonstra have pointed out that the articulation between the fibula and the astragalocalcaneum was a very extensive and intimate one, allowing no appreciable movement between them.

The above-mentioned authors stress the following points: The distal articular surface on the femur is directed more ventrally than distally and the crus could only have moved through an arc of 45 degrees. Furthermore, the non-functional articulation between the fibula and the proximal element must have prevented any flexure at the crurotarsal joint.

Hence, they conclude, and correctly, that the functional joint must have been mesotarsal in position.

They point out that the astragalocalcaneum must have been tilted forward in life, and being thus orientated, it could only have borne the weight of the body through the development of some sort of a cartilaginous heel-process along the distoventral border, thus giving the tilted elements a firm base. The same situation is present in the tarsus of *Diadectes*, with the astragalus and calcaneum inclined at about the same angle. It would appear unnecessary to postulate the presence of a cartilaginous heel when it is realized that the proximal element was well imbedded in the extrinsic flexor musculature and, undoubtedly, in a very thick plantar pad. If such a process were present, it would be a very unusual structure indeed.

As Haughton and Boonstra point out, the femur is of great interest, for the pareiasaurs are the most primitive tetrapods known in which the head of the femur is oriented at an angle with the long axis of the shaft, amounting to about 30 degrees. Hence, for the first time, the femur moved backward during propulsion in a more vertical plane and not the horizontal plane of the other cotylosaurs with a terminal femoral head. Furthermore, during the recovery phase the femur could swing forward in almost the same plane. The more detailed implications of the medially directed femoral head will be considered in the discussion of the locomotion of the alligator.

Haughton and Boonstra consider the tibia to be the weight bearing element of the pareiasaurian limb, and the fibula to be the regulator of the rotary movements of the foot. They do not elaborate further. It is certainly true that, as in the primitive tetrapods, the tibia makes an extensive articulation with the femur, while the fibula merely articulates with a small and more laterally directed facet on the outer condyle of the femur. The tibia is thus situated to bear by far the greater proportion of the body weight since, in addition, in the cotylosaurs it obtained for

the first time an articulation with the tarsus, which permitted weight distribution to the greater part of the foot. The fibula, however, still must have borne some of the weight, probably through a transference from the tibia to the fibula, which as pointed out earlier, must have been the case in the labyrinthodonts. The fibula must, furthermore, have had a steadying influence on the entire leg, in that its extensive and intimate articulation with the astragalocalcaneum would tend to prevent any displacement of the latter in the verti-

cal plane, and the fibula and tibia together offered a double support on which the femur could rotate, which was further strengthened by the fusion of the proximal tarsal elements. That the fibulotarsal articulation limited the abduction and adduction of the foot in the pareiasaurs may be accepted as true, although there must have been some rotary motion at the femorofibular joint. The somewhat medially directed head undoubtedly compensated for the inability of the tibia to assume the diagonal position during propulsion.

THE STRUCTURAL AND FUNCTIONAL DERIVATIVES OF THE UNSPECIALIZED COTYLOSAURIAN TARSI

The cotylosaurian tarsus, of a sort resembling that of *Labidosaurus*, gave rise roughly to three types of tarsi; ignoring, of course, the numerous variations of each of these types. They may be briefly listed as follows:

(1) The type found in the Mesosauria, Ichthyosauria, Protorosauria, and Sauropterygia—a modification of the captorhinomorph pattern for an aquatic habitat—to a greater or lesser degree depending on the order, the protorosaurian tarsus being the most conservative, as this group is mostly terrestrial.

(2) The type found in the Chelonians and Eosuchia and the reptilian orders considered to be derived from the latter. All the specializations in the tarsus in this group are built around one central theme, the development of a mesotarsal or intertarsal joint. Although the pareiasaurian tarsus might be included in this category, it is more convenient and logical to include it in the foregoing discussion of the cotylosaurian tarsus.

(3) The type found in the Pelycosauria, Therapsida, and finally culminating in the Mammalia. This group specialized in the development of a crurotarsal joint.

TYPE I

This rather heterogeneous assemblage of orders has, with few exceptions, aquatic tendencies and the tarsus has become modified from the *Labidosaurus* pattern with the usual end result that it simulates

a paddle. There is a tendency toward the convergence of the tarsal elements to simple rectangular or circular nodules and an increase in length, or multiplication in the number of phalanges.

The least modified tarsus within this group is that of the Mesosauria (Fig. 11). That of *Mesosaurus* resembles very closely the tarsus of *Procolophon*, except that the former has retained a fifth tarsale. Both agree in the loss of the centrale and the general configuration of the astragalus. The astragalus also bears a resemblance to that of *Labidosaurus* and to the L-shaped astragalus of pelycosaurs. The tibial facet is decidedly more distal than the fibular but is not rounded as in the pelycosaurs. The fibular facets on the astragalus and calcaneum are also plane surfaces, and there is no indication of extensive movement at the crurotarsal joint. There was undoubtedly movement between the tarsalia and the metatarsals, but, with the foot functioning as a paddle, the greatest movement must have been distal to the metatarsals. In swimming, the tarsal region, in fact most of the foot, must have been held rather rigid during the propulsion phase. Although the head on the femur is terminal, the foot was forwardly directed since the tibia articulated with the foot at a more distal level than the fibula.

The tarsus of the Ichthyosauria (Fig. 11) requires little comment. The tarsus was clearly not an independent functional unit, but rather the entire limb must be

considered as such. There was undoubtedly some movement between the phalanges, but little in the tarsal region.

The tarsus of the *Protorosauria* (Fig. 11) along with that of the *Mesosauria*, underwent but little modification from the captorhinomorph type. That of the terrestrial form *Araucoscelis* is, as Williston (1914) pointed out, unusual in a number of respects. The astragalus is a cube of bone with a flat tibial facet. The calcaneum is dorsoventrally compressed and of unusual shape. Williston refers to a lateral calcaneal process as a heel and point of insertion for the "Achilles tendon," which cannot be the case, for, as will be pointed out, the true tuber calcanei first appeared in the thecodonts and therapsids. From the structure of the proximal tarsals, it is evident that the ankle-joint could not have been crurotarsal but tarsometatarsal. The femoral head is terminal and the tarsus has none of the specialization of the lizard tarsus, hence there is no reason for assuming that the feet were oriented at right angles to the body during propulsion as Williston has done in his restoration (1914, p. 402).

The tarsus of *Protorosaurus*, as figured, is likewise unusual (Peyer, 1937). The astragalus and calcaneum are apparently dorsoventrally compressed and of unusual shape. There was but slight movement at the crurotarsal joint and again most of the action must have occurred at the tarsometatarsal joint. As this form was at least partially aquatic, movement in the tarsus was undoubtedly restricted.

The tarsus of the *Sauropterygia* is different for almost each suborder. That of the terrestrial form *Tanystropheus*, is poorly ossified. The astragalus and calcaneum are kidney-shaped elements, dorsoventrally compressed, and were probably surrounded by cartilage in life. The other diagnostic features suggest that the foot was forwardly directed during locomotion and that the functional ankle may have been partly crurotarsal, partly mesotarsal. The other members of this order were exclusively aquatic. In the nothosaurs and placodonts the tarsus was at least partly ossified, the bony portion consisting of

simple nodules. In the plesiosaurs (Fig. 11) the tarsus is completely ossified and must have functioned very much as in the ichthyosaurs. There was obviously no localized plane of flexion, but a slight amount of flexion between each row of elements, producing the gradual curve necessary for sculling movements.

TYPE II

THE CHELONIAN TARSUS

The chelonian tarsus (Fig. 11) is subject to considerable variation, principally due to the fusion of the proximal elements. That of *Chelydra* (Fig. 11) is of particular interest in that it has retained the primitive pattern both with regard to the number of elements and their relative disposition. The calcaneum is relatively much reduced in size, while the astragalus is relatively larger than in the *Cotylosauria*. There is a separate centrale in the *Chelydridae* and in most of the *pleurodires* (Zittel, 1932). That the tarsus might readily be derived from the *Labidosaurus* type is self-evident. Furthermore, the chelonian tarsus gives some clue as to the probable mode of origin of the mesotarsal joint. The first step was undoubtedly a flattening of the tibial and fibular articular surfaces on the astragalus and calcaneum, resulting in a total loss of movement at the crurotarsal joint. This was followed by a tendency toward very close articulation and finally fusion between the astragalus and calcaneum and a functional union of this proximal element with the crus. The latter was probably favored as a means of overcoming the disrupting influence of the torsion produced in the proximal tarsal region during propulsion. That this was the case, is supported by the fact that the completely marine cryptodires secondarily lost the localized plane of flexure in the tarsus. In this type, the tarsus is made up of a number of rounded nodules of bone (*Archelon*) with no indication of a tendency toward fusion of the astragalus and calcaneum or fixation of the crurotarsal joint.

The tarsalia are four in number, with

the fourth exceeding the others in size as in the cotylosaurs. There is no fifth tarsale in the adult nor any indication of it embryologically (Fig. 12,C); it may or may not be indistinguishably fused with the fourth throughout ontogeny.

Both the tibial and fibular facets on the astragalus, and the fibular on the calcaneum, are somewhat concave and are restricted entirely to the proximal surfaces. There is therefore no possibility of movement at the crurotarsal joint. By sectioning the hind-limb in the transverse plane, with the foot fixed in a flexed position, it can be demonstrated quite conclusively that the functional joint is mesotarsal in position. In the turtles the fusion of the proximal elements has occurred in many types, such as *Testudo*, and where it has not, as in *Chelydra*, the astragalus, calcaneum, and centrale are very intimately associated with no possibility of movement between them.

The manner in which the limbs operate, in spite of the presence of the shell, is probably, as Romer has pointed out (1933, p. 134), as close to the primitive tetrapod method of locomotion as can be found among living Reptilia. The femoral head is very well developed and approaches the perfection of the mammalian condition, even to the presence of a neck between the head and the femoral shaft. The orientation of the head relative to the shaft is, however, quite unique, for it is not medially but dorsally directed. The articular portion, however, has its center of curvature pointing in a proximodorsal direction and the acetabulum is correspondingly directed ventrolaterally.

Functionally, therefore, the head may be considered as terminal, for the movement of the femur is entirely restricted to the horizontal plane. The well-differentiated head and the orientation of the acetabulum may be looked upon as specializations associated with the restrictions of the shell and the fact that it prevents any marked movement in the vertical plane.

With the movement of the femur restricted largely to the horizontal plane, and the proximal tarsal elements at least functionally united, it is impossible for the tar-

sus to be forwardly directed during propulsion. This difficulty is partly overcome by the fact that the metatarsals are forwardly directed and are hence orientated at an angle of about 60 degrees to the long axis of the tarsus and crus. The tarsus is narrower on the preaxial side than the postaxial, mainly because the first tarsale is compressed proximodistally, while the fourth tarsale is cubical in shape. This condition further aids the metatarsals, particularly one and two, in orienting themselves in a forwardly directed position.

THE EOSUCHIAN TARSUS AND ITS DERIVATIVES

The captorhinomorph tarsus is without question at least the structural ancestor of the eosuchian tarsus; the number of elements, relative disposition, and many of the morphological features being essentially the same. The tarsal pattern is known in a number of eosuchians, specifically, *Youngina* (Fig. 14,A), *Palaeagama* (Broom, 1926), *Howesia* (Broom, 1906a) (Fig. 14,B), and *Saurosternum*, and, except for minor variation, the pattern is identical in all of them.

The astragalus of *Youngina* differs from that of *Labidosaurus* in lacking a well-differentiated tibial facet. This articular surface is apparently not rounded (Broom, 1924), but is located as a shallow concavity on the proximodorsal surface. It is entirely possible that its location is a heritage character, held over from the captorhinomorph position. The fibular facet on both the astragalus and calcaneum is restricted to the proximal borders. The calcaneum is dorsoventrally compressed, but, according to Broom, the medial portion is somewhat thickened for the fibular facet and the articulation with the astragalus. The primitive nature of the *Youngina* tarsus is further attested by the fact that the fifth metatarsal is not hooked, although it is hooked in all other eosuchians known. The tibial facet on the astragalus of the other known eosuchians is confined to the proximomedial border with no overlapping on the dorsal

surface. The nature of the articular surfaces at this point would seem to indicate greatly restricted movement in a dorso-plantar direction, if indeed, there was any movement at all. The principal plane of flexure must have been tarsometatarsal in position.

The femur is well preserved in *Palaeagama*, and although the head is terminal, the shaft has a very slight s-curve, suggestive of the condition found in the crocodiles

would restrict considerably the ability of the tibia to assume the diagonal position (cf. discussion of flexion in *Trematops* tarsus). It is evident, however, that the tibial facet is still somewhat more distal than the fibular. Whether this slight difference in level was great enough to permit the foot to remain forwardly directed throughout propulsion is impossible to determine. The nature of the femoral head plus the lack of a rounded tibial facet

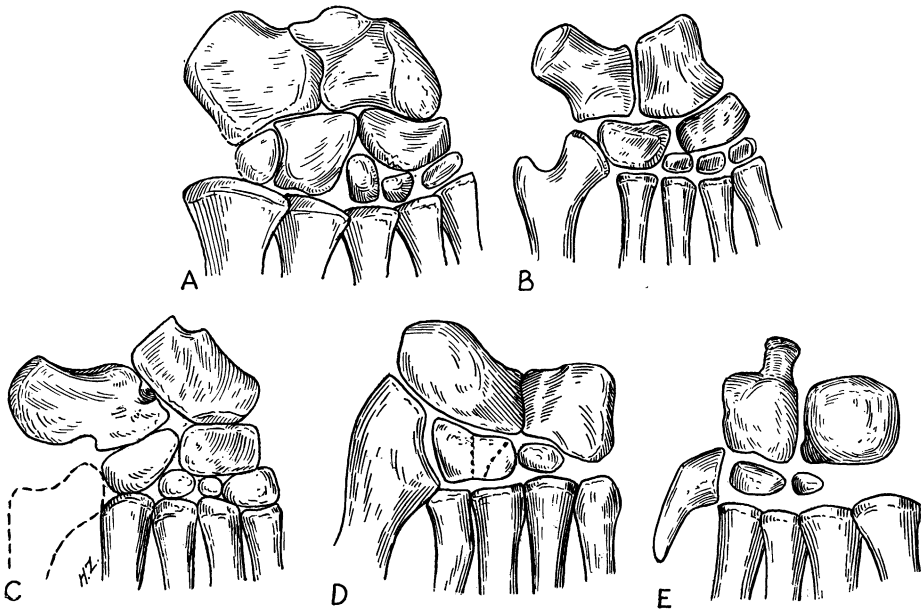


Fig. 14.—The eosaurian tarsus. A, *Youngina*, plantar view (after Broom); B, *Howesia* (after Broom).

The thecodont tarsus. C, *Chasmatosaurus* (modified after Broom); D, *Euparkeria* (from photograph, after Broom); E, *Aetosaurs* (after von Huene).

and lizards. In spite of the slight curve, the head is not directed medially to any appreciable degree, and the femur must have had its movement during propulsion largely confined to the horizontal plane. This being the case, and with the tibia and fibula articulating with the tarsus on the same horizontal plane, it is very difficult to see how the foot could have been forwardly directed to the same extent as it has been in all the previously discussed terrestrial tetrapod groups. The lack of movement between the proximal tarsals

on the astragalus are evidence for believing that the hind feet may have been forced into a moderate outward position as propulsion progressed.

