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# Note on *Psephophorus polygonus*, v. Meyer, a new Type of Chelonian Reptile allied to the Leathery Turtle

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# Notes



30. Note on Psephophorus polygonus, v. Meyer, a new Type of Chelonian Reptile allied to the Leathery Turtle. By Professor H. G. Seeley, F.R.S., F.G.S., &c. (Read May 12, 1880.)

(PLATE XV.)

WHEN I was in Vienna in the spring of 1879, Franz Ritter von Hauer, the Director of the Imperial Geological Survey, requested me to examine and describe the remarkable organism on which Von Meyer had founded the genus Psephophorus, which, although noticed by himself, by Von Meyer, and, more recently, by Dr. Fuchs, has never been figured. Its nature was at first sight so problematical that opinion leaned to the conclusion that it was the dermal covering of an Edentate closely allied to the Armadilloes. The dorsal surface of the fossil was perhaps insufficient to settle this question without a good deal of comparative work; but Von Hauer courteously allowed me to partially develop some fragments of bones, which are imperfectly preserved on the underside of the intractable sandstone matrix of the slab; and these fragments of procedous vertebræ proved to be altogether reptilian; and though differing from the vertebræ of known reptiles, yet, by the forward projection of the zygapophyses, they indicate the animal to be Chelonian, and therefore show the fossil to be more nearly allied to Sphargis than to any other type in the Chelonian order.

When Von Meyer first gave a name to this genus ('Jahrbuch,' 1846, p. 472), it was only known to him by isolated dermal plates; but subsequently a drawing was sent to him by Partsch, and on that he made a further note in the 'Jahrbuch' for 1847 (p. 579). This specimen, then in Pressburg, he describes as a fragment of a carapace, containing seventy bones touching each other, and showing the impressions of many others. Among these dermal bones rises a middle row, in which the plates are longer and more evenly pressed together in front and behind, while the other plates are placed together irregularly. He adds his conviction that it may be referred to the Dasypodia. It remained without further notice till 1868, when Von Hauer, in the 'Verhandlungen der k.-k. geologischen Reichsanstalt' (p. 387), mentioned briefly that the fossil had been acquired for the Museum of the Imperial Geological Survey in Vienna. He also, in 1870, in the same publication (p. 342), makes a note on Psephophorus, mentioning that the museum had acquired not only the original type specimen, but a second larger slab, fitting the first, and containing a larger portion of the same carapace; for while the first piece contained six median plates, characterized by a raised keel, extending in a straight line, and sixty-four smooth lateral plates in a connected position, on the second slab of sandstone are five more median plates and nearly a hundred more lateral plates. These form together an even arched shield,

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about thirteen Vienna inches long, and fifteen at its greatest breadth. Numerous bony plates are said to be scattered through the mass of the sandstone, besides other bone-fragments; and Von Hauer considers that there is a second shield, which lies parallel to the first, and under it, at an interval of scarcely half an inch. Von Meyer had made another short note on this fossil in the 'Berichte über die Mittheilungen von Freunden der Naturwissenschaften in Wien' for 1851 (p. 3), which Von Hauer well epitomizes by saying that although the animal had originally been regarded by Von Meyer as belonging to the Armadillo family, he subsequently showed the striking resemblance of the carapace from Neudörfl with one from the Zeuglodont Limestone of North America, which Müller had figured and compared with the dorsal shield of Dermatochelys in his work on Zeuglodon. But, beyond drawing attention to its resemblance to the Psephoderma alpina from the Upper Trias, and pointing out some resemblances which that genus presents to the crocodilian type of armour, Von Hauer expresses no opinion on the systematic position of the genus. Finally Dr. Th. Fuchs, in notes on his travels in Italy, printed in the 'Verhandlungen der k.-k. geologischen Reichsanstalt' for 1874 (p. 220), remarks that in the zoological department of the Museum at Florence he saw the remarkable shield of Sphargis coriacea; and adds, "the full resemblance to our Psephophorus is so evident that I cannot imagine that any one who had seen the two could remain a moment in doubt on this matter." Von Meyer appears to have inclined towards the Chelonian hypothesis, in consequence of Müller's account of the Sphargis in the Zoological Museum in Padua; and it only remained for Fuchs to confirm the accuracy of this interpretation.

