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THE PES OF *BAURIA CYNOPS* BROOM

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In several respects the bauriamorphs are farther advanced toward the mammals than the cynodonts and any additional information concerning the detailed morphology of the skeleton is of special interest. This study is based on an almost complete left pes of the type of the Bauriamorpha, *Bauria cynops*, which Broom found, along with the associated skull, at Winnaarsbaken, South Africa, in beds referred to the Upper Triassic. These specimens have been described by Broom (1937) and Boonstra (1938). Because of its undeniable evolutionary importance, further study of the pes was undertaken. As the result of extensive preparation, the use of roentgenograms, and the construction of a natural size model, certain features have been revealed which make a revised and more detailed description advisable.

The foot (A.M.N.H. No. 5622), with all the preserved elements in their natural positions, is complete, except for the more distal phalanges of the fifth digit. These are most certainly two in number and may be restored with confidence. The distal ends of the tibia and fibula are present and were in place when the fossil was found. The proximal ends of these bones, but from the opposite side, were also located elsewhere in the surrounding matrix.

The distal parts of the tibia and fibula were removed from the matrix before the present study was undertaken, and the proximal and distal articular surfaces were ground in an attempt to remove the very tenacious matrix. This makes it impossible to determine the exact nature of these surfaces. The distal end of the fibula has a greater diameter than that of the tibia and clearly shows two concave facets for articulation with the astragalus and calcaneum. The distal end of the tibia is but little expanded, with its astragalar face slightly concave. There is no indication of either an internal or an external malleolus. The upper extremity of the tibia is more expanded than that of the fibula and has a very mammal-like crest and tubercle for the attachment of the patellar ligament. Both the tibia and the fibula apparently have straight, slender shafts.

The astragalus and calcaneum are of particular interest. The latter possesses a short but well-defined tuber with a somewhat restricted neck. The presence of this tuber could not be definitely established by Broom. On the contrary, Boonstra describes a tuber, but because of an apparent detachment of its distal portion, he considers the latter to be a sesamoid bone. Further preparation for the present study demonstrates without question that the so-called sesamoid bone is merely a part of the tuber. The roentgenograms further support this conclusion.

A tuber calcis has been found by Watson (1931) on the calcaneum of the bauriamorph *Ericiolacerta parva*. It is also present on the calcaneum of the primitive gorgonopsian *Scymnognathus* cf. *whaitsi* (Broili and Schröder, 1935) and the therocephalian *Ictidosuchoides intermedius* (Broom, 1938). In *Ericiolacerta*, as in *Bauria*, the tuber meets the body of the calcaneum at an angle of about 140 degrees. This does not necessarily indicate, as Watson suggests, that the foot was digitigrade. The evidence rather indicates that it was plantigrade or semiplantigrade. Although, in *Scymnognathus*, the tuber does not make an angle with the body, the foot has likewise been restored as digitigrade. In mammals, true digitigradism is always associated with the development of an anticlinal vertebra