This is a rather crucial point in the evolution of this type of tarsus, for in all the orders derived from the eosaurs the tarsus had a functional mesotarsal joint. The functional factors favoring its appearance are difficult to determine. This much may be said: all the more advanced tetrapods arising from the cotylosaur stock tended to localize the functional

ankle-joint proximal to its primitive position between the tarsalia and the metatarsals. This migration resulted in producing a highly mobile and complex joint by the fusion or very close articulation of the elements on one or both sides of the joint, as pointed out in the discussion under the chelonian tarsus. By this means, complicated joint surfaces were perfected, definitely restricting movement in one particular direction (excepting in the mammalian foot), and, furthermore, in producing much greater stability at the joint. Such a process was never favored with the joint in its primitive location, for the obvious reason that fusion of the tarsalia or the metatarsals would greatly hinder locomotion. The development of a mesotarsal joint in one group and the development of a crurotarsal joint in another group may be looked upon as simply two different ways of producing the same general result, a consolidated tarsus acting at right angles to the crus and giving support to a diarthrodial joint.

The consolidation of the proximal portion of the tarsus was accomplished in two ways in the eosuchian descendants, either by fusion or very intimate articulation of the astragalus and calcaneum side by side in the same positions they assumed in the primitive tarsus, or, in one group, the Crocodilia, by a rather complicated interlocking that still permits movement between them. The latter simulates somewhat in form and function the superposition of the astragalus upon the calcaneum in the mammalian tarsus.

THE RHYNCHOCEPHALIAN AND LACERTILIAN TARSUS

The rhynchocephalians and the lacertilian are considered to be directly descended from the eosuchians, and this conclusion is borne out by the tarsus. The tarsi of the other orders all show specializations that were acquired first in the thecodonts, as will be pointed out shortly.

The Upper Jurassic rhynchocephalian *Homaeosaurus* (Lortet, 1892; Broili, 1925) has a tarsus resembling that of *Sphenodon* (Fig. 15,A). The astragalus and calcaneum are very intimately articulated,

although not coössified. The distal tarsalia are much reduced in size and there is no evidence of a separate centrale. The functional ankle-joint was intertarsal. It seems clear that the intertarsal joint was preceded by the loss of the centrale as a separate element and a reduction in the number and the size of the tarsalia. The fact that there is but one distal element in the tarsus that articulates with the astragalocalcaneum is an expression of the consolidation necessary to form a diarthrodial joint. The tarsus of *Homaeosaurus* is about as close to an intermediate condition as can be found between the eosuchian on the one hand and the rhynchocephalian and lacertilian tarsus on the other.

The tarsus of the Upper Triassic rhynchocephalian *Stenaulorhynchus* (von Huene, 1938) has, according to this author, a separate tibiale. That such is the case is again extremely unlikely. It would appear more reasonable to consider this element as the astragalus, and the extra element on the lateral side as a persistent fifth tarsale, although the presence of a hooked fifth metatarsal and a fifth tarsale in the same tarsus is unique. If this assumption is correct, the tarsal pattern is exactly like that found in *Youngina* and the joint must have been tarsometatarsal. Furthermore, there is then reason to believe that the fifth metatarsal became hooked before the fifth tarsale was lost, supporting Goodrich's contention (1916) that the hamate process was not produced by the fusion of the tarsale and the metatarsal.

The rhynchocephalian and the lacertilian tarsus may be characterized as consisting of an astragalocalcaneum that is dorsoventrally compressed, and extended medially and laterally beyond the tibia and fibula to a slight extent. Its proximal border has two shallow concave facets for articulation with the tibia and fibula. The crurotarsal joint is rendered completely immobile by ligaments that connect the crural bones with the proximal element very snugly at every point. There is a particularly strong system of ligaments running from the anterior face of the very distal portion of the tibia to the lateral face of the astragalar portion of the proximal tarsal element.

This branching of the ligamentous fibers indicates relatively greater stress in this region than in any other.

The detailed morphology of the astragalocalcaneum is somewhat different in *Sphenodon* (Fig. 15,B) and the lizards. In the former, the distal border of the proximal tarsal element has a slightly concave articular surface that fits over the somewhat convex proximal surface of the fourth tarsale. The second and third tarsalia and metatarsal five articulate with the dorsal surface of the astragalocalcaneum. Hence, the intertarsal joint is located laterally between the distal border of the astragalocalcaneum and centrale four, while medially it is located between

obviously very specialized tarsus such as in the geckos, the distal surface of the astragalocalcaneum possesses two rather prominent grooves, with the elevations between the grooves rounded. The groove between the medial and lateral elevations runs diagonally, or proximomedially, to the center of the anterior surface. The lateral wall of this groove is relatively high, forming a kind of lip that projects anteriorly. The groove between the central and medial elevations does not extend on to the anterior face, and its axis is directed anteroposteriorly. The distal portion of the tarsus is still more reduced; the two remaining elements are considered to be the tarsale three and the tarsale

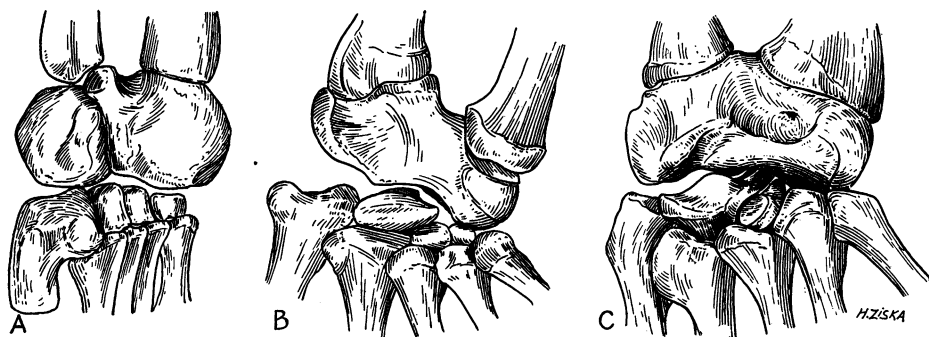


Fig. 15.—The rhynchocephalian tarsus. A, *Homaeosaurus* (after Broili, Lortet); B, *Sphenodon* (from specimen).

The saurian tarsus. C, *Iguana* (from specimen).

the dorsal surface of the astragalocalcaneum and the more distal elements. This arrangement tilts the astragalocalcaneum at an angle of about 40 degrees with the horizontal plane of the digits, with the result that the crural portion of the leg, particularly when the femur is at a right angle to the body axis, is tilted forward at least 45 degrees from the vertical plane. This condition undoubtedly arose along with the twisting of the femoral shaft, the distal portion having been rotated clockwise (or the proximal counter-clockwise), in the case of the right femur, about 50 degrees.

In the iguanids (Fig. 15,C) and other members of the Kionocrania, excepting an

four (by some four plus five). It is now generally agreed that the hooked portion of metatarsal five does not include tarsale five. Tarsale four is the only member of the distal tarsalia that forms a true joint with the astragalocalcaneum. Its proximal surface possesses a groove running in a diagonal direction, dorsomedial to ventrolateral. Into this groove fits the central elevation of the proximal element, thus forming a tongue-and-groove joint. Because of the diagonal direction of the elevations and the groove, the crus is directed medially in relation to the long axis of the leg. The nature of this articulation plus the twisting in the femur accounts in a large part for the characteristic pose of

the hind-limbs of the saurians, with the knee close to the ground and the long axis of the foot at an angle with the long axis of the body.

While all the metatarsals but the first articulate with the dorsal surfaces of the two tarsalia, the first metatarsal articulates directly with the dorsal surface of the astragalocalcaneum. A meniscus is present between metatarsal one and the astragalocalcaneum, where, in the primitive types, the torsion was the greatest. It is not extensively developed and is embedded in the ligamentous capsule that arises from the anterolateral surface of the astragalocalcaneum and covers the base of the first metatarsal. It acts as a sort of shock-absorber and creates a true articular surface between these elements.

In the varanids the saddle-joint between the astragalocalcaneum and tarsale four is modified into more of a concavoconvex articulation, with considerably restricted movement. In *Varanus komodoensis* the foot is permanently flexed on the crus, not only because all the metatarsals articulate with the anterior surface of the tarsalia but also because of the relative immobility of the intertarsal joint.

The transverse tarsal arch, so characteristic of the mammalian foot, is present to a slight degree in the saurian and the rhynchocephalian foot. The bases of the first three metatarsals are broader dorsally than ventrally, resulting in an arch when they are side by side in their natural positions. The origin of a transverse arch cannot be attributed to the effect of the transversely applied stresses in the primitive tetrapod foot, as Morton believes, for reasons previously stated. The fact that it is associated with the two types of diarthrodial ankle-joint suggests that it has developed along with, or as a result of, the tarsal consolidation in these types but in different ways.

Metatarsal five, having no direct contact with the tarsus has, however, a large, somewhat circular flange extending under metatarsal four, which articulates with tarsale four, and through which it receives its share of the body weight. Goodrich (1916) is of the opinion that while the

hooked fifth metatarsal may be of importance in the classification of the reptilia, it is not associated with any particular type of locomotion. The hook is present in the Chelonion and the Crocodilia, and the mesotarsal joint is differently constructed in each.

The characteristic manner in which the hind-limbs move during the locomotion of *Sphenodon* and the typical lizards is mainly due to the structure of the femur. In *Sphenodon* and all the saurians examined, the transverse axis of the femoral head is essentially parallel to the ground throughout most of the propulsive stroke. As pointed out earlier for *Sphenodon*, however, the distal portion of the femur is twisted around the long axis of the shaft, from 40 to 50 degrees in a clockwise direction in the case of the right femur. The articular surface for the tibia is thus directed ventrocaudally, forcing the crus to be likewise ventrocaudally directed. This situation, as pointed out above, accounts for the fact that in many lizards the knees almost touch the ground during the propulsive stroke.

Besides the twisting in the femoral shaft, the head is directed about 30 degrees away from the long axis of the shaft, medially and in the horizontal plane. With the femur moving in essentially the horizontal plane, this curvature has very little functional effect, except at the beginning of propulsion when it enables the shaft almost to parallel the long axis of the body.

The structure of the tarsus and the equal length of the tibia and fibula, however, as has been pointed out, do not permit the foot to be forwardly directed unless the crus is forwardly directed at the same time, as at the beginning of propulsion. Hence, as propulsion progresses, the foot is forced to assume a position at right angles to the long axis of the body. The position of the foot at the beginning of propulsion is subject to much variation. By permitting *Anolis* to walk over a rough, blackened surface that has been covered with a thin film of white powder it can be shown that, although the foot may be almost forwardly directed at the beginning of locomotion, it is rotated into the right-angled position

as the femur rotates backward. The body, as is the case in the caudates, is raised from the ground during locomotion, although the relatively very long tail is dragged. Hence, during propulsion the stresses are for the first time mainly transmitted transversely across the tarsal region as propulsion progresses.

THE THECODONT TARSUS

The thecodont tarsus is of considerable significance as the Thecodontia are ancestral to the pterosaurs, crocodiles, dinosaurs, and birds. The most primitive thecodont tarsus known is that found in *Chasmatosaurus*. The tarsus has most probably two elements in the proximal row, although Broom (1932b) believes there are three, with a separate intermedium and tibiale. After considering the tarsus of other closely related types, it would appear evident that the intermedium and tibiale of Broom are actually the astragalus and the centrale. It is difficult to believe that a separate tibiale appeared sporadically in various unrelated genera of terrestrial fossil reptiles, as some paleontologists would have us believe. It appears more reasonable to assume that the so-called tibiale is really a centrale that was displaced during preservation, or had shifted its position in the tarsal pattern in a group of genera of which we have only one or two representatives of the tarsus. It is certainly too profound a modification to be considered only as a generic difference. In the phylogeny of the reptilian tarsus (Fig. 11), that of *Chasmatosaurus* has been reproduced as figured by Broom, while in Fig. 14 the centrale has been placed in its probable natural position. Assuming the tibiale to be actually the centrale, this tarsus has the same number and disposition of elements, lacking one tarsale, present in the foot of *Youngina*. As far as can be determined from Broom's sketch, the calcaneum has a well-developed processus lateralis but no tuber. The functional ankle-joint, as in *Youngina*, was undoubtedly between the tarsalia and the metatarsals as none of the modifications resulting in a mesotarsal joint are present.

The next stage in the evolution of the thecodont tarsus, and of the mesotarsal joint, may be represented by *Euparkeria* (Broom, 1913a). The calcaneum still has a well-developed processus lateralis (Fig. 14,D) and, according to Broom, no indication of a heel. The centrale has disappeared as a separate element, however, and there are four (?) reduced tarsalia. There is definite evidence that the joint in this case was mesotarsal. Apparently the astragalus and the calcaneum were very closely associated, and the reduced tarsalia could have had no effect in maintaining the plane of flexure in the primitive position between them and the metatarsals. There is every reason for believing that the mesotarsal joint developed independently in the archosaurs and lepidosaurians, as it was not developed in either the eosuchians or the most primitive thecodonts.

Broom has pointed out (1932b) that the tarsus of *Chasmatosaurus* agrees very closely with that of *Hovesia* (Fig. 14,B), a Triassic eosuchian, and that it also agrees with that found in *Youngina*, which, in turn, agrees with the tarsal pattern found in *Labidosaurus*. In other words, the primitive cotylosaurian pattern is still present in the eosuchians and the thecodonts, showing the first sign of modification in *Euparkeria*.

Although *Saltoposuchus* (von Huene, 1921) is considered to be a primitive thecodont, there is a well-developed mesotarsal joint, and the calcaneum, while lacking the processus lateralis, does have a well-developed tuber (Fig. 21,D). The latter is a distinct advance over the condition found in *Euparkeria*.

Aëtosaurus (von Huene, 1920b), a somewhat aberrant thecodont (Fig. 14,E), which has a tarsus very similar to that of *Saltoposuchus*, has been figured for comparison with *Chasmatosaurus* and *Euparkeria*. The tibial and fibular facets are restricted to the proximal surfaces of the astragalus and calcaneum. The proximal elements are more cubical than the same elements in *Euparkeria* and were immovably articulated with the tibia and the fibula. With the remaining two tarsalia reduced to mere nodules, there is little

question but that the functional joint was mesotarsal (intertarsal).

The thecodont femur has a well-developed and medially directed head, a condition that first appeared in this order, although, as pointed out previously, the medial bending of the head was in an incipient stage in the eosuchians. The femur was thus able to swing in the vertical plane during propulsion and recovery, and the feet were brought into a forwardly directed position without any torsion at the ankle-joint as the tibia and fibula were able to remain parallel throughout propulsion.

Of the groups derived from thecodonts, the crocodiles and one primitive family of theropod dinosaurs are the only ones retaining the tuber calcanei. The loss of the tuber was likely associated with the perfection of bipedalism in both orders of dinosaurs. Since none of the crural flexors inserted entirely on the tuber, the secondary loss of the tuber would have but little effect on the musculature. The rôle of the foot in propulsion in the thecodonts and dinosaurs is discussed in the section on the reptilian musculature (p. 462).

