On parts of the skeleton of a mammal from Triassic rocks of Klipfontein, Fraserberg, South Africa (Theriodesmus phylarchus, Seeley), illustrating the reptilian inheritance in the mammalian hand / by H.G. Seeley.

PHILOSOPHICAL TRANSACTIONS

OF THE

ROYAL SOCIETY OF LONDON.

VOL. 179 (1888), B, pp. 141–155.

[PLATE 26.]

4

RESEARCHES

ON THE

STRUCTURE, ORGANIZATION, AND CLASSIFICATION

OF THE

FOSSIL REPTILIA.

III.—ON PARTS OF THE SKELETON OF A MAMMAL FROM TRIASSIC ROCKS OF KLIPFONTEIN, FRASERBERG, SOUTH AFRICA (THERIODESMUS PHYLARCHUS, SEELEY), ILLUSTRATING THE REPTILIAN INHERITANCE IN THE MAMMALIAN HAND.

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LONDON:

PUBLISHED FOR THE ROYAL SOCIETY

BY TRÜBNER AND CO., LUDGATE HILL, E.C.

1888.

Price One Shilling.

4.

V. *Researches on the Structure, Organization, and Classification of the Fossil Reptilia.*—III. *On Parts of the Skeleton of a Mammal from Triassic Rocks of Klipfontein, Fraserberg, South Africa* (Theriodesmus phylarchus, Seeley), *illustrating the Reptilian Inheritance in the Mammalian Hand.*

By H. G. Seeley, *F.R.S., Professor of Geography in King's College, London.*

Received October 24,—Read November 24, 1887.

[Plate 26.]

Among specimens collected from various localities in Cape Colony by Mr. Thomas Bain, and deposited in 1878 in the British Museum of Natural History, is a small counterpart slab, 8 inches long by 5½ inches wide, now registered under the number 49,392. It was labelled by its discoverer "The hand of a Saurian, from Klipfontein, Fraserberg, South Africa"; and this determination escaped question. Its exact geological horizon is unfortunately unknown, but is probably the same as that of the Dicynodont Reptiles collected with it, which are on many grounds regarded as Triassic. This slab is a natural mould of the bones of the fore-limb of one of the smaller Mammalia characterised by five digits. It also shows, in less satisfactory preservation, remains of the tibia and fibula, which are relatively longer than the corresponding bones of the fore-limb. The animal thus indicated was considerably larger than the Otter, and approximated to the dimensions of the Wolverine. In their general shape and elongation, the limb bones, as a whole, approximate to the smaller Carnivora, but are distinguished by many differences of detail. Thus, the bones of the fore-arm are more nearly equal in size, though the difference is one of degree rather than type; and the same is true of the bones of the fore-leg. But, except the tibia, and possibly the humerus, none of the bones give evidence of having terminated in epiphyses, and the forms of the distal ends of the ulna and radius are unlike those found in Carnivora. The carpus also shows some new points, though the bones are displaced, in giving evidence of a third row of carpal bones. The phalangeal bones of the digits, also, vary from the usual Mammalian type, and possibly, in one digit, give evidence of renewal after the digit had been lost, as among Amphibians. The vertebral column is only indicated by a portion of a single caudal vertebra. None of the differences, however, which the specimen shows from the skeletons of existing

Mammals can be regarded as making an approximation towards lower Vertebrates in the plan of the skeleton, or as throwing a doubt on the interpretation of the animal as a typical Mammal; but as evidences of inheritance, the carpus, metacarpus, and digits are singularly suggestive. I would express my thanks to Dr. Henry Woodward for permission to study and describe this remarkable fossil, and for his assistance in preparing the beautiful cast from the slab which was made by Mr. Hall, the mason, after the specimen had been cleared from some fragments of the original bone which adhered to the natural mould.

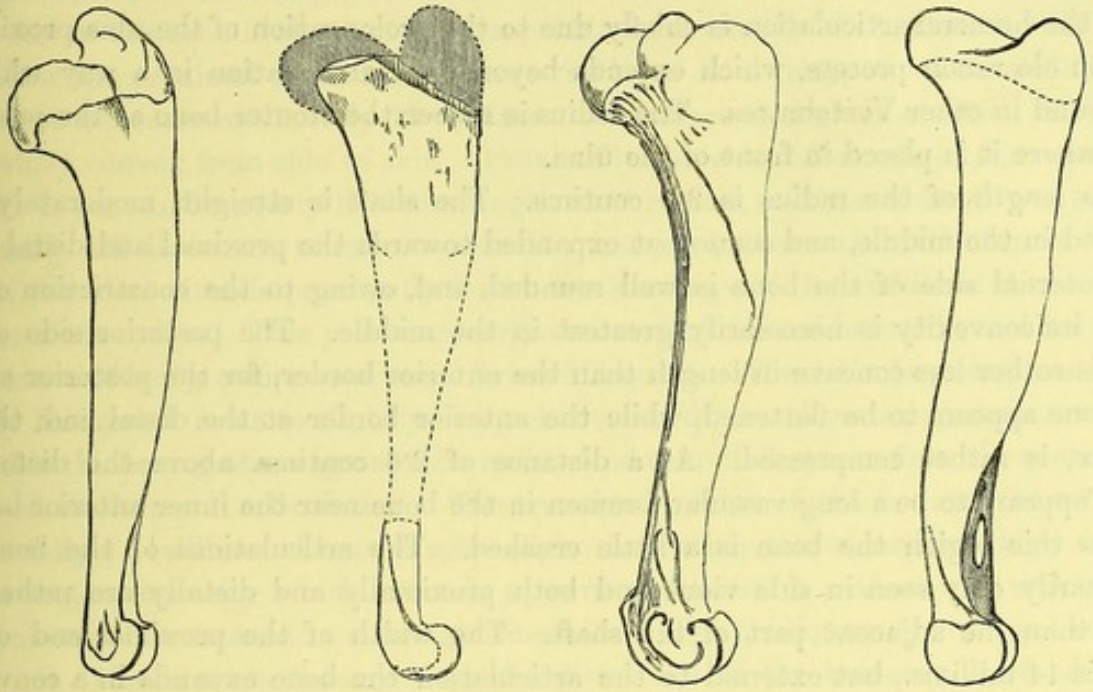
The Humerus.

