

The foveal photoreceptor mosaic in the pipefish, *Corythoichthyes paxtoni* (Syngnathidae, Teleostei)

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Summary. The foveal and non-foveal retinal regions of the pipefish, *Corythoichthyes paxtoni* (Syngnathidae, Teleostei) are examined at the level of the light and electron microscopes. The pipefish possesses a deep, pit (convexiclivate) fovea which, although lacking the displacement of the inner retinal layers as described in other vertebrate foveae, is characterised by the exclusion of rods, a marked increase in the density of photoreceptors and a regular square mosaic of four double cones surrounding a central single cone. In the perifoveal and peripheral retinal regions, the photoreceptor mosaic is disrupted by the insertion of large numbers of rods, which reduce spatial resolving power but may uniformly increase sensitivity for off-axis rays. In addition to a temporal fovea subtending the frontal binocular field, there is also a central area centralis subtending the monocular visual field. Based on morphological comparisons with other foveate teleosts, four foveal types are characterised and foveal function discussed with respect to the theoretical advantage of a regular square mosaic.

Key words: Fish, Retina, Fovea, Rods, Cones, Photoreceptor mosaic

Introduction

A retinal pit or fovea has been described in a number of vertebrate groups but was once thought to be restricted to primates (Weale, 1966), birds (Fite and Rosenfield-Wessels, 1975) and reptiles (Harkness and Bennett-Clarke, 1978; Fite and Lister, 1981). However, the syngnathid fovea was described over 100 years ago and since then a large number of marine teleosts have also been found to possess foveae. Found in various genera such as *Syngnathus* (Krause, 1889; Chievitz, 1890; Slonaker, 1897; Rauther, 1925; Verrier, 1928a,b;

Kahmann, 1934, 1936; Walls, 1942) and *Hippocampus* (Carriere, 1885; Krause, 1886; Slonaker, 1897; Verrier, 1928b; Kahmann, 1934, 1936), the syngnathid fovea was thought to subservise both binocular (aided by foveal fixation) and monocular vision due to its location in the central region of the fundus and the extreme mobility of the eyes (Kahmann, 1934; Walls, 1942). Moreover, it was even suggested that there was a strong correlation between the development of the fovea and the extent of voluntary eye movements (Walls, 1942).

More recently, the relationship between the presence of a fovea and increased eye mobility has been noted in a number of other teleosts including the cod, *Serranus cabrilla* (Verrier, 1928a), the kelp bass, *Paralabrax clathratus* (Schwassmann, 1968), the blenny, *Pholis gunellus* (Verrier, 1933), the sandlance, *Limnichthys fasciatus* (Pettigrew and Collin, 1995), the clingfish, *Gobiesox strumosus* (Wagner et al., 1976) and the sandperch, *Paraperchis nebulosus* (Easter, 1992). In fact, in addition to the approximately 10 syngnathid species described, foveae have now been confirmed in over 42 shallow-water (Rochon-Duvigneaud and Roule, 1927; Verrier, 1928b, 1933; Kahmann, 1936; Walls, 1942; Rochon-Duvigneaud, 1943; Schwassmann, 1968; Vrabc, 1969; Munk, 1969, 1971, 1975; Ali et al., 1973; Wagner et al., 1976; Collin and Collin, 1988a; Easter, 1992) and 30 deep-sea (Brauer, 1908; Walls, 1937, 1940, 1942; Vilter, 1954; Munk, 1966, 1968, 1975; Locket, 1977, 1985, 1992; Bertelsen et al., 1976; Collin et al., 1994; Wagner et al., 1998) species of teleosts.

In conjunction with an increase in photoreceptor (Zaunreiter et al., 1991; Beaudet et al., 1997) and ganglion cell (Collin and Pettigrew, 1988a,b; Collin, 1999) densities, areae centrales have been shown to subservise higher spatial resolution in specific regions of the visual field (Collin and Pettigrew, 1989; Van der Meer and Anker, 1984; Shand, 1997). However, although the foveal increases in receptor density may be included beneath this broad umbrella of retinal specialisations, the steep-sided retinal pit may also provide other optical advantages. These include image magnification (and therefore increased visual resolution) at the centre of the convexiclivate pit (Walls, 1942;

Snyder and Miller, 1978), the detection and maintenance of accurate fixation (Pumphrey, 1948), monocularly-mediated directional focus (Harkness and Bennett-Clarke, 1978) and the perception of depth (Munk, 1975; Locket, 1992). These foveal studies have all been undertaken in a range of vertebrate groups and, given the structural diversity described and the range of visual strategies, there may be a number of foveal types.

This diversity has been identified in the bifoveate retinae of anolis lizards (Fite and Lister, 1981) and birds (Fite and Rosenfield-Wessels, 1975; Moroney and Pettigrew, 1987), in which the two foveae even in the one species may differ both structurally and functionally. In both these predatory groups, a central steep-sided (convexiclivate) fovea subtends the lateral monocular visual field with high spatial resolving power, while the temporal shallow-sided (concaviclivate) fovea subtends the frontal binocular visual field with lower spatial resolving power (Fite and Rosenfield-Wessels, 1975; Fite and Lister, 1981). Moreover, the foveal characteristics may influence foraging behaviour and prey type. Although there are no reports of bifoveate teleosts, these appears to be a large degree of structural diversity where the shape, depth and position of the foveal clivus all show interspecific differences in fish inhabiting disparate ecological niches from shallow-water to deep-sea (Collin, 1997). The densities of retinal receptors (photoreceptors and ganglion cells) and the degree of lateral displacement of the inner retinal layers also show remarkable diversity suggesting different functional roles.

One way of assessing foveal function is to examine the arrangement, spacing and morphology of the photoreceptors that comprise the mosaic. The functional significance of particular cone mosaics is still unknown. However, a number of authors agree that most species which feed on fast moving prey and need high spatial resolution possess a regular cone mosaic which may improve the perception of movement (Lyll, 1957; Dathe, 1969; Bathelt, 1970; Wagner, 1972; Ahlbert, 1969, 1973). Following the characterisation of the spectral sensitivity of each photoreceptor type, the function of the mosaic may also be assessed with respect to the chromatic sampling of the image. The size and spacing of the photoreceptors comprising the foveal mosaic place limits on the spatial resolving power of the eye. Detailed analysis of the morphology of each photoreceptor type provides an index of sensitivity given the types of photoreceptors comprising the mosaic. Diurnal shallow-water species with foveae predominantly possess pure-cone foveae while nocturnal deep-sea species possess pure-rod foveae but the degree of sensitivity may be a function of receptor density and the degree of summation (Munk, 1975; Collin et al., 1994) where, given equal concentrations of visual pigment, cones may be as sensitive as rods (Munz and McFarland, 1973). Interestingly, the amphibious clinid, *Dialommus fuscus* (Munk, 1969) and the scarid, *Cryptotomus roseus* (Ali et al., 1973) are both diurnal but possess both rods

and cones within the fovea while the deep-sea notosudids, *Scopelosaurus hoedti* and *Ahliesaurus berryi*, which survive beyond the penetration limits of sunlight, both possess a pure-cone fovea (Munk, 1975). Although no analysis of these foveal photoreceptor mosaics has been undertaken, the incorporation of both types of photoreceptors into the mosaic suggests that different arrangements may provide functional advantages as has been suggested for non-foveal retinae (Engström, 1963a).

