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THE APPENDICULAR SKELETON OF THE PERMIAN EMBOLOMEROUS AMPHIBIAN *ARCHERIA*

BY

ALFRED SHERWOOD ROMER

1817

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CONTENTS

ALTHOUGH the name Embolomeri was created by Cope in 1885, little attention was paid to this group until the publication by Watson of his important series of papers on the labyrinthodont amphibians in 1919, 1926, and 1929. He pointed out that the embolomeres were a dominant Carboniferous group of amphibians which possessed many primitive characters and, further, showed many features suggestive of relationship to the ancestry of reptiles. The nature of embolomere structure is thus a matter of great importance in the study of tetrapod history, and Watson in his papers of 1926 and 1929 described as fully as possible the anatomy of the known embolomeres (and presumed embolomeres) of the Carboniferous.

Carboniferous amphibians, however, are for the most part preserved in slab form in a crushed, essentially two-dimensional condition, and despite his best efforts, Watson's account left many unfortunate lacunae in our

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knowledge of the group. Although the embolomeres were mainly a Carboniferous group, it had long been known that a surviving member was present in the Texas Permian red beds where, typically, proper three-dimensional preservation is the rule. Of this form, long called *Cricotus* but more correctly termed *Archeria,* two partial skeletons had been found as long ago as 1880 (Case, 1911, Pl. 24, etc.). These specimens were, unfortunately, contained in a refractory matrix which made them of relatively little value for morphological study, and although numerous fragmentary remains were found in later decades, these further specimens yielded little data of value. Case (1915) had found numerous vertebrae of the *"Cricotus"* type in the Briar Creek bone bed, and suggested that various isolated girdle and limb elements found there might well pertain to this form. It seemed to me that intensive search of these Texas beds should eventually result in the discovery of adequate skeletal remains of *Archeria,* making possible a distinct contribution to knowledge of embolomere structure and, hence, of tetrapod evolution.

In consequence, discovery of embolomere material was my prime objective when I began work in the Texas red beds. With youthful optimism I dreamed of gathering skeletons of *Archeria* on my first trip to these beds in 1926. As might be expected, I was disappointed; similar disappointment met me in subsequent years. Scraps were occasionally discovered, but no articulated material of value. By 1939 I had practically abandoned hope. That year, with a party of eight, a month was spent excavating in the Geraldine bone bed in Archer County, Texas; here numerous individuals of *Edaphosaurus* and *Eryops* were entombed, but *Archeria* appeared to be represented (as frequently) by isolated vertebral elements alone.

Toward the end of the season, however, there appeared, to my gratification and astonishment, a nearly complete skeleton of *Archeria.* Before the work ended for the year we had found three more articulated skeletons, in addition to a considerable number of isolated limb and girdle bones, jaws, skulls and partial skulls. Additional materials came to light in excavations in subsequent years by R. V. Witter and S. J. Olsen before the bone layer "played out." Study of the material was delayed by the war and other pressing duties. With the completion of preparation by R. V. Witter, F. R. Olsen, and S. J. Olsen, there is available sufficient material from this one locality for a satisfactory account of the anatomy of this animal.

In the present paper I shall describe the appendicular skeleton, leaving the accounts of the skull and axial skeletons for future publication. Although the descriptions given below are almost entirely based on the

Geraldine material in the Museum of Comparative Zoology collections, I am indebted to Dr. E. H. Colbert for the privilege of studying materials in the American Museum of Natural History, and to Dr. Claude Hibbard for access to the Briar Creek specimens collected and described by Case. I am greatly obliged to Dr. Erik Stensiö and Dr. Erik Jarvik, of Stockholm, for free access to the interesting skeletal materials (largely undescribed) of that most ancient of known amphibian groups, the ichthyostegids. It is with pleasure that I recall the many stimulating and profitable discussions which I had in years past with Dr. Case on the status of the embolomeres and on many other problems in the Permian history of the vertebrates.

Systematics and stratigraphy.—I propose to consider these topics fully in a paper dealing with the axial skeleton, and shall merely summarize them here. The generic name *Cricotus* was applied by Cope (1875, p. 405) to isolated vertebrae of embolomerous type from an Illinois deposit which he thought to be Permian in age. When, shortly afterward, embolomere vertebrae were found in the Permian of Texas, he not unnaturally applied to them the same generic term. The Illinois beds, however, are now known to be well down in the Pennsylvanian (see, for example, Romer, 1935, pp. 1635–36). Although diagnosis of the genus *Cricotus* is difficult because of the fragmentary nature of the material, it is highly improbable that the same genus was present in these two sets of beds, widely separated stratigraphically. I had felt for many years that it would be necessary to make a new genus for the Texas red beds embolomere. Through an unexpected turn of events this proved unnecessary. Case (1915, p. 170) had described as *Archeria robinsoni* a humerus of unusual pattern which, in the possession of an entepicondylar foramen, appeared to be that of a reptile. When, however, the Geraldine *"Cricotus"* material was prepared and a humerus was for the first time found in association with an embolomere skeleton, it was discovered that the bone was of the *Archeria* type, and that this generic name was thus available for the Texas *"Cricotus."*

Cope at first applied to the Texas specimens a specific name, *heteroclitus,* used for material from Illinois (Cope, 1875, etc.). Later, however, he described two species on the basis of Texas material—*C. crassidiscus* and *C. hypantricus* (Cope, 1884*a,* pp. 28–30). As will be discussed on a future occasion, the former term appears to be that appropriate to the material described in this paper; its proper designation being *Archeria crassidisca.* Certain embolomere specimens from the lowest and highest Texas red beds may differ specifically (and possibly generically), but all specimens on which the present paper is based appear to be cospecific, despite some apparent tendency for specimens from higher beds to be, on the average, somewhat larger in dimensions. All are from the Wichita group, currently considered as basal Permian, and from the Moran, Putnam, Admiral, and Belle Plains formations of that group. The detailed stratigraphy of these deposits, of continental nature in the collecting area, is incompletely known. I have treated stratigraphic position here as in the monograph on pelycosaurs (Romer and Price, 1940, pp. 23–27), and in an account of the Texas beds and their fauna now in press.

Almost all of the present account is based on material from the Geraldine bone bed, lying in the lower part of the Admiral formation of Archer County, Texas (Romer and Price, 1940, pp. 25, 175–76). This is a bog deposit with a lush flora, in which, as noted above, numerous individuals of *Edaphosaurus* and *Eryops* as well as of *Archeria* had been trapped. The matrix, which is readily removed, is in most cases a soft gray clay with a high organic content. There is seldom found any film of harder mineral matter on the bone surface (in contrast to conditions in many other Texas sites). The bone itself is soft and friable and in some instances has been disturbed or destroyed by the invasion of plant roots.

A second locality of importance is the Briar Creek bone bed, discovered by Case (1915, pp. 157–76, Pls. 21–24). This is a deposit of gray clay, presumably a bog deposit comparable to that at Geraldine and containing a similar fauna, except that *Dimetrodon* was common as well as *Edaphosaurus, Eryops,* and *Archeria.* Unfortunately, there is almost no evidence of association of any two or more skeletal elements in this deposit. Apart from these two "bogs," no great amount of *Archeria* material is to be found in any other bone "pocket" in the collecting area, although at least the characteristic vertebral elements have been found in a great number of Wichita Group localities.

Materials.—Below are listed by number, in stratigraphic sequence, those Texas specimens of *Archeria* which include girdle and limb material utilized in the present description. American Museum specimen numbers are prefixed by the letter *A,* those of the University of Chicago collections by *C,* those of the University of Michigan by *M.* All those numbers not prefixed by a letter belong to the collections of the Museum of Comparative Zoology.

From the Moran formation:

1. Little Bitter Creek, Young Co.: 2081

From the Putnam formation:

1. Archer City bone bed: 2214, *A* 7117
2. Four miles east of Archer City: 2220
3. Three and one-half miles southwest of Elbert, Young Co.: 2221

4. (horizon uncertain) One mile northeast of Anarene, Young Co.: 2219
5. (horizon uncertain) Two miles southwest of Belcherville, Montague Co.: 2208

From the Admiral formation, lower part:

1. Geraldine bone bed: 2045–2072, 2094, 2225, 2472 (2045–2049 and 2072 are associated skeletons including much girdle and limb material)
2. North of Little Wichita River, below Kickapoo Lake dam, Archer Co.: 2227

From the Admiral formation, upper part:

1. Briar Creek: 1176, 1177, 2473, *A* 4550, *A* 4550*a*, *C* 109, *C* 132, *M* 3034, *M* 3044, *M* 3246, *M* 3247, *M* 3355, *M* 3362, *M* 3363, *M* 3421–3424, *M* 3426–3427, *M* 3433
2. Rattlesnake Canyon, Archer Co.: 1170, 1172, 1173, 1180, 1287, 1288, 1290
3. South side of Godwin Creek, near mouth, Archer Co.: 1730, 2083
4. Between Kickapoo and Briar creeks, near mouths, Archer Co.: 2228

From the Belle Plains formation:

1. "Hay Camp" pocket, between the Little Wichita and Godwin Creek: 1289, 1748
2. Tit Mountain, Archer Co.: 2082
3. South side of the Little Wichita, opposite Fulda, Baylor Co.: 1363
4. Slippery Creek, south of Dundee: 2075, 2079

Shoulder girdle (Figs. 1, 2).—A complete set of partly articulated shoulder elements is present in No. 2045, and the description below is mainly based on this specimen. The scapulocoracoid is of a normal pattern for Carboniferous and Permian tetrapods. It includes a short scapular blade; below it, a broad coracoid plate curving medially and anteriorly; a strap-shaped glenoid cavity; a supraglenoid buttress pierced by a large foramen. There is no evidence of more than a single ossification. The scapular blade is, as usual, thickened along its rounded posterior margin, thin anteriorly. Its upper edge is unfinished. The seeming shortness of the blade is due to incomplete ossification; when the dermal elements are properly articulated it is seen that there was in life an unossified suprascapular extension of some height, reaching up to the cleithral expansion. In life, the scapular blade was obviously comparable to that of *Diadectes*. Below a point opposite the supraglenoid foramen the anterior margin of the bone turns strongly forward and then curves downward and finally posteriorly to form the margin of the broad coracoid plate. The anterior part of the plate is convex externally in section, forming a segment of a sphere which obviously followed closely the contours of the chest in life. More posteriorly the plate narrows, its ventral margin slanting upward (and outward). This posterior part of the plate is concave externally in anteroposterior section, the boundary between convex and concave parts being a rounded ridge running anteroventrally from the supracoracoid foramen. This foramen, of good size, pierces the bone dorsoventrally to emerge in a pronounced hollow below and in front of the anterior end of the glenoid. The nature (or existence) of the glenoid foramen in early tetrapods has been a point of controversy in many instances. It has been thought, for example, to be merely a nutrient foramen. In *Archeria,* however, there is definitely a small perforating foramen which emerges on the external surface well below the glenoid.

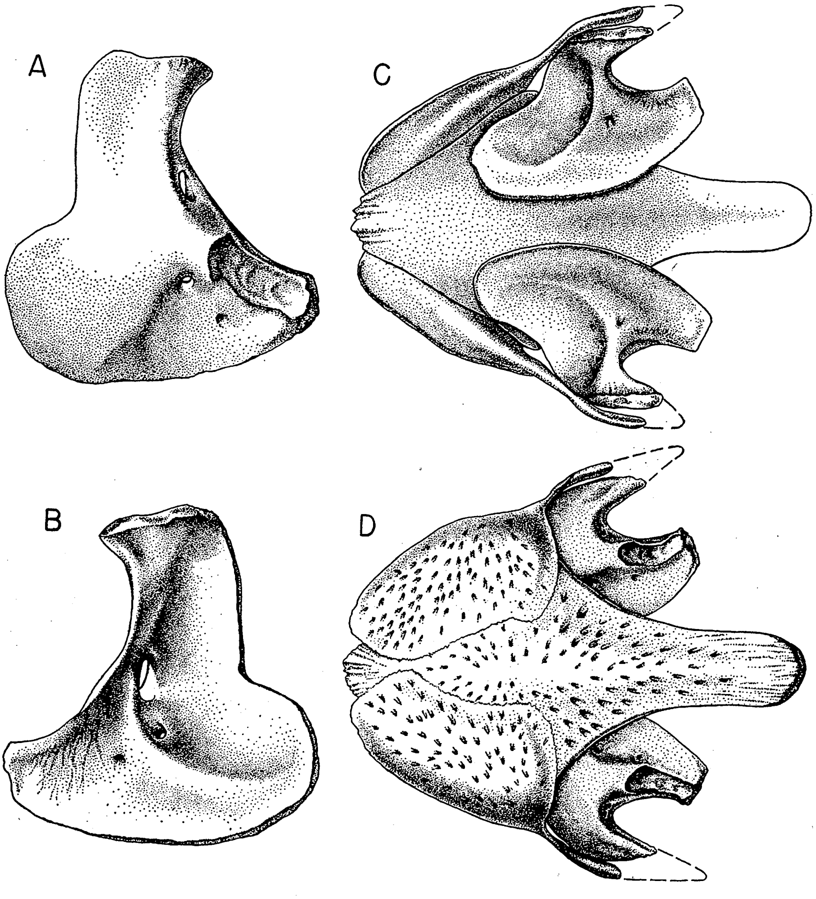

FIG. 1. Shoulder girdle. *A,* lateroventral view of scapulocoracoid; *B,* mediodorsal view of the same; *C,* dorsal view of assembled girdle; *D,* ventral view of the same. Based on No. 2045. *A, B,* × ¾; *C, D,* × ½.

The supraglenoid foramen is exceptionally large, fully occupying the width of the upper part of the supraglenoid buttress and in some specimens even encroaching on the ridge that bounds the buttress anteriorly. Below the foramen the buttress surface may be somewhat excavated or rugose. The glenoid cavity has the typical strap shape generally found in early tetrapods. It commences at a stout anterior buttress and extends back to the posterior end of the bone, curving over about a quarter circle in its course. There is relatively little of the spiral effect frequently noted in early tetrapods. The posterior end of the coracoid, as ossified, truncates the posterior end of this surface, and there was presumably a prolongation of modest extent in cartilage.

On the inner surface of the girdle the curved posterior margin of the scapulocoracoid is rounded and thickened through most of its length. This ridge loses its identity dorsally, where the bone tends to thicken for most of its anteroposterior width and forms a triangular surface for origin of the subscapular muscle. Medial to the supraglenoid foramen the posterior margin of the girdle forms a stout bridge between scapular and posterior coracoid areas. Anterior to this bridge there is a deep subscapular fossa from which the supraglenoid foramen takes origin dorsally and the coracoid foramen ventrally. The inner opening of the glenoid foramen lies posterior to the lower end of the subscapular fossa. Most of the inner surface of the scapulocoracoid follows the contours of the outer surface. In consequence, much of the anterior part of both coracoid and scapular regions forms a broad concave plate; the posterior coracoid region (below the dorsal ridge and behind the subscapular fossa) is, however, somewhat convex in section.

Interclavicle and paired clavicles and cleithrum are present. The interclavicle is roughly an elongate diamond in shape, with rounded anterior and posterior termini. Essentially the two anterior quadrants are shallowly excavated to receive the lower ends of the clavicles. The anterior tip of the interclavicle, somewhat striated longitudinally, is visible in ventral view in a V-shaped area between the diverging clavicles. This area, as well as most of the posterior end of the "diamond," has a surface which bears a somewhat punctate ornament. The posterior end of the bone, unlike that of typical temnospondyls, extends back as a short, broad stem which is longitudinally striated ventrally. That part of the ventral surface of the bone to which the clavicles attach is not visible in any specimen; to judge from the nature of the apposed clavicular surface, the bone was smooth here. The inner surface of the interclavicle is smooth; there are very low transverse ridges between the lateral apices of the diamond.

