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AN ATTEMPT TO CORRELATE PSEUDOPUPIL SIZES IN STOMATOPOD CRUSTACEANS WITH AMBIENT LIGHT CONDITIONS AND BEHAVIOR PATTERNS

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Abstract—1. The distribution of pseudopupils in the eyes of representatives of five genera of Stomatopoda has been studied.

2. A triple pseudopupil is seen when the eye is viewed perpendicularly to the specialized middle band on the cornea, but a double pseudopupil appears when the direction of viewing is moved five degrees away from the vertical, as a result of the skewing of ommatidia adjacent to the middle band.

3. Skewed ommatidia near the middle band constitute a monocular range-finder.

4. Species with the most complex behavior patterns have the most complex skewing patterns of ommatidia.

INTRODUCTION AND TECHNIQUES

Pseudopupil observations are commonly used for studying the direction of view of ommatidia, ommatidial angles and cone apertures (Stavenga, 1979; Kirschfeld, 1974, 1976; Horridge, 1978). In most arthropod eyes, ommatidia in different regions of the eye differ considerably in these three kinds of measurements (Horridge and Duelli, 1979).

Eye shape and the different structures of the middle bands in representatives of three superfamilies of stomatopods are discussed elsewhere (Manning *et al.*, 1984). We recognize four subcategories of corneal shape: cylindrical, semicylindrical, spherical, and elliptical.

All stomatopod eyes examined (except those of *Bathysquilla*, a deep sea form with degenerate eyes) have the cornea divided in two nearly bilaterally symmetrical halves by a middle band of either two (cylindrical, generally dim light eyes) or six (spherical or elliptical, mostly bright light eyes) rows of specialized ommatidia (Schiff *et al.*, 1984). The eyes of stomatopod crustacea have a characteristic system of skewing of ommatidia such that either two or three pseudopupils are present for any direction of viewing the eye. To analyze this system we first photographed the pseudopupils in living animals for different positions of the eye with respect to the viewing direction. Subsequently the eyes were excised, photographed, fixed and sectioned. Skewing of ommatidia was then measured in the sections by determining the inclinations of the anatomical axes of the ommatidia. Good correspondence was found between the data obtained by the two techniques. The probable errors in calculating acceptance angles (Snyder, 1979) and measuring skewing angles are almost certainly larger than the deviation between optical and anatomical axes. Furthermore, in the pseudopupil measurements the wide cornea–cone aperture is involved and not the acceptance angles of the rhabdoms. The pseudopupil observations are described here and an account of the histological results will follow (Schiff *et al.*, in preparation).

Sequences of ommatidia parallel to the middle band we call rows and the direction of these rows is horizontal. Sequences of ommatidia perpendicular to the middle band we call columns and their direction is vertical. Sides of the eyes are those parts of the cornea furthest away from the middle band; the submedian surface is between the middle band and the sides of the cornea. The back is defined as the margin with the stalk, and the front is opposite it. For more detailed definitions see Fig. 1 in Manning *et al.* (1984).

RESULTS

We have compared pseudopupils of stomatopod species from different luminous habitats which include depth *per se* and also localized niches. Pseudopupils were photographed from the following species and genera (systematics: Manning, 1980):

Squilla mantis (Squilloidea, Squillidae): Mediterranean from the dim light at 50–100 m depths, but also found in polluted surface waters.

Hemisquilla ensigera (Gonodactyloidea, Hemisquillidae): eastern Pacific, about 20 m depth in burrows.

Odontodactylus scyllarus (Gonodactyloidea, Odontodactylidae): Indian Ocean, about 5–10 m depths, living on coral reefs.

Gonodactylus festae, bredini, lalibertadensis, oerstedii, bahiahondensis (Gonodactyloidea, Gonodactylidae): American, 0–20 m, in rubble.

Pseudosquilla ciliata (Gonodactyloidea, Pseudosquillidae): Pacific, 0–1 m, in rubble or in burrows in sand.

While *Squilla* usually forages from a burrow and, to a lesser degree, so does *Hemisquilla*, the other species are more active. *Odontodactylus*, *Gonodactylus*, and *Pseudosquilla* move around and scan their environment continuously, hunting their prey actively. All stomatopods have a characteristic attention position of the eyes (and striking appendages) when optically stimulated. In the attention position the middle band is held approximately horizontal (about 30 degrees to the ground) except in *Gonodactylus* and *Pseudosquilla* which keep the middle band nearly vertical as seen from the front, and aligned with the body axis as seen from above.