Despite the widespread occurrence of foveae in teleosts, few detailed studies have investigated the photoreceptor types or their arrangement in foveal and non-foveal retinal regions at the ultrastructural level. In the pure-cone fovea of the sandlance, *Limnichthyes fasciatus*, four equal double cones surround a single cone with each photoreceptor unit tightly-packed into a regular square mosaic. Ultrastructural analysis shows that rods are present only in non-foveal retinal regions but in relatively low numbers with a ratio of 20 cones to one rod (Collin and Collin, 1988a). The convexiclivate fovea in the sandlance, as in some deep-sea alepocephalids (Wagner et al., 1998) is also characterised by the radial displacement of all the inner retinal layers (described by some authors as a «true fovea»), a marked concentration of visual cells and low summation ratios mediating high spatial resolving power (Collin and Collin, 1988b).

Despite the wealth of structural studies of the syngnathid fovea, there is no agreement regarding the foveal shape or the type and arrangement of photoreceptors within foveal and non-foveal retinal regions (Engström, 1963a). Müller (1874, as cited by Engström, 1963a) reported that there is only one type of visual cell in *Syngnathus acus*, while Krause (1886) reported both rods and cones in *Hippocampus sp.* Both Verrier (1928b) and Walls (1942) found only single cones in three species of syngnathids and considered that double cones were not associated with sharp vision and therefore were not present in any teleost fovea. Engström (1963a) found equal double cones and two types of single cones arranged in a regular square mosaic with only few rods in an undefined region of the retina in *Siphostoma typhle*. Munk (1975) describes the fovea of the deep-snouted pipefish, *Syngnathus typhle* as an asymmetrical slit-like depression with a regular square pattern of single and twin cones packed tightly into a density of 10.7×10^4 cones per mm^2 . Walls (1942) even claims that the syngnathid retina may possess two foveae, while Easter (1992) fails to find any foveae in the short-tailed pipefish, *Trachyrhamphus bioarctatus*, the spotted seahorse, *Hippocampus kuda* and one other unidentified species of seahorse.

This study investigates the morphology of the foveal clivus in the syngnathid pipefish, *Corythoichthyes paxtoni* with special reference to the characterisation and arrangement of the photoreceptors in foveal and non-foveal regions of the retina at the level of the light and discrepancies found in the published literature but also

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highlight the morphological diversity of the teleost fovea and the photoreceptor mosaic in an attempt to provide some functional bases for interspecific comparisons. This study also forms the basis of future developmental studies of foveal photoreception which will concentrate on the formation of chromatic sampling arrays.

Materials and methods

Five individuals (8 to 12 cm in length) of the pipefish, *Corythoichthyes paxtoni* Dawson 1977 (Syngnathidae, Teleostei) were collected on Heron Island Reef under permit by the Great Barrier Reef Marine Park Authority (GBRMPA) in Australia and maintained in large holding tanks at the University of Queensland Research Station under natural light/dark cycles. Two preserved adult specimens were donated by the Australian Museum.

Collected animals were killed with an overdose of tricaine methane sulphonate (MS222, 1:2,000) under the ethical guidelines of the National Health and Medical Research Council of Australia. The eyes were excised and either immersion-fixed in 4% paraformaldehyde in 0.1M phosphate buffer (pH 7.4) (light microscopy) or fixed in 4% glutaraldehyde in 0.067M sodium cacodylate buffer (pH 7.4) overnight following the removal of the cornea, lens and vitreous (electron microscopy). The museum specimens had previously been fixed in 10% formalin and stored in 70% ethyl alcohol and were only used for light microscopy. A total of eight whole eyes (including the formalin-fixed eyes) were embedded in either LR white resin or Histoiresin for light microscopy and 1 to 2 micron sections cut on a rotary microtome (American Optical) using a steel knife. Sections were stained with either Toluidine blue or Richardson's stain, dehydrated and coverslipped for analysis with a compound microscope (Olympus BH-2). The remaining six eyes were used for electron microscopy. Foveal and non-foveal retinal pieces were

post-fixed in a solution of 2% osmium tetroxide and 1.5% potassium ferrocyanide in 0.1M sodium cacodylate buffer. Tissue was then dehydrated in acetone and embedded in resin (Polybed/812, Polysciences Inc). Selected foveal and non-foveal retinal tissues were oriented carefully so that thick (1 μm) and thin (50 nm) sections of the photoreceptor array were obtained in both the transverse and tangential planes. Semithin sections were stained with either Richardson's stain or paraphenylenediamine and examined by standard light or phase-contrast microscopy, respectively. Ultrathin sections (50 nm) were stained with lead citrate and uranyl acetate and examined on a Siemen's Elmiskop 1A electron microscope.

All measurements were made on enlargements of electron micrographs using a magnifier and graticule. Lens dimensions used for the calculations of spatial resolving power outlined in the discussion were obtained from resin sections of the whole eye of the smallest individual (80 mm standard length) used in a previous study of the anterior segment of the pipefish, *C. paxtoni* by Collin and Collin (1995) after correction for shrinkage (Browman et al., 1990). Photographs were taken on either 35 mm Kodak Technical Pan film (rated at 50 ASA, light microscopy) or Kodak 4489 electron microscope film.

Results

General features of the fovea

The fovea of the pipefish, *Corythoichthyes paxtoni* is located in the temporo-dorsal region of the retina, 15° above the horizontal plane, subtending the frontal region of the visual field when the eyes are at rest. Therefore, the fovea subtends the region of the frontal visual field in front of the mouth which is situated at the end of an elongated snout. However, the eyes of the pipefish move independently and are highly mobile and are able to scan

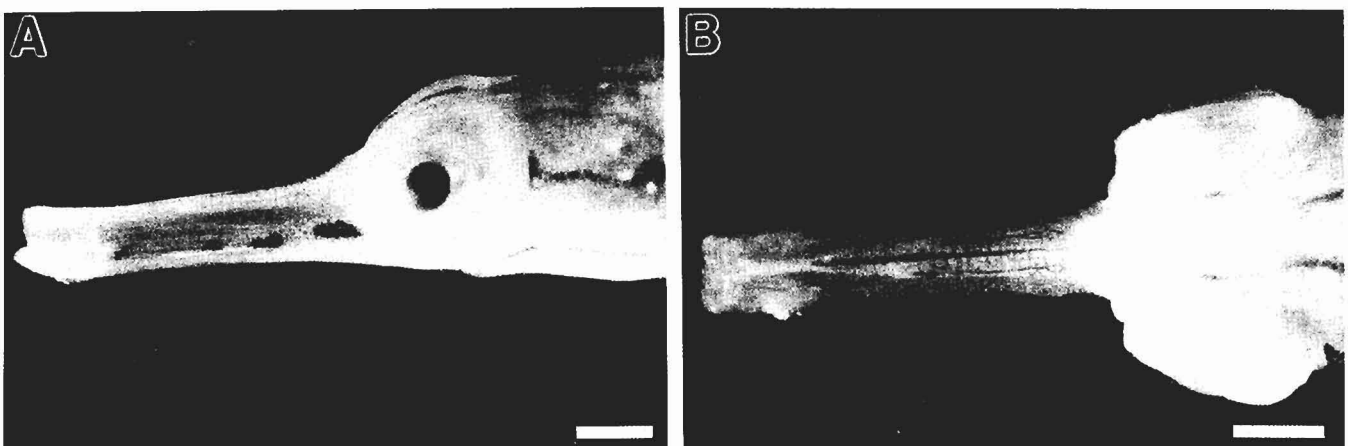


Fig. 1. **A.** Lateral view of the head of the pipefish, *Corythoichthyes paxtoni* showing its long snout and small mouth. Bar: 5 mm. **B.** Dorsal view of the head. The eyes are highly mobile and can subtend both monocular and binocular regions of the visual field. Bar: 5 mm.

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the upper and lower regions of their frontal visual field, often fixating on moving prey, such as small crustaceans, before sucking them into their small mouth (Fig. 1A,B).

