Quarterly Journal of the Geological Society

Further Evidence of the Affinity between the Dinosaurian Reptiles and Birds

T. H. Huxley

Quarterly Journal of the Geological Society 1870, v.26; p12-31.
doi: 10.1144/GSL.JGS.1870.026.01-02.08

Notes

third digits are quite distinct; but the distal end is entire only in the first, or that of the hallux, which measures 1·85 inch in length. It has a pulley-shaped articular surface, and is 0·5 inch wide. The shaft of the bone is greatly compressed from side to side, as in *Scelidosaurus*. The second and third metatarsals are much broader and stouter, with flattened superior faces. They also seem to have been longer than the first. The fourth metatarsal looks, at first, as if it were much wider than the other; but, on close examination, I think I can trace a line of matrix separating a true fourth metatarsal, of about the same size as the others, from a slender fifth metatarsal. A basal phalanx, which seems to have belonged to the middle digit, is 1 inch long, 0·6 inch wide at the proximal, and 0·35 inch at the distal end. The pes of *Hypsilophodon*, thus, was either tetradactyle or pentadactyle.

The length of the trunk and tail of *Hypsilophodon* was probably about 4½ feet; and, in all likelihood, it was mainly herbivorous.

[For description of Plates I. & II. see p. 50.]

---

4. Further Evidence *of the* Affinity *between the* Dinosaurian Reptiles *and* Birds. By T. H. Huxley, LL.D., F.R.S., President of the Society.

On my way to Birmingham, in October 1867, I chanced to meet with Prof. Phillips; and mentioning some palæontological inquiries, chiefly relating to the Ichthyosauria (with which I then happened to be occupied), he very kindly urged me, as I returned to London, to pay a visit to the collection under his charge in the University Museum at Oxford. I did so; but as we were traversing the museum towards the Ichthyosaurian cases, we stopped at that containing the Megalosaurian remains, and I may say with Francesca—

"Quel giorno più non vi leggemmo avanti."

It is indeed a wonderful collection, ample enough to occupy the working hours of many a day; and it was particularly attractive to me, as some difficulties in the organization of *Megalosaurus* and its allies had long perplexed me.

As Prof. Phillips directed my attention to one after the other of the precious relics, my eye was suddenly caught by what I had never before seen, namely the complete pectoral arch of the great reptile, consisting of a scapula and a coracoid ankylosed together. Here was a tangle at once unravelled. The coracoid was totally different from the bone described by Cuvier, and by all subsequent anatomists, under that name. What then was the latter bone? Clearly, if it did not belong to the shoulder-girdle it must form a part of the pelvis; and, in the pelvis, the ilium at once suggested itself as the only possible homologue. Comparison with skeletons of reptiles and of birds, close at hand, showed it to be not only an ilium, but an ilium which, though peculiar in its form and proportions, was eminently ornithic in its chief peculiarities.

Next came the question of the nature of the so-called "clavicle." The determination of the structure of the shoulder-girdle threw open the homology of this bone, which clearly could not be a clavicle, whatever else it might be. The alternative position once more lay in the pelvis, and this time between the ischium and the pubis; and as the ilium was bird-like, might not the ischium, or pubis, be also expected to be ornithic in form? At any rate the bone answered remarkably well to the ischium of one of the *Ratitæ*.

Resemblances to the structures found in some birds had already been noted by Prof. Owen * in the sacrum of the *Dinosauria*; but these specially ornithic peculiarities of the pelvic girdle had not been indicated by any anatomist, and opened up a very interesting field of inquiry. To this I devoted all my disposable leisure during the winter of 1867–8, occupying myself chiefly with a critical examination of the materials in the British Museum in order to ascertain how far the peculiarities of *Megalosaurus* were common to the *Dinosauria* in general. As I knew that Prof. Phillips had devoted a great deal of time and thought to the collection which he has done so much to form, I begged him to furnish me with a statement of the results at which he had arrived before my visit; and in the commencement of 1868 he favoured me with the following letter:—

"Oxford, 1st January, 1868.

"My dear Huxley.—I must no longer delay to send you a notice of some specimens of Megalosaurian bones in this Museum, and of the doubts which frequent examination of them had raised in my mind touching the true composition of the skeleton. Since I had the opportunity of speaking to you on this matter, with the specimens before us, you have made so much progress toward replacing doubts by decisions, that, in truth, there is little now to be said which can appear to you either new or important. Still it will be a pleasure to me to recall the process by which I was led to form a quite different idea of *Megalosaurus* from that which I had derived from Cuvier and Buckland—the great early and skilful explorers in this field. When I came to reside in Oxford, and to handle the noble collection of Dr. Buckland, I was speedily satisfied that only two groups of reptilian bones were *frequent* at Stonesfield and in the contemporaneous (geologically speaking) Oolitic beds of the vicinity, viz. *Megalosaurus* and *Teleosaurus*. To these must be added, as usually of somewhat later date, *Cetiosaurus* of Owen, and, still later, for the most part, *Steneosaurus*. *Teleosaurus* and *Steneosaurus* require *scrutiny* to be differentiated; the bones of *Cetiosaurus* in this collection are more easily separated from those of *Megalosaurus*; but there are not many homologous bones of these two reptiles in our collection, rich as it really is. I mention these things chiefly to satisfy you that, *exceptis excipiendis*, the large case which you

* Prof. Owen evidently attached no weight to the fact as indicating any affinity of the *Dinosauria* with birds, as in his 'Report on British Fossil Reptiles,' 1861, p. 102, he says that "the Reptilian type of structure makes the nearest approach to Mammals in the *Dinosauria*."

saw filled with the reliquiæ of the great land Saurian contained no other than his personal remains.

"When the Stonesfield fossils came before me for lectures to a practical class, it was often my desire to present a sketch of the skeleton for comparison with that of a crocodile, and a pleasure to me to employ in this way such knowledge of the osteology of reptiles as a few dissections, now thirty or forty years ago, of each great reptilian group had fixed in my mind. For making these drawings on a large scale I was obliged to examine and consider several times the great bone called by Cuvier 'coracoid,' and to *complete* it by adding, after the pattern of *Varanus*, the extensions toward the sternum. When this was done, the magnitude of the thoracic region became such as to terrify me, and I looked eagerly through the collection for anything to relieve my alarm. Not being able to find any trace of sternal or episternal bones, I examined the curiously bent bone commonly referred to clavicle, and perceived that *it* was of the same order of magnitude. Next a set of spatulate bones, in fragments, came under my notice, and I speedily decided, *ex necessitate*, these to be scapulæ*. When completely restored they presented long flattened bones, concave on one broad face, convex on the other. I know no scapulæ like them except those of birds; and among birds none appeared to fit so well in the comparison as *Apteryx*. Then I reflected—a scapula like this, how could it belong to a coracoid like that? Examining for this purpose the humeral extremity of the bone, and collecting all the examples, I found it was composed of two elements ossified together, these elements concurring on one edge to form an articular cavity. Of these elements the broader and shorter one, which extended toward the sternum, was coracoidian in form, and perforated in each of four specimens. If, as appeared now to be the case, this was the coracoid, surely the great heavy bone so long called by that name was a pelvic bone, and the restoration of the skeleton must proceed on an entirely new basis.