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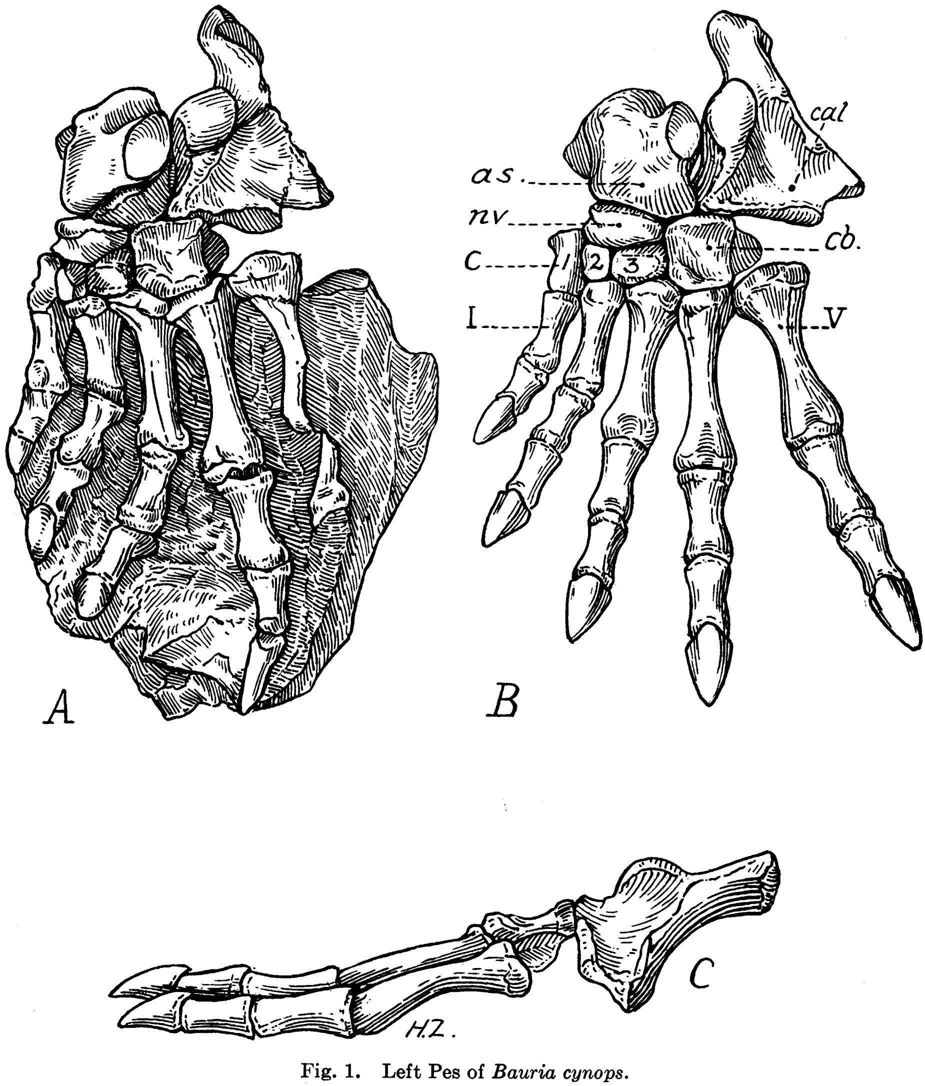

Fig. 1. Left Pes of *Bauria cynops*.
A. Dorsal view, from specimen. Natural size.
B. Dorsal view, from model. Natural size.
C. Lateral view, from model. Natural size.

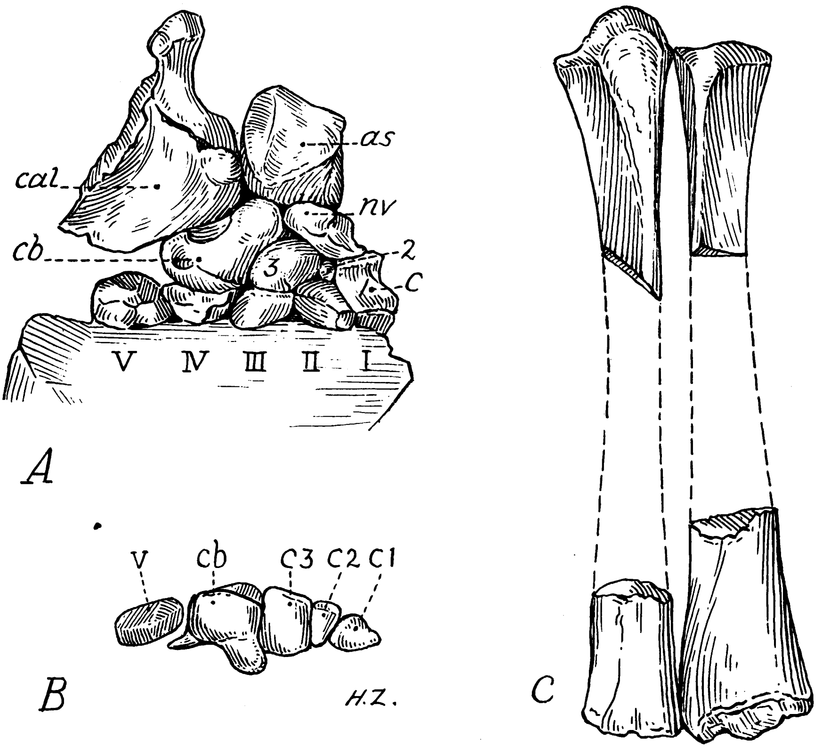

Fig. 2. A. Plantar view of tarsal region of left pes of *Bauria cynops*, from specimen. Natural size.