In the impression from the slab the humerus is crossed by the tibia and fibula, so that only its proximal and distal parts are shown: the middle parts of the shaft have been contained in the corresponding slab. The bone is 11·5 centims. long. It is twisted, so that the proximal end is turned inward at an angle of about 45°. Hence the distal end is shown in profile from the outer side, while the proximal end shows the expanded width of the bone, which is comparatively flattened, with a moderate side-to-side convexity. The part of the proximal end which is exposed has an antero-posterior extent of 4·1 centims. It is nearly straight on the anterior border, slightly concave on the posterior border, 3·2 centims. wide at the proximal end as preserved, and 1·7 centim. wide at the distal limit of the exposure. The proximal contour, owing to the shallowness of the impression probably, gives but an imperfect conception of the form of the proximal end of the bone. The proximal articular surface is very imperfectly preserved. What remains of it is convex from front to back, and 2 centims. wide. Its anterior extension is apparently compressed on the ulnar side, with the small hemispherical convexity of the articular head in the middle, somewhat thickened and extended inward, so as to rise convexly above the surface of the impression. Anterior to this boss is a saddle-shaped depression, concave in length and concave transversely, and then a small trochanteroid process rises, which extended to the border of the bone.

The distal exposure of the humerus shows its thickness to have exceeded 7 millims. The fragment seen is 3·1 centims. long. The anterior and posterior sides are subparallel till the distal extremity is reflected forward in the trochlear condylar articulation. The inner surface of the bone is somewhat flattened, and marked by a groove which ascends from the median lateral extremity of the distal condyle, and, extending upward and backward with a slightly concave curve for 2 centims., obliquely crosses the shaft. The slight elevation of this ridge causes all the distal part of the bone posterior to it, which forms the convex posterior part, to be wider transversely than the part of the shaft in front of it. This ridge is not closely paralleled by any structure known to me in the distal end of any humerus. Its direction is the reverse of the band which extends over the epicondylar humeral foramen in many Mammals, though it coincides with the direction of the vessel which such bars cover in

Marsupials and other Mammalia. Because it occurs on the outer side of the bone, I am led to interpret it as comparable to ridges similarly placed in Carnivora. The antero-posterior thickness of the distal end through the condyle is 1·3 centim.; and the vertical extent of the condyle on the anterior side of the bone is 1 centim. The condylar surface is well rounded from above downward and backward.

Diagram showing the right humerus in Mammals which resemble *Theriodesmus*.



Hyrax capensis. *Theriodesmus.* *Felis leo.* *Thylacinus.*

I cannot but suspect the possibility of this humerus having lost its proximal epiphyses; and, if so, the restoration of the missing portions might bring the bone into close correspondence with the Mammals, which it resembles in its distal end. In the outline here given a sufficiently close approximation may be seen to three Mammalian types to be suggestive of affinities. In form the bone is very like the humerus of a Leopard, in which there is a not dissimilar attenuation of the shaft distally; but this character is probably of small importance, since other Felidæ do not show quite the same proportions. And, while some of the Felidæ show a not dissimilar ridge on the outer side of the bone at the distal end, there is also a strong anterior tricipital ridge at the proximal end, to which the fossil offers no approximation. This ridge, however, assumes a more anterior marginal position in some Carnivora, and in others is less conspicuous; still its absence appears to show that the muscular relations of the humerus to the body were not identical with those of existing Carnivora. The resemblance to *Hyrax* is not less remarkable, though now it is the distal ridge that is wanting. A third resemblance is found in *Thylacinus*, which in general form and

character of the bone, and especially in the antero-posterior distal compression of the shaft, approximates to the fossil closely.

Ulna and Radius.

The ulna and radius are moderately elongated, but are somewhat shorter than the humerus. The two bones combine proximately to form a semicircular cavity for the distal end of the humerus to work in. This condition is characteristic of Mammals, since the humeral articulation is chiefly due to the prolongation of the ulna proximally into an olecranon process, which extends beyond the articulation in a way which is not found in other Vertebrates. The radius is rather the stouter bone at the proximal end, where it is placed in front of the ulna.