"It soon became evident that the bone so long regarded as a clavicle must be removed from the place it had occupied, with the so-called coracoid, to which it was proportioned. It could not be attached to the now ascertained scapulo-coracoidian arch. It seemed calumnious to assign such a bandy-legged bone to either the radial or tibial alliance—besides that there could be presented a better claimant for the honours of the fibula, if not of radius or ulna. What could this bone be? In this state of uncertainty you found me, and helped me to a clearer view of the whole case now opening. I showed you the long bones which seemed to me to have the best claim to be regarded as of the fore limb, remarking that every thing seemed to indicate the fore limb of *Megalosaurus* to have been comparatively light and applicable,—not merely a strong support to a heavy body, as was thought to be the case when the huge

* In his "Notice of *Megalosaurus*" (Brit. Assoc. Reports, 1841, p. 108) Professor Owen says, "The scapula is a thin, slightly bent plate, of equal breadth, except where it is expanded and thickened towards the humeral end, but thinning off again towards the articular margin."

oval bone was called a coracoid. I pointed to an incomplete bone which you quickly decided to be humeral—rather a small bone as compared with the femur.

"Turning now to the hinder extremity, it was easy to see that as the small glenoid cavity formed in the scapular and coracoidian bone was fitted for a small humerus, so the great hollow in the heavy, arched pelvic bone was adapted to the large head of the well-known femur, 3 feet long. But to name this great pelvic bone was a difficulty with me. I was under the impression that its broad, smoothly expanded surface might be best compared with that of an ischium * or pubis, and that this would be more suited to the broad depressed body (as I supposed it to be) of such a huge creature, than, by accepting it as an ilium, to admit the beast to have been narrow in the rear, like a bird, with the plane of the bone not much inclined from the vertical. The only points in favour of its being possibly an ilium were, first, its resemblance to that bone in birds, and specially in *Apteryx* (to which I confess I gave but little importance, as too unlikely to be accepted), and, secondly, marks apparently of bony attachment, on one face of the bone, such as might be left by the removal of cohering processes from the sacrum. To this I was reluctant to give weight for the same reason, viz. that it seemed to make *Megalosaurus* too 'sib' with primæval birds. In this state of mind you found me, and, to my surprise, took up *de novo*, and resolutely, to compare the bone with the pelvic arrangement of Ostrich and its congeners†. You also then seized upon the so-called "clavicle," and rapidly placed it in a probable manner to one of the tuberosities which project beyond the acetabular cavity, and called it an ischial or else a pubic bone, of struthious rather than lacertian analogy. Every observation which I have since been able to make goes to confirm this result, and the corollary from it, viz. a decided ornithic alliance of the pelvic, as we already found in the sternal, arrangement. Perhaps in the same direction may be cited the distinctly tubular character of the limb bones, which I have not perceived as yet in *Cetiosaurus*, though it may perhaps be found to be the case, and I think it will be.

"As you are now engaged in working out the true affinities of this uncommon creature, I propose to send you careful drawings of our most characteristic specimens, and will now only request your attention to one or two things which have occurred to my observation.

"These are two forms of the great pelvic (ilial) bone—the well-

* In his "Report on British Reptiles" (British Association Reports, vol. i. p. 109), Prof. Owen describes "a subcompressed three-sided bone, flattened and slightly expanded at one end, thickened and more suddenly extended transversely at the opposite end, which formed part of a large cotyloid cavity," as most likely an ischium. "Length 18 inches, breadth at the middle of the shaft 5 inches, at its articular end 9 inches, the thickness of this end 4 inches." Where is this bone preserved?

† It appears that Buckland had suggested to Cuvier, but unsuccessfully, what now appears to be the right view; for we read, "Toutefois je ne puis guère douter que ce ne soit un coracoïdien de Saurien: il ressemble beaucoup moins à leur os des îles, auquel M. Buckland l'a comparé" (Oss. Foss. v. pl. 2, p. 346).

known ordinary form, which occurs in several examples, and another, in one quite young. The difference is very considerable, too great, I suppose, to be explained as a mark of age.

"There are two forms of scapula, both very large: the largest (one example) is separate from the coracoid; the others (several) are joined to the coracoid by synostosis. You will see the differences in the drawings. I am disposed to admit the larger specimens as belonging to *Cetiosaurus*, of which one huge femur (*Cetiosaurus giganteus*, Owen) was found in a deposit not much differing in age, at Gibraltar, north of Oxford.

"We have several specimens of metatarsal bones from Stonesfield—Megalosaurian no doubt. Lately there came to hand three metatarsals from the Kimmeridge clay of Swindon, which appear also to be of the same reptile. These were in apposition, cemented by a thick crust of selenitic crystals. These have now been removed, and the bones appear clear.

"It seems to me that these three bones were all that were in the metatarsus, and that the creature was tridactyle; but of course there may be reason not to trust too much to one case for proof of a negative. Still that seems to me the probable inference. As we have plenty of information about the femur, tibia (fibula?), metatarsals, and claw-bone, the reconstruction of the animal seems now practicable. But we want in this museum information as to cervical* and anterior dorsal vertebræ, and the central part of the sternal arrangements: of ribs we have sufficient examples, from anterior very short bicipital ribs, to very long arched widely bicipital ribs about the middle of the body, or, rather, a little before the middle. The *Marsupialia* do not appear to me to offer any special resemblances to any of the Megalosaurian bones. Among reptiles Crocodiles furnish the most analogous forms, among birds the *Struthionidæ*.

"Wishing you well through the Deinosaurians,

"Believe me, ever yours truly,

"JOHN PHILLIPS."

