56.81,7E

Article III.—FURTHER EVIDENCE ON THE STRUCTURE OF THE EOSUCHIA

By R. Broom

Dedicated to the Memory of Samuel Wendell Williston

In 1912 I discovered at New Bethesda near Græff Reinet, South Africa, the skull and part of the vertebral column of a small diaptosaurian reptile of the very greatest interest. I gave a short description of the skull in "Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History, II. Permian, Triassic and Jurassic Reptiles of South Africa."[1] Here it is described under the name *Youngina gracilis*. Towards the end of 1914 I exhibited the skull before the Zoological Society of London and there described it at considerable length under the name *Youngina capensis*, forgetting that I had used a different specific name in the American paper. Owing to some delay in the publication of the American Catalogue, the London paper appeared a few weeks before it; so that the fossil must take the name *Youngina capensis*.

The type skull is, on the whole, remarkably well preserved but lacks the upper part and point of the snout and the quadrate region. The mandibles are in position and I did not think it wise to risk injuring the type by exploring the palate, but I believe Prof. D. M. S. Watson, with whom I left the specimen in care, has succeeded in revealing the palatal structure.

The great interest that attaches to this specimen is that it is the only known Permian skull which shows two arches. Other Permian reptiles, such as *Protorosaurus*, *Broomia* or *Heleosaurus*, may have had two arches, but *Youngina* is the oldest reptile in which two arches are clearly shown; and as the large majority of the reptiles known from the Triassic and later periods of the world's history are either reptiles with a two-arched skull or a skull derived from the two-arched type, we have in *Youngina* either an ancestral type or, at least, a type which will throw much light on the structure of the ancestor of the majority of the later reptiles.

As I showed, the skull has two arches not unlike those seen in *Sphenodon*, but *Youngina* differs from the rhynchocephalians in having a

[1]1915. Bull. Amer. Mus. Nat. Hist., XXV, pp. 161, 162.

large pineal foramen and in retaining a distinct interparietal bone and tabulars. The squamosal is large and forms most of the posterior border of the lower temporal fossa. The quadratojugal is small. The tabular lies above the squamosal and behind it and articulates with the paroccipital, the parietal and the postorbital as well as with the squamosal, and

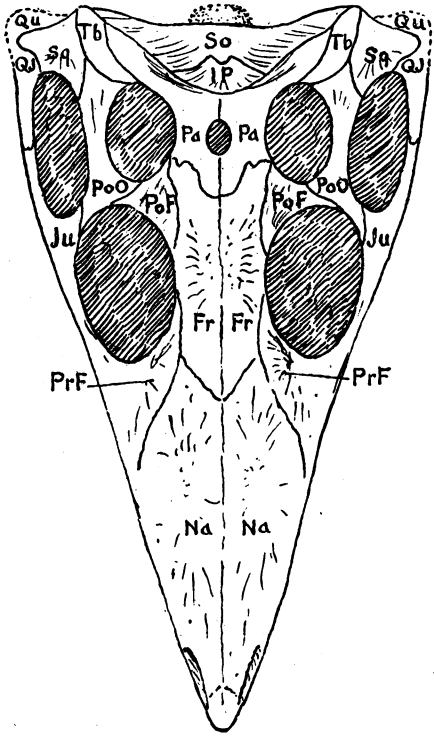

Fig. 1. Skull of *Youngina capensis* Broom. About one and one-half times natural size.

thus reveals to us the origin of such later skulls as are found in *Sauranodon* and *Pleurosaurus*, where a large tabular is found above the squamosal, and of the lacertilian skull, where the two bones—a small tabular above and a large squamosal below—are generally retained.