The length of the radius is 8·5 centims. The shaft is straight, moderately constricted in the middle, and somewhat expanded towards the proximal and distal ends. The internal side of the bone is well rounded, and, owing to the constriction of the shaft, its convexity is necessarily greatest in the middle. The posterior side of the bone is rather less concave in length than the anterior border, for the posterior side of the bone appears to be flattened, while the anterior border at the distal end, though convex, is rather compressed. At a distance of 2·6 centims. above the distal end there appears to be a long vascular foramen in the bone near the inner anterior border, but in this region the bone is a little crushed. The articulations of the bone are necessarily only seen in side view, and both proximally and distally are rather less wide than the adjacent part of the shaft. The width of the proximal end of the bone is 14 millims., but external to the articulation the bone expands in a convexity which is almost a process, which overlaps the ulna. The superior extremity of this convexity extends for 4 or 5 millims. further proximally than the anterior border, so that, while the anterior and lateral borders are sharp and well-defined, the articular surface is concave and inclined obliquely forward. This concavity, like that of the adjacent ulna, is parallel to the convexity of the distal articular end of the humerus, from which it is separated by an interspace as if for cartilage about 2 millims. wide.

The distal articulation is somewhat similar in character, except that the less prominent distal convexity and downward prolongation of the bone is on the inner border, while the shaft is concave on the ulnar side. The side to side width of the articulation is only 12 millims. In this direction the articular surface is concave and oblique, looking downward aud outward, because the inner border has a greater extension distally than the ulnar border. The margin of the articulation is sharp, and the surface is transverse to the shaft.

The ulna is a straight bone, somewhat compressed from side to side. It is 10 centims. long, and in form and extent of the olecranon process approximates to the ulna of the Wolverine and some of the smaller Carnivora. Its shaft has a slight curve by which the middle part bends inward towards the radius, while the

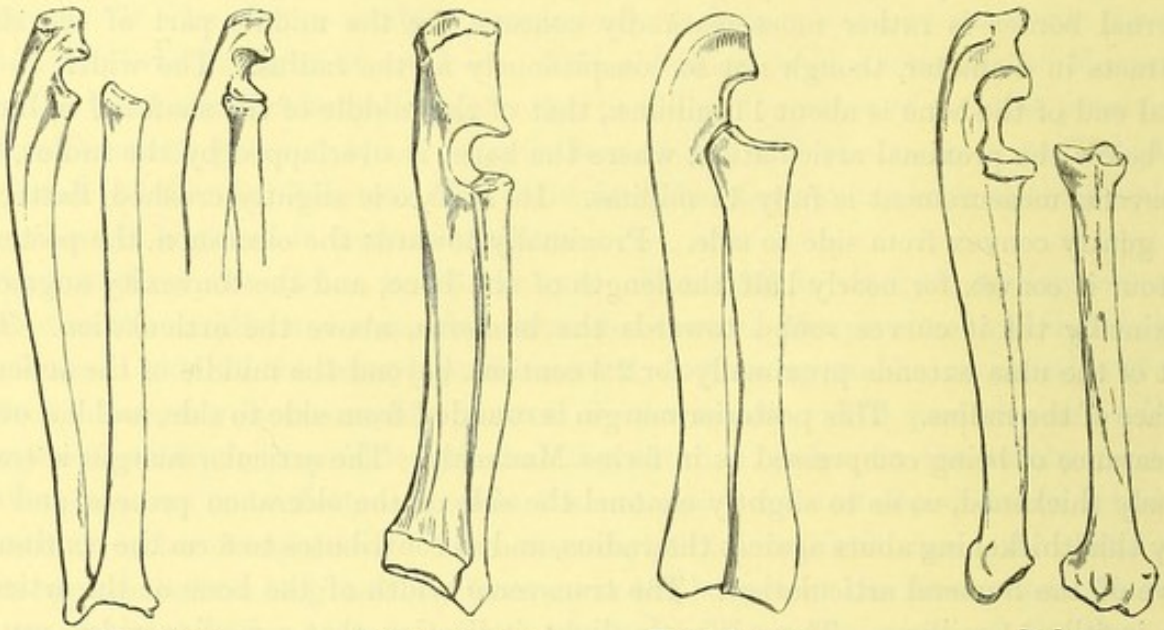
greater part of the proximal end of the bone is behind the radius. Distally the ulna is displaced so as to lie away from the radius and most of the carpal bones. The impression of the ulna in the stone is less deep than that of the radius, so that it is impossible to be sure that the entire width of the bone is exposed, and no estimate can be formed of its thickness. The anterior border of the shaft, below the olecranon articulation, is very slightly convex in length, and the corresponding posterior and external border is rather more markedly concave, for the middle part of the shaft contracts in diameter, though not so conspicuously as the radius. The width of the distal end of the bone is about 11 millims., that of the middle of the shaft is 7 millims., and below the proximal articulation, where the bone is overlapped by the radius, the transverse measurement is fully 11 millims. Its surface is slightly crushed, flattened, and gently convex from side to side. Proximally towards the olecranon, the posterior contour is convex for nearly half the length of the bone, and the convexity augments proximally till it curves round towards the humerus, above the articulation. This part of the ulna extends proximally for 2·4 centims. beyond the middle of the articular surface of the radius. This posterior margin is rounded from side to side, and has every appearance of being compressed as in ferine Mammals. The articular margin is transversely thickened, so as to slightly channel the side of the olecranon process, and distally this thickening abuts against the radius, and so contributes to form the continuous curve of the humeral articulation. The transverse width of the bone at the articulation is fully 11 millims. There is some slight indication that a median ridge ran up the articular concavity which extends upward and forward. Above the articulation the olecranon is truncated in a straight line with a slight obliquity; here it is 1 centim. deep. It extends some distance over the distal end of the humerus, in which there must have been a considerable olecranon pit. Thus the ulna and radius combine to make a perfect hemispherical cup for the humerus, which is nearly 16 millims. wide and inclined obliquely backward.

