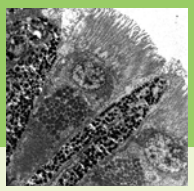
3D-reconstruction of bivalve compound eyes

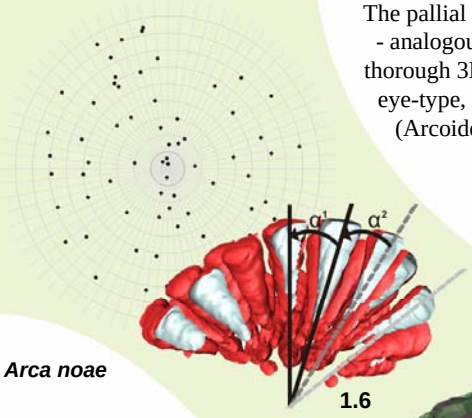
Florian Kretzler, Gerhard Haszprunar, Thomas Kunze, Martin Heß
BioZentrum der LMU München, Großhadernerstraße 2, 82152 Planegg, Germany
hess@zi.biologie.uni-muenchen.de



Introduction

The pallial eyes of some pteriomorph bivalve species are dome-shaped compound eyes - analogous to arthropod apposition eyes to a certain degree - up to now waiting for a thorough 3D investigation. To get deeper insight into the functional architecture of this eye-type, we investigated the three-dimensional cellular eye structures of *Arca noae* (Arcoidea) and *Glycymeris glycymeris* (Limopsoidea) on the light- and electron-microscopic level including some digital morphometry.

As a rule general histological descriptions of sense organs manage with the display of few selected cutting planes. Functional interpretations of sensor arrays with an inherent three-dimensional direction-sensitivity (e.g. eyes), however, require the acquisition of complete structural data volumes as well as the reconstruction, display and morphometric analysis of selected structures in 3D. Nowadays this venture is facilitated by up-to-date computer aided methods (e.g. Amira) based on digital images of complete semithin section series. Here this procedure is exemplified with the charming compound eyes of bivalves (Arcidae).



Arca noae

1.6 3D-morphometry: interreceptor-angles and visual space

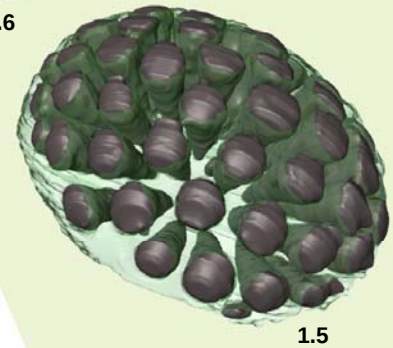
1.5 3D-rendering of an eye-dome with photoreceptor cells

1.4 Semithin section (horizontal, 1 µm) through a compound eye

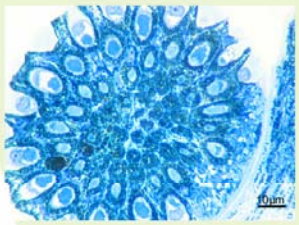
1.3 Semithin section (radial, 1 µm) through a compound eye

1.2 Eyespots at the mantle-edge

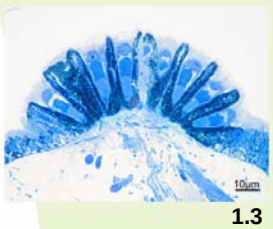
1.1 Conches of *Arca noae*



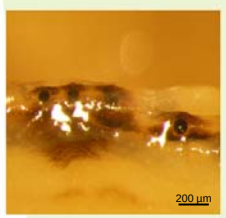
1.5



1.4

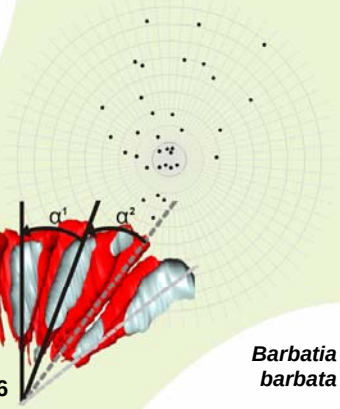


1.3



1.2

1.1



Barbatia barbata

2.6 3D-morphometry interreceptor-angles and visual space

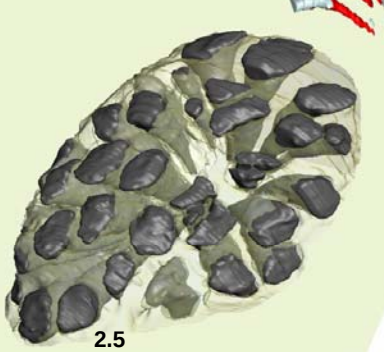
2.5 3D-rendering of an eye-dome with photoreceptor cells