On the 7th of February, 1868, I published the chief results of the studies to which Prof. Phillips gives his benediction, in a lecture "On the Animals which are most nearly intermediate between Birds and Reptiles," delivered at the Royal Institution, and subsequently published in the 'Proceedings' of that body, and also, with the addition of sundry illustrations, in the 'Popular Science Review.' But in this lecture I drew my illustration of Dinosaurian structure almost wholly from *Iguanodon*. My reason for this was that *Iguanodon* was the only typical *Dinosaurian* of which the remains of the greater part of the body of a single specimen were associated together, while, at the same time, detached bones, all the peculiarities of which can be clearly made out, are numerous.

The conclusions at which I had at that time arrived are thus enunciated:—

* Professor Phillips has now (January 1870) obtained a cervial vertebra. It suggests a smaller head than was calculated from the known portion of the lower jaw.

"The *Dinosauria*, a group of extinct reptiles, containing the genera *Iguanodon*, *Hadrosaurus*, *Megalosaurus*, *Poikilopleuron*, *Scelidosaurus*, *Plateosaurus*, &c., which occur throughout the whole series of the Mesozoic rocks, and are for the most part of gigantic size, appear to me to furnish the required conditions.

"In none of these animals are the skull or the cervical region of the vertebral column completely known, while the sternum and the manus have not yet been obtained in any of the genera. In none has any trace of a clavicle been observed.

"With regard to the characters which have been positively determined, it has been ascertained that:—

"1. From four to six vertebræ enter into the composition of the sacrum, and become connected with the ilia in a manner which is partly ornithic, partly reptilian.

"2. The ilia are prolonged forwards, in front of the acetabulum, as well as behind it; and the resemblance to the bird's ilium thus produced is greatly increased by the widely arched form of the acetabular margin of the bone, and the extensive perforation of the floor of the actabulum. The other two components of the *os innominatum* have not been observed actually in place; indeed, only one of them is known at all, but that one is exceedingly remarkable from its strongly ornithic character. It is the bone which has been called 'clavicle' in *Megalosaurus* and *Iguanodon* by Cuvier and his successors, though the sagacious Buckland had hinted its real nature *. But these bones are not in the least like the clavicles of any known animal, while they are extremely similar to the ischia of such a bird as an ostrich; and in the only instance in which they have been found in tolerably undisturbed relation with other parts of the skeleton, namely, in the Maidstone *Iguanodon*, they lie, one upon each side of the body, close to the ilia. I hold it to be certain that these bones belong to the pelvis, and not to the shoulder-girdle, and I think it probable that they are ischia; but I do not deny that they may be pubes.

* The so-called "coracoid" of *Megalosaurus* is the ilium, I am indebted to Prof. Phillips, and to the splendid collection of Megalosaurian remains which he has formed at Oxford, for most important evidence touching this reptile.

[I do not know how it came about that I have here confused Dr. Buckland's suggestions with one another. In his memoir "On the *Megalosaurus*" (Tr. Geol. Soc. 2nd ser. vol. ii. p. 396), Dr. Buckland says:—

"The bone represented in fig. 3 is the outside view of the ilium, slightly concave. The inner surface is slightly convex, and shows marks of articulation with the sacrum."

The bone in question is that of which Cuvier makes the remark quoted by Prof. Phillips.

All subsequent writers have followed Cuvier's determination, which was wrong, and ignored Buckland's, which was not only quite right, but the key to a great deal that is most important in Dinosaurian organization. The so-called "clavicle" was so named by Buckland himself. Cuvier hesitates to recognize it as such, inclining to the belief that it may be the fibula. According to Prof. Owen the presence of this clavicle is one of the chief features of the *Dinosauria*. "The chief marks of difference from the Crocodile structure of the scapular arch and of resemblance to the Lacertian type is the presence of a distinct pair of clavicles."—Fossil Reptilia of the Wealden Formation, p. 33.]

"4. The head of the femur is set on at right angles to the shaft of the bone, so that the axis of the thigh-bone must have been parallel with the middle vertical plane of the body, as in birds.

"5. The posterior surface of the external condyle of the femur presents a strong crest, which passes between the head of the fibula and the tibia, as in birds. There is only a rudiment of this structure in other reptiles.

"6. The tibia has a great anterior or 'procnemial' crest, convex on the inner, and concave on the outer side. Nothing comparable to this exists in other reptiles; but a correspondingly developed crest exists in the great majority of birds, especially such as have great walking- or swimming-powers.

"7. The lower extremity of the fibula is much smaller than the other; it is, proportionally, a more slender bone than in other reptiles. In birds the distal end of the fibula thins away to a point, and it is a still more slender bone.

"8. *Scelidosaurus* has four complete toes, but there is a rudiment of a fifth metatarsal. The third, or middle, toe is the largest, and the metatarsal of the hallux is much smaller at its proximal than at its distal end. *Iguanodon* has three large toes, of which the middle is the longest. The slender proximal end of a first metatarsal has been found adherent to the inner face of the second, so that if the hallux was completely developed it was probably very small. No rudiment of the outer toe has been observed.

"It is clear, from the manner in which the three principal metatarsals articulate together, that they were very intimately and firmly united, and that a sufficient base for the support of the body was afforded by the spreading out of the phalangeal regions of the toes.

"From the great difference in size between the fore and hind limbs, Mantell and, more recently, Leidy have concluded that the *Dinosauria* (at least *Iguanodon* and *Hadrosaurus*) may have supported themselves for a longer or shorter period upon their hind legs. But the discovery made in the Weald by Mr. Beckles, of traces of large, three-toed foot-prints, of such a size and at such a distance apart that it is difficult to believe they can have been made by any thing but an *Iguanodon*, lead to the supposition that this vast reptile, and perhaps others of its family, must have walked, temporarily, or permanently, upon its hind legs.

"However this may be, there can be no doubt that the hind quarters of the *Dinosauria* wonderfully approached those of birds in their general structure, and, therefore, that these extinct reptiles were more closely allied to birds than any which now live"*.

There is one part of the organization of the *Dinosauria* which is not mentioned in this enunciation, because I did not at that time see its bearing upon the problem under discussion, I mean the very singular structure of the distal moiety of the tibia.

It took me a great deal of trouble to comprehend the structure of

* Proceedings of the Royal Institution of Great Britain. Friday, Feb. 7, 1868.

this bone, the extant descriptions being very imperfect, and sometimes based upon bones which have been broken and put together the wrong way by the mender. In the British-Museum collection the only thoroughly trustworthy *Iguanodon* tibia I can find is the small one numbered 36,403. It has been broken into several pieces; but they are very well fitted together, and the bone is not at all distorted. A second tibia of *Iguanodon*, with a very good proximal end, is numbered 28,669. The distal end of the Megalosaurian tibia (No. 31,809), which has been figured, is imperfect; but there was a tibia of *Megalosaurus* in the collection, the distal end of which was still inserted in its matrix; and, at my request, it was very carefully worked out. This tibia is the most perfect I have seen.

