JANUARY 6, 1858.

The Rev. Arthur W. Ingram, M.A., Hawington, and Timothy Curley, Esq., Hereford, were elected Fellows.

The following communications were read:—

1. *On* CEPHALASPIS *and* PTERASPIS. By THOMAS H. HUXLEY, F.R.S., F.G.S., Professor of Natural History, Government School of Mines.

[Plates XIV. XV.]

THE genus *Cephalaspis* (Agassiz) was originally established to include four species of Devonian fishes,—*C. Lyellii*, *C. rostratus*, *C. Lloydii*, and *C. Lewisii*; but the differences between the first and the last of these species were so great, that the founder of the genus himself suggested the probability of their future separation.

The two groups of species are said by Prof. Agassiz to be contrasted not only by their forms, but also by their minute structure. In regard to form, the cephalic disc of *Cephalaspis Lyellii* is stated to possess an almost semicircular anterior outline, while its postero-lateral angles are greatly prolonged backwards. The middle part of the occipital region, Prof. Agassiz adds, is cut off almost square (coupée presque carrément). As regards this last point, however, my own observations are at variance with his description.

Several specimens in the museum of this Society show that the middle of the occipital margin is not truncated, but is greatly produced backwards, the margins of the produced portion being concave. The same peculiarity is clearly distinguishable in the specimen of *C. Lyellii* now in the British Museum, and figured by M. Agassiz, pl. 1. *a*. 2: indeed the artist has faithfully depicted the real contour of the occipital margin in the figure cited. The well-known occipital spine is supported by this produced portion of the disk.

The discoid bodies, corresponding to all appearance with the cephalic disc of *C. Lyellii*, upon which alone the species *C. Lewisii* and *Lloydii* were established, differ widely from *C. Lyellii*, being oval in contour and not prolonged into postero-lateral cornua.

The structural differences observable in the disk of *C. Lyellii* on the one hand, and of *C. Lewisii* and *Lloydii* on the other, are thus stated by Prof. Agassiz:—

"In *C. Lyellii* the head is covered with a pavement of polygonal plates, altogether similar to that which covers the head of *Ostracion*. Each plate is convex in the centre, and is marked by radiating grooves ending at the margin in denticulations, by which the scales interlock. These scales appear to be osseous and to have their external surface enamelled. At the circumference of the disk they become confounded together, and the enamel presents wrinkles parallel to the edge." Elsewhere these plates are said to be "true scales juxtaposed."

In the 'Recherches,' M. Agassiz describes "fibrous bones of the

head" under the "scales," and he particularly mentions and figures the radiating direction of these "fibres;" but in the 'Monograph of the Old Red Sandstone Fishes' I find the following general remarks applied to the whole of the *Cephalaspidæ*:—

"It would appear from the condition of the specimens preserved, that all the cranial bones were only protecting plates, which covered a cartilaginous cranium similar to that of the Sturgeons; at least I have never been able to discover any cranial bones deprived of that characteristic granulation, which indicates that the plates were in direct relation with the integument. Therefore, I think there can be no doubt that all these granular plates rested by their inner and smooth surface on a cranial cartilage, such as is found in cartilaginous fishes and in the embryos of osseous fishes."—*Monog. Grès Rouge*, p. 3.

Nevertheless, in speaking of the genus *Cephalaspis*, a few pages further on, Prof. Agassiz states that he has nothing to add to his previous account of the genus; so that I am puzzled to know what view I ought to ascribe to him at present. We shall see by-and-by that the last-quoted is the only one warranted by the facts of the case.

The disk of *Cephalaspis Lloydii* is said to consist of an external striated enamel, of a middle layer "composed of granules similar to those of the bones of Chondropterygious fishes," and of an internal layer made up of superimposed lamellæ. Prof. Agassiz considers that this structure "singularly recalls that of the test of the *Crustacea*."

Notwithstanding these, partly real and partly imaginary, differences between his different species of *Cephalaspis*, Prof. Agassiz found in *Cephalaspis rostratus* (a species which I have had no opportunity of observing) a form and structure of so transitional a character that he included them all under the same genus.

That so close an affinity obtains between all the species of *Cephalaspis* has, however, been disputed latterly by M. Rudolph Kner, who in 1847 published a memoir in Haidinger's 'Naturwissenschaftliche Abhandlungen' for the purpose of proving that *C. Lloydii* and *C. Lewisii* are not piscine remains at all, but that they are the internal shells of a Cephalopod allied to *Sepia*, for which he proposed the name of *Pteraspis*.

M. Kner's reasoning is based upon his examination of the structure of a fossil (evidently closely allied to *C. Lloydii*) from the Silurian rocks of Gallicia. The form of this fossil, says M. Kner, is very similar to that of *C. Lloydii*; but it is larger, having a length of about four inches by a width of two. It consists of three layers. The innermost is shining, bluish-green, enamel-like, and presents four or five distinct lamellæ. This layer forms one continuous surface marked in the centre by a longitudinal depression, smaller at one end than at the other, and by obscure radiating lines. The upper part of the conical depression is covered with minute pores or depressions, which are visible in the deeper as well as in the more superficial layers, but become evanescent in its lower part.

Between the layer of enamel and the prismatic layer which

succeeds it, there lies a thin dull layer, in some places of a brownish colour. This is followed by an excessively delicate lamina of enamel which lies upon the prisms.

The layer of prisms is one line thick, and in section presents a number of more or less hexagonal disks. The enamel passes for a short distance between the prisms. Externally the prisms lie on a granular layer, to which the outermost very delicate "epidermic" lamina marked with parallel striæ succeeds.