The importance of making a distinction between a true tuber calcanei and the processus lateralis of the calcaneum has been stressed by Tornier (1927). The tuber always points in a posterior direction and is always associated with the superficial extrinsic flexors of the foot. The processus lateralis, on the other hand, is definitely a lateral extension of the calcaneum around which the tendons of the peroneal muscles pass. The lateral process is always best developed in a calcaneum that is dorsoventrally compressed, as in the Cotylosauria, Rhynchocephalia, Lacertilia, Pelycosauria, and some Therapsida.

It is evident that the process is not associated with any particular type of locomotion. In the forms with a mesotarsal joint the process projects laterally, while in the cotylosaurs and the pelycosaurs it is directed more proximolaterally. This may be of functional significance. The forms having a well-developed tuber always tend to have a reduced lateral process.

The phytosaur tarsus was apparently

but poorly ossified. Camp (1930) has described an astragalus for *Myriosuchus adamanensis* which resembles that of *Aëtosaurus* rather closely.

THE CROCODYLIAN TARSUS

The tarsus found in the Crocodilia (Fig. 16,B) is in many ways unique and is not approached in any other reptilian group. The tarsus of the precrocodylian *Protosuchus* (Brown, 1933, 1934) is very similar to that of *Aëtosaurus*. The calcaneum has a well-developed tuber and the astragalus is a nodule cuboidal in shape. Although the tarsal region has not been completely worked out of the matrix, there is no indication of any tarsalia. The functional ankle-joint is definitely mesotarsal in position. In the Upper Jurassic *Alligatorellus* (Lortet, 1892) the tuber is reduced (Fig. 16,A), but otherwise the astragalus and the calcaneum are very similar to the same elements in *Protosuchus*. There are three ossified tarsalia in contrast to the two found in recent crocodiles. Apparently the movable interlocking of the astragalus and the calcaneum occurs only in the Crocodilia.

Morphological features of the crocodile tarsus have been considered in detail by Rabl (1910), with some attention paid to its function. He has pointed out that the tarsal joint is mesotarsal on the tibial side and crurotarsal on the fibular side, a fact that can be easily demonstrated in a preserved specimen.

The astragalus and the calcaneum (Fig. 16,C) are entirely separate and articulate with each other by means of a modified, double ball-and-socket joint. In the posterolateral articulation the astragalus has a convex surface and the calcaneum a concave, whereas in the anteromedial articulation the opposite condition exists. This arrangement permits the calcaneum to rotate on the astragalus through about 45 degrees. In other words, as the foot is dorsiflexed on the crus, the astragalus remains immobile and functionally united with the crus while the calcaneum moves with the foot (some movement is possible between the calcaneum and the adjacent tarsale). The fibula is held immobile by

its immovable articulation with the astragalus.

The fibular articular surface on the astragalus is on the lateral extension, which places the distal end of the fibula immediately above the middle of the fibular articular surface on the calcaneum. Hence, as in the advanced therapsids and mammals, the weight is passed to the foot in essentially a vertical plane. This method of weight distribution is apparently always associated with a ginglymoid ankle-joint with well-developed, concavoconvex articular surfaces. Furthermore, when this type of ankle-joint is present, allowing the foot to bend at right angles to the crus

tarsale and the calcaneum is a plane surface, prohibiting any movement between these elements, and there is likewise no movement between the tarsalia and the metatarsals.

THE LOCOMOTION OF THE ALLIGATOR

The locomotion of the alligator (*Alligator mississippiensis*) has been investigated in the present study by means of motion pictures, employing the same methods used for the caudate amphibians (Fig. 17). The peculiar structure of the tarsus in addition to the somewhat medially directed head on the femur would seem also to give some clue as to the type of locomo-

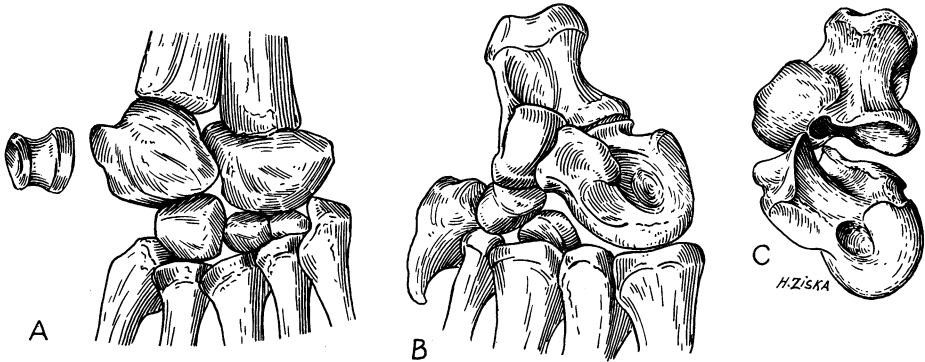


Fig. 16.—The crocodilian tarsus.

A, *Alligatorellus* (after Lortet), lateral view of calcaneum showing tuber on left; B, *Alligator* (from specimen); C, Astragalus and calcaneum of *Alligator*, slightly separated to show the nature of the articular surfaces.

(Fig. 21,E), and when the functional ankle-joint is between the calcaneum and the crus, at least on the fibular side, there is a tendency for the calcaneum to develop a tuber. The origin of the tuber will be discussed in the section on the therapsid tarsus, although the discussion applies equally well for the thecodonts and crocodiles.

The distal tarsalia are two in number. There is, of course, no free centrale, and Rabl considers it to be fused with the astragalus (Fig. 12,F). There is a meniscus between the medial tarsale and the base of the fifth metatarsal and the calcaneum, which forms a socket in which the astragalus rotates. The contact between the lateral

tion found in the thecodonts, dinosaurs, lacertilians, and even the advanced therapsids. The locomotion of the crocodile (*Osteolemus*) has been investigated by von Huene (1913) by direct observation and by footprints made in wet clay. The crocodiles have two methods of locomotion, one for rapid progression, the other for slow. When moving slowly, the body is dragged along the ground and the limbs are moved in a very lizard-like manner. When moving rapidly, however, the body is raised from the ground and the femur swings backward in more of a vertical plane. The ability of the crocodiles to raise the body relatively far from the ground when compared with a lizard may

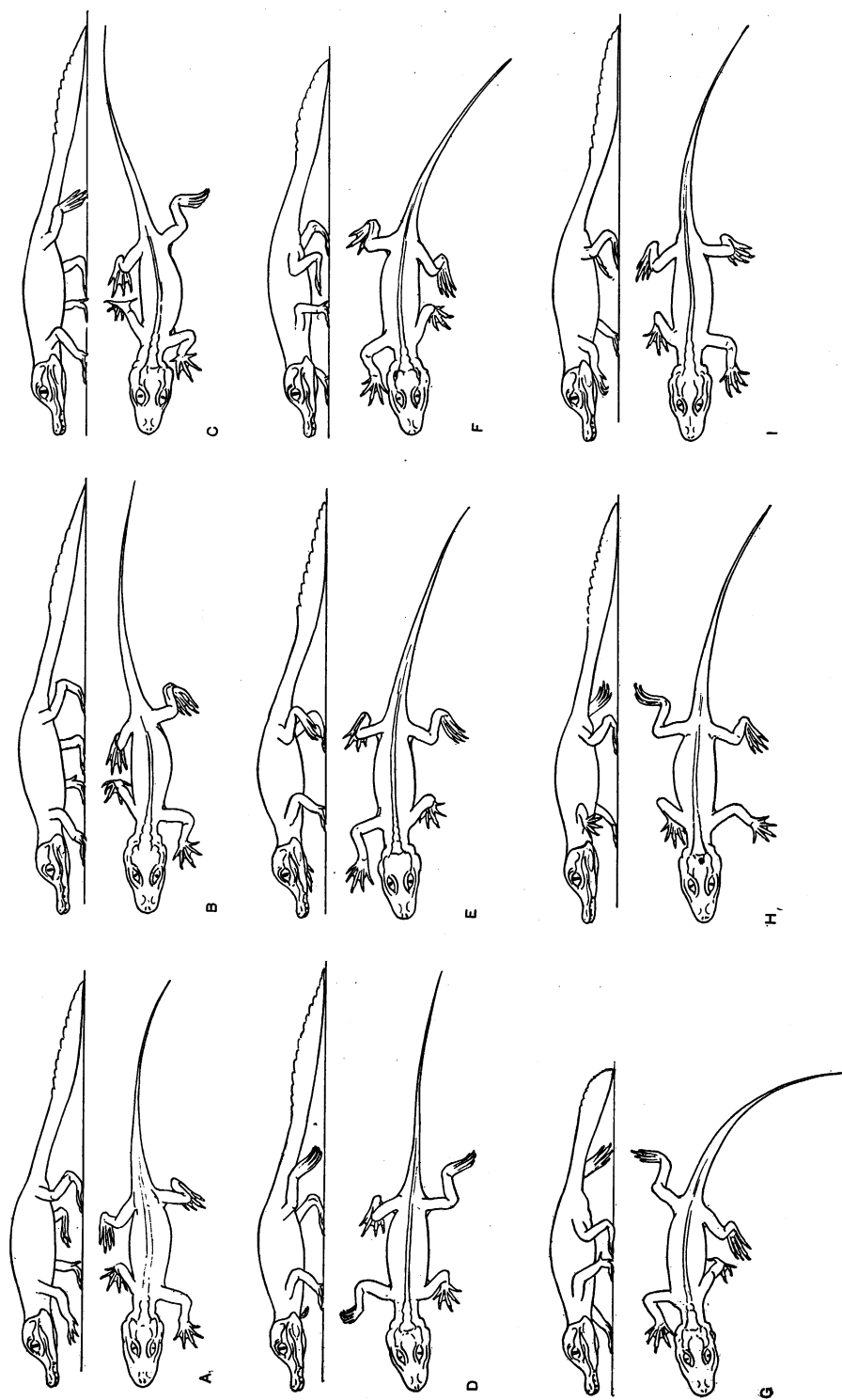


Fig. 17—Series of diagrams showing the position assumed by the limbs during locomotion of *Alligator mississippiensis*. Made from a motion picture by projection.

be associated with the extensive development of the pubo-ischio-femoralis externus and the adductor femoris as described by Romer (1923).

A direct comparison between the rapid locomotion of the alligator and the locomotion of an advanced therapsid such as *Bauria* appears plausible when the morphological similarities producing similar functional effects are considered. It will be recalled that the terminal head on the amphibian and on the primitive reptilian femur allowed the latter to move only in the horizontal plane, no appreciable vertical component of movement being present. In the form under consideration, as in certain of the ancestral thecodonts, however, the position of the femoral head permits a vertical component. The femoral shaft is twisted in the same manner as in the Lacertilia, the proximal and the distal ends being rotated about 50 degrees out of line with each other. The proximal end, furthermore, is directed away from the long axis of the shaft also at an angle of about 50 degrees in a dorsomedial direction. When the body is held close to the ground, the femur moves in the horizontal plane as in the lizards. When it is raised from the ground, the medial bend in the proximal portion of the femur becomes effective, permitting the femur to swing in a plane about 40 degrees off the vertical. In the dinosaurs, birds, some therapsids, and mammals the horizontal component is, of course, reduced to zero.

In both the advanced therapsids and crocodiles the tuber on the calcaneum increases the leverage action of the foot by increasing the effective distance through which certain of the flexors, which partially or entirely insert on the tuber, act (Fig. 21,E,H). Hence, the foot is able actively to participate in the propulsion phase. Von Huene points out that when the crocodile is moving very rapidly, the metatarsals and phalanges appear to snap plantarward, pushing the body forward. This motion he states, is favored by the tuber on the calcaneum, giving the extrinsic flexors of the foot a "lever grip." Finally, the ankle-joint, with its concavoconvex articular surfaces, allows greater freedom of move-

ment than the same joint in the lizards, functionally approaching the condition found in the higher therapsids and mammals. The typical tetrapod pattern of movement is present and the other details of locomotion common to all tetrapods are also exhibited, as described for the amphibian.

The movement of the hind-limb will now be described in detail. At the beginning of propulsion the crural portion of the leg is almost vertical in position in contrast to its forwardly directed position in the caudate amphibians. This is a function of the flexibility of the ankle-joint and of the position of the femoral head, and is associated with the fact that during recovery the limb is simply swung forward into the proper position rather than being brought forward "overhand," as is the case in the amphibian.

When the foot is placed on the ground at the beginning of the propulsion phase, its long axis is usually almost parallel with the body, but the exact position is by no means constant, as the diagrams demonstrate. Von Huene states that the foot is directed forward during propulsion in the crocodile, with the second toe parallel to the body axis, while the third and fourth toes are nearly always bent more or less sideways. As can be readily observed, this is true for both slow and rapid progression. The long axis of the foot, however, remains almost parallel with the longitudinal body axis, by the end of propulsion being oriented at an angle of about 20 to 30 degrees to this axis. Likewise in the therapsids there is every reason for believing that the feet were directed forward throughout propulsion as they were in the primitive tetrapods. In other words, the laterally directed foot of many reptiles is entirely secondary and not a heritance character as many have supposed. Under these conditions, stresses are applied transversely across the foot but not to the same degree that they would be applied in Morton's hypothetical tetrapod in which the feet are at right angles to the body. These stresses may be partly responsible for the low transverse arch in the lepidosaurian foot, although there is

no sign of such an arch in the alligator foot. Morton (1935) is of the opinion that the transversely applied stresses by producing the superposition of the astragalus on the calcaneum were responsible for the creation of the transverse tarsal arch in the therapsids and mammals, which in the light of the evidence here presented would appear improbable.

During rapid propulsion, the femur moves backward at an angle of about 60 degrees with the vertical plane. This has the effect of increasing the average angle between the femur and the crus during locomotion. The analysis of the forces at work on the amphibian limbs during locomotion is again applicable to reptilian locomotion. The component *c* (Fig. 8) which draws the limbs toward the body, is, however, not nearly as large with the femora in the vertical position. Although the values of the various forces involved may differ from those for the amphibian, there is no radical change in the nature of the forces until the femur assumes the vertical position and the effect of gravity is largely overcome by the position of the limbs under the body. Under these conditions, the force *w*, which tends to cause the foot to slip sideward, is practically non-existent, and the force *b* requires but little muscular exertion as most of the body weight is transmitted directly through the bones in the vertical plane.

It is obvious that the alligator foot does not slip off the ground as does the amphibian foot, but that it is lifted from the ground immediately after the weight is transferred to the heads of the metatarsals. The reptilian foot lacks the suppleness of the amphibian foot, particularly in the case of the digits. Furthermore, in the amphibian foot the metatarsals, phalanges, and the distal portion of the tarsus are the only parts making effective contact with the ground, while in the alligator the entire foot contacts the ground almost simultaneously at the beginning of propulsion, as von Huene also noticed. The proximal portion of the foot is then raised by flexion between the metatarsals and the phalanges. With the foot participating in the propulsive effort, a certain minimum contact be-

tween the foot and the ground is required for a successful thrust, and, furthermore, successful propulsion requires a firmly consolidated lever which, in this case, is simply the elongated metatarsals. In the case of the amphibian, as pointed out earlier, the foot, although it may be considered as a compound lever system as far as its intrinsic movements are concerned, is but a flexible base giving support to the propulsive movement of the leg.

