

A STUDY IN FOOT STRUCTURE.

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THE material and the direction of this study were suggested to me by Professor W. B. Scott of Princeton, and during its progress I have been much indebted to his candor and helpfulness. The original plan was to select a short phylogeny containing well-marked changes, and to study that closely, with the idea of drawing any conclusions possible as to the genesis of bone structures. The basis of the work is the manus of a *Perisodactyl* from the Bridger eocene *Palæosyops* [*Limnohyops*], an animal of tapirine proportions; while the White River genus *Menodus* has been used for comparison. *Menodus* was a slow-gaited form, with heavy body and head. It was undoubtedly derived from a form closely resembling *Palæosyops*, and the two serve practically as a phylum.

The foot of *Palæosyops* is a beautiful specimen with very few imperfections. Its articular surfaces are mostly simple, many being nearly plane, while they are generally strongly inclined to the axis of the digits. These peculiarities render this foot amenable to geometrical study, a method suggested and rendered valuable by recent arguments, based on palæontological material, for the mechanical evolution of structure. This method has in fact been applied. The volume of the bones was first got at. Next the area of the bearing surfaces and their inclination to the digits were measured. Then, giving to the thrust of each metacarpal a value proportional to its volume, the distribution of that thrust can, by resolution and composition of forces, be traced through the foot, and the pressure on each surface and bone approximately obtained. Conditions of course do not admit anything like exactness, and only general results are given. A diagram is given later on, illustrating the method, which through the foot has been applied as carefully as seemed advantageous or possible.

The key to structure is use, for which in this study the work *Animal Locomotion* by Harrison Allen has been taken as authority. According to this author, whose statements in turn are based on photographic studies, the following seems to be true of the gait of all terrestrial mammals with a broad foot. The foot while off ground is carried forward in partial pronation, and strikes the ground by its outer border. This it does with the limb straight, and directed well forward at an angle depending on the speed of the animal and the weight of its head and shoulders. The limb as it strikes arrests the downward plunge of the body—then it acts as a lever of the third class to bring the body forward. When the limb is vertical, the foot is planted squarely on the ground; as the perpendicular is passed, the foot rolls on to its inner border. The outer toes thus become free, and they are successively flexed. With a straight thrust, and from the inner border of the foot, the limb leaves the ground, its segments during early recover being flexed on one another to clear the ground and to offer less resistance to the air.

This much was true in all probability for the forms under consideration. It is evident that weight is borne by the limb in full extension. Pressure therefore occurs chiefly at the anterior face of the foot, while the ligaments which bind the carpal rows to one another and to the bones above and below are needed, as they are placed, at the posterior face.

Turning to the foot of *Palæosyops* with the facts of its use in view, the following principles of its structure are derived:—

(1) Direct thrust of the metacarpals is distributed by slanting surfaces from each side across the foot, and is met by the curve of the cubito-carpal joint.

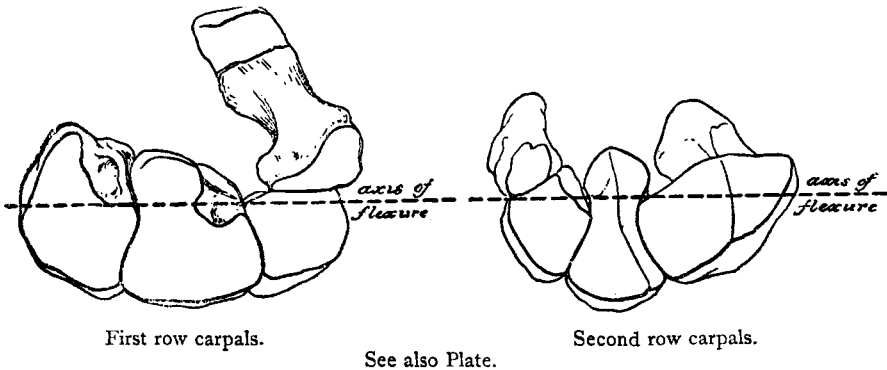
(2) The swinging strike of the foot and lateral thrusts from each side are met in the same way, also by interlocking surfaces which take little or none of the direct thrust of the digits. Such surfaces are those between metacarpals IV and V, IV-III, III-II, and II-magnum.

