IX. *On the Structure of the Optic Lobes of the Cuttle-Fish.*
By J. Lockhart Clarke, *F.R.S., &c.*

The brain of the Cuttle-fish is enclosed in a cartilaginous case or skull, which is pierced by foramina for the passage of the nerves which it gives off. It consists of several ganglia closely aggregated and united around the upper end of the œsophagus, as shown in fig. 1, Plate X. *Above* the œsophagus, the foremost or pharyngeal ganglion (*a*), which is much the smallest, is bilobed, somewhat heart-shaped, and closely applied, at the central line, to the junction of that tube with the large globular and powerful pharynx (*b, b, b*). Behind this ganglion, and joined to it by two nervous cords, is a large bilobed ganglion (*c c*), which is broader above than below. It rests on a kind of disk or collar-like layer of nerve-substance, which forms the *roof* of the ring or short canal (*d*) through which the œsophagus is transmitted.

Below the œsophagus, and forming the *floor* of the canal (*d*) that transmits it, is a large and broad ganglion (*e*) which extends forward and is partially divided into an anterior and a posterior portion. The latter portion is connected along the sides of the œsophagus with the *supra*-œsophageal ganglia, by means of bands which complete the œsophageal ring. It gives off nerves to the branchiæ, to the viscera, to the mantle, &c. The *anterior* portion of the subœsophageal mass supplies nerves to the feet and tentacles, and a connecting branch to the pharyngeal ganglion (*a*).

From each side of these cephalic masses, and connected as much, apparently, with the ganglia beneath the œsophagus as with those above it, springs the optic peduncle (*f*) which unites them with the large optic ganglion (*g g*). On its upper surface is a small pyriform tubercle attached to it by a short pedicle or neck. Each optic lobe is as large as the rest of the cephalic ganglia on both sides taken together, and bears a striking resemblance in shape to the human kidney. Fig. 2 represents the left one freed from the nerves in which it is enclosed. It is very convex on its outer side, with a deep notch on its inner side where the peduncle is attached. Its upper surface also is a little concave, and its under surface is convex in a corresponding degree. Every-where it is covered and entirely concealed by a thick stratum of optic nerves disposed in flattened bands, which issue from all parts of its substance and proceed at once to the back of the eye (*h*), in a layer or kind of fan-shaped expansion (*i i*), which, like the optic lobe itself, is somewhat concave at its upper surface and a little convex below. As they enter the back of the eye the bands of the layer decussate; those proceeding form the *upper* surface (*i'*, *right side of figure*) sloping downward over the convex border

of the lobe, to the *under* side of the eye; while those which proceed from the *under* surface of the lobe, ascend in a similar way between the others to reach the *upper* side of the eye at i''. Moreover, at the upper surface, this layer of fibres is curiously folded over each end of the lobe, as shown at $g\,g$.

After removing one of the optic lobes with its peduncle and layer of nerves, if a thin longitudinal section be made through the middle line, and magnified about seven diameters, it presents the appearance delineated in fig. 3. Here it will be seen that the optic nerves at j proceed outward in almost straight lines, while those nearer the end and at the opposite side of the lobe (k, k, k) are successively more curved in their course to join the others for the formation of the fan-like expansion which is attached to the globe of the eye. The substance of the lobe consists of two distinct portions, which differ from each other considerably both in structure and general appearance. The outer portion (l, fig. 3) resembles a thin rind or shell, and is very delicate and very easily separated from the substance which it encloses. It may be said to consist of three concentric layers,—an external layer (m), an internal layer (n), and a broad pale layer between them, containing two thin and concentric layers (o) of a somewhat darker hue.

When this outer or cortical portion of the lobe is subjected to higher magnifying powers, it is found to possess a very beautiful and a very elaborate structure. Fig. 4, p represents a thin vertical section magnified 220 diameters. The first or outer layer (q) to which the optic nerves ($r\,r$) are attached, is composed of small round nuclei of nearly uniform size, together with a few nucleated cells of either an oval or a poly-angular shape. Near the surface the nuclei are comparatively few, but increase in number as they descend, and on approaching the border, which is very sharply defined, they are crowded closely together. Through this layer the nerves enter in separate bundles which diverge as they descend. The majority, at least, of their fibres are connected with the nuclei, and form with them a close network; but whether any of them run directly through to the next subjacent layer I have not determined satisfactorily.

