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Review

The frontal eyes of crustaceans

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Abstract

Frontal eyes of crustaceans (previously called nauplius eye and frontal organs) are usually simple eyes that send their axons to a medial brain centre in the anterior margin of the protocerebrum. Investigations of a large number of recent species within all major groups of the Crustacea have disclosed four kinds of frontal eyes correlated with taxonomic groups and named after them as the malacostracan, ostracod-maxillopodan, anostracan, and phyllopodan frontal eyes. The different kinds of eyes have been established using the homology concept coined by Owen [Owen, R., 1843. Lectures on the comparative anatomy and physiology of the invertebrate animals. Longman, Brown, Green, Longmans, London] and the criteria for homology recommended by Remane [Remane, A., 1956. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. 2nd ed. Akademische Verlagsgesellschaft, Geest und Portig, Leipzig]. Common descent is not used as a homology criterion. Frontal eyes bear no resemblance to compound eyes and in the absence of compound eyes, as in the ostracod-maxillopodan group, frontal eyes develop into complicated mirror, lens-mirror, and scanning eyes. Developmental studies demonstrate widely different ways to produce frontal eyes in phyllopods and malacostracans. As a result of the studies of recent frontal eyes in crustaceans, it is concluded by extrapolation that in crustacean ancestors four non-homologous frontal eye types evolved that have remained functional in spite of concurrent compound eyes.

Keywords: Frontal eyes; Crustacea

1. Introduction

Frontal organs innervated from the medial protocerebral portion of the crustacean brain were hot stuff in carcinology during end of 19th and first half of the 20th centuries. Nowadays they are cold. The reason for bringing them up again is to review those so-called frontal organs that are eyes. Further the diversity of frontal eyes in crustaceans is much neglected in phylogenetic discussions and they deserve a more careful consideration. Their role in photoreception has never been approached seriously and it is an interesting issue that could benefit from more recent knowledge available about frontal eye morphology. This is especially interesting regarding the so-called extraretinular photoreception involved in perception of solar day information (Page, 1982).

From the first report of frontal eyes their history covers more than 200 years and numerous scientific articles. Reviews of the older literature are found in Elofsson (1963, 1965, 1966a). Developing an understanding of frontal eyes has been studded with obstacles. Some frontal organs were in fact eyes, whereas others were part of a complex of organs connected with the protocerebrum, shown nowadays to be non-visual sensory organs. Still other structures interpreted as frontal organs were other unrelated kinds of cells.

The rich literature on the subject is mainly derived from light microscopy and thus suffers from the limited resolution of details. Many discussions around what is known as microvilli forming rhabdoms, are outdated. The investigations also centred around few species to begin with, and the phylogenetic speculations were far-reaching. Even though there exists more recent contrary knowledge, earlier speculations have not been revised.

The term frontal eyes, which is preferred here, relates to eyes, which are not compound eyes, and which in crustaceans

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are innervated from a specific centre medially in the dorsal portion of the protocerebrum. Often three eyes appear joined together in an eye having two lateral cups and one ventral cup, formed by pigment cells, and containing sensory cells. This is the naupliar eye in older terminology or nauplius eye *sensu stricto*. These three eyes will be referred to below as the three-partite eye when joined and when separated as the lateral frontal eyes and the unpaired ventral frontal eye.

In addition to these eyes, more frontal eyes can exist, and they occur in different combinations. They are termed in relation to the three-partite eye. They can be dorsal, ventral, and caudal, paired or unpaired. The terms are neutral and do not imply common decent even if they happen to be e.g., paired ventral in two of the groups mentioned below. Most of these eyes have been termed frontal organs in the past. Since the term nauplius eye does not encompass all small frontal eyes, the new term frontal eyes is suggested here.

A study of a large number of frontal eyes of recent crustaceans has revealed four morphological patterns attributable to taxonomical entities; the malacostracan, ostracod-maxillopod, anostracan, and phyllopod, which will be presented below.