The slab of hard sandstone in which the specimen is preserved is 46 centimetres long, and about 41 centimetres wide. It only shows a small portion of the shield, which originally covered the back of the animal, the principal part preserved being 33 centimetres long and 35 centimetres wide. It is divided into two portions by an elevated longitudinal median keel or crest. The lateral parts are inclined to each other at an angle of about 155 degrees. The keel does not appear to be quite straight; and it would be difficult to assert positively that it occupied a lateral position in the body, though this probably was the case. The keel is rounded, and formed by a single row of polygonal plates, portions of eleven of which are preserved; nine occupy a length of 28 centimetres. Nothing could be more remarkable than the extreme irregularity of size and form of the ossicles which make up the lateral portions of the carapace. Some small ossicles are nearly circular, others ovate, triangular, subquadrate, but mostly of irregular forms with five, six, or more sides, which are sometimes convex, sometimes concave, and often with sharp angles at the points where they join the neighbouring little plates. Occasionally a minute plate occurs which is hardly a centimetre in diameter; but most of the plates are from two centimetres and a quarter to two and a half centimetres in diameter. Their substance is very dense, almost like the palatal teeth of Plethodus or

the armour of a ganoid fish. There is no trace of the plates having been ankylosed together; for although they for the most part still retain their natural positions, they have separated sufficiently to show that the original connexion was maintained by a fibrous or coriaceous investiture. On the dorsal surface the plates, except in the median keel, nearly all show a beautiful radiating sculptured ornament, which certainly recalls that seen in some of the larger Armadilloes, rather than the condition in any reptile. On the under surface the plates are perfectly smooth. As arranged, the transverse measurement of the plates appears to be greater than the longitudinal measurement, five plates occurring transversely in one place in a distance of twelve contimetres, and six or seven occupying the same distance longitudinally.

It is difficult to say which should be regarded as the anterior part of the fossil, as the remains are so fragmentary that they give no indication whatever of its complete form or size; but I incline to believe, from the analogy of the curved ridge in Sphargis, that it is an anterior fragment from the left side. The plates are remarkable for their thickness, which sometimes amounts to nearly a centimetre, though most of them are thinner. Towards one corner of the slab are a few plates, much thinner, partly covered with matrix, which look as though they might have belonged to an under or ventral armature; but having regard to the state of preservation of the fossil, it would be unsafe to overlook the probability that they may be a portion of the carapace displaced and inverted, or of its margin, which would naturally have an inverted position. But Psephophorus, unlike Sphargis, may have also possessed a ventral shield of thin plates. A question may arise as to whether the fragmentary bones on the other side of the slab, which is about six centimetres thick, are portions of the skeleton of the same animal; but all probabilities seem to me to lean in that direction; for this fessil was evidently stranded, much as porpoises and other animals are thrown up on sandy shores at the present day, and the skeleton, becoming knocked to pieces, has been scattered. The resemblance of the carapace to that of a mammal is certainly sufficiently close to have justified any one in so regarding it: and the large size of the armour-plates, as well as their sculptured surfaces, would support this resemblance; but the elevated rounded keel, increasing in height as it passes onwards, with the somewhat flattened sides of the shield, are more in harmony with Sphargis; and if skeletons of the covering of Sphargis had been prepared in our Museums, it is certain that the same kind of irregular arrangement of the plates would have been recorded. There is little, except the relatively large size of the plates in the fossil and their perfect ossification, to distinguish them from the comparatively small elements which make up the bony skeleton of the covering of the leathery turtle.

So far as I am aware, the dermal shield of *Sphargis*, though often figured, has never had its osteological characters described; for the thin epidermic covering conceals bones which constitute a shield which is only comparable to a tessellated pavement, corrugated by