The fovea is convexiclivate where the retina forms a deep invagination or slit-like pit with steep, sloping sides

(Fig. 2A). The retina is 250 μm in thickness within the foveal pit, increasing to 420 μm in the perifoveal region before falling again to approximately 230 μm in the periphery (Fig. 2B). The boundaries of all the neuronal layers within the retina, including the inner (ILM) and

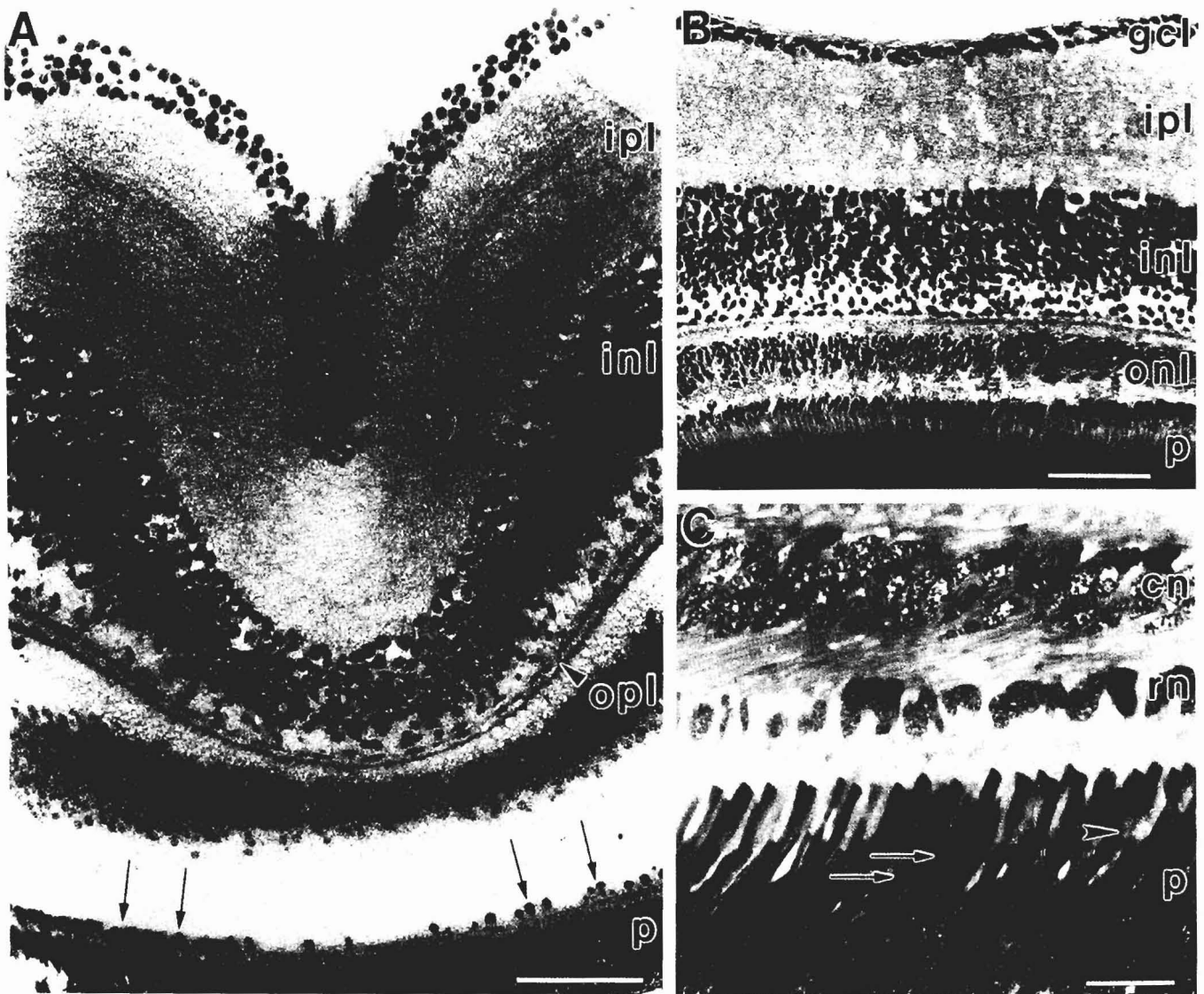
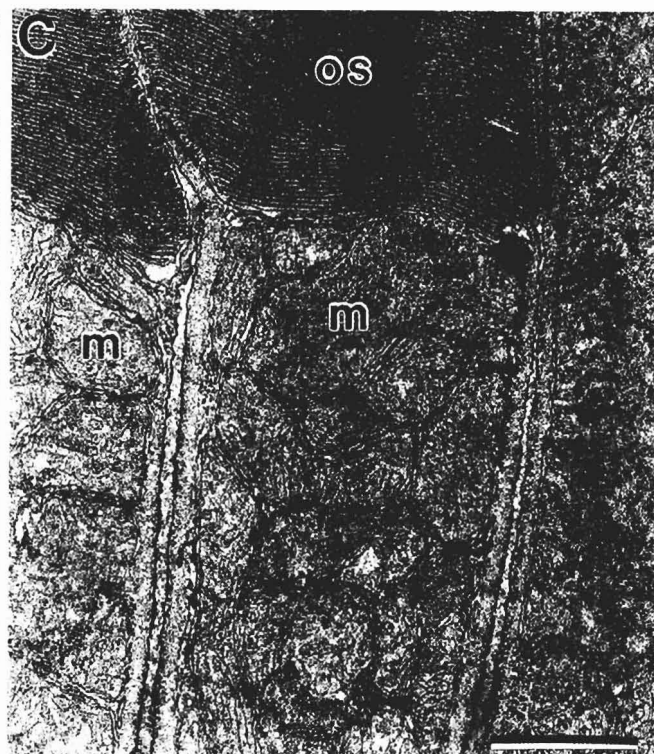
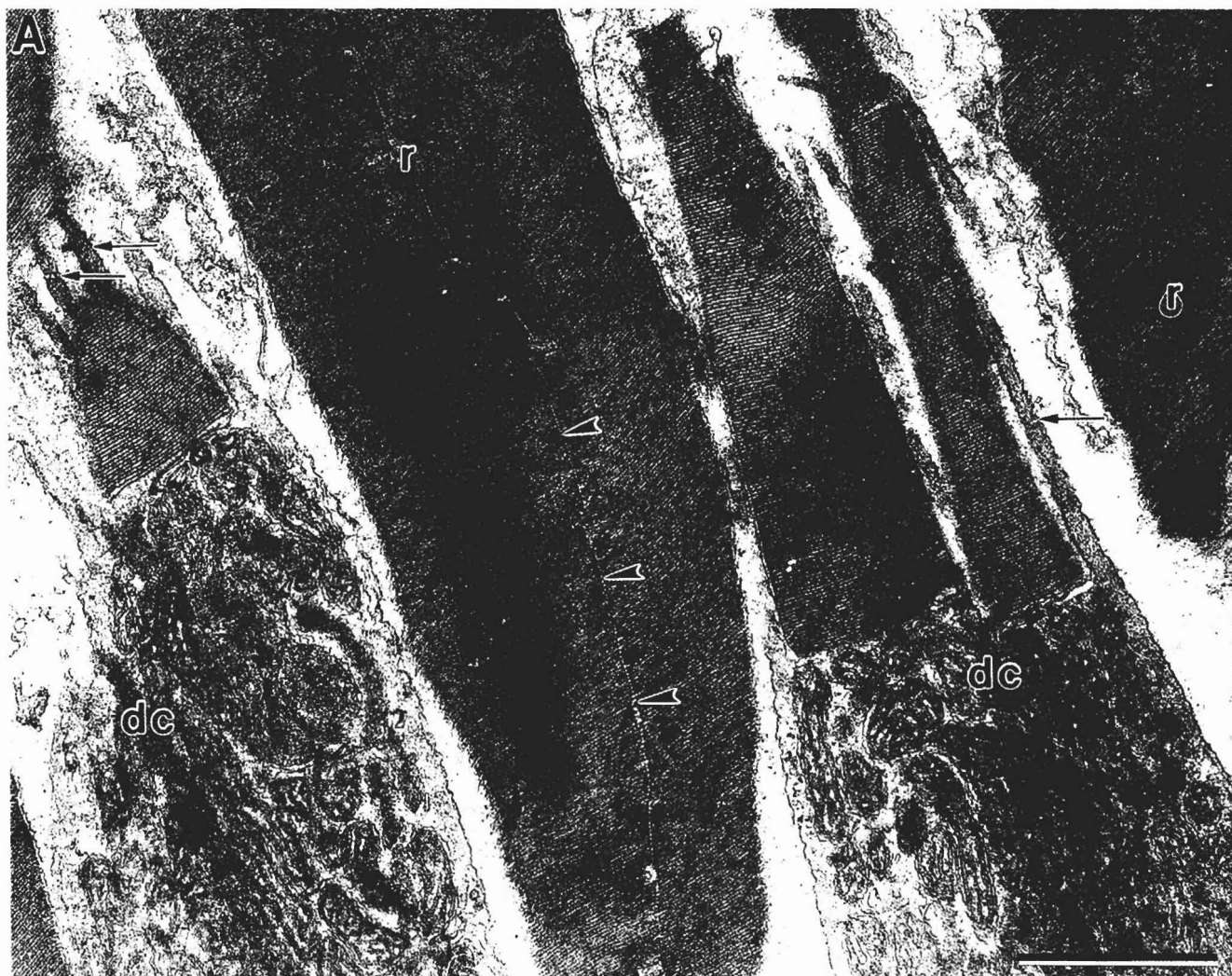


