Journal of Anatomy and Physiology.

THE RELATION OF STRUCTURE AND FUNCTION AS ILLUSTRATED BY THE FORM OF THE LOWER EPIPHYSIAL SUTURE OF THE FEMUR.

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THE interdependence of Structure and Function has been universally recognised, though whether structure determines function or function originates structure, is a question about which there is much disagreement. As Mr Herbert Spencer[1] says:—"To answer this question is not easy, since we habitually find the two so associated that neither seems possible without the other, and they appear uniformly to increase and decrease together." The following observations, apart from their strictly anatomical details, appear to have an important bearing on the question above referred to.

The growth of a long bone is provided for by independent centres of ossification for the shaft and extremities. The former (diaphysis) appears long before the latter (epiphyses), and at birth, in the human fœtus at least, only a few of the epiphysial centres of ossification have as yet made their appearance, and most do not begin to ossify until a very much later period. Maturity is reached when all these independent centres have fused, a process which occurs at widely different times in different animals. Meanwhile, it is important to note that throughout a considerable portion of this adolescence the bones involved

[1] *Principles of Biology*, 1898, vol. i. p. 197.

are subject to the same statical conditions; that is to say, their function as means of support is the same as that exercised by the completely developed bones. But in the earlier stages of development the epiphyses and diaphysis are still separated by a considerable layer of bone-producing cartilage. At first this layer is indefinite in form, but with the increase in size of the ossific nucleus of the epiphysis, and the extension of ossification from the diaphysis, it becomes attenuated, and ultimately forms the thin epiphysial layer which determines the form and mode of union of the epiphysis with the shaft. Throughout the period of growth the epiphyses and diaphyses are subjected to the same forces which affect them after union has taken place between them. As must be evident, the statical conditions met with in one group of animals vary greatly from those which occur in other groups. Consequently, we would expect to meet with differences in the form of the epiphysial suture, such differences as would be best adapted to withstand the strains to which the joint between the shaft and epiphyses are habitually subjected. If on examination such proved to be the case, we would have a clear instance of function determining structure.

A consideration of the following observations will, I trust, justify the correctness of such an assumption.

For the following reasons, the lower epiphysis of the femur was selected for the purposes of this inquiry:—1st, because it ossifies from a single centre; and 2nd, because in different groups of animals the femora are subjected to different strains according to the habitual posture and use of the limb. It is sufficient to refer to the bipedal method of progression as opposed to the quadrupedal gait, to illustrate what is meant.

The material at my disposal to conduct this inquiry was not great, but, thanks to the kindness of Professor Weldon, the stores at the department of Comparative Anatomy were placed at my disposal, and I have thus been able to examine a considerable number of young skeletons. I am also indebted to Professor Paterson and Mr F. G. Parsons for the loan of specimens. For the time being I have confined my observations to mammals. Of these I have examined the following:—

MARSUPIALS.—

1 Didelphys Virginiana (Virginian opossum).
3 Macropus fuliginosus.
1 Halmaturus Bennetti (Bennet's wallaby).
1 Kangaroo (?).
1 Phascolomys platyrrhinus (platyrhine wombat).
7

EDENTATES.—

1 Bradypus tridactylus (three-toed sloth).
1

UNGULATES.—

1 Tapirus Americanus (Brazilian tapir).
1 Equus (horse).
2 Sus scrofa (pig).
1 Capra ibex (Alpine ibex).
1 Ovis aries (sheep).
1 Ovis musimon (mouflon).
1 Cervus elaphus (red deer).
1 Cervus (?).
9

CARNIVORA.—

1 Felis leo (lion).
1 Canis familiaris (dog).
1 Canis lupus (wolf).
1 Canis vulpes (fox).
1 Meles taxus (badger).
2 Lutra vulgaris (otter).
1 Nasua narica (white-nosed coati).
1 Ursus arctos (brown bear).
1 Melursus labiatus (sloth bear).
2 Phoca vitulina (common seal).
12

PRIMATES.—

1 Presbytes Thwaitesii (?).
4 Anthropithecus troglodytes (chimpanzee).
1 Semnopithecus entellus (entellus monkey).
1 Cercopithecus mona (mona monkey).
1 Cercopithecus (?).
1 Macacus cynomolgus (macaque monkey).
1 Macacus (?).
1 Cynocephalus anubis (anubis baboon).
1 Cebus capucinus (weeper capuchin).
12

A total of 40 altogether.

