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Conference paper

CHANGEABLE COLORATION OF CORNEA IN FISHES AND ITS DISTRIBUTION

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Some shallow-water fishes, both sea- and fresh-water, belonging to several groups of teleosts, are able to change the corneal coloration according to illumination level. Quite colorless in the dark, their corneas become yellow, orange or even deep red (depending on species) under direct sunlight, in an hour or so. This phenomenon is based on the redistribution of colored cytoplasm between cell bodies and dendrites of the highly specialized corneal chromatophores, which form compact cell masses outside the pupil area, at the corneal border, their flat ribbon-like processes protruding over the pupil corneal area. Fishes of interest have been encountered in all aquatoriae around the globe, and it would be of interest to look for them in the Mediterranean Sea. A list is presented of fish species known to express the described

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phenomenon to different extent.
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It is common to treat fishes as 'lower vertebrates' although, occupying a wide range of ecological niches, they developed many intriguing adaptations, among which we find a number of specific features concerning their vision, unparalleled by other vertebrates. One of them is the ability of some fishes to change the coloration of their cornea in response to illumination conditions. Surprisingly, this phenomenon has not been investigated for a long time, although ichthyologists correctly described 'ruby-red' or 'cherry-red' eyes, ignoring what eye structures were responsible for the unstable coloration. The first description of this phenomenon concerned *Hexagrammos octogrammus* (*Hexagrammidae, Scorpeniformes*), common in coastal waters of the Peter the Great Bay, Japan Sea (Orlov *et al.*, 1974; Orlov and Gamburtzeva, 1976). It turned out later that many shallow-water fishes, both sea and freshwater ones, from several taxonomic groups of teleosts, possess this ability. Quite colorless in the darkness or under weak illumination (as in most fishes), their cornea becomes yellow, orange or even deep red (depending on species) under direct sunlight, not only in fish kept in an outdoor aquarium, but in their natural habitat as well. In the dark, the cornea becomes again colorless, tens of minutes being necessary for a full color change in either direction.

This phenomenon is dependent on the presence in the cornea of highly specialized chromatophores, concentrated at the border between cornea and sclera, and forming, in some cases, a kind of a circle or a pair of sickle-shape cell masses (as in *Hexagrammos*) at the upper and lower corneal border. These pigment cells have a typically pear-shaped cell body, and a single, long and flat, more or less wide, process protruding to the pupil corneal area or even crossing it. A network of such processes forms a kind of veil. Its coloration dynamic depends on the redistribution of a deeply

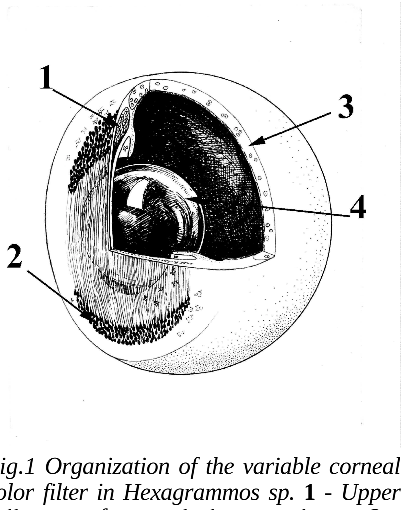

Fig.1 Organization of the variable corneal color filter in Hexagrammos sp. **1** *- Upper cell mass of corneal chromatophores;* **2** *- Lower cell mass;* ***3*** *- Lens.*

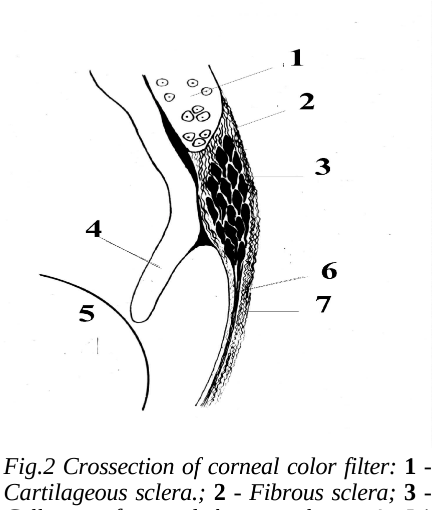

Fig.2 Crossection of corneal color filter: **1** *- Cartilageous sclera.;* **2** *- Fibrous sclera;* **3** *- Cell mass of corneal chromatophores;* **4** *- Iris; 5 - Lens;* **6** *- Processes of corneal chromatophores;* **7** *- Fibrous cornea.*

