ARTHROPOD
STRUCTURE &
DEVELOPMENT

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.
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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.

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
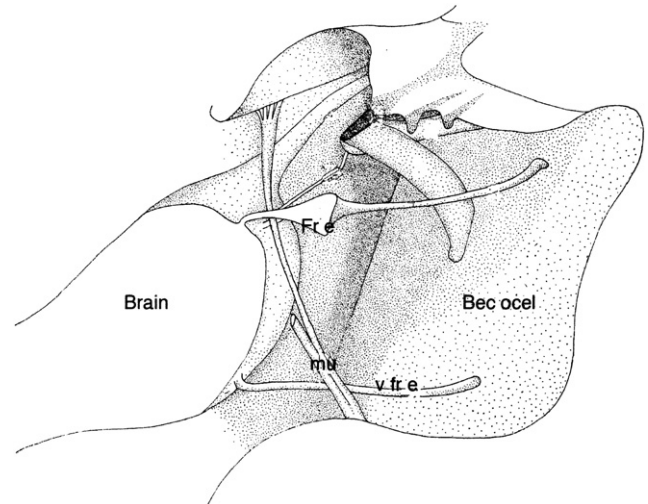

Fig. 1. *Pandalus borealis*. Drawing illustrating bec ocellaire (bec ocel) with frontal eyes in an animal cut midsagittally. Anterior to the right. The left portion of the three-partite frontal eye combined with the paired dorsal frontal eyes (fr e) connects to the top of the brain and to the epidermis 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.

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
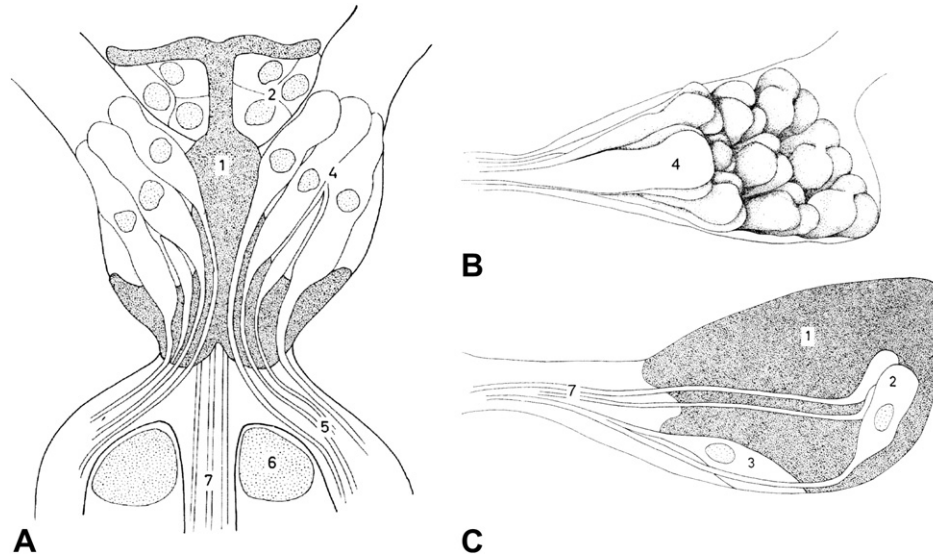
Fig. 2. *Pandalus borealis*. Detailed drawings of the combined three-partite and paired dorsal frontal eyes. (A) Horizontal section through the eye (anterior to the top of figure). (B) Sagittal view of the retina-like arrangement of the sensory cells in one of the paired dorsal frontal eyes. (C). Sagittal view of the three-partite eye with the paired dorsal frontal eyes removed. 1, pigment lamella; 2, the lateral eye and 3, the ventral eye of the three-partite eye; 4, the paired dorsal frontal eye; 5, the nerve from the paired dorsal frontal eye to the brain; 6, m. oculi basalis distalis; 7, The median nerve from the three-partite eye. Anterior to the right in B and C. Reprinted with modifications from Elofsson (1963) with kind permission of Taylor and Francis.

the next. A general feature of reduced frontal eyes is a stepwise withdrawal of the eyes into the brain, together with a reduction of the sensory cells.

Some of the eyes can be entirely lacking. Brachyurans lack frontal eyes with a few exceptions where reduced eyes can appear (Elofsson, 1963). When reduced eyes exist, more or less withdrawn towards the brain, the dorsal and three-partite frontal eyes have rhabdoms, or remains of rhabdoms, formed by three sensory cells, thereby clearly separated from the ventral frontal eyes where two sensory cells form the rhabdom. The three nerves from the combined eye (three-partite and dorsal frontal eyes) do coalesce during reduction and can be difficult to distinguish as three nerves. Paterson (1970) gives an example of reduction that confirms the reduction seen in reptantians. The phyllosoma larvae and juveniles of three palinurid species have well developed frontal eyes that degenerate in the adult but are still found outside the brain.

Elofsson (1965) investigated the frontal eyes of 115 species of malacostracans, other than decapods. Wherever frontal eyes were found they mimicked the morphology of those of decapods. An interesting coherence with regard to the presence of frontal eyes was seen in the species of the different subtaxa.

Stomatopods have three-partite, paired dorsal and ventral frontal eyes (Fig. 3). The combined eye, consisting of the paired dorsal frontal and the three-partite eyes, has fused nerves leading to the brain. Compared to the well-developed decapod eyes, those of stomatopods are more reduced. Slight variations can occur in that one species lacks the rhabdoms of the reduced ventral eyes, or that the ventral frontal eyes are absent.

Euphausids have the three-partite frontal eye and the reduced paired ventral frontal eyes. In cases like this, when the dorsal frontal eyes are missing, the tubular connections of the three cups of the three-partite eye with the epidermis

is very obvious. Each cup of the three-partite eye houses three sensory cells.

Anaspidaceans have three-partite frontal eyes and presumably reduced paired dorsal frontal eyes. The few species investigated allowed no firm conclusion.
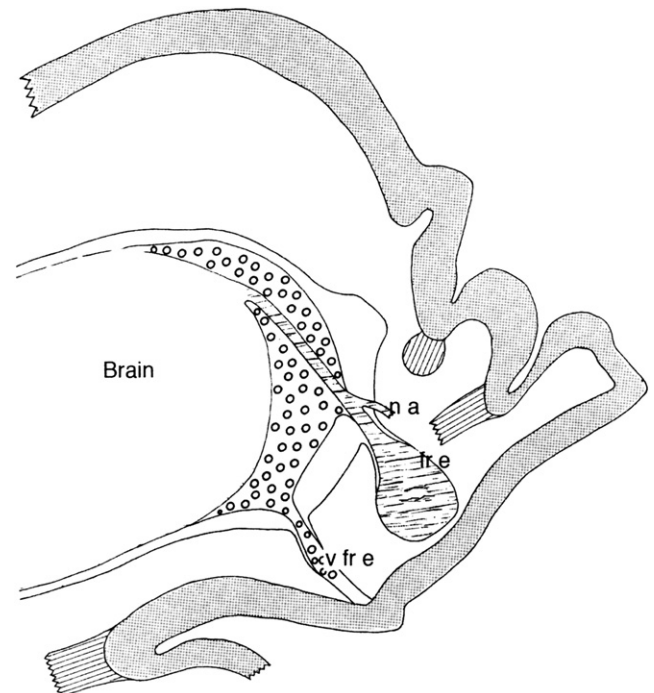

Fig. 3. *Squilla armata*. Drawing of a sagittal section through the bec ocellaire and the anterior portion of the brain. The combined three-partite and paired dorsal frontal eyes are labelled ''fr e''. Nervus apicalis (n a) to the muscles follows the eye nerve for a distance before it meets the muscles. The paired ventral frontal eyes are labelled ''v fr e''. Anterior to the right. Reprinted with modifications from Elofsson (1965) with kind permission of Taylor and Francis.
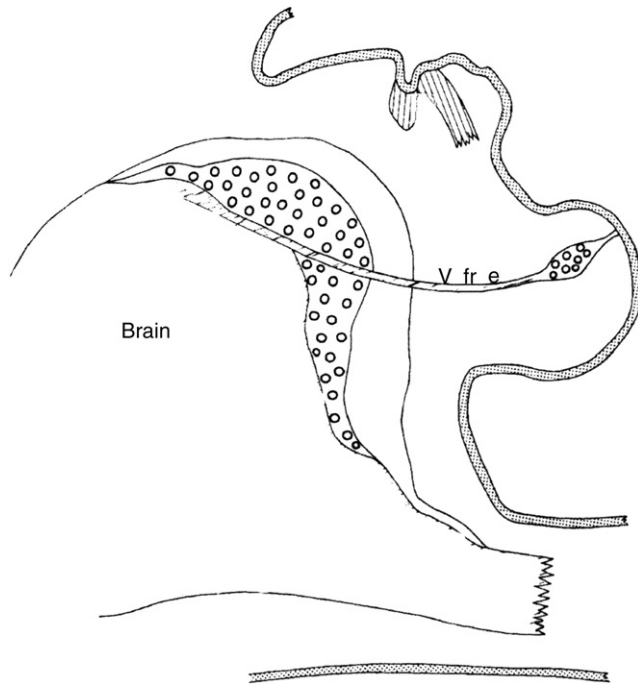
Fig. 4. *Boreomysis arctica.* Drawing of a sagittal section through the head. The reduced paired ventral frontal eyes (v fr e) end in the bec ocellaire. Anterior to the right. Reprinted with modifications from Elofsson (1965) with kind permission of Taylor and Francis.