The clavicles have, in primitive fashion, an expanded, essentially triangular, and flattened ventral area apposed to the interclavicle; the two bones come close together toward the mid-line for a short distance but diverge anteriorly and posteriorly. Like the interclavicle, the ventral parts of the clavicles bear a punctate pattern of ornamentation. The inner surface is essentially smooth, but slightly striate in a pattern radiating from the external angle of the triangle. For the most part, the ventral expansion of the bone is thin, but somewhat back of the anterior edge a transverse ridge is developed. This ridge increases in height toward the lateral margin of the clavicular plate and, curving upward and posteriorly, is continuous with the ascending shaft of the bone. The shaft turns rather sharply upward and backward from the ventral plate, following the outer contours of the animal's shoulder. Posteriorly, the lower part of the shaft is followed upward for a short distance by a continuation of the thin ventral plate; this, however, constricts rapidly in width above, and the upper part of the shaft is essentially rodlike. It is here excavated posteroexternally for an overlap of the cleithrum, and shouldered internally for apposition to the anterior edge of the scapula. When scapula and clavicle are placed in articulation, it is seen that the broad anterior end of the coracoid plate extended far forward median to the clavicle—the two bones presumably separated by a gap occupied by the supracoracoid muscle.

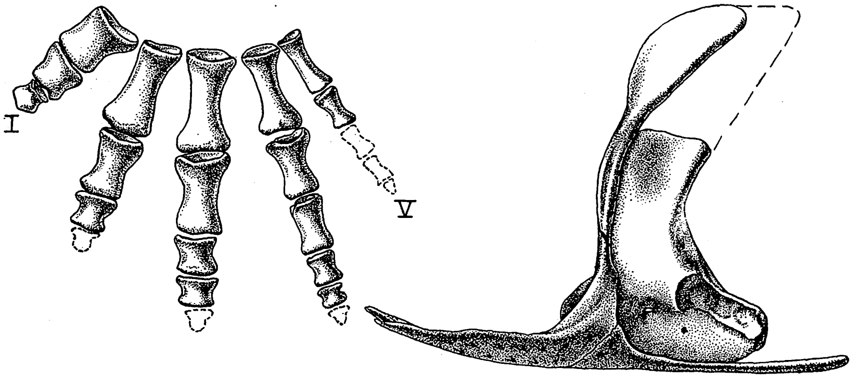

FIG. 2. *Left,* restored manus, × 1. *Right,* lateral view of shoulder girdle, × ½.

The cleithrum includes a shaft and a somewhat expanded upper extremity. The shaft is essentially triangular in section. There are flat external and anterointernal surfaces, but the shaft is grooved on its posterior aspect for articulation with the margin of the scapula. Presumably, its ventral tip overlapped the upper end of the clavicle slightly, but the bone is imperfect here. The upper end of the bone is somewhat expanded and curved backward over the presumed cartilaginous "suprascapula."

Case (1915, pp. 163–64, Fig. 37 *a–c;* Nos. *M* 3421, *M* 3422) correctly identified scapulocoracoids of *Archeria* from the Briar Creek bone bed, and the MCZ collections include another specimen from that locality, No. 1177. Additional Geraldine specimens showing shoulder girdle material are Nos. 2046–2049, 2072, and 2472.

As has been seen from the description above, the shoulder girdle of *Archeria* is of the general pattern found in many early tetrapods; this pattern is present, on the one hand, in such temnospondyls as *Eryops* and the dissorophids, and on the other, in such an archaic reptile as *Diadectes.* It differs from many early forms in the low degree of ossification of the scapula, but this does not presume any difference in morphology. A similar lack of distal scapular ossification is seen in *Seymouria* and other early tetrapods; even in pelycosaurs there may remain a considerable unossified dorsal region (Romer and Price, 1940, p. 124, Fig. 18). From *Eryops* there is little difference except in the development of a short stem on the interclavicle. The clavicles and interclavicle are similar to those of *Pholidogaster* and those possibly pertaining to *Crassigyrinus; Diplovertebron* and the seymouriamorphs and typical early reptiles differ only in the greater development of an interclavicular stem (Romer, 1947, p. 75, Fig. 14). *Diadectes* has a capping cleithrum similar to that of *Eryops* and *Archeria.* The morphology of the scapulocoracoid in such an early reptile as *Diadectes* is very similar to that of *Archeria*—even to the presence of a glenoid foramen.

It would appear certain that this type of girdle construction was set up at a very early stage in labyrinthodont history, since little divergence is seen in either typical temnospondyls, on the one hand, or embolomeres and early reptiles, on the other. This girdle is already far advanced over the crossopterygian condition (Jarvik, 1944) in dermal bone reduction dorsally, except for a modest cleithral cap and loss of a skull connection. It is further advanced in the considerable development of the scapular blade and the evolution, in the glenoid and coracoid regions, of distinctive features common to temnospondyls, anthracosaurs, and early reptiles. The endochondral girdle in fishes is, in contrast, universally small (see, for example, Romer, 1924) and, despite some basic similarities in pattern, lacks many of the typical amphibian features of glenoid and coracoid plate. Most notably, there is no expanded scapular blade, a structure which appears to have developed in connection with terrestrial locomotion. A separate coracoid ossification is present in all early reptiles and even in the Seymouriamorpha. Since the embolomeres are surely related to reptilian ancestors, the presence of a coracoid would have caused no surprise. There is, however, no indication of a distinct coracoidal ossification in any specimen. Among modern amphibians a coracoid is present in the Anura, and a separate coracoid is reported in *Diplocaulus* among ancient lepospondyls. Presumably, the situation is the result of parallelism.

It is to be hoped that Dr. Jarvik will be able to publish fully on the ichthyostegid material in the not too distant future, for the shoulder girdle is of an almost ideal transitional fish-to-amphibian type (Jarvik, 1955, Figs. 11, 12). Even here there is considerable reduction of the dermal girdle, and the lower part of the endochondral girdle is already typically amphibian in nature; on the other hand, the scapular blade is undeveloped.

Watson (1926, pp. 232–35, Figs. 25, 26) tentatively associated with the embolomere *"Eogyrinus"* a restored shoulder girdle based mainly on material from Newsham. This is of an exceedingly primitive and piscine pattern, with, as restored, a cranial connection, cleithrum and clavicle very broad throughout, and an endochondral girdle which not merely lacks a scapular blade but lacks ventrally any of the typical amphibian features already present in the Devonian *Ichthyostega.* I am inclined to doubt the association of this girdle material with *"Eogyrinus,"* since (1) the construction is much more piscine than in the far older Devonian type, and (2) *Archeria* and *"Eogyrinus"* appear to be so basically similar in many structures that it is difficult to believe that they would differ radically in shoulder pattern. The bone restored as a supracleithrum, as Watson noted, was not found in position, and the presumed posttemporal, forming the skull connection, is not from Newsham, but is a girdle bone belonging to the type of *Pholiderpeton* from Bradford; it is comparable in shape to the cleithrum of *Archeria.* The broad plate of dermal bone which is identified as cleithrum plus clavicle is sculptured in the fashion seen in rhipidistian crossopterygians, and the plate as a whole seems highly comparable, in reversed position, to the cleithrum of such a form as *Eusthenopteron* (see, for example, Jarvik, 1944, Fig. 23). Quite possibly the Newsham girdle is that of one of the large Carboniferous crossopterygians.

Pelvic girdle (Fig. 3).—All three elements of the girdle are ossified, but in available specimens ossification has proceeded so slowly that the three tend to separate at their union in the acetabulum. Specimens of the ilium are common; few identifiable specimens of pubis or ischium are known. The illustrations are based primarily on No. 2045 with details added from other Geraldine specimens, including material with several of the skeletal series of Nos. 2046–2049 and 2072, and from Nos. 2070 and 2472. The ilium is present in *A* 4550, one of the "type" specimens of *A. crassidisca* (Cope, 1884*b,* Pl. 5, etc.). Case (1915, p. 161, Pl. 22, Figs. 2, 3) correctly identified ilia from the Briar Creek bone bed (*M* 3034); the pubes and ischia from that deposit which he believed to belong to *"Cricotus"* are, however, those of small ophiacodonts (Case, 1915, p. 162, Fig. 35, Nos. *M* 3217, *M* 9655). Ilia, or partial ilia, from a number of other localities are included in Nos. 1173, 1176, 1180, 1730, 2081, 2083, 2214, 2220, 2221, and 2227.

The iliac blade is of a type long recognized as characteristic of the embolomeres. Above the acetabulum is a narrow neck, beyond which there is a bifurcation into a long posterior projection and a vertically directed shovel-shaped blade. The bone is thick at the neck; the blade, however, thins dorsally, although the anterior edge tapers gradually in thickness. The internal surface of the blade shows clearly a set of markings associated with articulation to the apposed sacral rib, and the size of the blade seems clearly correlated with that of the sacral rib. In contrast with the

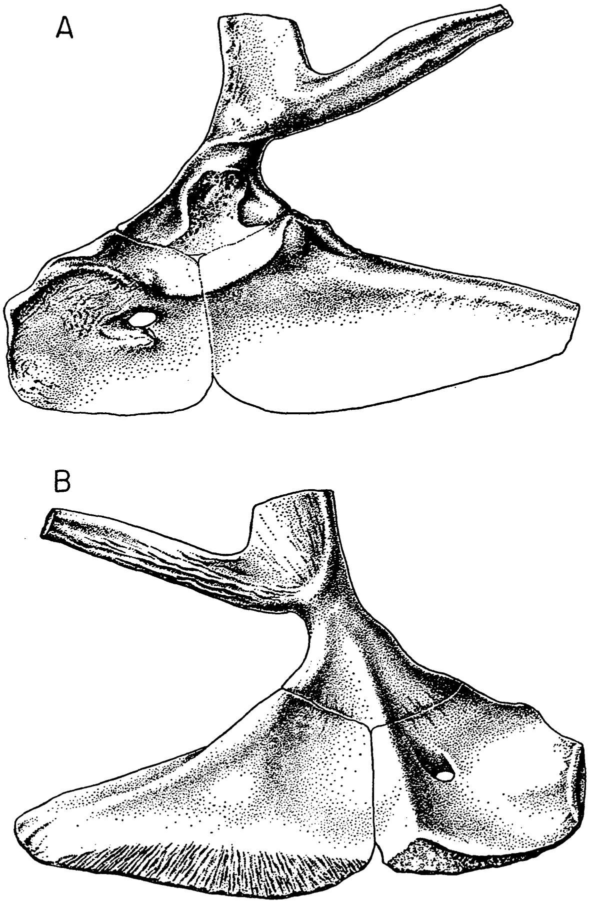

FIG. 3. *A, B,* left pelvic girdle, external and internal views, × ½. Based mainly on No. 2045.

blade, the long posterior prong remains relatively thick throughout its length. Near the base it is triangular in section—essentially flat medially, but with a rounded longitudinal ridge externally. More distally, this external ridge slants upward to continue distally along the upper border. A second ridge extends along the lower border of the prong; between the two ridges the prong is somewhat thinner in section. The inner surface (and to a less extent, the outer) bears variable longitudinal striations. The prong ends posteriorly in an unfinished oval surface, presumably for tail tendon attachment.

A ridge which curves backward from the front margin of the ilium above the neck presumably marks the upper limit of the very restricted area for attachment of dorsal limb musculature. Below this the external face of the bone expands in triangular fashion to form part of the acetabular area. Anterior and posterior borders, both with marginal ridges, give this surface a somewhat concave outline. The supra-acetabular buttress characteristic of early tetrapods generally is present; it faces somewhat posteriorly (and ventrally) rather than laterally. Its surface is unfinished and variably pitted; below it the ilium bears a major part of the acetabular area. This iliac surface is likewise unfinished; it is outlined by slightly raised borders and broadens ventrally toward pubic and ischiadic contacts. The lower margin of the ilium is somewhat convex in outline.

Internally, below the neck there arises a prominent ridge slanting forward and downward. This divides the inner surface of the bone into two very distinct areas, an anteromedian triangle leading down onto the inner surface of the pubis and a broader surface facing inward and slightly posteriorly, continued by the ischium. The posterior border of the acetabulum is thick and rounded, the anterior border thinner and sharp-edged.

The pubis is short anteroposteriorly, but deep; it meets the ilium in a diagonal suture and the ischium in a vertical suture at about the level of the center of the acetabulum. The posterodorsal portion of the outer surface is part of the acetabular area. This surface is deeply concave; it is bounded anterodorsally by a sharply rounded ridge, forming part of the margin of the bone, and below by a thickened outswelling which is continuous posteriorly with a similar ventral buttressing of the acetabulum by the ischium. The surface of this part of the bone is not well preserved in available material, but appears to have been of unfinished type. An extension of this unfinished surface runs a short distance forward beyond the acetabular region in the form of a groove close to the upper border of the bone. The short upper margin of the bone in front of the acetabulum is moderately thick. Part way along this margin there develops a low rugose pubic tubercle; beyond this point the margin dips down and forward. The anterior margin of the bone is thick and vertically placed; there was obviously an anterior cartilaginous continuation of the pubis, probably of modest dimensions. Ventrally, the anterior edge of the bone thins and curves backward toward the symphysis. As is general in reptiles and early amphibians, the pubis is sharply outturned dorsally and anteriorly so that the outer face of the bone faces downward and somewhat backward as well as outward. Below the anterior part of the acetabulum the outer surface is interrupted by the outer opening of the large obturator foramen.

Most of the inner surface of the pubis forms, as in many early tetrapods, a triangular area facing somewhat upward and forward as well as inward; this was occupied in life by the origin of the puboischiofemoralis internus muscle. This area of origin, the upper part of which lies on the ilium, is bounded posteriorly by a strong ridge running ventrally, medially, and somewhat anteriorly from the ilium to the symphysis; it is bounded anterolaterally by the upper lateral margin of the pubis. The base of the triangle is formed by the anterior margin of the bone and the anterior part of the pelvic symphysis. The plane of this surface is parallel to that of the outer surface and hence the bone, in contrast to that of such an animal as *Eryops,* is nowhere greatly thickened. This surface is interrupted at about mid-height by the inner opening of the obturator foramen. This pierces the bone vertically, and a rounded, grooved channel in the bone leads down to it from above. The pubis extends somewhat back of the ridge forming the posterior boundary of the triangular pubic surface just described. The symphysis begins some distance back along the lower margin of the pubis, increases rapidly in depth to a peak at the lower end of the internal vertical ridge on the pubis, and then rapidly thins. This part of the symphysial surface shows irregularities indicating a close interlocking of the pubes.

The ischium is notably elongate, its length being nearly twice that of the pubis. The posteroventral part of the acetabulum lies on the ischium; the surface here is not well preserved, but appears to have been unfinished. There is a well-defined lower acetabular rim, continuous with that on the pubis, formed by a thickened outturned part of the bone. Posteriorly, this rim rises to a pronounced buttress, with the acetabular surface here directed somewhat upward and well anteriorly. From this buttress a prominent ridge continues backward to form most of the upper border of the ischium, diminishing in strength and curving gently downward posteriorly. Above the buttress, however, the posterior boundary of the bone is a distinct flange set at a more median level than the buttress ridge.

The main outer surface of the ischium, forming with the pubis the extensive puboischiadic plate, is tilted outward dorsally, but to a lesser degree than the pubis. Anteriorly, it has, of course, the same depth as the pubis, but it tapers posteriorly, so that its height has decreased by half at its short vertical posterior border. The contours of the inner surface of the ischium correspond closely to those of the outer surface, so that, except for the acetabular region and the ridge at its dorsal margin, the bone is thin throughout. The inner surface faces medially and somewhat dorsally. Although conditions are obscured by crushing in available specimens, this surface appears to have been essentially flat but perhaps slightly convex in vertical section. Just within the dorsal margin for the distal two-thirds of the length of the bone there appears to be a beveled surface which, as is probable in many other early types, may have carried a slender ischiotrochanteric muscle. Presumably, the remainder of the inner surface carried no musculature. At about the level of the posterior end of the pubis the articular faces of the apposed pelvic halves, forming the symphysis, change to a series of vertical striations, indicating not a structural union of the two ischia, but rather an apposition of the bones with fibrous tissue as the binding element.

