TRIMERORHACHIS, A PERMIAN TEMNOSPONDYL AMPHIBIAN

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No genus of vertebrates occurs so abundantly in the Permian deposits of Texas and Oklahoma—it is unknown elsewhere—as *Trimerorhachis* Cope. Almost always the remains are found in bone-beds as masses, more or less cemented together, of isolated and disturbed bones, often broken, sometimes waterworn, never in anatomical relation. Isolated specimens are not often found, and in such cases where parts of a single skeleton are associated they are more or less jumbled together. The clavicular girdle only is sometimes found closely associated with the skull, filling out more or less the interval between the mandibles posteriorly. In the Chicago collections there are probably parts of at least five hundred individuals. I have counted seventy-five isolated occipital condyles, nearly as many articular ends of the mandible, and scores each of humeri, femora, ilia, scapulae, clavicles, and epipodials, for the larger part fragmentary. Very often the bones are associated with disconnected bones of *Diplocaulus;* not rarely with teeth of *Diplodus* and dipnoans; and sometimes with the smaller disconnected bones of land reptiles. All of which go to prove that the various species of *Trimerorhachis* were purely aquatic animals, living probably in shallow waters near the shores.

Different writers have expressed the opinion, and I have shared it, that *Trimerorhachis* is the most generalized of our American temnospondyl amphibians. I am now about convinced that it is the most specialized, for the following reasons:

We have very good reason to believe that this and other groups of stegocephs were, by the beginning of Permian times, already very old. The origin of terrestrial amphibians surely dates from at least as early as late Devonian times and of land reptiles from early Pennsylvanian if not Mississippian times. There can be little doubt that *Eosauravus*, from the Coal Measures of Linton, Ohio, is a real reptile; and Watson has recently figured[1] a femur from the Lower Carboniferous of Scotland that he believes to be of a true reptile, or at least of a "precocious" amphibian. I think that he is right.

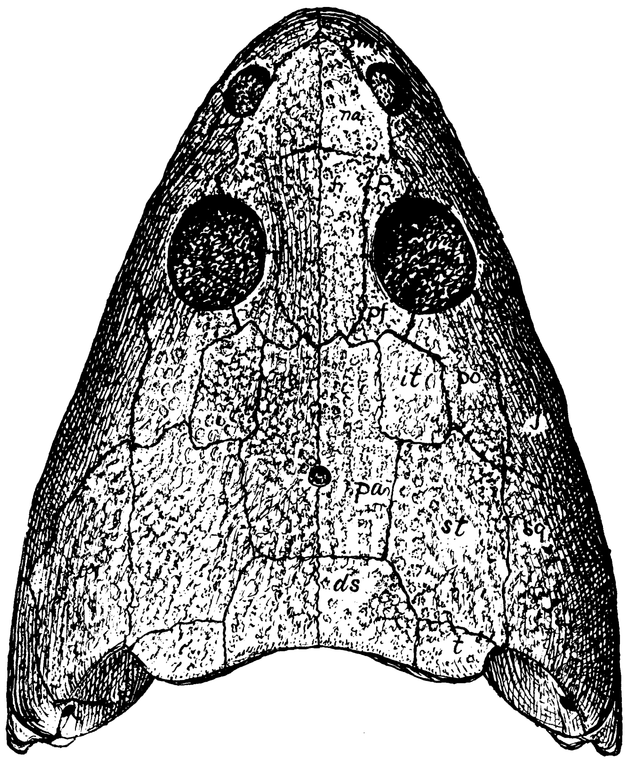

FIG. 1.—Skull of *Trimerorhachis insignis* Cope. One-half natural size: *pm*, premaxilla; *na*, nasal; *p*, prefrontal; *pf*, postfrontal; *po*, postorbital; *it*, intertemporal; *pa*, parietal; *st*, supratemporal; *j*, jugal; *sq*, squamosal; *ds*, dermosupraoccipital; *t*, tabulare; *l*, lacrimal; *m*, maxilla; *qj*, quadratojugal; *sp*, splenial; *psp*, postsplenial; *an*, angular; *art*, articular.

