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On Thecospondylus Daviesi (*Seeley*), *with some* Remarks *on the* Classification *of the* Dinosauria.

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

In the Fox Collection in the British Museum is the anterior third of a vertebra, with the number $\frac{R}{181}$, from the Wealden Beds of Brook, in the Isle of Wight, which indicates an animal of a type which hitherto has had but one other representative in Europe. With his usual acumen Mr. William Davies, F.G.S., recognized it as being the cervical vertebra of an animal closely allied to the genus *Cœlurus* of Marsh. No one would have been more competent than that veteran palæontologist to have written its history; and if I gladly undertake the task, it is because it enables me to suggest this honour to the work of a distinguished pioneer, whose labours on the Fossil Vertebrata have smoothed the way and facilitated the studies of every student of the National Collections for the last quarter of a century.

Imperfect as the specimen is, it may serve as a nucleus round which knowledge will accumulate, until the genus becomes as well known as the larger Wealden reptiles.

The centrum is elongated, compressed from side to side, with a flattened base, and flattened subquadrate anterior articular face, with the sides of the face prolonged backwards as subparallel sides, and as a ventral surface which is subparallel to the neural canal. The cervical ribs are co-ossified with the centrum and neural arch. The bony tissue, not unlike that of Ornithosaurs for its relative thickness, forms a dense external film, which defines the form of the bone, and is connected with some delicate internal supports in the chambered neural arch; so that there is no solid tissue in neural arch or centrum, and the densest layer is the film around the large neural canal. The neural arch forms a long pent-house ridge, which is penetrated in front above the neural canal by a large subtriangular cavity.

The only European genus hitherto described in which the vertebræ are similarly elongated, compressed from side to side, and enveloped in a dense external film of bone, is that indicated by the sacrum named *Thecospondylus Horneri*. The internal mould of that specimen, and the fragmentary vertebra of this, are confessedly scanty materials for comparison; but as they agree in characters which define them from all other animals, I believe it will be legitimate to refer both to the same genus, though there is the possibility of their belonging to distinct genera which are nearly allied. In the type of *Thecospondylus Horneri* the sacral vertebræ are about 11 centimetres long, and I estimate the vertebra about to be described as having been 9 centims. long, so there is no great difference in size. But since *Thecospondylus Horneri* has the sacral vertebræ convex trans-

versely on the ventral aspect, while the ventral aspect of this vertebra is transversely subquadrate, I regard the remains as indicating distinct species, because I have often noticed among Ornithosaurs that the flattened or rounded ventral condition, as the case may be, in the cervical region also obtains in the sacrum.

Fig. 1.—*Anterior aspect of the vertebra, which has lost the pre-zygapophyses and cervical ribs.*

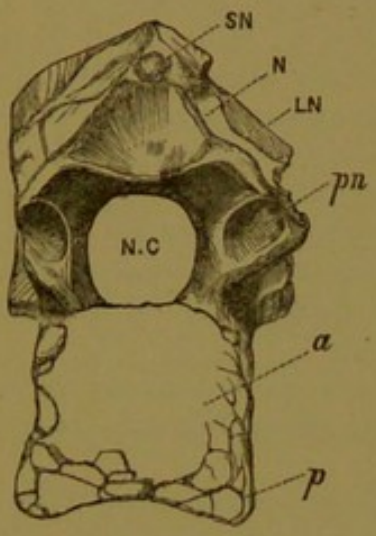


Fig. 2.—*Right lateral aspect of the same specimen.*

Fig. 3.—*Ventral aspect showing the base of the centrum.*

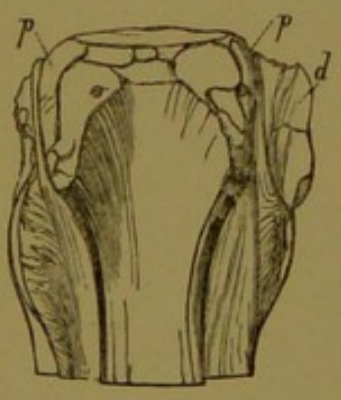
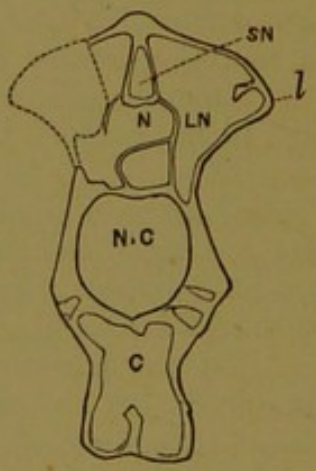


Fig. 4.—*Polished vertical section of the vertebra, showing the chambers in the neural arch and centrum.*



a, articular face of centrum, showing coarse cellular tissue on its slightly worn margin; *p*, attachment for the cervical ribs on the centrum; *d*, attachment for the cervical ribs on the neural arch; N.C, neural canal; *pn*, pneumatic foramen; N, cavity in neural arch, and corresponding air-chamber in fig. 4; SN, supra-neural air-chamber; LN, lateral air-chamber in the neural arch; C, centrum.