M. Kner asserts (supporting his statement by the authority of Heckel) that in no known fish does any such epidermic or prismatic layer exist, and assuredly no such continuous internal enamel-layer, as in the fossil; and he then proceeds to compare the latter with the cuttle-bone.

M. Kner would hardly have published his views, had he subjected his sections to a more minute and careful microscopical examination. But, even apart from the characteristically piscine structure of these disks, very strong objections suggest themselves. In fact, to get at any sort of resemblance, M. Kner has to compare the outer layer of the fossil with the inner of the cuttle-bone, and *vice versâ*; and even the superficial resemblance in the striation of the two bodies is anything but close.

In Dunker and Von Meyer's 'Palæontographica' (B.iv. H.3. 1855) Roemer gives an account of a fossil, which he refers to the *Sepiadæ*, under the name of *Palæoteuthis*. Whether this body is or is not a Cephalopod, is a point I will not enter upon here; but Roemer in referring to Kner's Memoir, expresses the opinion that the *Pteraspides* are *Crustacea*.

Mr. Salter and myself described two new species of *Cephalaspidæ* allied to *C. Lloydii* (Ag.), in a note* appended to a paper read before this Society by Mr. Banks, in December 1855. Without acceding to Kner's views respecting the zoological affinities of such Cephalaspids, we adopted his name. The facts to be detailed in the present paper will, I believe, fully justify this step; and I shall hereafter speak of *C. Lloydii* and its allies under the generic name of *Pteraspis*.

Professor Pander† has recently described two Silurian species of *Cephalaspis* (*C. verrucosus* and *C. Schrenckii*) both from Rootsiküle. The former somewhat resembles *C. ornatus* (Egerton), having a highly ornamented and tuberculated upper surface. In the broad tuberculated antero-dorsal plates, separated from the head by a suture, it foreshadows *Auchenaspis*, Eg. *C. Schrenckii* has hexagonal ornamented plates upon its disk.

Professor Pander appears to think that the margins of the disk represent jaws, being led to this conclusion, apparently, by their production into short quadrate serrations, which he regards as teeth. Sections of these "jaws" and "teeth," examined microscopically, exhibited "a homogeneous base, in which clear and dark cells of the most various forms—rounded, elongated, and angular, with fine radiating branches, lay scattered, and were frequently disposed in concentric

* Quart. Journ. Geol. Soc. vol. xii. p. 100.

† Monographie der fossilen Fische des Silurischen Systems. 1856.

layers, where a tubercle rose above the general surface. Although they have not the same regular form as ordinary bone-lacunæ (such as occur in *Pterichthys* and *Coccosteus*), yet they can hardly be called by any other name. The very thin narrow teeth, closely united with the margins of the jaws, and coalescent with them, have a porous basis, and shining, broad, sharp upper and lateral edges. If both surfaces are carefully rubbed down, the basis is seen to consist for the most part of a homogeneous transparent mass, full of small dark cells, from which the very fine tubuli radiate in all directions, branch out, unite with the neighbouring ones, and by their many anastomoses form a most complex network. Towards the shining surface, as well as anteriorly and posteriorly—at least, certainly, towards one surface—the cells cease; the tubuli, winding irregularly in the base, take a straight course, and ascend apparently with an enlarged diameter, without convolutions and rarely branching, towards the external sharp angle." (*l. c.* p. 46.)

I am not aware of the existence of any other account of the minute structure of *Cephalaspis* and *Pteraspis* beyond these; and I will therefore now proceed to the immediate subject of this paper, which is, to describe that structure more fully and, I hope, more accurately than previous observers have done,—to compare *Pteraspis* and *Cephalaspis*, pointing out their real differences and resemblances,—and finally to consider the bearing of the structural facts upon the question of the zoological position of these ancient fishes.

Cephalaspis. (Pl. XIV.)

In but few of the specimens of *Cephalaspis Lyellii* which I have had the opportunity of observing, has the external surface of the cephalic shield been well exhibited, or preserved over any considerable surface. Where best shown it is somewhat uneven, and presents that curious apparent division into polygonal (usually hexagonal) areæ which has been described by Professor Agassiz. On examining the apparent sutures closely, however, they have not presented to my observation precisely the appearance figured in the pl. 1 *b*. fig. 2. of the 'Recherches.' They appear rather as if short, delicate, reddish-brown lines had been ruled across the line of junction of the sides of the hexagons, for some way towards the centre of each hexagon; and these lines are so gently convergent as to seem nearly parallel. Neither do I remember to have met with such strongly marked central elevations as those represented in the figure cited.

The inner surface of the disk has presented itself well preserved in more than one specimen. It never exhibits any trace of the apparent sutures of the outer surface (compare Agassiz's 'Recherches,' pl. 1 *b*. fig. 3, where this fact is clearly shown), but appears whitish, enamel-like, and very smooth where it is not furrowed by certain shallow and narrow depressions which radiate from the region of the orbits and occiput towards the margin, before reaching which they repeatedly subdivide and anastomose. I do not doubt that these are the impressions of the vessels which ramified under the disk during life. Sometimes, by the elevation of the substance of the disk into a

wall on each side of one of these depressions, the latter may become almost converted into a canal, so as to retain a portion of the matrix. This however is a rare occurrence.

When the concave inner surface of a disk and the convex cast of another specimen are compared, it is at once seen that the "radiating fibres" of the one correspond with the grooves and furrows of the other. The surface of the cast is remarkably darker than the surrounding matrix, and might not unreasonably at first be supposed to be of a different nature. When the inner surface of the disk is carefully examined with a magnifying glass, a number of reddish-brown minute dots appear scattered irregularly over its surface. It will be seen immediately that these are the internal openings of vascular canals which enter the substance of the disk.