Trimerorhachis was a purely aquatic amphibian, as its mode of occurrence indicates and as its structure demonstrates. The characters showing aquatic adaptation are found in the anterior position of the orbits and their direction upward; in the relatively

[1] *Geological Magazine* (1914), p. 347.

small size of the limbs and the attachment of the anterior pair almost at the angle of the mandible; in the shape of the humerus, very unlike that of the terrestrial types, with the planes of its extremities but slightly divergent and with strong muscular rugosities, as in the plesiosaurs and marine turtles, situated low down; in the absence of the adductor ridge on the femur; in the relatively very short epipodials, a certain indication in crawling reptiles of swimming habits; in the conspicuous lack of ossification at the ends of the long bones; in the almost certain chondrification of the mesopodials and pubes; in the short scapulae, utterly unlike those of terrestrial amphibians; in the structure of the clavicular girdle, so like that of *Diplocaulus* as to be almost indistinguishable at first sight; and in the certainly bare skin. Further evidence is scarcely needed.

It may be granted that the first amphibians were aquatic animals, perhaps as much so as is our modern *Necturus*, although of that I am not convinced. If then, *Trimerorhachis* is a generalized amphibian, it naturally follows that it has retained its primitive structure and habits from Devonian times; that its peculiar clavicular girdle is primitive, as also the unossified mesopodials and the relatively feeble ossification of the vertebrae, the very small size of the pleurocentra, etc. It necessarily follows that if the clavicular girdle is primitive, that of the stereospondyl amphibians of the Upper Trias is also, for the buckler-like structure in these, the last of the stegocephs, is much more pronounced. On the other hand, I believe that the clavicular bones in the direct line of the ancestry of the reptiles were never large and rugose, that they began as small dermal elements and continued so in those amphibians which gave origin to the reptiles.

The occipital condyle of *Trimerorhachis* is remarkably different from that of all other known American Permian amphibians, as will be seen by reference to the figures (Fig. 5, I, J, K), in that it is single and deeply cupped, fishlike. Granted that this a primitive character, and it may be, it does not necessarily disprove the argument I make that *Trimerorhachis* was descended from terrestrial forbears, that its aquatic characters are acquired, not hereditary. Watson urges that the primitive amphibians had a closed palate, like that of the reptiles; *Trimerorhachis* has very wide parasphenoidal vacuities, though only a slender parasphenoid. Certainly the resemblances between *Trimerorhachis* and *Diplocaulus* in the eyes, clavicular girdle, and small limbs are adaptive, not genetic, for *Diplocaulus* is a holospondylous amphibian.

In the evolution of the feet we know that aquatic adaptation has frequently resulted in the more or less complete chondrification of the mesopodials. One need only to study the progressive evolution of the mosasaurian paddle to be convinced of this.[1] And the cetaceans are still better examples.

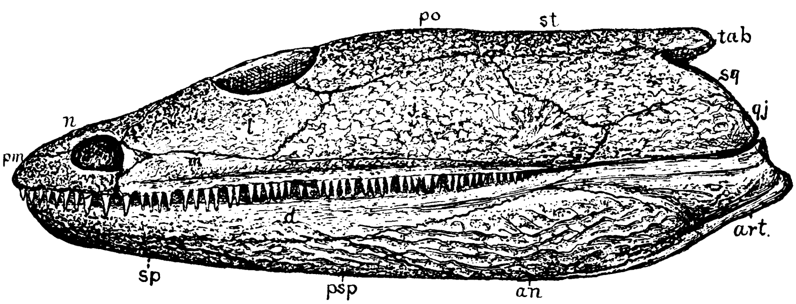

FIG. 2.—*Trimerorhachis insignis*, skull, from the side. Explanations as in Fig. 1

In the progressive adaptation of the tarsus to terrestrial life, there has been a continued loss of elements and a strengthening and closer articulation of those remaining, not only in the mammals, but in the reptiles as well. In the most primitive known tarsus, that of *Trematops*,[2] there are not less than thirteen ossified bones, four in the first row, four in the second, and five in the third. The early amphibian was a truly crawling animal, dragging its body over the surface of the ground. Its feet were directed outwardly, and the motion of the tarsus on the leg was chiefly lateral; the angle between the over-extended foot and the leg was always obtuse. In the evolution of the reptiles greater speed was attained by the elevation of the body from the ground in locomotion. No modern reptiles crawl, in the strict sense of the word, except the snakes and legless lizards—for the most part at least; many even

[1] Williston, *American Permian Vertebrates*, p. 45.