The anterior end of the vertebra (fig. 1) is imperfectly preserved, having lost the cervical ribs and adjacent tissue of the neural arch to which they were attached, as well as the adjacent prezygapophyses. If these parts were restored they probably would approximate in shape to those of *Cœlurus fragilis*, Marsh, except that the lateral extension of the ribs was less, and their supra-neural development was much less, for the lateral expansion of the neural arch has a relatively higher position than in that genus. As preserved, the anterior aspect of the bone is remarkable for narrowness relatively to its height. The articular face of the centrum (fig. 1, *a*) is flat or slightly concave, inclined slightly forward, subquadrate, being horizontal on the neural surface above, vertical laterally, and on the base it is concave from side to side, owing to the anterior corners having a downward development to form the basal attachments for the cervical ribs (fig. 1, *p*). The transverse width of the articular face of the centrum is 19 millim., and its vertical depth in the middle is about as much. The margins are somewhat worn, and show large cells defined by delicate tissue. The subtriangular facets of the cervical ribs at the inferior anterior corners of the centrum are probably but little worn, and in a line with the original sutures. They are oblique, and look downward, forward, and outward, and measure 13 millim. long by 9 millim. wide in front, where they are separated by an interspace of half a centimetre, which is convex as it descends from the articular surface on to the base of the centrum. The surface of the rib-facets is divided into two or three cells.

Above the articular face of the centrum is the transversely expanded subhexagonal entrance to the neural canal, 2·5 centim. wide and half as high in the middle, where the thin transverse bony plate which forms the upper limit of the arch extends from side to side with a downward curve. The neural canal itself (fig. 1, N. C) is higher than wide. The lateral angular expansions or antrum in front of the canal contain on each side an oval transversely oblique foramen (*pn*), which was probably pneumatic. It is situate in the lateral angle of the arch in such a way that the bone above it appears as though excavated, and that below it descends to form the stout pedicle of the neural tunnel, which has a transverse measurement of half a centimetre. The plate which limits the neural canal above is 8 millim. behind the articular face of the centrum. Upon this plate is a large aperture of a cavity in the neural arch, apparently penetrating conically, which is only inferior in size to the neural canal. It is 12 millim. wide at the base, and about 8 millim. high, with the sides converging upward to a transverse width of half a centimetre, while the upper border is 2 centim. behind the articular face of the centrum. The cavity penetrates far into the bone, and I regard it as having given attachments to ligaments which were attached to the extremity of the neural spine. The whole supra-neural region retreats backward as it ascends. Above this neural cavity is a circular foramen about 4 millim. in diameter, which assists in completing the triangular contour of the area above the

neural canal (fig. 1, N, SN). The lateral margins of this triangular area are approximately parallel to the external surfaces of the neural arch; only much of the external bone is broken away with the cervical rib which it supported. The interval was occupied by lateral air-cavities, one on each side, which included some delicate supporting bony films. The four supraneural chambers thus indicated appear to extend longitudinally throughout the neural arch.

The superior external surface of the neural arch is very imperfect. In the median line it forms a longitudinal blunt ridge from which the smooth flat lateral halves of the neural arch diverge outward at a wide angle (fig. 4), becoming convex as they descend, and terminating outward in a blunt ridge, which ascends from the hinder border of the diapophysial attachment of the rib, and defines the upper border of a large lateral concavity on the side of the arch, like an impression of the finger (fig. 2). Its lower half rests against the upper half of the neural arch, and its upper part, which has a thin wall, is bounded by the lateral air-chamber of the neural arch. There is a small foramen in the upper anterior part of the concavity. This concavity is bordered below by a strong longitudinal ridge, which is placed below the middle of the side of the neural canal (fig. 4). As this ridge extends forward it expands to form the anterior border of the concavity, which is 2·5 centim. behind the articular face of the centrum. It is prolonged further forward, decreasing in height (fig. 2). Its inferior surface is horizontal and sinuous; as preserved, it is 2 centim. long. The greatest transverse measurement on it, through the centrum, is 2·5 centim. It is apparently upon the line of junction of the neural arch with the centrum, 1½ centim. from the base of the centrum, and 2½ centim. from the median ridge of the neural arch. The remainder of the neural arch is badly preserved, and does not admit of description.