Since the type skull was discovered, two other specimens have been found at the same locality—the second specimen about eight yards from

[1]References to lettering in the figure: *Fr.*, Frontal; *Ip.*, Interparietal; *Ju.*, Jugal; *Na.*, Nasal; *Pa.*, Parietal; *Po.F.*, Postfrontal; *Po.O.*, Postorbital; *Pr.F.*, Prefrontal; *Qu.*, Quadrate; *Q.J.*, Quadratojugal; *So.*=*Sa.*, Supra-occipital; *Sq.*, Squamosal; *Tb.*, Tabular.

the type and the third about thirty yards away, but all in the same horizon. The second specimen was apparently a nearly perfect skeleton, but Mr. J. Venter, who discovered it, removed it in a most unskilful manner, with the result that all that remains of it is a few fragments now in the collection of the Pretoria Museum. These fragments, however, are of very great value. Of the skull there remains much of both mandibles, of both maxillæ and premaxillæ and most of the palate. Of the shoulder girdle we have remains of one scapula and much of one coracoid. There are one good humerus and portions of the other, a radius and ulna and some fragments of the fore foot. Two sternal ossifications are preserved in fair condition. Of the pelvis there remain only one fair pubis and a few fragments, but much of both hind limbs is preserved and one tarsus fortunately is preserved in almost perfect condition.

The third specimen which has been found was discovered by myself. It consists of a good skull, which is somewhat crushed and has lost the occipital region with the tabulars and most of the parietals. The specimen is of great value in showing most of the squamosal with some of the quadrate, much of the palatal structure and almost the whole of the snout in good condition.

With the help of these later specimens it is possible to give a much more perfect restoration of the skull than could be done with the type skull alone.

The snout is long and very pointed. The premaxillaries are small and narrow and each has three teeth and possibly four. The nostril is far forward and low down.

The maxilla is long and slender and has about twenty-one round-pointed teeth, which lie in a groove as in *Ichthyosaurus*, but some of the older teeth in front seem to have their bases anchylosed to the bone, like the teeth in *Varanus*.

The structure of the lachrymal and prefrontal cannot be clearly made out. The upper part of the prefrontal is clear enough, but I cannot find any suture dividing it from what one would expect to be the lachrymal. Possibly the lachrymal is already lost, as in *Sphenodon*. More likely, one is present but either small or united with the prefrontal.

There is no trace of a preorbital vacuity.

The nasal bone is unusually large and broad. It is ornamented by a number of radiating ridges and little knobs.

The frontals, parietals, postfrontals and postorbitals have already been described in the type skull, and the one further point which may be

noted is that, like the nasals, they are ornamented by little radiating ridges and bony knobs.

The squamosal, though not quite perfect in this third specimen, luckily has its lower end preserved. The quadratojugal is displaced and crushed and of the quadrate we have little more than the impression of the anterior side. But the additional evidence enables us to restore the articular regions of the skull with considerable confidence.

The palate is not well preserved in either of the new specimens, both showing the bones considerably crushed. Still the main structure is sufficiently revealed. In front are a pair of prevomers not unlike those in *Proterosuchus* but with the internal nares farther back. As in *Proterosuchus*, the prevomers have a row of small teeth. The palatines are very much larger than in *Proterosuchus*, but, when viewed from the under side, they are considerably hidden by the anterior processes of the pterygoids. I cannot find any teeth on the palatines, but these bones are not sufficiently displayed to show for certain that none exists.

The pterygoids are very large and long bones. Posteriorly they appear to agree in structure with those of most primitive diapsidan reptiles. They articulate with the basisphenoid, as in *Sphenodon* and other rhynchocephaloids. There is a strong transverse process which passes almost directly outwards. This process has, as in *Proterosuchus*, a row of fairly large rounded teeth. The anterior part of the pterygoid is, as in *Proterosuchus*, long and broad, and, as in that genus, it has a large number of small rounded teeth which are arranged in rows. A little in front of the articulation with the basisphenoids, the pterygoids approach each other closely in the middle line, and along this inner portion of each bone there are three or four long rows of small teeth. A little farther out, along a thickened portion of the bone, are two or three rows of rather large teeth very similar to the outer rows in *Proterosuchus*, and in addition to these are a few small teeth still farther out.

The ectopterygoid is small and situated well out, as in *Proterosuchus;* and the infraorbital vacuity is also apparently small.

The mandible is not well preserved in either of the specimens I have on hand. The jaw agrees in many respects with that of the crocodile. The splenial is large and extends forward to near the symphysis, but whether it takes part in the symphysis the evidence does not show. There is a large angular not unlike that of *Erythrosuchus*, and there is a lateral vacuity in the jaw.