If a vertical section of the cephalic shield of *Cephalaspis Lyellii* is carried through the orbits and perpendicularly to the axis of the body, it will be seen that the disk is exceedingly thin, hardly anywhere attaining $\frac{1}{40}$th of an inch in thickness, except at the margins and the spine, which are thicker. At the lateral margin the thin lamella is bent abruptly and almost horizontally inwards for about a quarter of an inch. It then suddenly thins so much as to be little more than a flexible membrane, which in the specimen now under description is pressed up into close proximity with the dorsal part of the shield (fig. 4).

The thinness and fragility of the disk of *Cephalaspis* render it difficult to obtain good sections for microscopical examination. The best I have seen (Pl. XIV. fig. 1.) is taken at an angle of about 45° to the longitudinal axis of the head, and intersects the occipital spine just beyond its origin. The section of the spine is in the best condition, and may be described first.

It is about $\frac{1}{40}$th of an inch thick in its thickest part, which corresponds with the median ridge of the spine, and presents three regions or layers, distinguishable from one another partly by their minute structure, and partly by the different mode of distribution of the vascular canals by which the tissue is permeated in each. The innermost or deep layer (*d*) is made up of superimposed lamellæ not more than $\frac{1}{2000}$th of an inch thick, each of which sometimes appeared to be still more finely laminated.

Interspersed among these, at greater or less distances, are numerous osseous lacunæ, whose long axes are parallel with the planes of the laminæ (fig. 3). The length of these lacunæ varies greatly, but may be taken at $\frac{1}{2000}$th of an inch on the average; some, however, are twice or three times this length, while others are much less. The transverse diameter is equally variable; but none that I measured exceeded $\frac{1}{3000}$th of an inch in this direction. The form of the lacunæ is very irregular in consequence of the long branching and anastomosing canaliculi which are given off not only from their ends but from their sides. In some parts the innermost layer appears almost black when viewed by transmitted light, in consequence of the quantity of air retained in the multitudinous lacunæ and canaliculi.

Large vascular canals, measuring from $\frac{1}{200}$th to $\frac{1}{400}$th of an inch

in diameter, whose inner openings correspond with the brown spots on the inner surface, traverse the innermost layer very obliquely, in their course towards the middle layer (fig. 1, *e*.) Their branches are few, and for the most part run parallel with the main trunk; but they give off a great multitude of minute canaliculi, which anastomose with those of the nearest lacunæ. Such of these canals as I have seen in section were oval, their long diameters being parallel with the planes of the lamellæ. In the specimen described the walls of the canals are lined with a reddish matter (like oxide of iron); and a similar substance obstructs many of the canaliculi.

The middle layer (*c*) is distinguished from the inner by the rarity or entire absence of the lacunæ, and by the indistinctness of the lamination as compared with that of the deep layer. Such striations of the nearly homogeneous base as seem to indicate lamination are, in the middle and inner parts of the middle layer, so disposed as to be nearly perpendicular to those of the deep layer, appearing to follow the course of the vascular canals.

The latter are continuous with the large vascular canals of the deep layer, but they are smaller and form a close network. Each of the large canals, on reaching the middle layer gives off several branches, which run nearly parallel with the surface (and therefore greatly inclined to the course of the great canals), and anastomose with those around, above, and below them. In this particular part of the disk, in fact, a large canal gives off as many as three tiers of these lateral branches, separated from one another by not much more than their own diameter, and all ramifying and anastomosing with one another. These lateral vascular canals have at first a diameter of about $\frac{1}{900}$th of an inch; but many of their anastomotic branches are much smaller.

Sooner or later all these branches appear to end in a close "superficial network," *b*, which lies in the boundary between the middle and the superficial layers. The latter or third layer of the disk (*a*) sometimes appears structureless, at others presents an obscure vertical striation, as if it were, like enamel, made up of minute fibres. The superficial vascular network sends into it a great number of minute short processes, which branch out abruptly at their ends, like a thorn-bush or a standard rose-tree, and end in excessively fine tubuli, like those of dentine. The tubuli appear empty and are much finer than the vascular processes, which are usually full of the dark red matter before referred to. Hence, when the section is viewed by transmitted light, the vascular canals are very distinct, and appear to end abruptly in the deep half of the superficial layer, while the tubuli have the aspect of fine, clear, sparsely ramified lines, by no means so readily visible. In some cases they seem to open on the surface. This substance, it will be observed, corresponds very closely in structure with the "cosmine" of Professor Williamson. I have been unable to find any trace of a "ganoin" layer external to it.

The superficial layer does not form a continuous whole, but is seen in the section to be divided into masses of various length by interspaces or gaps, which extend as far as the superficial vascular net-

work, the canals of which appear indeed to open into the bottom of the interspaces.

A structure in every essential respect similar to that just described is to be found in all other completely ossified parts of the cephalic shield, whether dorsal or ventral. In other regions of the dorsal part, however, the lamination of the inner layer is far more marked; and as a general rule the middle layer in these parts of the shield is thinner and contains fewer layers of lateral vascular ramuscules. The like is true of the inner part of the ventral region, in which only a single layer of close-set vascular canals makes its appearance (Pl. XIV. fig. 5). The flexible part of the ventral layer appears to be composed of the lamellar inner layer only; and the thick margins of the disk resemble the spine in structure.