When looking at the cornea with the viewing line perpendicular to the corneal surface of the middle band (zero degree), three pseudopupils are seen, one on each submedian surface and one in the middle band. These pseudopupils extend over nearly the whole cornea across the middle band in three separate, elongate sections. They do not extend into the sides and they are interrupted on each side of the middle band. When the eye is rotated along the middle band such that the viewing direction remains perpendicular to the middle band but different regions along it are viewed, the three-partitioned pseudopupil wanders over the cornea, shifting from one column to the next.

Rotations of the eye across the middle band so that the viewing direction is no longer perpendicular to the surface of the middle band causes the pseudopupils in the middle band and on the submedian surfaces to become gradually shorter. As the viewing angle increases beyond about 5 degrees, the pseudopupil in the middle band vanishes and the pseudopupils in the submedian surfaces transform into two smaller, round pseudopupils. These are not symmetrically located. The nearer to the middle band the pseudopupil is located in one half of the cornea, the further away it is on the other half.

Over the range of viewing angles from 5 to 25 degrees the pseudopupil across the middle band becomes a thin line a few facets long, parallel to the middle band. This line jumps to the next row for every 3–5 degree rotation for the first 4–5 rows next to the middle band.

At the far side of the cornea, small "false" pseudopupils are found which do not change with the direction of viewing the eye. These pseudopupils are due to ommatidia without cones.

The long, triple pseudopupil means that columns of ommatidia have parallel optical axes pointing out of the eye in the direction perpendicular to the corneal surface of the middle band.

The double pseudopupils derive from groups of ommatidia on the surfaces with optical axes in the viewing direction: the pseudopupil near the middle band indicates skewing of ommatidia towards the middle band on each side of it. That pseudopupil indicates ommatidia that are progressively smaller and more skewed the nearer they are to the middle band. The four rows of ommatidia nearest to the middle band are the most skewed and change skewing angles in steps 3–5 degrees. The other pseudopupil derives from ommatidia on the submedian surface where the optical axes turn and follow the curvature of the cornea. When looking at the eyes from the sides only one round pseudopupil is seen.

Pseudopupils in the different genera

Squilla mantis (*dim light*). *Squilla* has triple pseudopupils 3–4 ommatidia wide in its cylindrical corneas. Ommatidial apertures are wide and small turns of the eye (less than 5–8 degrees) do not significantly shift the position of the pseudopupil. The pseudopupil shape in the middle band is relatively broad, being spindle shaped on the two submedian parts of the cornea, broader in the middle parts of the two halves, and slimmer at the sides and near the middle band (Fig. 1). Moving the direction of view away from the strictly frontal direction results in a double pseudopupil composed of half-spindles comprising about half of each hemisphere of the cornea, never actually becoming round spots as in other stomatopods.

Hemisquilla ensigera (*dim to medium light*). Pseudopupils in *Hemisquilla* are more difficult to observe than in other stomatopods because the pseudopupils are only one ommatidium wide and are seen on a dark brown background (pigments of the retinula cells and accessory cells). Other stomatopods have green and white reflecting pigments over all of the retina surface and the dark pseudopupils show up in strong contrast. *Hemisquilla* eyes contain these pigments only on the sides of the eye.

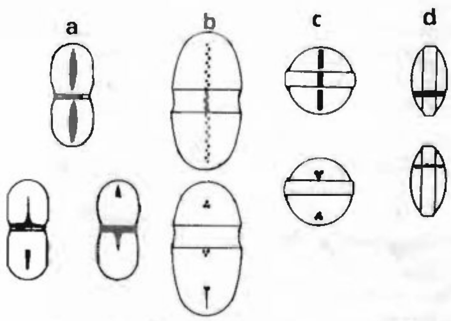

Fig. 1. Schematic drawing comparing pseudopupils in different genera. (a) *Squilla*. (b) *Hemisquilla*. (c) *Odontodactylus*. (d) *Gonodactylus*. Top, viewing direction perpendicular to surface of the middle band; bottom, viewing direction at an angle with respect to corneal surface of middle band.