The region below the neuro-central ridge is the side of the centrum. Anteriorly it rises into the bases of the pedicels of the neural arch, which curve obliquely outward and upward towards the rib (fig. 2). So much of the side of the centrum as is preserved is approximately vertical, concave from the neuro-central ridge to the angle at the base of the centrum, and more gently concave from front to back. At more than 1½ centim. behind the articular face, and half a centim. from the base, is a transversely oblique foramen, over half a centim. long, margined superiorly by a slight arched border (fig. 2, *pn*), which extends beyond it. This was probably covered by the cervical rib, and appears to have been pneumatic. The least transverse measurement in the middle of the centrum is 8 millim. at the posterior fracture (fig. 4). There is a slight constriction anteriorly at the base of the neuro-central angle, so that the centrum bulges a little below it.

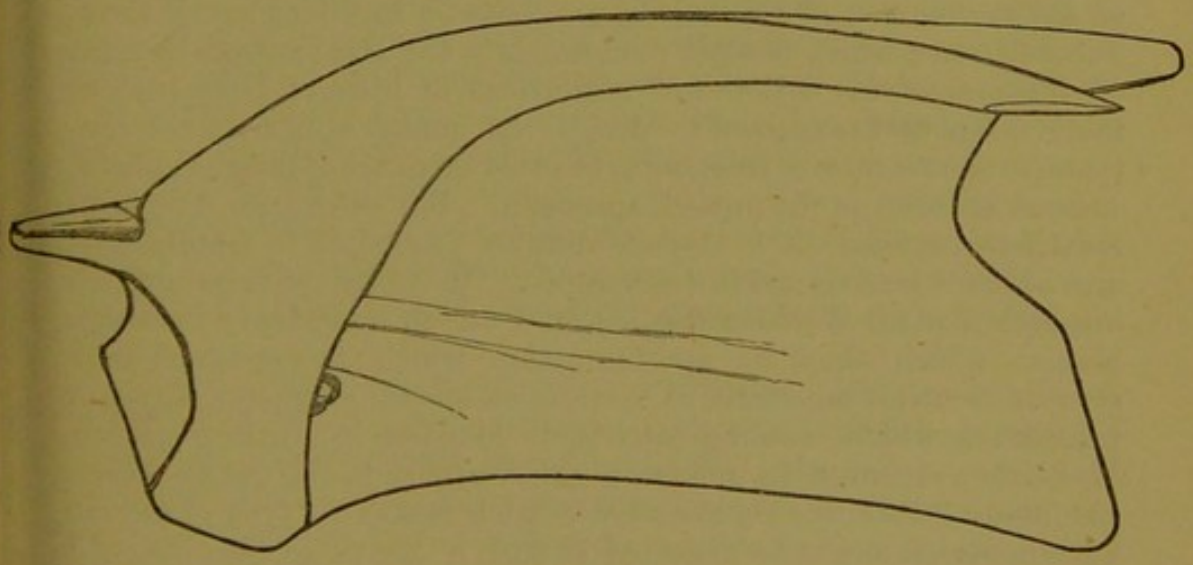
The base of the centrum is elongated, flattened, with concave sides. It is concave transversely, and widened anteriorly (fig. 3) by the development of the parapophysial tubercles for the rib, which extend the base till it is as wide as the centrum. At the posterior fracture the transverse measurement is one centimetre, so that it

has become narrowed to about one half of the anterior width. A long foramen runs in the anterior part of the left lateral angle of the base.

The posterior vertical fracture of the specimen has been polished (fig. 4); it shows the vertical height of the vertebra to be 4 centim. The transverse width of the neural arch at its superior expansion was 2·3 centim.; the transverse width at the neuro-central suture is 1·7 centim., and at the base 1 centim. The height of the centrum to the neural canal is 13 millim.: so its form is vertically oblong in section, concave above and at the sides, and margined all round by a thin wall of dense bony tissue, forming a perfect box, as in the vertebra of an Ornithosaur. The neural canal is slightly higher than wide, and measures 1 centim. transversely. The lateral walls of the neural canal are thick, 3 millim. on the left side, and 4 millim. on the right side, which includes two small foramina. The section of the neural arch is subpentagonal. It is divided into four chambers. First, a vertically oblong cavity with the angles rounded (N) is placed above the neural canal; secondly, a small and narrow isosceles triangle extends from above that cavity to the neural ridge (SN). Externally on each side are the large lateral subtriangular chambers (LN). These cavities are defined by the thinnest films of bone (fig. 4).