Its proximal end is produced into a great cnemial crest, which is concave on its outer, convex on its inner side. But when the backs of the condyles rest upon a plane surface, the outer edge of the crest does not project beyond the outer side of the bone. The inner and outer condyles of the proximal end are not very unequal, though the outer is the smaller. On the outer side of the proximal end of the bone there is a strong longitudinal ridge for the attachment of the fibula. The shaft of the bone is somewhat flattened from before backwards, and the distal end is still more flattened and expanded. Moreover the direction of its faces is quite different from that of the principal faces of the proximal end of the bone. These look inwards and outwards, supposing the condyle to rest upon a posterior plane surface. But the faces of the distal moiety of the tibia look forwards and outwards, and backwards and inwards, the plane of the distal end of the bone being nearly at right angles to that of the proximal end. The antero-external face of the distal end presented a somewhat smooth surface, apparently for the articulation of a bone; and this surface was bounded above and internally by a sharply defined edge, which terminated the face of the shaft of the bone. This edge at first passed outwards and backwards, and was convex downwards; but having reached the middle of the surface of the bone, it turns upwards and is lost at about $\frac{1}{5}$ the length of the tibia from its distal end. The distal articular surface is wider internally than externally, and its external moiety projects further than the internal, so that its inferior contour is oblique and slightly sinuated.

The tibia of *Iguanodon* is similar in its general characters to that of *Megalosaurus*; but the two condyles at the proximal end are more unequal, and the great cnemial crest is bent over in such a manner as to project far beyond the outer side of the tibia when the posterior edges of the condyles rest upon a plane surface. There is a small facet just beneath the outer condyle, for the proximal end of the fibula; but no crest for that bone is developed from the outer face of the tibia. The distal half is not so flattened as in *Megalosaurus*, but more trihedral. Its plane is twisted in the same way in relation to the antero-posterior plane of the bone, as in *Megalosaurus*. The distal extremity is divided into a larger antero-internal, and

a smaller postero-external moiety. The former presents a convex articular surface, which looks obliquely downwards and outwards. The postero-external moiety is an irregularly concavo-convex surface, which projects suddenly and considerably beyond the level of the other.

Fig. 1. Fig. 2.

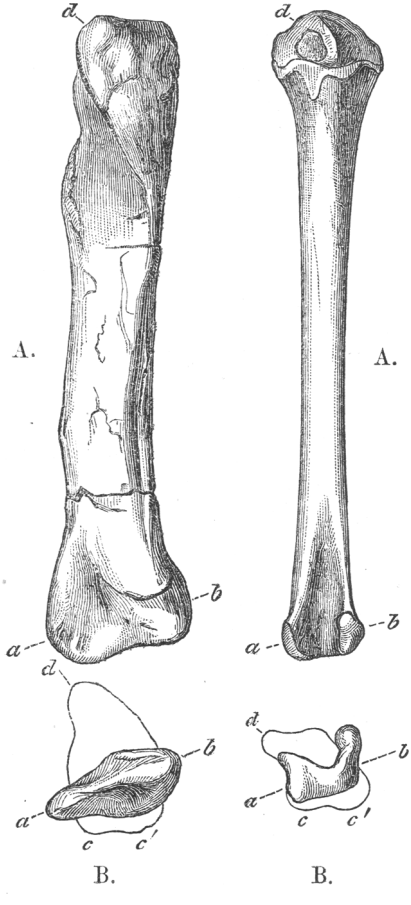

Fig. 1. A, the right tibia of *Megalosaurus*. The posterior margins of the articular condyles are supposed to be in the plane of the paper; *a–b*, a line traversing the median plane of the distal end of the bone; *d*, the summit of the cnemial crest. The strong fibular ridge is seen on the outer surface of the proximal third of the bone.

B, the distal extremity of the same bone projected upon the proximal end, which is drawn in outline. The letters as before, except *c* the outer and *c′* the inner condyle.

Fig. 2. A & B, corresponding views of the tibia of a young Fowl. The letters have the same signification.

The determination of the true form of the distal end of the tibia of *Megalosaurus* had some interesting consequences.

In the 'Ossemens Fossiles' (éd. 4me, t. ix. p. 204, "Sauriens Fossiles"), the following passage occurs:—

"A lower portion of a tibia from Honfleur, with the astragalus, another bone of the tarsus, and a fragment which possibly belongs to the fibula indicate a hind foot of very extraordinary structure.

"To understand its nature, it is necessary to conceive that the leg to which these bones belonged was much compressed from side to side, so as to be sharp behind, like the tarsus of a duck, instead of being flattened from before backwards, like that of the Crocodiles, and still more that of the Monitors. Bearing this conception in mind, the bone *a a*, figs. 34–36, has some similarity in form to the astragalus of the Crocodile; but one sees that the calcaneum must have been altogether posterior and very small.

"The articular face of the tibia is 0·14 metre long; its greatest width (0·04) is towards its anterior fourth, which is acutely angulated; posteriorly, the inner edge is undulated. A curved crest ascends obliquely along the inner face of the tibia, and articulates with the ascending and compressed process of the astragalus. In consequence of its compression, the form of this astragalus is so curious that it mght be taken, at first sight, for the calcaneum of a mammal.

"Below, it presents a convex cylindrical surface; above, it is irregularly concave, to adjust itself to the sinuosities of the articular face of the tibia; from its inner edge, posteriorly, arises the compressed process of which I have spoken. The internal face is semilunar. Behind, it is truncated, presenting a little concave facet, which undoubtedly articulated with the calcaneum.

"The animal to which this lower part of a leg and this tarsus belonged cannot have been less than thirty-six feet long, supposing it to have nearly the same proportions as the Gavials. If it had the proportions of a Monitor, its length must have amounted to forty-six feet."

Now, on comparing the distal end of the tibia of *Megalosaurus* with that of Cuvier's Honfleur Saurian, it was quite obvious that the two were closely analogous, and that *Megalosaurus* must have had an astragalus very like that of the Honfleur reptile. Evidence confirmatory of this conclusion was derived from another quarter.