The distal end of the bone is truncated, and the oblique surface in which it terminates gave attachment to two carpal bones, which are smaller than the single carpal which was attached to the radius.

When these bones are compared with those of other Mammalia, no one genus combines all their characters. In general aspect they are like the same bones in the Wolverine, except for the simpler forms of their distal extremities. The proximal end of the radius perhaps finds its nearest parallel in the Aye-aye and other Lemurs, in which there is a similar concave oblique surface. The ulna is perhaps more like that of *Meles* or *Gulo*. But the distal ends are unlike the corresponding surfaces of Lemurs or Carnivora, and the simplicity of the surfaces is almost Reptilian. Still Mammals like the *Hyrax* make an approximation in the form of the distal ends, which is the more interesting from the somewhat *Hyrax*-like form of the humerus, though there is no close resemblance in form or proportion between the bones of the fore-arm in the two types, and both Sirenians and Seals approximate to the fossil in

the form of the distal ends of the ulna and radius. But, whatever may be the taxonomic value of these resemblances in the distal ends of the bones, their predominant characters otherwise suggest Civets, Weasels, and Badgers, with frequent reminders of the bones in Lemurs and Monkeys.

Diagram of ulna and radius.



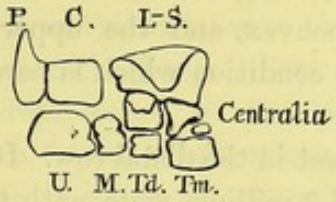
Cheiromys. *Hyrax capensis.* *Theriodesmus.* *Meles.*

The Carpus.

Although the carpal bones are not in compact articulation, they are so displaced as better to show the forms of the bones without disordering their relations. The distal row of four carpal bones remains in contact with the metacarpus. Two carpals are in contact with the ulna, and one with the radius, and these form the proximal row. But between these two rows is a portion of the third row, consisting of three bones which are towards the radial side. The largest, and most centrally placed, may be identified with the centrale of Monkeys, Lemurs, and some other Mammalia; but the other bones external to it, on the radial side, rather suggest the condition in the carpus of some Chelonians and Amphibians, and appear to throw some light on the relation of the carpus to the tarsus in Mammals.

The large bone, which is equal in size to the distal end of the radius, and is in contact with it, I regard as the scapho-lunar; and two bones, which are faintly outlined in contact with the ulna, would then be the cuneiform and pisiform bones. The four bones of the distal row of the carpus, being *in situ*, are easily identified as the trapezium, trapezoid, magnum, and unciform bones. There is no possibility of the row having included more bones, since the unciform bone supports two metacarpals. The intermediate row may be distinguished as centrale 1, 2, and 3. This interpreta-

tion may be better understood from the following diagram, in which I have made a restoration of the scheme of the carpus.



Scheme of the carpus of *Theriodesmus* restored.

The scapho-lunar bone is so far displaced by being twisted forward on the ulnar side that much of its proximal surface is exposed. It is a sub-quadrate bone, and, like all the other carpal elements, has its articular margins sharp and well defined. The proximal surface is 12 millims. wide, smooth, with a cartilaginous articulation which is defined by a linear margin. It is convex from back to front, in harmony with the concavity at the distal end of the radius. The distal surface is somewhat smaller, and develops a prominent mammilate convexity in the middle. The external surface, which was towards the ulnar side, is only 3 millims. deep, concave vertically, convex transversely, with prominent superior and inferior margins, and it shows a few vascular foramina in the middle. The other external surface has a vertical depth of about 9 millims., but diminishes in depth as it extends forward. It is flattened, but is slightly concave both from above downward and behind forward; the measurement in the latter direction is 7 millims., and is limited laterally by a vertical ridge.

The bones which articulate with the distal end of the ulna are much less perfectly indicated, showing only ill-defined impressions of their lateral contours. First, there is a transversely oblong bone on the side towards the radius, which is the cuneiform. It measures a centimetre from back to front, and is 7 millims. deep, and articulates with the principal distal facet of the ulna. The other carpal, adjacent to it, I regard as the pisiform bone. It is a sub-triangular or pear-shaped bone, which has its chief extension behind the ulna. Its transverse measurement is about 6 millims., and its vertical measurement about 1 centim., terminating proximally in a point. These three bones now described I regard as forming the proximal row of the carpus, because, if the distal end of the ulna were brought into contact with the radius, the cuneiform bone would be in contact with the lunar side of the scapho-lunar.

In the distal row, beginning on the inner side, the bones Tm, Td, M, U, present a type common among pentadactylate Mammals, in which the first three bones each support one metacarpal, while the last two are supported by the unciform bone. The trapezium is sub-quadrate or somewhat lozenge-shaped, flat, inclined inward, and measures $5\frac{1}{2}$ millims. in height and breadth.

The external surface of the trapezoid is much smaller, being only about half the width of the proximal end of the second metacarpal on which it rests. Its proximal

and distal surfaces are convex, its sides are flattened ; it is about 4 millims. high and 3 millims. wide.

The magnum is a larger bone, being 5 millims. wide and 7 millims. high, with the proximal surface prominently convex, and the upper half of its quadrate anterior aspect triangularly excavated, a condition which is paralleled in the magnum of many Carnivora.

The unciform bone is the largest in the distal row. Its lateral aspect is sub-quadrate, being about 8 millims. deep and 7 millims. wide, with the inner distal angle prolonged as a slight talon, and the outer proximal angle is rounded. The superior and external borders are convex in length, and the external surface is concave.