The *Archeria* pelvis appears to be of a primitive and generalized early tetrapod type. The triangular acetabular region, with its characteristic dorsal buttress, is found in all well-known Paleozoic labyrinthodonts and early reptiles. Equally common in the older tetrapods is the presence of an extensive ventral puboischiadic plate, unbroken except by the opening of the obturator foramen, strongly outturned anteriorly and dorsally, terminating in a high unfinished pubic margin anteriorly and tapering posteriorly in a relatively narrow ischiadic area. A short pubic region is probably primitive. It is seen, on the one hand, in *Ichthyostega* and, on the other, in captorhinids and some ophiacodont pelycosaurs (Romer and Price, 1940, Fig. 25); in such reptiles as the sphenacodonts the pubis is more elongate. The ischiadic part of the plate is, in contrast, relatively long in *Archeria*. This is perhaps to be correlated with active use of the hind limbs in swimming; the strength of the internal trochanter of the femur (noted later) indicates a powerful development of the puboischiofemoralis muscle, which arises from the plate; ischiadic length suggests especial development of the posterior part of the muscle to give a powerful backward stroke to the femur.

The sharply marked internal triangular area on the pubis, from which arose the puboischiofemoralis internus muscle, is, again, a feature common to all well-known early tetrapods. It is usually highly developed in labyrinthodonts—overdeveloped, so to speak, in *Eryops,* where the surface is turned sharply forward and the pubis grossly thickened in consequence. It tends to be less pronounced in reptiles, but is clearly demarcated in most forms through the earlier Permian.

The pelvic symphysis is relatively poorly known in early tetrapods, since the surfaces concerned are well seen in only a small percentage of preserved specimens. It seems highly probable, however, that the type of symphysis seen in *Archeria*—with a firm pubic union which reaches its greatest depth near the posterior end of that bone, and a less-developed ischiadic union—is primitive in nature. The *Ichthyostega* symphysis appears to be much the same as is that of various labyrinthodonts, and an essentially similar symphysis can be seen even in such a relatively advanced reptile as *Ophiacodon* (Romer and Price, 1940, Fig. 49 B).

The ilium of *Archeria,* with its vertically directed blade for sacral articulation and its distinct and slender posterior process for caudal tendon attachment, is certainly of a primitive type which was widespread among early amphibians. Watson's deduction that this type was characteristic of embolomeres seems unquestionably true. Examples, apart from *Archeria,* which appear to be embolomerous include that which he figured from Nova Scotia (Watson, 1926, Fig. 27) and various specimens described by Fritsch (1889, Pl. 52, Fig. 2; Pl. 53, Fig. 14; Pl. 66, Figs. 1, 2; Pl. 67, Figs. 1, 2; Pl. 69, Fig. 1) as pertaining to *Diplovertebron* and *"Macromerion."* Other examples among primitive labyrinthodonts include Joggins (Nova Scotia) specimens described by Steen (1934, Figs. 8, 17) and the protorhachitome *Pholidogaster* (Watson, 1929, Fig. 9). Most interesting of all examples is the *Ichthyostega* pelvis which Jarvik (1952, Fig. 5; 1955, Fig. 11) has figured in preliminary fashion. As noted above, the dorsal "blade" seems clearly associated with attachment to a sacral rib, and it is of interest to see that this attachment had developed before the end of the Devonian. The equally characteristic posterior process was presumably associated with powerful tendons from the tail musculature.

In later labyrinthodonts generally, iliac evolution was mainly in reduction of the posterior process, represented in *Eryops,* for example, merely by a spur projecting from the posterior edge of the blade. A transverse line at the base of the blade marking the upper limit of limb muscle attachment is already visible in *Ichthyostega;* and in later amphibians also it would appear that as a rule the blade had little other function than sacral rib articulation.

Quite different was the course of iliac evolution in early reptiles (Romer, 1922, pp. 559–60; 1956, p. 317, Fig. 151). In such primitive forms in this line as the seymouriamorphs, the iliac surface is expanded by ossification of the area between blade and posterior process. Following this, the original outer surface is folded over to the upper inner aspect of the bone, with a new external expansion of surface for limb musculature; *Diadectes–Ophiacodon–Dimetrodon* form a morphological (although not phylogenetic) series showing this evolution.

Humerus (Figs. 4 *A–D,* 5 *D, E*).—The *Archeria* humerus is basically of the tetrahedral type common to all early tetrapods, but is unusual in a number of features, most notably in the great expansion of the entepicondylar region, the relatively low degree of "twisting" of the ends of the bone, and the prominent lateral keel; it is further unusual, for an amphibian, in the presence of an entepicondylar foramen. An appearance of massiveness is given the bone because of the development of a lateral flange and of the broad entepicondyle; basically, however, the humerus is a relatively lightly built structure.

The proximal articular surface is strap-shaped, as in early tetrapods generally, curving in a semicircular fashion around the head of the bone. In many early tetrapods this surface twists around the head in screw fashion, with the anterior end of the articular surface turned far dorsally, the posterior end, in contrast, facing rather ventrally. Less complete ossification and imperfections in most of the specimens tend to obscure conditions in *Archeria,* but there is little evidence of this spiral twist, and the surface throughout its length appears to face in a nearly proximal direction. As in *Eryops,* but in contrast with many early reptiles, the articular face extends some distance along the anterior border of the bone toward the deltopectoral crest. The articular surface is deepest somewhat anterior to the middle of its length, but narrows rapidly toward its anterior termination.

On the relatively narrow proximal dorsal surface a pit with an unfinished surface is present at the head near the posterior end of the articular area; in an especially well-ossified specimen this area is transformed into a rugose swelling presumably associated with a powerful joint ligament. Distal to this structure is a smaller tubercle, probably affording insertion to the latissimus dorsi muscle. A tuber at the posterior margin of the head may have been for the subscapularis. At the anterior margin of the head a shallow depression, sometimes with small rugosities at its distal border, may mark the attachment of the scapulohumeralis anterior.

Rising distally from the posterior margin of the head is a rounded ridge which develops into the ectepicondyle. In most specimens this process is unossified terminally; in one, however, it is well ossified and is seen to project, in a fashion similar to the ectepicondyle of many other early tetrapods, well above and beyond the distal articular region of the bone.

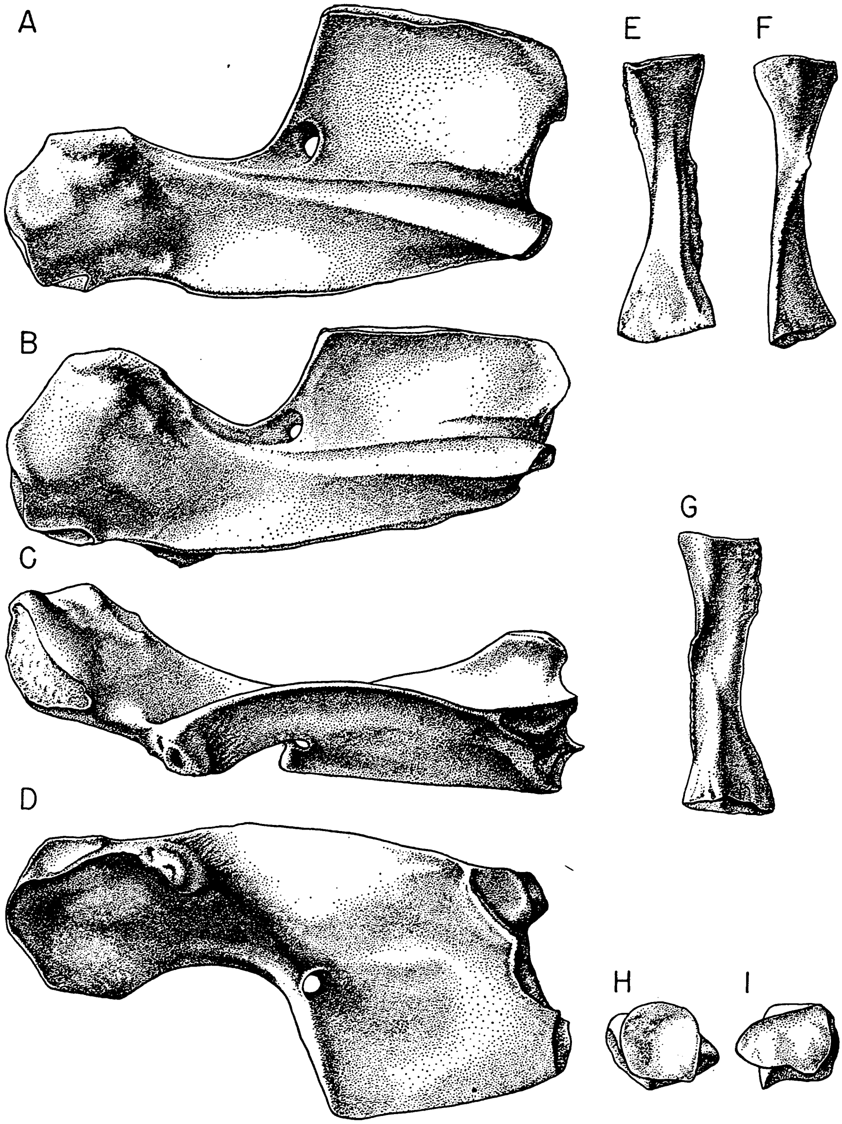

FIG. 4. *A–D,* left humerus; *A,* in the plane of the distal dorsal surface; *B,* in the plane of the proximal dorsal surface; *C,* from an anterior direction; *D,* in the plane of the distal ventral surface; *E, F, G,* left radius in dorsal (extensor), lateral, and ventral (flexor) aspects, respectively; *H, I,* proximal and distal ends of the radius, dorsal surface above. Composites, based primarily on No. 2045. For end views of humerus, see Fig. 5. × 1.

The deltopectoral crest is well developed at the anterior margin of the head. Its areas of muscular attachment form in most specimens an unfinished surface which is in continuity with that of the proximal articulation. In better-ossified specimens, however, a finished bone surface is developed along the anterior margin between the two areas, and the crest itself may attain a finished surface except for small pits presumably representing deltoid and pectoralis tendon attachments. The deltopectoral crest in *Archeria* is essentially an expansion of the anterior face of the head region of the bone, rather than a ventrally directed process, as in most early tetrapods. If the head of the bone is considered horizontal in position, the "summit" of the crest faces anteroventrally.

The nature—indeed, the presence—of the deltopectoral crest is obscured by the presence in *Archeria* of a highly developed flange of bone which projects anteriorly from the "normal" anterior margin of the humerus and extends longitudinally the entire distance from the deltopectoral crest to the distal end of the bone, although decreasing in width distally. Its outer margin, thin for most of its length, is curved upward from the plane of the head of the bone; it terminates distally at a level well below the elevated epicondyle. In many early tetrapods no such flange is present, and the anterior margin of the humerus is concave in outline from the deltopectoral crest to a point near the epicondyle, where there is found an anterior projecting supinator crest. A flange of a nature somewhat similar to that of *Archeria* is present in reduced form in *Trimerorhachis* and is well developed in certain other rhachitomes, such as *Parioxys*. But in these amphibians the flange terminates at the position of the supinator crest, beyond which there is a notch in the anterior margin, presumably for the radial nerve and artery.

The posterior margin of the head is thin-edged proximally; beyond this there develops a shallow rounded groove, directed ventrodistally, affording access for vessels and nerve to the entepicondylar foramen. This opening, of modest size, is situated close to the proximomedial corner of the entepicondyle. This last structure is developed to a high degree as a large subquadrate plate of bone, of no great thickness, which extends laterally from the ectepicondylar region for about the distal half of the length of the humerus. The plane of this sheet of bone is "twisted" downward at an angle of 20° to 25° from that of the proximal dorsal surface—an angle considerably less than that seen in most early tetrapods. Its dorsal surface is gently concave. The proximal margin is a thin, finished surface which turns abruptly in a lateral direction from the shaft. The long posterior face, slightly convex in outline, is somewhat thicker and has an unfinished surface. The plane of the entepicondyle lies well below the summit of the ectepecondylar ridge. Parallel to the ridge the bone distally is gently channeled longitudinally; at the distal margin there is, lateral to the channel, a slight swelling above the ulnar articulation.

The proximal ventral surface is gently concave; it bears slight and apparently variable rugose markings presumably associated with attachment of the supracoracoideus musculature. Distally, as in early tetrapods generally, this surface is terminated by a diagonal ridge extending down the bone from the deltopectoral crest and curving posteriorly onto the proximal edge of the entepicondyle. This ridge is little developed (in contrast to many other early types), due to the fact that proximal and distal planes are separated ventrally, as dorsally, by only a small angle.

Because of the development of the anterior flange there is a broad proximal continuation of the distal ventral surface up to the region of the deltopectoral crest; presumably, this surface was occupied by a humeroradialis muscle. The major area of the distal ventral surface is constituted by the under aspect of the great entepicondyle. This surface is slightly concave toward the proximolateral angle of the entepicondyle. At the proximomedial boundary of the entepicondyle the entepicondylar foramen opens onto this ventral surface. A low swelling traverses the bone diagonally from a point anterior to the foramen to about the middle of the distal border.

In typical early tetrapods the articular areas for the forearm bones are conspicuous on the ventral surface; here these areas are small and crowded distally, suggesting a normally more extended position of the forearm in correlation with dominantly aquatic habits. The radial articular surface is in most known early tetrapods a large hemispherical structure projecting ventrally; in *Archeria* it is a small triangular area at the anterodistal corner of the bone, beneath the ectepicondyle. It is a nearly flat unfinished surface which faces in a somewhat anterodistal rather than in a directly ventral direction; very probably it was completed in life by a cartilaginous swelling. The surface for ulnar articulation is an unfinished area on the distal margin back of the radial area and partly continuous with it. Above this area lies the slight dorsal swelling mentioned earlier, but here the bone is, nevertheless, of no great thickness. Lateral to these two articular areas the distal margin in most specimens continues without break, as an unfinished surface, to the posterodistal area. In particularly well-ossified forms, however, there is here a distinct projecting process with an unfinished circular tip from which there obviously took origin part of the forearm flexor musculature.

The humeri referred tentatively to *"Cricotus"* by Case (1915, pp. 162–63, Figs. 36 *a–f;* Pl. 22, Figs. 4, 5; *M* 3419, 3420) pertain to small rhachitomes. *Archeria* humeri, as may be seen from the list in Table I, are not uncommon at Geraldine, but are almost unknown from any other localities. When the *Archeria* humerus was first discovered it was naturally assumed to pertain to a reptile, since the presence of an entepicondylar foramen was then thought to be diagnostic of the Reptilia as opposed to the Amphibia. In more recent years, however, an entepicondylar foramen has been reported in at least two early temnospondylous amphibians (Steen, 1934, Figs. 7, 23). Hence the discovery that this structure was present in an amphibian related to reptile ancestry need not cause surprise; it could be reasonably concluded that the foramen was present in the common ancestor of the rhachitomes on the one hand, and of embolomeres and reptiles on the other.

The humerus, nevertheless, showed a puzzling type of structure. Both typical rhachitomes, such as *Eryops,* and primitive reptiles, such as *Diadectes, Seymouria,* and even pelycosaurs, possess a humerus which is in marked contrast to that of *Archeria,* lacking the projecting anterior flange and having instead a constricted "waist" between proximal and distal expansions and, further, having the two ends of the bone much more sharply twisted upon each other than is true of *Archeria.* As noted above, a few rhachitomes (as *Parioxys*) show some resemblance to *Archeria* in humeral build, but the sum of the available evidence suggested that this was an aberrant type of structure. New light is, however, shed on the matter by the ichthyostegid material. As noted by Jarvik (1955, Fig. 11), the humerus of *Ichthyostega* is complex in structure; however, it is one from which, by simplification, that of *Archeria* can readily be derived. Presumably, this type is one suitable for amphibians which are dominantly aquatic in habits, as is still the case in *Archeria.* The more "typical" tetrahedral type seen in such forms as *Eryops* and *Diadectes* was presumably developed in parallel fashion by forms which tended more toward a terrestrial mode of existence.

Radius (Fig. 4 *E-I*).—As may be seen from Table I, the two forearm bones are represented by a limited number of specimens from Geraldine and Briar Creek. The radius is of the typical early tetrapod pattern: a stout cylinder, somewhat flattened dorsoventrally in the shaft, with a rounded and somewhat concave head for humeral articulation and a distal end somewhat broadened for an articulation with the radiale. The bone is much more slender than in *Eryops.* It is comparable in proportions with *Seymouria* except for greater shaft breadth in *Archeria;* the radius of such archaic (and large) cotylosaurs as *Diadectes* and *Limnoscelis* is rather stouter, most notably at the distal end. Since support is the dominant function of the radius, absolute size of the animal presumably is an important factor in the development of disproportionate thickness of the shaft in large forms.