The 'Mémoires de la Société Linnéenne de Normandie' (tome vi. 1838) contain a very remarkable paper by M. Eudes Deslongchamps, "Sur le *Poikilopleuron Bucklandii*, grand Saurien Fossile intermédiaire entre les Crocodiles et les Lézards," discovered in a Caen-stone quarry. The remains of this animal indicate that it had a length of from 25 to 30 feet; and as teeth of *Megalosaurus Bucklandi* occur in the Caen stone, Deslongchamps is inclined to suspect that *Poikilopleuron* may be identical with *Megalosaurus*. Among the bones of his *Poikilopleuron*, Deslongchamps obtained two astragali, the resemblance of which to the bone described by Cuvier in the 'Ossemens Fossiles,' was exceedingly striking; and applying one of these bones to the end of a fragment which he had

previously considered to be a femur, he found that it was really the distal end of the tibia, corresponding in all its broad features with Cuvier's specimen from the Honfleur clays. Deslongchamps's very just appreciation of the close affinity between his *Poikilopleuron* and *Megalosaurus* would have been immensely fortified if he had been acquainted with the true structure of the distal end of the tibia of the latter reptile.

I had got thus far in February 1868, and it was on the strength of the facts just mentioned that I included *Poikilopleuron* in the list of the *Dinosauria*, in the lecture which has been cited. At that time, however, I had not seen the following notes by Prof. E. D. Cope, of Philadelphia, which are contained in the 'Proceedings of the Academy of Natural Sciences of Philadelphia,' for November 1866 and December 1867, and in the 'Proceedings of the Boston Natural History Society' for June 1869, and which constitute important additions to his previously published account of the American Megalosauroid *Lælaps*.

The similarity of Prof. Cope's general conclusions to my own, in his second note, render it necessary for me to point out that I could not possibly have known anything about them when my lecture was delivered, still less at the time when the letter from Prof. Phillips which I have cited, was written.

"E. D. Cope pointed out the anomalous relations existing between the tibia and the fibula in certain of the *Dinosauria*, as illustrated by the genus *Lælaps*. He remarked, the distal extremity of the tibia is transverse and much compressed, and does not exhibit any of the usual appearances of an articular surface, neither the reptilian condyle, nor a cotyloid cavity sufficient for an astragalus of the size necessary for an animal of such bulk. A bone presenting a broad hour-glass-faced articular surface was discovered with the other remains, and had puzzled the anatomists who had seen it. This piece exhibits along its whole posterior aspect two faces, which form a reentrant angle for a fixed articulation; this is found to have been applied to the extremity of the tibia exactly, and to have been fixed by strong articular ligaments. The medianly constricted condyle, presenting forwards and a little downwards, exhibits so little analogy with the astragalus, as to suggest other interpretations; and after a careful examination, it seems evidently the distal extremity of the fibula. This element furnishes a small articular surface at the knee, and fitting the tibia by the concavity of its inner face, becomes greatly attenuated at its distal third, where it is, in consequence of the obliquity of its direction, applied to the anterior face of the former bone. It then spreads into a plate extending to the inner margin of the tibia, while the solid shank is continued along the outer margin, and both terminate in the massive condyle, which embraces the whole extremity of the tibia, like an epiphysis.

"One other example only of this structure is known in the Vertebrata, of which I only find mention in Cuvier, 'Ossemens Fossiles,'

x. p. 204, tab. 249. figs. 34, 5. This author studied the distal extremity of a tibia, with applied fibular condyle, from Honfleur, which he was not able to assign to any known species or genus, but which he, with his usual sagacity, included in the chapter devoted to *Megalosaurus*. He however regarded the face of the tibia receiving the condyle-bearing bone as the inner instead of the anterior, stating that the tibia is laterally instead of antero-posteriorly compressed; so anomalous is this structure among Vertebrates. He regarded the bone as the astragalus, and did not perceive any connexion between its ascending apophysis and a fibula, partly because a fibula with distinct distal articulations was received with the same bones.

"The fibular condyle possesses an articular facet on its exterior extremity (anterior, Cuvier), probably adapted to a corresponding face of a calcaneum. Its plane is transverse, and does not cover the whole extremity, the anterior margin and a knob on the antero-superior part of the extremity projecting beyond it. Exterior to the middle of the upper margin of this piece, and at the internal base of the ascending apophysis, it is perforate, as is the cavity above the condyles of the humerus in the higher apes, and may have received a similar coronoid process of an astragalus.

"As compared with the species examined by Cuvier, this fibular condyle has a less elevated form; in Cuvier's specimen the ascending apophysis was flatter, broader, and directed towards the calcaneal facet instead of from it; it lacked the submedian perforation. Its tibial face appears to have been rounded, not angulate. The tibia presented an ascending ridge to the face by which the ascending apophysis was applied; in the *Lælaps aquilunguis* there is no ridge, the apophysis reposing in a slight concavity. This apophysis, like the slender portion of the fibula, is composed of dense bone . . . . . .

"The direction of the condyle indicates the articulation of the tarsal elements to have been at a considerable angle with the shank of the leg, and that the animal was entirely plantigrade and was unable to extend the foot in line with the lower leg. The animal's weight was, no doubt, shared by another tarsal bone, besides the astragalus, owing to the anterior position of the former.

"In most known *Dinosauria* the relations of the tibia and fibula are similar to those in the modern *Lacertilia*. It would appear, then, that the class existed under two ordinal modifications: the first, including *Scelidosaurus* (Ow.), *Hylæosaurus* (Mant.), *Iguanodon* (Mant.), and *Hadrosaurus* (Leidy), may be called the ORTHOPODA; the second, including *Lælaps* (Cope), and probably *Megalosaurus* (Buckl.), may be termed the GONIOPODA."*

Prof. Cope's description leaves no doubt that *Lælaps* had the tibia and the anomalous bone which articulates with it, distally fashioned in the same way as in *Megalosaurus*, the Honfleur reptile, and *Poikilopleuron*; but it will become clear by and by that the

* Proceedings of the Academy of Natural Sciences of Philadelphia, Nov. 13, 1866.

anomalous bone is certainly the astragalus, as Cuvier determined it to be, and not a part of the fibula; it will also appear, I think, that Cuvier was right, from a morphological point of view, when he declared the tibia to be laterally compressed, and that there is no proof, but rather a presumption the other way, as to the plantigrade character of *Lælaps*. Finally, I shall bring forward evidence to show that the structure of the tibia and astragalus in question obtained in all the genera mentioned, so that the groups of *Orthopoda* and *Goniopoda* must be disestablished.