2.4 Semithin section (horizontal, 1 µm) through a compound eye

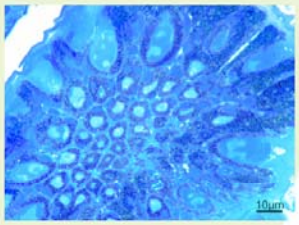
2.3 Semithin section (radial, 1 µm) through ca ompound eye

2.2 Eyespots at the mantle-edge

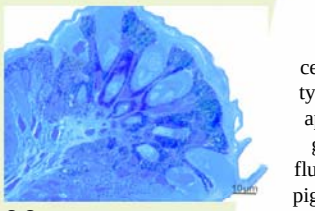
2.1 Conches of *G. Glycymeris*



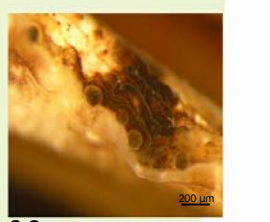
2.6



2.5



2.4



2.3

2.2

Material & Methods

The animals were relaxed in seawater-isotonic $MgCl_2$-solution, fixed with buffered glutaraldehyde, dissected, postfixed with OsO_4, dehydrated in a graded acetone series and embedded in epoxy resin. Complete semithin section series were cut with a Histo-Jumbo diamond knife, mounted on glass slides and stained with Richardson's reagent. Digital images of the slices were imported in Amira®, followed by manual alignment and segmentation. Surfave rendering, 3D-angle measurements and volumetry were carried out also with Amira, mapping was accomplished with IDL. In addition thin sections were made for transmission electron microscopy.

Results

In *G. glycymeris* a single dome, for instance, is made of 36 photoreceptor cells embedded in about 260 pigment cells (dome height 47 µm, oval profile: 127 µm x 89 µm). The "ommatidia" cover a field-of-view of about 90% of a hemisphere with interreceptor angles between 15° and 20°. Deep embedding of the photosensitive membranes within hollow pigment cones (see TEM-picture top right) restricts the actual collecting angle due to collimation effects. The photoreceptor cells vary in size (length and volume, range 1:6) and show a somewhat irregular distribution with an acentric density maximum.

A single eye of *A. noae* is almost hemispheric (radius 60 µm) and, e.g., made of 64 "ommatidia" embedded between about 315 pigment cells. The interreceptor angles amount to 13°-16° in an almost iso-distant alignement. The photoreceptor cell volumes slightly decrease from apical to basal positions. The photoreceptor and pigment cell fine structures are very similar in both species.

Discussion

A couple of bivalve species from the genera *Arca*, *Glycymeris* and *Barbatia* form compound eyes at the mantle edge with some geometrical analogy compared to those of polychaets and arthropods. We have reason to believe that this is not an incidental architecture but evolved and stabilized thanks to any advantageous function, exceeding sheer shadow-off reactions, e.g. the capability to rapidly close the shell once a perturbing shadow appears and to discriminate between potentially dangerous approaches and survival-irrelevant intensity-fluctuations. The dome-shaped eye, the cornet-shaped pigment pits, and the limited number of photoreceptor cells all together result in an hemispherical field-of-view with a low spatial sampling frequency, and some overlap of neighbouring apposition cones. The perception of "pictures" appears unlikely and we have no clue about the processing power of the bivalve's central visual system (i.e. the visceral ganglion). The eyes of arcidae rather may subserve edge- and motion detection by analyzing the speed (and direction?) of the successive shading of neighbouring photoreceptors and/or eyes.

Literature

Will F (1844) Froriceps neue Notizen … 29: 81-103
Carríere J (1883) Quart J Micr Sci 24: 673-681
Patten W (1886) Mittlg Zool Stat Neapel 6: 542-756
Braun R (1954) Zool. Jb 65: 91-125
Levi & Levi (1971) J Microscopie 11: 425-432
Waller TR (1980) Smithson Contrib Zool 313
Morton B (1982) Sarisa 67: 269-282
Nilsson DE (1994) Phil Trans R Soc Lond 346: 195-212
Morton B, Peharda M (2008) Acta Zoologica 89: 19-28