Fig. 2. **A.** Radial section of the convexiclivate fovea of the pipefish showing the lack of rods beneath the retinal pit (rod nuclei within the perifoveal region are depicted by the arrows). Note the other retinal neurons are not displaced in this region but only reduced in density. Bar: 50 μm . **B.** Radial section of the peripheral retina showing the marked difference in thickness from the foveal retina and the high density of rods (darkly-staining sclerated layer of nuclei within the bistratified outer nuclear layer, onl). Bar: 50 μm . **C.** Higher magnification of the outer nuclear and photoreceptor layers in the retinal periphery showing the division of rod (rn) and cone (cn) nuclei. Arrows depict the long cylindrical outer segments of the rods and the arrowhead depicts an equal double (twin) cone. Bar: 15 μm . gcl: ganglion cell layer; inl: inner nuclear layer; ipl: inner plexiform layer; opl: outer plexiform layer; p: photoreceptor layer.

Fig. 3. **A.** Electron micrograph of a radial section of peripheral retina showing the equal double (twin) cones (dc) and rods (r). The arrows depict the calycal processes surrounding the outer segments of the double cones and the arrowheads depict a longitudinal incisure within the membranous discs of a rod outer segment. Bar: 0.5 μm . **B.** Higher magnification of the outer segment discs of a single cone (sc) and a rod (r). Arrowheads indicate a rod incisure. Bar: 2.0 μm . **C.** Radial section of three rods at the level of their ellipsoids. os: outer segment; m: mitochondria. Bar: 1.0 μm .



outer limiting (OLM) membranes closely follow the contours of the foveal invagination to approximately a radius of 280 μm from the base of the foveal pit. In the perifoveal region, each of the retinal layers increases up to double its peripheral thickness. This translates into a marked increase in the density of all neuronal cell types within the perifoveal region (with the exception of the rod photoreceptors, Fig. 2A and see below). The foveal depression is asymmetrical with the exact curvatures of the sloping sides difficult to describe definitively due to histological processing. However, in the horizontal plane, the temporal perifoveal region has a larger radius of curvature than the rostral perifoveal region. In the vertical plane of section, the sides of the foveal pit are steeper, more symmetrical and although artificially-exaggerated in Fig. 2A, are convex in shape. The inner retinal layers are not displaced laterally as is classically described for some vertebrate foveae with all retinal classes of neurons lining the inner aspect of the foveal curvature.

In the central region of the fundus, the retina is also specialised. The retina of the area centralis is thicker due to a localised increase in photoreceptor length (by a factor of 40%) and an increase in both inner and outer nuclear layer neurons. Slight increases in ganglion cell and photoreceptor density may also exist but no detailed topographic analysis was undertaken. This second specialisation appears as a bulge in the retina and contains both rods and cones.

Classification of photoreceptor types

Based on morphological criteria, two types of cone photoreceptors underlie the foveal invagination; single cones and equal double (twin) cones in a proportion of 1:4. No rods lie within a radius of 90 μm from the base of the foveal pit (Figs. 2A,C, 3A-C).

The single cones are up to 86 μm in length (measured from the vitread limits of their nuclear membrane to the sclerad limit of their outer segment discs) and 2.0 μm in diameter (measured at the base of the outer segment). Their outer segments are tapered, surrounded by up to 16 calycal processes and are attached to a mitochondria-rich inner segment via a non-motile connecting cilium (Fig. 3B). Beneath the ellipsoid, the myoid region of the single cones tapers substantially to penetrate the OLM. The outer nuclear layer is divided into two sublaminae: a sclerad layer of rod nuclei and a vitread layer of cone nuclei separated by the thin myoid processes of the cones (Fig. 2C). This arrangement of sclerad rod nuclei and vitread cone nuclei is in contrast to the opposite arrangement in most other teleosts and may spread the large numbers of cone nuclei, bipolar cells and ganglion cells over a wider retinal region avoiding the need to further increase retinal thickness in such a small eye (Munk, 1975), possibly accounting for the oblique displacement of the cone myoid fibres in the region of the fovea and the area centralis. Although differentiation of the cone nuclei into single and double cone nuclei was

not attempted, a thin layer of darkly-staining (osmiophilic) nuclei situated more vitread may correspond to the single cones which appear in lower density than the double cones throughout the retina. The nuclei of both the single and double cones are up to 6 μm in diameter and, although some cone nuclei extend across the base of the foveal pit, many cone nuclei which contribute an inner and outer segment to the densely-packed photoreceptor array within the fovea, lie in the perifoveal region sending long myoid processes towards the foveal pit at an oblique angle.

The equal double cones are up to 92 μm in length (measured from the vitread limit of the nuclear membrane to the sclerad limit of the outer segment discs) and are up to 2.6 μm in diameter (measured at the base of the outer segment). The outer segment discs of both single and double cones are 15 nm in diameter with an interdisc space of 25 nm (Fig. 3A,B). The outer segment of each component of the double cone is of equal size, tapered and surrounded by up to 20 calycal processes (Fig. 3A). Both single and double cones possess accessory outer segments. The two components of each double cone are contiguous along the length of their inner segments as far as the OLM where their juxtaposed membranes appear thicker and more darkly staining. Beneath each apposing membrane lies a subsurface cistern. The mitochondria within the ellipsoid region are densely-packed, slightly smaller in diameter than those of the single cones and are often elongated longitudinally (Fig. 3A).