The second layer (s) is composed entirely of fine nerve-fibres which run in two different directions at right angles to each other, the one being vertical, and the other horizontal or concentric with the layer. The vertical fibres are by far the more numerous. They issue from the under surface of the first layer as prolongations of the nerve-roots, but they have no fascicular arrangement, being uniformly disposed in parallel lines. Some of them, particularly at the lower part, abandon their original direction to become continuous with the horizontal fibres (t, t'), while the rest are prolonged across these fibres as far as the next layer (u). The horizontal fibres, for the most part, are collected into separate bands. The highest of these (t) is very slender, and below it are delicate fibres running in the same direction, but with wider intervals between them. The other two bands are at the lower end of the layer. They are much broader, and are separated only by a narrow interval. The lowest is in contact with the third or subjacent layer (u).

This third or internal layer (u, fig. 4, and n, fig. 3) of the cortical portion of the lobe

is composed of round and closely aggregated nuclei of nearly the same size as those of the first layer. The nuclei are united in a network of fibres, which at the upper border (*w*) are directly continuous with both the transverse and longitudinal fibres of the layer next above. At the lower border (*w'*) is a single row of nucleated cells, which send their processes upwards, inwards, and sideways.

But the cortical substance, consisting of these three layers, forms only a very small portion of the optic lobe, the chief bulk of which has a structure and appearance of quite another kind. From the nuclear network and nucleated cells of the third or inner layer (*u*, fig. 4) of the cortical portion of the lobe, a continuous series of fine nerve-fibres may be seen to issue at its lower border (*w*). At first these fibres are vertical, parallel, and arranged side by side in a nearly uniform series; and between them are scattered without regularity a number of round, oval and triangular nuclei like those of the cortical layer; but immediately after their exit the fibres begin to arrange themselves in bundles, which, as they descend, deviate from their former vertical direction, and decussate each other in a plexus or network (*x, x, x*); while the nuclei, in corresponding proportion, collect at first into small irregular groups (*y y*) between the bundles, and then into groups that are larger and more compact, within the meshes of the plexus (*y' y'*); they are not, however, completely isolated, but communicate with each other, to a greater or less extent, by means of lateral offsets. At first the meshes and the groups which they contain are more or less fusiform and disposed with their longer axes vertical, so as to constitute a system of communicating rays at right angles to the cortical layers (*y' y'*, figs. 4, 3, 5, & 6); but as they reach the centre of the lobe, where the bundles of the plexus are more divergent and decussate each other, in every direction, at greater angles, the groups contained in the meshes become more globular, more isolated, and at the same time larger; but still they communicate by lateral offsets like a number of stellate cells (figs. 3, 5, & 6). Fig. 5 represents a transverse section of the lobe along the line *a'*, fig. 2, and shows the globular and stellate form of the cell-groups in the centre, with their elongated form and radiate arrangement near the surface*. Fig. 6 represents another transverse section through the peduncle and its tubercle, along the line *b'*, fig. 2. Here the cell-groups in the centre are still more globular, and consequently, in section, many of them appear much larger than the elongated groups which are cut transversely in fig. 5.

Under a magnifying power of 60 diameters, thin sections made in different planes through the central parts of the lobe present the appearances delineated in fig. 7. Here the blank, communicating spaces, so well seen in fig. 5 between the central groups of cells, are occupied by the most intricate part of the plexus, where the bundles interlace in every possible direction. The fibres of each bundle are connected with the cells of different groups by means of their processes, which are turned to every side.

On examining the cell-groups under still higher powers, they were found to consist of round, oval, pyriform, and triangular nuclei, confusedly mingled with small and large

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* Fig. 5 should have been reversed from right to left by the engraver.

nucleated cells of every variety of shape, as represented in fig. 8, magnified 220 diameters.

From the plexus on the inner side of the lobe the bundles converge and unite to form the fibrous portion of the peduncle (z, figs. 3 & 6). In fig. 3, which represents a longitudinal section of the lobe, they are seen to decussate in a very striking manner; but in planes at right angles to it there is no appearance of decussation, as may be seen in fig. 6, which represents a transverse section through the middle of the lobe and peduncle in the direction of the line b', fig. 2. Moreover, it may be here observed that the fibres occupy only the inferior half of the peduncle, the superior half (z') consisting chiefly of masses of nuclei and *small* cells like those of the lobe, and giving attachment to the tubercle (z'') by a short and narrow pedicle or neck. This little body is pyriform, inclined somewhat outward, and composed of closely-aggregated nuclei connected with a multitude of fibres which converge to the neck and then spread through the cells of the peduncle.

