CHAPTER VIII

THE EYES OF PROTO-CHORDATES

THE Chordates constitute a phylum characterized by a dorsal tubular nerve-cord, a dorsal supporting axis (a notochord) and pharyngeal gill-slits ; the last two, however, may be temporary in duration. The Vertebrates constitute a sub-phylum within the Chordates which possesses as distinctive characters a head and skull, a brain with eyes, a vertebral column, and (generally) paired limbs. Stumbling on the

FIG. 232.—*BALANOGLOSSUS.*

The long tongue-like proboscis (Pr) resembles an acorn (βαλανος, an acorn ; γλῶσσα, a tongue).

border-line between Invertebrates and Vertebrates are three classes of animals (Proto-chordates) possessed of a rudimentary nerve-cord, a notochord and gill-clefts—the Hemichordates, the Tunicates, and the Lancelets. Apart from the pelagic Tunicates, these lowly creatures are either sessile or burrowing in habit.

The HEMICHORDATA are typified in *Balanoglossus*, a worm-like marine creature burrowing in the sand and mud of most seas (Fig. 232).

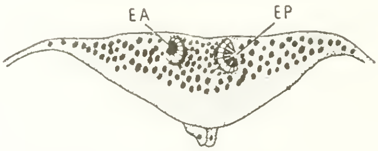

FIG. 233.—THE EYES IN THE TORNARIA LARVA OF *BALANOGLOSSUS.*

Antero-posterior section through the apical plate showing the anterior, EA, and posterior, EP, eyes (after Morgan).

The nervous system arises as a longitudinal groove of ectoderm which becomes tubular but gives no evidence of visual out-pouchings. In the larvæ (tornaria) of some species situated on the apical plate there are two eye-spots consisting of cup-shaped depressions of clear cells surrounded by pigment (Fig. 233), but in the adult there are no special sense organs (Spengel, 1893 ; Stiasny, 1914).

FIG. 234.—THE SEA-SQUIRT, *ASCIDIA*.

The adult covered by its tunic (*test*), the lower end attached to a rock, the upper end ending in an inhalant siphon (mouth), and on the morphological dorsal surface an exhalant siphon (atrial opening). Around both apertures there are sometimes pigment spots of unknown character. During life, the animal draws water in through the first and expels it from the second ; if irritated, water is forcibly expelled from both, hence the name "sea-squirt."

The TUNICATA (UROCHORDATA) are typified in the Ascidians or sea-squirts (Fig. 234). *Ascidia* in its free-swimming larval stage is a tadpole-like creature, about 1·0 mm. in length, possessing the chordate characteristics of a brain and a dorsal tubular nervous system, a notochord and gill-slits. At this stage it is provided with a single cerebral eye associated with a statocyst, but as the hermaphroditic adult settles to its sedentary plant-like life within its thick tunic of cellulose and attaches itself to rocks or weeds, the nervous system is reduced to a single ganglion above the pharynx and the eye disappears. In some of these forms the siphons respond to light by retraction. It is true that pigmented spots are found around the siphonal openings, which used to be considered " ocelli", but in *Ciona*, at any rate, they are in fact not light-sensitive (Millott, 1957).

The transient eye of the larval Ascidian is of unusual interest (Kowalevsky, 1871 ; von Kupffer, 1872 ; Froriep, 1906). It arises as an out-pouching of the cerebral vesicle which forms a single sensory organ consisting of a sac containing a statocyst and an extremely elementary eye on its dorso-posterior wall (Fig. 235). The retina is composed of a few sensory cells derived from the inner wall of the neural tube ; it is capped with pigment and above it lies a rudimentary cellular lens. It is interesting that the visual cells are morphologically inverted inasmuch as they face towards the cavity of the sensory vesicle while the intrinsic lens faces towards the brain as if it would be effective only for light traversing the transparent body of the animal.

In free-swimming Tunicates visual organs may persist ; thus in the asexual form of *Salpa* there is a single median horse-shoe-shaped ocellus and sometimes smaller accessory ocelli on the dorsal aspect of the animal closely associated with the single nerve ganglion.

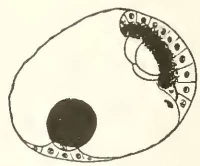

FIG. 235.—THE EYE OF THE ASCIDIAN TADPOLE

Diagram of the sensory vesicle with a unicellular otolith and an ocellus (above right) with retinal cells, pigment and 3 lens cells situated towards the cavity of the vesicle (Berrill, *The Origin of Vertebrates*, Oxon., 1955).

The LANCELETS (ACRANIA ; CEPHALOCHORDATA) are variously regarded as a pioneer off-shoot from the chordate stock or as a degenerate member of the phylum. They possess a dorsal tubular nerve-cord, a notochord and gill-slits but lack a differentiated brain or eyes. They are typified in the common lancelet, *Branchiostoma* (*Amphioxus*) *lanceolatum*, a small translucent fish-like marine creature about 2 in. in length the body of which is divided into 62 myotomes (Fig. 236). Although possessing no definitive eyes, the animal is strongly photo-negative and sensory organs occur, some possibly in the surface ectoderm and others deeply placed in relation to the neural tube which tend to enforce upon the animal its burrowing habit.