The structure of the ventral layer, enclosed as it is on both sides by the matrix, is usually very well displayed in sections, and the better, on account of the dark reddish-brown hue which is acquired by the matrix, for some little distance from its line of contact with the animal substance. But neither in these nor in any other sections can any trace of bony substance be discovered beyond that which enters into the composition of the thin cephalic shield itself. I believe, therefore, that the so-called "fibrous bone" is nothing but the surface of the matrix impressed by the inner surface of the disk, and stained of a darker colour than elsewhere.

If flakes of the inner layer of the shield be detached and well soaked in hot Canada balsam, they become transparent, and their structure is well displayed in a superficial view (fig. 3). At their broken edges, the lamellæ of which they are composed are seen cropping out one beyond the other; but their most striking feature consists in the long lines of lacunæ which lie in parallel and equidistant series in each layer, so that under a low power it appears to be composed of broad flat fibres arranged side by side. The axes of the lacunæ of each layer are directed nearly at right angles to those of the layers above and below, so that under a low power the section appears cross-hatched by a series of dark lines. The great vascular canals are well seen traversing the successive lamellæ very obliquely.

In flakes of the disk similarly treated, but containing more of the middle and outer layers, fig. 2, it is obvious that the great canals divide into the branches of the middle layer which have already been seen in the vertical section, chiefly, if not only, along lines corresponding with the apparent sutures between the so-called "polygonal scales." The canals of the middle layer are very singularly arranged, passing from their origin, across these sutural lines and nearly parallel with one another, towards the centre of the adjacent "scales." The appearance of distinct "scales," and of the curious lines along their boundaries, is entirely due to this vascular distribution, the canals with their reddish lining showing very distinctly against the whitish general substance. In these views, again, the fissures by which the superficial layer is interrupted in the sectional view are seen to be nothing more than the expression of the valleys between the irregular and inconspicuous tubercles into which the superficial layer is raised (Pl. XIV. fig. 2).

Pteraspis. (Pl. XV.)

A fragmentary specimen of *Pteraspis Banksii* (belonging to Mr. Marston) affords by far the best view I have yet met with of the general structure of the shield of this genus. A cast of the outer surface is exhibited, and for the greater part of its extent the substance of the shield is absent; but in the centre a patch is left, exhibiting all the layers in their natural condition and relations (fig. 2).

The innermost layer (*d*) is composed of a reddish-white nacreous substance, exhibiting a distinct appearance of lamination at its free edges: its surface is somewhat uneven, and presents scattered rounded apertures about $\frac{1}{400}$th of an inch in diameter. The edges of these apertures were not unfrequently somewhat raised; and their cavities were full of a reddish matter. External to the innermost layer is the middle layer (*c*), composed of vertical plates of a laminated substance of similar appearance to the inner layer, and varying in thickness from $\frac{1}{200}$th of an inch downwards. These plates are so disposed as to form a network, enclosing polygonal (4–5–6-sided) cells of an average diameter of about $\frac{1}{50}$th of an inch.

The inner apertures of these cells are closed by the inner layer. Externally, they are also closed by a substance of the same nature as their walls, but perforated by a variable number of apertures somewhat smaller than those in the inner layer (*b*). The inner surface of this substance presents in many cases a striation more or less parallel to the sides of these apertures; and when it is broken away the thickness of the layer which closes the outer apertures of the cells is seen to be permeated by numerous small canals which give it a sort of worm-eaten or reticulated appearance. I will call this the "reticular layer." Lastly, outside the reticular layer is a white substance, very imperfectly visible in this specimen, in which no canals are visible, and which constitutes the external layer (*a*).

A view, the precise complement of that just described, is afforded by another of Mr. Marston's specimens of *Pt. Banksii*. This exhibits, for the most part, a cast of the internal surface; but towards the edge a considerable portion of the shield is left in a very perfect state of preservation, and with its external surface intact. The external layer is produced into strong ridges, the summits of which are turned outwards and their bases juxtaposed. The summits of the ridges are as much as $\frac{1}{160}$th to $\frac{1}{170}$th of an inch apart. In some cases they were sharply angular, in others more rounded. Where this layer was broken away, the reticular layer beneath it, and the polygonal cells of the next layer were well displayed. The bottoms of these cells were seen to be closed by the inner layer, and in this apertures were visible, corresponding with those on its inner surface. I have not examined transverse sections of this species; but the structure of *Pt. Lloydii* is so similar, that its transverse section perfectly elucidates the appearances presented by *P. Banksii*.

I have seen no specimen exhibiting the unaltered external surface of *Pt. Lloydii*; but its internal surface and its other layers, where the inner one is broken away, are well displayed in two specimens belong-

ing to the Geological Society. The inner layer is thin, whitish, and nacreous, and presents, scattered over its surface, apertures of a similar character and size to those shown by *Pt. Banksii*.

The next layer appears, at first, to be very different, inasmuch as it seems to be composed of irregular reddish prisms with white interspaces. The prisms have a diameter of $\frac{1}{80}$th of an inch, more or less.

The reticular layer is hardly distinguishable in this view; but when the apparently prismatic substance is broken away, either a thin filmy outer substance is visible, or a peculiar striation. A thin section of the shield of *Pt. Lloydii* (fig. 1), taken perpendicularly both to its plane and to its long axis, exhibits the following appearances when viewed with a low power by reflected light.

The total thickness of the section is about $\frac{1}{40}$th of an inch, and of this amount about $\frac{1}{110}$th of an inch is occupied by the inner layer, $\frac{1}{140}$th of an inch by the second layer, $\frac{1}{300}$th of an inch by the next, and $\frac{1}{200}$th by the outermost layer.