The 11 investigated species of mysidaceans all point to the presence of reduced paired ventral frontal eyes and no others (Fig. 4). In one of the *Eucopia* species the reduced ventral frontal eyes are enormously exaggerated, as are the reduced dorsal frontal eyes of the decapod species *Processa edulis* and *Sergestes kröyeri.*

Martin (1971) first discovered reduced frontal eyes in isopods. Medially inside the protocerebral cell layer in *Porcellio dilatatus,* three groups, two latero-dorsal and one ventral, containing two sensory cells each, are found. They form microvilli on their adjoining sides. Martin et al. (1990) found the same condition in the phreatoicid *Paramphisopus palustris* a freshwater Gondwana relic. Martin (1976a,b) showed reduced frontal eyes inside the cell layer of the brain to be present in 32 out of 35 isopod species in six suborders. The number of reduced frontal eyes varies between five and two. Usually two, sometimes three sensory cells were present in the eyes. Although the reduced eyes allow little speculation as to the relationship with the frontal eyes of other malacostracans they stay within the presumed maximal number of seven. It also indicates that there is no such constancy of number and kind of frontal organs as in other malacostracans.

No frontal eyes, so far, have been found in amphipods, cumaceans, tanaidaceans, and leptostracans.

2.2. Development

Elofsson (1966b) investigated the development of the frontal eyes in malacostracans. In most malacostracans, the entire development of eyes takes place in the egg, and studies of early development can be difficult. Usually the larvae hatch in a fairly advanced stage with both compound and, when present, frontal eyes. Penaeid shrimps, however, hatch as nauplii and go through a series of naupliar stages where the eye development can be followed. The peneid shrimp *Penaeus duorarum* (Dobkin, 1961) has five naupliar, three protozoeal, and three mysis stages until they reach the first postlarval stage. In the first naupliar stage the anlage of the eyes is a "U"-shaped structure anterior to the brain anlage. The legs of the "U" give rise to the compound eyes whereas the bend of the "U" gives rise to the frontal eyes. The anlage is a neuroectoderm and its cells differ from others by being large, extending into the head, and having a large nucleus. At this stage the anlage of each compound eye is undifferentiated, as is also that of the paired dorsal and ventral frontal eyes. The three-partite eye, however, is formed with one ventral and two lateral cups in one pigment cell. There are two sensory cells in each cup, but no rhabdom.

In the second nauplius, the anlagen of the dorsal and ventral eyes start to develop. They separate from the three-partite eye and project inwards. The anlagen of the compound eyes also begin to change.

In the third nauplius, the three-partite eye has two pigment cells, and there are two to three sensory cells in the cups. The dorsal frontal eye has made contact with the brain anlage (as have also the compound eyes) and has lively mitotic activity. The paired ventral frontal eye is still largely in the epidermis but with a weak connection with the "brain".

No large difference is seen in the fourth nauplius.

In the fifth nauplius a clear demarcation is seen between the three-partite eyes and the anlagen of the compound eyes. There are still no rhabdoms. The paired dorsal frontal eyes are retained inside the cell layer of the brain, but the ventral frontal eyes are connected with the epidermis.

The first protozoea displays a fully developed three-partite eye. It is close to the epidermis and has well-developed connections with it. Rhabdoms begin to appear. There are no large changes in the dorsal and ventral frontal eyes.

The major step in the second protozoea is that the compound eyes become stalked and have pigment and rhabdoms. No changes occur in the frontal eyes.

From the third protozoea and onwards, small changes occur in the frontal eyes. The three-partite eye is retracted towards the brain. In the first postlarva traces of rhabdoms in the dorsal frontal eyes are seen.

An example of a malacostracan that hatches at a more advanced state is *Caridion gordoni* (Elofsson, 1966b). The larvae have an egg-nauplius and hatch as zoea. Already in the second stage, the three-partite frontal and the compound eyes are well developed with pigment and rhabdoms. The former has two pigment cells and three sensory cells in each cup. The paired dorsal and ventral frontal eyes, however, are seen only as strands of cells from the future brain to the epidermis.

Not until the sixth zoea do the dorsal frontal eyes start to develop, and in this stage they attach to the three-partite eyes and have developed rhabdoms formed from three sensory cells.

In the postlarva the dorsal frontal eyes are fully developed, with 21 sensory cells in groups of three. There are still no rhabdoms developed in the ventral frontal eyes.

Scattered evidence indicates a similar development of the frontal eyes in prawns.

Stomatopod larvae of *Lysiosquilla occulta, Squilla mantis* and *S. desmaresti* hatch with the same organization of the frontal eyes as those in *Caridion*. Jacques (1976) confirmed that in these species the paired dorsal and ventral eyes also develop later than compound eyes and the three-partite eye. Any similarities in organ development within malacostracans find support in the similarity in malacostracan naupliar development (Scholtz, 2000).

2.3. Experiments

Aoto (1963) showed in a series of experiments that white chromatophores of the prawn, *Palaemon paucidens*, reacted to light in spite of excised compound eyes. He concluded that the nauplius eye promoted that change. *Palaemon paucidens* can be expected to have frontal eyes similar to those reported for palaemonids (Elofsson, 1963), i.e. all seven frontal eyes. Aoto's experiments thus show that the frontal eyes are functioning. Some problems encountered by Aoto excising also the frontal eyes can be explained by the fact that he did not know of the complexity of the eyes and probably did not extirpate the ventral frontal eyes.

Eaton and Boyd (1970) performed the first electrophysiological experiments on frontal eyes in malacostracans. Using extracellular electrodes they measured the light-sensing capabilities of the three-partite frontal eye combined with the dorsal frontal eyes of *Pandalus borealis*. They concluded that the responses showed a photosensory capacity, and preliminary studies indicated maximum peak sensitivity at 475 and 500 nm.

An unintentionally similar experiment was conducted on the crayfish *Cherax destructor* (Sandeman et al., 1990). An extraretinular photoreceptor was found in the superficial layers of the brain; this is, in fact, the reduced frontal eyes. Another astacid *Astacus fluviatilis* was found to have all seven reduced frontal eyes inside the anterior cell layers of the brain (Elofsson, 1963). They were in the same position and with the same appearance as reported for the extracellular receptor of *Cherax*. Electron micrographs show the microvillous rhabdoms. Two or three cells form them, which indicates the presence of both the ventral, three-partite and dorsal frontal eyes. Axons terminate in a specific neuropil centre, although small in this case, in front of the protocerebral bridge as expected. The experiments gave the benefit of showing that the reduced frontal eyes react to a monoclonal antibody against *Cherax* rodopsin, that the axons end in the frontal eye neuropil and that the reduced eyes still react to light. The intracellular measurement was performed in green light (540 nm). In an earlier immunocytochemical investigation retinal S-antigen, involved in phototransduction, was found in the frontal eyes of the shrimp *Macrobrachium rosenberghii* and the crayfish *Pacifastacus leniusculus* (van Veen et al., 1986).

Another experiment where the frontal eyes may have played a trick on the investigators was the entrainment of circadian locomotor activity in a crayfish *Procambarus clarkii* (Page and Larimer, 1972). Ablation of both the compound eyes and the presumed caudal photoreceptor did not abolish entrainment. The authors assumed that there must be another photoreceptor outside the above mentioned. It is highly probable that the frontal eyes, which the authors did not know of, are the photoreceptor in question.

3. Ostracodan and maxillopodan frontal eyes

A common construction of the frontal eyes is found in ostracods and members of the maxillopodan constellation of taxa, of which the subclasses Thecostraca, Branchiura, and Copepoda are treated here (Elofsson, 1966a). There is an unsettled discussion going on regarding the relevance of the maxillopod assemblage. A contribution to this is outside the scope of the review and the term Maxillopoda is retained here since the frontal eye type unites in the taxa investigated.

The frontal eyes consist of three eyes, sometimes united as a three-partite eye or separated from each other. The tendency to split the three-partite frontal eye is specific for the ostracod-maxillopod group. When split, they occur as one ventral unpaired frontal eye and two lateral or paired frontal eyes. The frontal eyes send their axons to a common centre in the brain on top of the middle of the protocerebrum. Four types of cells build the frontal eyes; pigment, sensory, tapetal and lens cells. Sometimes a cuticular lens is present. These features are diagnostic of the ostracod-maxillopod group of frontal eyes. The sensory cells are inverse, i.e. they turn their apical portions towards the tapetum and pigment, and the axons leave the cell towards the incoming light. This feature is common to all non-malacostracan frontal eyes and is similar to vertebrate retinular cells. The rhabdoms are usually formed around the apical portion of the sensory cells in non-malacostracans. In a cross section of the rhabdomeres they form a honeycomb pattern.

3.1. Ostracod frontal eyes

3.1.1. Morphology

Members of the subclass Myodocopa have both compound and frontal eyes whereas those of the subclass Podocopa only have frontal eyes. The frontal eyes are more developed in the podocopan ostracods, which may be connected with the absence of other eyes. The frontal eyes appear both separately and as a three-partite eye in this subclass.

The brain of all ostracods is deflected dorsally to be perpendicular to the long axis of the body. The three frontal eyes are situated on top or dorsal to the brain. The centre of the frontal eyes in the brain is detached from the brain neuropil and forms three rounded balls on top of the protocerebrum.

There are three to five large pigment cells centrally where the frontal eyes are united as a three-partite eye e.g., in *Pilomedes globosus, Cypris* sp., *Cyprinotus incongruens, Leptocythere* sp. and *Palmella limicola* (Elofsson, 1966a).