(3) Torsions are taken up by these surfaces which are largest at their anterior and posterior ends; also by backgrowths of the carpals. Projections of scaphoid and lunar centre down from each side on that of the magnum.

(4) Differentiation in the two sides of the foot. The limb

in forward reach is under severe leverage. This extra leverage the outside of the foot bears chiefly. In adaptation to this the following structures are noted. (a)¹ The pisiform holds off the flexor muscles of the outer digits, putting those muscles at a better advantage. (b) The articular surfaces on the two sides of the foot are differently arranged, and with some doubt I interpret the fact as a mechanism to relieve pressure at the anterior face of the carpus and to distribute it through the depth of the bones. Thus the upper surfaces of the unciform and its joint with metacarpal V are large arcs of small circles, while the bearing surfaces of the median side of the foot are nearly plane. To this advantage, too, I attribute the different shape of the heads of metacarpals II and IV. II is cut squarely across, while the upper surface of IV is inclined downward and forward.

(5) The bones of each carpal row were closely bound together by ligaments, and in flexure move round a common axis. To



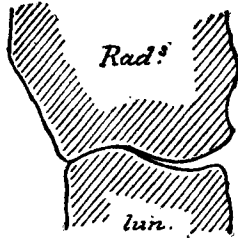
this fact and to the conformation of the joint surfaces the accompanying diagrams furnish a key. The front face of the carpus is strongly arched into an arc to which the axis of flexure is a cord. This cord, the axis of movement, in the mid-line of the foot falls far back of the anterior carpal surface. The utility of the backgrowth of the magnum, and above it of the scaphoid and lunar, is here made evident. Their articular

¹ The musculature of the tapir as given in *Jour. Anat. and Phys.*, Vol. VI, is the authority for this statement. Dissection of the pig's manus, and the markings of the bones of this one, are the key to the arrangement of ligaments.

surfaces guide the parts in flexure ; they do not bear the weight of the body.

Systematic examination of the articular surfaces, bearing in mind the two functions of weight-bearing and flexure, gives the following results : —

Cubito-carpal Joint. — The complication of surface here is evident from the figures. The proximal faces of scaphoid and



Antero-posterior section through radius and lunar.

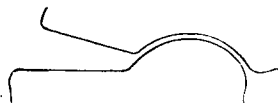
cuneiform are nearly plane, while the proximal surface of the lunar in vertical antero-posterior section is a double curve, corresponding to another in the lower end of the radius. With the foot on ground, the radius and ulna are bearing on the anterior portion of all these surfaces. In flexure the radius, by reason of the curvatures, retains a firm bearing on the back part of the lunar,

while contact with scaphoid and cuneiform is practically that between a plane and a cylinder. At all times a slight twist seems to be possible here. Motion in this joint is a rolling one, and it is evidently considerable.

Inter-carpal Joint. — The position of the axis of movement in this joint has been indicated in the woodcut. However, as the articular surfaces are convex upward, the axis is really beneath those surfaces and within the body of the bones. During



(a) During plantation.



(b) During flexure.

Relation of scaphoid to magnum.

plantation the scaphoid and lunar are well forward, and the contact between the posterior surfaces of these bones and the magnum is very slight. In flexure the lunar and scaphoid slip back on the magnum, bringing the posterior surfaces to bear ; the joints open at their anterior face, and movement takes place by sliding between the posterior surfaces. The scaphoid at

the same time slips back, down, and medially across the long axis of the trapezoid, while the unciform revolves in place. The last-named bone, in accordance with the general plan of weight-bearing in the foot, lies in an angle between the lunar

and cuneiform. Thus placed, the only conformation of surface that would allow movement is that of two truncated cones placed base to base. This is to all appearance the case, the axis of the figure lying at an angle with the face of the bone in the axis drawn.

The metacarpals appear to move somewhat independently of one another. Their proximal surfaces are quickly curved off behind, and with the exception of metacarpal V, very little surface is bearing during flexure. Movement takes place chiefly by sliding between the surfaces, as in the intercarpal joint, and is hardly more extensive than in that joint.