Having thus concluded my description of the optic lobes and their peduncles, I will offer a few brief remarks on the general structure and connexions of the remaining cerebral centres, with the view of determining their homologies. The foremost or bilobed pharyngeal ganglion *in situ* is rendered quadrangular by the roots of the nerves which it gives off. In front it gives off from each angle a thick nerve-trunk (a, a), which soon divides into two branches. One of these is distributed on the outer side of the mouth to the powerful muscles which move the beak, while the other turns inward to the laminæ or turbinated folds of the palate. These folds are muscular, but have a strong resemblance to the nasal laminæ of fishes and other vertebrata, and are everywhere lined with mucous membrane and epithelium*. Between the large nerves given off from the angles of the ganglion, numerous smaller branches proceed directly forward to different parts of the mouth. Some of them may be traced to the muscular bands that descend to the base of the spiniferous tongue, which is situated at the bottom and in front of the turbinated palate. The ganglion itself has a composite structure. A longitudinal section, that is, a section behind-forward, is oval or fusiform. Examined under a sufficiently high power, it is found to consist of two kinds of tissue—(1) a central, oval, and whitish nucleus ($_1$, fig. 9) composed of the closest interlacement or network of the finest nerve-fibres, with some intervening granules; and (2) a surrounding grey layer of nucleated cells ($_2, _2$), in connexion with fibres proceeding from the central nucleus. Above, and especially below, the nucleus reaches nearly to the surface of the ganglion, so that at those parts the layer of nucleated cells is very thin; but in front ($_2$) and behind ($_{2'}$) it is much deeper. From the distribution of its nerves to the muscles of the mouth and tongue, and to the turbinated laminæ of the palate, this ganglion would seem to correspond to the centres of the fifth, the ninth or hypoglossal, and perhaps the olfactory and gustatory nerves of vertebrated animals.

The second and larger ganglion ($c\ c$, fig. 1), which is connected with the former by two

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* They communicate with the mouth by openings or fissures in the palate, and appear to be the olfactory organs.

nervous cords, has also a composite structure. Its superficial, smooth, and convex portion consists of two comparatively thin caps or shells, joined in the middle line, but separated in front by a notch (see fig. 10, *c c*). It is composed of a very close inter-lacement or network of the finest fibres, interspersed with fine granules, with nuclei, and with small cells of different shapes ; and in these respects bears a strong resemblance to the cerebral lobes of fishes. Beneath the convex caps is a large mass of an entirely different structure. This consists of a kind of plexus, or interlacement of coarser fibres in every direction, with intervening but irregular and coalescing groups of nucleated cells and nuclei. It has some resemblance to that of the central parts of the optic lobes, but is finer. At its base, where it overlays the canal for the œsophagus, it presents a somewhat diversified appearance, and projects in front (₃, fig. 10) and behind (fig. 1, ₃) in the form of a kind of collar, as already stated. Whether this central portion of the ganglion constitutes any part of the nervous apparatus for vision, or whether it should be considered as a cerebellum, is not easy to determine. It is certainly in connexion both in front and behind with the optic peduncles and lobes; but then so is the cere-bellum in vertebrate animals, especially in fishes; and it can scarcely be expected that a distinct cerebellum would be wanting in an animal whose cerebral development approaches so closely to that of fishes in which that organ is very large.