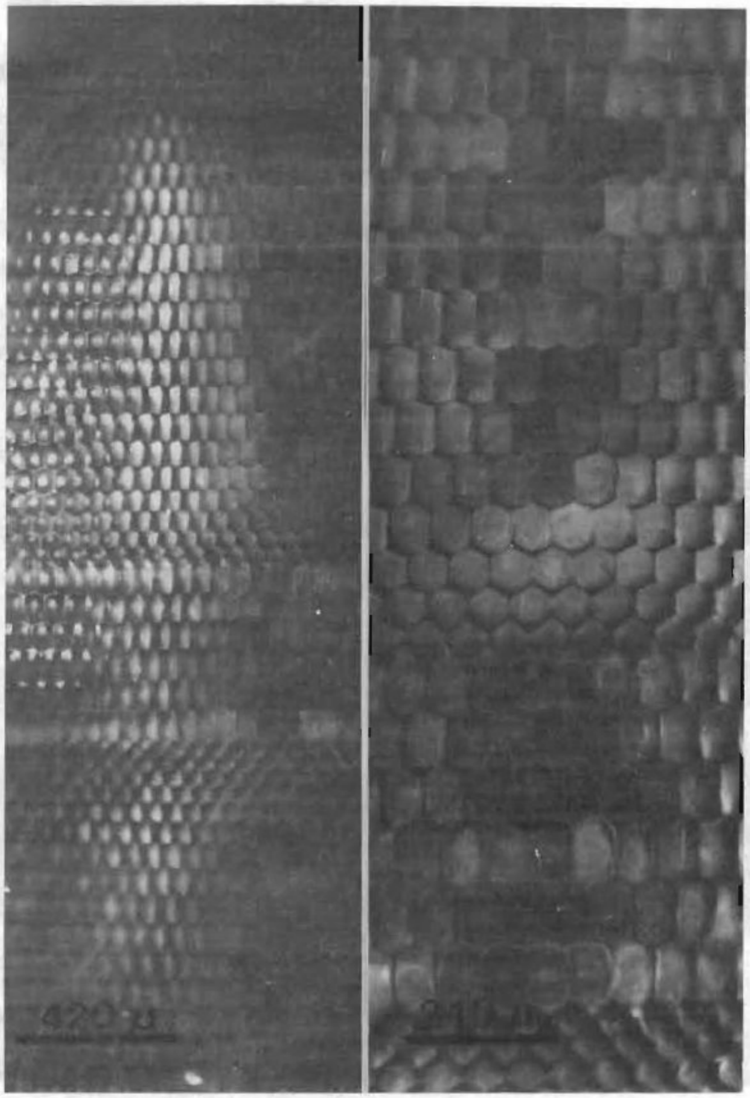

Fig. 2. Corneal surface of *Hemisquilla ensigera* showing the pattern of black and grey facets within the triple pseudopupil.

The triple pseudopupil is long and slim, indicating small cone apertures as confirmed by histological measurements (Schiff *et al.*, in preparation) and further confirmed by the small, 2–3 degree viewing angle within which the pseudopupil is seen. It is formed by a zig-zagging line of a single column of ommatidia interrupted for about 5 rows of ommatidia neighboring the middle band. If the eye moves very slightly away from the frontal view, but not enough to transform the triple into the double pseudopupil, the pseudopupil becomes a band with a complex pattern of dark and grey ommatidia. The dark facets, the ones that truly constitute the pseudopupil, are distributed in separate small groups along the stripe of the original triple pseudopupil (Fig. 2). Around these cluster the grey facets, where the viewing direction is not exactly aligned with the optical axes.

If the eye is moved even more, the double pseudopupil appears and wanders over the cornea with small (3–4 degrees) displacements of the eye. Here also the deeply dark facets are surrounded by facets of different shades of grey. The small pseudopupils and correspondingly small cone apertures and acceptance angles (Schiff *et al.*, in preparation) in the eye of *Hemisquilla* would indicate an animal from a bright habitat with good detail vision. However, *Hemisquilla* lives under medium light conditions, less bright than the environment of *Odontodactylus*, even though the eye structurally resembles the eye of *Odontodactylus* in several respects.