THE FOOT OF MENODUS.

Menodus was a heavily built animal with slow gait and short step. When compared with that of *Palæosyops*, its manus exhibits the following changes in proportion :—

- (1) Metacarpals are shorter, broader, and more erect.
- (2) Metacarpal V is longer in proportion to the others.
- (3) The carpals are thinner proximo-distally.
- (4) Surfaces which take up lateral thrust are smaller.

THEORETICAL APPLICATIONS.

Recent American Palæontology has been largely identified with Lamarckianism. It has claimed to show that change of structure has been the result of changed function and conditions, directly, not selectively. Inferring inheritance from the marked changes produced and the length of time involved, it is stated as the law of evolution of bone structures that growth and atrophy, following lines natural to them under changing mechanical relations, produce and perfect those structures.

This is the general thesis. Before examining it further, I feel justified in saying that the discussion on the Lamarckian side has been loosely conducted. There has often been a great want of clearness, while some facts have been adduced as evidence which, from their lack of self-consistency, seem to discredit the theory which they were cited to support. Thus when Professor Cope¹ attributes to the longitudinal impact of running the lengthening of the limb bones of many groups of mammals,

¹ *Journal Morphology*, Vol. III, pp. 149-154.

to stretching in arboreal habits the length of the fore limbs of the sloths, to cross pull of the wing the great elongation of the calcaneum of some bats, few, I think, will believe that the uses which he points out can, in any other than a selective sense, be said to condition those structures. Similar effects are here attributed to the most diverse causes. To prove the Lamarckian case, it is not enough to attach to a structure its use. It must be shown that use puts the bone under such physiological conditions that by the "natural processes of growth" the structure will be produced.

The proposition is that evolution has followed natural laws of growth in the individual. One of these laws formulated is that already implied, that use determines growth. This is undisputed as a physiological law operative, within limits, in the lifetime of animals; but it has been extended into Phylogeny. To take the Lamarckians in this matter on their strongest ground, it is the cause of the reduction of digits through disuse of the shorter ones following erection into digitigradism and change of habitat to hard ground.¹ Atrophy of metacarpals has followed, of carpals also except when put to use by other digits.

The physiology is that of bone cells. Impact on the bone surface stimulates its cells to more active deposit; lack of use inhibits that deposit. The same bone in a series of feet and corresponding bones in the same foot are proportioned to their use. In the metacarpal series of any foot, as in its carpal series, there is a physiological balance of the elements with the impact they receive.² Specialization among the teeth has been explained by the neo-Lamarckians in the same way.

Now from the nature of the case it is evident that under selection alone this relation would hold true approximately and in the main; but when such a constantly adjusting principle is brought in, the facts must be rigidly questioned. Now in the foot I have been studying the trapezoid is too small to harmonize with this law. It is a thin bone especially. The disproportion-

¹ This for Ungulata only.

² The foot of *Menodus* furnishes an excellent illustration of the principle. The assumption of a heavy body must tend to spread out the digits, and bring the shorter metacarpals more into action. Thus metacarpal V is much larger in proportion in *Menodus* than in *Palæosyops*. The advantage to a heavy animal of having a broad foundation is, however, perfectly evident.

tion can be seen in the figures, but it has been subjected to geometrical demonstration. The method of inquiry has been previously explained. By it I find that the trapezoid has from a third to a half the volume it should have. The reason for its thinness is plain; it allows metacarpal II to complete the system of interlocking by a bearing on the magnum; but with the Lamarckian principle the facts are incompatible. The same disproportion continues in *Menodus*, and it can be seen, in perhaps a less degree in the recent tapir, hippopotamus, and rhinoceros.

But the principle of use stimulating growth and the opposite has been applied far more minutely. To elucidate, I find Professor Osborn's summaries¹ most available, stating that in the evolution of teeth, new cusps have arisen where, in earlier forms, were shown the effects of wear. Here on a single centre differential use has resulted in differential growth. The place and the direction of growth have been determined by impact.