The proximal (humeral) articulation is subcircular in outline, somewhat flattened on the flexor margin, and gently concave. It is essentially terminal, but faces slightly toward the medial side. In *Eryops* the tilt of the articular surface is more pronounced; in reptiles the posterior surface is usually more flattened. The sides and extensor surface in the head region in *Archeria* are smoothly rounded. Practically the same condition is seen in early reptiles generally; in *Eryops* the lateral margin of the extensor surface is pronounced in the head region, so that the section of the bone here is essentially triangular, and the articular surface has a similar outline.

In *Archeria* a sharp keel develops on the lateral margin of the radius slightly above the middle of the shaft and continues down to the end of the bone, curving somewhat dorsally in its course. A ridge in *Eryops* which is possibly homologous is placed farther down the lateral surface and faces ventrally rather than laterally as in *Archeria.* I do not have at hand much well-preserved cotylosaur material for comparison, but there appears to be little keel development here in *Diadectes; Limnoscelis,* however, has a ridge seemingly comparable to that of *Eryops*. In *Archeria* a low but sharp longitudinal ridge appears medially near the head, well toward the flexor margin. This ridge continues downward most of the length of the bone; its tip faces more ventrally than medially and is rugose at its upper end. In *Eryops* there is a somewhat comparable medial ridge, which is quite rugose at its proximal termination, but it faces medially rather than ventrally; there is little development of a medial ridge on such early reptile material as is available to me. Presumably, lateral and medial ridges mark the boundary between extensor and flexor muscle groups; the rugosity at the head of the medial ridge probably afforded attachment to the humeroradialis and to a biceps, if present.

The dorsal surface of the radius becomes distally broadened and flattened, rather in contrast to the gently convex surface present in most early tetrapods. Seemingly peculiar to *Archeria* is a low but distinct dorsal longitudinal ridge which arises in the shaft region and subsides distally toward the lateral border.

The ventral (flexor) aspects of head and shaft, between medial and lateral bounding ridges, is essentially flat. Distally, in preparation (so to speak) for development of the distal articular surface, the bone thickens by the development of a stout longitudinal ridge which curves out ventrally from the general line of the shaft. This ridge divides the distal portion of the ventral surface into two parts—a narrow lateroventral area and a broad medioventral one. Both are nearly flat, but the medioventral area bears a shallow longitudinal groove. In *Eryops* there is a variable development of a distal ventral keel which separates two distal surfaces; but the two lie in much the same plane, facing ventrally rather than toward either side.

In relation to the high development of this ventral distal keel in *Archeria* the distal articular surface, which faces in a slightly lateral direction, is relatively narrow and deep, essentially triangular in outline. This is in strong contrast to *Eryops* and to certain cotylosaurs as well, in which the articular surface is much expanded mediolaterally. Only in *Seymouria* among archaic tetrapods is the distal articular surface comparable in its proportions. The nature of this surface is, of course, correlated with the structure of the carpus and pes; unfortunately, the *Archeria* carpus is little known. The extreme breadth of the articular surface in *Eryops* is presumably correlated with the fact that the bone articulated distally not only with the radiale and intermedium, but with the proximal centrale as well. One might assume, on this basis, that the *Archeria* carpus was constructed in a reptilian fashion. But the articular face remains very broad in *Diadectes* and *Limnoscelis,* despite the presumed elimination of the centrale from a radial contact.

Ulna (Fig. 5 *A-C*).—The proportions of the short, broad ulna are similar to those of *Seymouria.* The bone in most other representative archaic tetrapods is to a variable degree stouter, a factor attributable in part, at least, to larger absolute size of the forms concerned. As in many other early forms, the olecranon is slow to ossify; in No. 2045, however,

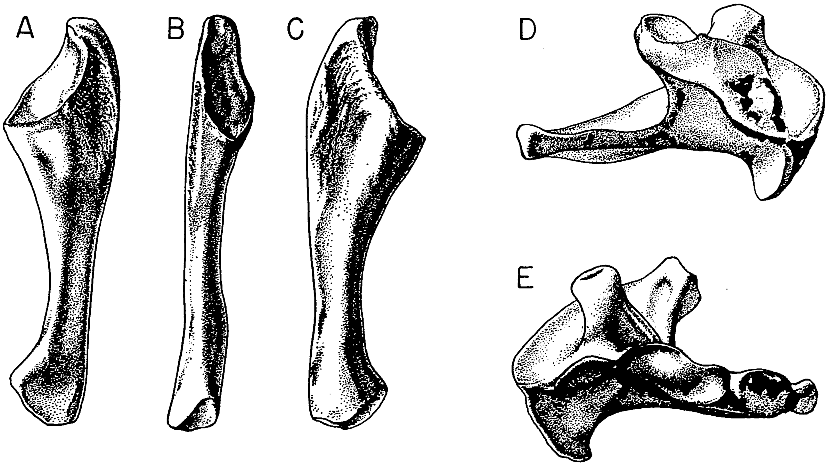

FIG. 5. Left ulna, in *A,* dorsal (extensor), *B,* medial, and *C,* ventral (flexor) aspect. Composite, based primarily on No. 2045. *D, E,* promixal and distal views of left humerus; see Fig. 4. × 1.

this structure (as figured) is well developed and proves to occupy about one-third of the total length of the bone. As is generally true, the proximal articular face—the sigmoid notch—faces somewhat anteriorly as well as medially. The articular surface is relatively narrow. Although the rugose tip is thickened, the lateral edge of the olecranon is much thinner than is the case in *Eryops*.

As in early tetrapods generally, the lateral margin of the shaft is but gently concave in outline, the medial margin notably concave. The lateral margin is a rather thin ridge for most of its length; the medial margin is more rounded in section. The dorsal (extensor) surface of the bone is gently convex in section in the region of the sigmoid notch; the shaft and lower part are nearly flat. The posterior (flexor) surface of the olecranon is somewhat concave in section and is rugose in more mature specimens. The major ventral surface of the shaft, descending from the olecranon, is flat; however, a faint ridge, descending ventrally from the lower end of the sigmoid notch, separates the main ventral surface from the rounded medial margin of the bone. Near the distal end the bone expands laterally and its lower surface curves ventrally to afford greater breadth and thickness for the distal articular surface. As is generally the case in early forms, the distal outline of the ulna is curved as seen from dorsal or ventral aspect, curving farther up at the expanded medial margin than at the lateral side. The unfinished articular surface as seen in end view is an elongate oval, much thicker medially than laterally. In *Eryops,* in contrast to *Archeria,* this distal surface is distinctly divided into two parts, apposed to intermedium and ulnare, the smaller lateral part slanting as far proximally up the bone as does the medial.

Carpus (Figs. 6, 7 partim).—Although a number of carpal elements are present in the material, they do not permit a satisfactory restoration of the carpus. In the left front foot of No. 2048 four carpals are present, but are disarticulated. One, found close to the base of the radius, is definitely a radiale. It is essentially an oval disc, with subcircular "upper" and "lower" surfaces, presumably applied, as in a primitive reptilian foot, to the lower end of the radius, on the one hand, and to the medial centrale, on the other. The proximal surface is large enough to form a contact with most of the relatively narrow lower end of the radius. In this it resembles the radiale of a primitive reptile rather than that of a rhachitome, in which the radiale only articulates with a fraction—the outer part—of the very broad radial surface. Much of the medial margin of the radiale has a finished surface, as in a reptilian radiale; however, the bone thins, in wedge fashion, toward the presumed lateral side. Here the intermedium or the proximal centrale (in rhachitomous fashion) may have aided to some extent in sustaining the radius; however, the radiale is poorly ossified and when fully developed may have occupied the entire base of the radius.

The three other elements present in this carpus are too poorly ossified to make their nature at all certain. A second element close to the end of the radius is somewhat suggestive of the medial centrale of a primitive pelycosaur. An element to the left is peg-shaped, with a somewhat concave "upper" finished surface rather comparable to one of the more medial distal carpals of a primitive reptile. A fourth element, adjacent to the ulna, is unossified superficially except for a crescentic finished dorsal(?) surface and is of uncertain nature.

With No. 2045 a single element of relatively large size was present with the right foot. This is essentially an imperfect cube. Presumed upper and lower surfaces are finished and somewhat concave; the deep margins are unfinished on every side. If compared with a primitive reptilian carpus, only the fourth distal carpal is at all similar; no element of the carpus of such a rhachitome as *Eryops* is comparable.

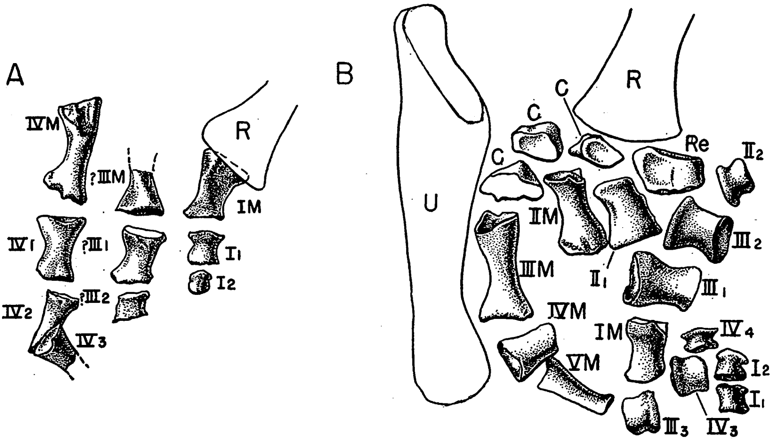

FIG. 6. *A,* partial front foot of No. 2048; *B,* nearly complete front foot of No. 2051, as described in text. Forearm bones shown in outline. Abbreviations as in Fig. 7. × 1.

Such meager evidence as there is regarding the carpus suggests (as is seen to be true of foot structure as a whole) a protoreptilian condition, rather than that known in temnospondyls and considered to be of normal amphibian type.

Manus (Figs. 2, 6, 7).—Apart from isolated elements, associated parts of the manus are present in three specimens. These are nearly completely disarticulated. Study of the three in conjunction allows reconstruction of the entire manus with a fair degree of probability. Since, however, the reasoning is involved, a detailed statement of the evidence is (unfortunately) necessary.[1] In primitive tetrapods generally, differences in articular surfaces in successive joints in a digit (Romer and Byrne, 1931) enable one to distinguish with reasonable accuracy between metapodials, first phalanges, intermediate phalanges, and penultimate phalanges, as well as unguals. Although ossification of articular surfaces is incomplete in *Archeria,* these differences can be distinguished in many cases.

In No. 2048 a partial right foot is present. Directly below the radius there is a metacarpal with a very broad head, followed by two phalanges, the second a tiny ungual; these elements seem certainly to be those of digit I. Lateral to this is an incomplete digit, probably III. Still farther lateral is a digit most reasonably interpreted by comparison with other specimens as IV. The elements are relatively long; they include a metacarpal, two complete phalanges, and part of a nonterminal third phalanx which from its length does not appear to be penultimate. This suggests a digit of five phalanges.

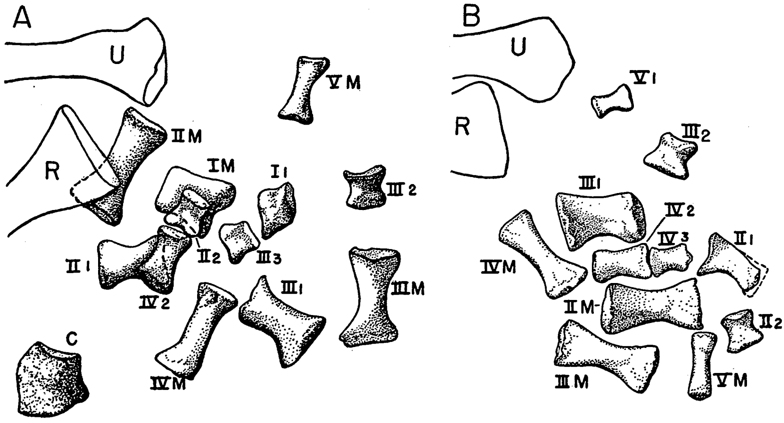

FIG. 7. *A,* bones of right manus of No. 2045; *B,* bones of left manus of same. Elements in position as found, except right presumed III M, which was isolated. Forearm bones shown in outline. In this and later figures of feet, digits are indicated by Roman numerals, specific phalanges by Arabic numerals; abbreviations: *a,* position of perforating artery, *C,* carpal, *F,* fibula, *Fe,* fibulare, *In,* intermedium, *M,* metapodial, *MC,* median centrale, *PC,* proximal centrale, *R,* radius, *Re,* radiale, *T,* tibia, *Te,* tibiale, *U,* ulna.

In No. 2045 parts of both the left and the right foot are present. Although neither is complete, the two together appear to show a nearly complete set of elements except for unguals, none of which is present. A complete set of five metacarpals is present in the right foot, of which

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[1] In the description and figures of manus and pes, digits are given in Roman numerals, phalanges in Arabic, metapodials = m or M.

four are matched on the left. Seven phalanges are present on the right, and the same number on the left. Five phalanges appear to be common to the two series, leaving two elements on either foot which have no apparent mates on the other. This brings the total of nonungual phalanges to nine as a minimum, which is close to the typical reptilian number of 12 preunguals in a phalangeal formula of 2,3,4,5,3.

On the right foot ten elements (plus a carpal) were found, as figured, close to the lower end of radius and ulna; two more podials, figured at the right, were found in the matrix close by. Five of the 12 represent the complete series of metacarpals. One, very short and broad, appears certain of identification as a I_m, comparable to that in No. 2048, and a long and slender element is comparable to that identified as IV_m in that specimen. At the upper edge of the figure is seen a shorter slender element which I at first believed to be a phalanx, but which proves to have a metapodial structure; it is presumably the metacarpal of a weak fifth digit. The two remaining metacarpals are obviously those of the second and third digits, the longer reasonably interpreted as III_m.

The identification of the phalanges is less certain, but a comparison of the material of the two feet leads to a reasonable identification of the material present. A short stout phalanx to the right of I_m, appropriate for articulation with this element, appears to be I_1. Close to II_m are elements which appear to be II_1 and II_2. Three moderately stout elements can be reasonably articulated in series with III_m as III_1–III_3. This interpretation gives us the three inner toes complete (except for unguals). Of the two outer toes, however, there are no phalanges except one element which comparison suggests to be IV_2.

In the left foot four metapodial elements interpreted as II_m–V_m are present. Phalanges comparable to those interpreted as II_1 and II_2 on the right foot are present and, as in the former case, are close to II_m, the positions in the two cases mutually confirming each other. Elements comparable to III_1 and III_2 of the right foot are present, close together. Distal to IV_m are two relatively slender phalanges which presumably belong to that digit. They are, however, too short to reasonably follow on IV_m and are best interpreted as IV_2 and IV_3. A small slender phalanx is interpreted as belonging to V.

The interpretations above were arrived at after making, and rejecting, various alternatives, none of which fitted as well as those here given. These interpretations seem to be further confirmed by a study of a final specimen, a left manus of No. 2051. This is, again, disarticulated, but with the elements clustered close to the bones of the forearm. As found, this assemblage lay in a three-dimensional cluster, in which it was impossible to figure them in any meaningful fashion; in Figure 6B they have been arbitrarily "flattened" into a plane, but their mutual positions have been retained as closely as possible.

Here, as in the right manus of the last specimen, all five metacarpals are present, and except for displacement of I_m they are arranged in sequence from a relatively short broad element identified as II_m to the slender metapodial identified as V_m. Obviously, the hand had not been completely disarticulated when burial occurred. The fourth metatarsal is incomplete; the other four elements are comparable to their supposed equivalents in 2045 and 2048.