[2] Williston and Case, *Carnegie Publication, No. 181* (1913), p. 56.

rear themselves on the hind legs in running. In such locomotion the leg is brought more nearly at right angles with the plane of the plantigrade foot, and the result has been a closer union of the proximal bones of the tarsus, either with each other or with the leg bones. The earliest known reptile, from the Coal Measures of Ohio, had only two bones in the proximal row, the astragalus and calcaneum, and, even as early as the beginning of Permian times, the centralia and fifth tarsale had begun to disappear. In the elevation of the heel from the ground a further union of the proximal bones took place in some forms, *Pareiasaurus*, for instance, and some living lizards and turtles. In modern reptiles the foot is plantigrade. Among the first results of digitigradism was the closer union of the astragalus with the tibia, as seen in *Ornithomimus* and other bipedal dinosaurs, becoming more intimate in a more or less sutural union in *Rhamphorhynchus*, and the sutural obliteration in *Pteranodon* and birds, and the final union of the tarsalia with the metatarsals in the latter. In known reptiles the chief joint between the leg and foot is intratarsal, that is between the first and third rows. In the mammals it is between the tibia and the astragalus. One wonders how the change occurred in the ancestral reptiles.

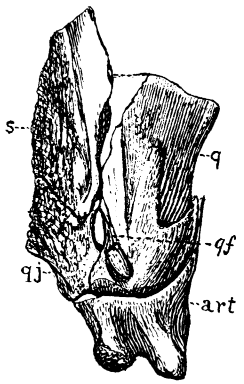

FIG. 3.—*Trimerorhachis*, part of skull, from behind: *q*, quadrate; *qf*, quadrate foramen; *art*, articular; *s*, squamosal; *qj*, quadratojugal. One-half natural size.

Not only has the vertical posture of the leg been the cause of the loss of tarsal bones, and of the change of the chief tarsal joint to the immediate end of the tibia, as in mammals, or its functional equivalent in the dinosaurs, ptderodactyls, and birds, but it has also been the cause, I believe, of the reduction of the phalanges in turtles, theriodonts, and mammals. In the most rectigrade posture of the lower leg and foot of all turtles, the land tortoises, but two phalanges remain in each toe. In the rectigrade Sauropoda no toe has, I believe, more than four phalanges; and the tarsal bones are much reduced.

Notwithstanding the abundant but disconnected material, I have been frustrated in the attempt to make out the complete anatomy of *Trimerorhachis*, and it will only be by the fortunate discovery of a connected skeleton that the tail, ribs, and feet will be made known. The figures of the skull herewith given are based chiefly upon three specimens. The most perfect of these, so far as form is concerned, is a solitary skull and clavicular girdle found by Mr. Miller in the same horizon as, and in the immediate vicinity