The rods first appear singly within the perifoveal region and progressively increase in density towards the periphery, although there appear to be few, if any, rods present in the central zone of retinal thickening or area centralis. Each rod is up to 75 μm in length (measured from the vitread limit of its nuclear membrane to the sclerad limit of its outer segment discs) with an outer segment diameter of up to 3.8 μm (Figs. 2C, 3C). The rod outer segment is cylindrical and possesses discs which are 15 nm in diameter and separated by an interdisc space of 12 nm. These dense stacks of discs are often interrupted by longitudinal seams or incisures where the discs are pinched off leaving a small space invaginating from the surface in one or two regions of the outer segment which may allow contact with the extracellular space (Fig. 3A,B). No accessory outer segments or calycal processes were observed in rods. The rod inner segment is cylindrical with a prominent ellipsoid of mitochondria, which is sclerad to a myoid region rich in polysomes, rough endoplasmic reticula and Golgi apparatus (Figs. 2C, 3C). Rod nuclei show a less dense chromatin pattern than cone nuclei, stain more darkly, are slightly smaller in size (up to 5 μm in diameter) and can be differentiated by their position within the sclerad substratum of the outer nuclear layer. The rod nuclei are also elongated with a substantial portion of their area perching the OLM.

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The foveal photoreceptor mosaic

In tangential section, the photoreceptors immediately beneath the foveal pit form a regular square mosaic

comprising four equal double (twin) cones surrounding a central single cone with the osmiophilic subsurface cisterns apposing the inner segment membranes of each cone doublet oriented perpendicularly to each other

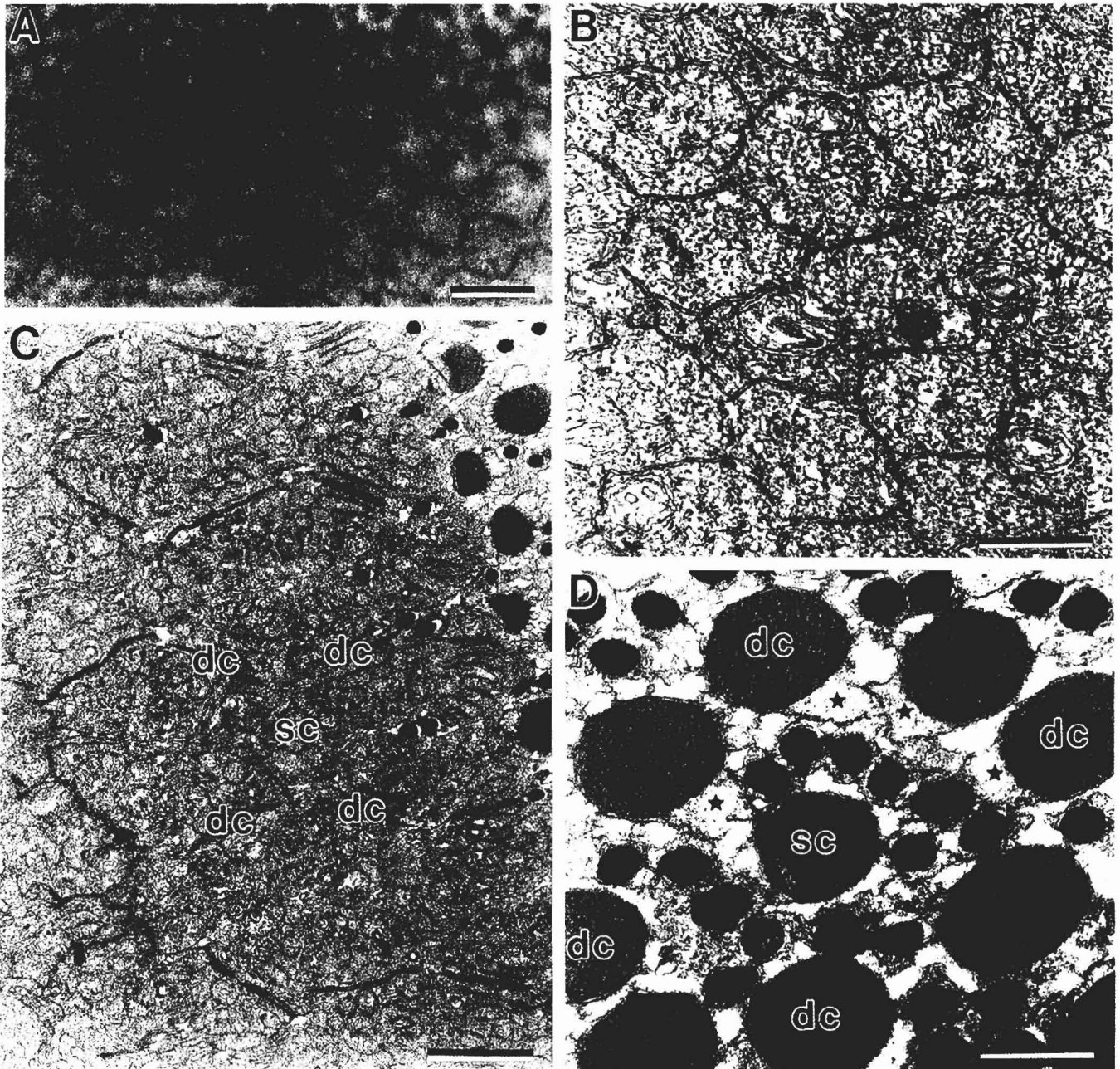


Fig. 4. **A.** Low power electron micrograph of the regular arrangement of photoreceptors in the foveal region observed in tangential section. The dark lines are the contiguous surfaces of each of the double cones in the array. Bar: 5 μm . **B.** Electron micrograph of a tangential section of the foveal photoreceptors at the level of their myoids. Note that at this level, the square mosaic is not present with each component of a double cone adopting an optimal hexagonal packing interrupted by the inclusion of the smaller myoid of a single cone (stars). Bar: 1.0 μm . **C.** Tangential section of the foveal photoreceptor array at the level of the ellipsoids. The array comprises a regular square mosaic with four double cones (dc) surrounding a single cone (sc). Bar: 2.5 μm . **D.** The foveal square mosaic at the level of the outer segments surrounded by melanosomes of the retinal pigment epithelium in the light-adapted state. Note the accessory outer segments (stars) of each component of the double cone are oriented towards the central single cone. Only one component of each double cone is labelled (dc). sc: single cone. Bar: 1.0 μm .

(Figs. 4A,C, 6A). This regular pattern is not evident at the level of the myoids although small diameter profiles, which may represent the myoids of single cones, are inserted haphazardly into an otherwise hexagonal array (Fig. 4B). Within this zone, the accessory outer segments of the double cones are oriented towards the central single cone of each repeating unit (Fig. 4D). There are no rods within the foveal mosaic.

The non-foveal photoreceptor mosaic

The perifoveal and peripheral photoreceptor mosaic is markedly altered by the insertion of rods. Although the square mosaic of four double cones surrounding a central single cone is still evident, the mosaic is disrupted with an irregular increase in cone spacing with eccentricity (Fig. 5A). In the more peripheral retinal regions, each double cone is surrounded by between 5 and 8 rods and each single cone by 4 rods (Fig. 5A-C; 6B). At both the light and electron microscopic levels, the darker-staining rods form fairly regular rosettes or rings with a ratio of approximately 22 rods:4 double cones:1 single cone if one includes all the rods, either inserted or surrounding the regular square mosaic (Fig. 5A,C; 6B). The orientation of the accessory outer segments of the double cones seems to be identical to that found for the double cones within the foveal mosaic.