Nine phalanges are present, including only one ungual. Most of these are comparable to those seen in the other specimens. Two small phalanges (including the ungual) are close beside I_m and presumably are the phalanges of digit I. Two stout elements fairly close to one another and to II_m are comparable to II_1 and II_2 of No. 2045. A series of large phalanges is fairly comparable to III_1–III_3 of the last specimen, although there is nothing in their position to prove this. The inner toes are thus well represented; of the outer digits, however, there is nothing except two phalanges which are rather small but too stout to pertain to V and hence are assigned to IV. The longer of the two is comparable to that interpreted as IV_3 in No. 2045, and the shorter is hence presumably IV_4.

The sum of available evidence enables one to make a restoration of a hand of essentially reptilian nature, with a formula which was rather certainly as high as 2.3.4.5 for the four inner toes, for which there is, except for unguals, complete material. The fifth digit is incompletely known; it seems certain that at least the reptilian count of three phalanges was present, but I have restored it with four phalanges by analogy with the relationship described later for the pes. It will be seen that the inner digits were short but with broad elements; the two outer digits are slender, especially digit V.

Femur (Figs. 8, 14 *C, D*).—The bone is of the general type familiar in all primitive tetrapods, essentially a stout cylinder with expanded ends and with developed ventral structures associated with muscular attachments. Its stout build, which contrasts with that of many advanced amphibian and reptilian types, is comparable to the build of many early tetrapods. It is somewhat less robust than in various cotylosaurs with which I have compared it, particularly in a lesser expansion distally; on the other hand, it is somewhat stouter than in such a temnospondyl as *Eryops,* despite the much larger size of that amphibian.

The proximal articular surface is, as in all typical early tetrapods, a band-shaped oval extended anteroposteriorly, relatively narrow dorsoventrally, convex in outline dorsally and concave ventrally, and convexly curved between anterior and posterior boundaries. Ossification of the femur is usually so incomplete that in most specimens the unfinished articular surface appears to be continuous with that of the internal trochanter. The anterior part of the articular surface is somewhat thicker

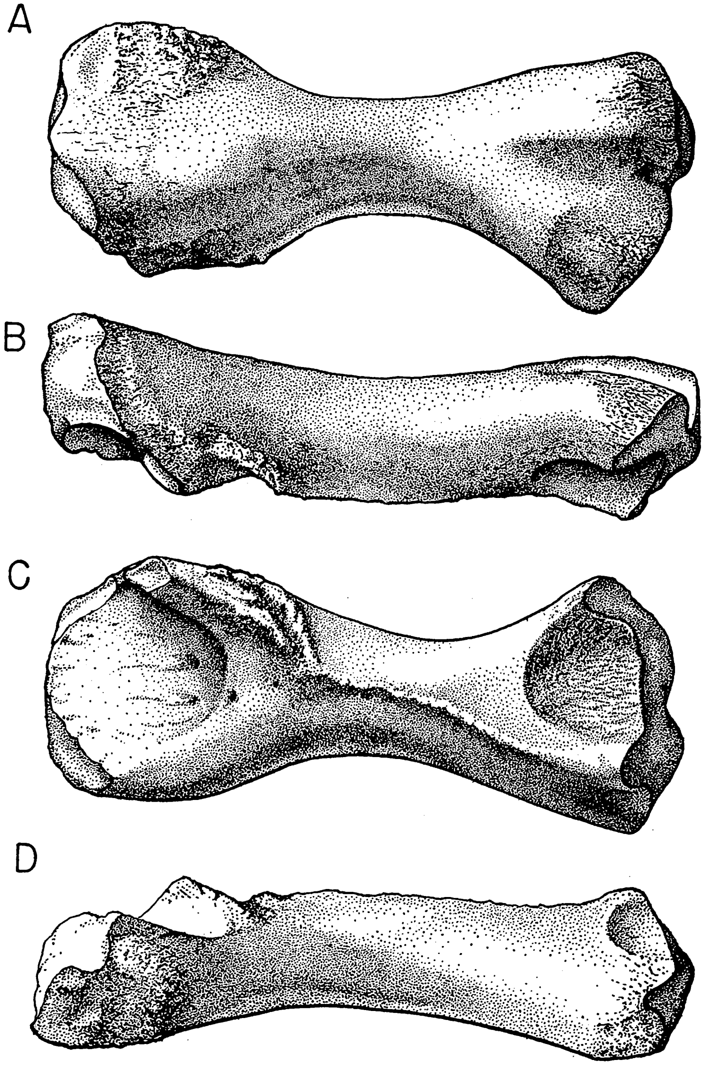

FIG. 8. Left femur in *A,* dorsal, *B,* anterior (medial), *C,* ventral, and *D,* posterior (lateral) views. In *B* extensor surface is at the top, in *D,* at the bottom. Composite, based primarily on No. 2047. For proximal and distal aspects, see Fig. 14 *C, D,* × 1.

and more projecting than the posterior part, but this difference appears to be less than in most early tetrapods. As is usually true in early forms, the posterior part of the articulation faces somewhat dorsally rather than directly proximally, and the posterior part faces somewhat ventrally.

The proximally expanded dorsal surface of the bone is gently convex; posteriorly, it terminates in a broadly rounded longitudinal ridge which curves ventrally into the intertrochanteric fossa. Anteriorly, the proximal dorsal surface curves downward onto the outer face of the internal trochanter. Rugosities near the head, and especially a well-defined transverse rugosity near the posterior edge, were presumably associated with joint ligaments; a more distal posterior rugose area may have served for attachment of the ischiotrochantericus muscle. The rounded dorsal surface in the narrower shaft region was presumably covered in life by the femorotibialis muscle. The plane of the dorsal surface of the distal expansion of the bone is tilted anteriorly about 35° from the plane of the head, primarily because of elevation of the posterior (lateral) condyle. The breadth of the distal end of the bone is mainly due, as in most early tetrapods, to a sharp outturning of the anterior margin. The posterior (or external) margin of the bone distally is gently convex, whereas in many other early forms it is essentially straight or even somewhat concave. The intercondylar groove for the triceps tendon is moderately developed (it lacks the peculiar accentuation seen in *Eryops*). As is general, the outer or posterior condyle extends farther distally than the anterior; presumably it was continued in cartilage into a typical projecting epicondylar process. Both condyles bear rugosities for extensor muscles and knee ligaments on the distal part of their smoothly rounded dorsal surfaces.

The nature of the distal articulations is obscured by the incomplete ossification of the end of the bone in even the largest specimens, but they appear to be of the generalized pattern familiar in both typical rhachitomes and early reptiles. The anterior articular surface, as far as it is ossified, is a flattened oval, convex in outline above, concave below, facing somewhat anteriorly and ventrally; presumably, in life the cartilaginous articular surface was somewhat convex instead of flattened. It is much broader anteroposteriorly than dorsoventrally, resembling in this regard *Seymouria, Limnoscelis,* and pelycosaurs, but differing from such a rhachitome as *Eryops* and also from the cotylosaur *Diadectes,* in each of which this surface is broad dorsoventrally. The lack of depth in this surface is in strong contrast with the depth of the seemingly apposed articular surface of the tibia; it must be remembered, however, that part of this apparent articular surface of the tibia in life formed the projecting upper end of the cnemial crest. In no specimen is the femur sufficiently ossified to interpose a finished surface between anterior and posterior articulations in the region beneath the intercondylar notch. *Archeria,* most exceptionally among contemporary tetrapods, presents a convex ventral margin on the distal surface at this point. The distal end of the posterior (lateral) condyle as typically ossified in *Archeria* has the form of an inverted V or check mark, with its major branch vertical in position and a minor wing extending laterally; the surface as a whole is moderately convex in section. Comparison with better-ossified specimens of *Eryops* renders identification of subdivisions of this area reasonably certain: the central part and the lower end of the major "wing" of the V bore the lateral tibial articulation; the upper part and the short lateral "wing" bore a facet for the fibula below a projecting tip of the epicondyle. It seems probable, however, that the fibular facet would not have descended the lateral margin of the condyle as it does in *Eryops* and in *Diadectes* and pelycosaurs. The shape of the area in *Archeria* corresponds well with that in the femora (equally imperfectly ossified) of *Seymouria* and *Limnoscelis.*

The ventral surface of the femur possesses the usual structures seen in early tetrapods—a deeply excavated and extensive intertrochanteric fossa, internal and fourth trochanters, a longitudinal adductor crest, a concave popliteal space. The arrangement and degree of development of these structures are generally the best diagnostic features of the femur, and *Archeria* is no exception. The internal trochanter lies close to the head of the bone at the proximal end of a high and thick ridge. As noted above, its unossified tip is usually confluent with the proximal articular area, but in one unusually well-ossified femur the two are distinct, the terminus of the trochanter for muscular attachment being a large oval area facing ventrally and proximally. Distally, as the ridge continuing the trochanter descends into the general contours of the shaft, it bears a prominent pit and associated rugosities which appear to represent the fourth trochanter; these rugosities continue proximally onto the medial side of the internal trochanter. In contrast with many of the older tetrapods there is no development of ridges on or toward the posterior (external) border of the intertrochanteric fossa. The adductor crest is a low rugose ridge which arises near the fourth trochanter, essentially in line with the base of the internal trochanter. It slants distally across the shaft to terminate laterally at the ventral tip of the outer tibial articular surface. It divides the ventral surface of the shaft into two essentially plane surfaces which meet one another at the crest at about a right angle. The more medial surface expands distally to terminate in the popliteal space, which bears rugosities for joint ligaments and is shallowly excavated toward the medial side. The more lateral ventral surface is restricted distally to become the lateral face of the bone, terminating in a depression between the two rami of the distal articular V described above.

The ventral structure just described differs markedly from that seen in such a rhachitome as *Eryops*. In that form there is little development of the internal trochanter, but there is present a very deep and stout ventral ridge, tilted posteriorly, with a great V-shaped fourth trochanter at its apex, well down the shaft at the deepest part of the ridge; further, in *Eryops* the deep adductor crest bifurcates distally, its two branches enclosing the popliteal space on either side. *Seymouria* differs from *Archeria* and agrees with *Eryops* in the great development of a V-shaped proximal pair of ridges, although the V is more widely open than in *Eryops*. *Diadectes* has a fourth trochanter developed somewhat as in *Archeria;* there is little development of the adductor crest. In various rhachitomes the fourth trochanter and adductor crest are situated on a long and prominently developed ridge. In early reptiles generally the internal trochanter is, as here, well developed, but the fourth trochanter is usually centrally situated and very prominent, occupying, in contrast to *Archeria,* the most elevated position in the ridge system. In various amphibians and reptiles the adductor crest extends directly distally along the mid-ventral surface rather than by the diagonal course seen in *Archeria*.

The femur from the Briar Creek bone bed figured by Case (1915, p. 169, Fig. 42, Pl. 24, Fig. 5; *M* 3363) as that of an "unnamed reptile" clearly pertains to *Archeria*. On the other hand, the femora which he assigned tentatively to *"Cricotus"* (1915, p. 163, Fig. 36*g, h,* Pl. 22, Figs. 6, 7; *M* 3361, 3366) appear to be immature pelycosaur bones. Other specimens including whole or partial femora of *Archeria* are (as may be seen from Table I) numerous in the available material, particularly from Geraldine.

The femur of *"Papposaurus,"* from the Mississippian of Scotland, which Watson (1914) suggested might be that of a reptile, is, as White (1939, p. 383) has noted, very similar to that of *Archeria* in almost all respects, the only differences of any note being the more elongate contour of the head and a slightly more distal (and probably more primitive) position of the presumed fourth trochanter. Watson (1929, p. 232, Fig. 9) noted that it is comparable to that of *Pholidogaster*. As far as the material is prepared, the ichthyostegid femur appears to be basically of a type similar to that of *Archeria,* but with a lesser development of the internal trochanter, a more distally placed fourth trochanter, and a higher adductor crest.

Tibia (Fig. 9).—The tibia is of the pattern common to most early tetrapods—a broad head with a pronounced cnemial crest, a somewhat narrowed shaft, and a modest distal expansion for tarsal articulation. The medial margin is markedly concave in outline; the outer margin is, on the whole, moderately concave, but, in contrast with most early tetrapods, is straight for much of the shaft length, with a strong outward slant both proximally and distally. The bone is remarkably short and broad, even for primitive tetrapods.

The cnemial crest, probably due in part to imperfect ossification of the head of the tibia, does not project markedly; it is simply a massive but low rounded swelling at the outer margin of the bone. This is in strong contrast with the marked projection of the crest at its head in all early reptiles (including even *Seymouria*), and is also in contrast with such a rhachitome as *Eryops,* in which the crest projects moderately. This lack of projection is reflected in the shape of the proximal articular surface of the tibia, which is much broadened in subcircular fashion laterally, but with little indication of distinction between lateral and medial areas. In other early types there is a marked "incision" medial to the cnemial crest on the extensor surface of the head, and a consequent V-shaped contour of the extensor margin of the articular surface. The broad medial part of the *Archeria* articular surface faces almost directly proximally and is in most specimens gently convex in section, as is the case in many reptiles. The lateral surface, which tends to be essentially flat or even somewhat concave, faces laterally for about 20°. This is in contrast to *Eryops,* in which inward tilt of the lateral surface is about 40°; but in

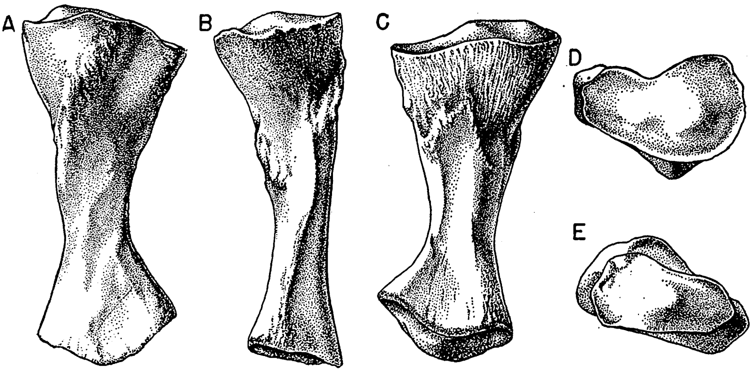

FIG. 9. Left tibia in *A,* dorsal (extensor), *B,* lateral, and *C,* ventral (flexor) views; *D, E,* proximal and distal ends, dorsal surface at the top. Composite, based primarily on No. 2047. × 1.

early reptiles generally the tilting is less than in typical rhachitomes, and in cotylosaurs it approximates that in *Archeria.*

A prominent rugose ridge develops a short distance below the head of the cnemial crest; distally, this slants toward the medial margin of the bone. This marking may have been associated with attachment of the quadriceps femoris muscle, which hence would have had an insertion much more distally and laterally than is usual; it may be, however, that this ridge is associated with a puboischiotibialis insertion which has extended much farther than usual onto the extensor aspect of the bone. Below the end of this rugose area the medial margin of the bone forms a sharp crest, presumably separating areas covered by extensor and flexor muscle groups. No such prominent crest is present in other early tetrapod material available to me. A considerable stretch of the lateral margin of the tibia, terminating below at the narrowest part of the shaft, forms a flattened narrow longitudinal ridge which is variably rugose. Presumably, this served as a point of attachment for interosseous ligaments and musculature.

The upper part of the flexor aspect of the tibia is heavily marked with longitudinal striations, indicating attachments of knee ligaments and fascia. About one-third the distance down the shaft occurs the most distinctive feature of the *Archeria* tibia. This is a highly rugose ridge, which descends diagonally across the bone from the lateral side toward the medial border. Presumably, this formed the major area of attachment of the flexor musculature of the thigh. I have seen no comparable structure in any early tetrapod material available to me, although in some specimens of *Eryops* a much fainter muscle scar is present toward the medial margin of the flexor surface below the head. The distal part of the flexor aspect includes a broad major surface extending down the shaft, broadening distally, and curving toward the flexor aspect so that the bone is much thickened; there is, further, a much narrower medial surface, facing strongly inward and tapering distally. This second area lies below the medial part of the prominent flexor muscle scar and bears longitudinal striations. The topography of the flexor surface contrasts with that found in *Eryops.* In the latter the main flexor surface is narrow proximally and is traversed for most of its length by a low but distinct longitudinal ridge, whereas the medial surface expands above and merges into the general flexor surface below the head; in the shaft region there is a deep longitudinal groove. In early reptiles, generally, a similar longitudinal groove is present (although there is no notable proximal expansion of the medial flexor surface).