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the seven longitudinal ridges which extend along it. The main median ridge is most elevated posteriorly; but the three lateral ridges on each side maintain about equal elevation throughout their respective lengths, and converge towards each other very slightly anteriorly, and more markedly towards the posterior end. A specimen in the British Museum has a length of a hundred and fifty centimetres; the greatest transverse width round the curve of the back is more than a hundred centimetres, though the width from side to side in a straight line in the same position is not much more than seventy centimetres. The bones which form the median ridges are often three centimetres long, and abut against each other by transverse sutures, much as in the fossil; but the ridges in the recent Sphargis are sharper and more broken by irregularities, owing to the fact that some plates have the ridge developed to a greater height than others. In the wide part of the carapace, the transverse width between two lateral ridges is about sixteen centimetres, and in this distance fourteen or fifteen polygonal bones may usually be counted. riorly the plates become rather smaller, and seventeen or eighteen plates may be counted between two ridges; and it is also here observed that the transverse measurement of each plate is usually greater than its longitudinal measurement. The plates mostly vary from half a centimetre to over a centimetre in diameter. Some of the plates appear to give indications of a slight radiated surfacewrinkling, like that seen in some parts of the fossil; so that, as Müller first suggested and Von Meyer afterwards asserted, the resemblance of Psephophorus to Sphargis is close, and quite justified Fuchs in stating that it was only necessary to see the two types to admit their general identity. In fact, there is nothing but difference in the size of the plates to distinguish the two genera, as far as the shield is concerned. It is, of course, impossible to say how many longitudinal ridges may have extended along the carapace of Psephophorus. If there were many, the interspaces between the ridges certainly wanted the concave character visible in the recent genus; and this apparent flatness of the carapace leads me to suspect that in Psephophorus the ridges may have been fewer than in Sphargis. The slight longitudinal curvature visible in the median ridge in the fossil, together with the slight transverse elongation of the bony plates, would lead me to regard the specimen as being probably part of a lateral ridge from the anterior portion of the shield, and not far from its margin; for what has appeared to be the under shield formed of thin plates, imperfectly seen at its posterior end, where many plates of the skeleton have been broken away, would well correspond to that part of the carapace of Sphargis which is bent round inferiorly at the outer sides of the shield; so that when fossilized, these portions might then present the appearance of two shields superimposed on each other.

It will readily occur to any one familiar with the Chelonia that the type which is represented by *Sphargis* and *Psephophorus*, differs from all the other members of the order, not only in having the ribs entirely separate from the carapace, but also in the fundamental

plan upon which the representative of the carapace itself is constructed; and I believe that we have here an indication of a primary division of the Chelonia to which palæontological discoveries may hereafter give more importance than can at present be claimed for it. From the point of view of evolution, it may fairly be anticipated that the pavement-shielded type of Chelonian preceded that in which the dorsal shield is formed of symmetrical bones. Perhaps the most remarkable character in the dermal skeleton of Sphargis is the fact that the bones of the plastron, although only forming an outer ring to the ventral surface, are already defined and homologous with those of the ordinary Chelonian, in which the carapace is specialized. And this leads me to draw attention to the fact that the dermal bones of Sphargis, which may be detected without difficulty on the dorsal surface of any ordinary shield, are altogether invisible on the interior side of the shield, which was in contact with the neural arches of the dorsal vertebræ and the slender flattened ribs; so that it is quite evident that the ordinary carapace of a Chelonian is in no way represented by the dermal skeleton of Psephophorus or Sphargis. Impressed by the fact that the dorsal ribs of Crocodiles bear upon their hinder margins plates of fibro-cartilage, which in the Hatteria also exist and are sometimes converted into bone, and believing that these plates are homologous with the epipleural elements or uncinate processes which become greatly developed and blended with the ribs of certain birds. I have been led to speculate on the probable occurrence of such cartilaginous elements upon the dorsal surfaces of ribs of Chelonians, and to believe that the development and ossification of such plates upon the Chelonian rib would lead to a transference of the osseous matter from the superficial portion of the skin to its deeper-seated layer, and hence to the growth of epipleural plates, which would become the costal plates of the carapace. The granulations on the shield of Trionyx, on such a view, indicate dermal bones like those of Sphargis—which were originally separate, but have become blended with the bony elements which were subsequently developed beneath them. The costal plates are said to be always distinct from the ribs in the young turtle when first hatched. They are certainly very small in the young of some of the Trionychidæ, in which, indeed, they remain throughout life but partly united with the endoskeleton. It is the impossibility of logically accounting for the development of the Chelonian carapace without the aid of this hypothesis that leads me to attach more than ordinary importance, in a classificational point of view, to the characters presented by Psephophorus, which are only otherwise paralleled by the small specimen which Müller figures from the Zeuglodont Limestone of North America, and by the living Sphargis.