The vertebræ are not very well seen in the Pretoria specimen, but they are biconcave and apparently notochordal. Large intercentra are present.

The shoulder girdle is not very well preserved. The scapula is represented only by a portion of its cast. It is apparently short and rounded. The coracoid is single and, so far as preserved, resembles that of *Sphenodon*. It has a well-marked foramen.

The left humerus is completely rotated, so that, though the ventral aspect of the animal is displayed, it is the upper or posterior surface that is seen. In general the humerus resembles more closely the lizard type than any other with which I can compare it. Quite manifestly, there have been fairly large cartilaginous pads on each end and it would agree

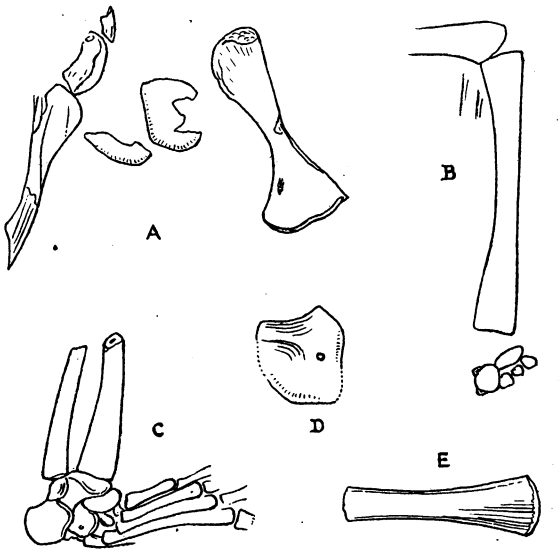

Fig. 2. Figures of portions of the skeleton of *Youngina capensis* Broom. Natural size.

A. Pectoral region with remains of right coracoid, both humeri and sternal ossifications.
B. Portions of right limb from front and outer side. The portion of the tarsus is in undisturbed position, the tibiale having fallen out.
C. The left tarsus and metatarsus with portions of tibia and fibula and of some phalanges, viewed from the inner and plantar surface.
D. The right pubis.
E. Distal portion of left femur.

pretty closely with the lizard humerus if the epiphyses were removed. The upper end is expanded somewhat as in *Varanus*, but, as will be seen by the figure, the curving is slightly different. The lower end is much expanded and fairly flat. There is a small ectepicondylar foramen but no entepicondylar. The shaft is much constricted in the middle.

One of the most interesting points in the skeletal structure is the presence of two thin flat ossifications which lie in the sternal region.

These cannot well be anything else than ossifications of the sternum. Neither is perfect, but it is possible to make a restoration from the two which is practically complete. I have figured the remains as they occur. Quite manifestly they are ossifications in cartilage. Though crushed, it is evident they must have been fairly flat and they are thin.

Of the pelvis the only bone that is preserved is the right pubis and this is not quite perfect. The bone is a modification of the plate-like type. It is very slightly broader than long. There are a short but strong anterior and outer process and a very small pubic foramen.

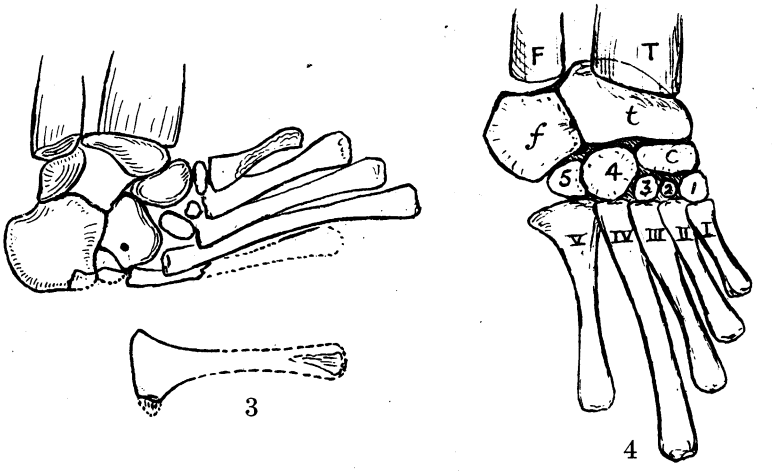

Fig. 3. Left foot of *Youngina capensis* Broom. Slightly more than twice natural size. With, below, fifth metatarsal as viewed from its true under side.