Each cup of the combined eyes is lined with two tapetal cells meeting in the middle of the cup. Together they are formed like the blade of a spoon. They contain the reflecting material formed as crystal-like plates. The sensory cells are usually few, varying between two to five, but more in the specimens of *Cypris* sp. The rhabdoms are large. In addition to the sensory cells each cup has two fairly large lens cells, which bulge halfway out, from the cups. These cells have a light cytoplasm. Myodocopan species, for example cypridinids, lack lens cells. The nerves from each of the cups have separate courses to the brain. Older investigations, e.g. Nowikoff (1908), confirm the findings, *mutatis mutandis*, on a number of *Cypris* species.

In *Loxoconcha tamarindus* and *L. granulata* as well as *Xestoleberis aurantia* the three frontal eyes are separated from each other. In *Cytheridia* and *Cythereis* species the paired lateral frontal eyes are situated quite a distance from the brain, being close to and in connection with the epidermis. In these cases a cuticular lens is often present in podocopan ostracods. The unpaired ventral frontal eye of the three-partite eyes is closer to the brain. *Conchoecia elegans* is the only species investigated that lacks any traces of frontal eye.

The results of light microscopy are confirmed by ultrastructural studies on the myodocopan ostracods *Cypridina norvegica* and *Philomedes globosus* (Andersson, 1979) and the fresh water podocopan ostracod *Notodromas monachus* (Andersson and Nilsson, 1981). The frontal eyes of the two myodocopan species are united in a three-partite eye. They have five pigment cells and one tapetal cell with up to 50 crystal layers. The sensory cells number 35 to 40 in the lateral eyes and 20 to 25 in the ventral eye. Their microvilli are formed around the apical portion of the cells. There are no lens cells. The three frontal eyes of *Notodromas monachus* are separated, but have four pigment cells that keep a sort of connection. Each eye of the frontal eyes has two tapetal cells containing 15 to 20 layers of crystals in the paired lateral eyes and 25 to 35 in the unpaired ventral eye. The lateral eyes have 18 retinular cells, whereas the ventral has nine. Here two sensory cells form one rhabdom, and the lens is formed by one cell. In addition to this internal lens the lateral eyes, which are situated close to the cuticle have a cuticular lens.

3.1.2. Experiments

In *Notodromas monachus* (Andersson and Nilsson, 1981) optical properties have been investigated, and the frontal eyes proved to have a combination of lens and mirror optics. The cuticular lens contributes by prefocusing and the crystalline layers of the tapetal cells reflect an image up onto the rhabdoms of the retinular cells. This type of eye occurs in animals of widely separated systematic position (Land, 1965, 1978). It was also shown that in *Notodromas*, the visual fields of the two lateral frontal eyes overlap 35°. Although the poor resolution and few rhabdoms indicate restricted information capacity, nothing is known about the neuronal architecture and possible neuronal compensations to allow for a fairly good manoeuvring in their natural habitat. The brain centre of the frontal eyes of *Heterocypris incongruens* may contain nerve endings of monoaminergic associative neurons (Aramant and Elofsson, 1976).

In the deep-sea species of *Gigantocypris* the frontal eyes have reached their most elaborate structure and function in ostracods. Their morphology was described by Lüders (1909) for *Gigantocypris agassizii*. The lateral frontal eyes are almost unrecognizably transformed into two large mirrors, which are parabolic seen from above and spherical from the side. The resulting focus is a line, along which the great number of very long sensory cells have developed their microvilli. (Land, 1984). The frontal eyes act as a massive light gathering device.

3.2. Maxillopodan frontal eyes

3.2.1. Subclass Thecostraca

3.2.1.1. Infraclass Facetotecta. The nauplius Y larva, previously presumed to belong to cirripeds, has a three-partite eye with two pigment cells and two sensory cells in each eye (Elofsson, 1971).

3.2.1.2. Infraclass Cirripedia

3.2.1.2.1. Morphology. Fahrenbach (1965) produced the first ultrastructural study of adult cirripede eyes. The two investigated species, *Balanus cariosus* and *B. amphitrite*, display three widely separated frontal eyes. The medial, unpaired ventral frontal eye is situated a considerable distance anterior to the brain. It contains seven sensory cells. The paired, lateral frontal eyes contain three sensory cells each. They are situated dorsocaudally of the brain, also quite a distance from it. The lateral frontal eyes contain, apart from the sensory cells, pigment and tapetal cells. Each eye sends a separate nerve to the brain. A peculiar feature is the branching sensory cells. They divide into numerous dendrites, which end in a large number of microvilli facing the pigment. Glial cells insulate the dendrites. Krebs and Schaten (1976) have verified these observations for the adult lateral frontal eyes of *Balanus eburneus*.

Gwilliam (1965) remarked that *Balanus tintinnabulus, B. balanus, B. crenatus, B. balanoides* also have one unpaired ventral and two lateral frontal eyes constructed like those of *B. cariousus* and *B. amphitrite*. Clare and Walker (1989) studied the unpaired ventral eye of *Balanus hameri* ultrastructurally and found ten cells eight of which were sensory cells and the remaining two possibly neurosecretory. They also made the observation that insulating glial cells separated the distal microvilli-bearing dendrites of the sensory cells.

3.2.1.2.2. Development. The eye of the sixth larval stage of *Balanus crenatus,* and *B. balanoides*, were investigated by Kauri (1962). There is a three-partite eye with three cups formed by two pigment cells. Four sensory cells are housed in the lateral eyes, and six in two layers in the ventral eye. The lateral eyes have an outer non-sensory cell that could represent a lens cell. There are no tapetal cells. The separated nerves join the brain in a neuropil that is separated from the protocerebrum and consists of three balls, one for each eye.

In the transition from cypris to adult, the eyes separate. The number of sensory cells changes somewhat, and the dendritic shape of the distal portion develops, as do tapetal cells.

Takenaka et al. (1993) followed the transformation of the three-partite larval eye, containing five sensory cells in the lateral eyes and four in the ventral eye, into the adult eyes of *Balanus amphitrite hawaiisensis*. The three cups of the larval eye in the nauplii and cypris separate, and form the adult configuration upon settlement. In the adult eye only three sensory cells remain in the lateral eyes. The tapetum and the finger-like dendrites with microvilli on the sensory cells are formed in the adult eyes.

The sensory cells of balanids are unique in crustaceans, as repeatedly shown, in that they terminate in a number of dendrites each branch ending in a large number of microvilli and being insulated by glial cells.

3.2.1.2.3. Experiments. Experiments on the function of cirriped frontal eyes for vision started with the demonstration of shadow reflexes (Gwilliam, 1963). Passive electrotonic conduction of a depolarizing potential occurred when the photoreceptors were illuminated. Later Gwilliam (1965) extended his study to intracellular recording and could establish that all the frontal eyes contributed to the photoreceptor response. The large axons also explained the absence of action potentials and supported the idea of long-distance electronic conduction. The pathway of the shadow reflex from the ventral frontal eye to the central nervous system was reported by Millecchia and Gwilliam (1972).

A group of scientists studied the receptor potentials and their dependence on the visual pigments. They concluded that *Balanus* has two thermally stable pigments with different absorption spectra, one peaking near 495 nm and one near 532 nm (Hillman et al., 1973; Hochstein et al., 1973; Minke et al., 1973). The cirriped frontal eyes are convenient preparations for investigation of molecular mechanisms of photoreception (e.g. Werner et al., 1992). The transmitter released by the sensory cells of the barnacle *Balanus nubilus* is histamine (Callaway and Stuart, 1989).

3.2.2. Subclass Branchiura

3.2.2.1. Morphology. The five investigated species (Elofsson, 1966a) are remarkably uniform with respect to the frontal eyes. There are only three frontal eyes, and all are combined into a large, three-partite eye situated on top of the brain and in contact with the epidermis. Each eye of the combined eyes has two pigment cells and two tapetal cells, which are very prominent. The number of long and slender sensory cells is large. In *Argulus coregoni* there are approximately 220 cells, whereas they vary in other species between 60 and 120. Two small lens cells are situated outside the sensory cells but still inside the cup formed by the pigment. The U-formed axons from the sensory cells run separately from each eye to the brain. The brain centre of the frontal eyes is large and occupies a considerable portion of the protocerebrum.

3.2.3. Subclass Copepoda

3.2.3.1. Morphology. In copepods, there are three frontal eyes that are often combined into a three-partite eye. Within this subclass, the frontal eyes are frequently transformed. Vaissière (1961) described seven species with a three-partite eye and 13 with transformed frontal eyes. Elofsson (1966a) demonstrated the transformation from the three-partite, fairly simple eyes to very elaborately transformed frontal eyes, using 12 species of each type.