The recovery phase of the reptilian and mammalian limb is relatively simple compared to the amphibian. That is to say, in all tetrapods having a terminal head on the femur the recovery phase is very similar to, or some modification of, the recovery described for the caudates. As pointed out several times previously, the medially directed head allows the femur to move in a more vertical plane. Hence, during recovery the crus is flexed on the thigh and the foot on the crus, and the entire limb simply swings forward. As recovery progresses, the segments are extended so that the foot is parallel with the ground and the crus is almost vertical by the time the foot contacts the ground at the beginning of propulsion. Although therapsid locomotion differed from this only in detail, the causes for this difference are of great importance (cf. section on therapsid foot).

THE TARSUS OF THE DINOSAURS, PTerosAURS AND BIRDS

The final stage in the perfection of the mesotarsal joint is found in the Saurischia, Ornithischia, Aves, and Pterosauria. They have paralleled one another in producing a tarsus in which the astragalus and the calcaneum tend to be proximodistally compressed, and in which the number of the more distal tarsal elements is greatly reduced.

In the primitive members of both the Saurischia and the Ornithischia (Fig. 11), the tarsus consists of a number of distinct elements that have been identified as the astragalus, calcaneum, and two to four tarsalia. A tuber calcanei was retained in the Hallopodidae, but was lost in all other dinosaurs. Its implications are dis-

cussed in the section on reptilian musculature (p. 462). In the more advanced members of both orders, there is a tendency for the astragalus and the calcaneum to articulate very intimately with the crus and for the crural elements to do the same with each other, preventing any possible movement between them. The distal surfaces of the astragalus and calcaneum are rounded off and form a continuous articular surface. This transversely rounded surface, in the living animal, must have fit into a concave surface composed of menisci and ligaments, the ossified tarsalia forming all or part of the floor of this concavity.

The tibia was the main weight bearing axis, the fibula being a much thinner bone. Apparently, whenever the femur develops a medially directed head, the tibia becomes the main weight bearing axis of the crus. This is true of all the members of this group, and of the advanced therapsids and mammals as well. Accompanying the dominance of the tibia, there is always a consolidation of the proximal part of the tarsus. In the dinosaurs, this was accompanied by the development of a flange on the distal portion of the tibial shaft that extended laterally around the fibula, for example, in *Tyrannosaurus*, *Trachodon*, *Protoceratops*, and *Stegosaurus*. This tibial flange was undoubtedly firmly attached to the fibula by ligaments, thus reenforcing the ligamentous attachment of the astragalus with the calcaneum. Furthermore, as is well known, the astragalus developed a dorsal process in some members of both orders; for instance, *Tyrannosaurus* and *Trachodon*, which attached it even more securely to the tibia. That this flange should have developed on the anterior rather than the posterior surface of the astragalus may be associated with the fact that in the bipedal forms the digits, meeting the tarsus at an angle might have tended to rotate the astragalus anteriorly during propulsion. The dorsal process, being firmly attached to the tibia, counteracted this tendency.

The pterosaur tarsus (Fig. 11) is quite dinosaur-like. The astragalus and the calcaneum are ossified and fused with the

tibia, the fibula being entirely absent. There are but two tarsalia, the lateral one, undoubtedly the result of fusion of several of the elements in this series, is the larger. These were firmly united by ligaments to each other and to the metatarsals. The metatarsal joint is again concavoconvex. Exactly how the pterosaurs used their hind-limbs is still a moot question and the matter will not be speculated on here, except to say that movement must have been largely restricted to the anteroposterior plane as in the birds. Furthermore, the presence of a well-developed and medially directed head on the femur indicates that the entire hind-limb moved in the same plane.

In the birds (Fig. 11), the consolidation has been carried a step further, with the astragalus and the calcaneum fusing together and ossifying with the tibia. The fibula has been reduced to a mere vestige. The remaining tarsalia indistinguishably fuse with the remaining metatarsals, which have likewise fused. This extensive fusion of the tarsal elements not only makes for rigidity at the tarsal joint, but also has the effect of preventing movement in more than one plane. The restriction of movement to the anteroposterior plane is actually due to a combination of factors. The tibia and the tarsometatarsus are firmly united by ligaments, forming a capsulated, diarthrodial joint. Secondly, the proximal end of the tibia and the base of the tarsometatarsus are transversely widened, and the former is convex and the latter is concave. These factors, together with the arrangement of the insertion tendons of the extensor and the flexor muscles, prevent any movements of one element on the other in the lateral plane.

TYPE III

THE PELYCOSAURIAN TARSUS AND ITS DERIVATIVES

The morphology of the pelycosaur tarsus has been very thoroughly described by Romer (1940), including a discussion of its functional aspects. The complete tarsus of *Varanosaurus* (A.M.N.H. No. 4174) and parts of the tarsus of *Dimetrodon*, together with a cast of an entire foot of the

latter, have been available for study. This tarsus has retained to a greater degree than did the eosuchian the unmistakable mark of the older captorhinomorph pattern (Fig. 18). There are two proximal elements, the astragalus and the calcaneum; two centralia; and five distal tarsalia. The presence of two centralia in the pelycosaurs is a unique condition among reptiles. *Labidosaurus* has but one and but one is present in *Dimetrodon*, *Youngina*, and other primitive reptiles.

As Romer points out, the astragalus is L-shaped, the vertical arm of the L articulating proximally with the fibula by a hinge-joint. The horizontal arm of the L, however, articulates with the tibia by means of a well-rounded articular surface, permitting gliding movements for the first time between these elements. In the types derived from the eosuchians, as just pointed out, the torsion on the medial side of the foot was relieved in several cases by the shortening of the tarsus on the medial side, but mostly by the development of a medially directed femoral head. In the pelycosaurs, this same torsion problem was partly alleviated by the formation of a rounded articular surface on the astragalus, permitting the tibia to move freely over the astragalus as propulsion progressed.

The long axis of the foot must have been directed forward during locomotion. The ability to do this, when the proximal ends of the tibia and the fibula were directed laterally, he attributes to the ability of the freely movable astragalotibial joint to allow the necessary rotational movement. There is one other feature, however, which must not be overlooked, namely, that the tibial articulation is on a more distal level than the fibular (Fig. 21,B). Because of this, the foot has to be oriented with its long axis directed forward, otherwise the tibia and the fibula could not articulate with the foot at the same time. Although the tibia articulates with the tarsus at a more distal level than the fibula in the primitive tetrapods, the pes was not directed forward throughout propulsion because of this condition. As already pointed out, the relative immobility of the tibiotarsal

articulation required that the tibia assume a diagonal position as the femur moved backward. This difference in level, however, did decrease the amount of tilting required of the tibia.

The L-shaped astragalus, as already noted, first appeared in the cotylosaurs, specifically the captorhinomorphs. It was apparently secondarily lost in the other cotylosaurian types except possibly in *Procolophon*. It will be recalled that it persisted in the Mesosauria and the more primitive Protorosauria. There is every reason to believe that this form of astragalus served the same purpose in all these types, that of directing the long axis of the foot forward and relieving the stress in the proximomedial region of the tarsus at the same time.

The calcaneum of the pelycosaurs is dorsoventrally compressed and only thickened where it articulates with the fibula, astragalus, and tarsalia four and five. The more distal elements are in most cases merely rectangular or rounded, and must have had cartilaginous peripheries in life. It would appear that Romer is correct in stating that there was no movement between these elements.

The locomotor methods of the pelycosaurs have been discussed by Romer. The movements of the femur with its terminal head, as he deduces them, were almost identical with those described for the primitive tetrapod. Actually, the only real advance is the organization of the crurotarsal articulation on two different levels, and the rounded astragalotibial articulation relieving the stress produced by the torsion in the medioproximal region of the tarsus. While this may be considered as an advance, it has actually modified the locomotor movements very slightly, the principal difference being, as just pointed out, that the tibia was no longer required to assume a diagonal position during the last part of the propulsion phase.

According to Romer, the femur has a greater forward than backward swing. At the beginning of propulsion, the femur was lower distally than proximally, and the crus was directed anteriorly and some-

what outward from the knee. At the end of propulsion, the femur was raised distally and was rotated counter-clockwise (on the left side), resulting in the tibial articulation facing directly downward, while the crus was in an almost vertical position.

The method of weight transfer during propulsion was, even at this stage, typical of the crurotarsal foot. At the beginning of propulsion, the body weight was transmitted to the ground through the astragalus and the calcaneum by way of the heel pads. As soon as the body moved forward and the posterior part of the foot was raised from the ground, the weight was transferred to the heads of the metatarsals or the ball of the foot. The wide tarsus, plus the length of the metatarsals, must have imposed tension-compression stresses of considerable magnitude on this region when the heel region was off the ground. These stresses could have been counteracted only by the efforts of the plantar ligaments and the intrinsic muscles of the foot. Not until the mammalian stage was reached, was a longitudinal tarsal arch created to counteract the stresses. Even in the mammals, the integrity of this arch is only maintained by the action of the ligaments and the intrinsic musculature (Jones, 1941).

The tibial articular surface on the pelycosaur astragalus shows one further point of interest. As Romer points out, this surface is directed not only medially but also dorsally. In other words, it has migrated somewhat on to the dorsal surface of the astragalus (Fig. 21,B). This tendency, again associated with the relief of the torsion on the medial side, must have first appeared in the cotylosaurs, and there is definite evidence of it in *Labidosaurus*. In the advanced therapsids, as will be pointed out shortly, not only has the tibial articular surface migrated entirely on to the dorsal surface of the astragalus, but the fibular articular surface has done likewise on both the astragalus and the calcaneum (Fig. 21,H). In the more specialized pelycosaurs, the tibial articulation is more dorsally located (*Dimetrodon*) than in the primitive types (*Ophiacodon*).

THE THERAPSID TARSAUS

According to Romer, the pelycosaurian family Sphenacodontidae, which includes *Sphenacodon* and *Dimetrodon*, is most probably ancestral to the therapsids. Although this may be true, it is rather difficult to reconcile the relative specializations of the *Dimetrodon* tarsus with the rather primitive tarsus found in the Dromosauria, and even the Dicynodontia and the Dinocephalia. (The tarsus of *Haptodus* is, however, more primitive.) As far as the tarsus alone is concerned, that of *Ophiacodon* appears better suited to be an ancestral type, as Romer (1940, p. 180) implies in noting the resemblance between the tarsus of *Ophiacodon* and *Labidosaurus*.

The therapsid tarsal pattern is again the same as that found in the pelycosaurs, except for the loss of the medial centrale (Fig. 18). This centrale tends to be displaced medially in the advanced pelycosaurs and is finally lost (Romer, 1940). The remaining centrale is the homologue of the mammalian navicular and will henceforth be called by that name.

The tarsus of the therapsids evolved along several distinct lines, as can be readily seen on the accompanying chart (Fig. 18). The Dromosauria, Dinocephalia, Dicynodontia, and Theriodontia probably represent four distinct evolutionary lines and the differences in the tarsus tend to support this conclusion.

There is some indication that the L-shaped astragalus was carried over into the therapsids. The astragalus of the gorgonopsians *Lycaenops* and *Aelurognathus* is somewhat of this shape. There was a definite tendency in all the suborders to transform the astragalus into a more rounded or cubical element, with its tibial articular surface either on the proximal border, as in the Dromosauria, Dinocephalia, and Dicynodontia, or on the dorsal or anterior surface as in the Gorgonopsia and the groups derived from this infraorder. In all of them the crurotarsal joint tends to be on the same level proximodistally, rather than the tibial articulation being more distal than the fibular.

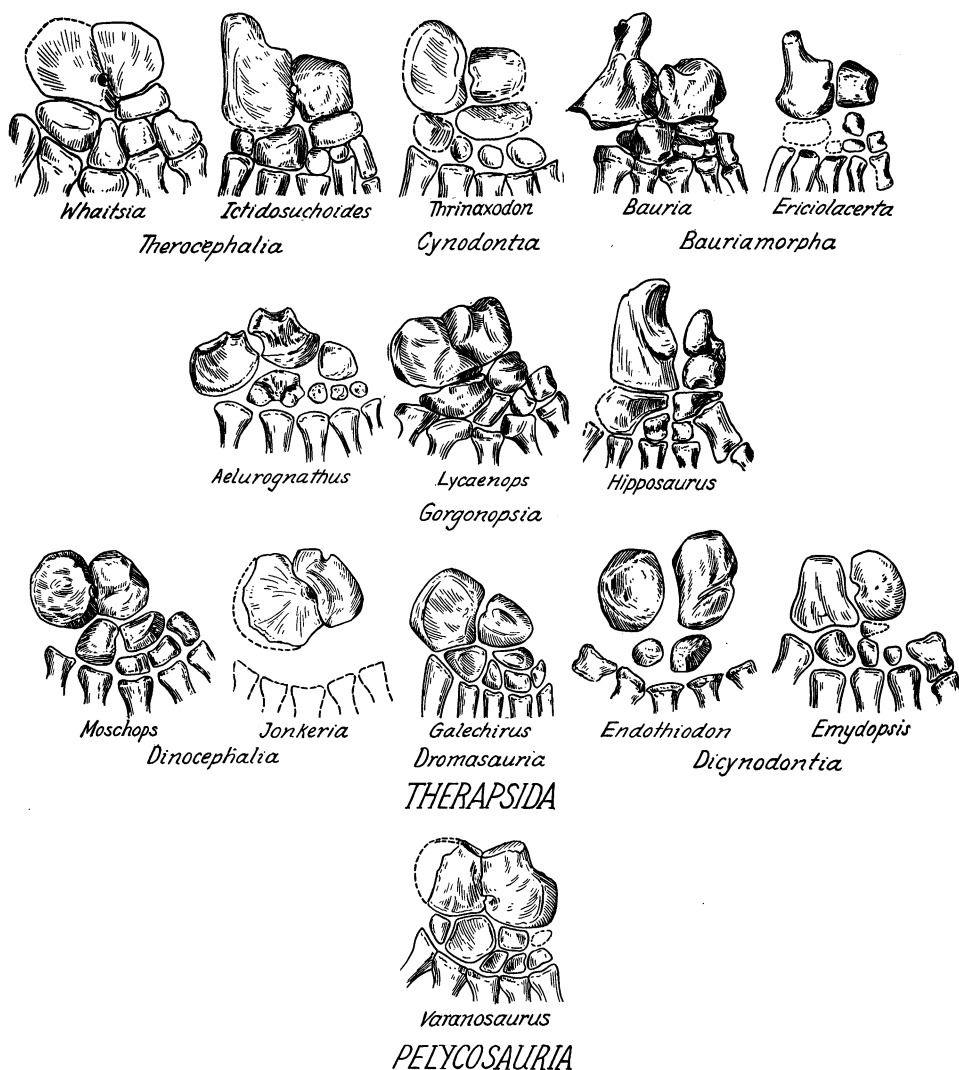


Fig. 18.—The therapsid tarsus. (Compiled from the literature and specimens.)

This leveling off in the crurotarsal articulation had no great effect on the position of the foot relative to the body during locomotion. In all therapsids the femur has a head that is medially directed to a greater or lesser degree, but minus the twisting of the ends in opposite directions, depending on the group and the extent of specialization in the direction of the mammals. This undoubtedly compensated for the leveling off, and permitted the long axis of the foot to parallel the long axis of the

body without the necessity of the tibia crossing in front of the fibula as was the case when the head was terminal.