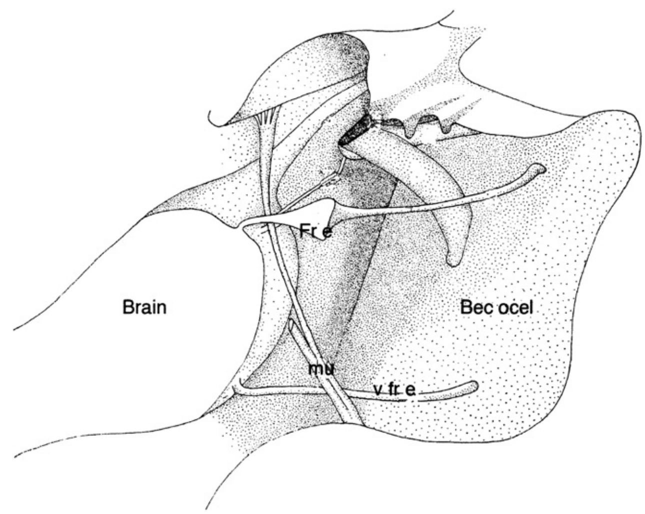

Fig. 1. *Pandalus borealis*. Drawing illustrating bec ocellaire (bec ocel) with frontal eyes in an animal cut midsagittally. Anterior to the right. The left portion of the three-partite frontal eye combined with the paired dorsal frontal eyes (fr e) connects to the top of the brain and to the epidermis of the bec ocellaire. The three nerves from the combined frontal eyes (the median and the left seen here) are separated by the musculi oculi basalis distalis (mu). The paired ventral frontal eyes (v fr e) run inside the cell body layer of the brain for a distance and then turn anteriorly ending in the ventral portion of the bec ocellaire (the left seen here). Reprinted with modifications from Elofsson (1963) with kind permission of Taylor and Francis.

2. Malacostracan frontal eyes

2.1. Morphology

In recent Malacostracan crustaceans there are maximally seven frontal eyes. Usually all seven do not reach the fully developed stage as organized eyes, and they are present in varying number in the different taxa of malacostracans (see below). Three of the eyes are united in the three-partite eye, mentioned above, housing only a few sensory cells. In addition, there are paired dorsal and paired ventral frontal eyes. They usually contain many sensory cells. Where the dorsal frontal eyes appear as an eye and are united with the lateral eyes of the three-partite eye, the whole structure has been referred to as the nauplius eye *sensu lato*.

Characteristic features of the malacostracan frontal eyes are, besides their innervation, the everse sensory cells where the frontal eyes are well developed. Rhabdoms are formed only on adjoining sides of the sensory cells, which is the case also when the eyes are reduced.

The most developed frontal eyes in malacostracans are found in decapods. They are especially well developed in the common prawn, *Pandalus borealis* (Elofsson, 1963).

Frontal eyes are found anterior to the dorsal margin of the brain, which in this species bends upwards. They are housed in a stem-like anterior portion of the body, the bec ocellaire, below the rostrum and present in many malacostracans (Fig. 1).

The dorsal frontal eyes of *P. borealis* are well developed containing 30 sensory cells in a small retina (Fig. 2A,B). They are intimately connected with the three-partite frontal eye, in which each cup contains three cells (Fig. 2A,C). All these sensory cells unite in groups of three forming a long rhabdom on adjoining sides. From the dorsal lateral eyes a tube of connective tissue continues to the epidermis of the bec ocellaire. From the combined eye one medial nerve containing the axons from the three frontal eyes in the three-partite eye proceeds to the brain. The axons from the sensory cells in the dorsal frontal eyes unite in two lateral bundles that run separated on each side of the former. There are thus three nerves from the combined eye to the brain. The pigment cells of the dorsal and three-partite frontal eyes form cups in which the sensory cells are housed. The axons pierce the pigment on their way to the brain.

The ventral frontal eyes consist of a paired strand of tissue that follows the ventral (or frontal) surface of the brain from the medial frontal eye centre until they turn anteriorly and end at the epidermis in the ventral portion of the bec ocellaire (Fig. 1). These are reduced eyes and the sensory cells appear in pairs with a mill-stone-like rhabdom in between.

The medial frontal eye neuropil is a large well-defined structure and covers a large portion of the dorsal protocerebrum. It is dorsal and anterior in relation to the protocerebral bridge. Differentiation within the neuropil is associated with large frontal eyes exemplified in *P. borealis* by a specific area for the ventral frontal eyes.

The best-developed frontal eyes in adults thus consist of five obvious eyes, the paired dorsal and three-partite eyes, and two reduced eyes, the ventral frontal eyes. A similar situation in decapods is found in the families Amphionellidae, Hoplophoridae, Pandalidae, Hippolytidae, Palaemonidae, and Processidae of the infraorder Caridea. In other representatives of decapods reductions have taken place (in all, 54 decapod species were investigated; Elofsson, 1963). A first step of reduction is smaller sensory cells. Fewer pigment cells can be