Odontodactylus scyllarus (*medium to bright light*). *Odontodactylus* (Fig. 3) has brilliant, bright green eyes in which the pseudopupils are seen very easily. In spite of the spherical shape of the cornea the pseudopupils have a three-sectioned, elongated shape similar to that in the cylindrical cornea of *Squilla* and in the semi-cylindrical eye of *Hemisquilla*, indicating,

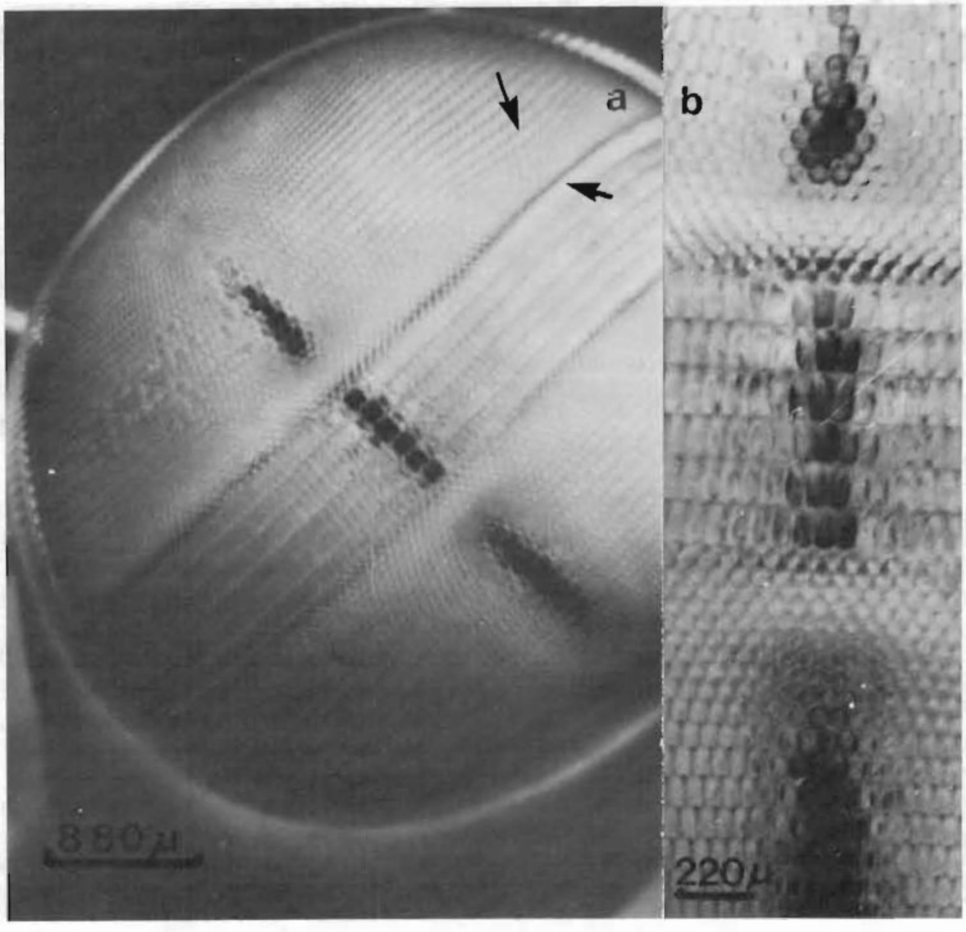

Fig. 3. (a) Frontal view of the eye of *Odontodactylus scyllarus* with a triple pseudopupil turning into a double pseudopupil. Arrow indicates the "acute" zone where facets are larger. The larger facets on the submedian surfaces restrict the area of skewed ommatidia next to the middle band. (b) Enlarged pseudopupil showing the distribution of deeply dark facets surrounded by facets with different shades of grey.

as confirmed by histological measurements (Schiff *et al.*, in preparation), that the ommatidia on the two hemispheres are skewed against the curvatures of the cornea so that their optical axes along a column are parallel to each other and to those in the middle ommatidia and perpendicular to a plane in front of the eye. This includes, of course, the first 5–6 rows of strongly skewed ommatidia on each side of the middle band and the ommatidia on the sides.

The usual double pseudopupil is seen on moving away from the frontal view. The skewed ommatidia on either side of the middle band have small facets and therefore the corresponding pseudopupil adjacent to the middle band is small.

The three-partitioned stripe-pseudopupil contains a small number of deeply dark ommatidia and only one in its middle part. All other ommatidia are different shades of grey. While optical axes of the deeply dark facets of a pseudopupil point straight into the observer's eye, the grey facets indicate deviation of optical axes from the viewing direction (see also Stavenga, 1979), a deviation which is less than the cone aperture. The different shades of grey indicate different amounts of reflections and absorptions in the optical equipment of the ommatidia with different angles of viewing directions with respect to their optical axes. There is slight skewing upward and downward in the middle band. A pattern of dark ommatidia distributed over the pseudopupil exists which comprises all those ommatidia which have exactly parallel optical axes.