THE DROMASAURIAN TARSUS

The Anningiamorpha having been demonstrated to be pelycosaurs (Romer, 1940) and the position of *Galesphyrus*, which Broom referred to this group, now open to question, the dromasaurian tarsus represents the earliest specialized offshoot from the primitive therapsid stock. The

tarsus of *Galechirus* (A.M.N.H. No. 5516) is the only well-preserved dromasaurian tarsus known (Fig. 18). The astragalus has lost the L-shape and has become a triangular element, with a rounded surface for articulation with the tibia. The calcaneum is disk-shaped and dorsoventrally compressed. As in the pelycosaurs, its proximal and lateral borders are thickened for articulation with the fibula and the astragalus, respectively. Its center is slightly concave, a characteristic of all therapsid calcanei, even including the bauriamorphs.

The navicular is directly distal to the astragalus in the typical mammalian position. It articulates with the three medial tarsalia that are in turn homologous with the three mammalian cuneiforms. The cuboid is a triangular element that barely articulates with metatarsal five. It is not possible to determine whether the fifth metatarsal actually articulated with the calcaneum in life.

The composition of the therapsid (and mammalian) cuboid bone presents the same sort of problem as that of the astragalus. Both Schmalhausen (1908b) and Holmgren (1933), studying the embryology of the tarsus of *Mus* (Fig. 12,G) and *Sus*, are of the opinion that the cuboid is composed of tarsale four and tarsale five. Dollo (1929) was also of this opinion. Most paleontologists, on the other hand, consider it the homologue of the fourth tarsale only. Again, it would appear impossible to solve this matter with paleontological evidence only, and its dual origin must be considered as a distinct possibility.

The ankle-joint in the dromasaurians must have been crurotarsal in position and must have functioned in the same manner as that of the pelycosaurs, with a freely movable joint between the tibia and the astragalus, and a hinge-joint between the fibula and the astragalus and the calcaneum.

The Dromasauria possessed the mammalian digital formula of 2-3-3-3-3. This must have been acquired independently, as many of the more advanced therapsids have the old reptilian formula.

THE DINOCEPHALIAN TARSUS

The dinocephalian tarsus is very poorly known considering the amount of material belonging to this suborder that has been uncovered. Apparently, the only titanosuchid tarsus known is that of *Jonkeria* (Broom, 1939) and it is incomplete, the astragalus and the calcaneum being the only elements preserved. It is quite possible that the titanosuchid tarsus generally was but poorly ossified. The astragalus of *Jonkeria* (Fig. 18) is rounded in much the same fashion as in *Galechirus* and undoubtedly there was movement between it and the tibia. The tibial articulation was at a somewhat more distal level than the fibular, a probable heritage character derived from the pelycosaurs. As the illustration shows, however, the astragalus is not L-shaped. The fibular facet on the astragalus appears to be also somewhat rounded. The calcaneum is again a disk-shaped element, compressed dorsoventrally and somewhat concave on its dorsal surface. It is thickened along the proximolateral and medial borders where it articulated with the fibula and the astragalus.

The only tapinocephalid tarsus that has been described is that of *Moschops* (Gregory, 1926). Since it was assembled from disassociated elements the distal portion is regarded as largely conjectural (Fig. 18). The element thought to be the astragalus is much more dorsoventrally compressed than that of *Jonkeria*. The tibial articular surface is but slightly rounded as compared with *Jonkeria* and is restricted to the proximal border. The calcaneum is in all respects similar to that of *Jonkeria*. Although the distal tarsals could not be identified with certainty, there is every reason to believe that there was the same number of elements, arranged in the same manner as in *Galechirus*.

The location of the ankle-joint in *Moschops* is somewhat of a problem. The articular surfaces on the astragalus and the calcaneum are relatively restricted in size, indicating but little movement between the crus and the tarsus. It would appear probable that the functional joint was actually located more distally between the

tarsalia and the metatarsals or between the proximal row and the next more distal elements. This point cannot be settled unless a foot is found preserved in place.

THE DICYNODONT TARSUS

The tarsus of the dicynodonts varies greatly in the extent of ossification. In the case of *Emydopsis* (Broom, 1906, 1932) and *Kannemeyeria* (Pearson, 1924), the tarsus is fully ossified, while those of *Lystrosaurus* (Watson, 1913a), *Dicynodon*, and *Endothiodon* are but partly so. The lack of ossification in this group has generally been associated with a semiaquatic or a fully aquatic habitus, but again, to some degree at least, the cartilaginous state may be genetic, as it appears to be in the caudate amphibians.

The tarsi of *Emydopsis* (Fig. 18) and *Kannemeyeria* are very similar to each other and to that of *Lycaenops*. The astragalus has a rounded dorsal surface for the articulation of both the tibia and the fibula and the calcaneum also appears to have a rounded fibular facet on its dorsal surface. The location and relative size of these facets indicates a functional crurotarsal joint with the foot assuming a semiplantigrade or plantigrade position during propulsion. The femoral head was medially directed to a marked degree, giving the hind-limbs a pose clearly resembling that indicated in Pearson's restoration of *Kannemeyeria*.

The single specimen available (A.M.N.H. No. 5635) of the foot of *Dicynodon platyceps* would seem to indicate that the astragalus and calcaneum are fused, although this is not certain. The tibial facet is rounded and dorsally located, as is the fibular facet, indicating that the foot could assume the same position as that of *Kannemeyeria*. Except for an unidentifiable splinter, the remainder of the tarsus is unossified.

The astragalus and calcaneum of *Endothiodon* (A.M.N.H. No. 5613) and *Lystrosaurus* (Watson, 1913) are, in contrast to their form in the genera just mentioned, dorsoventrally compressed with the tibial and fibular articular surfaces restricted to the proximal borders. The remainder of

the tarsus is not ossified, except for two very small distal nodules in the *Endothiodon* tarsus (Fig. 18).

THE GORGONOPSIAN TARSUS

The most primitive gorgonopsian tarsus known is that of *Lycaenops* (Fig. 18). A complete and perfectly preserved specimen has been studied in great detail (A.M.N.H. No. 2240) and a model has been constructed in order to restore the tarsal elements in their probable natural positions.

The astragalus is more or less rectangular in shape and is well rounded on its dorsal surface. This area is divided into two parts or articular surfaces by a shallow groove running in a proximodistal direction. The medial articular surface for the tibia is directed in a medial and dorsal direction in the same manner as is the homologous surface on the pelycosaur astragalus. The lateral fibular articular surface is relatively smaller and is in line with the rounded proximal border of the calcaneum, which, of course, also articulates with the joint. The astragalus overlaps the calcaneum to a slight extent proximally and the calcaneum overlaps the astragalus to a greater extent distally. There is no evidence that this is due to crushing as the elements have been clearly preserved in almost their natural positions, with no sign of mediolateral compression. In Broom's drawing of a *Lycaenops* tarsus (1930) there is, however, no indication of this interlocking. This method of articulation absolutely precluded any possibility of movement between the astragalus and the calcaneum. As will be seen shortly, the development of a medial process on the calcaneum was favored for the same reason in the bauriamorphs.

The calcaneum is very similar to that found in *Galechirus*; in other words, it still resembles the primitive therapsid type, being disk-shaped and concave in the middle of the dorsal surface. Its medial border is notched for the reason mentioned above. The proximal border is relatively thicker and the curved surface more extensive than in *Galechirus*.

In *Lycaenops* there is evidence for the first time that the fibula was able to rotate

somewhat on the calcaneum in the vertical plane. This slight amount of movement reduced still more the torsion at the ankle-joint, which must have increased somewhat when this joint leveled off in the primitive therapsids.

The cuboid is transversely elongated, tapering laterally to almost a point. The other elements do not require special comment, except that the navicular is oval in outline and barely contacts the entocuneiform.

When the *Lycaenops* foot is properly oriented, the midtarsal axis passes either along the third digit or slightly to the fibular side of that digit and then approximately between the astragalus and the calcaneum. If this axis is raised into a vertical position, it is found that a rather well-developed transverse arch supported by plantar pads was required in order that all the heads of the metatarsals could touch the ground at one time. It is highly probable that the foot was semiplantigrade and not digitigrade as figured by Broom (1932, p. 129), although he has described it as plantigrade (1929, p. 35). In fact, there is no reason for believing that any of the therapsids were digitigrade, although they have been commonly restored as such. This matter has been fully discussed in a previous paper (Schaeffer, 1941).

Two more gorgonopsian tarsi have recently been described by Boonstra (1934), belonging to *Aelurognathus microdon* and *Hipposaurus boonstrai*. In both cases Boonstra considers the proximal row of the tarsus to contain three elements: the tibiale, the intermedium, and the fibulare. Boonstra does admit, however, that his interpretations may be incorrect in both cases, which is very probable.

The tarsus of *Aelurognathus* (Fig. 18) undoubtedly contains all the elements possessed by that of *Lycaenops*. The element considered by Boonstra to be a tibiale would appear, however, to be the slightly displaced navicular. It has the same oval shape and relative size as the *Lycaenops* navicular. His intermedium is then, of course, the astragalus.

The tarsus of *Hipposaurus* (Fig. 18) is of great importance as it is the first known example of a gorgonopsian tarsus in which the calcaneum possesses a true tuber. In fact, the resemblance between the calcaneum of *Hipposaurus* and *Bauria* is remarkably close. In both cases the body of the calcaneum is still basin-shaped on its dorsal surface as in the more primitive types. The fibular facet, however, consists of a rounded knob that is elevated above the surface of the body. The tuber projects in both cases backward just lateral to the facet, and is relatively more robust in *Hipposaurus* than in *Bauria*.

The nature of the astragalus cannot be made out from Boonstra's description. He considers it to be a composite element, the "conjoined" intermedium and tibiale, with each part containing a knob-like process. It is quite possible that further preparation would reveal that there is but a single element, the astragalus, with two rounded surfaces, the more medial one for the tibia and the more lateral one for the fibula, as in *Bauria*.

The more distal portion of the tarsus is also very difficult to interpret. Boonstra is of the opinion that the medial, proximal mass may also contain the navicular which is absent as a distinct element. In any case, the illustration shows but four distal elements instead of the usual five, and the presence of a fifth may be strongly suspected.

The method of locomotion must have been almost mammalian. The femoral head is medially directed almost to the same extent as in the mammals. As the head became more medially directed, the importance of having the tibia and the fibula articulate on the same level is obvious. If the pelycosaur condition were still maintained, the foot would be inverted and almost supinated to the extent of causing the animal to walk "pigeon-toed." The axis of the ankle-joint was at all times at approximately right angles to the long axis of the body. This relationship imposed the least amount of lateral strain on the hip-, knee-, and ankle-joints.

THE METHOD OF PHALANGIAL REDUCTION AS
ILLUSTRATED BY THE GORGONOPSIA

The question of the reduction from the reptilian to the mammalian phalangeal formula has been discussed by Broom (1913b). In the manus of *Scymnognathus* there figured, and also in the manus of *Lycaenops* (Broom, 1929), digits one and two and five have the mammalian formula, while digit three has four phalanges, and digit four has five phalanges. In digit three, the second most distal phalanx, and in four, the second and the third, are mere disks. The second most distal phalanx of the third digit of the *Hipposaurus* pes is also of this sort. It would appear that certain of the phalanges were reduced to disk-like proportions and finally either fused with the adjoining unreduced ones or were eliminated altogether. The cynodont *Thrinaxodon* also shows this condition, having exactly the same arrangement of the disk-like elements.

THE THEROCEPHALIAN TARSUS

Whether or not the gorgonopsians will prove to be the ancestors of the therocephalians and the more advanced therapsids groups, it seems evident that the tarsus of *Lycaenops* is clearly, at least structurally, ancestral to the tarsus of these forms. Of particular importance is the rounding off of the tibial and fibular articular surfaces on the astragalus and the calcaneum, and of the migration of these surfaces on to the dorsal surface of these elements.

The tarsus of the therocephalian *Whaitsia* (Broom, 1930a, Fig. 4, B) is very similar to that of *Lycaenops*. The calcaneum is still disk-like with no indication of a tuber (Fig. 18). The astragalus is very similar except that its dorsal surface is not divided into distinct tibial and fibular facets as is that of *Lycaenops*. The navicular is relatively wider transversely and articulates with the entocuneiform, but barely contacts the ectocuneiform.

The tarsus of *Ictidosuchoides* (Broom, 1938) is of great interest in that the calcaneum possesses a tuber (Fig. 18). The body of the calcaneum is transversely widened as in the gorgonopsian *Hippo-*

saurus. Apparently the fibular facet is not a knob-like elevation as in *Hipposaurus* and *Bauria* but is simply a part of the body. The astragalus does not have its dorsal surface divided into facets and in this respect resembles *Whaitsia*. The navicular articulates with all three cuneiforms. The entocuneiform tends to simulate the first metatarsal in its proximodistal elongation. This tendency, which is also evident in *Bauria* and *Emydopsis*, has been noted by Romer (1941) in the tarsus of the pelycosaurs. One curious feature is the apparent presence of a fifth tarsale. This is apparently the only case among the therapsids where this element is separately present. If it does not turn out to be simply a part of the fourth tarsale or cuboid, it presents strong evidence for believing that the mammalian cuboid is a compound bone. The presence of a cartilaginous fifth tarsale must also be considered as a distinct possibility in the case of *Bauria*.

Broom figures (1932, p. 76) an unidentified scaloposaurid that apparently also has a tuber on its calcaneum. The foot has, however, unfortunately been restored as digitigrade, a criticism that also applies to Watson's restoration of the bauriamorph *Eriaciolacerta*.

THE CYNODONT TARSUS

The cynodont tarsus has not been completely described, although it is known in *Cynidiognathus*, *Thrinaxodon*, and *Diademodon*. That of *Thrinaxodon* (Fig. 18) as figured by Broom (1932, p. 270) has an astragalus and calcaneum very similar to that found in *Lycaenops*. The calcaneum is oval in shape and lacks a tuber. Broom quotes Watson as saying that a tuber is present on the calcaneum of *Diademodon* (1930b, p. 133). The other tarsal elements resemble very closely those of *Ictidosuchoides*. As pointed out above, the phalanges appear to be in a state of reduction toward the mammalian formula.

THE BAURIAMORPH TARSUS

The tarsus of the bauriamorph *Bauria* (Fig. 18) has been described by Broom (1937), and Boonstra (1938), and further

prepared and redescribed by Schaeffer (1941). Its more important features may be listed here. The calcaneum has a well-developed tuber and has lost its disk-like or oval outline, being more rectangular in shape. The fibular facet is in the form of a rounded knob that is directly opposite the fibular facet on the astragalus. The astragalus has two distinct articular surfaces divided by a shallow groove much as in *Lycaenops*. It has a rather extensive articulation with the cuboid, a condition usually found in the ungulate mammals. The navicular articulates only with the meso- and the ectocuneiform, barely contacting the entocuneiform. The latter, as pointed out above, simulates the first metatarsal. The cuboid only articulates with the fourth metatarsal, the fifth has no apparent bony support whatsoever. This matter is fully discussed in a previous paper (Schaeffer, 1941). The plantar surface of the calcaneum has a short medial process that extends under the lateral border of the astragalus, and it has been suggested that this may be the beginning of the sustentaculum tali. The cuboid also has a medially directed process extending under the navicular for a short distance, which is probably a specialized feature for additional consolidation.