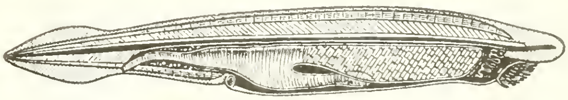

FIG. 236.—THE LANCELET, *AMPHIOXUS*.
The head end is towards the right, the tail end to the left (after Haeckel).

The superficial sensory organs are the large isolated CELLS OF JOSEPH (1904–28), associated with the surface epithelium on the dorsal aspect, which were claimed by this investigator to be light-sensitive (Fig. 237); this view, however, is by no means substantiated.

The neural photosensitive organs are of two types (Fig. 237). Towards the cephalic end of the animal a small median area of ependymal cells lining the central canal of the nerve-cord is specially differentiated to form an INFUNDIBULAR ORGAN which appears to be light-sensitive and is functionally allied to a

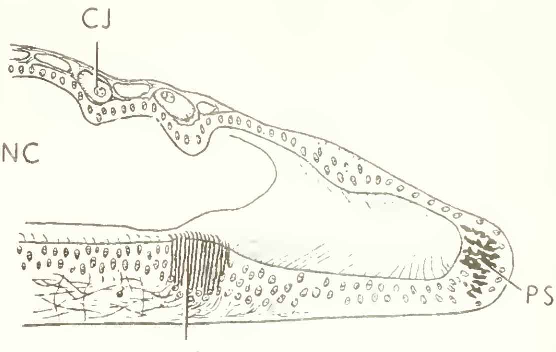

FIG. 237.—SAGITTAL SECTION OF THE ANTERIOR PORTION OF *AMPHIOXUS*.
CJ, cells of Joseph; Inf, infundibulum; NC, neural canal; PS, anterior pigment spot (after Boeke).

dark pigment-spot situated at the head end of the animal. The pigment-spot was originally described as an "eye-spot" by Johannes Müller in 1842, and used to be credited with light-sensitive properties and specific connections with the central nervous system [1]; it was indeed held to be the phylogenetic precursor of the vertebrate eye. Its specific innervation, however, was contested initially by Kohl (1890) and conclusively by Franz (1923), and a visual function excluded

[1] See the writings of W. Müller (1874), Langerhans (1876), Ayers (1890), Joseph (1904–28), Edinger (1906), Boeke (1908), Pietschmann (1929).

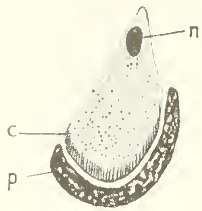

Fig. 238.—Visual Cell of *Amphioxus*.

n, nucleus ; c, striated margin ; p, pigment mantle.

by the experiments of Nagel (1896) and Hesse (1898) and more particularly by those of Parker (1908) and Crozier (1917). There would seem little doubt that it is not a vestigial eye but that its function is to endow the infundibular organ with directional ability by casting a shadow upon it when the animal or the light source moves, a primitive role we have already seen in the eye-spot of the Protozoon, *Euglena* [1] (Franz, 1912–34 ; Wollenhaupt, 1934).

A second photosensitive mechanism is seen in the ORGANS OF HESSE (1898), individual cells scattered on the ventral and lateral aspects of the nerve-cord towards its posterior end (Figs. 238 and 239). These are single large ganglion cells variously orientated, each provided with a brush-like ciliated margin and an issuing nerve-fibre, each capped by a crescent-shaped pigment cell to give it directional ability. The distribution and structure of these unique cells have been fully studied by a number of observers (Franz, 1923 ; Joseph, 1928 ; Kolmer, 1928 ; Wollenhaupt, 1934) and their photosensory function established by Parker (1908) and Crozier (1917).

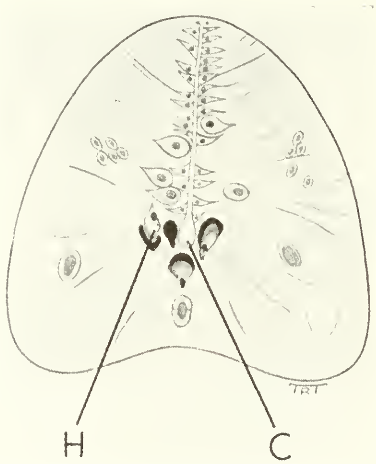

Fig. 239.—The Neural Visual Cells of *Amphioxus*.

Section through the spinal cord in the region of the 5th segment, showing the central canal, C, and the large visual cells of Hesse, H, with their associated pigment cells (after Hesse).

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[1] p. 126.

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