The distal articular face of the tibia is, as is usual in early tetrapods, a transversely elongate oval, convex in outline on the extensor margin and flat to slightly concave on the flexor rim. This surface is essentially flat in cross section, but may be slightly convex in the most mature specimens. The more medial part of the articular surface is broad and faces almost directly distally; this area was presumably apposed to the tibiale. The lateral part of the surface, presumably in contact with the intermedium, is narrower, tapers laterally, and faces distinctly laterally at an angle of 40° with the shaft. The condition here contrasts with that in *Eryops,* in which the surface is relatively shorter mediolaterally and is of about the same width throughout. In *Seymouria* and *Limnoscelis* the articular area is still long mediolaterally, but is of about the same width laterally as medially; in *Diadectes* and pelycosaurs, with the development of an astragalus, the distal articular area is a single surface which is relatively short and deep dorsoventrally and tilted somewhat laterally.

In *Archeria* the distal end of the bone is "twisted" on the shaft in such fashion that the plane of the extensor surface of the distal end is turned medially about 30° on the upper end of the shaft; this, of course, is associated with the forward turning of the foot. In both *Eryops* and *Seymouria* the "twist" is approximately 40° to 45°; it is possible that *Archeria* represents in this regard a condition associated with persistent water-dwelling habits, in which the use of the foot as an "oar" was more important than its use in land locomotion.

As may be seen from Table I, tibiae are relatively abundant, particularly in the Geraldine material, due, in part at least, to the stoutness of the bone and its consequent favorableness for preservation. The Briar Creek specimen tentatively assigned by Case to *"Cricotus"* (Case, 1915, p. 164, Fig. 37 *e, f*) is apparently the tibia of a small sphenacodont; on the other hand, the tibiae of an "unnamed reptile" (Case, 1915, p. 172, Figs. 46 *a–e, M* 3433, *M* 3355) are *Archeria* elements.

Fibula (Fig. 10).—The fibula has the characteristic shape seen in many early tetrapods: a somewhat broadened and thickened head with a terminal articular surface for the femur, a flattened shaft, and a broad and relatively thin distal segment with a terminal surface for articulation with the tarsus. The bone is relatively stout compared with later reptilian types, but is comparable in its proportions to that of various early tetrapods. As contrasted with the fibula of *Eryops* (and other rhachitomes) the bone is notably broad distally. This feature is presumably correlated with expansion of the fibulare and proximal end of the astragalus as in reptiles, with which (in contrast to temnospondyls) the fibula articulates by a broad hinge joint.

As is usual in primitive tetrapods, the two ends of the bone are "twisted" upon each other, with the effect of turning the flexor aspect of the head inward toward the femoral articulation; the rotation of head on shaft is about 35° in *Archeria*. The bone, as in all early tetrapods, is strongly concave along its inner (tibial) margin; the outer edge is nearly straight, with a gentle concavity at the mid-shaft region and a convex outline toward the distal end. This is in contrast with *Eryops*, in which the *Seymouria, Diadectes*, and *Edaphosaurus* show contours here which are in general comparable to those of *Archeria*.

The articular surface for the femur is a crescentic oval, somewhat convex in outline along its extensor margin, concave on the opposite edge; the medial part of the surface is concave in cross section. The surface is seemingly broader towards the lateral border, but this may be due to a lack of ossification at the externolateral angle; at this point there may well have been a cartilaginous continuation of the outer corner of the bone, as in *Eryops*. As in general, this articular surface faces strongly inward to appose the articular surface on the femur. This inward turning is, however, considerably less than in *Eryops*, for the plane of the articular surface is turned only about 30° from the line of the shaft, whereas in *Eryops* this angle is about 60°. The general concavity of the articular surface is a feature found in *Eryops* and *Seymouria*, but in primitive reptiles, generally, the lateral part of the articular surface tends to assume a convex section. Were ossification more complete, the apparent peculiarities of this area in *Archeria* might well disappear.

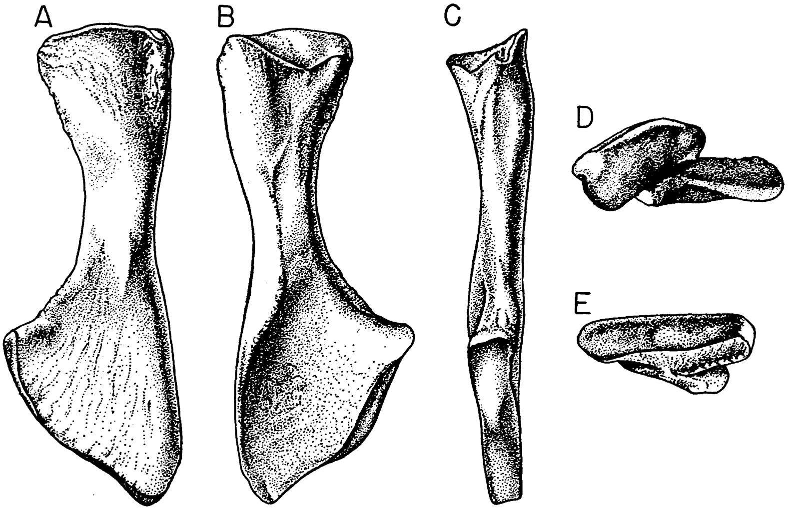

FIG. 10. Left fibula in A, dorsal (extensor), *B*, ventral (flexor), and *C*, medial views; *D, E*, proximal and distal ends, dorsal surface at the top. Composite, based primarily on No. 2047. × 1.

In the articular region the external surface of the shaft is nearly flat; this part of the bone is moderately thick, with a convex inner surface. This is in contrast with *Eryops,* in which the outer surface is markedly convex, whereas the bone is somewhat concave in section on its inner surface. This contrast between the two is associated with the fact that the articular face in *Archeria* is only gently curved mediolaterally, whereas that of *Eryops* is bent to form a considerable segment of a semicircle. Both *Eryops,* on the one hand, and many early reptiles, on the other, have a pronounced external rugosity, or tuber, on the outer surface of the head, presumably for joint ligaments and perhaps as an accessory quadriceps insertion; this is absent in *Archeria,* although the external surface is generally rugose. On the lateral margin, below the head, the bone has a sharp rugose margin, presumably associated with the iliofibularis muscle attachment. This is present in *Eryops* but not seen in the material of primitive reptiles available to me.

Associated with the notable constriction of the shaft below the head, the bone at mid-length is proportionately stout and convex on both extensor and flexor surfaces, as in pelycosaurs, and in contrast with the flattened shape of *Diadectes* and *Seymouria,* and with *Eryops,* in which the bone is markedly convex above but concave on the opposite, or flexor, surface. In *Eryops* a strong rugose ridge, facing ventrally, descends the external margin of the shaft; this presumably afforded origin for lateral elements of the flexor system. This ridge is absent in reptiles generally (although the imperfect material of *Seymouria* available to me shows indications of such a lateral ridge). In *Archeria,* however, a seemingly homologous ridge arises on the lateral part of the ventral surface at about the mid-length of the bone, and, becoming increasingly prominent, attains the lateral margin distally.

As stated above, the *Archeria* fibula is notably broad distally, as in early reptiles generally, and is greatly flattened here, quite in contrast with *Eryops,* in which the distal end is relatively narrow and thick. In *Eryops* a distinctive groove curves inward and downward along the ventral surface distally; no such feature is seen in *Archeria* or in primitive reptiles. The lateral ridge noted above continues as a prominent structure down most of the length of the distal expansion, giving the ventral surface a somewhat concave section. A similar ridge, much less developed, appears to be present in *Diadectes,* but is not present in material of other reptiles available to me.

The distal articular surface is very elongate mediolaterally but narrow dorsoventrally. As a whole, it faces as much medially as distally, but is divided into two parts. The distal part is thinner and faces more distally, presumably articulated with the fibulare, whereas the longer, thicker, and more medial segment presumably met the intermedium. This breadth of apposition is in strong contrast with the rhachitome type, in which there is a very short area of apposition to the fibulare and a moderately short articulation with the intermedium, both parts being, however, relatively broad dorsoventrally. In reptiles there appears to be likewise a strong trend for a shorter and thicker type of distal articular area. This, however, is due to a different situation. It is presumably associated with the "construction" of the astragalus out of its amphibian tarsal components and a consequent rearrangement of proximal tarsal connections.

Case correctly assigned to *"Cricotus"* a fibula from the Briar Creek bone bed (1915, p. 164, Fig. 37 *g*, No. *M* 3426). A few other fibulae are known from both Briar Creek and Geraldine.

Tarsus (Figs. 11–15).—Left intermedium, fibulare, and fourth centrale are preserved in connection with the major hind limb elements of No. 2047, an unusually mature and well-ossified individual. The right foot elements of No. 2045, in which ossification is less complete, include an intermedium and fibulare of smaller size; in the left foot of the same specimen are present these elements, and in addition the tibiale and fourth centrale(?), but in a crushed and broken condition. Except for a peculiar bone in No. 2065, which may be a medial centrale, no remains of distal tarsals or of the distal row of centralia are identifiable, and it is not improbable that they were in general persistently cartilaginous or but feebly ossified.

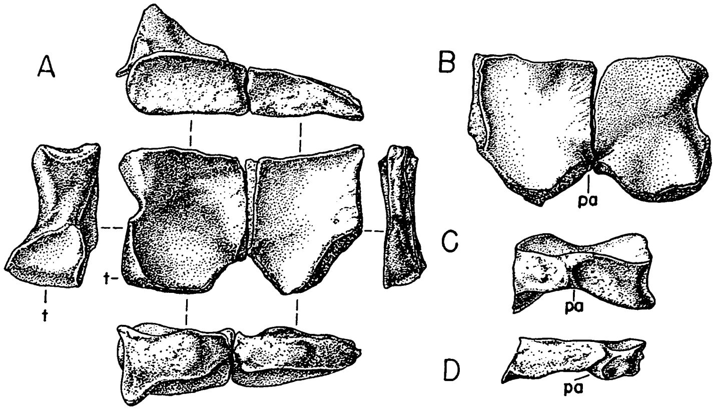

FIG. 11. Left intermedium, and fibulare of No. 2047. In *A*, the two elements in dorsal view in the center, with proximal, medial, lateral, and distal faces adjacent to the related margins; *B*, ventral view of the two bones; *C*, lateral surface of intermedium; *D*, apposed medial surface of fibulare. Abbreviations: *pa*, groove for perforating artery; *t*, surface for tibial articulation. × 1.

The fibulare of No. 2047 is quite unlike this same element in rhachitomes, where it is, as far as known, thick and elongate proximodistally. The *Archeria* fibulare is, in contrast, a relatively flat plate which corresponds more closely to that of primitive reptiles, such as *Ophiacodon*. The bone is pentagonal in shape. An extended proximal margin articulates with the outer half of the fibula; at right angles to this is a medial margin articulating with the intermedium and a lateral margin which, as preserved, does not project beyond the line of articulation with the fibula, but may have been somewhat extended in cartilage. Distally, there are diagonal margins, the lateral one (which appears to be somewhat imperfect), the longer. The dorsal surface of the fibulare is essentially flat, but somewhat concave, with the edges raised except at the distomedial margin. The ventral surface is likewise somewhat concave, but here there is little elevation of the margins at the proximolateral angle and at a point part way down the medial edge, where a groove forms part of the border of the opening for the perforating artery. On the other hand, the diagonal mediodistal margin, distal to this groove, and certainly articulating with centrale 4, is distinctly elevated. The five marginal surfaces are "unfinished" and presumably continued in cartilage, except for a diagonal groove with a finished surface forming part of the arterial channel; the bone is thickest (and these surfaces hence broadest) at the proximomedial corner, thinnest proximolaterally. The proximal marginal surface, together with its continuation on the intermedium, was articulated with the broad distal end of the fibula. The lateral surface was no doubt, as in general, in contact only with ligaments and, possibly, with muscle tendons. The medial margin was apposed for its whole length to the corresponding surface of the intermedium. Beyond the notch for the artery the thick mediodistal surface was presumably in contact with centrale 4; the laterodistal surface was no doubt in contact with one or more of the lateral distal tarsals.

Both fibularia are present in No. 2045, but although the animal is not much smaller than No. 2047, these are much smaller, due presumably to a much lesser degree of ossification. The "lip" of the arterial groove can be identified as a landmark on the right fibulare, and it is evident that the unossified areas are mainly the distal and lateral parts of this element.

The well-ossified intermedium of No. 2047 exhibits a structure generally comparable to that seen in rhachitomes, on the one hand, and to the proximal part of the astragalus of primitive reptiles, on the other. It is much thicker and less platelike than the fibulare. The bone is roughly oblong (its long axis directed proximodistally), but with its distolateral angle truncated and its medial border concave. The dorsal surface is relatively flat, but with distinct elevation at its proximal and distal medial borders. On the ventral surface the bone is seen to be greatly thickened at the proximal end and at the medial part of its distal end; laterodistally is seen the lower end of a notch which, like that in the adjacent surface of the fibulare, formed part of the boundary of the channel for the perforating artery. The lateral margin articulated with the corresponding margin of the fibulare, terminating distally at a distinct dorsoventral groove for the arterial channel; beyond this point is a diagonal surface presumably apposed to centrale 4. The distal border, and the distal end of the medial border continuous with it, presents a very broad unfinished surface. At first sight one tends to compare this entire area with that of a somewhat similar structure of the astragalus on which the tibia moved in *Ophiacodon* and other primitive reptiles. Here, however, it is more reasonable to assume that the distally facing part of this area was apposed to an independent tibiale, and that only the more lateral part of this broad surface was in direct tibial contact, the bone in this regard being built on an amphibian plan. Proximal to the tibiale area the medial margin of the intermedium has a finished surface, contracting to a "waist" part way up the bone and expanding again in breadth proximally. The broad proximal surface formed the medial part of the fibular articulation.

On No. 2045 the intermedium is well preserved on the right side; present but badly crushed and broken on the left. As in the case of the fibulare, ossification has proceeded here to a much lesser degree than in No. 2047; the general structure, however, is similar.

Unfortunately, no tibiale is present in No. 2047, but on the left side of No. 2045 a bone distal to the crushed intermedium is presumably this element. It is to be regretted that the relatively low degree of ossification of this specimen results in a paucity of data as to the nature of the tibiale. As preserved, it is triangular in shape and somewhat concave dorsally; from this surface descend vertical side walls with unfinished surfaces, suggesting that, in contrast to described rhachitomes, the tibiale did not reach the medial margin of the limb, but, as in the astragalus of reptiles, met the foot of the tibia medially. On the medial surface, presumably in contact with the tibia, the bone is as deep as the intermedium, and the same depth is present at the medial edge of the proximal face, for presumed contact with the intermedium. The ventral surface of the bone, however, is somewhat tilted, so that its depth is less at its presumed proximomedial angle, a feature agreeing with a lateral narrowing of the associated facet for its articulation with the intermedium. By analogy with the fibulare and intermedium of this individual, the cartilaginous areas of this bone were probably extensive in life; it thus affords, unfortunately, few data as to the structure of the adjacent region of the tarsus.

In No. 2045 a small bone found on the left side in the notch between fibulare and intermedium is presumably the proximal centrale; it possesses a rather flat, finished, dorsal surface, but contracts in a wedge shape ventrally. I interpret also as a proximal centrale a well-preserved wedge-shaped element found close to the intermedium and fibulare of No. 2047, although not in contact. Some doubt may exist, however, as to its identity since its dorsal surface is distinctly concave; that of No. 2045, as preserved, is somewhat convex. Below, the element of No. 2047 constricts in wedge fashion to a ventral termination forming a keel parallel to the long axis of the dorsal surface. The side which I interpret as the distal face is quite flat except for a small notch which may have housed a ligament and was presumably apposed to one or more distal tarsal elements. On the opposite (presumed proximal) side, a large area has a finished surface, V-shaped, with raised margins and a dorsal apex; this would appear to have formed a funnel-shaped lower entrance to the canal for the perforating artery, the finished surfaces being continued above on intermedium and fibulare. About this V are articular surfaces which, with some allowance for intervening cartilage, articulate reasonably with the adjacent borders of fibulare and intermedium.