The one other baurimorph tarsus that has been described is that of *Ericiolacerta* (Watson, 1931). The astragalus and the calcaneum (Fig. 18) are very similar to those found in *Bauria*. The more distal tarsals were apparently poorly ossified. The navicular, ento- and mesocuneiforms are represented by nodules, and there is no sign of the ectocuneiform and the cuboid.

To date, the ichtidosaurian tarsus is unknown. If this group is as close to the mammals as is now supposed, the calcaneum should have a well-developed tuber, and possibly the superposition of the astragalus upon the calcaneum is in an incipient stage.

THE FUNCTIONING OF THE THERAPSID FOOT

In spite of all the advances in the construction of the foot toward the mammalian condition which appeared in the higher therapsids, there is no evidence that the foot

had more than one axis of rotation, producing dorsoplantar movement at the crurotarsal joint. As will be seen later, the complicated movements of the mammalian foot are directly associated with the superposition of the astragalus on the calcaneum. Supination and pronation, or any rolling movement of the foot from side to side, must have been negligible as they could only have occurred by an actual dislocation of either the tibio- or the fibulotarsal joints. It is evident therefore that the locomotion of the therapsid, no matter how mammal-like the construction of the hindlimb, lacked the fine degree of postural adjustment that the relatively unspecialized mammalian foot makes possible. Movement, particularly over uneven terrain, must have been relatively slower as more effort had to be expended in preventing a shifting of the center of gravity during progression. With the body raised well off the ground and the legs swung under the body, this factor was of greater importance than in the primitive tetrapods. It would thus appear that superposition was favored when the hindlimbs assumed the mammalian position, as a means of vastly improving the mechanism of postural adjustment.

In other types in which the femur assumed a vertical position, such as the dinosaurs and the birds, a relatively smaller portion of the foot touched the ground at any one time, and also the toes were capable of a certain amount of independent movement. Furthermore, the architecture of the foot with the extrinsic flexors inserting directly into the plantar surface would assist in necessary adjustments.

ASTRAGALAR SUPERPOSITION

The superposition of the astragalus in its relationship with the calcaneum is a distinctly mammalian characteristic and the one major difference between the mammalian and the baurimorph foot. It is the final step in the transformation of the therapsid foot into the mammalian. The construction of the tarsus among mammals is subject to but relatively minor variation associated with the posture of the

foot. This is in sharp contrast to the great variation in the structural design of the tarsus among the reptiles.

The superposition was brought about at first not so much by an actual overriding of the calcaneum by the astragalus as by the development of a medial process on the calcaneum that finally extended under the astragalus. This process is present in an incipient stage in the foot of *Bauria*. As pointed out in the description of the *Bauria* foot, the tuber calcanei appeared long before the astragalus became superimposed on the calcaneum, and although the former may be of arboreal significance, the development of a tuber definitely is not.

The extension of this medial process of the calcaneum, which may be called the sustentaculum, produced three important functional changes in the therapsid foot. First, the fibula lost its important functional contact with the tarsus as a weight bearing element and the tibia became the main weight bearing axis of the crus. A single weight bearing column for each leg is a less stable means of support than a double column, for the latter tends to stabilize the crus on the foot in the transverse plane. The two remaining changes are associated with maintaining stability between the crus and the foot.

Superposition caused the astragalus and the calcaneum to act as a functional unit, at least so far as movement of the foot in the sagittal plane is concerned. The development of the tuber changed the foot into a lever of the first order with the fulcrum at first at the joint formed by the tibia and the fibula on the one hand and the astragalus and the calcaneum on the other. This must have been a rather inefficient system for, with the astragalus and the calcaneum side by side, most of the force exerted on the tuber by the triceps surae must have been transmitted directly through the calcaneum to the distal portion of the foot, with very little being transferred to the foot via the astragalus. There was, therefore, an unequal distribution of the muscular force applied at the tuber. This arrangement had no appreciable effect on the weight distribution at this stage, as the body

weight was transferred both to the astragalus and the calcaneum through the tibia and the fibula, although most of the weight must have been carried by and transferred to the former. Thus, it seems evident that while the calcaneum transmitted the greater part of the muscular force, the astragalus transmitted the greater part of the body weight to the more distal portion of the foot. As a result of the superposition, a certain proportion of both forces was transmitted to both proximal elements and then through them to the more distal portions of the foot, specifically, directly to the heads of the metatarsals. The fulcrum was then located at the talocalcral joint.

Finally, the appearance of the sustentaculum was undoubtedly followed by a certain amount of actual superposition. It was this superposition that actually brought about the loss of the calcaneofibular articulation. With the development of the extensive articular surface between the astragalus and the calcaneum in a plane almost paralleling the plane of the foot, the functional subastragalar joint (talocalcaneal) was established, permitting for the first time so-called pronation and supination.

The effect of the superposition of the astragalus upon the calcaneum has been discussed by W. Abel (1930). He believes that it caused two major changes in the foot, one in the creation of a two-layered condition in the tarsus, and the other, a result of the first, an alteration in the axis of motion of the foot. Along with the superposition of the astragalus, the navicular was pushed above the cuboid, forming, along with the astragalus, what Abel calls the upper layer. The cuneiforms, no longer able to remain in the same horizontal plane as the cuboid, were thrown into an arcuate arrangement. As the cuboid was tilted to complete the arch, it resulted in the creation of the transverse arch of the mammalian foot. Morton (1935, p. 17) also is of the opinion that the transverse arch was created by the superposition of the astragalus.

In order that the subastragalar joint might be functional, or in other words, in

order that the foot might pronate and supinate, the astragalus assumed a functional role as part of the crus. This made it necessary for movement to occur between the astragalus and the navicular. This situation undoubtedly favored the development of a rounded head on the astragalus and a concave proximal surface on the navicular. Abel's contention that the tarsus may be divided into two layers can, it would seem, only apply to the proximal elements of the tarsus, in that the astragalus moves on the calcaneum. The more distal portion of the tarsus, although it is thrown into an arc, cannot be considered as either structurally or functionally two-layered.

The one remaining joint that is characteristic of the mammalian foot is the transverse tarsal joint. It is situated between the astragalus and the calcaneum on the one side and the cuboid and the navicular on the other. The function of this joint in man and the chimpanzee has been discussed by Elftman and Manter

(1935a). They are of the opinion that the longitudinal arch of the human foot is the result of the transverse tarsal joint being locked in a plantar-flexed position.

If the longitudinal arch be defined as an arch resulting from permanent plantar-flexion of the transverse tarsal joint, strictly speaking, man may possibly be the only animal possessing it, although this point will bear future investigation. This joint reaches its extreme in mobility in the artiodactyl where it is just as functional as the upper ankle-joint. In this case the arrangement of the joint planes allows dorsiflexion only. By definition, therefore, there is no true longitudinal arch in the therapsids or any of the other reptilian groups. Furthermore, there is no indication that a transverse tarsal joint was ever developed in any of the therapsids without the support of plantar pads, as in the *Lycaenops* foot. The articular surface between the astragalus and the navicular is a simple, plane surface that allowed no movement.

THE EXTRINSIC AND INTRINSIC MUSCULATURE OF THE REPTILIAN HIND-FOOT AND ITS RELATION TO LOCOMOTION

Although there are some variations in the cruropedal and pedal musculature in the existing orders of limbed reptiles, it is possible, as the work of Ribbing (1909) demonstrates, to observe fundamental similarities. The musculature of this region in *Iguana* (Fig. 19) is quite typical and represents about the maximum degree of differentiation found in this class. In order to clarify a number of points dissections were made of the cruropedal and pedal musculature in *Chelydra*, *Sphenodon*, *Iguana*, *Varanus*, and *Alligator*. The papers of Osawa (1898), Sieglbauer (1909), and Rabl (1916) were found helpful in this connection.

Extensor Series

In the reptiles, the tibialis anterior (extensor tibialis of amphibia) arises from the proximal portion of the tibia, while in the Caudata, Anura, and presumably in the labyrinthodonts, this muscle arises from the lateral condyle of the femur. This

shift in origin undoubtedly occurred when the femorotibialis and the ilirotibialis became the principal extensors of the crus. The insertion on the base of the first metatarsal in all reptiles indicates that its action has always been to dorsiflex the foot, particularly the medial border.

The extensor digitorum longus (communis) has retained its primitive point of origin on the lateral femoral condyle. In the Lacertilia and *Sphenodon* and also in the Crocodilia its insertion has been limited to the base of the second and third metatarsals, while in the Chelonia it inserts on all but the first metatarsal. In all recent reptiles the tendons of insertion are attached to the base of the metatarsals, while in birds and mammals they have migrated out to the distal phalanges. In the latter groups this muscle functions not only as an extensor of the foot as a whole, but also as an extensor of the digits. In other words, the extrinsic extensor of the digits has taken over more complete control, supple-

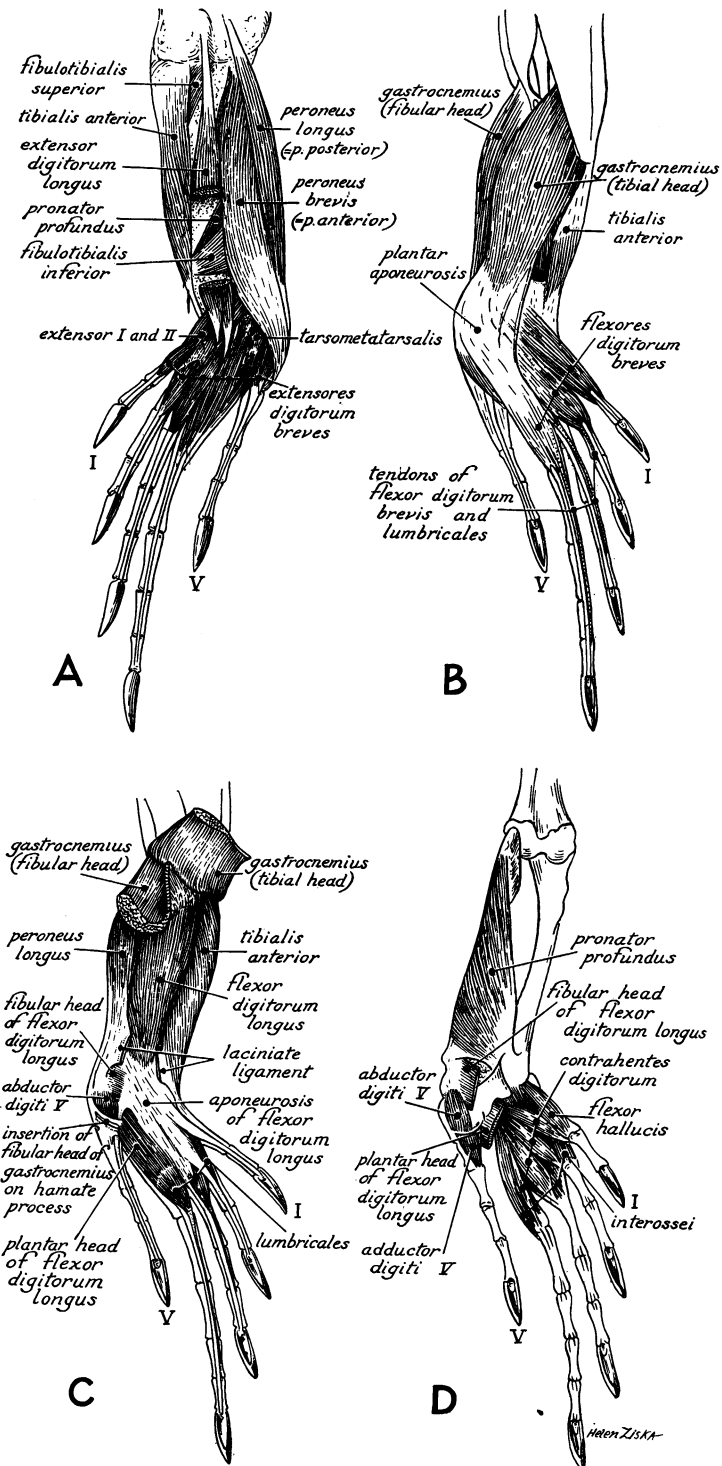


Fig. 19.—The crural and the pedal musculature of *Iguana*. A, extensor musculature; B, C, D, successively deeper layers of the flexor musculature.

menting the action of the extensor digitorum brevis. The migration to the distal phalanges was probably favored by the arboreal habitus of the earliest birds and mammals as a means of effectively and quickly extending the toes after relaxing the hold on a branch.

Although the reduction in the number of tendons of insertion of the extensor digitorum longus is evident in the lizards and crocodiles, there is no evidence of such reduction in the birds and mammals in which the tendons of insertion run out to the distal phalanges. The nature of the insertion cannot be ascertained in any of the extinct orders with reasonable certainty. It would appear logical to assume that the tendons of insertion were attached to the proximal ends of the metatarsals in the cotylosaurs, the eosuchia, the thecodonts, and possibly the pelycosaurs and at least the more primitive therapsids. It is probable that they migrated out to the distal phalanges in the dinosaurs and pterosaurs.

One of the most interesting problems in the evolution of the foot musculature is that of the changes in the peroneal musculature that occurred in the lizards, crocodiles, birds, and undoubtedly in the most advanced therapsids. By an alteration in its topographical relationships, one or both divisions are changed from an extensor into a flexor. As in the caudate amphibians, the peroneus (extensor fibularis) of the *Chelonia* is divided into several parts and this is also the case in the lizards and the alligator. In *Sphenodon*, on the other hand, the muscle appears to be undivided. Its origin on the fibular shaft and its insertion on the lateral surface of the fifth metatarsal just anterior to the axis of the mesotarsal joint causes it to extend the foot to a slight extent and to elevate the lateral border.

In the lacertilians, as in the crocodiles, the peroneus has differentiated into brevis (anterior) and longus (posterior) portions. The brevis arises from the fibula and inserts on the dorsal and the lateral surfaces of the fifth metatarsal. It dorsiflexes the foot to a slight extent and elevates the lateral border. The longus arises from

the lateral condyle of the femur and inserts into the ligamentum laciniatum and also by a strong tendon into the hooked portion of the fifth metatarsal. Hence, as Tornier (1927) has pointed out for *Varanus*, it runs along the ventral surface of the processus lateralis. Being posterior to the axis of rotation of the mesotarsal joint, the peroneus longus functions as a flexor. This change in function was probably brought about by the development of the processus lateralis, separating the brevis and the longus near their insertion.

As Morton has stated (1935, p. 75), the changes in the course of the tendons of the longus and the brevis, as they appear in mammals, must be associated with the superposition of the astragalus upon the calcaneum. Superposition had the immediate effect of narrowing considerably the posterior portion of the foot, and, associated with this narrowing, the tendons of both the peroneus longus and brevis slipped behind the lateral malleolus. This shift placed the line of pull of these muscles behind the axis of rotation of the crurotarsal joint instead of in front, as in all amphibians and most reptiles. Under these conditions the muscles must necessarily act as flexors rather than extensors. Jones (1941) has pointed out, however, that the chief action of the peronei during propulsion is the distribution of weight among the metatarsals.