The pseudopupils in *Odontodactylus* are wider with 2–3 columns of facets participating and are seen within a wider angle of viewing, indicating wider cone apertures than in *Hemisquilla*.

Gonodactylus (*very bright light*). *Gonodactylus* (Fig. 4) has an elongated eye the largest part of which is normally kept dorsal. The cornea extends over the frontal end of the eye, and covers a small area on the ventral surface. When looking from above into the larger dorsal part of the cornea, a triple pseudopupil appears only in a small part of the cornea, just a little behind the middle of the dorsal part of the cornea. Because the ommatidia in the anterior part of the eye are skewed forward the pseudopupil is biased towards the front. Therefore the pseudopupil can be

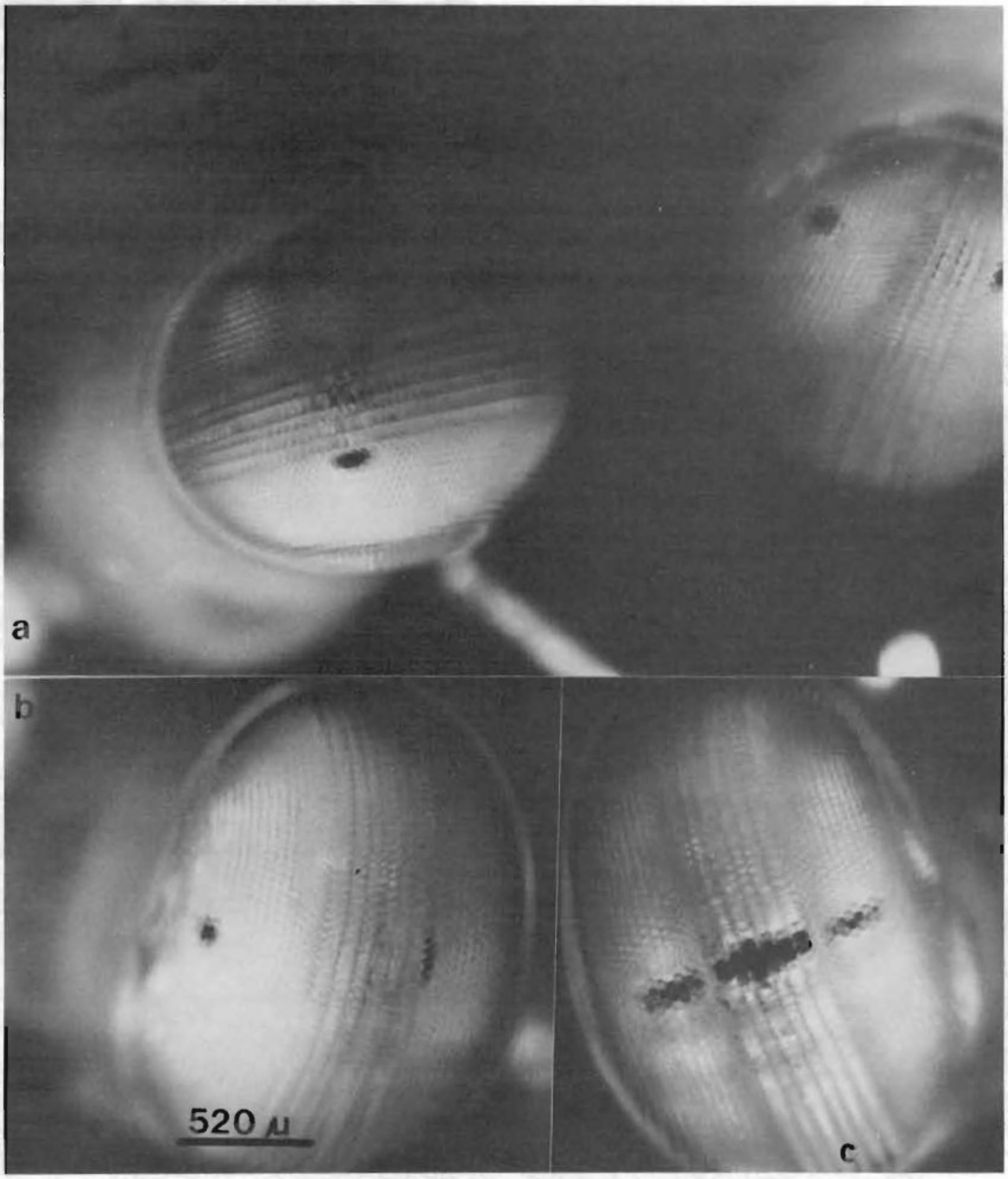

Fig. 4. Pseudopupils in *Gonodactylus oerstedii*. (a) Double pseudopupil. (b) Double pseudopupil when viewing at an angle of 25 degrees with respect to corneal surface of the middle band. The dark facets next to the middle band belong to the ommatidia most skewed towards the middle band. (c) The triple pseudopupil on the dorsal surface of the eye. Viewing direction is from frontally above. The front tip is on the top of the figure.