Between these bones, forming the distal row and the proximal row, is the intermediate row of three bones which was placed on the radial side. There are one or sometimes two bones in this position in the carpus of Chelonians, and at least one in the carpus of Lemurs, of certain Quadrumana, and of some Rodents like the Beavers, while the centrale is a well-known element in the carpus of Salamanders. But in no Vertebrate have three bones been found in the position described.

The first bone (*g*) of this series, counting from the radial side, is situate at the upper inner angle of the trapezium. It is a small ossification, 2 millims. in diameter, and sub-quadrate in form. It may be connected distally with a minute ossification external to the trapezium.

The second bone (*h*) is triangular. As preserved, it rests by its flat distal surface upon the trapezium and trapezoid, while the two inclined proximal faces, which are about equal in size, meet to form a sharp pent-house ridge. It is 8 millims. long, and half as high. It is obviously displaced, and one of its superior surfaces was received under the internal half of the scapho-lunar bone.

The third bone (*i*) is much larger than the others, and of sub-quadrate form. It is 8 millims. high, about 7 millims. wide distally, and 4 millims. wide proximally. The proximal surface is flattened to articulate with the lunar portion of the scapho-lunar bone. The distal surface may have fitted upon the trapezoid or the magnum. Laterally the bone has two surfaces, separated by a sharp vertical oblique ridge. The surface on the ulnar side is concave in the vertical antero-posterior direction, and convex from front to back. The other lateral surface faced towards the second centrale already described.

I regard these three bones collectively as homologous with the naviculare in the tarsus. That bone is situate between the astragalus and the three cuneiform bones which carry the first three metatarsal bones, so that the naviculare, originally, may also have included three ossifications. Since the third central bone in this fossil is the largest, that fact may help to account for the internal position taken by the representative ossification in Mammals in which it is still found. This carpus is more primitive than any Mammalian carpus hitherto known, and, on the whole, better

compared with that of Amphibians and Reptiles. Dr. R. Wiedersheim, in a paper * on the central bones in the carpus and tarsus in the Axolotl, shows some remarkable conditions of the carpus to be developed with age. There are at first three bones in the proximal row, and four bones in the distal row, though ultimately the latter series numbers five † on the left side of the body. Between these rows is the centrale, at first single, and ultimately represented by two cartilages on one side and three on the other. I should desire to see preparations before affirming that a linear series of three central elements is a normal characteristic of the Axolotl, but this number appears probably to be present. The presence of two central bones in certain Reptilia is much better established. Dr. Franz Bayer has figured and described ‡ two central elements in the young *Hatteria* which have a linear arrangement, and are placed above the second and third tarsals of the distal row. And this condition appears to have been observed independently by Dr. G. Baur and by M. L. Dollo. It is among Chelonians, however, that the two centralia are most strikingly developed in linear arrangement towards the radial side. But, though the condition of the carpus in this fossil is thus shown to be Amphibian and Reptilian, it is typically Mammalian in all points except that of the central bones. But no Mammal shows more than one central bone, and the number of types in which that one is persistent throughout life is not large. Dr. G. Baur, indeed, affirms § that a centrale has been shown to occur at some period of life in all orders of Mammals except Ungulata and Cetacea, but figures and detailed descriptions have yet to be given to demonstrate the proposition for some orders. Perhaps the carpus of *Cheiromys* nearly parallels *Theriodesmus*, except that in the Lemur the scaphoid and lunar bones are not united. The one large centrale is in contact proximally with the scaphoid and lunar, and it meets all the bones of the distal row. The bone is relatively smaller in the Orang-utang, but the structure is the same. Vrolik remarks ‖ that this bone is found in the Gibbons, and appears to exist in all the lower Monkeys. Vrolik also figures (*loc. cit.*, p. 204) a second ossification between the trapezium and scaphoid, regarded by him as a sesamoid bone for the tendon of the adductor longus pollicis. Baur (*loc. cit.*) states that he has evidence of the centrale in Man, the Cat, and Dog. In the embryo of *Lutra* the central bone was quite free and very fully developed, while the radiale and intermedium [= scapho-lunar] were coalesced. *Hyrax capensis* has a free centrale, though it is only free in this species of the genus. The presence of this bone cannot but mark an ancient connection between the orders in which it is found; just as the two or three central bones of

* "Über die Vermehrung des Os centrale in Carpus und Tarsus des Axolotls," von R. Wiedersheim, 'Morphol. Jahrb.,' vol. 6, 1880, p. 581, Taf. xxx.

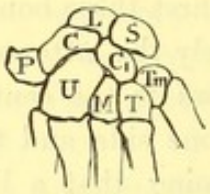
† The unciform bone in *Thylacinus* appears to be formed by union of two elements.

‡ "Über die Extremitäten einer jungen *Hatteria*," von Dr. Franz Bayer, in Tabor, 'Wien, Akad. Sitzber.,' vol. 90 (Abth. 1), 1885.

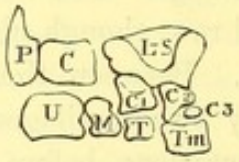
§ 'American Naturalist,' February, 1885, p. 195.

‖ "Quadrumana," 'Todd, Cyclopædia Anat.,' vol. 4, part 1, 1852, p. 203.

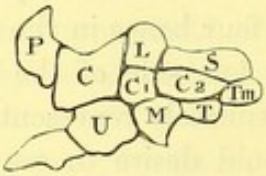
Amphibians, *Hatteria*, and certain Chelonians must indicate a closer genetic relation between *Theriodesmus* and some of the lower Vertebrata.