The three-partite eye can be situated close to the brain or an eye length or more anteriorly from the brain, close to the ventral surface of the animal (Fig. 5A). The eye has three pigment cells, forming three cups, and each cup has two tapetal cells. The ventral frontal eye (the ventral cup) has ten sensory cells, and they are arranged in two layers, one containing six cells and the outer layer four cells. The lateral eyes have nine sensory cells. The sensory cell number in the frontal eyes is rather stable in a large number of the copepods investigated; *Macrosetella gracilis*, however, has fewer. All sensory cells are inverted, although in some cases the axons are slightly
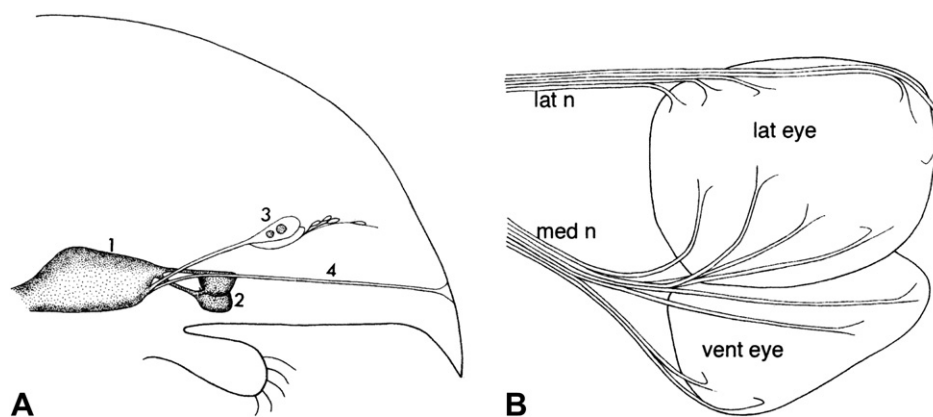

Fig. 5. *Pareuchaeta norvegica*. Drawing of (A) the anterior portion of the head from a sagittal view and (B) a detail of the three-partite frontal eye. Anterior to the right. (A) The brain (1), the three-partite eye (2), Gicklhorns organ (eye) (3) and the cavity receptor organ (4). (B) Illustration of how the median (med n) nerve from the eyes receives axons from both the ventral (vent eye) and lateral (lat eye) eyes, whereas the lateral nerve (lat n) receives axons only from part of the lateral eye. Reprinted with modifications from Elofsson (1966a) with kind permission from Taylor and Francis.

displaced to one side of the sensory cell. Microvilli develop mainly on the adjoining sides of the sensory cells. There are three nerves from the eyes to the brain, apart from *Calanus* species, which have one. In contrast to the condition in malacostracans, the median nerve contains a blend of axons from the eyes. It collects all the nerves from the ventral eye and four from the lateral eyes (Fig. 5B). The paired lateral nerves contain only five axons from the lateral eyes. The nerves end in a centre at the anteriormost end of the brain, which is fairly large and has a broad contact with the brain neuropil. There are no structurally visible specializations in the centre. Together, the two investigations above agree with regard to the morphology of the three-partite eye in 18 species of different families.

Fahrenbach (1964) investigated the ultrastructure of the three-partite eye of *Macrocyclops albidus*. Four pigment cells form three eyecups, each with two tapetal cells. The paired dorsal cups contain nine sensory cells, and the ventral five. Five flat conjunctival cells cover the eye surface. Fahrenbach found a single afferent axon to the dorsal eye, an observation not confirmed so far. Dudley (1969) performed an ultrastructural study of the three-partite frontal eye in the copepod *Doropygus seclusus*. Her study corroborates in general the description above, but some differences occur. She observed two pigment cells serving all three cups, and noted that glial cells covering the eyes also functioned as accessory pigment cells marginally. There were no lens cells. Each eye had eight sensory cells. Her study also included the development within five naupliar and five copepodid stages. Pigment and tapetal cells appear from the first naupliar stage, whereas the glial cells with accessory pigment develop in the fifth naupliar stage. Only three sensory cells are ''functional'' in each eye in the naupliar stages; six primordial cells are present in the lateral eyes and five in the ventral. The ninth sensory cell in the lateral eyes degenerate in the moult to the first copepodid at which point rhabdoms and axons are fully developed.

The transformation to be described next involves 25 species from the two investigations mentioned above (Vaissière, 1961; Elofsson, 1966a). Different species from the families Sapphirinidae, Copilidae, Corycaeidae and Caligidae unite and confirm the studies.

An early transformational step is seen in *Chiridius armatus*, which still has a three-partite eye, but the lateral eyes are much larger than the ventral (Fig. 6). Here, and in subsequent steps, there are lens cells in each eye. The unpaired ventral eye still has ten sensory cells with microvilli facing the tapetum and pigment. The eye looks a little more reduced than in the species with unmodified three-partite eyes. The nine sensory cells of the lateral eyes are arranged as a bowl or hemisphere, in the centre of which the two lens cells are enclosed. Four cells forming the bottom of the sphere send their axons as the medial nerve, whereas the ''rim'' cell axons form the lateral nerves. Microvilli abut the pigment also in this eye. The fundamental pattern of a three-partite eye is still to be recognized. *Caligus acutus* resembles *Chiridius* except that a solid lens is formed in the lateral eyes pointing out from the bowl formed by the eye.
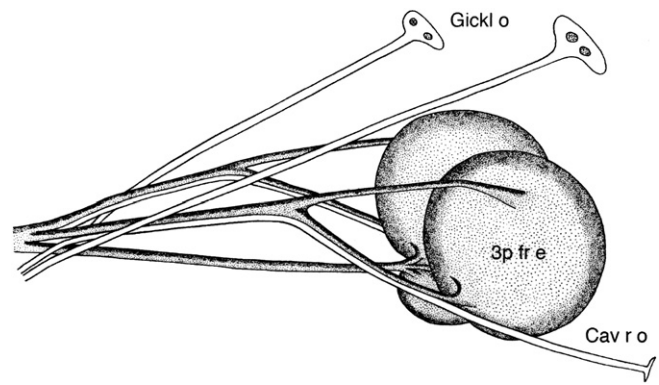

Fig. 6. *Chiridius armatus*. A drawing of the three-partite eye (3p fr e) with associated organs in a sagittal view. Anterior to the right. The three-partite eye shows a beginning transformation with large lateral eyes. The Gicklhorns (Gickl o) and cavity receptor (Cav r o) organs are closely apposed to the eyes. Note also here the mix of axons from the ventral and lateral eyes in the median nerve and the lateral nerves containing only some of the axons from the lateral eyes. Reprinted with modifications from Elofsson (1966a) with kind permission of Taylor and Francis.

The *Sapphirina* species display the same basic frontal eye morphology, although they seem radically different from the previously described eyes. The spacious interior of these animals house, to almost a fourth of the animal's length, the enormous lens apparatus. It belongs to the lateral frontal eyes, separated from one another and from the unpaired ventral frontal eye, and starts anteriorly with a biconvex lens at the cuticle. From here, a cone-shaped tube tapers posteriorly to end in an oblong lens. Here, four small sensory cells are attached anteriorly to the ventral side of three huge sensory cells almost 0.1 mm in length. All sensory cells are wrapped in two different kinds of pigment cells. The orientation of the whole lateral eye has rotated from antero-lateral to frontal. The large sensory cells are stacked upon each other with their long axis parallel to the long axis of the animal. They reach from the brain to the interior lens and create a setting for it. The microvilli are situated on the lateral sides of the cell and extend the whole length of it. The axons leave the cell about midways. Tapetal cells are present. They are presumed to contain guanine crystals at least in pontellids (Frasson-Boulay, 1973).

An ultrastructural study of *Sapphirina angusta, S. auronitens,* and *S. ovatolanceolata-gemma* confirmed the general structure of the frontal eyes in *Sapphirina* (Elofsson, 1969) and established with better precision cell numbers and boundaries. Two pigment types, red and black, were found to invest the lateral eyes (Fig. 7A). The black pigment in particular contained rootlet-like fibrils 0.15 μm thick.

The unpaired ventral frontal eye is situated anterior to the brain and turned ventrally (Fig. 7B). It contains nine sensory cells with distal microvilli, pigment and tapetal cells. Four of the sensory cells contain a bladder-like structure. The axons appear first as three nerves uniting as one before the entrance into the brain. The ventral eye has not undergone any large changes and is modest compared to the paired lateral frontal eyes.
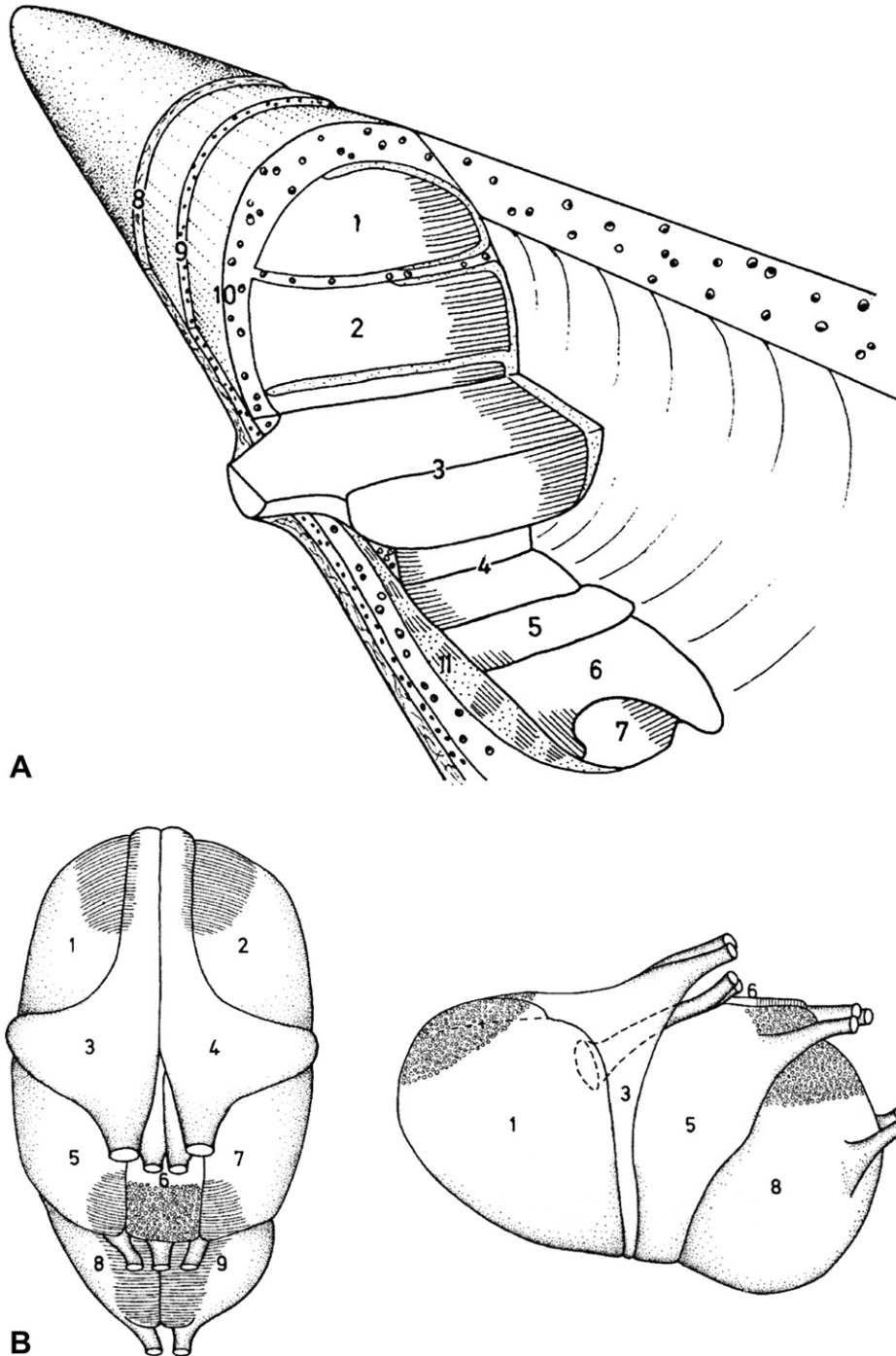
Fig. 7. *Sapphirina angusta*. Drawings showing (A) a dissected lateral eye (without the lenses) seen from the front and (B) the ventral frontal eye seen from above and from one side. In A, 1–3 are the large and 4–7 the small retinular cells; 8, connective tissue sheath; 9, red pigment; 10, black pigment; and 11, tapetal cells. In B the cells are numbered and the direction of the microvilli is indicated. Anterior to the top of figure. Reprinted from Elofsson (1969) with kind permission of Springer Science and Business Media.