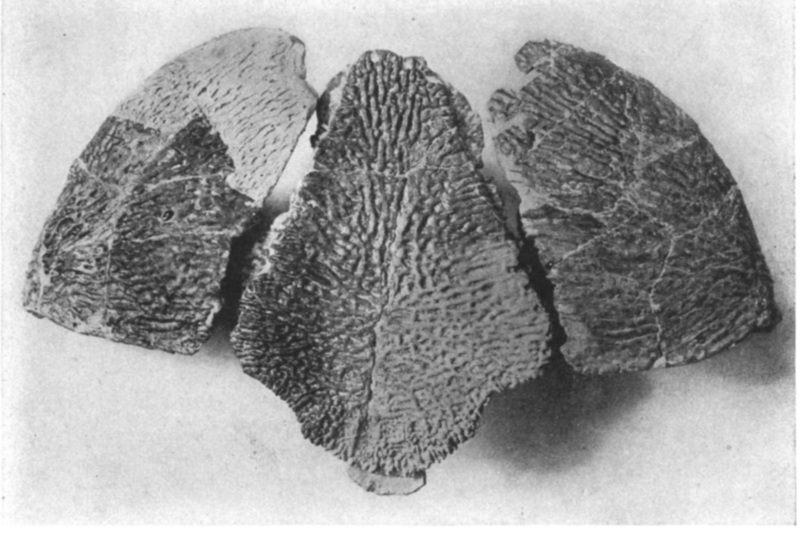

FIG. 4.—Clavicular girdle of *T. insignis*, from below; four-fifths natural size

of, the skeleton of *Seymouria* described by me in a previous paper. The specimen originally was perfect and undistorted, but weathering had carried away much of the thin roof, leaving the cast very smooth and complete. These parts have been completed from two other specimens of identical size and character, specimens collected in Texas nearly twenty years ago by Professor Case. The sutures separating the elements have been determined chiefly from these three specimens, aided by parts of several others, and I think can be relied upon. In their general courses and relations there is but little novelty in the figures. All of them, except the more anterior ones, were first determined by Professor Case.[1] Dr. Huene completed our knowledge of the anterior ones, and Dr. Broom has corroborated the most of them. The most striking peculiarity of the skull is seen in the large size and posterior extension of the lacrimal.

The figure of the clavicular girdle is made from one of the numerous isolated specimens agreeing closely with that attached to the first-mentioned skull. Its comparison with that of *Cacops*[2]

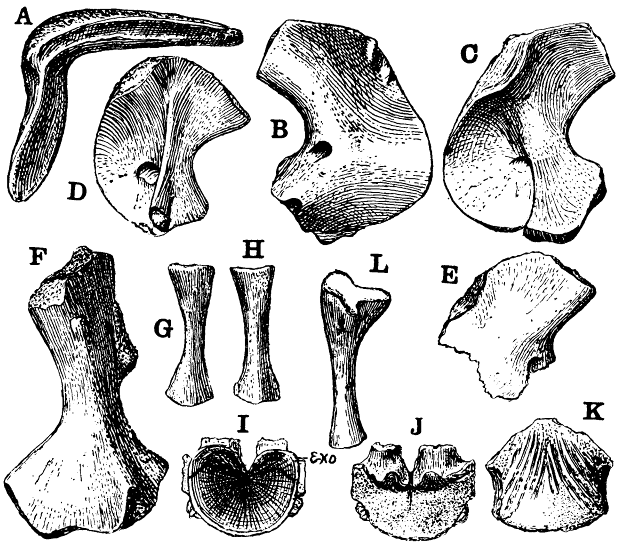

FIG. 5.—*Trimerorhachis*. *A*, right interclavicle, from behind; *B*, right scapula, from without; *C*, the same, from within; *D*, scapula of a smaller individual or species; *E*, fragment of another scapula; *F*, humerus; *G*, *H*, radii; *I*, occipital condyle from behind; *exo*, exoccipital; *J*, the same bone from in front; *K*, the same from below; *L*, ulna. All figures three-fourths natural size.

will show the extraordinary differences from the more terrestrial type of the contemporary temnospondyl amphibians. The scapula is also very peculiar in its short, rounded shape. The thickened part on its front border is apparently for articulation with the ascending process of the clavicle (Fig. 5, C). The foramen is the supraglenoid. The bone agrees closely with that figured by Case

[1] *Carnegie Publication, No. 146, (1911)* pp. 107 ff., A, B.

[2] *Bulletin American Geological Society*, XXI, Plate II, Fig. 1.

(*op. cit.*, p. 113), referred provisionally to *Zatrachys*. The coracoid has not been certainly recognized. The bone figured (Fig. 5, E, F) is probably correctly identified; possibly it is the ischium. There are no other evidences of pelvic bones, except of the ilia, of which more than fifty are in the Chicago collections. I have figured the relations of the quadrate in a specimen in which the different elements had been separated (Fig. 3). The sutural roughening for the pterygoid is very conspicuous. The separated quadrate is not very rare in collections.