The posterior part of the subœsophageal mass, as already stated, gives off nerves which supply the branchiæ, some of the viscera, and the auditory apparatus, and may therefore be considered as homologous with the medulla oblongata ; while the anterior part, which supplies nerves to the feet and tentacles, may be regarded as the spinal cord, concentrated, like those organs, in the neighbourhood of the head.
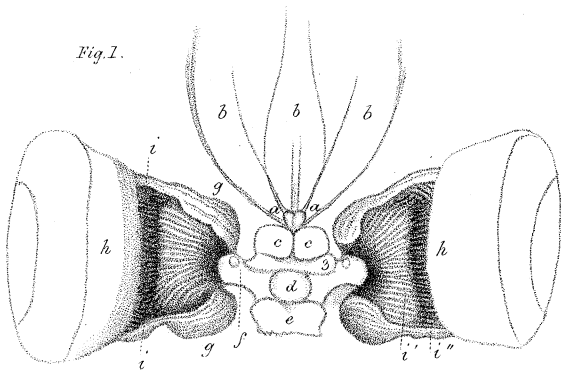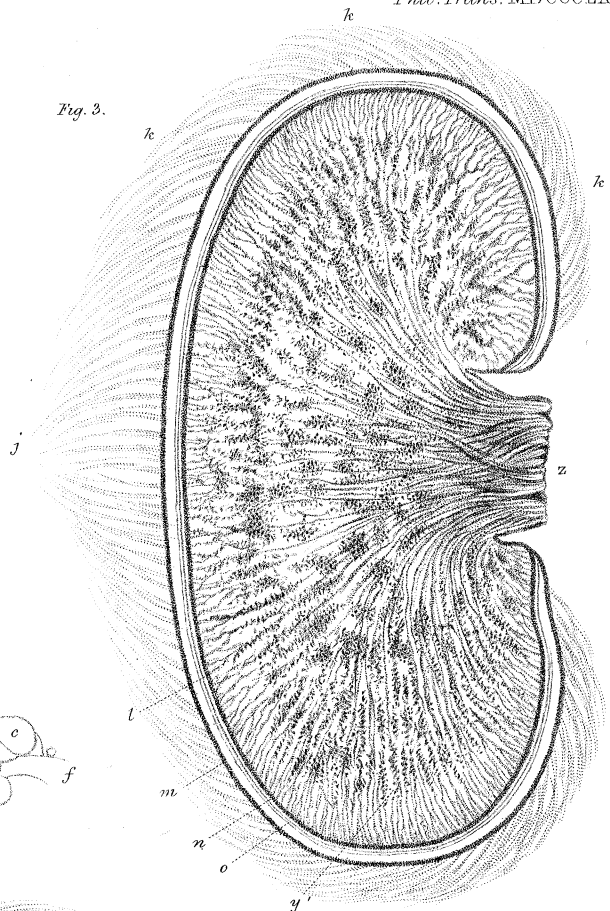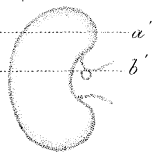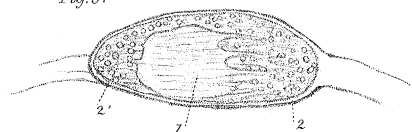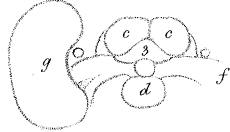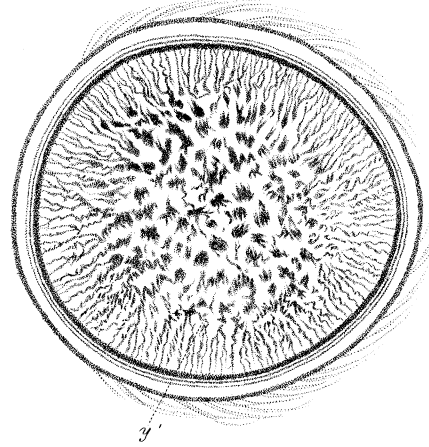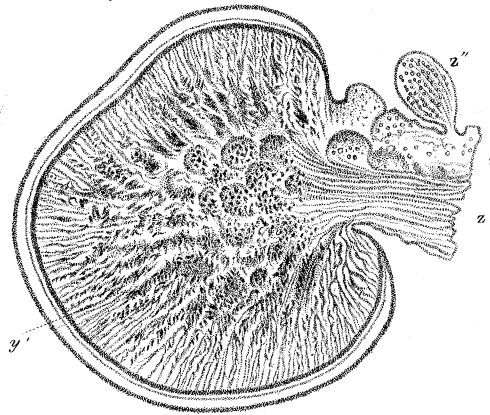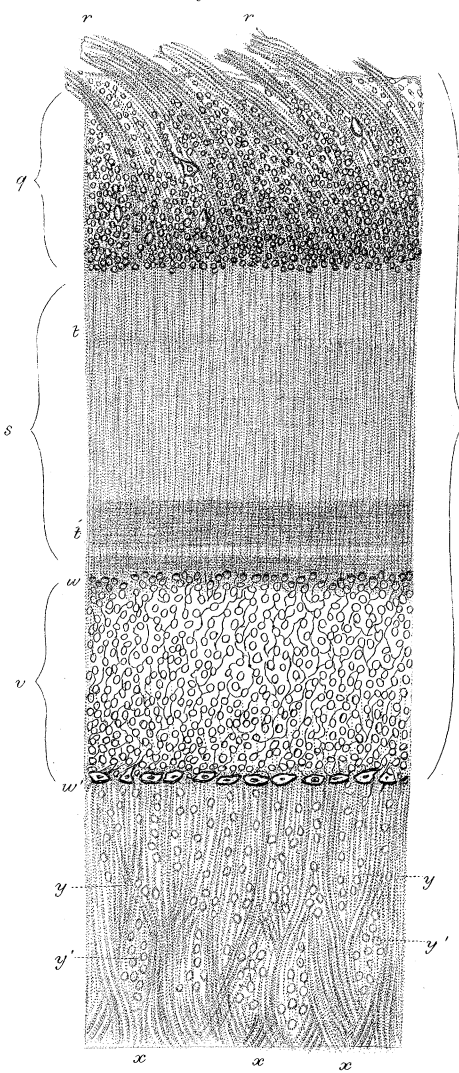
Fig. 1.

Fig. 2.

Fig. 9.

Fig. 3.

Fig. 4.

Fig. 10.

Fig. 5.

Fig. 6.

Fig. 7. × 60

Fig. 8. × 220

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