Discussion

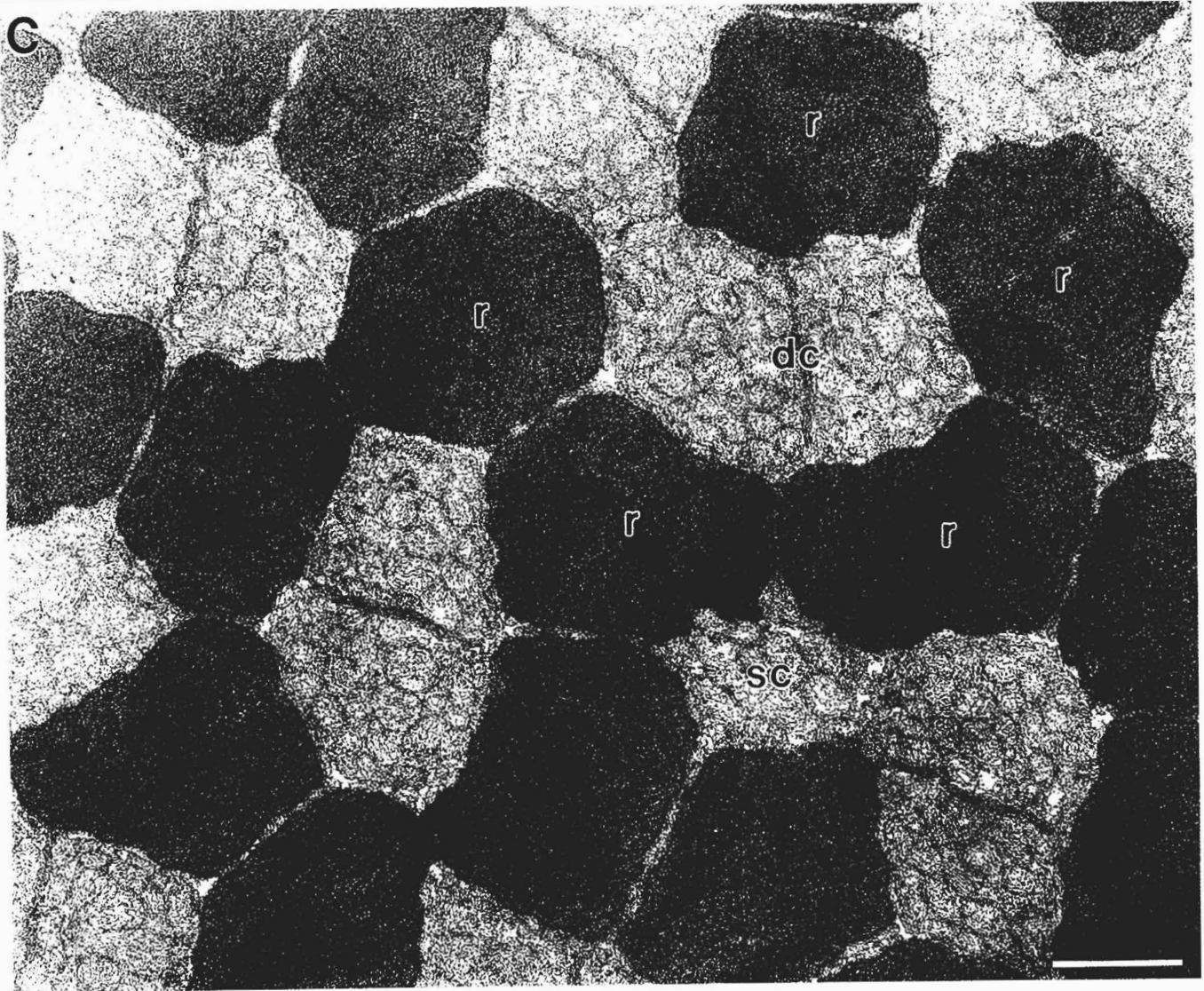
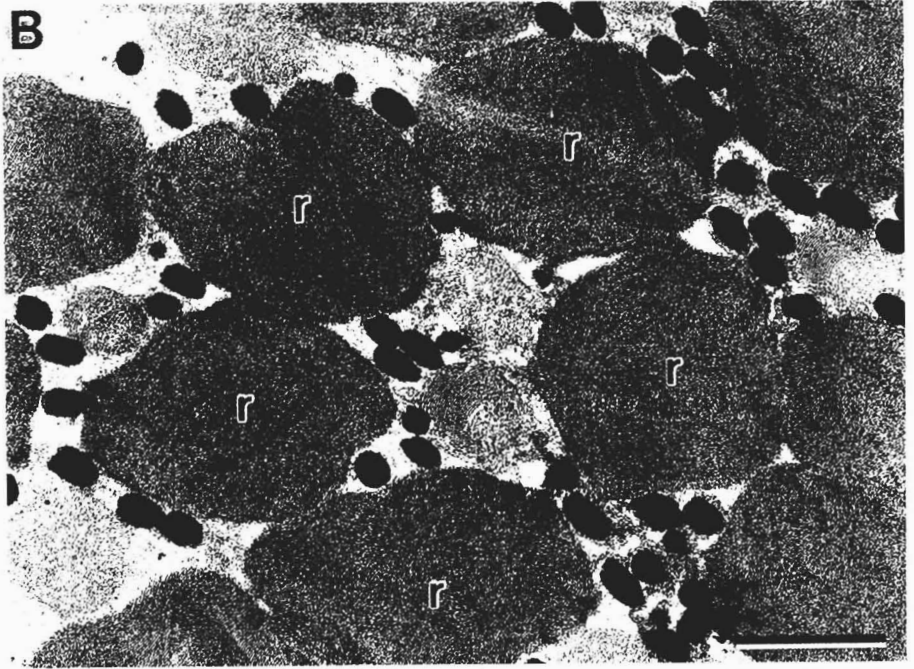
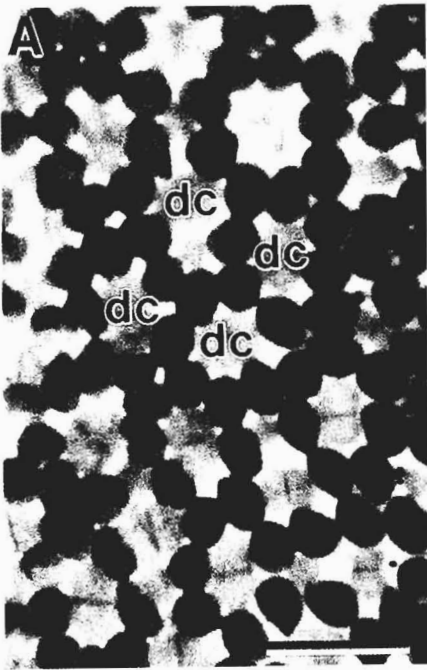
The structure and function of the pipefish fovea

This morphological study confirms that the pipefish, *Corythoichthyes paxtoni* possesses a steep-sided (convexiculate) fovea in temporal retina and a retinal thickening thought to be an area centralis (pending quantitative analysis) in central retina, confirming a previous description of the syngnathid retina in the deep-snouted pipefish, *Syngnathus typhle* (Munk, 1975). The morphology and location of these two retinal specialisations suggest disparate functions given that the area centralis is a thickening of the retina and the fovea is a retinal indentation. Both regions contain high densities of receptors and a concomitantly low convergence ratio thereby mediating increased spatial resolving power in the monocular (area centralis) and binocular (fovea) regions of the visual field. However, up to three areae centrales have previously been found in both monocular and binocular retinal regions of some teleosts (Collin and Ali, 1994; Collin, 1999). This implies there may be specific advantages in possessing a foveal invagination. Although conjectural, several

hypotheses have been put forward to elucidate the function of the vertebrate fovea. Image magnification may result from a marked change in refractive index between the vitreous and the sloping sides of the foveal retina thereby increasing visual resolution (Walls, 1937, 1940, 1942; Snyder and Miller, 1978; Locket, 1992; Collin et al., 1994). The fovea may play a major role in the detection and maintenance of fixation providing an increased sensitivity to small angular movement as the image of a moving object is distorted by the curvature of the pit (Pumphrey, 1948). In conjunction with a high degree of independent eye mobility, a deep foveal pit may also act as a directional and monocular indicator of accommodative focus as has been found in the chameleon (Harkness and Bennett-Clarke, 1978) and in the marine sandlance (Pettigrew and Collin, 1995). In addition, where the foveal axes fall within a pronounced binocular overlap, skewing of eccentric images may also provide a useful cue about range and possibly a method of breaking luminescent camouflage in a number of foveate teleosts which have ventured into the deep-sea (Steenstrup and Munk, 1980; Locket, 1985, 1992; Wagner et al., 1998).