As was to be expected, a great variety of outline of the epiphysial suture was displayed in the specimens examined, varieties which depend, no doubt, on the uses and strains to which the limbs are habitually subjected, such as posture, range of movement of the knee joint, and such actions as climbing, leaping, and springing. Interesting, too, are the modifications in form displayed in some aquatic mammals, where the limb is largely relieved from the strain thrown upon it as a means of support, and where the suture is better adapted to withstand the resistance opposed to it when used as a paddle or flipper.

The results obtained may best be studied by taking illustrations from individual members of a series which are more or less typical of the group to which they belong.

As a rule, the joint between the epiphysis and the diaphysis assumes the form of a series of conical projections arising from the lower end of the shaft, which are embedded in corresponding hollows on the upper surface at the epiphysis. In man's lower extremity, where the limb is mainly subjected to a vertical strain associated with the bipedal position, the joint assumes its simplest form. Here the general shape of the lower end of the femur (fig. 1, 5) is rounded from side to side, and from before backwards, so as to fit into a shallow concavity on the upper surface of the epiphysis; but if more carefully examined, the lower end of the femur is seen to be pitted centrally at the point of confluence of two shallow furrows which cross each other at right angles, and so sub-divide the joint surface into four slightly projecting areas. The upper surface of the inferior femoral epiphysis is correspondingly divided into four shallow fossæ, mapped out by a slight ridging of the surface, these ridges being arranged in harmony with the grooves on the lower end of the femur, and displaying a more or less prominent tubercle at the point where they cross; this tubercle fits into the central fossa on the under surface of the femur. The articular surfaces so described are admirably adapted to resist a vertical strain when placed in contact with each other, but are not well suited to withstand thrusts having an antero-posterior direction.