The outer layer (*a*) appears to consist of a series of papillary elevations which have a broad free end, and are attached by narrow bases, so that a triangular interspace with its apex outwards is left between every pair of elevations. The matrix filling these interspaces, and for some distance in the immediate vicinity of the outer surface, is much darker than elsewhere, and has a deep brown hue. The attached ends of the elevations pass into a whitish substance, which, under this power, looks similar to their own. It is traversed by many reddish canals, which send diverticula into the elevations (*b*); and hence this substance clearly represents the "reticular layer" of *Pt. Banksii*. At intervals of about $\frac{1}{70}$th to $\frac{1}{110}$th of an inch or thereabouts, thin septiform processes are given off from the reticular layer, and pass perpendicularly inwards to the inner layer; they thus subdivide the second layer into a series of irregularly quadrate spaces, corresponding with the prisms seen in the superficial view.

The inner layer is, like the rest, whitish, and is traversed parallel with its surface by four or five much whiter streaks, so that it appears to be composed of only a corresponding number of lamellæ; but on allowing the light to pass through the section, it is at once obvious that each of these apparent lamellæ is in reality made up of many of the primitive laminæ which constitute the inner layer, and that the bright and dull white streaks are due entirely to a difference of texture or composition in the successive groups of laminæ.

Under a high power the laminæ are seen to have a thickness of about $\frac{1}{4300}$th of an inch, and to run nearly parallel with, and closely applied to, one another. They present an indistinct vertical striation, but exhibit no canals nor lacunæ. The septa of the second layer are composed of similar laminæ, but less distinct, and curved in various directions, usually more or less parallel to the walls of the large cavities which they bound. A fragment of the inner layer (fig. 4), rendered transparent by Canada balsam, and viewed by transmitted light, shows that it contains no lacunæ; nor have I been able to detect any distinct structure in its laminæ, unless an obscure and very delicate striation, visible here and there, may be regarded as such.

A similar disposition of curved laminæ can be traced in the "reticular layer;" but in the elevations of the external layer, such laminæ are no longer distinctly visible, although here and there traces of them may be seen. Each elevation, in fact, nearly resembles the tooth or dermal defence of a placoid fish. It contains a central cavity, commonly filled with a dark red matter, which usually occupies the centre of the basal half of the elevation and then suddenly ends in a number of excessively minute branches, which pass towards the surface, ramifying as they go, and closely resembling the canals of dentine or cosmine. They appear to terminate on the surface, on which I have been unable to discover any trace of laminated structureless ganoin. The central canals of the elevations open internally into the network of vascular canals which lies in the reticular layer. These canals rarely exceed $\frac{1}{700}$th to $\frac{1}{800}$th of an inch in diameter, and they are rendered particularly obvious by the dark red granules with which their walls are dotted.

Internally they open directly into the interspaces of the septa which connect the reticular with the inner layer, and the granules are continued on to the walls of the septa, which are themselves occasionally traversed by short canals. The interspaces (*e*) are full of a more or less transparent inorganic matter, identical with that of the matrix. It follows, therefore, that the "bony prisms" or "granules" which have been described have no existence, these so-called prisms being nothing but the matrix which has filled up the cavities of the polygonal cells, visible in their natural empty condition in *Pt. Banksii*. Canals resembling those of the reticular layer, as I have said, traverse some of the septa and put their chambers in communication.

In the section under description, the inner layer is for the most part devoid of canals; but one (*f*) is exhibited very beautifully. It has in the middle a diameter of about $\frac{1}{350}$th of an inch, but is wider at both ends, and traverses the inner layer almost perpendicularly. The laminæ are bent outwards for a certain distance, where they impinge upon its walls.

The structure just described is that of the central part of the section. At one of its ends, near the margin of the disk, the arrangement of the vascular channels is more like that in *Cephalaspis*,—the reticular layer assuming a much greater development, and the areolar character of the sinuses of the second layer becoming greatly obscured.

On comparing together the appearance of a section with those presented by the internal and external views of *Pteraspis*, there can be no doubt that the elevations of the outer layer of the one are the sections of the ridges of the other; and it is remarkable that there should be so striking a difference in the form of these ridges in *Pt. Banksii* and *Pt. Lloydii*. The ridges seen in concave casts probably always correspond with the whole interspaces between the ridges of the outer layer in *Pt. Banksii*; but it is quite conceivable that in *Pt. Lloydii* the ridges, in consequence of their peculiar form, might sometimes be held by the matrix and sometimes not; so that at one time the ridges of the cast would be very narrow, corresponding only

with the intervals between the summits of the ridges of the disk, sometimes broad, and corresponding with the intervals between their bases.

Comparison of PTERASPIS *and* CEPHALASPIS.

If the exposition which has just been given of the structure of *Cephalaspis* and *Pteraspis* be correct, it follows that neither the resemblances nor the differences in the structure of these two genera have hitherto been rightly apprehended.

The sole important differences consist, 1st, in the absence of osseous lacunæ in *Pteraspis*—their presence in *Cephalaspis*; 2nd, in the different general character and arrangement of the vascular sinuses; 3rd, in the different mode of arrangement of the external layer. These differences appear to me to be in themselves fully sufficient to warrant a generic distinction, but not more; for they are not greater than may be found among closely allied genera.

It will be observed that the account of the structure of *Pteraspis* given by M. Kner coincides, so far as it goes, with mine; and the examination of one of his *Pteraspides* (of which Sir Philip Egerton, with his usual liberality, has permitted me to have a section made), though not so satisfactory as I could have wished, still leads me to entertain no doubt that his fossils are really *Pteraspides*, and closely allied to *Pteraspis Lloydii*.