Fig. 4. Tarsus and metatarsus of *Youngina capensis* Broom, as they would appear when viewed from dorsal side. About twice natural size.

The femur, tibia and fibula are all rather slender bones without any striking characters, and they will be best understood by the figures given.

The left tarsus is almost perfectly preserved, with much of the foot, and there is an important portion of the right tarsus also preserved.

Though the left tarsus has its plantar surface exposed, all the elements can be perfectly made out. There are two large proximal elements and five distal tarsals and an eighth large element which occupies the position of the navicular in the human tarsus. The resemblance of the tarsus to that of the Therapsida is so striking that I think we may safely regard the elements as homologous, and I shall therefore speak of the two proximal elements as tibiale and fibulare and the navicular-like element as the centrale.

The tibiale is the largest element of the tarsus. It gives a large articulation to the lower end of the tibia and its outer portion gives part of the articulation for the fibula. The tibiale is curiously twisted, so that, while the plantar surface of the inner two-thirds is nearly in a plane with the plantar surface of the fibulare and the centrale, the plantar surface of the outer one-third is much recessed from the general plane. A foramen passes between the tibiale and the fibulare as indicated in the figures. The tibiale articulates with the fibulare, the large fourth tarsale and the centrale.

The fibulare is a rounded bone whose outer half is thin and flat and whose inner side is thickened to give part of the articulation to the lower end of the fibula and to articulate with the tibiale and the fourth and fifth tarsalia.

The centrale is an element about one-quarter of the size of the tibiale. It articulates with the distal tarsals 1, 2, 3 and 4, and also with the tibiale.

Tibialia 1, 2 and 3 are all small. The appearance as viewed from both above and below is shown in the two specimens.

Tibiale 4 is a large element which articulates with tibialia 3 and 5 and with the centrale, the tibiale and the fibulare. The articulations with all the elements except the fifth tarsal are freely movable, but that with the fifth tarsal must have admitted of very little movement.

The fifth tarsal is a fair-sized element a little larger than either tarsalia 1, 2 or 3. It is firmly united with tarsale 4 by a suture which is straight on the plantar side but curved on the upper. It has a large articulation with the fibulare. Though the outer half is missing, there is probably little doubt that it was a rounded element as figured.

The metatarsals are fairly well preserved. They are moderately straight slender bones which increase in length from the first to the fourth. The fifth is slightly shorter than the fourth. Though not perfectly preserved, enough remains to show that it is a slender bone fairly similar to the other metatarsals but with a larger head. The proximal end is flat and broad and has a short posterior and inferior process which is probably attached by a ligament to the fibulare. In no way is this metatarsal hooked like the fifth metatarsal of *Sphenodon* and most other Diapsida.

The phalanges are long and slender.

When the characters of *Youngina* are looked into, it will be observed that we have in it one of the most important missing links that have yet been discovered. It is undoubtedly a diapsid, and as it is the oldest

diapsid known and the only one yet discovered in Permian beds, it shows, as might be expected, a number of very primitive characters.

The presence of a distinct bone which I believe to be the tabular, above the large squamosal, gives us the clue to the two bones in the lizard skull. Though some doubt may remain as to whether the upper bone is a tabular or a supratemporal, as held by Boulenger and others, no doubt whatever remains that the lower and outer bone is the squamosal. The skulls of *Sphenodon*, of *Pleurosaurus* and of the lizard may be regarded as three different modifications of an ancestral skull of the *Youngina* type.

The shoulder girdle is practically of the same type as is seen in *Sphenodon*. The presence of two large sternal ossifications is very interesting in view of the presence of similar ossifications in some dinosaurs.

The pelvis as shown by the pubis is of the plate-like type found in most Permian forms.