From this fragment it is only possible to attempt a restoration of the vertebra on the basis of general principles and the structure of allied animals; and such an outline, of the natural size, is here given (fig. 5).

Fig. 5.—*Outline of the Vertebra of* Thecospondylus Daviesi, *restored.* Nat. size.



The restoration, no less than the specimen described, indicates a close resemblance and affinity with the cervical vertebra of *Cœlurus fragilis*, Marsh*, which I suppose to indicate an animal not more than two thirds as large as this, or smaller. Both have a similar plan of vertebral construction, as shown in the elongated form, and

* Am. Journ. Sci. vol. xxi. pl. 10. fig. 1 (1881).

the correspondence extends to the lateral compression of the centrum and neural arch, inclined articular face of the centrum, mode of attachment of the ribs, the convex external surface of the neural arch, almost total suppression of the neural spine, thin texture of the bone, and internal chambers in the neural arch and centrum. Yet this strong evidence of affinity does not, I think, amount to generic identity. The following points seem to me important differences :—First, in this specimen the anterior part of the neural arch is much higher, ascends as it extends backwards, shows a large cavity above the neural canal, has no trace of a neural spine, and much more extensive diapophysial attachment for the ribs. Secondly, the chambers in the neural arch of *Cœlurus* are divided by a vertical median septum ; while in this specimen there are two important median chambers in addition to the lateral chambers. I attach less importance to the differences in the lateral walls of the neural canal, in the character of the forward extension of the postzygapophysial ridge, and in the form and condition of the articular face of the centrum, or to the other minor differences which are evident on comparison of the figures. But the sum of the differences seems to define a genus, but so close to *Cœlurus* that other parts of the animal may be expected to conform to the general construction of that type.

The sacrum of *Thecospondylus* being only known from a cast (Quart. Journ. Geol. Soc. vol. xxxviii. pl. xix.), from which the external film of bone has almost disappeared, is compared with some disadvantage ; and the resemblances which can be detected are limited to the thinness of the investing layer of bone, the smoothness of its internal surface, the elongation and lateral compression of the vertebræ, and a certain approximation in their general form. The difference which is most remarkable is the absence from the cast of *Thecospondylus Horneri* of indications of films of bone such as might have been expected to divide the neural arch from the centrum, or the sacral ribs from both, or other evidence of internal plates, such as are seen in the present specimen. But since such structures must have existed, their absence may be attributed to fossilization, and is no evidence of organic difference. It is because these animals are both British Wealden fossils that I attach importance to resemblances which show an approximation which is consistent with generic identity, especially as there is no known character, direct or inferential, which would justify their location in distinct genera. If I am warranted in referring this vertebra to the genus *Thecospondylus*, it follows that the identification makes the type of sacrum known, which might be expected in such a genus as *Cœlurus*, and completes a knowledge of the vertebral column in the family which that genus evidences.

I should infer that *Thecospondylus Daviesi* had the head elongated, with long slender jaws ; that the neck was over half a metre long, that the back and sacrum together were less than a metre and a third long ; so that the measurement from the tip of the snout to the extremity of the tail may have been under three metres. The

narrowness of the sacrum in *Thecospondylus Horneri*, which measures 20 centimetres between the iliac bones, no less than the elongation of the ilium over six or seven vertebræ, and the general build of the animal, lead to the conclusion that its habits were active, its limbs long, and its extremities specialized.

In endeavouring to form an opinion on the systematic position of *Thecospondylus*, there is little evidence available beyond these British specimens. For although Professor Marsh * states that he possesses portions of ten or twelve individuals of *Cœlurus fragilis* from the middle Secondary rocks of Wyoming, which yielded the Atlantosaurs, little is known of their structure beyond what his figures demonstrate. He places the animal in a new subordinal group, and observes (p. 340):—"its remains preserved suggest resemblance to Dinosaurs, to Pterodactyles, and more remotely to Birds, and it is apparently a generalized Sauropsid which, when fully investigated, may serve to bridge over some of the present breaks in the lines of descent. The sum of its known characters indicates that it is a reptile and not a bird. Its structure, so far as known, presents more similarity to Dinosaurs than to Pterodactyles; but for its nearer affinities we must await the discovery of further remains." I concur in the general spirit of these conclusions, but they admit of some elaboration.