The elaboration of the paired lateral frontal eyes is taken one step further by *Corycaeus speciosus, C. limbatus, C. flaccus,* and *Corycella carinata*. Here the three large cells are much longer and reach the posterior part of the thorax on each side of the stomach. They are situated beside each other, with the rhabdomeres pointing dorsally. There is also a cuticular lens outside the distal lens of the combined lens apparatus.

Although the frontal eyes of *Copilia mirabilis* are in essence constructed as in the preceding species, they may represent another step towards the dominance of the three large cells of the paired lateral frontal eyes. The unpaired ventral frontal eye and the four small sensory cells of the paired lateral frontal eyes are more reduced in this species. The unpaired ventral frontal eye sits on the antero-dorsal margin of

the brain, since in *Copilia* the brain is tilted almost 180° backwards. The large sensory cells of the widely separated paired lateral eyes bend medially, approximately in the middle, by approximately 90°. The axons leave the cells after the bend. Vaissière (1961) observed a sexual dimorphism in *Copilia*, and the description above refers to females. In males the frontal eyes are united, and the extreme situation in the lateral eyes described for the females is less pronounced.

Miracia efferata has gone another step further. The unpaired ventral frontal eye is minute, with a few cells, and is situated below and in the anterior end of the large paired lateral eyes. The latter adjoin each other dorsally in the head. Each eye contains three large cells stacked upon each other vertically. The rhabdoms are found in the caudal portion. They are large and developed ventrally. The axons leave from the proximal third of the sensory cells. The two lenses are contiguous, and there are two large biconvex cuticular lenses.

The paired lateral frontal eyes dominate in the development described above. Another and parallel transformation of the frontal eyes to more elaborate structures in which the unpaired ventral frontal eye dominates, is found in pontellid copepods (Vaissière, 1961; Land, 1984). A beginning of this change is found in *Centropages typicus*, which has a three-partite eye, but small lateral eyes and a large ventral eye supplied with a prominent lens. Vaissière (1961) found the frontal eyes in the genera *Anomalocera, Labidocera,* and *Pontellopsis* to be well separated and with cuticular lenses. The copepodan features are also present here, viz. the pigment, tapetal, sensory, and lens cells. The unpaired ventral frontal eye of *Pontellopsis regalis* is very large and bulges out anteriorly. The lens cell occupies a large portion of the eye and abuts six sensory cells behind, arranged in two groups. Two different pigment layers envelop a tapetal layer, as in *Sapphrina*. The pigment covers most of the eye except for a pupil anteriorly. The unpaired ventral frontal eye is similar in the males of *Anomalocera patersoni* and *Labidocera wollastoni*. Sexual dimorphism is present in these species although reversed in comparison to *Copilia*, in that the ventral eye is much less developed in females. Cohen et al. (2005) investigating the large ventral lens of male *Anomalocera ornata* found that the crystallins, responsible for the optical properties of animal lenses, are the same in this species as in vertebrate lenses.

The paired lateral frontal eyes of *Anomalocera patersoni* have two cuticular lenses each. Behind these, a hyaline lens-like structure extends to the sensory cells. These are arranged in three lobules, containing two sensory cells each. Tapetum and pigment encircle the eye. The paired lateral frontal eyes of *Labidocera wollastoni* and *Pontellopsis regalis* resemble *Anomalocera*, apart from having one cuticular lens in the former species, and none in the latter.

3.2.3.2. Experiments. Gregory et al. (1964) showed that the large cells of the paired lateral eyes of the female *Copilia* performed a scanning movement of their proximal lenses powered by muscles attached to the large sensory cells at their bend. They move apparently across the image plane of the anterior biconvex, cuticular lens. Gregory and co-workers

thought of the eye and its performance as "transmitting spatial information by conversion into a time-series by scanning, as in television". Later Wolken and Florida (1969) investigated the optics of the lateral frontal *Copilia* eyes and their ultrastructure. Their estimates of the optical capacity led them to the conclusion that the lens system functioned as a light amplifier. Downing (1972) reached another conclusion regarding the optic properties, but more interestingly showed that the receptor movement was involved in vision, and that *Copilia* gives an example of optical scanning. Land (1984) remarked that a one-dimensional scan did not use the whole field of view. Interesting research lies ahead concerning these highly modified copepod frontal eyes.

Land (1984) investigated the optical design and function of the male *Labidocera acutifrons*, which has large lateral eyes, and *Pontella spinipes,* with a large ventral eye. The lateral eyes of *Labidocera* are directed towards the sky, with a lens, unique in crustaceans, that presumably has an inhomogeneous refractive index, high in the middle and low in the periphery, making a short focal length, as with lenses in fish and cephalopod mollusc eyes. A muscle attached to the eye could provide scanning movements that moved the focus across a correspondingly extended line of rabdoms. Friedrich (1931) had already reported the muscles in *Labidocera wollastoni*.

The ventral eye of *Pontella* has a triplet lens built after the principle of multiple surfaces, as in a microscope objective lens. Further, the outer surface is parabolic to eliminate spherical aberration. The organization of the rhabdoms in the six sensory cells is not less interesting. One of the two dorso-medial cells has a ball-shaped rhabdom encircled by the ring-shaped rhabdom of the other. They are situated in the lens focus, and the construction makes them capable of detecting spots. The other two pairs of cells have rhabdoms that are outside the focal plane, but able to receive a refocused image thanks to the tapetal cell layer behind them.

The brain centre of the frontal eyes has developed accordingly. It is large almost equal to half the brain proper. The thick lateral nerves enter the dorsal, main part, and the ventral nerve enters the ventral portion. There is a broad zone of contact between the frontal eye centre and the protocerebrum.

3.3. Gicklhorn's organ

Gicklhorn (1930) described in *Cyclops strenuus* a paired so-called frontal organ that consisted of two large bi-nucleated cells, situated quite a distance anterior to the brain (Figs. 5A and 6). Similar structures were found in a number of copepods (Elofsson, 1966a): *Pareuchaeta norvegica, P. marina, Calanus finmarchicus, C. hyperboreus, C. gracilis, Augaptilus* sp., *Chiridius armatus, Sapphirina nigromaculata, S. ovatolanceolata* and *Sapphirina* sp. All but the *Sapphirina* species, which had one nucleus in each cell, were bi-nucleated. The nerves from the cells entered the brain laterally on the protocerebrum.

An ultrastructural study (Elofsson, 1970) on *Euchaeta norvegica, Calanus finmarchicus* and *Chiridius armatus* revealed microvilli around the cells of the organ, except in *Calanus* where

microvilli were present only on the adjoining cell borders, thus forming a simple rhabdom. The cell nuclei are large approximately 20 μm and the nerves are long approximately 0.5 mm. The axons measure 6—10 μm. They terminate in the brain without a discernible contact with the frontal eye centre. It was concluded that this organ is a simple eye, but a connection to either compound or frontal eyes could not be established.

The statement by Paulus (1972) that I had established an eye transformed to a gland is not true. The satellite cell axons connected to the organ contained dark granules that I unfortunately termed neurosecretory. They are more properly compared to the cavity receptor organ of *Artemia salina* (Elofsson and Lake, 1971), which contains a transmitter substance (Aramant and Elofsson, 1976).