Morton (ibid, p. 75) is of the opinion that the separation of the primary fibular extensor mass into the peroneus longus and brevis did not occur until after the change in the course of the tendon of insertion. In every type examined, except *Sphenodon* and *Varanus*, however, as pointed out above, the peroneus is divided, and was certainly divided at the stage represented by the baurimorphs. Morton states that the superposition of the astragalus upon the calcaneum so altered the position of the latter relative to the fibula, that the displacement of the tendon occurred. Possibly the most important step in the shift was the slipping of the tendons behind the lateral malleolus, and this must have occurred at the time when the superposition caused a certain amount of

forward displacement in the articulation of the tibia and the fibula relative to the tarsus. The peronei, on the other hand, maintained their old insertion on the base of the fifth metatarsal, with the result that the fibula was displaced relatively to a position in front of the tendons.

The fibula of *Bauria* does not have a well-developed, lateral malleolus, although it is possible that the peronei could have functioned as flexors with the longus and possibly also the brevis passing along the plantar surface of the lateral process of the calcaneum. The lateral process on the *Bauria* calcaneum is certainly not a peroneal tubercle nor is it necessarily homologous with that tubercle on the mammalian calcaneum, but is, more likely, an extension of the entire lateral border, homologous with the processus lateralis. The peroneal tubercle is simply a projection on the lateral surface that must have developed along with or after superposition. It is of great importance, however, in directing the tendons more ventrally and thus increasing the flexing power.

In the alligator the peroneus brevis inserts for the most part on the fifth metatarsal, but to some extent on the distal outer surface of the calcaneum. It functions as an extensor (dorsiflexor). The relatively much larger peroneus longus, on the other hand, inserts on the outer surface of the tuber, posterior to the axis of the ankle-joint and is, hence, a flexor. Its migration into this position was accomplished simply by a posterior migration of the broad tendon of insertion.

In the birds, the peroneus longus arises from the upper half of the dorsal surface of the tibia and inserts mostly into the tibial cartilage (a block of fibrocartilage situated on the ventral surface of the tibia between the condyles), and the tendon of the flexor of the third toe. Thus, by virtue of its insertion posterior to the axis of the ankle-joint, it functions as a flexor of the tarsometatarsus.

The abductor and extensor hallucis, or the so-called supinator of the Amphibia, is well developed in the Chelonina, Lacerilia, and Crocodilia. It still arises from the distal end of the fibula and the fibulare

and inserts on the first and sometimes on the second digits. It functions almost entirely as an extensor of the first and second digits.

The presence of the separate extensor hallucis longus in birds and mammals, arising from the tibial shaft and inserting on the terminal phalanx of the first digit, is again a specialization associated with the arboreal habitus. It must have split off from the extensor digitorum longus.

The extensor digitorum brevis is usually divided into a number of slips and two layers. The divisions arise for the most part from the proximal tarsal elements and their tendons insert into the bases of the distal phalanges. In mammals all the parts tend to converge toward an origin on the calcaneum, although some parts still arise from the fibula (i.e., *Caenolestes*). This condition must have arisen in the therapsids, and very probably *Bauria* had a completely mammalian arrangement of these slips.

It is highly probable that the dorsal musculature did not differ extensively in any of the orders of reptiles in spite of the different trends in tarsal evolution. The most important change was the shift in the insertion of the peronei in the lacerilians, crocodiles, birds, and presumably in the advanced therapsids, causing these muscles to act as flexors rather than as extensors. It is not possible to determine whether such a shift occurred in the dinosaurian orders or in the pterosaurs, although it is quite possible in both cases.

Flexor Series

At some early stage in reptilian evolution the flexor primordialialis communis split into two layers, the superficial becoming the gastrocnemius, and the deeper, the flexor digitorum longus (flexor profundus). The mechanical causes favoring such a division are obscure, although in a thick muscle-mass, such as the flexor primordialialis communis, certain regions are undoubtedly more concerned with the complete flexion of the digits, while other regions are more concerned with flexing the foot as a whole. This differential action of groups of fibers within the same

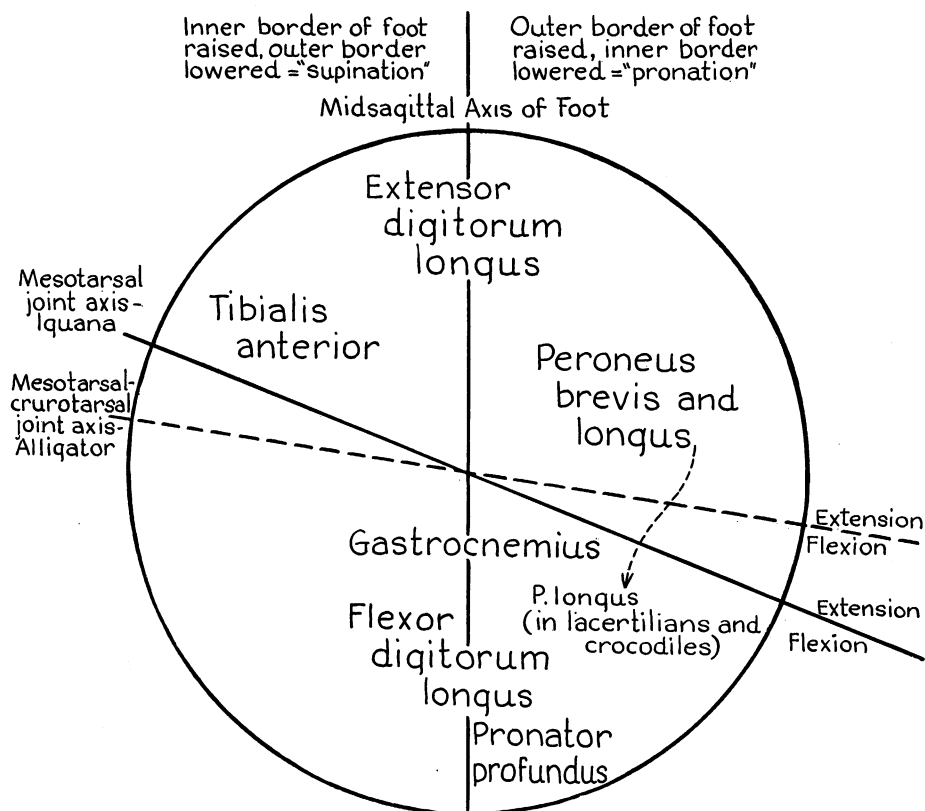


Fig. 20.—A diagrammatic representation of the action of the extrinsic pedal musculature in a lacertilian (*Iguana*) and an alligator. Note the change in the action of the peroneus longus from the primitive condition found in the chelonians and *Sphenodon*.

muscle due to slight differences in origin, insertion, or in direction, could very well result in such a subdivision.

The gastrocnemius was apparently split into tibial and fibular portions soon after it separated from the primitive flexor mass, or it may have separated off into two parts. The origin of the tibial portion is subject to some variation, arising either from the femur or tibia or both. It inserts, for the most part, into the plantar aponeurosis, but in many cases with a small slip to the base of the fifth metatarsal, as in *Iguana* and *Sphenodon*. In the Recent Reptilia, the fibers of the tibial head run diagonally across the crus with the lateral border of the muscle inserting on the fifth metatarsal. The femoral head of the gastrocnemius springs from the lateral surface of

the lateral condyle of the femur. It inserts for the most part into the plantar fascia, although it has a supplementary insertion on the fifth metatarsal. In the Crocodilia, the tendon of the relatively much larger fibular portion passes directly over the tuber and is partially attached to it, although the actual insertion is into the plantar aponeurosis. The tibial head joins the fibular at the tuber, as does also the long tendon of the flexor tibialis. The latter, through this tendon, amplifies the action of the gastrocnemius and peroneus longus to a slight degree.

The usual function of the gastrocnemius is stated to be plantarflexion of the foot in association with propulsion. Another important phase of its action, particularly in the more primitive reptiles, is to prevent

the foot from sliding forward as the body-weight is shifted to one or the other hind-limb at the beginning of propulsion. This is essentially the same function performed by the flexor primordialis communis in the caudate amphibian foot.

It was stated in the section on amphibian locomotion (p. 419) that the primitive tetrapod foot takes a very small part in the propulsive effort. This was probably the case when the very supple nature of the foot is taken into account, as well as the body-weight compared with the size of the flexor primordialis communis, and the angle of application of this muscle (discussed below). In the Anura, on the other hand, the work of Hirsh (1931) demonstrates that the elongated tarsal elements, motivated by the homologue of the flexor primordialis, usually called the plantaris longus, plays a very active role in propulsion. The plantaris longus, however, is relatively very large and powerful compared to the size and weight of the animal and the size and length of the segments moved by it.

It would appear that the ability of the flexors to enable the foot to participate actively in the propulsive effort is dependent on the size and weight of the animal, on the relative size of the flexors concerned, on the degree of consolidation within the tarsus, and, finally, but of great importance, on the angle of application (the angle between the axis of the muscle and the axis of the part moved). Steindler (1935) has pointed out that if the angle of application is under 30 degrees the force exerted by the muscle has a greater stabilizing than rotary component. He figures the condition in the human knee, a type of joint basically similar to the mesotarsal type of ankle-joint. In the former the angle of application is increased by the presence of the patella, forcing the applying tendon to make an angle in its course instead of running in a straight line from the femur to the cnemial crest. With all these variables that must be considered, it is very difficult to determine, with a reasonable degree of accuracy, the importance of the foot in the propulsive effort in many of the fossil reptiles.

It would seem, in the case of the cotylosaurs and in the terrestrial forms grouped under "Type I," that the foot could have exerted relatively little forward thrust during propulsion. There is no evidence indicating that the gastrocnemius was relatively larger in these groups than in the labyrinthodonts, although the body-weight was certainly as great in many cases. Furthermore, the gastrocnemius was inserted into the plantar aponeurosis, which in turn was practically parallel to the plane of the foot, resulting in a very small angle of application. A similar situation must have existed in the eosuchians and pelycosaurs (Fig. 21,B), and in the therapsids lacking a tuber calcanei. Romer (1940, p. 165), has stated that a portion of the gastrocnemius was inserted on the thinned proximolateral border of the pelycosaur calcaneum. This being the case, the angle of application would indeed be very small.

In the lizards and *Sphenodon* there is evidence of the active participation of the foot in propulsion to at least a limited degree. The axis of the fibular head of the gastrocnemius, when continued distally, passes through the hooked-portion (hamate process) of the fifth metatarsal. This portion of the gastrocnemius, furthermore, has a very strong insertion on the elevated and thickened distomedial border of the hook, as pointed out before (Fig. 21, C). This arrangement has the effect of increasing the angle of application, and the ventrally extended portion of the hook may be looked upon as the functional analogue of the tuber calcanei. In *Varanus komodoensis*, this portion of the hook amounts to a ventrally directed tuber. The position which the lizard's foot is forced to assume during the latter half of propulsion, however, is not favorable for its active participation as the leverage action of the foot cannot be employed to full advantage.

In the more advanced thecodonts and, as mentioned earlier, in one primitive family of theropod dinosaurs, the Hallopodidae, the calcaneum possessed a tuber, although the calcaneum was functionally united with the crus. This tuber did, however, influence the orientation of the

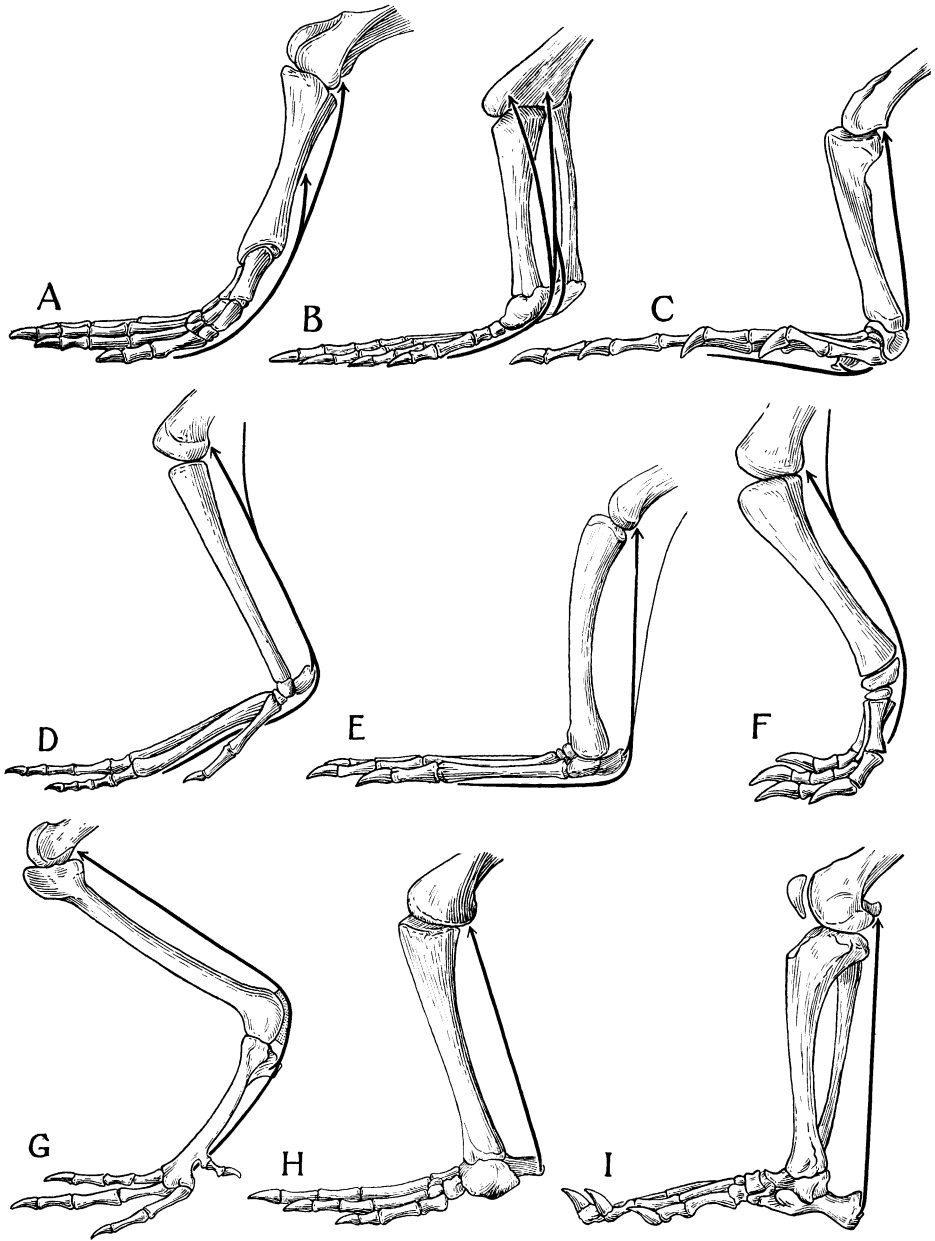


Fig. 21.—Medial views of the lower leg and foot of A, *Trematops* (from model); B, *Varanosaurus* (after Romer and specimen); C, *Iguana* (from specimen); D, *Saltoposuchus* (after von Huene); E, *Alligator* (from specimen); F, *Plateosaurus* (from specimen); G, *Gallus* (from specimen); H, *Bauria* (from model); I, *Taxidea* (from specimen). The heavy black lines indicate the course of the gastrocnemius (the flexor primordialis communis in the case of *Trematops*).

tendons so that they inserted at a slight angle to the plane of the foot, thus presumably enabling the gastrocnemius to exert a more effective pull on the foot by increasing the angle of application. In view of its functional importance, it is rather puzzling that this tuber should have been lost in all the other descendants of the thecodonts, except the crocodiles. With the exception of the Hallopodidae, neither the saurichian nor the ornithischian dinosaurs have any indication of a structure that would increase the angle of application. In view of this fact, the extrinsic flexors had to be of relatively great size to permit the active cooperation of the foot. The same reasoning would seem to apply to those therapsids in which the tuber calcanei is lacking.