seen at the tip when viewed frontally, it can be seen on the anterior dorsal half when viewed frontally above the tip, and on the ventral part when viewed from slightly below. The stepwise change in position of the frontal pseudopupil when the eye is tilted up or down is due to the grouping of axes in the anterior ommatidia.

As indicated by the pseudopupil, ommatidia in the posterior dorsal half have optical axes which are directed upward in about the middle of the dorsal part of the eye and turn backward on the more proximal parts.

The transition from the triple into the double pseudopupil with the adequate changes of the viewing direction is as in other stomatopods provided the differences in shape and forward–backward skewing are taken into account.

Facets are surprisingly large for these animals from extremely bright habitats. A peculiarity of several species of *Gonodactylus* is that the whole layer of cornea and cones is relatively transparent as if optically nearly isotropic. The entire retinal surface with its pigments can be seen on focusing down without a clear subdivision in ommatidial units. This indicates that light passes through the walls of the cones and is not funneled into the rhabdom as in other stomatopods but is reflected out of the eye by the reflecting pigments on the retinal surface.

There are, however, white blotches on the eyes of many species of *Gonodactylus* and white stripes in *Pseudosquilla ciliata*. The blotches comprise about 30 ommatidia and consist of white pigment sleeves around the distal cones. In these regions the ommatidia are separated from each other and transparency is interrupted.

"Acute" zones

Regions of the eyes of *Odontodactylus*, *Gonodactylus*, and *Pseudosquilla* have larger facets and pseudopupils. Regions such as these were called foveas (Collett and Land, 1975) or acute zones (Horridge and Duelli, 1979) implying that here vision is more detailed. Though these regions in the above species are located where detailed vision would be most important, we are not sure whether this holds true also for stomatopods where visual fields largely overlap. The location of the "acute" zone is at the frontal tip of *Gonodactylus* (Fig. 5) and in the inner frontal part of the eye in *Odontodactylus*. In *Odontodactylus* the facets of the submedian surfaces and the middle band in the "acute" zone are larger while the facets of the skewed ommatidia adjacent to the middle band are smaller allowing the larger facets on the submedian surfaces to occupy more space.

The larger pseudopupils in the acute zones are determined partly by the larger facets and partly—or in *Gonodactylus* entirely—by including a larger number of facets in the pseudopupil.

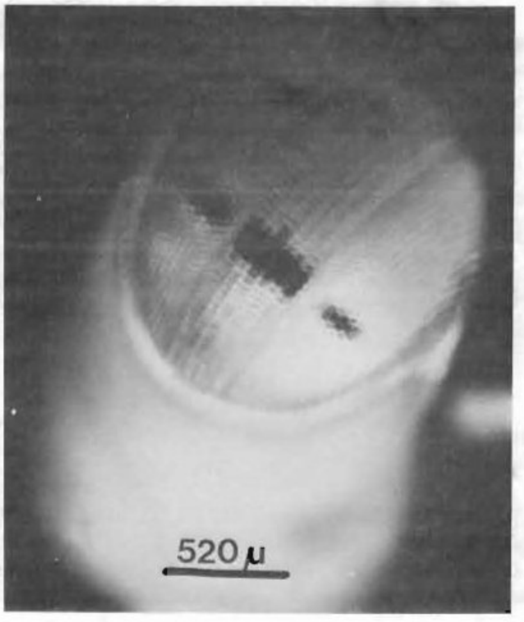

Fig. 5. Pseudopupil in the acute zone of the frontal tip of the eye of *Gonodactylus*. More facets (*cf* Fig. 4(c)) participate in the pseudopupil which therefore becomes larger.

Reflection patterns in ommatidia belonging to a pseudopupil

Light patterns appear in each facet when focusing below the corneal surface in the ommatidia of a pseudopupil. These are seen in the middle of each facet where the cone is attached on the inside of the cornea. They are of the size of the distal cone (Schiff *et al.*, in preparation) and of different patterns: circles in *Odontodactylus*, circles with a line connecting them along a row of ommatidia in *Hemisquilla*, and clover shaped in *Gonodactylus* (Fig. 6). We still do not know whether these appear only in certain regions of the eye or elsewhere.