In this specimen, however, the histological characters which have been described are almost all undistinguishable. All that remains of the *Pteraspis* is a yellowish substance, without any definite structure, which appears in the section to form loops broader at their free than at their attached ends, and to send in longer or shorter reticulated processes of a similar character into the interior of the matrix. The interspaces of the loops are filled up with crystalline masses of carbonate of lime (?).

The length of the loop-like processes is about $\frac{1}{210}$th of an inch, and the breadth of their wide end about the same; the width of their necks is not more than $\frac{1}{330}$th, or thereabouts.

Now these are, as nearly as may be, the average dimensions of the sections of the ridges of *Pteraspis*.

No one can, I think, hesitate in placing *Pteraspis* among Fishes. So far from its structure having "no parallel among Fishes," it has absolutely no parallel in any other division of the animal kingdom. I have never seen any Molluscan or Crustacean structure with which it could be for a moment confounded. Its relations with *Cephalaspis*, on the contrary, are very close. In each the shield is excessively thin, and composed of three or four layers:—1st, an "internal," composed of lamellæ parallel with the surface, and traversed more or less obliquely by vascular canals; 2nd, next to this is a "middle layer," containing the network of wide canals or areolæ; 3rd, the "reticular layer," described in *Cephalaspis* as part of No. 2, from which it is not distinctly marked in that genus; 4th, the "external layer," consisting of a cosmine-like substance raised into ridges or tubercles.

The "bony granules," or "prisms," supposed to be characteristic

of *Pteraspis*, the "polygonal ossicles" and the "fibrous bony layer," supposed to be peculiar features of *Cephalaspis*, have, as I have shown, no existence. Supposing that the shield of *Pteraspis*, like that of *Cephalaspis*, covered the animal's head (though there may be some ground for entertaining a doubt on this point), then it may be said that the presence of orbits in one, and their absence in the other, indicates a wide difference between the two genera. It must be remembered, however, that there is precisely the same difference between *Pterichthys* and *Coccosteus*, which are admitted by all to be closely allied.

Though I have had no opportunity of examining the Russian species, I believe I do not err in regarding what Pander describes as the teeth of *Cephalaspis* as merely an excessive development of the marginal tubercles of the outer layer. It does not appear to me that there is any evidence that the mouth was situated at the margin of the shield; on the contrary, the inward prolongation of the reflected ventral layer leads me to suspect that the under surface of the head of *Cephalaspis* resembled that of *Loricaria* or of *Acipenser*.

Zoological position of Cephalaspis *and* Pteraspis.

Leaving for the present Professor Pander's "Conodonts" out of view, *Cephalaspis* and *Pteraspis* are among the oldest, if they are not the very oldest, of known fishes; and it is therefore highly interesting to inquire into their position in the scale of ichthyic nature.

Palæontologists in general, following Agassiz, classify them as "Ganoids;" but it is to be feared that few persons who have not paid special attention to recent Ichthyology and to Comparative Anatomy have a clear conception of what is meant by the term "Ganoid."

The founder of the Order, allowing himself to attach an undue weight to mere secondary characters, included under the head of "Ganoidei" a heterogeneous assemblage of Fishes characterized by very few common characters, save their hard and shining scales, and the abdominal position of their ventral fins, but embracing the Siluroids, the Gymnodonts, and the Ostracionts, while the genus *Amia* was allowed to remain among the *Clupeidæ*.

If these are all Ganoids, and if such are the characters of the Order, then doubtless *Pteraspis* and *Cephalaspis* are Ganoids.

Since the publication of the admirable and philosophica researches of Johannes Müller, however, the term *Ganoidei* has been received in a very different sense by the great mass of naturalists. Müller showed that the great majority of the recent Fishes classed as Ganoid by Agassiz, viz. the Siluroids, the Gymnodonts, the Ostracionts, &c., were in no essential respect different from the *Teleostei*, or true bony fishes, while the true recent Ganoids formed a small but extremely remarkable assemblage, characterized by a structure in many respects intermediate between that of *Teleostei* and that of the *Elasmobranchii* (or what are commonly called cartilaginous fishes). Müller showed, furthermore, that the character of the surface and the histological texture of the scales are of little systematic value, and reduced the

diagnostic marks of a Ganoid, visible in the external skeleton, to two —the presence of "fulcra" and the articulation of the scales by gomphosis. The rest of the essential characters of the Ganoids are entirely derived from the soft parts—the brain, the heart, the branchiæ, and the air-bladder. A Ganoid is in fact distinguished from any other fish by the following peculiarities.

The optic nerves form a chiasma; the bulbus aortæ is rhythmically contractile, and provided with several series of valves; the branchiæ are free; there is an air-bladder connected by an open duct with the intestine; the ventral fins are abdominal. These essential characters are shared by only six genera of existing fishes—*Lepidosteus, Polypterus, Amia, Acipenser, Scapirhynchus,* and *Spatularia* —which are no less singular in their distribution than in their anatomy. All are essentially freshwater fishes; all are found in the northern hemisphere; three—*Lepidosteus, Amia,* and *Spatularia*—are exclusively North American; *Polypterus* is only known in the Nile, while *Acipenser* is common to Europe, Asia, and North America.

Now what evidence have we that either *Cephalaspis* or *Pteraspis* are in the proper sense Ganoids? There is nothing about their dermal covering peculiarly characteristic of Ganoids; and as to the rudimentary state of ossification of the vertebral column, there are Teleostean fishes (e. g. *Helmichthys*) quite as imperfect in this respect as any Ganoid.