Carpus of *Cheiromys*.



Carpus of *Theriodesmus*.



Carpus of *Hatteria*.

Carpus of *Axolotl*.

The Metacarpus.

The metacarpus consists of five stout bones, which are deep from back to front at their junction with the carpus, and wide from side to side at their distal ends. The transverse width over the proximal end of the metacarpus is 2·6 centims. These bones successively augment in length from the first to the fourth, but the fifth is shorter than the second. As a whole the metacarpus is very Mammalian, being like that of the Otter, and several of the smaller Carnivora. But the plan of the metacarpus is also interesting from its resemblance to the metatarsus in *Protorosaurus* and the Scaphosaurians.

The first metacarpal is 1 centim. long, the second 2·1 centims. long, the third measures 2·7 centims., the fourth 2·8 centims., while the length of the fifth metacarpal is reduced to 2 centims. The middle three bones have their distal ends strong, and are flattened superiorly. Their relative length is characteristic of the Carnivora. The several bones have their sides concave, but the concavity is most marked on the external side. The superior surface is convex from side to side, with the oblique convexity most marked on the outer side in the outer digits, and on the inner side in the inner digits.

The depth of the proximal end of the first metacarpal is 6 millims.; its width at the proximal end is 2 millims., and rather less at the distal end. The proximal articulation is truncated and flat. The distal articulation is well rounded from above downward.

The second metacarpal is between 5 and 6 millims. wide proximally, contracting in the middle to 4 millims., and expanding distally to a width of nearly 8 millims. The distal articulation is nearly straight transversely, and the convexity from above downward is less distinctly shown. The lateral border, which faces the third metacarpal, is more concave than that which faces the second. Above the distal condyle there is a slight transverse depression, but all the bones want the supracondylar grooves which are commonly found among Mammals.

The third metacarpal is 5 millims. wide proximally, it soon contracts to 4 millims., and expands distally to 9 millims. The outer corner of the distal end is obliquely truncated, and is not articular, so that neither in this digit nor the next is the proximal end of the first phalange as wide as the metacarpal with which it articulates.

The fourth metacarpal is 5 millims. wide proximally, contracts to 4 millims., and expands distally to 9 millims.; but, though these transverse measurements are the same as in the third, the configuration of the bone is different, because the distal widening is here gradual from the proximal third of the bone, while the third metacarpal widens rapidly near the distal end. A short ridge descends obliquely from the inner angle of the proximal articulation.

The fifth metacarpal bone has its proximal articular end directed inward. It is 6 millims. wide, the distal end is about equally wide, and in the middle the shaft contracts to between 3 and 4 millims. The inner lateral border is nearly straight, except that there is a marked concavity below the articulation, which may result from the inflexion of the inner proximal angle, such as is seen in the fourth metacarpal. Distally there is some appearance of a ridge on the superior inner border of the bone.

The Digits.

The digits are imperfectly preserved. In each the first phalange is large and strong, but the other phalangeal bones are short. In the fifth digit there are three phalanges, and the fourth has the same number, but the third appears to have had four phalanges. In the second digit only two phalanges are preserved, and the first has but one preserved and a second indicated.

In the first digit the first phalange is 8 millims. long. It is wide at the proximal end, where the articulation is concave from side to side. It appears to have a well-developed anterior end, with a rounded articulation, margined superiorly by a slight groove. In close contact with this surface is a small hemispherical ossification which appears to represent a second phalange.

In the second digit the stout first phalange is 12 millims. long. It is 7 millims. wide proximally and 5 millims. distally, but contracts rapidly below the proximal articulation. The second phalange is similar in form, but smaller, being 7 millims. long. Its distal extremity appears to have been articular, but there is no trace of a third phalange, which may have been preserved in the counterpart slab.

In the third digit the first phalange is relatively long and slender. It measures 13 millims. in length, is 8 millims. wide proximally, and about half as wide distally. The second phalange is hardly more than 3 millims. long; and the third is nearly 7 millims. long. It has a good trochlear distal end, and beyond it is an indication of a fourth bone, but there is no evidence to show whether it was a complete phalange.

In the fourth digit the first phalange is 15 millims. long, so that the first phalangeal bones follow the same law of progressive elongation as the metacarpals. The bone is rather stouter than the others, being less contracted distally. The second phalange is about 3 millims. long, but more than 5 millims. wide. Anterior to this is a curved mass of most irregular form, with a striated surface, which I regard as being the extremity of the digit, but the absence of definition of the joints leads me to believe

that the original bones had been lost, and replaced, as among some of the lower Vertebrata, by fibro-cartilage imperfectly ossified, and that this tissue, with the attached ligaments, has been preserved, but only defines the third phalange, which is not terminal.

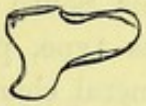
The fifth digit is well preserved. The first phalange is 1 centim. long, the second 5 millims. long, and the third is a slightly curved claw phalange 5 millims. long. These three bones steadily diminish in size.

The characters in this hand, which are new, are first evidence of an augmentation in the number of phalanges in the middle digits. But, although the three phalanges in such digits are singularly constant in the Mammalian class, the existence of so remarkable a departure from the usual rule as is found in the Cetacea, will show that the increased number is not inconsistent with the Mammalian plan, and not inconsistent with the number being different in nearly allied genera. Still the increased number in *Theriodesmus* is suggestive of a lower Vertebrate type, just as is the possible replacement of the extremity of the fourth digit. The form of the metacarpals, enlarged distally and flattened superiorly, is suggestive of the Marsupial *Thylacinus*, while the shortness of the phalanges and the character of their articular ends is not unlike the condition in *Echidna*. Still, neither Monotremes nor Marsupials make any approach to carpus in character. But the *Echidna* has the distal end of the ulna and radius simpler than in most unguiculate terrestrial Mammalia.