DISCUSSION

The small pseudopupils near the middle band, seen only when looking across the middle band, are essential for the monocular range finding device in stomatopod eyes (Schiff *et al.*, in preparation). The

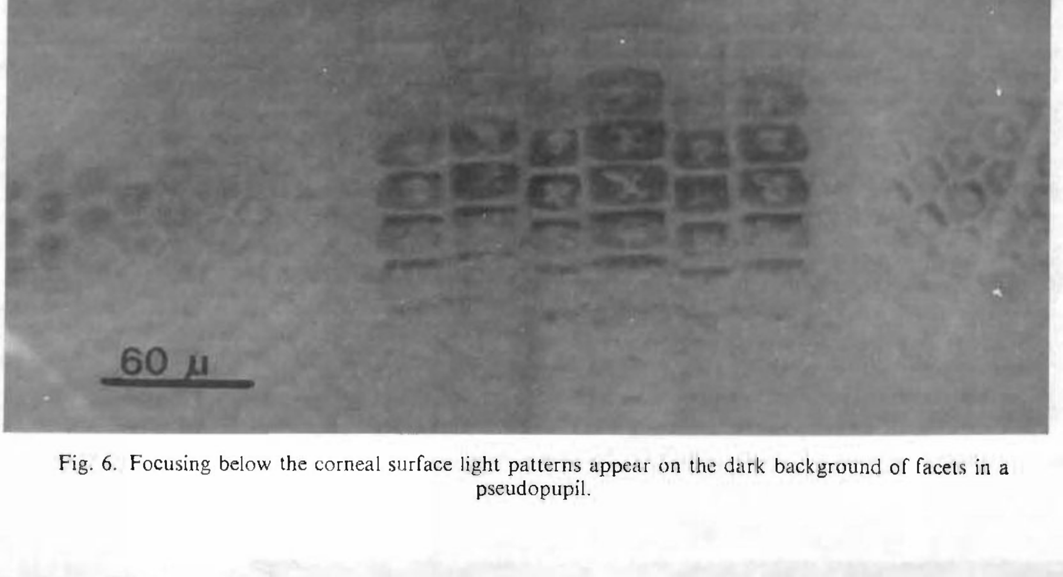

Fig. 6. Focusing below the corneal surface light patterns appear on the dark background of facets in a pseudopupil.

underlying cause is that ommatidia are skewed towards the middle band so that their optical axes from the two halves of the eye cross each other. This device is intimately coupled to mechanisms measuring angular velocity of a moving object in the visual space, and probably also to a mechanism for recognizing specific shapes and colors which are of particular importance in the complex behavior patterns (Dingle and Caldwell, 1969).

In stomatopod eyes, only the most skewed ommatidia, which we believe are responsible for computing angular velocities of organisms approaching the animal, have separate visual fields. Ommatidia belonging to a pseudopupil have overlapping visual fields and should be considered as a whole, not divided into separate ommatidial units. The pseudopupil comprises groups of ommatidia which, in cooperative action, cut out and view certain areas in the visual space around the animal. The entire visual field around the eye is seen as an ensemble of areas, each one of which is seen by a set of ommatidia in a particular composition and not as a mosaic. As pointed out for amphipods by Land (1981), pooled information from groups of ommatidia may not only be possible for animals in a homogeneous, unstructured environment but may even be advantageous. We think it enhances the ability of an animal to recognize specific shapes and patterns, probably wired into the eye genetically. There is some similarity to the "Innate Release Mechanism" of Tinbergen or the "Angehorener Ausloesermechanismus" of Lorenz known in vertebrates. In vertebrates the IRN is wired into the brain and determined either genetically or by early imprinting. In stomatopods, similar mechanisms necessary for pattern recognition as part of their complex behavior seem to be wired into the eye.