4. Anostracan frontal eyes

4.1. Morphology

The order Anostraca of the subclass Sarsostraca differs markedly with respect to the frontal eyes from the subclass Phyllopoda and the term anostracan frontal eyes is used to denote it specifically. One species each from five families of the Anostraca were investigated, and all are very similar with respect to the frontal eyes.

There are five frontal eyes in anostracans (Elofsson, 1966a), three joined in a three-partite eye and two constitute paired ventral frontal eyes (Fig. 8). Pigment and sensory cells are the only components of the eyes. The sensory cells are inverse, and their rhabdomeres are formed around the apical border facing the pigment. There is one nerve from each eye. Their nerve centre in the brain is well separated from the rest, and forms a sphere in the cell body layer. A structure close to the lateral eyes of the three-partite eye has been described as the (dorsal, paired, lateral) frontal or X-organ and, because of this, has been misinterpreted in the past. It is a cavity receptor organ connected with the lateral protocerebrum (Elofsson and Lake, 1971).

The three-partite eye contacts the epidermis. The eyes are lodged in two large pigment cells. The lateral eyes are large containing 25 to 75 cells, depending on species, and there is also individual variation. The ventral unpaired eye contains 20 to 40 sensory cells. It faces the anterior surface of the animal.

The unpaired ventral eye of the three-partite eye, the paired ventral eye, tissue from the excretory system, and connective tissue forms a complicated structure that can be difficult to resolve (Fig. 8). The paired ventral frontal eyes are filled with reduced sensory cells and run from the epidermis to the centre in the brain. From its paired beginning at the epidermis, the two cell strings unite in front of the unpaired ventral eye of the three-partite eye, then divide again and run on each side of the ventral cup to the brain. Rasmussen (1971), Anadón and Anadón (1980) and Anadón (1983) confirmed the observations in *Artemia salina* and could show, ultrastructurally, microvilli in all eyes.
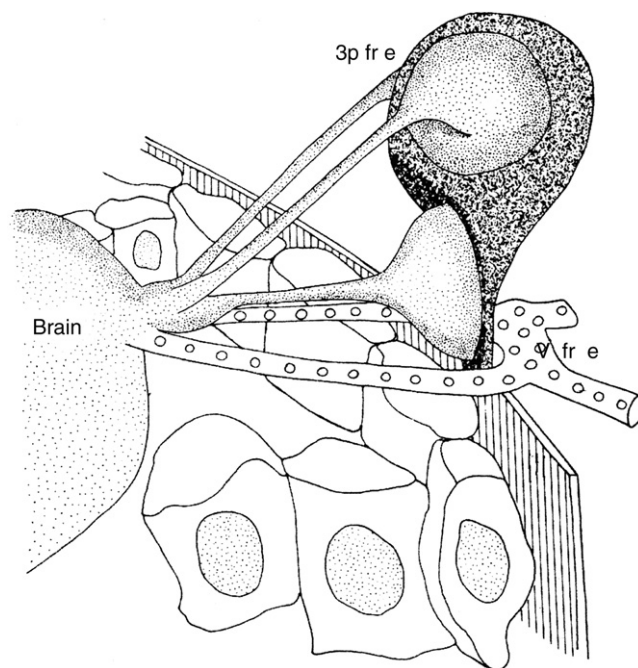

Fig. 8. *Branchinecta paludosa*. Drawing of the anterior part of the head in a sagittal view. Anterior to the right. The relation between the three-partite (3p fr e) and paired ventral frontal (v fr e) is illustrated. The large cells and the sheath of connective tissue unrelated to the frontal eyes are indicated below the eyes. Reprinted with modifications from Elofsson (1966a) with the kind permission of Taylor and Francis.

4.2. Development

In a short contribution Vaissière (1956) stated that the three-partite frontal eye of *Artemia salina* does not emanate from the epidermis, but from anlagen common to the nervous system. Benesch (1969), however, in an extensive investigation of the development of *Artemia salina*, showed that the anlagen of the frontal eyes appear in the first naupliar stage as invaginations from the ectoderm. First, two pigment cells appear, followed by retinular cells and the paired ventral frontal eyes. The three-partite eye is formed in the third naupliar stage, with pigment and retinular cells. The ventral frontal eyes are less developed.

The whole brain and eye complex originates as "V"-formed anlagen, the frontal eyes being the tip of the "V", and the compound eyes and the brain the legs of the "V".

5. Phyllopodan frontal eyes

5.1. Morphology

Members of the subclass Phyllopoda have frontal eyes that resemble each other, and can be treated as a specific type that sets them apart from other crustacean frontal eyes. The phyllopodan frontal eyes have a rather complicated structure. A common feature is a four-partite eye with pigment and inverse sensory cells that send their axons in a large centre medially on the dorsal surface of the protocerebrum. The rhabdomeres

are formed around the distal or apical portion of the sensory cells. Apart from the four-partite eye the number of frontal eyes varies, and there seems to be no stable number of eyes uniting all phyllopods.

The frontal eyes of *Lepidurus arcticus, L. apus, Triops cancriformis,* and *T. namaquensis*, which belong to the order Notostraca, are very similar (Elofsson, 1966a). Their eyes are very large and fill the space between the epidermis and the brain (Fig. 9). The pigment is contained in a tissue formed by many cells. This tissue can form lamellae that compartmentalize the lateral eyes. The most prominent frontal eyes are the two large lateral eyes, which consist of several hundred sensory cells on each side of the pigment lamella. These can be divided in two groups; one is ventro-caudal and has larger cells sending a thin nerve to the brain; and one is much larger and gives rise to a thick nerve to the brain outside the former. There is individual variation in that the two nerves can coalesce and even coalesce on one side and be kept as two on the other in the same individual. In addition to these two large lateral eyes, there are two unpaired eyes, one situated on the ventral side of the pigment, and one situated on the caudal margin of the pigment lamella. Each eye contains approximately 30 sensory cells and they send their nerves separately to the brain. Another eye is reduced, unpaired and runs behind the caudal frontal eye in a tube connected with the epidermis.

The nerve runs parallel to the nerve from the caudal eye, and they both end in the centre of the frontal eyes.

Caenestheria var. *salberghi, Cyzicus cycladoides, Limnadia lenticularis,* and *Lynceus brachyurus* belong to the phyllopodan group previously named Conchostraca (Elofsson, 1966a). The frontal eyes resemble those of the notostracan phyllopods in all essential features. The large lateral eyes of the four-partite eye contain either a few large cells or 50 to 150 depending on species. Rhabdomeres are formed around the apical portion of the sensory cells. All species have unpaired ventral and caudal eyes, each containing approximately 25 sensory cells. The two former species have only these four frontal eyes whereas the latter two have the reduced unpaired eye behind the caudal eye and another pair of eyes situated ventrally and distal to the combined four-partite eye, in all seven frontal eyes. The nerves from the paired ventral frontal eyes run caudally, passing the lateral eyes of the four-partite eye, sometimes joining the lateral eye nerve, and end in the frontal eye centre. The sensory cells form rhabdoms around the apical portion of the cells.

The frontal eyes of species of the suborder Cladocera (Elofsson, 1966a) showed a specific, common arrangement. The species *Daphnia magna, D. pulex, D. longispina* and *Eurycercus lamellatus* are very similar. They have a four-partite eye, as all phyllopods, with few cells in each eye, four to eight depending on species and eyes. The rhabdomeres are well developed. The nerves from the eyes are long in *Eurycercus*, but hard to see in the daphnid species where the eyes sit on the brain. The lateral eyes of the four-partite eye send their axons to the middle area of the frontal eye centre in the brain. The unpaired ventral and caudal eye nerves run together to the same place as the lateral ones, and thus there are seemingly three nerves from the four-partite eye (Fig. 10). There is no counterpart in the cladocerans to the reduced frontal eye behind the caudal eye in the other phyllopods.

The remaining frontal eyes of cladocerans have a peculiar construction. From the lateral sides of the frontal eye centre,
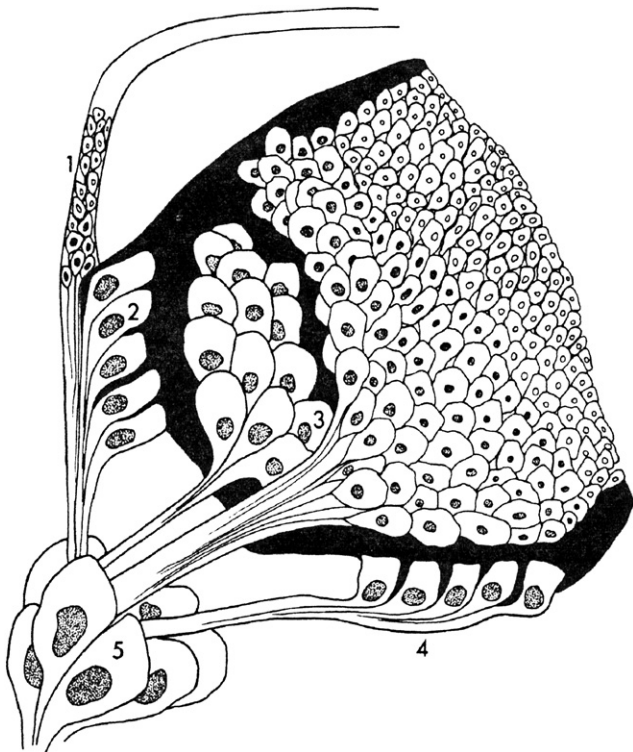