If we take as our type the femur of an animal whose limbs

are subjected to constant shocks and jars, due to its habits of

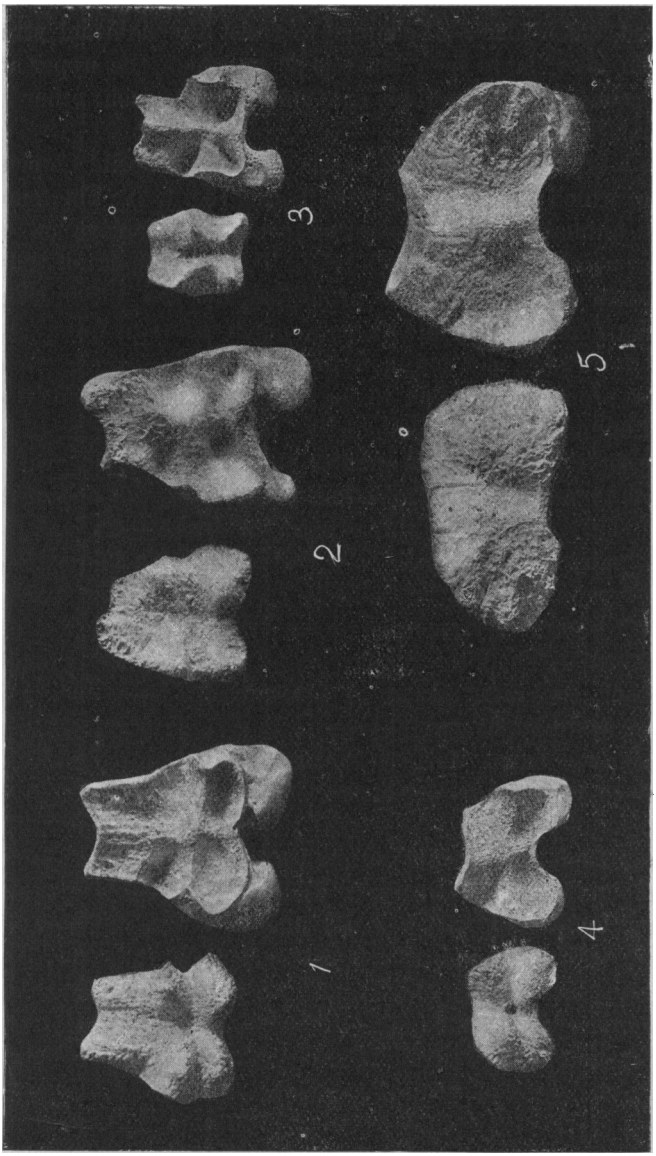

FIG. 1.—Photographs of the lower end of the femoral diaphysis and upper surface of the inferior femoral epiphysis. 1, mouflon ; 2, red deer ; 3, wolf ; 4, baboon ; 5, man.

leaping from rock to rock, we will find a much more complex joint between the shaft and the epiphysis. The alteration in

the character of the opposed surfaces is not only designed to withstand the sudden strains to which it is from time to time subjected, but is also well adapted to resist the habitual stress to which it is liable in a knee joint in which the upper and lower segments of the limb are united with each other in angular fashion.

Such a type is exemplified in the mouflon or wild Corsican sheep, of which a specimen is here figured (fig. 1, 1). The femur of this animal in the adolescent condition displays on its inferior extremity three pairs of cone-like projections: of these, the anterior pair are but little projecting, and are rather ridge-like than conical; the middle pair, much the most prominent, project downward, and end more or less pointedly; the posterior pair, less prominent, incline to be wedge-shaped. The inferior femoral epiphysis of this animal, the diameter of which in an antero-posterior direction is greater than its transverse width, is pitted to receive the projections from the lower end of the femur. There are thus three pairs of fossæ — an anterior shallow pair, a middle pair deeply excavated, and a posterior pair less pronounced. The middle and the posterior pair of fossæ are separated from each other by well defined lips and sharp edges. When the diaphysis and epiphysis are brought in contact, the interlocking of the surfaces described is so intimate as to withstand strains in every direction: in consequence we have, during adolescence, a joint admirably adapted to withstand the shocks incident to the habits of the animal.

It is difficult in any illustration to give an accurate idea of the complexity of the joint. To some extent, however, this is indicated by the disposition of the outline of the union of the epiphysis with the diaphysis on the surface of the bone, such as is represented in fig. 2, *a*, which is a view of the inner side of the lower end of the femur. Here the downward projection of the inner of the central pair of cones is well represented, though the degree of projection of the anterior and posterior tubercles is but little indicated by the outline on the surface. As, however, the same objection applies in all cases, the comparison of the superficial epiphysial outline forms a convenient method of grouping the specimens. As will be seen in figs. 2