B. View of proximal articular surfaces of metatarsal V, cuboid (cb), and cuneiforms (c3, c2, c1) of left pes of *Bauria cynops*, from model. Natural size.

C. Anterior view of left tibia and fibula of *Bauria cynops*. Proximal portion of tibia from right side, reversed in drawing. Natural size.

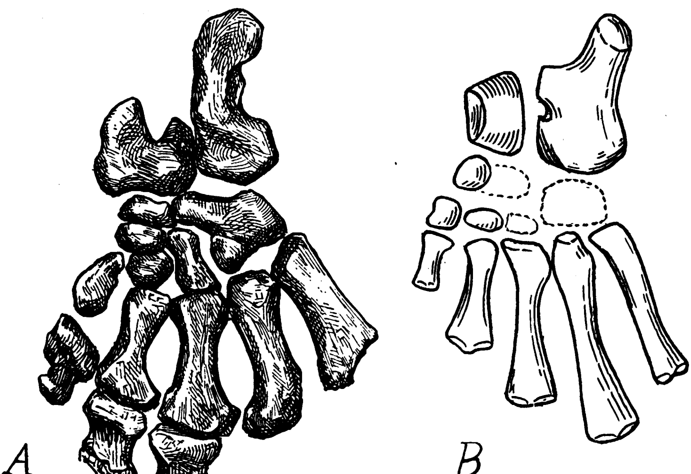

Fig. 3. A. Plantar view of right pes of *Scymnognathus* cf. *whaitsi* Broom. Astragalus should be rotated so that notched border faces laterally. After Broili and Schröder. ×1/2.

B. Plantar view of left pes of *Ericiolacerta parva*. Modified and reversed, after Watson, ×3.

and with elongated spinous processes which slope more or less caudad anterior to and craniad posterior to this vertebra. Thus the digitigrade condition, permitting greater speed, developed coincidently with the modifications producing a more efficient spring-like action of the vertebral column. The neural spines of *Ericiolacerta* are short and directed upward or slightly caudad. This is the condition found in *Varanus* and most slowly moving mammals such as *Ornithorynchus*, *Didelphys*, and *Myrmecophaga*, which are essentially plantigrade or semiplantigrade.

The tuber of the calcaneum of *Didelphys* has an inclination similar to that of *Bauria* and *Ericiolacerta*, but as the plantar surface of the foot is covered by a fibrous, fatty pad, the distal end of the tuber is well protected, and does not project ventrally beyond the plane of the sole. Such a pad was very probably present on the sole of the bauriamorph foot.

It is quite evident that the tuber made its appearance before the calcaneum lost its contact with the fibula, and that it developed primarily to increase the leverage of the foot. Morton (1935) has stated that the tuber developed, along with the superimposed astragalus, as an arboreal adaptation, permitting differentiation of the extrinsic flexors into digital flexors for grasping and into the triceps surae (gastrocnemius and soleus) inserted on the tuber for increased leverage action. The pes of *Bauria*, however, is definitely not arboreal, although there was undoubtedly almost complete differentiation of the triceps surae. The raising of the astragalus onto the calcaneum probably occurred during the stage in which the tibia became the main weight-bearing axis of the lower leg, and the fibula, reduced in importance, lost its articulation with calcaneum. This step in the evolution of the foot, together with the enlargement of the tuber, may be of arboreal significance.

The body of the calcaneum is dorsoventrally compressed, is more or less rectangular in shape, has a raised lateral border, and a basin-like central portion. The articular surface for the fibula is proximomedial in position and is a very prominent and well-rounded knob. The cuboid facet of the calcaneum is not rounded as in *Ericiolacerta* but is quite flat. This facet articulates only with the proximolateral corner of the cuboid, but it extends laterally out over a gap above the fifth metatarsal. In *Scymnognathus* the calcaneum does not articulate with the cuboid, which is very probably the more primitive condition. The calcaneoastragalar contact is weak, as the articular facets of the related bones are narrow, plain surfaces. The roentgenograms reveal the presence of a foramen between the astragalus and the calcaneum which is not evident in the fossil itself. The plantar surface of the calcaneum is decidely concave. There is a well-developed and knob-like medial process which extends just under the lateral border of the astragalus and serves to strengthen the calcaneoastragalar articulation. This may be the beginning of the sustentacular process.