Based on morphological, ecological and functional diversity, we propose that the teleost fovea may be characterised into at least four distinct types. Type I is exemplified by the syngnathid fovea, such as that in *C. paxtoni*, and is characterised by a steep-sided (convexiculate) retinal pit without a lateral displacement of the inner retinal layers. Other examples of this type are found in the bass, *Paralabrax nebulifer* (Schwassmann, 1968) and the barred sand perch, *Parapercis nebulosis* (Easter, 1992). A Type II fovea is also convexiculate but the inner retinal layers are displaced laterally leaving an unimpeded path for the incident light to strike the underlying photoreceptors. Examples of a Type II fovea are found in the sandlance, *Limnichthyes fasciatus* (Collin and Collin, 1988a) and the notosudid, *Scopelosaurus hoedti* (Munk, 1975). Type III foveae are similarly convexiculate but possess a thick foveal lining of radial fibre processes putatively thought to be refractive. Examples of this foveal type are found in the deep-sea alepocephalids, *Conocara macroptera* (Collin et al., 1994; Wagner et al., 1998) and *Alepocephalus bairdii* (Locket, 1992). Although changes in refractive index within foveal and perifoveal retinal regions still remain to be tested in any species, indices of 1.3353 (vitreous) and 1.3494 (retina) measured in *Chondrostoma nasus* (Nicol, 1989) suggest that this gradation may have an optical effect. Changes in foveal thickness, the displacement of the inner retinal layers and variations in the shape of the foveal clivus will

Fig. 5. **A.** Light micrograph of the photoreceptor array in tangential section showing the regular rosette pattern of rods which have been inserted within the square mosaic of double (dc) and single cones in non-foveal regions of the retina. Note that the regular square cone mosaic observed is still present but with an increased spacing. Bar: 10 μ m. **B.** Electron micrograph showing the rosette pattern of rod outer segments (r) surrounding a double cone in tangential section. Bar: 1.5 μ m. **C.** Tangential section at the level of the rod outer segments (r) and double (dc) and single (sc) cone inner segments. Bar: 1.5 μ m.



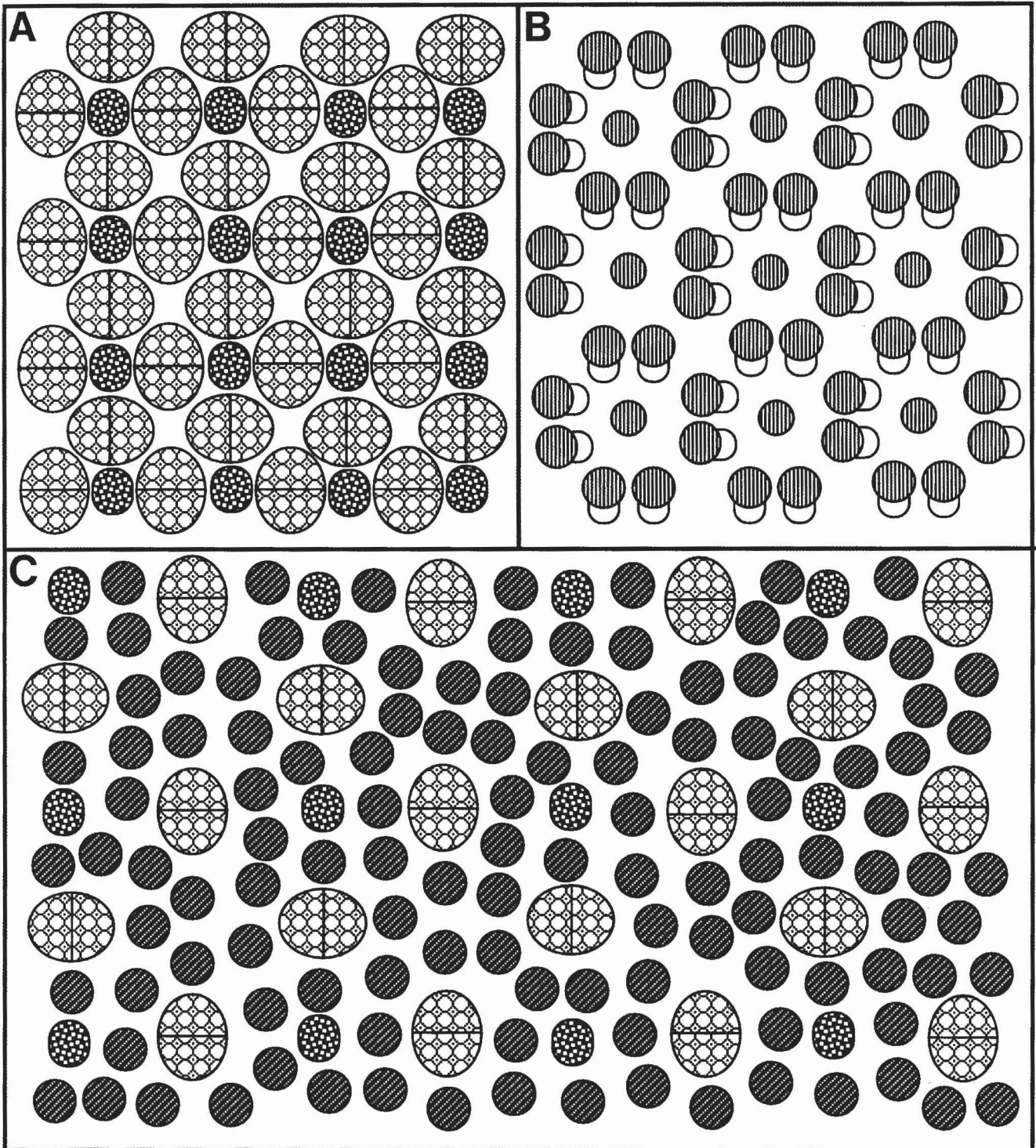
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Fig. 6. A, B. Schematic diagrams of the foveal photoreceptor mosaic in the pipefish sampled at the levels of the inner (A) and outer (B) segments. At the level of the inner segments, four double cones surround a central single cone in a tightly-packed array. More sclerad, the orientation of the outer segments of each unit remain the same with the accessory outer segments of at least two double cones facing towards the central single cone. C. Schematic diagram of the non-foveal photoreceptor mosaic at the level of the cone inner and rod outer segments. Note the regular square pattern is still evident but interrupted by the insertion of rods which form rings around each double cone.

Photoreceptor mosaic in the pipefish retina

undoubtedly produce different optical effects to satisfy specific ecological needs. Type III foveae may prove to be of particular interest given the widespread occurrence of the foveal lining in other vertebrates, such as birds (Locket, 1992), where the relative thickness of the dense radial fibre processes may comprise up to 40% of the foveal thickness (Locket, 1992; Wagner et al., 1998). Finally, the Type IV fovea is a shallow (concaviclivate) invagination of the retina where there is neither a lateral displacement of inner retinal layers or a radial fibre lining. Examples of this type are found in the banded toado, *Sphaeroides pleurostictus* (Collin, 1987) and the deep-sea, *Bathylagus benedicti* (Vilter, 1954). Further subdivisions may also be forthcoming as detailed morphological analyses of more foveate species are completed, the refractive indices of ocular media are measured and the optical importance of a sclerad evagination of the retina underlying the fovea (or foveae externae, reviewed in Collin, 1997) are better understood.