The best-preserved vertebral fragment (Pl. XV. fig. 2), as already mentioned, is Chelonian in its characters. A few scattered plates occur intimately associated with the vertebræ. Altogether there are fragments of five vertebræ preserved. None shows the whole of either centrum or neural arch; nor do they collectively throw much light upon each other. It is difficult to affirm with certainty the region

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of the vertebral column to which they belong, though I am disposed to believe that they chiefly pertain to the later cervical or dorsal series, and there is a fragment which appears to be a portion of a rib. The best-preserved specimen rests on its side, partly imbedded, and fractured through its length. The centrum is about five and a half centimetres long, or but little longer than the later cervical vertebræ of Sphargis. It shows cancellous tissue along its fractured length; but in the processes this is covered by a dense outer layer. The base is concave in length, the constriction being greatest towards the anterior end. The anterior end is cupped concavely, is about two and a half centimetres deep, and has the articular cup vertical. The posterior articular end was a well-rounded ball, and considerably deeper than the anterior cup. The neural arch is, unfortunately, much less perfect than the centrum. Projecting anteriorly just above the neural canal is a small process; and above this is the right side of the neural arch, which reaches forward and upward in a wedge-shape. having a total length, from its posterior termination near the middle of the centrum, of about five centimetres, and gives no indication of facets of the zygapophyses, which could not have looked inward. Its total height from the base of the centrum, as preserved, is about six centimetres; the distance for which it extends anterior to the articular face is about two and a quarter centimetres. From the middle of the right side of the centrum, at about its junction with the neural arch, is given off a transverse process, which has a strong expanded base, is somewhat compressed, and directed outward and, possibly, upward. It is imperfectly preserved at the end. Imperfect as these indications are, they amply show that we have here to do with an animal which differs not only generically from Chelonians, but in characters in which all other genera agree.

Two other centrums are exposed so as to show their length. Both appear to be moderately concave at the expanded anterior end, and slightly convex at the narrower posterior end. These vertebræ are about five and a half centimetres long. One shows the hinder part of the centrum to be rounded from side to side (it probably had a descending process in front); the other shows a strong flattened transverse process, which is directed slightly forward, and expands a little anteriorly towards its free end. The fourth fragment indicates a smaller vertebra, apparently caudal, which has the prezygapophyses strong and short, and curved apparently forward and upward, with the facets looking inward. The points in which these vertebræ differ from those of all Chelonian reptiles are, the apparently massive character and great development and height of the neural arch, and the extraordinary transverse processes, which are both ankylosed to the centrum.

In Chelonians such processes are limited to the caudal region; but in no respect have we here the characteristics of caudal vertebræ, except in the small and imperfect specimen, in which the end of the centrum appears to be flattened. And I believe the evidence rather points to the vertebræ belonging to the later cervical or dorsal region.

It would appear that the absence of transverse processes in the Chelonian, while so characteristic of the crocodile in the dorsal region, may have come to be correlated with the mode of development of the carapace, and the consequent way in which muscular tension on the bones was changed; but when the carapace is free from the ribs, the condition of the dermal skeleton is not very different, as regards its position and relation to the endoskeleton, from what obtains among the Crocodilia; and although *Sphargis* does not develop transverse processes for the attachment of the ribs, it must be remembered that *Sphargis* is the only member known of a great division of the Chelonia which must have included many types of organization, and is probably as important morphologically as all the other Chelonia put together.

The anterior position, however, of the transverse process in one vertebra, just behind the anterior articulation, is altogether in harmony with the Chelonian plan. There is no indication that the ribs were attached by a double articulation to the transverse processes, as among Crocodiles; but then it may be remembered that this character is only found in the first six or seven dorsal vertebræ of the crocodilian skeleton; so that I am led to believe that the many points in common, both in soft and hard structures, which the Chelonian and Crocodilian orders possess, lead us here to look for a group which may have more nearly connected them than any form previously known. In the characters which can be compared, Psephophorus seems to me to differ more from existing Chelonians than they differ among themselves; and hence I believe it will prove to be the type of a new subordinal division, which, however, it is impossible at present to fully define in the absence of the more important osteological characters. The following classification gives in a condensed form the results to which this study of Psephophorus has led up.