Tibia and Fibula.

The right tibia and fibula are parallel bones, imperfectly displayed, and imperfect proximally. Little more is known of the fibula than that it equalled the tibia in length; it was apparently more slender, similarly straight, was contracted at the distal end, and slightly expanded proximally, where it is 13 millims. wide.

The tibia is a stout strong bone, somewhat disfigured by crushing. The postero-exterior side is exposed in which the bone faces towards the fibula. At the distal end it is fully 13 millims. wide; it there thickens from front to back so as to make a convex outline towards the articulation. The middle of this convexity is inclined towards the inner side of the bone, up which it runs as a narrow, rounded, marginal ridge, which separates the convex anterior surface from the flattened and sub-concave posterior surface. In the middle third the width of the shaft is 1 centim., but the width increases proximally to 1·7 centim. at the fracture, partly by the great increase in strength of the convex lateral ridge, and partly by expansion towards the fibula. The distal articular end of the bone is inclined obliquely backward; the surface, partially exposed, is as deep as wide, is gently convex, and not smooth, but slightly irregular, as though it were cartilaginous. Below it, separated by a distance of a centimetre, is a bone which from its form might well be the distal epiphysis. It is 11 millims. wide and 8 millims. deep on the inner side, where its contour is vertical, with the distal surface notched out so as to give the bone a descending talon, which



apparently would have fitted on to an astragalus. No affinities can be inferred from these bones, which are little more than 10 centims. long.

Caudal Vertebra.

An impression of a caudal vertebra exhibits the under side, transverse processes, anterior articular end, and some indication of the small depressed neural arch.

The centrum, as displayed, is 14 millims. long, with the anterior articular end of the centrum transversely ovate, 6 millims. wide, and about 4 millims. deep. The articular margin is rounded, and there is a marked concavity occupying the larger part of the articular surface.

The ventral aspect is very slightly constricted transversely, with blunt, longitudinal, lateral ridges margining the base, which is flattened, slightly concave between the ridges, and gently concave in length. The transverse processes are thin, compressed from above downward, about half a centimetre long, directed obliquely outward and backward. They are given off from the middle of the height of the side of the centrum, near to its anterior end, the sharp anterior ridge of the process rising immediately behind the articular face, though the process on the left side is carried further back than that on the right side. The transverse width over the processes is 12 millims.

The neural arch is only indicated by a slight trace of the prezygapophyses, which

Ventral aspect, caudal vertebra.

shows that the neural canal was very depressed. No affinities can be found in an isolated caudal vertebra like this, though its characters are Mammalian.

Conclusion.

From the foregoing description it is manifest that *Theriodesmus* is a primitive Mammal of a generalised type, which diverges much less from existing orders than might have been expected, seeing that no limb bones have hitherto been known from the secondary rocks, with the exception of the small humerus and femur from the Stonesfield slate.* With that type this fossil has nothing in common. If the

* 'Geol. Soc. Quart. Journ.,' vol. 35, 1879, p. 456.

humerus only had been found in this South African animal, it would have been regarded as indicating a Carnivorous type, probably Marsupial. The ulna and radius in their proximal ends and general character correspond with Carnivora and Lemuroids, but in their distal ends are more like certain Rodents and the Monotreme *Echidna*. This I take to indicate that there may have been no supination, and that the distal extremities of the bones acquired their modification after the Carnivorous characteristic had been developed. Some caution may be needed in drawing inferences from the carpus, because the bones are not all in natural articulation. But the presence of the bones of the central series seems beyond question. The prevalence of the central ossification in the Quadrumana, Lemuroidea, and certain Rodents points to a collateral affinity with those groups, the former two of which have obvious points of contact with Carnivora. The absence of the centrale in the Monotremata and Marsupialia suggests that, if *Theriodesmus* is not Placental, it has no close kinship with any surviving type of Marsupial, while the fact that as many as three central bones are present, tends to show that it is of a more ancient stock, even if it should prove to be an offshoot from the Lemuroid division of Mammalia. The close general rememblance of the carpus, but for the central bones, to the carpus of a Carnivore is suggestive of relations to the Carnivora as well. The metacarpus is that of a Carnivore like the Otter, simplified in details in a way found among Marsupials. The phalanges are short as in terrestrial Chelonians, and have the superior surfaces but little modified, indicating a plantigrade movement, or very little motion between the phalanges of the digits.

Hence I conclude that this fossil cannot be placed in any defined order of existing Mammals. It would appear to belong to that group or sub-class which Professor Cope has named Bunotheria, but not to any order of it which has been indicated. For, while it is like the Bunotheria in being on a lower grade than the existing Placental Mammals, it is of higher type than the Creodonta, and the structures described suggest that higher Placental types may have diverged from the order of which it is the first indication.