Prof. Cope * gave an account of the extinct reptiles which approached the birds. "He said that their approximation appeared to be at two points, the first by the *Pterosauria*, to which the modified bird *Archæopteryx* presented points of affinity. The second, and one not less striking, is by the *Dinosauria* of the orders *Goniopoda* and *Symphopoda*. He showed the essential differences between the ordinary *Dinosauria* and the birds to consist in the distinct tarsal bones in two series, the anteriorly directed pubes, and the presence of teeth, of the first class. In the genus *Lælaps* (Cope), type of the *Goniopoda*, the proximal series of the tarsal bones was principally represented by one large astragaloid piece, which had a very extensive motion on those of the second series. This was immovably bound to and embraced the tibia, and was perhaps continuous with the fibula, much resembling the structure of the foot of the chick of the ninth day, as given by Gegenbaur. The zygomatic arch was of a very light description. He was convinced that the most bird-like of the tracks of the Connecticut sandstone were made by a nearly allied genus, the *Bathygnathus* (Leidy). These creatures, no doubt, assumed a more or less erect position, and the weight of the viscera &c. was supported by the slender and dense pubic bones, which were to some extent analogous to the marsupial bones of implacental Mammalia, though probably not homologous with them.

"He said he was satisfied that the so-called clavicles of *Iguanodon* and other *Dinosauria* were pubes, having a position similar to those of the *Crocodilia*—also that a species of *Lælaps* had been observed in France, by Cuvier, which was different from the *L. aquilunguis*, and which he proposed should be called *Lælaps gallicus*.

"*Compsognathus* (Wagner), type of the *Symphopoda*, expressed the characters of the latter in the entire union of the tibia and fibula with the first series of tarsal bones—a feature formerly supposed to belong to the class Aves alone, until pointed out by Gegenbaur. This genus also offered an approach to birds in the transverse direction of the pubes (unless this be due to distortion in the specimen figured by Wagner), their position being intermediate between the position in most reptiles and in birds. Other bird-like

* Proceedings of the Academy of Natural Sciences, Philadelphia, Dec. 31st, 1867. I may remark that my memoir "On the Classification of Birds" was published in the summer of 1867 in the 'Proceedings of the Zoological Society.' Prof. Cope has evidently done me the honour to study it carefully.

features were the great number and elongation of the vertebræ of the neck, and the very light construction of the arches and other bones of the head.

"He thought the Penguin, with its separated metatarsals, formed an approach on the side of the birds; but whether the closest approximation to the *Symphypoda* should be looked for here or among the long-tailed Ratitæ (Ostrich, &c,) he was unable to indicate."

The 'Proceedings of the Boston Natural History Society' for June 18th, 1869, state that Prof. Cope "gave an account of the discovery by Dr. Samuel Lockwood, of Keyport, of a fragment of a large Dinosaur, in the clay which immediately underlies the clay-marls below the Lower Greensand bed in Monmouth County, New Jersey. The fossil represented the extremities of the tibia and fibula, with astragalo-calcaneum ankylosed to the former, in length about sixteen inches, distal width fourteen. The confluence of the first series of tarsal bones with each other and with the tibia he regarded as a most interesting peculiarity, and one only met with elsewhere in the reptile *Compsognathus* and in birds. He therefore referred the animal to the order *Symphopoda*, near to *Compsognathus*, Wagner. The extremity of the fibula was free from, and received into a cavity of the astragalo-calcaneum, and demonstrated what the speaker had already asserted, that the fibula of *Iguanodon* and *Hadrosaurus* had been inverted by their describers. The medullary cavity was filled with open cancellous tissue. The species, which was one half larger than the type-specimen of *Hadrosaurus Foulkii*, he named *Ornithotarsus immanis*."

It is very satisfactory to me to find that so able an anatomist as Prof. Cope should have been led by the force of facts to arrive, simultaneously with myself, at conclusions so similar in their general character with my own. It will be observed, however, that we differ a good deal in details. For example, it appeared to me that it was more probable that the so-called "clavicles" of the *Dinosauria* were ischia, rather than pubes; and in my diagrammatic restoration of *Iguanodon*, they are directed backwards in a manner approaching that in which the ischia of Birds are disposed, rather than in Crocodilian fashion, forwards, as Prof. Cope supposes. Prof. Cope does not allude to the strongly ornithic characters of the ilium and of the proximal ends of the tibia and fibula. In describing the astragalus of *Lælaps*, Prof. Cope states that "one other example only of this structure is known in the Vertebrata," referring to Cuvier's Honfleur reptile; but, as I shall show immediately, the astragalus is altogether similar in the commonest Birds, and probably in the whole class Aves.

Prof. Cope states that the fibulæ of the *Dinosauria* have been turned upside down by the describers of *Iguanodon* and *Hadrosaurus*. I am quite aware that the fibulæ of the former reptile have been figured the right way up by the artist and carefully inverted in the text by the describer; but if Prof. Cope will refer to my lecture, published in the 'Popular Science Review,' he will see that

what I say about the fibula is consistent only with a knowledge of the proper relations of its ends.

The further evidence as to the ornithic affinities of the *Dinosauria* which I have to bring forward in the present paper consists, first, in the structure of the pelvis, as shown by *Megalosaurus*, *Iguanodon*, and *Hypsilophodon*, and, secondly, in that of the distal end of the tibia and of the astragalus, as evidenced by *Poikilopleuron*, *Megalosaurus*, and *Lælaps*.

If the pelvis of any existing reptile be compared with that of any existing bird, the following points of difference will be observed:—

1. In the Reptile the ilium is not prolonged in front of the acetabulum; and the acetabulum is either wholly closed by bone, or presents only a moderate-sized fontanelle, as in the *Crocodilia*.

In the Bird the ilium is greatly prolonged in front of the acetabulum, and the roof of the acetabular cavity is a wide arch, the inner wall of that cavity remaining membranous. The anterior pier of the arch or præacetabular process extends further downwards than the posterior pier or postacetabular process.

Now, in all the *Dinosauria* which I have yet examined, the ilium extends far in front of the acetabulum, and furnishes only a widely arched roof to that cavity, as in Birds. It retains a reptilian character in the further proportional extension of the postacetabular process downwards.

2. The ischium in the Reptile is a moderately elongated bone, which becomes connected with the pubis in the acetabulum, and extends downwards, inwards, and somewhat backwards, to unite with its fellow in a median ventral symphysis. The obturator space is not interrupted by any forward process of the outer and anterior half of the ischium.

In all birds the ischium is elongated and inclined backwards, the backward direction being least marked in *Apteryx*, and most in *Rhea*. The ischia never come together directly in a median ventral symphysis, though they unite dorsally in *Rhea*. The anterior edge of the external half of the ischium very generally sends off a process which unites with the pubis, thus dividing the obturator space.