The tarsus is extremely interesting in many ways. In the first place, though undoubtedly a diapsid tarsus, it agrees so closely in structure with the tarsus of therapsids and even of living mammals that the homology of the bones can be determined with certainty, and we are thus able for the first time definitely to fix the homologies of some of the bones in later reptiles.

A few years ago, I figured the tarsus of a small reptile under the name of *Galesphyrus capensis* and referred it to the Dromasauria. But, while it has a general resemblance to the dromasaurian tarsus, all the points in which it differs are points in which it agrees with *Youngina*. There is thus much more probability that *Galesphyrus* is really an eosuchian.

Howes and Swinnerton, when investigating the development of the *Sphenodon* tarsus, found that the large proximal tarsal element in an early embryo is composed of "the intermediare and fibulare chondrified and separated by a foramen . . . the centrale and tibiale being procartilaginous." Their figures, however, do not show a very clear separation of the "centrale" and "tibiale," and anyone who has studied "procartilage" much knows how fallacious the appearances may be. If we assume, as I think is very probable, that the "centrale" and "tibiale" of Howes and Swinnerton are really a single element, then the agreement is fairly close with the tarsus of *Youngina*, but *Youngina* shows that the large supposed intermediale is really the tibiale, and the centrale and tibiale really only the centrale.

Osborn in discussing the tarsus of the primitive "Diaptosauria" says: "No ideally primitive tarsus with three distinct proximal elements (tibiale, intermedium, fibulare), free centrale or centralia, and five separate distal tarsalia, has yet been found among the Diaptosauria. More or less coalescence (astragalus = tibiale + intermedium + centrale) or degeneration of these elements has occurred in every known type. Five separate distal tarsalia are observed only in certain Protorosauria (*Palæohatteria*) and Proganosauria (*Mesosaurus* and *Stereosternum*), a unique feature among reptiles; in all other Diaptosauria distal tarsalia 4 and 5 are united."

Youngina gives us what is probably the most primitive tarsal type where there are still five distal tarsalia, but in addition a distinct centrale. There is no evidence of an intermedium.

The occurrence of a simple unhooked fifth metatarsal in *Youngina* is a point of great importance. The majority of diapsidan reptiles have a peculiarly modified and hooked fifth metatarsal such as is seen in *Sphenodon*. Goodrich considers that the ancestral diapsidan must have had such a character and that all reptiles with this character belong to a common group. As the chelonians also show the character, we must either conclude that they are aberrant descendants of a primitive two-arched reptile or that this modification of the fifth metatarsal has been independently evolved in two different groups. As will be seen from the discussion of this question in my paper on the classification of the reptiles,[1] I favor the latter alternative.

There is good hope that in South Africa we shall yet be able to give a very complete account of the evolution of the Permian ancestors of the diapsid reptiles and perhaps also discover the ancestors of the Ichthyosauria, Plesiosauria and Chelonia.

ADDENDUM

In the three years that have elapsed since the above paper was written, a few additional facts have been discovered which give greater definiteness to certain points in the classification. In the past six months, I have been fortunate in discovering the full details of the structure of the skulls of the tapinocephalian and titanosuchian dinocephalians. These show that the dinocephalians are more nearly related to the anomodonts and to the gorgonopsians and therocephalians than had hitherto been supposed, and not quite so nearly related to the pelycosaurs. The mammal-like reptiles, or Therapsida, have probably

[1] 1924. Bull. Amer. Mus. Nat. Hist., LI, pp. 39–65.

originated from an at present unknown pro-gorgonopsian or pro-therocephalian group that lived in Lower Permian times. From this primitive group, there arose by three diverging lines of descent: (1) the Dinocephalia, which became subdivided into two suborders, the Ṭapinocephalia and the Titanosuchia; (2) a line of carnivorous therapsids, branches of which gave rise to the Gorgonopsia, the Therocephalia, the Burnetiamorphia, the Bauriamorpha, the Cynodontia and the Mammalia, and (3) a line which resulted in the specialized group the Anomodontia. The exact relationship of Dromasauria to the other therapsids will remain doubtful until we get the details of the structure of the skull and jaw. (4 Nov., 1923.)