The question arises whether *Tritilodon*, founded on the anterior part of the skull, described by Sir R. Owen, from the Trias of Thaba-chou, Basutoland, South Africa, may be the skull of the same animal? I regard the two animals as having no close family relation. The skull, as judged by its dentition, is a Bunotheroid Rodent; while this fore-limb is that of a Bunotheroid type which lies between the Lemurs and Carnivora; yet the distal ends of ulna and radius do not indicate a typical Carnivorous dentition. These remains are probably but the beginnings of a Mammalian fauna which the South African rocks may be expected to yield to systematic exploration, which will show other evidences of Reptilian inheritance. It is in the Mammalia that many characters of extinct Amphibian and Reptilian ordinal groups must be sought for.

Explanation of Plate.

PLATE 26.

Fig. 1. A slab showing the right fore-limb and some bones of the hind-limb of a Mammal from South Africa (*Theriodesmus phylarchus*). Natural size.

a. Humerus.
b. Ulna.
c. Radius.
d. Scapho-lunar bone.
e. Cuneiform and *f*. pisiform.
g, *h*, *i*. Centralia.
k, *l*, *m*, *n*. Trapezoid, trapezium, magnum, and unciform.
o, I., II., III., IV., V. The metacarpus.
p, I., II., III., IV., V. The first phalange in the five digits.
q, I., II., III., IV., V. Second phalange.
r, III., IV., V. Third phalange.
s, III., ? Fourth phalange.
t. Mass at the extremity of the fourth digit, drawn enlarged in fig. 2.
v, *w*. Tibia and fibula.
x. Distal epiphysis of tibia.

Fig. 2. The fourth digit enlarged three times, showing the first, second, and third phalanges, *p*, *q*, *r*, and a mass *t* extending distally. The processes which extend from *r* are regarded as ossified ligaments, and it is possible that the part of the digit from *r* downward may have been lost and replaced by fibro-cartilage.

Fig. 1.

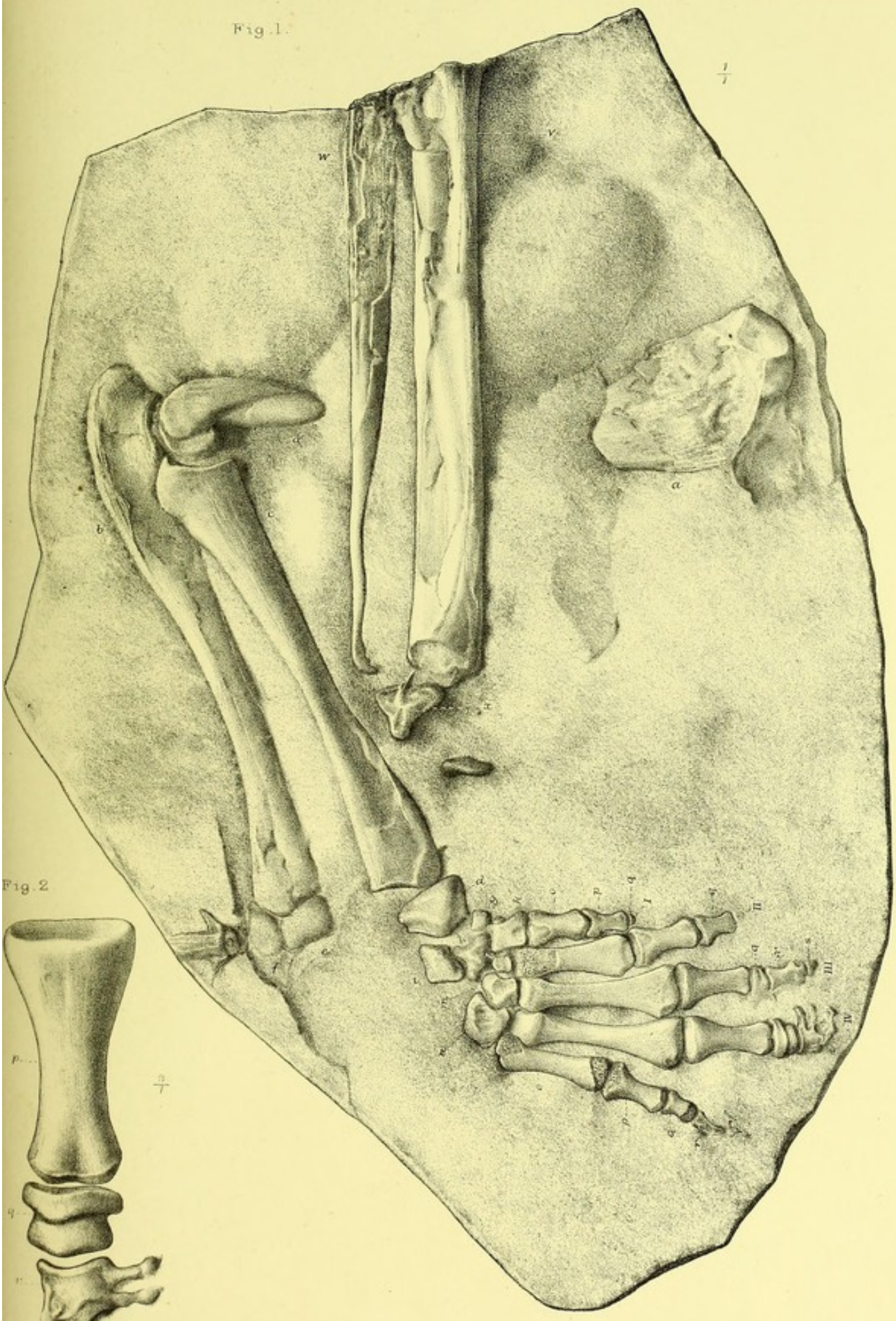


Fig. 2

West, Newman & Co. imp.