The characters of the carapace indicate three primary divisions of the Chelonian order:—First, the

Aspidochelyidæ, comprising Turtles, Emydians, and Tortoises, in which the symmetrical bony carapace is covered with symmetrical horny scutes; secondly, the

Peltochelyide, including the Trionychide, in which the symmetrical bony carapace has a granular surface-structure, and is covered by an undivided dermic substance without scutes; and, thirdly, the

DERMATOCHELYIDÆ, represented by the Sphargidæ, in which the carapace is not developed, but is represented by a bony skeleton within the skin, resembling a tessellated pavement.

The remains are from Neudörfl, near the river March, which forms the boundary between Austria and Hungary. Von Hauer refers the sandstone there to the second or upper Mediterranean series of the Austrian Neogene. Fish-remains from this formation have been described by Count Münster in his 'Beitrage zur Petrefactenkunde;' and the deposit also yields Gasteropods, Bivalves, and Echini.

I would express my grateful thanks to Professor Suess for direct-

ing my attention to this remarkable specimen; to Director von Hauer, not only for facilities afforded me in studying the specimen, but for the beautiful photographs which accompany my paper; to Dr. Günther, of the British Museum, for the opportunity of demonstrating its affinities with *Sphargis* by studying the skeleton of that type; and to the Council of the Royal Society for assistance in investigating this type in a distant locality.

#### EXPLANATION OF PLATE XV.

#### (Figures half the natural size.)

- Fig. 1. Portion of dermal shield of *Psephophorus polygonus*, Von Meyer, showing part of an elevated longitudinal keel with polygonal plates on each side of it, which differ in form and size and mostly show a superficial radiated ornament. Beyond the point where the figure 1 is placed, the slab shows thin plates with a smooth surface, which may be marginal.
  - 2. Vertebra from the under side of the slab, probably cervical, fractured longitudinally and imbedded in the matrix. a. The anterior cup. b. The posterior ball. c. A fragment of the neural arch blended with the centrum. d. Transverse process of the right side, imperfect, but directed outward and upward.

# Discussion.

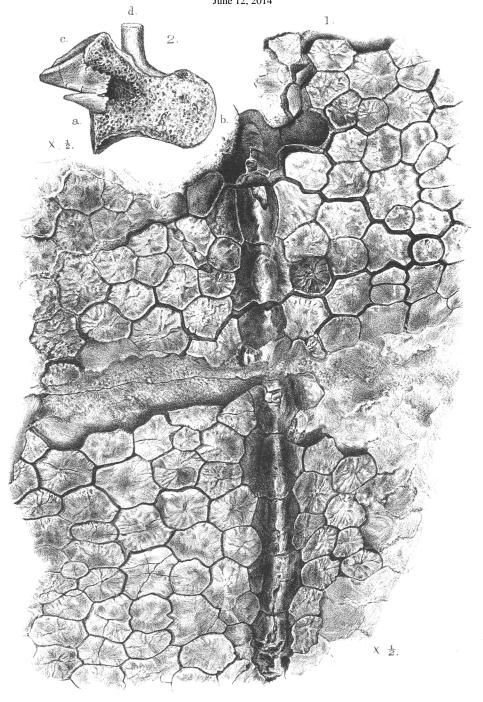
Mr. HULKE agreed with the view taken by Prof. Sceley of the specimen. As to the classification proposed, it would require careful consideration.

Prof. Duncan said the possible existence of something like ribs in the cervical region was interesting. The position of the shoulder-girdle in the Chelonians was always a difficulty. This, however, might have been gradually assumed during the early stages of life; but the presence of cervical ribs rendered the former existence of the scapula outside the dorsal ribs and in front very difficult of comprehension. The classification of the Chelonians was at present in great confusion. He thought there was much to be said for the simplicity of Prof. Seeley's classification.

The President asked whether these dorsal-shielded forms preceded the others in time or not.

Prof. Seeley said the specimen was Pliocene, i.e. the newer division of the Tertiary. It comes from Neudörfl, near the borders of Hungary and Austria, and is associated with Manatees and Chelonians of ordinary type. It has been compared by von Hauer with Psephoderma alpina from the Trias in the Munich Museum. This specimen he had seen, which he thought was not a Chelonian, though it might be an antecedent form or even a fish, like Ostracion. It was curious that the Mesozoic Chelonia belong, so far as known, to those with well-developed carapaces; but he thought that Sphargis was nevertheless the more primitive type.

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