and 3, the angle formed by the anterior and middle tubercles of

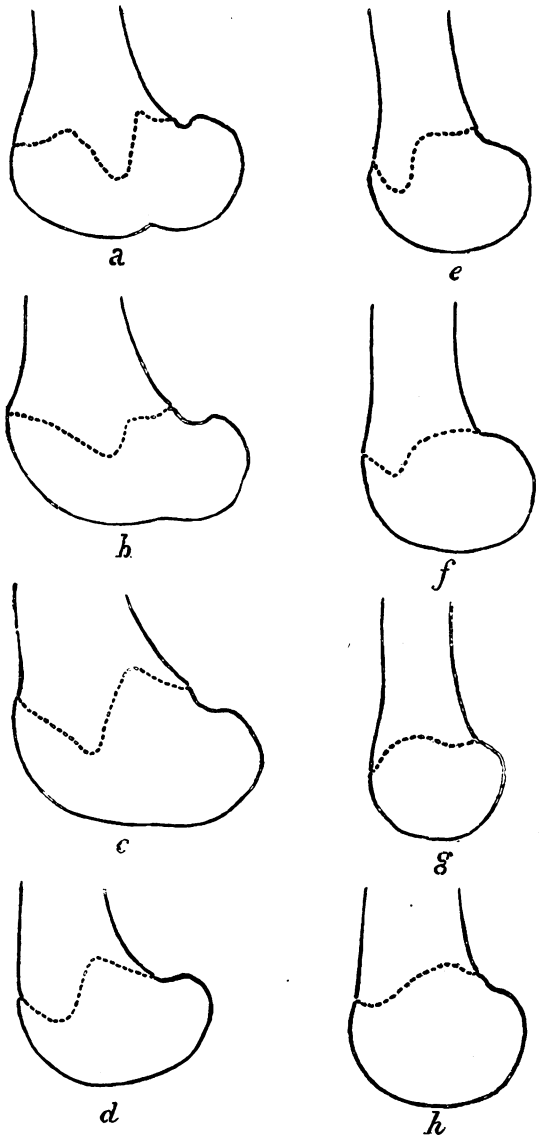

FIG. 2.—Diagrams showing the arrangement of the epiphysial line on the inner surface of the right femur in—*a*, mouflon; *b*, red deer; *c*, wolf; *d*, kangaroo; *e*, baboon; *f*, gorilla; *g*, chimpanzee; *h*, man.

the femur forms a convenient shoulder to resist the strain to

which the patellar surface of the epiphysis is subjected, whilst the condylic surfaces, which are subjected to an upward and forward thrust as they are supported on the tibiæ, are wedged in between the anterior and posterior tubercles.

Whilst it is by no means easy to group the varieties to which these epiphysial joints are subject, an intermediate type such as that represented in the wolf may be examined. This is shown in fig. 1, 3. The most noteworthy difference between this type and that already described as characteristic of the mouflon, is a reduction in the number of cones or tubercles displayed on the under surface of the femoral diaphysis: in place of there being three pairs, as in the case of the mouflon, there are only two pairs. This reduction in the number of the cones seems to be due to the disappearance of the anterior pair, or the coalescence and fusion of these with the middle pair. On the other hand, there is more equality in the size of the two pairs of cones than is the case in the middle and posterior pairs in the mouflon. The upper surface of the epiphysis displays correspondingly two pairs of fossæ of nearly equal depth; the resulting joint, whilst not possessing the same power of resistance to shock in various directions as that possessed by the corresponding parts in the mouflon, is yet sufficiently strong to meet all the requirements of such an animal as a wolf. The angle into which the tibial condyles is recessed is broad and deep, whilst the patellar surface abuts on an oblique notched area on the anterior aspect of the under surface of the femur.

A somewhat similar pattern is displayed in the Cervidæ (fig. 1, 2), though here the patellar slope is more extensive than in the wolf, and the recess into which the tibial parts of the condyles fit less deep.

As we pass to forms in which the range of extension of the knee is much increased, as evidenced by the confluence of the patellar and tibial surfaces, we find the whole epiphysis undergoing an antero-posterior compression, so that its transverse diameter now much exceeds its antero-posterior width. Correspondingly, there is an alteration in the form of the lower end of the femoral shaft.

I have taken as a type of this variety the forms displayed in the femur of a baboon (fig. 1, 4). There the lower end of