The astragalus has a large and well-rounded tibial facet with no definite indication of a trochlea. This articular rolling surface is, of course, a heritage character, as its beginning can be traced back to such a form as the cotylosaur *Diadectes* (Romer, 1931), in which there already is considerable torsion between the crus and the foot when the leg is directed backward at the end of a stride. The articular surface for the fibula is a distinct knob with a flattened lateral surface. It is comparatively smaller in size than in other therapsids. The astragalus also possesses what may be interpreted as a true, but weakly developed head. In the actual specimen the head appears to be a separate bone, but the roentgenograms clearly demonstrate the presence of a partially matrix-filled crack running through the astragalus and calcaneum. A neck is not differentiated from the head, and the latter is not rounded distally but has two rather concave facets which articulate with the navicular and cuboid, respectively. The head cannot be observed from the plantar surface, as it is covered both by the navicular and a medial extension of the cuboid.

The navicular is a small bone with a moderate transverse elongation. The astragalar facet is convex, while the distal articular surface is quite flat. The latter articulates with the ecto-, meso-, and proximolateral corner of the entocuneiform. The nature of the cuboid facet is difficult to determine, but it is probably somewhat convex.

Viewed from its dorsal aspect, the cuboid has a rectangular outline. In articulating with the astragalar head, it must have shared about equally with the navicular the weight stresses transmitted by the astragalus. Distally it articulates with the base of the fourth metatarsal. It does not articulate with the base of the fifth metatarsal and there is, in this fossil, a large gap between the distal end of the calcaneum and the base of the fifth metatarsal. Without question, the cuboid bore by far the greater part of the weight stresses transmitted from the fibula through the astragalus and calcaneum. The gap may have been filled with a lateral, fibrocartilaginous extension from the cuboid or possibly by a persistent fifth tarsale, either of which would have been capable of transmitting some pressure from the calcaneum to the base of the fifth metatarsal. Such a gap is indicated in the pes of the therocephalian *Whaitsia*, as restored by Broom (1932) and is definitely present in certain other therapsids. Granger and Simpson (1929) have recorded the presence of a large gap in the same position in the multituberculate *Eucosmodon*, although in this case the fifth metatarsal does articulate with the extreme lateral border of the cuboid. This gap certainly was not filled by a cartilaginous fifth tarsale. Whatever the significance of the gap may be, the evidence indicates that no osseous element has been lost in the *Bauria* pes.

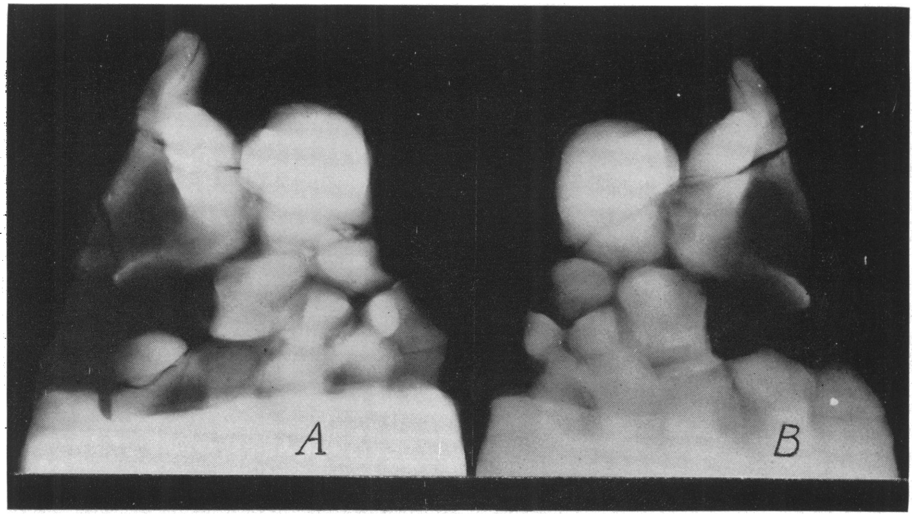

Fig. 4. Roentgenograms of Left Pes of *Bauria cynops*.
A. Plantar view of tarsal region. Natural size.
B. Dorsal view of tarsal region. Natural size.