With the appearance of the tuber in the advanced therapsids, and with its retention in the crocodiles, in both cases associated with a calcaneum, which, in turn, is functionally united with the foot, the mechanical setting is much clearer. The foot is, under these conditions, definitely a lever of the first class, as was pointed out earlier, and the muscular force, being applied at almost a right angle, goes almost entirely into the rotary component. In other words, the foot definitely participates in the propulsive effort and, assuming other things to be equal, the longer the tuber, the less the amount of power required of the gastrocnemius, but the slower the action.

In the birds, the angle of application of the gastrocnemius is increased by the presence of the hypotarsus and by the tibial cartilage. Both structures are grooved to guide the tendons of the gastrocnemius over the ankle-joint and, therefore, they bring about the active participation of the foot in propulsion. The gastrocnemius has an attachment on the hypotarsus and finally inserts on the sheath of the digital flexor tendons. A soleus arises from the tibia and inserts on the tibial cartilage.

With the development of the tuber in the therapsids, the gastrocnemius lost its insertion into the plantar aponeurosis and inserted directly on the tuber. Also at this stage, the fibular head of the gastroc-

nemius subdivided into three parts, the largest retaining the same name, the other two becoming the soleus and the plantaris. The soleus undoubtedly represents a portion of the gastrocnemius externus that migrated on to the tibia and the fibula and was separated from the gastrocnemius through differential action. The plantaris, on the other hand, while arising from the lateral condyle, maintained its ancient insertion into the plantar fascia. The latter gives every indication of being the only part of the gastrocnemius that did not develop a new insertion on the tuber.

The other derivative of the flexor primordialialis communis, the flexor digitorum longus, has in all reptiles several heads of origin: from the lateral condyle of the femur, from the upper third of the fibula, and one or two transverse tendinous bands from the distal end of the fibula or the fibulare and the fifth metatarsal. These divisions unite in the lower third of the crus to form a broad, flat tendinous sheet covered by the plantar aponeurosis. The former then splits into five, or sometimes less, tendons that extend to the distal phalanges, where they become attached.

In the primitive tetrapod foot, and also in the types with a metatarsal joint, the flexor digitorum longus has a relatively broad plantar tendon. It becomes narrowed somewhat in the Sauria as it passes through a shallow groove on the plantar surface of the astragalocalcaneum. In *Alligator*, the presence of the tuber has forced the tendon toward the medial side as it has in the mammals, and undoubtedly did in the therapsids having this structure. In birds, the digital flexor musculature has reached an extreme stage of differentiation, each digit being flexed by separate muscles, a condition obviously associated with prehension.

The pronator profundus (sometimes called the tibialis posterior in reptiles) is a very powerful muscle. In all cases it arises from the entire length of the fibular shaft and inserts by means of a strong tendon into the base of the first metatarsal, and in some cases, also, the second metatarsal. The pronator profundus functions to some extent as a flexor, but it is

also an adductor of the hallux. That such a powerful muscle should function mainly as an adductor seems unlikely. A more important function would appear to be, as in the primitive tetrapod, that of slightly pronating (in the lacertilians) and adducting the foot at the end of the recovery phase. During propulsion its contraction can only evert the knee.

There has been considerable disagreement regarding the origin of the mammalian flexor fibularis. Without discussing the matter in detail here, the conclusion of Howell (1939) appears most reasonable, namely, that it has been separated from the flexor digitorum longus (flexor tibialis) and has no relationship with the pronator profundus, which is probably the homologue of the mammalian tibialis posterior.

The deepest layer of the extrinsic series of muscles is divided into proximal and distal parts. The proximal portion, the interosseus cruris or fibulotibialis superior, arises from the medial side of the fibula and the interosseus membrane and inserts on the proximal half of the tibia at a more distal level. The distal portion, the fibulotibialis inferior, arises from the distal half of the fibula and inserts on the lower third of the tibia. This layer is concerned with the maintenance of the normal relations of the tibia and fibula during propulsion.

The Plantar Musculature

The plantar musculature was presumably but little altered from the primitive tetrapod plan until the tuber calcanei appeared in the advanced therapsids, or the highly specialized tarsometatarsus developed in the birds, favoring its reduction. It is composed of two basic layers (Howell, 1939), each being subdivided into several minor layers. It is not required here to discuss this musculature in detail, or to trace its homologies. Briefly considered, it is concerned with the flexion of the digits, in some cases amplifying the action of certain of the extrinsic flexors, and, in some mammals, with the maintenance of the longitudinal arch.

The superficial layer consists of the

flexor digitorum brevis and the lumbricales. The former has its origin for the most part from the plantar aponeurosis, although a deeper layer may arise from the aponeurosis of the flexor digitorum longus, and inserts into the proximal phalanges. It is not only concerned with flexing the digits, but also with amplifying to a slight extent the action of the gastrocnemius. With the development of the tuber in the therapsids this continuity was broken, the gastrocnemius inserting on the tuber and the plantar aponeurosis, and the flexor digitorum brevis arising from the plantar surface of the tuber.

The quadratus plantae of mammals is considered by Howell to be a remnant of the extrinsic musculature interposed between the superficial and deep layers. This observation would appear tenable in view of the fact that the quadratus plantae has no homologue in the amphibian intrinsic musculature. It may represent a distal muscular portion of the flexor digitorum longus, which was left behind on the sole during the alteration in the orientation of the distal portion of this muscle necessitated by the development of the tuber.

Among recent reptiles there is no tendency for the superficial layer to develop independent abductors of the marginal digits; they are very probably associated with the arboreal ancestry of the mammals, where the independent action of the first and fifth digits was favored.

The lumbricales arise from the dorsal surface of the plantar aponeurosis of the flexor digitorum longus and insert into the tendons of the flexor digitorum brevis. They are likewise flexors of the digits, amplifying the action of the flexor digitorum longus to some extent.

The deep layer is made up of the contrahentes digitorum and the various divisions of the interossei. The contrahentes digitorum has maintained its identity from the amphibian stage and is present in all recent reptiles. In the caudates it arises mostly from a tendinous band attached to the second to the fifth tarsalia, while in the reptiles it arises from the fifth metatarsal. In the reptiles it has, therefore,

shifted and concentrated its origin on the lateral side of the foot. The contrahentes are mainly adductors of the digits, particularly of digits one, two, and three. If a slip is present for the fourth digit, it can only act as a flexor. The adductor of the fifth digit, and possibly also the abductor, are probably derived from this layer.

The interossei (flexor breves profundi), having their origin on one digit and inserting on the adjacent digit at a more distal level, act as adductors and flexors. They are usually divided into several layers.

The plantar musculature in the extinct orders must have been very similar to that just described, except in the aquatic forms and in those types in which it was reduced. In such types as the ichthyosaurs and pleisosaurs there must have been a reduction and secondary simplification of the extrinsic and intrinsic musculature, as the more distal portion of the paddle could only be flexed to a very limited degree. In the less specialized aquatic forms, such as some of the protorosaurs, it was probably not reduced.

SUMMARY

1.—Both the number and the disposition of the elements in the tarsus of the rhachitome *Trematops* indicate that it is the most primitive completely preserved tetrapod tarsus known. This tarsal pattern is dominated by a convergence of the elements, excepting those along the preaxial border, toward the fibula, a condition inherited from the rhipidistian pelvic fin and persisting into the caudate amphibian tarsus. Although movement could occur between most of the tarsal elements in varying degrees, the important plane of flexure during locomotion was between the tarsalia and the metatarsals, as is the case in the caudates.

2.—The known tarsi of other rhachitomes, the embolomeres, and stereospondyls are incompletely and variably ossified. The available evidence indicates a general agreement with the *Trematops* pattern, although there may be a reduction in the number of elements present.

3.—The tarsus of the Lepospondyli, an order now considered to be ancestral to the Caudata, is known in only two forms. That of the nectridian *Scincosaurus* cannot be ancestral to the reptilian tarsus, as Broom believes, nor is there any evidence to support his view that the tibiale is homologous with the mammalian navicular. The tarsus of the *Microsauria*, considered to be directly ancestral to the caudates, is known only in the case of the poorly preserved although completely ossified tarsus of *Hylloplesion*.

4.—The pertinent literature on the

caudate tarsus is discussed and its marked resemblance to the primitive tetrapod tarsus is stressed by description and by a pictorial phylogeny. The sporadic occurrence of ossification in the amphibian tarsus, excepting the anuran, is considered to be genetic and not related to the habitus of the animal.

5.—The variation in the centrale region of the tarsus is discussed. It would appear that the number of centralia present is of no functional importance and hence that there has been no selection toward a constant number.

6.—Previous work on the embryology and phylogeny of the anuran tarsus is critically reviewed. It is concluded, on embryological evidence, that the two elongated proximal tarsal elements are the fibulare and the tibiale plus several centralia and possibly the intermedium. There are no paleontological data to support or refute this view. The relationship between specialization in the tarsus and the lack of variation is discussed.

7.—The basic resemblance between the caudate and the labyrinthodont tarsus is evidence against the theory that the caudates were independently derived from the Dipnoi, and the Anura from the Labyrinthodontia. The very early embryonic stages of the tarsus are very similar in the Caudata and the Anura, although the specializations of the anuran tarsus are evident as soon as the anlagen of the tarsal elements are formed.

8.—All the evidence indicates that the

labyrinthodonts, like the caudates, had their hind-feet forwardly directed during locomotion, although the femoral head is terminal and there are no diarthrodial tarsal joints. The necessary adjustments allowing this were made in the crus. The tibia assumed a diagonal position, lessening the functional length of the inner side of the crus, and thus permitting the foot to be forwardly directed throughout propulsion.

9.—By means of motion pictures of the locomotion of *Triturus* and *Ambystoma* it is possible to describe in detail the movement of the hind-limb during propulsion and recovery. With this information, deductions are made concerning the movements of the hind-limb in the labyrinthodonts.

10.—The pressure-distribution of the amphibian foot, as deduced from fossil footprints, is discussed, together with the forces acting on the hind-limb during locomotion and their relation to the structure of the crus and tarsus. The foot probably did not enter actively into the propulsive effort to any great extent in the primitive tetrapods, but functioned mainly as an expanded base through which the tractive forces centered around the femur were applied to the ground through the crus.

11.—The extrinsic and intrinsic musculature of the amphibian hind-foot is described with particular emphasis on the functional grouping of the muscles in producing the characteristic movements of locomotion. There is no true pronation and supination in the amphibian foot, these movements occurring only in a limited degree in the mammalian foot.

12.—The origin of the reptilian tarsus is critically examined. Both ontogenetic and phylogenetic evidence is presented. The position is here taken that, although the calcaneum is only the fibulare, the astragalus is compound in origin, being made up of the intermedium, a centrale, and possibly the tibiale.

13.—The evolution of the tarsus within the Cotylosauria resulted in a number of distinct types. That of *Labidosaurus* is considered to be representative of the primitive, definitive reptilian type. The

tarsus of *Seymouria* is essentially amphibian, while that of the diadectomorphs is specialized, culminating in the pareiasaurian condition in which the astragalus and calcaneum are coössified, and the functional ankle-joint is mesotarsal.

14.—The reptilian tarsus originating from a *Labidosaurus*-like type evolved roughly along three different lines:

TYPE I.—Retention of the primitive pattern or a modification of it for an aquatic habitus, to a greater or lesser degree, in the Mesosauria, Ichthyosauria, Sauropterygia, Protosauria.

TYPE II.—Modifications leading to the mesotarsal joint as the functional ankle-joint, in the Chelonians and the orders descended from the Eosuchia. The joint probably developed independently in the archosaurs and lepidosaurs, as it was not developed in the eosuchians and possibly not in the most primitive thecodonts.

TYPE III.—Modifications leading to the crurotarsal joint as the functional ankle-joint in the pelycosaur, therapsids, and mammals.

15.—In the first type the functional ankle-joint remained tarsometatarsal unless the foot degenerated into a paddle with most of the flexion in the digits, as in the ichthyosaurs and plesiosaurs.

16.—In the second type the mesotarsal joint was elaborated in various ways. In all the orders in this category, excepting the Crocodilia, the astragalus and calcaneum are functionally part of the crus. In the latter there is movement between the astragalus and the calcaneum and between the latter and the fibula. In every case there is a marked reduction in the number of distal tarsal elements, a modification that occurred along with formation of the mesotarsal joint.

17.—The locomotor movements of the hind-limb are determined as much by the morphology of the femur as by the structure of the tarsus. Regardless of the plane in which the femur moves throughout propulsion, the foot is directed forward, unless, in the case of the *Sphenodon* and the lizards, the twisting of the femoral shaft and the structure of the tarsus forces it to rotate laterally as retraction progresses.

18.—The crurotarsal joint, characteristic of the third type, first appeared in the pelycosaur. Although the femoral head

is terminal and the knee-joint permanently crooked, the rounded tibial facet on the astragalus, plus the fact that the tibial articulation is on a more distal level than the fibular, permits the foot to be forwardly directed. Although the fibular facet is restricted to the proximal border, the tibial has migrated somewhat on to the dorsal surface.

19.—The development of the mesotarsal and the crurotarsal joints may be looked upon as two different ways of treating the stress in the proximomedial region of the primitive tarsus. In the case of the former the joint is constructed to resist the stress, in the latter to eliminate it.

20.—The therapsid tarsus evolved along several distinct lines. In the dromasaurians, dinocephalians, and dicynodonts, the calcaneum remained dorsoventrally compressed and the astragalus tended to lose its rounded facet. In the gorgonopsians, therocephalians, cynodonts, and bauriamorphs the rounded tibial facet on the astragalus was retained, and the tibial and fibular facets on the calcaneum tended to migrate completely on to the dorsal surface. This migration freed the proximal border of the calcaneum, permitting a tuber to develop.

21.—The therapsid femur early developed a medially directed head without any accompanying twisting in the shaft, and the femur swung more and more in a

plane approaching ninety degrees. The well-rounded tibial and fibular facets eliminated the torsion in the tarsus and formed a highly mobile hinge joint.

22.—The tuber calcanei developed independently in the Thecodontia and the Therapsida. Of the orders derived from the thecodonts, the tuber was retained only in a primitive family of theropod dinosaurs, the Hallopodidae, and in the Crocodilia.

23.—At some stage between the therapsids and the mammals the astragalus became superimposed upon the calcaneum. This alteration relieved the fibula of its articulation with the calcaneum and the tibia became the weight bearing axis of the crus. The functional implications of the superposition are discussed, the most important being the creation of the subastragalar joint, permitting so-called supination and pronation for the first time, and the formation of the transverse tarsal arch.

24.—The extrinsic and intrinsic musculature of the reptilian foot is described with emphasis on function. The role of the foot in propulsion is evaluated, particularly in relation to the angle of application of the gastrocnemius. In this connection, the ventrally directed portion of the hook on the fifth metatarsal of lizards is considered to be the functional analogue of the tuber calcanei, in that it increases the angle of application of the fibular head of the gastrocnemius.

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