Now if this principle is true in the teeth, it must be of general application. The carpus is a better field for its operation, since the bones in weight-bearing are held rigidly together. Indeed, displacement in the carpals has been thus explained,² while the terms *impact* and *strain* have been freely connected with all foot structures. Inclination and complication of surfaces and correlation must be accounted for. Is it in accordance with the law that regions of special pressure are regions of growth, compensating for that pressure, and producing structure adapted to meet it? I propose here to apply the principle to one test case, discussing it more generally later on.

There is and always has been a region of special impact and strain in the anterior face of the foot as compared with the posterior face, and especially in its outer border, which is in action under severe leverage when the limb first strikes the ground. Applying here the physiological principle derived from the teeth, it is found that while in that case it produced a structure presumably adapted to the circumstances, here it would spoil the joint. Wherever applied in the carpus, its tendency is to lift the bones apart on points and ridges. I have pointed out structures in this foot which I think meet and distribute

¹ *Am. Nat.*, 1888, pp. 1074; July, 1889; February, 1891.

² OSBORN, "Evolution of the Ungulate Foot," *Trans. Am. Phil. Soc.*, Vol. XVI.

this strain, but they are not in accordance with this principle. Later on the same is applied to variation and correlation.

A third law has been announced as operative in osteological evolution. Instancing the production of new joint sockets and tendinal grooves in cases of dislocation, the formation of joint surfaces phylogenetically, the production of trochlear crests, the sculpturing of tooth walls¹ is thought due to a similar process re-enforced by heredity. Here bone tissue yields to mechanical force, either physiologically or by molecular processes. This is, then, contradictory to the principle last dealt with. If certain teeth have developed opposing cusps and ridges, and other teeth are mutually arranged like shears with cusps shoved out of the way of direct impact,² the two structures may be equally adapted to their respective uses; they have not behaved the same under their mechanical relations.

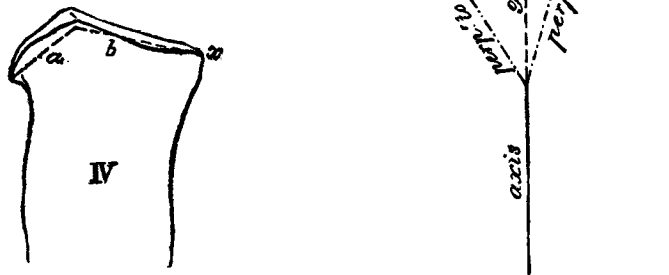
The last principle stated involves plasticity in bone, either physiological or molecular. As applied to the bones or the teeth, it must be supposed to be operative within limits imposed by the hardness of the structure, its rate of growth and metabolism, its hereditary form. I propose to enter with it into the structure of the foot under consideration, having special reference to the phenomena of variation and correlation. This matter of adjustment and correlation through the foot seems to me the hardest thing in osteological structure to account for without the aid of some form of mechanical evolution.

The results of the geometrical study of this foot, though the problem does not permit of exactness, point toward the conclusion that among those surfaces on which the weight of the body is thrown, pressure is equal. The diagram, representing the head of metacarpal IV, will illustrate this. The amount of thrust to be taken on surface *a* or *b* is determined by their inclination to the axis of the bone. *A* with its great obliquity

¹ See papers of Cope and Ryder on subjects mentioned.

² COPE, *Proc. Am. Ass. Adv. Sci.*, 1887, p. 256; *Jour. Morph.*, Vol. III, p. 233. Professor Cope, in these papers and in "The Origin of the Fittest," reiterates that wear is shown on the inner face of the upper sectorial of the Carnivora, on the outer face of the lower sectorial; also that the anterior internal cusp of the upper sectorial, supported by but one root, has been shoved out and forward by the opposing cusp of the lower sectorial which is supported by two roots. Compared with the facts cited by Professor Osborne, diverse effects are seen to have been assigned to similar causes.