Without doubt there is a singularly close resemblance, in the structure of the dermal plates, between *Cephalaspis* and *Megalichthys*— the last being very probably a true Ganoid; but the point of difference is noteworthy: *it is precisely the characteristic ganoin-layer which is absent in Cephalaspis.*

On the other hand, the arrangement of the hard tissues in *Pteraspis* reminds one almost as strongly of *Ostracion,* an undoubted Teleostean.

The existing fishes to which *Cephalaspis* presents the nearest resemblance in form, viz. *Loricaria* and *Callichthys,* are Siluroid Teleosteans, and not Ganoids; and, if we take the immediate allies of *Cephalaspis* and *Pteraspis,* viz. *Coccosteus* and *Pterichthys,* their analogies with Siluroids, such as *Bagrus* and *Doras,* are as strong as those with *Acipenser.*

A careful consideration of the facts, then, seems to me to prove only the necessity of suspending one's judgment. That *Cephalaspis* and *Pteraspis* are either Ganoids or Teleosteans appears certain; but to which of these orders they belong, there is no evidence to show.

If this conclusion is valid, it is clear that the ordinary assumption, that the earliest fishes belonged to low types of organization, falls to the ground, whatever may be the relative estimation in which the different orders of fishes are held.

But it is said that the great development of the dermal skeleton, combined with the rudimentary condition of the endo-skeleton, shows that these early fishes occupied a low place within their own group.

Mere *à-priori* argumentation on such questions as these would be a waste of time; but, happily, we can put the principle involved in

this reasoning to the test by direct observation. This principle clearly is, that the development of the exo- and endo-skeletons stands in some ratio to the general perfection of the organization of a fish.

Now the existing genera of Ganoids are, as I have said above, characterized by certain anatomical peculiarities common to all; and, in every essential of organization, no one can be said to be superior or inferior to another. The same kind of brain, heart, and respiratory organs are to be found in all; nevertheless, Nature seems to have amused herself with working out in this small group every possible variety and combination of endo-skeleton and exo-skeleton.

Lepidosteus has a greatly developed exo-skeleton, and the most Salamandroid vertebra known among fishes.

Polypterus has an equally well-developed exo-skeleton, and a well-ossified but piscine vertebral column.

Amia has scales as thin and flexible as those of a carp, with a well-ossified skeleton like that of an ordinary Teleostean fish.

Acipenser and *Scapirhynchus* have large enamelled dermal plates, constituting a well-developed exo-skeleton, with a cartilaginous vertebral column and persistent chorda dorsalis;

While, finally, *Spatularia*, with its mainly cartilaginous endo-skeleton, has a smooth skin, without dermal plates at all.

In the face of these plain anatomical facts, what is the value of the argument from the development or non-development of the skeleton to the grade of organization of a fish?

EXPLANATION OF THE PLATES.

PLATE XIV.

Cephalaspis.

Fig. 1. Vertical section of the shield of *Cephalaspis*, magnified 100 diameters. *a*. Outer layer. *b*. Reticular layer. *c*, *d*. Middle and innermost substance. *e*. Vascular canals. *f*. Matrix.

Fig. 2. Horizontal section of the same, viewed from the outer side, showing the peculiar arrangement of the vascular canals along the so-called "sutures," magnified 50 diameters.

Fig. 3. Thin scale of the inner substance showing the osseous lacunæ of two laminæ, magnified 200 diameters.

Fig. 4. Outline of a vertical section through the shield of *Cephalaspis*, showing its inflected margin (*a*) and inferior flexible wall (*b*), magnified 2 diameters.

Fig. 5. Section of the inferior wall at the point of transition of the ordinary substance of the shield (*a*) into the thin flexible under layer (*b*), magnified 100 diameters.

PLATE XV.

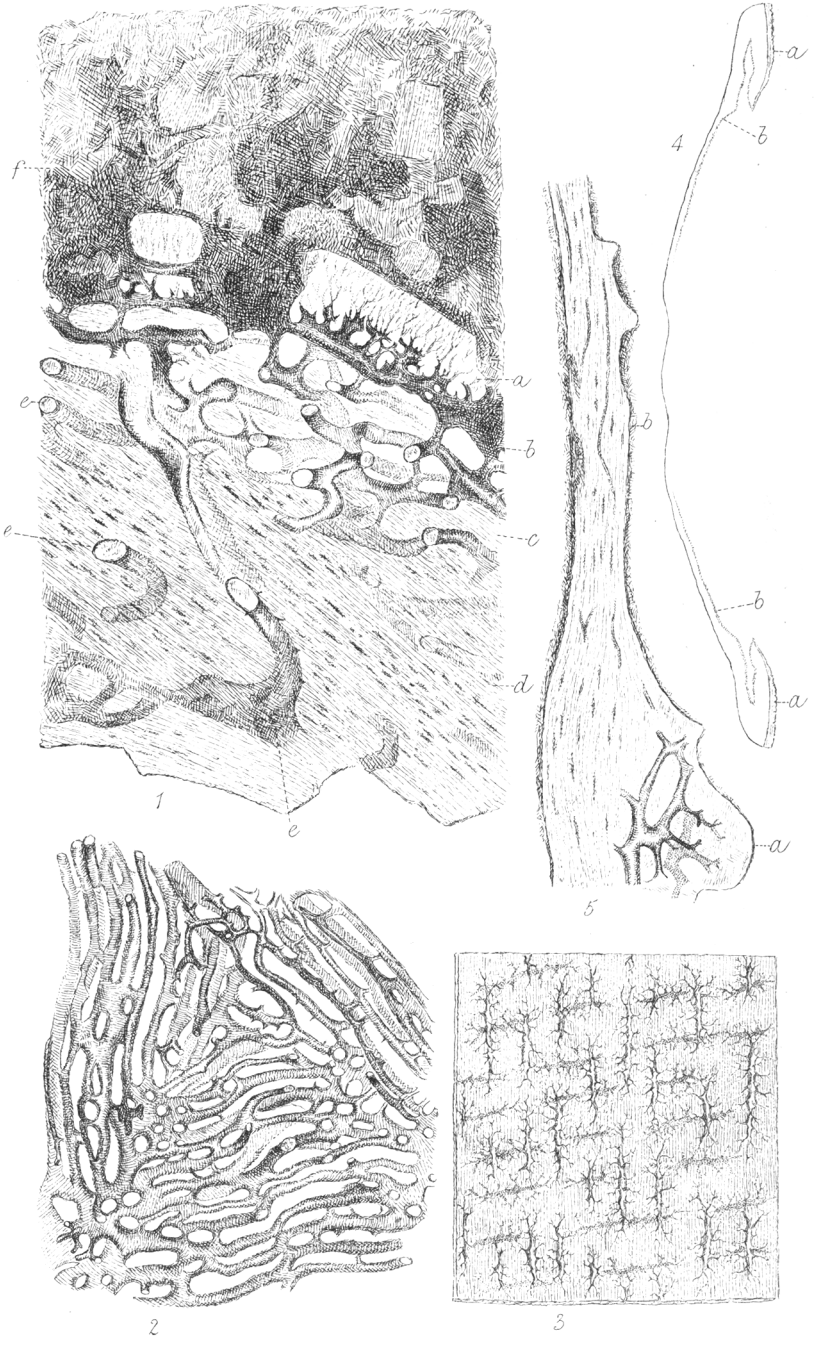
Pteraspis.