Not a trace of any dermal ossicles has been detected in any of the abundant material; the skin unquestionably was bare. Certain skin ossifications or calcifications, however, have been detected in a few specimens, first mentioned by Cope and later by Case. They consist of very thin sheets, like leaves of thin paper, probably of calcified cartilage, overlying each other, a dozen or more, in places. They probably sheathed the under side of the abdomen.[1]

The bones figured were all found dissociated, and probably belong to different species, though there is not much difference in size. A number of species of *Trimerorhachis* have been described, though it is a futile and almost hopeless task to identify them. I assume that the skull and pectoral girdle belong to *T. insignis*, because they agree, so far as I can determine, with the species so named. I cannot forbear entering a protest here against the heedless naming of species of fossil reptiles, and especially of the Permian vertebrates, based upon fragmentary material or, much worse, upon difference in size. Such names seldom advance science. Nor does anyone care much, at the present time, about species; they are, for the most part, a nuisance. Specific determinations will become of use only when precise differences

[1] Rather singularly dermal ossicles have very rarely been observed in the air-breathing vertebrates of the American Permian—so far as I am aware only in *Eryops*, though ventral ribs or scales are a rather common characteristic of the reptiles. Very recently I have observed in *Pantylus*, the strange reptile of which only the skull has been known hitherto, a continuous covering extending probably over the whole body, though possibly only on the under side, composed of a mosaic of small, smooth, bony scutes two or three millimeters in diameter. The vertebrae and ribs show as great peculiarities as does the skull.

are required for geological correlations, or for minor problems in evolution, and their naming should, so far as possible, be deferred until much more material is available for comparison. As I have said elsewhere, the genus is practically our unit for most of the older vertebrates. In very few of the Permian vertebrates do we yet know what specific differences really are; we have few measuring sticks yet to measure them by; and it is only the morphological characters of the genus and higher divisions that concern us much in paleontology. Perhaps this protest is a sort of belated

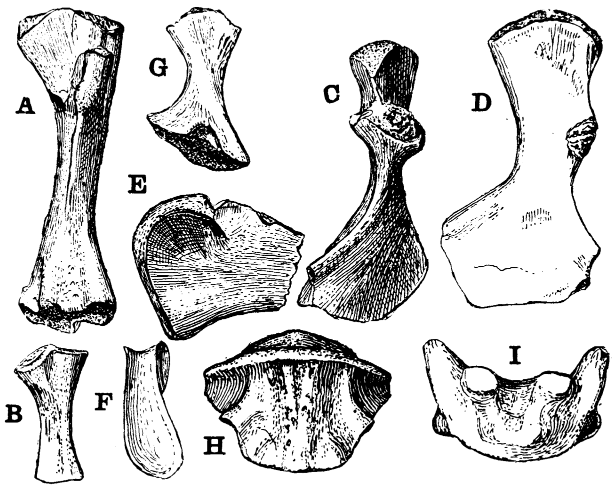

FIG. 6.—*Trimerorhachis*. *A*, left femur, from behind; *B*, tibia; *C*, humerus, radial side; *D*, another humerus, dorsal side; *E*, coracoid (?); *F*, the same, end view; *G*, right ilium, outer side; *H*, anterior intercentrum, from below; *I*, the same, from behind. All figures three-fourths natural size.

repentance on the part of one who has himself contributed hundreds of specific names to zoölogical and paleontological literature, but the many hours he has spent in the endeavor to identify organisms from vague and imperfect descriptions at least give him the right to urge temperance in the making of more or less worthless types! About twenty-five specific names were given to the mosasaurs of Kansas. The most diligent search of abundant material has resulted in the recognition of scarcely a half-dozen. The same fate probably awaits the great majority of the specific names which have been given to the Permian vertebrates.

There are various species among the material known as *Trimerorhachis;* of that there can be no question; as also of *Eryops;* but when one species is based upon an isolated scapula, for instance, another on the comparative size or minor distinctions of a skull, and a third upon a vertebra, one is tempted to ask: What is the use?

It need not be said that the differences of occipital condyle, pectoral girdle, vertebrae, and limbs in *Trimerorhachis* are of more than family importance. Doubtless some day, when we know the forms better, the genus or genera will be separated into a group of higher rank.