When the first notices of *Ornithopsis* were published, Dinosaurs with a pneumatic skeleton were unknown; and it was remarked of the type specimens (Annals and Mag. Nat. Hist., April 1870):—"both vertebræ agree in being constructed after the lightest and airiest plan, such as is only seen in Pterodactyles and Birds; and they agree in possessing pneumatic foramina, which are an Avian and Ornithosaurian peculiarity. The foramina are of enormous size, and approximate to those of the Pterodactyles rather than to those of birds." On its affinities it was observed "it does not conform closely in the shape of vertebræ to either Pterodactyles or birds. And from the bones preserved, and many indications of allied animals which I have seen from the Wealden and Potton Sands, I anticipate that it will form the type of a new Order of animals, which will bridge over something of the interval between birds and Pterodactyles, and probably manifest some affinity with the Dinosaurs."

At that time, *Hypsilophodon*, *Iguanodon*, *Hadrosaurus*, and *Scelidosaurus* gave the best conception of the Dinosauria. It has been the fortune of others to elaborate the group thus indicated. Mr. Hulke has admirably described *Ornithopsis*, and Professors Cope, Huxley, and Marsh have investigated the structure of its allies, and their classification. But it has seemed to me that the classificational value of the pneumatic skeleton has been underestimated in the results which have been formulated. Professor Marsh has been led to form an order of animals for the type to which *Ornithopsis* belongs. This order was named Sauropoda†, and has for its European types *Cetiosaurus* and *Ornithopsis*.

* Amer. Journ. Sci. vol. xxi. (April 1881).

† *Ibid.* vol. xvi. p. 412 (Nov. 1878), vol. xxiii. p. 83 (Jan. 1882).

As early as December 1874* I suggested the name Cetiosauria as an ordinal division of the Dinosauria, and therefore am in harmony with Professor Marsh in separating these types from the remainder of the Dinosauria, though the separation may be based upon different data from those adopted by Professor Marsh. These animals are characterized by pneumatic vertebræ. And therefore when an additional order is instituted for animals with cavernous or pneumatic vertebræ, the Theropoda of Marsh†, under which *Cœlurus* is grouped, it becomes necessary, in order to determine the systematic position of *Thecospondylus*, to briefly review its relations to allied animals. I have no doubt that the two ordinal groups Sauropoda and Theropoda should be united into one order, the Saurischia, while the Stegosauria and Ornithopoda should be united into an order, the Ornithischia.

If Prof. Marsh is correct in attributing to *Cœlurus* the pelvic bones which have been figured (Amer. Journ. Science, vol. xxvii. pl. xi., April 1884), then there can be no doubt that the genus correctly finds its place in the Saurischia, in some such position as its discoverer suggests; for its pubis does not show a generic difference of form from *Allosaurus*. But in his account of the vertebral column (Amer. Journ. Science, vol. xxi., April 1881) it is said that the ribs preserved have undivided heads, and in the figure of a dorsal vertebra (*l. c.* pl. xi. fig 2 *a*) there is no sign of a capitular facet on the neural arch, while the fractured, compressed, transverse process is subcrocodilian. This is a remarkable divergence from the divided rib-articulation hitherto found in the Ornithischia; but is an intelligible modification of the Saurischian type. Its chief interest lies in the rib being attached to the transverse process as in the Ornithosaurian genus *Pachyrhamphus*, with a vertical compression of the process, which is Crocodilian or Avian. But while the Saurischia may thus be exceptionally modified in vertebral characters, the pneumatic skeleton is an approximation towards Ornithosaurs and Birds, which may be a stronger evidence of organic affinity. And it serves to demonstrate the way in which the pneumatic skeleton was developed, in animals which not only did not fly, but show no sign of degeneration from flying types. It cannot therefore be classed as an adaptive modification of structure consequent on flight. Hence it may be regarded as indicative of a community of plan of vital organs so far as the respiratory system is concerned. It is curious that while the Saurischia thus make an approximation to Ornithosaurs, and the pelvic structures and hind limb to some extent support the comparison,—the pelvic structures and the hind limb, in the Ornithischia, on the other hand, rather approximate towards Birds in plan of the skeleton, although the pneumatic condition of the vertebræ is not a character in common between them.

* Quart. Journ. Geol. Soc. vol. xxx. p. 690.

† Amer. Journ. Sci. vol. xxi. p. 423 (May 1881), vol. xxiii. p. 84 (Jan. 1882), vol. xxvii. p. 337 (April 1884).

Discussion.

The President congratulated the Author on the opportunity afforded him for paying a tribute to that excellent palæontologist Mr. William Davies, which he cordially endorsed.

Mr. Hulke would not enter into the question of classification. He had great hesitation in accepting the Author's identification with *Thecospondylus*. It was difficult to institute a comparison between a structure such as the fossil under description and one which has no structure. Then there was the great difference in size. On the whole the resemblance of the fossil to *Cœlurus* was so close that he was inclined to refer it to that genus.