In all the *Dinosauria* in which I have been able to identify the bone (*Thecodontosaurus*, *Teratosaurus*, *Megalosaurus*, *Iguanodon*, *Stenopelyx*, *Hadrosaurus*, *Hypsilophodon*), the ischium is greatly elongated. In *Iguanodon* it has the *obturator* process characteristic of the same bone in Birds; and I imagine that the same process is seen in *Compsognathus*. In *Hypsilophodon* there can be no mistake about the matter, and the remarkable slenderness and prolongation of the ischium gives it a wonderfully ornithic character. In *Iguanodon* this slenderness and prolongation are carried beyond what is to be seen in Birds. I am disposed to think, however, that, as was certainly the case in *Hypsilophodon*, the ischia united in a median ventral symphysis in all the *Dinosauria*.

Fig. 3.

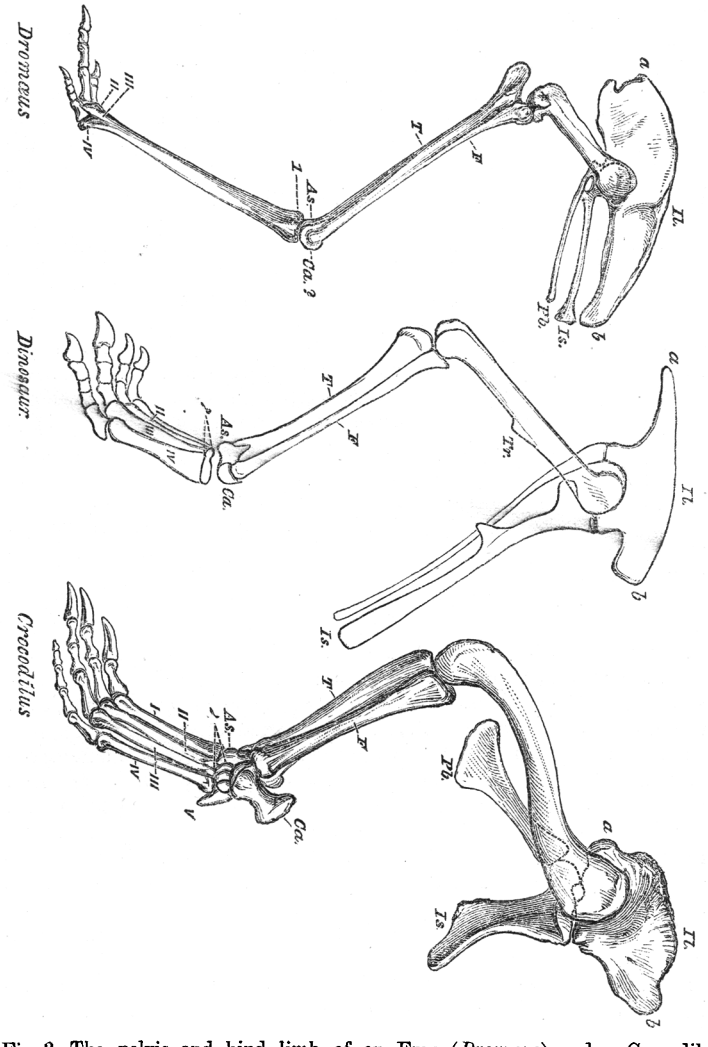

Fig. 3. The pelvis and hind limb of an Emu (*Dromæus*) and a Crocodile (*Crocodilus*), for comparison with the diagrammatic restoration of the corresponding parts in an Iguanodontoid Dinosaurian. The bones of the Bird are in their natural position; in the Dinosaur it may be a question whether the metatarsus was so much raised; in the Crocodile the foot would, naturally, be flat upon the ground, and the thigh turned out nearly at right angles to the body. The letters have the same signification throughout; *Il*, ilium; *a*, *b*, its anterior and posterior extremities; *Is*, ischium, *Pb*, pubis; *Tr*, trochanter of the femur of the Dinosaur; *T*, tibia; *F*, fibula; *As*, astragalus; *Ca*, calcaneum; 1, the distal division of the tarsus; I, II, III, IV, V, the digits.

Thus the ischia of a Dinosaurian are more bird-like than those of any existing reptile, but retain the reptilian union in a symphysis.

3. In all reptiles the pubis is inclined forwards as well as downwards towards the ventral median line. In all except the Crocodile it takes a considerable share in the formation of the acetabulum; and in all, except the Crocodile again, the ossified pubis unites directly with its fellow in the middle line. In the Crocodiles, the inner extremities of the pubes remain cartilaginous for a great extent, and consequently the ossified parts of the pubes remain widely apart in the dry skeleton.

Prof. Phillips has shown me what I believe to be fragments of the pubes of *Megalosaurus* in the Oxford Museum. If the determination is correct, they resembled those of the Ostrich in many respects. As they are detached, there is no certainty respecting their direction. The pubes of *Compsognathus* are, unfortunately, obscured by the femora. They seem to have been very slender; and they are directed forwards and downwards, like those of lizards. Some lizards, in fact, have pubes which, if the animal were fossilized in the same position as *Compsognathus*, would be very similar in form and direction.

Hypsilophodon, however, affords unequivocal evidences of a further step towards the bird. The pubes are not only as slender and elongated as in the most typical bird, but they are directed downwards and backwards parallel with the ischia, thus leaving only a very narrow and elongated obturator foramen, which is divided by the obturator process. I suspect that if only the pubis and the ischium of *Hypsilophodon* had been discovered, they would have been unhesitatingly referred to *Aves*.

Thus, as far as its pubis is concerned, *Hypsilophodon* affords an unmistakable transition between *Reptilia* and *Aves*. It remains to be seen how far the hypsilophodont modification extended among the *Dinosauria*. The remains of *Compsognathus* and of *Stenopelyx* lead me to suppose that it was by no means universal. In fact in this, as in many other respects, I have reason to think that the *Dinosauria* present us with serial modifications leading from the Parasuchian* type of structure, on the one hand, to that of Birds on the other.

The evidence yielded by the distal end of the tibia and the astragalus has the same tendency.

In the splendid collection of Megalosaurian remains in the possession of Mr. James Parker, of Oxford, which I had the good fortune to see a few weeks ago, I recognized the astragalus of that reptile, which, as I had already divined from the structure of the tibia, is altogether like the corresponding bone in *Poikilopleuron*.