The plantar surface of the cuboid presents a very different picture. A short, rounded, dorsoventrally flattened process extends laterally into the gap. This process may have offered some support to the fibrocartilaginous portion and acted as a point of ligamentous attachment, but is otherwise, apparently, of no functional importance. There is also a very strongly developed knob-like process which extends medially and proximally, overlapping somewhat the lateral border of the navicular. This process affords a bracing mechanism which, with the aid of ligaments, would tend to prevent the separation of the cuboid and navicular and thus functionally unite these bones against any possible wedging action of the astragalar head. The blood vessel passing between the astragalus and calcaneum ran above this process to reach the plantar surface.

The ecto- and mesocuneiforms articulate proximally with the navicular and distally with the third and second metatarsals. The mesocuneiform is a wedge-shaped element with its apex just slightly visible on the plantar surface. The entocuneiform is the largest of the cuneiforms and is proximodistally elongated. It barely contacts the navicular on its proximolateral corner. The position of the entocuneiform in *Scymnognathus* is most unusual. It is wedged in between the relatively small cuboid and the mesocuneiform. Whether it has been displaced or is in its natural position cannot be ascertained.

The metatarsals, as Boonstra noted, are very mammal-like in appearance. They all have expanded, well-developed osseous articular surfaces proximally and distally. The proximal surfaces, except in the case of the fifth, are flat facets, making for rather intimate contact with the tarsals. The base of the fifth is more or less rounded and somewhat rugose as if it were capped with fibrocartilage in life. The shafts of the metatarsals and also of the proximal and middle phalanges are quite circular in cross section in contrast to the flat oval condition found in more primitive therapsids. The heads are very mammalian in character, being rounded and separated from the shafts by a distinct groove.

The phalangeal formula is 2–3–3–3–3. The bases of the proximal phalanges are expanded and concave. The heads are transversely cylindrical. The middle phalanges have a concave base with a fairly well-developed proximodorsal process for the attachment of the extensor tendons. The terminal phalanges taper to a blunt point and are not transversely compressed. They also have a proximodorsal process.

MEASUREMENTS IN MILLIMETERS

Metatarsals	Middle Phalanges
I—10	
II—12.5	II— 7.5
III—20.5	III— 9.5
IV—24	IV—10.5
V—23	V—?

Proximal Phalanges	Distal Phalanges
I— 7.5	I—7.5
II— 8.5	II—?
III—10.5	III—?
IV—13	IV—9.5
V—?	V—?

The pes as a whole exhibits a degree of consolidation not found in any of the lower therapsids, possibly excepting *Scymnognathus*. The more or less interlocking condition of the tarsal bones, so characteristic of the mammalian foot, is definitely indicated. Several features support the conclusion that there was a low transverse tarsal arch, namely, the indication of a well-developed cuboideonavicular ligament, the wedge-shaped mesocuneiform, and possibly the rudimentary sustentacular process. The digits increase in length up to the fourth, with the fifth about the same length as the third. The fifth digit was probably slightly divergent. That the type of locomotion was like that of a modern lizard, as Boonstra suggests, would appear very doubtful in view of the fact that the long axis of the foot must have been almost parallel to the long axis of the body. The pes of *Bauria* is unquestionably the closest known approach to the mammalian foot among the therapsid reptiles.

The roentgenograms have been of great assistance in this study, and some information concerning them may be of interest. A properly exposed roentgenogram can be of great value in many types of paleontological research, as many of Peyer's papers will testify. In this case it is only through the use of the x-rays that the true existence of a crack in the astragalus can be demonstrated. The outlines of the bones are also very clearly defined. The extremely hard and tenacious matrix has made complete preparation almost impossible. It consists of a very resistant hematitic limestone which is almost impervious to the x-rays, and good results were only attained after the greater part of the matrix was removed from the tarsal region. The foot was successfully roentgenographed at a focal target distance of 30 inches, kilovoltage 55, milliamperage 50 for 3 seconds. The type, density, and thickness of the matrix, as well as the fossilization of the specimen, are all factors which must be considered.

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