Fig. 9. *Lepidurus arcticus*. Drawing of the large and complicated frontal eyes in a lateral view. 1, the posterior unpaired reduced eye; 2, the caudal medial unpaired eye apposed to the pigment lamella; 3, the large lateral eye with its two components and nerves; 4, the ventral medial unpaired eye; 5, the so-called giant cells unrelated to the frontal eyes. Anterior to the right. Reprinted from Elofsson (1966a) with kind permission of Taylor and Francis.
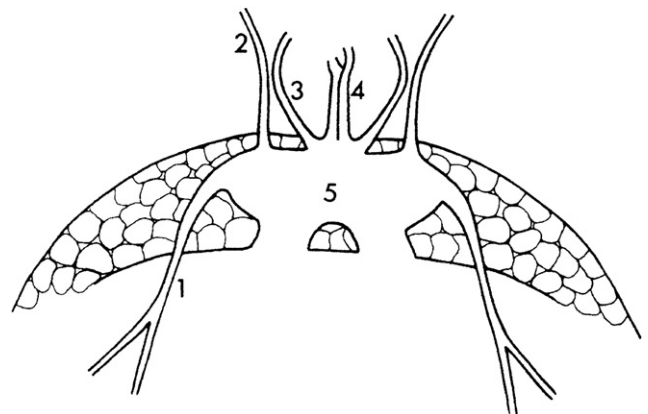

Fig. 10. *Eurycercus lamellatus*. A horizontal drawing of the frontal eye centre in the brain (5) illustrating the nerves from the frontal eyes. 1, nerve from the dorsal portion and 2, from the ventral portion of the split frontal eyes; 3, the nerve from the lateral cups of the four-partite eye; 4, the nerve combining the axons from both the unpaired caudal and ventral eyes. Anterior to the top of figure. Reprinted from Elofsson (1966a) with kind permission of Taylor and Francis.

two nerves depart from each side (Fig. 10). One passes the lateral eyes of the four-partite eye and ends in the sensory cells at the epidermis. These nerves are two in *Eurycercus* but are fused anterior to the four-partite eye into one in daphnids, which has caused much confusion. The other nerve from the frontal eye centre makes a loop dorsally, and along its course, ends in separate groups of sensory cells. There can be three such eyes. This is subject to much variation. In one specimen of *Daphnia magna*, five small, separate groups containing two sensory cells were found.

Reduced frontal eyes are present in some cladoceran species. *Leptodora kindtii* has a disorganized group of cells in the brain cell layer that form microvilli. These were seen by Scharrer (1964), although not recognized as the frontal eyes. *Sida crystallina* has reduced frontal eyes arranged around a pigment cell. Three species of the family Polyphemidae had no frontal eyes whatsoever.

5.2. Development

An important contribution to the development of frontal eyes was made by Dahl (1959) on the phyllopod species *Triops cancriformis*. When the embryos of the genus *Triops* hatch, a three-partite eye, which is slightly more differentiated than surrounding tissues, is present frontally. It is surrounded by a horseshoe-shaped anlage of the brain and compound eyes. The main portion of the dorsally directed arms is the future optic lobe. During development, the caudal frontal eye comes from cells in the inner (medial) and lower part of these lobes, but possibly also from the brain anlage. Thus, this eye has a paired origin. The same area of the anlagen also contributes to the growth of the lateral eyes and perhaps also to the unpaired ventral eye. The dorsolateral lobes of the anlage eventually split longitudinally into the anlage supplying frontal eyes and the one intended for the compound eyes. It thus partly mimics vertebrate eye development, which starts in the central nervous system.

As development proceeds, the dorsolateral lobes and a connecting dorsal bar of cells change to a proliferation zone that occupies the medial side of each future compound eye. This zone contributes still more cells to all frontal eyes of the four-partite eye.

If the ontogenetic development of the frontal eyes in the genus *Triops* is valid for all phyllopods it explains the four-partite frontal eyes, which in fact should be six-partite since the caudal and the ventral frontal eyes are paired. If all new contributions to the originally three-partite eye should be recognized, a still more complicated eye (nine-partite) should be the result. It also explains the varying number of frontal eyes in phyllopods.

6. Other crustaceans

Ultrastructural investigations of cephalocarids (Elofsson and Hessler, 1990) and mystacocarids (Elofsson and Hessler, 2005) have established that these two groups have no eyes whatsoever. It is important to repeat here that Burnett (1981) mistook the olfactory lobes for compound eyes in cephalocarids; this was corrected in Elofsson and Hessler (1990) but nevertheless quoted in Paulus (2000).

7. Discussion

The frontal eyes in crustaceans have been considered to be homologous in the sense of common ancestry even throughout arthropods (Paulus, 1972) or euarthropods (Bitsch and Bitsch, 2005). This has been widely accepted. There are features in crustacean frontal eyes that could suggest this. All frontal eyes are situated anteriorly and send their axons to a medial neuropil in the protocerebrum. The transmitter substance is histamine in barnacle eyes (Callaway and Stuart, 1989) and many other invertebrate photoreceptors (Hardie, 1987; Schmid and Duncker, 1993). Finally, there is a tendency in crustaceans to form a three-partite eye.

Salvini-Plawen and Mayr (1977) concluded in their basic work on the evolution of eyes that eyes had evolved many times during evolution. Land and Fernald (1992) concluded that convergent evolution of eyes is common. Nilsson (1996) came to the same conclusion considering the acquisitions used by multifunctional ancient master genes to form different eyes. Fryer (1996), an astute reviewer of phylogenetic speculations, although neglected, gives ample evidence of a separate origin of eyes from ancestors with simple eyes or eyeless as well as arthropod polyphyly in general (Fryer, 1998). Fernald (2000) reviewed eye-forming genes, molecular and other structures forming eyes in animals. He concludes that an interactive gene network regulates all complex organs, that different tissues have been recruited to build eyes, and thus, it seems unlikely that eyes have a single origin. Also molecular evidence favours a separated origin of eyes (Oakley and Cunningham, 2002). Can this possibility of separated origin of eyes apply to the frontal eyes of crustaceans?

It is an uphill road to advocate different types of frontal eyes in crustaceans. In spite of that, the need to do so in the present review, and in earlier work, is compelled by morphological evidence and a semantic analysis of terms used in morphology and the criteria for homology. Homology is a central concept in morphology and was used intuitively until Owen (1843) rendered morphology the outstanding service to offer a valuable tool. He coined the terms homology and analogy. At that time no idea of common descent was available. The reasons to use the terms in their original sense are forcefully analysed by Boyden (1973; several works reviewed). The criteria, by which homology could be established, were, however, not settled until Remane introduced his criteria of homology (Remane, 1956, 1961). He pointed at positive, observable structures that had to be applied and evaluated before accepting or refuting homology. His main criteria are (1) similarity in position and connections of the parts, (2) similarity in quality of resemblance of structures, and (3) continuity or similarity through intermediate species. He also made it clear that common decent is one result of homology analyses not one of the methodological criteria. Boyden (1973) and Remane (1956, 1961) give more exhaustive arguments for the use of

the homology concept as a strict morphological tool not influenced by common descent. This separation of observable morphological features from speculations of common or separate descent has unfortunately been neglected in the past in phylogenetic studies, irrespective of method.

Thus, following the original use of homology, given by Owen, I have handled the structural criteria according to Remane in the following way: the position and connection criterion is valid for all eyes in a bilateral, mobile animal and for all eyes between the compound eyes. There are no alternatives. The first criterion of Remane is thus valid in a general way.

The similarity criterion in structure is the main one used to establish the four morphological groups of frontal eyes (Fig. 11). First, there is a deep trench between the malacostracan frontal eyes and the three other groups, due to the everse sensory (or retinular) cells of the former and the inverse of the other. The ostracod-maxillopod group stands apart because of their frontal eyes being formed by four elements, and the capacity to form complicated eyes that are functionally unique in crustaceans. Molecular data indicate an independent origin of compound eyes in myodocop ostracods, whereas frontal (median) eyes are homologous within all ostracods. Further the frontal eyes in ostracods and maxillopods are considered homologous in the sense of common decent (Oakley and Cunningham, 2002). Within this group their peculiar dendritic retinular cells unite the cirripeds. The fairly simple anostracan frontal eyes differ from the complicated phyllopodan eyes with their, judging from development, six-partite eye.

Within each group, a large number of species have frontal eyes with the same construction. Seemingly different eyes in the groups, such as in copepods, can be seen to connect to one another by transitional frontal eyes. This utilizes the third criterion, that of continuity. The continuity criterion is demonstrated elegantly by decapods. Thus a few cells, hidden in the cell layer of the brain, can be homologized with fully-fledged eyes through a series of intermediates (Elofsson, 1963). It is also obvious from the survey of recent species that there are no connecting links between the four established groups of frontal eyes. The term homologous, meaning common decent, can thus be used for the frontal eyes within each of the four groups.

Turning now from the observed facts gathered from the morphology of the frontal eyes of recent crustaceans to speculation, I venture to say that present day frontal eyes extrapolated into a distant past, evolved along four different lines. This is based on the use of the homology concept in a strict sense leaving the non-morphological tool of common descent beside. The result is that the frontal eyes are not homologous. Carrying the speculations one step further to state that they also originated separately can neither be denied nor supported with the morphological methods used.