In another specimen the distal end of the tibia and the fibula were in place, and there was the impression of the ascending process of the astragalus, with a fragment of its bony substance, exactly where it should be. With this complete knowledge of the

* By the generic name *Parasuchus* I indicate a reptile from the Indian Trias, which I hope shortly to describe, and which is clearly allied to *Belodon*.

tibia, fibula, and astragalus of such a typical Dinosaurian as *Megalosaurus*, let us compare these bones with the corresponding bones of Reptiles and Birds, as we have compared the pelvis.

In Reptiles (ordinary *Lacertilia* and *Crocodilia*, namely, which are alone at present under consideration),—

1. The proximal end of the tibia has but a very small or quite rudimentary cnemial crest, and it presents no ridge for the fibula on its outer side.

2. The flattened sides of the distal end of the tibia look, the one directly forwards, or forwards and inwards; and the other backwards, or backwards and outwards. And when the posterior edges of the two condyles of the proximal ends of the tibia rest on a flat surface which looks forwards, the long axis of the distal end is either nearly parallel with that surface, or is inclined obliquely from in front and without backwards and inwards.

3. There is no depression in the anterior face of the tibia for the reception of an ascending process of the astragalus.

4. The distal end of the fibula is as large as, or larger than, the proximal end, and articulates largely with a facet on the outer part of the astragalus.

5. The astragalus is not depressed and flattened from above downwards, nor does it send a process upwards in front of the tibia.

6. The astragalus remains quite free from the tibia.

In all these respects any ordinary bird, say a fowl, is very strikingly contrasted with the reptile.

1. The proximal end of the tibia is produced forwards and outwards into an enormous cnemial crest; and, on the outer side, there is a strong ridge for the fibula.

2. When the posterior edges of the condyles of the tibia rest upon a flat surface, the one flat surface of the distal end of the bone looks outwards as well as forwards, and the other inwards as well as backwards, and the axis of the distal end is inclined at an angle of 45° to the flat surface from within and in front, backwards and outwards, thus exactly reversing the direction in the Reptile.

3. There is a deep longitudinal depression on the anterior face of the distal end of the tibia, which receives an ascending process of the astragalus.

4. The distal end of the fibula is a mere style, and does not directly articulate with the astragalus.

5. The astragalus is a much-depressed bone, with a concave proximal and a convex, pulley-like distal surface. A process ascends from its front margin in the groove in the front face of the tibia. This process is comparatively short, and perforated by two canals for the *tibialis anticus* and *extensor communis* in the Fowl, while in the Ostrich and Emu it is extremely long and not so perforated.

6. The astragalus becomes ankylosed with the tibia (though it remains distinct for a long time in the Ostrich and *Rhea*, and in some breeds of fowls).

Now in every one of these particulars, except perhaps the last, *Megalosaurus* is far more like a bird than it is like a reptile.

1. There is a great cnemial crest and a ridge for the fibula.
2. The disposition of the distal end of the tibia is literally that observed in the bird.

Fig. 4.

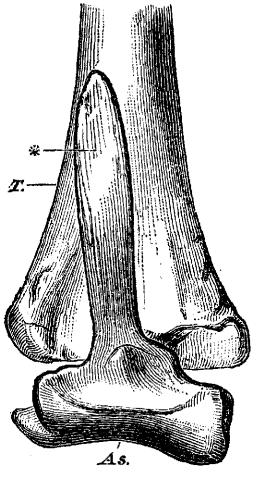

Fig. 4, front view.

Fig. 5.

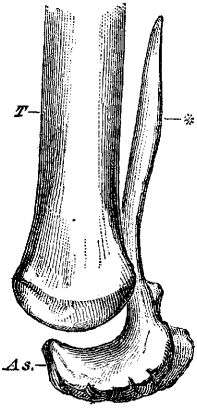

Fig. 5, side view.

The distal end of the tibia (*T*), with the astragalus (*As*), of a young Ostrich in the Museum of the Royal College of Surgeons. * the ascending process of the astragalus.

3. There is a fossa for the reception of the ascending process of the astragalus.
4. The distal end of the fibula is much smaller than the proximal, though not so slender as in *Aves*. It cannot articulate with the astragalus in the precise way observed in Reptiles.
5. The astragalus is altogether similar to that of a bird, with a short ascending process. I suspect that the perforation observed in this process in *Lælaps* by Prof. Cope, is the opening of a canal or canals for tendons, as in the fowl.
6. The astragalus appears to have remained distinct from the tibia throughout life in *Megalosaurus*; but it seems to have become ankylosed in *Compsognathus*, and Prof. Cope describes it as ankylosed in *Ornithotarsus*. I believe I have evidence of the same coalescence in *Euskelosaurus*.

I find that the tibia and the astragalus of a Dorking fowl remain readily separable at the time at which these birds are usually brought to table. The cnemial epiphysis is also easily detached at this time. If the tibia without that epiphysis and the astragalus were found in the fossil state, I know not by what test they could be distinguished from the bones of a Dinosaurian. And if the whole hind quarters,

from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us from referring them to the *Dinosauria*.

Discussion.

Sir Roderick Murchison, who had taken the Chair, inquired as to the habits of the *Hypsilophodon*.

Mr. Hulke mentioned that Mr. Fox had two blocks containing remains of a large portion of the *Hypsilophodon*, all procured from a thin band of sandstone near Cowleaze Chine. On one the pelvis is almost entire, as well as the right femur, the tibia (which is longer than the femur), four long metatarsal bones, and an astragalus. All the long bones are hollow. Portions of at least eight individuals have been found in the same bed.

Mr. Seeley doubted whether these animals should be called Reptiles at all, as they seemed to him to form a group distinct alike from reptiles, birds, and mammals, but occupying an intermediate position. In the hinder limbs of *Pterodactylus* the analogies were closer with mammals than with birds. He thought it possible that the peculiar structure of the hinder limbs of the Dinosauria was due to the functions they performed rather than to any actual affinity with birds.

The President, in reply, stated that *Hypsilophodon*, from the character of its teeth, probably subsisted on hard vegetable food. He expressed a hope that Mr. Fox would allow a closer examination of his specimens to be made. He was unable to agree with Mr. Seeley's views. He was inclined to think that the progress of knowledge tended rather to break down the lines of demarcation between groups supposed to be distinct than to authorize the creation of fresh divisions.

November 24, 1869.

Robert Arnold Barker, M.D., Civil Medical Officer, Cachar, Bengal, was elected a Fellow of the Society.

The following communications were read:—