Only species living in medium and bright light conditions have the possibility to see colors and shapes and can develop more complex behavior patterns. Species in the genera *Odontodactylus*, *Gonodactylus*, and *Pseudosquilla* have brightly colored patterns in white, blue, green, red, orange, and yellow, whereas animals from dim habitats are paler with dark reddish colors. Members of *Gonodactylus* (and probably also *Odontodactylus* and *Pseudosquilla*) have one of the most complex behavior patterns among invertebrates (Dingle and Caldwell, 1969). In agonistic behavior the meral spots on the striking appendages are exposed. These spots are shape- and color-coded for the species. This position exposes three sets of colored shapes and is seen by the front part of the opponents' eye with its triple pseudopupil while it is in the optical attention position. The pseudopupils on the submedian surfaces may recognize the meral spots by shape and color. The pseudopupil in the middle band—having larger and more complex ommatidial compositions—may be able to recognize finer patterns and movements of the antennae, antennules, antennal scales, etc., still as a unique whole pattern of colored shapes.

Nerves

We have found in stomatopods large, presumably integrating fibers (described for *Squilla* in Schiff *et al.*, in preparation), which we relate to the different tasks performed by the eye. We think that in the first ganglion, the lamina, a fiber with many horizontal branches, collects inputs from successive rows of cartridges and is used in determination of angular velocities expressing time delays in the successive inputs by different spike frequency patterns.

In the middle externa we find two giant fibers branching throughout the medulla. Here, for the first time, inputs from the two halves of the eye flow together, and we correlate distance measurements with these giant fibers.

In the lamina several large fibers branch out, distributed in a way that resembles the shape of the part of the triple pseudopupil on the submedian surface. We think these fibers integrate information from groups of ommatidia externally represented by a pseudopupil and subserving instant recognition of particular shapes and colors in agonistic behavior.

Correlation to ambient light conditions

Larger pseudopupils have been found in *Odontodactylus* than in *Hemisquilla*, which would indicate a brighter habitat for *Hemisquilla*. This is not so. Other contradictions like this have been found in the structure of the ommatidia (Schiff *et al.*, in preparation). These make it difficult to correlate pseudopupils and eye structure with luminous environments. It should be kept in mind, however, that the depth of the ocean is not always an exact indicator of the availability of light. Similarities in eye structure observed in these two genera and the distantly related *Pseudosquilla* may be a reflection of their phylogenetic affinities rather than a function of the luminosity of the environments they inhabit. If these organisms shared a common ancestor, then it would not be surprising to find that their eyes are similar structurally, even though they now use them in different ways under different environmental conditions. Unfortunately, we still know very little about stomatopod habitats, prey, behavior, origins of the taxa recognized today, and we are still in the beginning of understanding their vision.

Neither the size of the pseudopupils or facets nor that of the rhabdom or the calculated acceptance angle can give a definite answer to what each ommatidium or ensemble of ommatidia actually sees. Differences in skewing angles or subtle differences in optics may determine large changes in vision. For example, whereas in *Squilla* light is funneled into the rhabdom the transparency in the *Gonodactylus* eye indicates that light is not funneled. Thus by changing refractive indices in the various parts of the optic equipment the same width of facet and cone may transmit larger or smaller amounts of light.

In *Gonodactylus* part of the ommatidia are looking upward and backward and those with larger facets and smaller acceptance angles look forward. In *Pseudosquilla* there are certain areas of the eye with ommatidia which look in particular directions. Only the ommatidia looking forward frontally can be of any use for locating and hitting a prey as the animals cannot strike upward and backward. All other regions of the eye therefore must have different tasks in the behavior patterns.

SUMMARY

Observations of pseudopupil distribution in stomatopod eyes have been made by viewing and photographing the eyes from many directions in order to analyze the directions of the optical axes.

When viewed frontally and perpendicular to the specialized middle band of ommatidia that is present in all but a few deep-sea species, a linear three section (or triple) pseudopupil is seen. As the eye is rotated but still viewed perpendicularly to the middle band, the triple pseudopupil persists, moving along the columns of ommatidia. For this to occur, the ommatidia in each column on the submedian surface must face the same direction. This is automatic in a cylindrical cornea, but necessitates skewing in all other shapes.

When the direction of view moves more than 5 degrees away from perpendicular to the middle band (i.e. viewing across it), a double pseudopupil is seen asymmetrically in the two halves. One of these derives from the rows of ommatidia next to the middle band that are skewed toward the middle band, and the other is due to ommatidia on the submedian surfaces and sides that follow the curvature of the cornea.

Our observations indicate three uncommon aspects in stomatopod vision: (1) Ommatidia near the middle band are skewed towards it, constituting a monocular range-finder. (2) Sets of ommatidia with parallel optical axes view selected regions in space. (3) Species with the most complex behavior also have the most complex skewing patterns of ommatidia.

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