The contradictory results on homology emanate from two different methods of approaching phylogenetic problems. Paulus (1972, 1979) starts from a "Grundbauplan" ("ground pattern"), with the notion that its frontal organs (eyes) are all similar and that the ancestral forerunners of mandibulates (euarthropods) had eight frontal eyes. From here the present situation of frontal eyes in chelicerates, insects and crustaceans are deduced by reductions and coalescence. Lauterbach (1983) accepts Paulus' ideas, and, seemingly unaware of earlier work on frontal eyes, bestows anostracans with eight frontal eyes, and repeats some other misinterpretations. Wägele (1993) adheres to the ground pattern, created by Paulus. He states that leptostracans have eight ommatidia (!) being the frontal
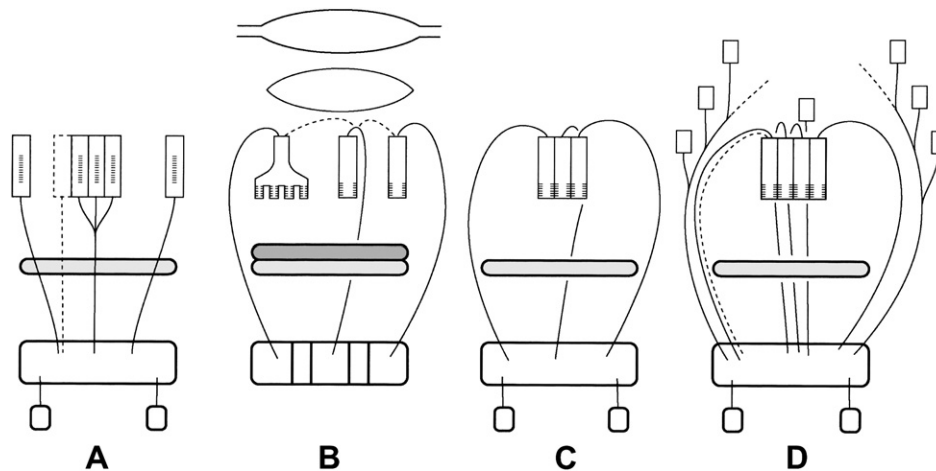

Fig. 11. Schematic presentation of the four groups of frontal eyes. Anterior to the top of figure. (A). Malacostraca; (B) Ostracoda-Maxillopoda; (C) Anostraca; (D) Phyllopoda. The following symbols have been used: Long, vertical, rectangular boxes = a frontal eye; short, vertical boxes = reduced frontal eyes; lines = nerves; large, horizontal boxes = frontal eye centres in the brain; thin, horizontal boxes (light shade) = pigment; thin, horizontal box (dark shade) = tapetum. Rhabdoms are indicated as small striations inside the boxes in A and on the box margins in B−D to indicated the different positions. Ventral frontal eyes are located below the frontal eye centre box, three-partite (four-partite) and dorsal frontal eyes above. In A the dotted box and line to the left indicate that the three-partite eye and the dorsal frontal eyes can be united. In B lens cells and the cuticular lens are situated above the eye boxes. The tendency to split the three-partite eye is indicated by the distance between the large, vertical boxes. The dendritic retinular cells of cirripeds are suggested in the left box and the dotted lines indicates the mixed median nerve in copepod three-partite eye. The partition of the brain centre relates to its appearance as separate neuropil in, e.g., ostracods. In D the dotted line from the left eye box relates to the split nerve from the large lateral cups of the four-partite eye and the dotted lines of the dorsal frontal eyes indicate that more than three frontal eyes can occur.

eyes. According to my knowledge, there are not even remnants of frontal eyes in that taxon (Elofsson, 1965). Further, he states, a symplesiomorphic character for Mandibulata should be the median complex (maybe the three-partite eye) with four (ommatidia!) eyes reduced to three in crustaceans. It is difficult to find this idealized type among the actual eyes in recent species. The frontal eyes are also claimed to co-evolve together with protocerebral neurohemal organs. The functional connection of these entities, and the reason why they are connected is not provided (Wägele, 1993). If the protocerebral innervation is the reason, the organ of Bellonci and cavity receptor organ are left without explanation. Thus this type of phylogenetic work lacks acceptance of the true nature of the frontal eyes of crustaceans.

Numerous cladistic, or numerical systematic works, supplement the "classical" phylogenetic approaches. The cladistic method can be based on descriptions of structures. In that case, with regard to the frontal eyes, the underlying notion up to present time is that they are homologous (common decent) in crustaceans or even arthropods. Character codes used for the cladograms only signal present or absent, four or five cells, etc. A deeper understanding of structure and relationships is thereby lost. The evolution of frontal eyes in crustaceans is more tuned-up than hitherto grasped and the cladistic methods need to include this.

My method is opposite to those above beginning with a generalized type of frontal eyes and a preconceived view of common descent. The starting point is the study of the structure of the frontal eyes in as many living crustaceans as possible, and applying the homology criteria, mentioned above, to establish similarity or not, and after that speculate on ancestral conditions. Thereby one avoids arguing in a circle, or as Remane (1961) phrases it "Die Gefahr eines Zirkelschlusses besteht in gleicher Weise bei einer Definition der Homologie aus dem Typus. Es ist umgekehrt, der Typus wird erst aus der vollgezogenen Homologisierung heraus konstruiert,…" (The danger of arguing in a circle remains in the same way by definition of homology from a type. It is the other way round; the type should be designed after a completed homologization…). It should also be mentioned that the view of separated lines of development of frontal eyes is influenced by the fact that the speed of organ development is much faster than previously believed (Nilsson and Pelger, 1994).

The three additional criteria coined by Remane (1961) have not been widely used, but they do add to the distinctness of the four groups of frontal eyes of the malacostracan, ostracod-maxillopodan, anostracan, and phyllopodan lines. The first states that even simple structures are homologous if they occur in a number of similar species. This is valid here since many species in the four groups have been shown to have similar frontal eyes. The second criterion valid for simple structures says, that, if more features appear in closely related species, they support homology. The ostracod-maxillopodan frontal eye type exemplifies this criterion. The third criterion states that the probability of homology decreases if the structure occurs in a number of species that are not related. The eye types above are restricted to species within one of the four groups and there are no transitional forms. Thus the concept of separate frontal eye types is strengthened. This third criterion is much neglected, but has a bearing on, e.g., cases like transmitter substances, such as histamine, ubiquitous in the animal kingdom or microvilli as a surface increasing structure, present in many unrelated animals.

The morphological arguments for the four types of frontal eyes are supported by functional experiments. Land (1984) reminds us that the Crustacea offer a greater diversity of eye types than any other invertebrate group. The frontal eye optics of the ostracod-maxillopodan line display a number of mirror, lens, and lens-mirror combinations as mentioned above. Crustaceans are thus capable of forming elaborate eyes, working after other principles than the compound eyes, the main visual organ. Molecular data referred to above (Oakley and Cunningham, 2002) give further support to those of morphology and function.

The entire organogenesis of the frontal eyes has been studied in three groups; in phyllopods (Dahl, 1959) malacostracans (Elofsson, 1966b) and anostracans (Benesch, 1969). The frontal eyes develop from ectodermal anlagen anterior to the brain. The early appearance of a small three-partite eye depends on the pelagic life of the first naupliar stages of the euphausids and dendrobranchiate decapods (penaeids belong to them) since the nauplius larvae are, according to Scholtz (2000), secondarily developed from an egg-nauplial stage. A common feature of the frontal eyes of crustaceans is that the frontal eyes, apart from the early three-partite eye, lag behind and become functional at the same time as the compound eyes or even after. The ectodermal anlagen of the frontal eyes are the only contributors to the frontal eyes in malacostracans and anostracans, whereas the phyllopod three-partite frontal eyes differ considerably, receiving additional eyes from the anlagen of the compound eyes, and maybe the brain. The consequence is large eyes and an irregular number of frontal eyes. The caudal and ventral frontal eyes are derived from two sides and thus in effect two frontal eyes which gives a six-partite eye.

The frontal eyes of crustaceans are considered primitive. In fact the frontal eyes of all arthropods have been thought to be so. A general assumption that simple eyes preceded other more complex visual organs, such as the compound, and ostracodan and copepodan eyes, seems reasonable (Nilsson, 1989; Elofsson, 1992; Nilsson and Osorio, 1997; Bitsch and Bitsch, 2005). The complex ostracod and copepod visual organs can, as a matter of fact, in recent species illustrate this process. Thus the general idea that frontal eyes are primitive and present in ancestors of arthropods, in the absence of evidence otherwise has to be accepted. It does not, however, support the idea that all simple eyes are similar. The study of recent crustaceans tells another story.

Coexistence of compound and frontal eyes constitutes a phylogenetic and a functional problem. Regarding the phylogenetic problem, if the frontal eyes are simply the forerunners of compound eyes, they should have become obsolete millions of years ago. The construction of the malacostracan frontal eyes admittedly makes them a plausible developmental base for ommatidia, but that does not apply to the inverted

non-malacostracan frontal eyes. There is thus no simple solution to be found in the present day frontal eyes. Coexistence of compound and frontal eyes is also a functional problem. In those cases where the frontal eyes are the only eyes, it is easy to comprehend their raîson d'étre. But when they occur together with compound eyes they seem more like a fifth wheel. Division of labour between compound and frontal eyes is, of course, an explanation for the persistence of frontal eyes. Sadly, apart from the highly developed frontal eyes of ostracods and copepods, which substitute for compound eyes, the function of the frontal eyes is unclear. The experimental work done on frontal eyes has mostly concerned whether they have a function at all, and no study has addressed their precise role in the visual process and cooperation with compound eyes.

Having varying kinds of frontal eyes of crustaceans does not necessarily assault a common decent of the Crustacea. It needs, however, difficult enough, an acceptance of separate and parallel evolution of non-homologous organs, which in this case leads toward a varied solution to visual problems, within the evolution of crustaceans.

Acknowledgements

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