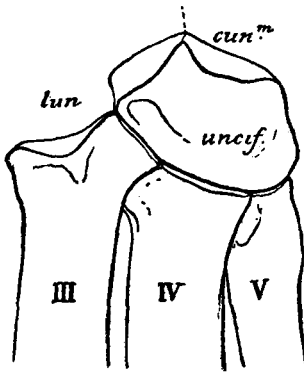
takes but little of the thrust, and has a proportionately small area on which to distribute it. But supposing the bones plastic and flattening out on one another according to the pressure between them, this is just what should be expected. The tendency of use during the life of an animal would be constantly on the line of adjustment. To make the fact clearer, suppose the plane *b* in a given individual to be more nearly perpendicular to the axis of the bone. In that case if the unciform above has a corresponding surface, *b* is under greater pressure than *a*; but plasticity being admitted, the whole tendency of use will be to flatten out the surface *b*, broaden it in proportion to *a*, until an adjustment is produced. But suppose while *b* has this new angle the corresponding unciform surface remains as



Resolution by plotting of the thrust of metacarpal IV on metacarpal III and the unciform. Parts given are the thrust of the metacarpal, which is let equal to its volume, and the inclination of the surfaces obtained by measure.

formerly. A region of special pressure is then produced at *x*. Use again, having its effect through plasticity, would tend to flatten out the surface at *x*, bring the whole surface to bear, and produce an adjustment as before. Observe what an opposite and destructive effect growth in the region of special impact would have. From the following diagram the effects can be car-

ried a step further up the foot. A little consideration will show, moreover, that increase in size and thrust of metacarpal V will,



through plasticity, produce a relative increase in the size of the unciform-lunar surface — a state of things which is found in *Menodus*.

Similarly as to the production of curvatures. A femur, say, slipped from its socket, may form a new joint with its girdle. The process so far forth is but a yielding of the bone to the pressure and movement of the femur head. If such is the physiology of bone tissue, the process must

be supposed operating in the history of each animal past and present, producing and perfecting the curved surfaces by which bones bear and move. The process kept within limits is, so far as I can see, a wholly adaptive one; but with the marked examples put before us, of changes wrought during the lifetime of animals, the office of heredity in the matter is not to be taken for granted. The crest and grooves on the lower metacarpal ends in some forms, produced apparently in relation to the sesamoid bones,¹ is one of the most marked examples of probable mechanical evolution. But before such structures can be said to prove the inheritance of acquired characters, the question should be tested whether they are not produced somewhere in the history of each individual by the necessary interaction of parts. It is understood that many structures, such as tooth forms which are cut in their adult shape, cannot be explained without heredity. To this it is answered that the correspondence of these structures to their mechanical surroundings has not been so definitely shown.

In conclusion it will be well to limit clearly the inferences pointed at in the preceding discussion.

1. Plasticity of bone, using the word *plasticity* not in a physical sense merely, but to include absorption under pressure, will probably account for much structure in the foot and elsewhere,

¹ The crests in certain highly specialized forms, like the horse and deer, reach round to the anterior face of the bone and apparently cannot be thus interpreted or assigned to any mechanical origin that is obvious.

especially in connection with the joints and in the fields of variation and correlation.

2. The determination of growth by pressure and strain is a complicated matter. The palæontological writers, however, I understand to have advanced two propositions on the subject: first, that the bones are governed in size by the mechanical stimulus they receive; second, that their conformation is determined in the same way, — regions of growth being determined by regions of pressure and strain. Facts have been shown inharmonious with both principles, while as to the second it has been pointed out that the testimony of the literature is conflicting.

That lines of evolution have progressed with but few useless side variations seems to be the uniform testimony of palæontologists; but that race changes follow those produced in the individual life, or that they are directly caused by their mechanical surroundings, I do not think has been satisfactorily shown.

EXPLANATION OF PLATE.

Fig. 1. Manus of Palæosyops in anterior view.

1 *a.* Trapezoid and trapezium of same.

1 *b.* Proximal view of 1st row carpals.

1 *c.* Proximal view of 2d row carpals.

Fig. 2. Manus of Menodus. $\times \frac{1}{4}$.

Sc, Scaphoid. *Lun*, Lunar. *Cun*, Cuneiform.

Tm, Trapezium. *Td*, Trapezoid. *Mg*, Magnum.

Un, Unciform. II, III, IV, V, Metacarpals.