With partial foot No. 2065 is a tarsal which, with doubt, I identify as a left medial distal centrale. The "finished" dorsal surface is diamond-shaped; a finger of bone, which is unfinished on its dorsal surface, extends in what I believe to be a lateral direction; on the opposite side the finished dorsal surface curves smoothly down along the margin, indicating that the element lay on the margin of the tarsus. The presumed proximal articular surface appears to be a single one, although convex medially and concave laterally; on the opposite, presumed distal, margin there are two distinct articular facets which I assume to be for distal tarsals 1 and 2. The ventral surface has a deep pit medially. Although I cannot readily interpret this element in any other way, a high development of C_1 and, of necessity from topographic relations, a concomitant reduction of C_2 (as well as C_3) is the reverse of the apparent reptilian trend, in which the pelycosaur evidence, at least, indicates C_2 to have been the "dominant" distal centrale.

In Figure 15 I have attempted a restoration of the tarsus, supplying a series of five distal elements, with the fourth the largest, as in most known early tetrapods, and indicating the presence of but two distal centralia (the third of this series being at best small in rhachitomes and absent in reptiles). I have indicated an extended area for the tibiale on the assumption that the degree of ossification of the single known specimen (figured) was comparable to that of the other (poorly ossified) tarsals with which it was associated.

As restored, the tarsus is in contrast with that described for the typical rhachitomous labyrinthodonts (Schaeffer, 1941) and is essentially protoreptilian; there are points of comparison (apart from lack of fusion of elements to form an astragalus) with such a Permian type as *Ophiacodon,* for example. As in early reptiles generally, the articulation with the fibula is of a very broad and relatively shallow hingelike type, in contrast with the rhachitomes, in which this articulation is narrower and deeper. Whether or not the element I have so identified is the proximal centrale, it is obvious from the structure of fibulare and intermedium that this centrale was a small bone, definitely not in contact with the tibia, and contrasting strongly with the large proximal centrale of rhachitomes. Although the only known tibiale is poorly ossified, it seems certain from the structure of the tibia that this major element had a free rocking motion on intermedium and, presumably, on tibiale. The distal end of the tibia, it will be noted, slants upward laterally, whereas the rhachitome tibia—wedged rather firmly between tibiale and intermedium—is beveled in exactly the opposite direction.

Pes (Figs. 12–15).—In No. 2045 the greater part of both hind feet is preserved, although nearly completely disarticulated; specimens Nos. 2047 and 2094 consist of isolated foot material. The restoration shown is based mainly on an interpretation of the feet of No. 2045, supplemented by data from the two other specimens. It will be noted that the hind foot is very much larger than the forefoot. This restoration is essentially reptilian, except for the presence of an extra phalanx in the fifth toe. But although I feel that the available material warrants the reconstruction of the foot as figured, there is one peculiarity in the material which may justly raise doubts of its authenticity in the mind of the reader, as it long did in my own mind. This is the fact that in the feet of the best preserved specimen, No. 2045, four toes, in almost complete form, are preserved on both sides, but, by some extraordinary chance, no trace of the presumed second digit is present on either side.

In the left foot of No. 2045, 17 metapodials and phalanges were preserved. Four of the stoutest of these have oval proximal articular areas, indicating their metapodial nature, and two are unguals, leaving 11 as "normal" phalanges. This in itself gives a potential phalangeal count close to that of typical primitive reptiles, in which 13 nonungual phalanges are present. In the right foot there are 15 elements, including four presumed metapodials and three unguals, leaving eight nonterminal phalanges.

Most of the metapodials and phalanges are relatively stout in comparison with their length; there are, however, series in both feet which are relatively long and slender; these I interpret as pertaining to a fifth digit. In the right foot of this specimen such elements are clustered in a discrete group seen in the figure above the tibia. One is a slender metatarsal; the others I assume to be associated phalanges. There is, however, a slight difficulty in that the presumed second phalanx is too broad distally to articulate properly with the presumed penultimate phalanx, suggesting that a phalanx was lost here from the block and that the unusual phalangeal count of five was present. This seems to be confirmed by a study of the left foot. In this, elements comparable to those identified on the right side as V_m and V_2 are seen at the lower left of the figure, and others comparable to the presumed V_1 and V_4 toward the right, and, in addition, there is at the center top a slender element of appropriate size and structure for the presumed V_3 element.

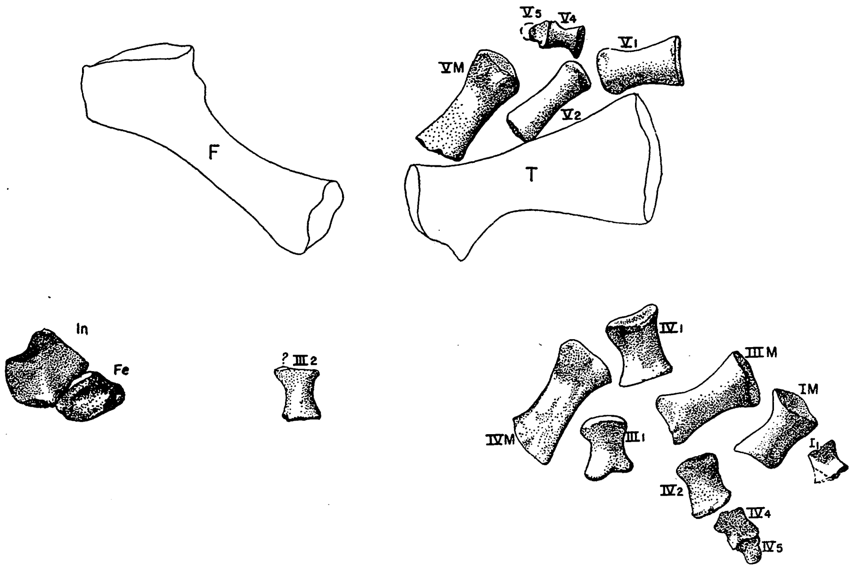

Fig. 12. Right hind foot of No. 2045, with elements in position in which they were found. Abbreviations as in Fig. 7. × 4/5.

In both feet of No. 2045 there are present three metapodials in addition to the presumed V_m. Each of the three present in either foot can be readily paired with an element from the other (except for crushing undergone by the supposed left IV_m). One of the three resembles the supposed V_m, but is slightly longer and slightly stouter; a second is somewhat shorter and very stout; a third is stout and very short, with a head facing somewhat diagonally. I interpret these elements as the metatarsals of digits IV, III, and I, respectively, with a II_m, which should be intermediate in length between III_m and I_m, missing in both cases. As noted below, most of the phalanges associated with these metatarsals are present in both feet, but none is easily attributable to a digit II.

The reader may immediately object to this interpretation and suggest that my supposedly missing digit II is imaginary, and that, as the evidence of this specimen implies, I am dealing with a four-toed pes. But although I find it very difficult to believe in a peculiar quirk of fate by which digit II, and digit II alone, happened to be lost by pure chance from both feet of a single fossil animal, I find it still more difficult to believe that the *Archeria* pes was four-toed. In temnospondyls there is a trend for loss of a digit in the front foot, but never in the hind. The form concerned is related to reptile ancestry, in which there is likewise no early trend for digital reduction. Further, the *Archeria* foot, as noted below, appears to be a highly developed paddle in which toe reduction would be very improbable. Still further, Dr. Donald Baird, who has studied widely the abundant material and literature of Paleozoic footprints, informed me that there appears to be no indication of any four-toed hind foot. And, finally, another specimen shows, as is mentioned later, a complete and articulated digit which fulfills all the requirements for the missing digit II.

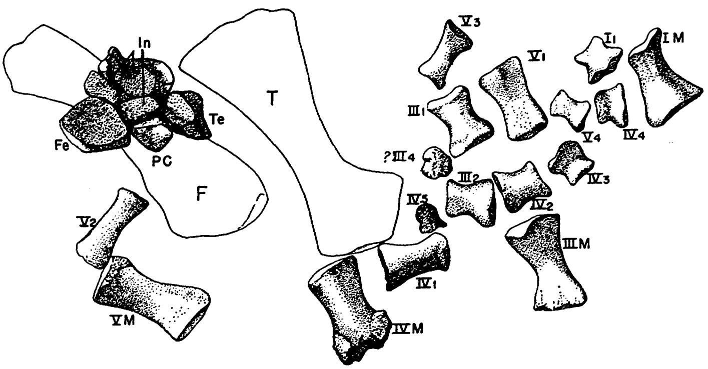

FIG. 13. Left hind foot of No. 2045, with elements in position in which they were found. Abbreviations as in Fig. 7. × 4/5.

To return to the feet of the main specimen, No. 2045, on the left side four phalanges extending irregularly toward the right from IV_m appear to be those of digit IV; these grade downward in size from left to right and articulate well, the whole suggesting the presence of a fourth toe with five phalanges. On the right, a similar series of phalanges is present in rough alignment, except that there is none which equates with the presumed IV$_3$ of the left foot.

Of possible digits of toe III, on the right side an element of appropriate size for III$_1$ lies adjacent to the distal end of III$_m$, and on the left a comparable element is found, plus one which articulates well with this and may be III$_2$. An element similar to the last was found on the right side in the screenings.

On the right side of the left pes assemblage, adjacent to the element interpreted as I$_m$, is a phalanx appropriate for identification as I$_1$; a comparable element is present in the right pes, likewise adjacent to its metatarsal.

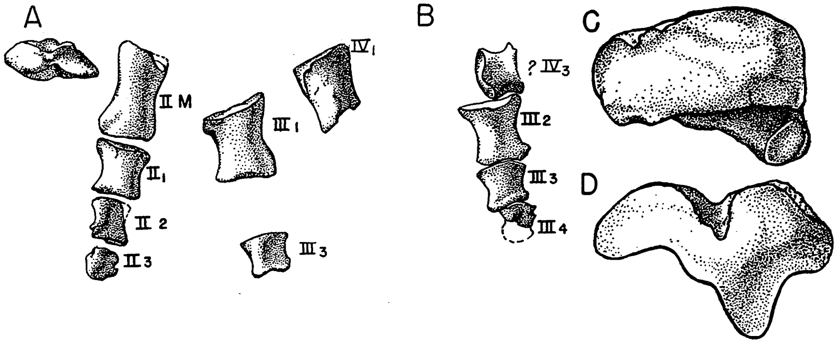

FIG. 14. *A,* partial left hind foot of No. 2047, with elements in position in which they were found. A tarsal (?medial centrale) at upper left; *B,* fragment of hind foot, found isolated (No. 2094); *C,* proximal view of left femur; *D,* distal view of same. × 1.

Of the unguals present, those of the right pes are, by association, presumably those of digits IV and V; the two disarticulated elements on the left are of uncertain nature; they may be those of digits III and IV.

The data from the two pedes of No. 2045 give nearly complete information on the outer three toes and digit I as well. Nothing is, however, present of digit II on either foot of No. 2045, according to the present interpretation.

Apart from a few isolated elements, the only other available materials of pes digits are those of Nos. 2094 and 2047. The former was isolated in developing the blocks from the Geraldine quarry; the elements are too large to pertain to the manus. Of a series of three articulated phalanges in No. 2094, the proximal is closely comparable to that identified above as III$_2$; this specimen thus appears to give a completion of digit III with the reptilian count of four phalanges. (The isolated phalanx lying above this series of three is presumably a phalanx of II or IV, most probably IV$_3$.)

The right foot of No. 2047, in addition to a tarsal, has parts of three digits. At the right of the figure is an incomplete phalanx comparable to IV_1. In the center are two elements which may be III_1 and III_3. At the left is a metatarsal with three phalanges, including an ungual, in articulation. This is presumably digit II, with a reptilian formula. This presumption is strengthened by the fact that the metatarsal is intermediate in length between those assigned to digits I and III in No. 2045.

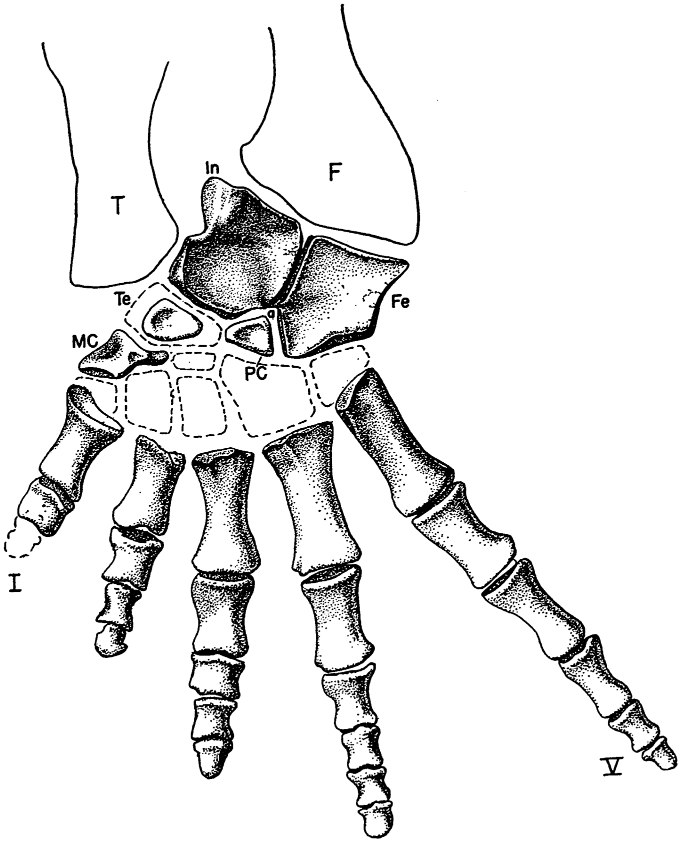

FIG. 15. Attempted restoration of left hind foot. Abbreviations as in Fig. 7. × 1.

As is seen, the reconstruction of the hind foot is quite hypothetical; nevertheless, the foot as figured is the only reasonable restoration possible on detailed consideration of the material. As reconstructed, it is essentially reptilian in its phalangeal formula and has, as does the manus, a phalangeal count well above that known or assumed to be present in rhachitomous labyrinthodonts. This is not unexpected in view of the presumed relationship of embolomeres and reptile ancestors. Certainly the 2.3.4.5.4 formula was characteristic of early reptiles, and a comparable count might be expected in anthracosaurs. The only feature of the reconstruction which might raise serious question on theoretical grounds is restoration of digit V with five phalanges. The material, however, tended to force me to this. I may note that a similar elongation and mild hyperphalangy of digit V is found in *Mesosaurus,* an animal of similar habitus. One may not unreasonably assume that the feet were webbed in both instances and were actively used in swimming movement.

Limbs (general).—In Figures 16 and 17 are given reconstructions of front and hind limbs from several points of view. Any attempt to study limb posture and movement in terrestrial locomotion in *Archeria* is handicapped by the feeble ossification of the articular surfaces of the limb bones and the consequent difficulty of placing them in proper articulation.

In the shoulder region the apposed surfaces of scapulocoracoid and humerus are, as in all typical early tetrapods, strap-shaped. In *Archeria,* however, the two surfaces, although elongate, show less of the spiral curvature usually present in early tetrapod shoulder articular surfaces. It is hence probable that the major movement at the shoulder was an essentially straight fore-and-aft movement of the humerus with little rotation of the distal end of the bone during the stroke; the entepicondyle, which is "twisted" downward but little from the plane of the head of the bone, presumably remained essentially horizontal throughout.

In most contemporary tetrapods the radial articulation is a hemispherical swelling facing directly downward beneath the distal end of the humerus, with the ulnar articular area adjacent. In *Archeria,* in contrast, the radial articulation is at the extreme anterodistal corner of the humerus beneath the ectepicondyle and faces as much laterally as ventrally, together with a slight forward inclination. This surface, as preserved in available specimens, is nearly flat; some convexity may have been present in cartilage in life, but even so, it is difficult to imagine that the radius in average position was as sharply bent on the humerus as was usually the case. The forearm would appear to have been much less flexed and to have extended, on the average, outward, diagonally downward, and forward with an essentially hingelike movement on the humerus. This difference is presumably correlated with aquatic habits; such an articulation would more readily allow the limb to be turned back along the body, "out of the way" during swimming, as in a newt, for example. On the other hand, this posture would make the limb less effective during periods of terrestrial locomotion, because of greater difficulty in bringing the forearm and front foot forward into proper walking position.