Fig. 1. Vertical section, magnified 100 diameters. *a*. "Enamel"-ridges forming the outer layer. *b*. Reticular layer. *c*, *d*. Middle and inner substance. *e*. Cavity filled with matrix—one of the supposed "ossicles." *f*. Vascular canal. *g*. Matrix.

Fig. 2. Portion of the shield of *Pteraspis Banksii*, viewed from within: letters as in fig. 1: magnified 10 diameters.

Fig. 3. Vertical section of inner layer of *Pteraspis*, showing the laminæ and one of the vascular canals, magnified 100 diameters.

Fig. 4. A flake of the inner layer viewed from within, magnified 25 diameters. *a*. Vascular canals.



CEPHALASPIS

Geo. West del et sc.

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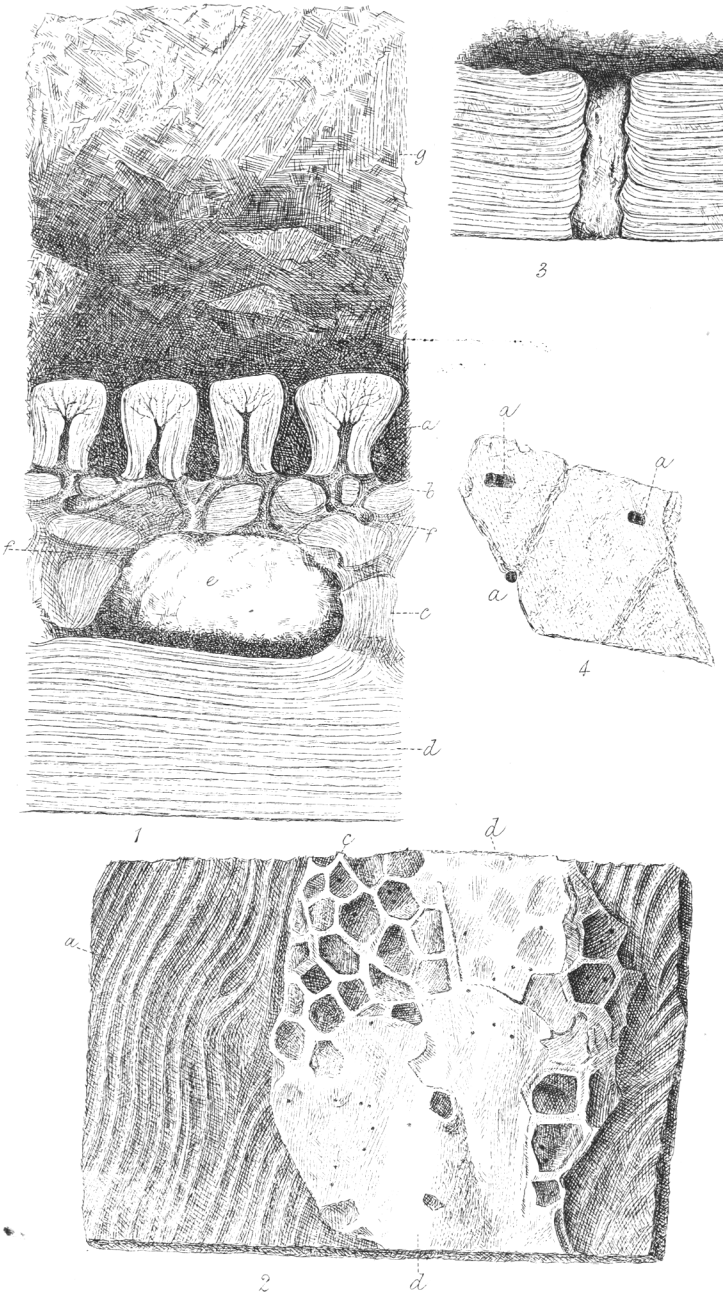

PTERASPIS