The Type I convexiclivate fovea of the pipefish, *C. paxtoni* is characterised by a deep retinal pit, the exclusion of rods, a marked increase in the density of all retinal neurons, a low summation ratio between the photoreceptors and the ganglion cells and high spatial resolving power. The resolving power in foveal and non-foveal retinal regions can be calculated using the formula; $\alpha = 2c/f$ in radians where α is the minimum separable angle in minutes of arc, c is the distance between the centres of adjacent cones and f is the focal length of the lens (Tamura, 1957). The focal length of the lens can be calculated using Matthiessen's ratio which states that the focal length of the spherical lens is 2.55 times the lens radius (Matthiessen, 1880). Although this ratio is thought to show interspecific variation (between 2.4 and 2.82), in the absence of direct measurements, a mean reported value of 2.55 is used here. Therefore, according to Matthiessen's ratio, focal length can be calculated by the formula; $f = 2.5r$ where r is the lens radius. Spatial resolving power can now be represented by; $\alpha = 2c/2.55r \times 180/\pi$ in degrees. So for an 80 mm (standard length) individual of *C. paxtoni* with a lens diameter of 0.5 mm, the foveal resolving power is 22.2 minutes of arc compared to 42.5 minutes of arc in the periphery. This compares to a foveal resolving power of 8.5 minutes of arc based on the average cone density calculated in a larger individual of the deep-snouted pipefish, *Syngnathus typhle* with a lens diameter of 0.9 mm (Munk, 1975). Therefore, with the incorporation of rods into the photoreceptor mosaic in non-foveal retinal regions in *C. paxtoni*, spatial resolving power is reduced, presumably providing increased rod-mediated sensitivity for off-axis rays.

The morphological differentiation of photoreceptor types

The photoreceptors of the syngnathid retina can be classified on ultrastructural criteria into three types;

double (twin) cones, single cones and rods. The foveal mosaic is comprised entirely of double and single cones with the incorporation of rods into the mosaic only occurring within the perifoveal and peripheral retinal regions. This refutes much of the earlier literature regarding the classification of photoreceptor types and confirms the findings of Munk (1975) who described the foveate retina of the deep-snouted pipefish, *Syngnathus typhle* at the level of the light microscope. Although, the two types of foveal cones require microspectrophotometric analysis, diurnal vision in the frontal region of the visual field is optimised. The two components of the double cones increase the cross-sectional area, the area of photon capture and therefore sensitivity. This increase in surface area, in conjunction with the fact that many double cone components possess visual pigments with different spectral absorptions, further enhances the sensitivity of the couplet to broad-band ambient light.

The function of the foveal square mosaic

Four double (twin) cones surrounding a central single cone form a regular foveal mosaic in *C. paxtoni*. Although present in the perifoveal and peripheral regions of the retina, rods are excluded from the foveal clivus which suggests this arrangement of cones provides some advantage in either high acuity sampling and/or the detection of prey in a diurnal environment. Although species which possess a square mosaic pattern have previously been associated with both an active, predatory lifestyle (Lyll, 1957; Boehlert, 1979; Van der Meer, 1992) and the optimisation of visual acuity in brightly-lit environments (e.g. in the weever fish, *Trachinus vipera*, Kunz et al., 1985, and the coral trout, *Plectropoma leopardus*, Collin 1989), this relationship is not always fulfilled. For example, the northern pike, *Esox lucius* is an active predator but possesses a regular flower petal arrangement of a central single cone surrounded by six double cones (Braekevelt, 1975) which suggests that both the composition and the arrangement of each photoreceptor unit may be of equal importance to some predatory species.

Theories put forward to elucidate the function of the square mosaic vary. This type of mosaic may increase visual acuity (Engström, 1963a,b; Anctil, 1969; Ahlbert, 1976) although both Willmer (1953) and Lyll (1957) consider that double cones are associated with vision in deep water (or low light) and thus should be intermediate in sensitivity between rods and single cones. Therefore, they would not contribute greatly to increases in visual acuity. The square mosaic may increase contrast (Ahlbert, 1976; Marc and Sperling, 1976; Van der Meer and Anker, 1984) and provide a more uniform spectral sampling (Bowmaker, 1990). Although the spectral sensitivities of the visual pigments in each component of the double cones in *C. paxtoni* are unknown, the regular arrangement of different types of photoreceptors into a square mosaic is also another way of sampling an image using different visual pigments

tuned to absorb maximally in different regions of the spectrum. The "alternating symmetry" of the double cones and an offset single cone may allow detailed chromatic patterns to be resolved (Lythgoe, 1979). The square mosaic may also mediate the detection of polarised light (Cameron and Pugh, 1991; Cameron and Easter, 1993; Rowe et al., 1994; Novales Flamarique et al., 1995) and possibly compensate for chromatic aberration of the lens provided the cone types are spectrally distinct and vertically-separated within the retina (Eberle, 1968). However, the most convincing theory, and not mutually exclusive, for the function of the square mosaic may be that it assists in the analysis of movement (Lyall, 1957; Engström, 1963a; Anctil, 1969; Bathelt, 1970).

Bathelt (1970) considers that the function of a row mosaic, as apposed to a square mosaic, relates to the perception of movement in different directions e.g. a row mosaic is suited to register movements in two directions and a square mosaic is used to register movements in all directions. This correlation is confirmed for a number of predatory salmonids that strike at moving prey in a three-dimensional environment and possess a square mosaic (Lyall, 1957; Ahlbert, 1976; Beaudet et al., 1997) compared to schooling salmonids which rely less on accurate strikes for prey and perceive a more two-dimensional environment along the horizontal plane and possess a row mosaic. Similarly, the non-schooling coral trout, *Plectropoma leopardus* (Collin, 1989), the sandlance, *Limnichthyes fasciatus* (Collin and Collin, 1988a; Pettigrew and Collin, 1995), the tuskfish, *Pseudolabrus miles* (Fineran and Nicol, 1974), the weeverfish, *Trachinus vipera* (Kunz et al., 1985) and the archerfish, *Toxotes jaculatrix* (Braekevelt, 1985) all strike moving prey with precision in a three-dimensional environment and possess a regular square photoreceptor mosaic. Therefore, in the foveate pipefish *C. paxtoni*, the square mosaic may be used primarily for the perception of movement of small approaching prey in conjunction with high visual acuity provided by an increased photoreceptor density, as has been suggested for the deep-snouted pipefish, *Syngnathus typhle* (Munk, 1975). In contrast, the row pattern of foveal cones in the deep-sea, *Scopelosaurus hoedti* (Munk, 1975) may aid in the fixation of more remote prey where the perception of depth may be subserved along a more two dimensional binocular axis (Locket, 1992).

Individual rods are not usually arranged into regular patterns in either foveal or non-foveal retinal regions but are randomly distributed amongst the single and double cones. However, the regular rosette pattern of rods in the perifoveal and peripheral retinal regions of *C. paxtoni* suggests an almost uniform sampling and an increase in sensitivity for the perception of off-axis images. It is currently unknown whether the rods in many deep-sea foveae which are arranged into a tightly-packed hexagonal array (Lloyd, 1994; Collin, 1997; Wagner et al., 1998) are simply optimising sampling or underlie other chromatic functions given the finding of more than

one visual pigment in the pure-rod retina of some species (Partridge et al., 1992).

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