The hind leg would appear to have been essentially of a normal early tetrapod type in posture and movements. Although, as in the case of the forelimb, imperfect ossification of the articular surfaces obscures the situation, these surfaces (as noted above) are reasonably comparable with those of many other early tetrapods. The proximal surface of the femur is like that of other early forms in which this element in average pose is thought to extend nearly directly outward from the acetabulum. The build of the distal end of the femur suggests the presence of tibial and fibular articulations comparable with those of other primitive tetrapods. The fibular shaft is, as usual, twisted so as to allow a forward direction of the associated tarsal elements. The tarsus, although incompletely preserved, suggests a beginning of the primitive reptilian type of articulation of crus and foot, with relatively free movement at the tibiotarsal joint.

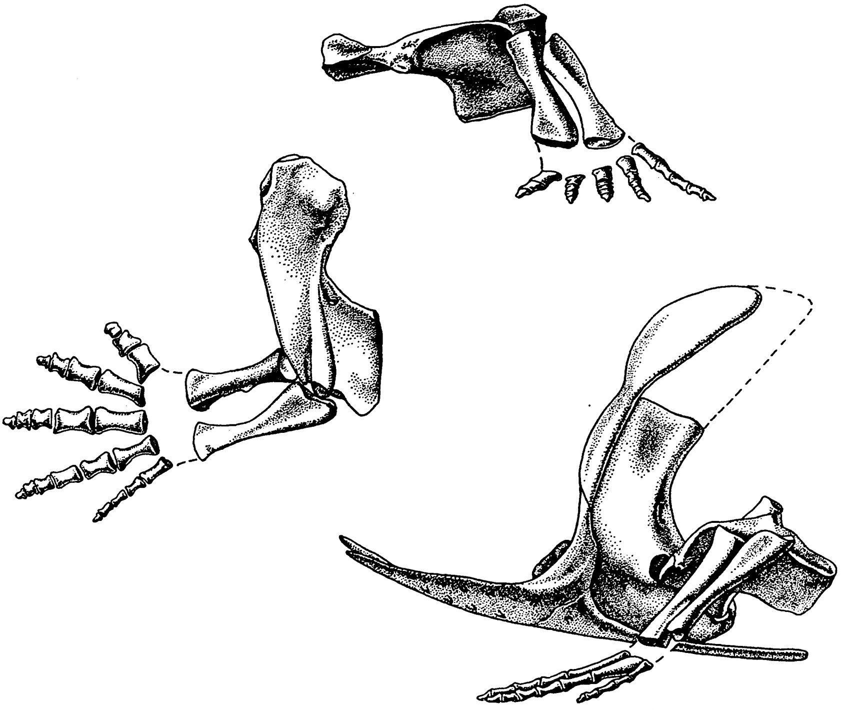

FIG. 16. **Left front leg, restored in articulated pose; *above,* front view; *left,* dorsal view; *below,* lateral view, articulated with girdle. × ½.**

As I have noted on earlier occasions, one has difficulty, when mounting an early tetrapod, in twisting the hind foot forward on the leg into the fore-and-aft position which all Paleozoic footprints show it to have assumed. In fact, in some mounts the attempt has not been made at all, and the feet project laterally (Williston, 1911, frontispiece, *Casea*). In temnospondyls, particularly, presumably proper articulation is difficult to obtain. In reptiles the solution is simpler, for the tibia articulates laterally rather than directly proximally on the tarsus, and the foot can hence be more readily swung inward on the lower leg. *Archeria* appears to show a transitional condition.

In Table I measurements are given of all known limb elements. Although these bones are from a variety of horizons, there seems to be little indication of any progressive increase in size during the time occupied by deposition of the Admiral and Belle Plains formations. In various elements there are variations in size of as much as 20 per cent or more. This seeming variation is, however, deceptive. It is in considerable degree due to the fact that ossification of the ends of the limb bones is slow. A relatively young animal may have had limbs which were in life as long as those of an older individual, but show much smaller length measurements because there were at either end of the "bones" considerable lengths of cartilage which are, of course, absent in the specimen as preserved. (Seeming length differences due to differences in degree of ossification are

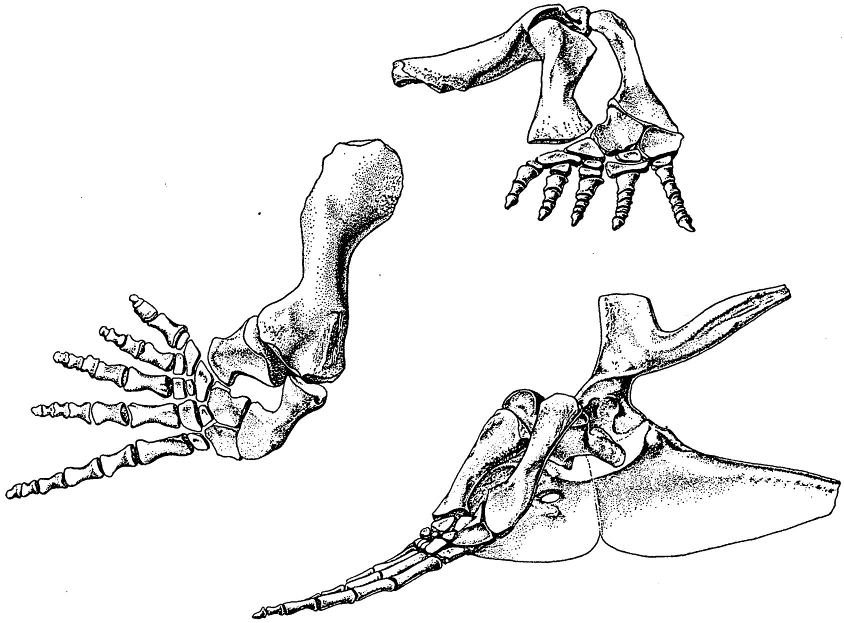

Fig. 17. Left hind leg, restored in articulated pose; *above,* front view; *left,* dorsal view; *below,* lateral view, articulated with girdle. × 1/3.

most striking in the ulna, where the olecranon is notably slow to ossify.) The tardiness in ossification is much greater than in such a contemporary amphibian as *Eryops*. This adds strength to the reasonable belief that *Archeria* was almost exclusively aquatic in habits; in general, a trend toward retention of cartilage is indicative of water life in amphibians and reptiles.

Inspection suggests that the limbs of *Archeria* are short in relation to body size as compared with many other early tetrapods. How can this be tested objectively? A comparison (such as is often made) between limb length and trunk length is in general of somewhat dubious value, since body length is a variable, and is especially dangerous here because of the obvious elongation of the trunk. In pelycosaurs (Romer and Price, 1940, pp. 7–9; Romer, 1948) I have attempted to attain a comparative objective standard for consideration of linear measurements by establishing an "orthometric linear unit" based upon the assumption that the cross section of the vertebral centrum is roughly proportionate to weight and hence to the cube of all linear body measurements. It is doubtful whether use of such a figure is justified in the case of a presumed water dweller such as *Archeria,* in which weight support by the column was of lesser functional importance than in the case of a land vertebrate, but, with this qualification, the facts may at least be presented.

In *Edaphosaurus,* a moderately advanced Permian reptile, the lengths of the main element of the limbs—humerus and radius, femur and tibia—are about 50 orthometric linear units for the front leg, 53 for the hind; in *Diadectes* the same lengths are about 38 and 42 units; in *Limnoscelis,* 31 and 32 units; in *Seymouria,* 37 and 40 units. These last three are typical short-limbed early terrestrial tetrapods; *Eryops* is in the same general category, although in temnospondyls the nature of the vertebral centra makes a computation of this sort difficult. In contrast, the major pectoral limb bones in *Archeria* are but 20 units long, those of the hind leg 27 units. The figures thus tend to support the subjective conclusion from "inspection" that the limbs in *Archeria* are unusually short, and are only about two-thirds as long, relative to the general size of the animal, as in such a seemingly short-legged form as *Seymouria.*

It is the epipodials which are particularly short. In *Archeria* they are only about 55 per cent of the length of the propodials; in *Eryops* and various other rhachitomes and archaic reptiles the figure is from 65 to 70 per cent. Probably this shortness is truly primitive, for the ichthyostegid epipodials are very short indeed.

This shortness of limbs can reasonably be associated with the presumed aquatic mode of life of *Archeria,* in which movement was mainly by swimming, with the powerful tail as the main locomotor organ; terrestrial locomotion probably occurred but rarely. Comparison is suggested here, as in other regards, with *Mesosaurus,* a roughly contemporaneous aquatic reptile of similar body proportions. I have no accurate measurements of vertebral centra in *Mesosaurus,* but such data as I have available suggest limb lengths in orthometric linear units of 32 and 33; i.e., *Mesosaurus* is not unusually short limbed for an early tetrapod. This is due mainly to the length of the propodials.

In early tetrapods generally the hind legs are somewhat the longer. In *Edaphosaurus,* for example, the length of humerus and radius combined is but 95 per cent of the length of the corresponding hind limb bones—femur and tibia; in *Diadectes* the figure is 91 per cent; in *Eryops* 80 per cent. In *Archeria* the contrast is notable; in associated specimens the figure is only 76 per cent. Not only are the major limb bones much longer (and more powerful) in the hind leg, but, as may be seen by comparing Figures 2 and 15, which were made to the same scale, the hind foot is very much larger, in both length and breadth, than the forefoot. This suggests a type of swimming in which, as suggested above, the front legs were held at the sides, but the hind feet (presumably webbed) aided the tail in forward locomotion.

Mesosaurus lacks the contrast seen here in limb lengths, for the major limb bones are only a little shorter in the front limb than in the hind. The two forms agree, however, in the fact that the hind foot is very much larger than the forefoot (cf., for example, McGregor, 1908, Fig. 1). It seems probable that locomotion was similar in these two parallel types.

Summary.—Above are described in some detail the girdles and limbs of the early Permian embolomere *Archeria.* The carpus and the distal part of the tarsus are poorly known, and the phalangeal formula cannot be told with certainty; otherwise the material is adequate. The endochondral bones are slow to ossify, and individuals showing nearly complete ossification are rare—a condition indicative of aquatic life. The limbs are as a whole small compared with body bulk, again suggestive of water dwelling. The hind legs are much larger than the fore, with large feet, presumably webbed; it is probable that they were actively used in locomotion, in addition to the tail.

The shoulder girdle is of a generalized type, with a structure comparable to that of typical contemporary rhachitomes, on the one hand, and many contemporary reptiles, on the other. Obviously this type of girdle is one of considerable antiquity. There is a small cleithrum of a capping type, but no connection of dermal girdle with head; the interclavicle has a modest stem development. The supraglenoid foramen is of large size. There is but a single ossification in the scapulocoracoid.

The pelvic girdle exhibits an ilium of primitive character with a narrow blade for articulation with a sacral rib and a narrow posterior prong; from this type the temnospondyl ilium has evolved by reduction of the posterior prong, the reptilian ilium by longitudinal expansion of the blade. Acetabulum, puboischiadic plate, internal puboischiadic area, and symphysis are all of a generalized type from which the structures seen in both typical temnospondyls and early reptiles can have evolved with little change.

The humerus is of a type not common among known early tetrapods but one derivable by simplification from that of ichthyostegids. The entepicondyle is but little "twisted" on the head. It would appear that the more typical tetrahedral type seen in many temnospondyls and early reptiles has developed in parallel fashion in the two groups. The entepicondylar foramen, lost in most temnospondyls, is retained, as in reptiles. The femur is of the usual primitive type except for an unusually large internal trochanter and a fourth trochanter which has little prominence and is placed close to the former. The forearm and lower leg bones are of generally normal build, except that there is little development of a cnemial crest on the stout tibia; they are, however, very short in relation to the propodials. It is probable that the phalangeal formula was essentially reptilian, rather than with the reduced count of typical temnospondyls. However, it is probable that the fifth digit of the pes was unusually long, with five phalanges.

In most regards, the appendicular structure of *Archeria* is thus seen to be of a primitive tetrapod type, more advanced, it is true, than that of the Devonian ichthyostegids, but one from which, in most regards, that of more progressive labyrinthodonts and ancestral reptiles might well have been derived. It is only in small limb size, particularly of the front legs, but with a relatively high development of the hind "paddles" that there appear to be specializations associated with a long continuation of a piscivorous water-dwelling mode of life.

TABLE I

Limb Bone Measurements of *Archeria*

Lengths are greatest lengths on perpendiculars to line of shaft; widths are taken at right angles to line of shaft in the plane of the extensor surface of the bone; ulnar length is from base of sigmoid notch (not including olecranon). Measurements in millimeters. Except for Nos. 2045–2049, 2495 and 2496, there is no positive association of the included elements.

Bone	Length	Proximal Width	Shaft Width	Distal Width
Humerus				
1172	70	30	23	..
2045	65	26	20	29
	66	22	19	29
2046	75	22	17	..
	..	20	..	27
2047	75	28	19	32
2048	52	21	18	..
2049	63	22	19	32
2057	73	25	19	32
2072	68	22	20	..
2472	67	23	20	..
2473	75	25	21	38
2500	70+	23	19	..
	..	..	..	30
	..	..	19	32
	..	25	..	..
M 3426	87	29	26	43

	Length	Proximal Width	Shaft Width	Distal Width
Radius				
2045	35	11	7	12
	35	11	6	13
2048	40	12	7	13
	..	11	7	12
2049	34	10	6	10
	33	11	6	10
2496	42	12	8	15
2498	39	10	7	11
	40	13	7	14
	..	10	7	..
	..	10	..	..
	..	11	7	..
M 3424	44	13	7	14
Ulna				
2045	36	15	6	11
	36	13	5	11
2048	38	15	6	11
	38+	13	..	..
2049	34	12	5	10
	32	13	5	10
2075	40	18	8	14
2496	..	18	7	11
2499	..	21	..	..
	..	19	..	..
	..	19	..	..
	..	16	..	..
	..	13	..	..
	..	13	..	..
	32	12	..	11
M 3423	40	19	9	15

Bone	Length	Proximal Width	Shaft Width	Distal Width
Femur				
1176	..	34	..	..
	..	33	..	..
1287	..	..	15	38
	76	31	14	34
1289	..	..	18	32
1363	87	34	17	35
2045	87	29	12	31
	84	30	11	30
2046	69	27	10	28
	69	23	11	28
2047	95	34	14	39
2048	72	24	11	28
	68	25	10	26
2049	..	27	12	..
	74	25	12	28
2079	77+	33	14	31
2082	..	..	10	28
2083	..	..	..	38
2208	..	..	12	27
	..	28	..	30
2214	..	..	16	31
	..	..	..	32
	..	..	..	27
2228	66	27	12	28
2472	97	35	12	31
	82	33	13	36
	..	..	15	34
	..	..	..	27
	..	..	17	38
	..	..	..	31
	..	..	12	31
A 7117	73	32	15	31
M 3362	87	..	..	..
M 3363	92	32	12	35
M 3427	68	..	..	..

Bone	Length	Proximal Width	Shaft Width	Distal Width
Tibia				
1176	..	29	..	..
	51	29	16	21
1288	48	28	13	21
1748	46	25	10	19
2045	46	23	9	18
	45	22	9	20
2046	40	23	8	18
2047	52	28	12	23
2048	42	22	9	19
	42	21	9	19
2049	42	21	9	18
2066	47	25	11	21
	..	..	..	18
	48	26	11	20
	46	24	9	20
	59	31	15	25
	48	24	9	20
	47	26	11	22
	48	27	12	20
2067	46	23	11	19
	46	21	12	19
2068	43	23	10	19
2495	41	24	10	20
C 109	53	28	10	24
M 3355	48	24	9	21
	46	22	8	20
M 3433	55	..	..	..
	48	..	..	..
	51	..	..	..

Bone	Length	Proximal Width	Shaft Width	Distal Width
Fibula				
2045	51	14	6	18
	50	14	7	18
2047	60	17	9	23
2049	47	13	7	18
2214	..	19	9	..
2495	52	16	8	..
2497	51	17	8	20
	54	17	8	24
	43	12	6	17
	..	17	10	..
C 132	62	19	10	23
M 3426	43	14	8	20

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