the bone displays four blunt wedge-shaped processes, differ-

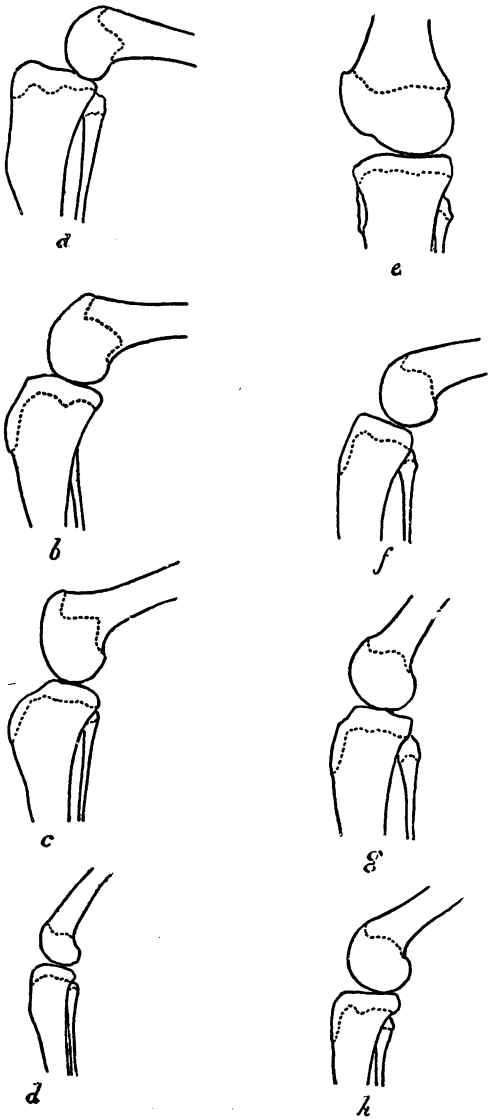

FIG. 3.—Diagram to show how the arrangement of the epiphysial joint at the lower end of the femur is modified as the range of extension of the knee joint is increased. *a*, kangaroo; *b*, polar bear; *c*, lion; *d*, wallaby; *e*, elephant; *f*, entellus monkey; *g*, chacma baboon; *h*, gorilla.

ing much in their projection from those already examined,

yet still displaying a conformity to the general type in that they are arranged in pairs. There are two pairs, and the anterior pair do not differ much in their development from the posterior pair. The upper surface of the epiphysis in general outline and shape is remarkably like that in man, but on closer inspection the fossa with which it is pitted are deeper and more clearly separated by upstanding crests than is the case in the human femur.

Unfortunately, the specimens of anthropoids at my command do not enable me to represent what, there is every reason to believe, would be an intermediate type between the baboon just described and man. I am only able to figure the lower end of the femur of a chimpanzee (fig. 2, *g*), in which, unfortunately, the ossification is not sufficiently advanced to give the precise and definite forms displayed in the other specimens.

Of interest are the modifications displayed in the form of the epiphysial suture in mammals of aquatic habits. As a type of this class, the femur of the seal may be taken. Here the lower end of the femur is much compressed antero-posteriorly, and the inferior surface of the diaphysis is divided into two rounded tubercles, separated mesially from each other by a fairly well marked antero-posterior furrow: slight evidence of a further subdivision of these tubercles into anterior and posterior parts may be observed, but for all practical purposes may be disregarded, so feeble are the indications of any such separation into pairs. Mention is made of the fact, however, as tending to display a conformity to the more general type, which has here undergone modification to a simpler form. The upper surface of the epiphysis displays a pair of fossæ in conformity with the tubercles of the shaft, and the suture between the two is such as best to withstand a side-to-side strain, but ill adapted to withstand a force acting parallel to the axis of the shaft of the bone, or a strain in an antero-posterior direction. An examination of the skeleton of the hind limb of the seal proves that the strains to which it is most subjected in action are just those which this suture at the lower end of the femur is best calculated to withstand.

In the elephant, in which the hind limb is straighter than in most other mammals, the epiphysial joint, subjected as it is to

a vertical strain, is simpler in its form and resembles more closely the arrangement displayed in man than is ordinarily the case in the quadrupedal type (fig. 3, *e*).

In the sloths, a group of animals in which, on account of their arboreal habits, an entirely different kind of strain is thrown on the limb, we would naturally expect to find a modification in the form of the epiphysial suture; nor in this are we disappointed, for in the specimen which I exhibit we find a remarkable difference in the form of the opposed surfaces from that which we have hitherto examined. In these animals there is a complete reversal of the arrangement already described; for in place of the lower end of the femur being tubercular, it is pitted, displaying two well marked hollows on either side of the middle line, the sides of these fossæ being channelled by a series of irregular grooves. On the other hand, the upper surface of the epiphysis, instead of being hollow and pitted, is elevated on either side over each condyle into irregular fluted projections, which fit into the corresponding recesses on the under surface of the femoral shaft. The resulting suture withstands admirably strains directed against it in all directions; but it is obvious that during the life of the animal it is more subject to a tearing than a crushing strain, as is the case in most of the types already referred to.

From a consideration of the foregoing facts, it seems to me that we are left with no other conclusion than that the form of the epiphysial suture is determined by the function of the limb; and since that function is exercised during a period of life in which the structure is still undeveloped and incomplete, we have a clear case, at least in this instance, of structure being determined by function.

Note.—Since the above was written, I have had an opportunity of examining a number of other specimens. The results, however, are entirely confirmatory of my previous conclusions.