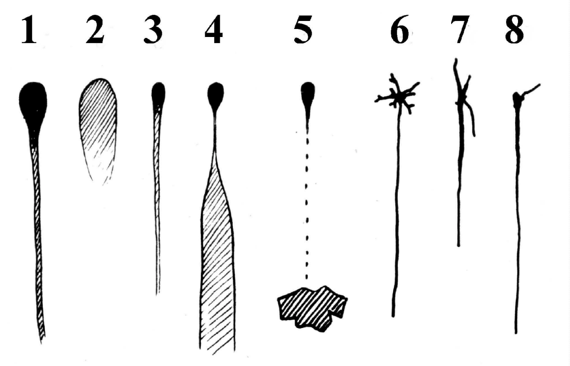

Fig. 3 Shape variations of corneal chromatophores: **1** *- Typical form (all species of Hexagrammos);* **2** *- Myoxocephalus brandti, Bero elegance, Blepsias cirrhosus;* **3** *- Myoxocephalus stelleri, Opisthocentrus ocellatus;* **4** *- some species of Myoxocephalus;* **5** *- Hemilepidotus gilberti;* **6** *- Corneal melanophores with long branches directed towards the pupil zone;* **7**, **8** *- Two types of corneal erythrophores with long branches directed towards the pupil zone*

colored cytoplasm between cell bodies (where cytoplasm is aggregated in the dark) and processes which become pigment-filled in the light-adapted state. The cytoplasm coloration is determined by carotenoids. Chromatophores within the same cornea may belong to different color types, different spectral properties being due to different carotenoids dissolved in cytoplasm. An abundance of lipid globules in which carotenoids are possibly dissolved, numerous microtubules underneath the cell membrane, and pinocytotic/exocytotic activity of the membrane of these pigmented cells can be observed by electron microscopy.

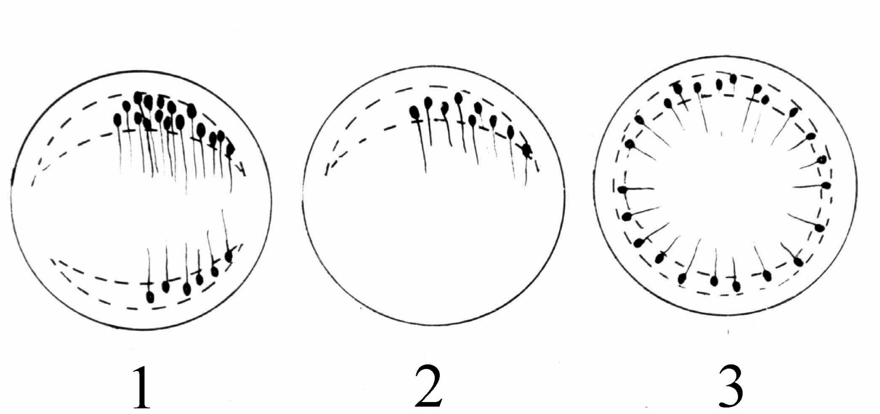

Fig. 4 Cell mass types of corneal color filters: **1** *- Double sickle-shaped (Hexagrammos sp.);* **2** *- Single sickle-shaped (Pleurogrammus);* **3** *- Circular (Myoxocephalus).*

The described phenomenon is expressed in fishes with a diurnal activity, inhabiting shallow water. They live under bright illumination and may sacrifice a part of it in favor of other advantages. The yellow coloration of ocular media (cornea, lens etc.) is

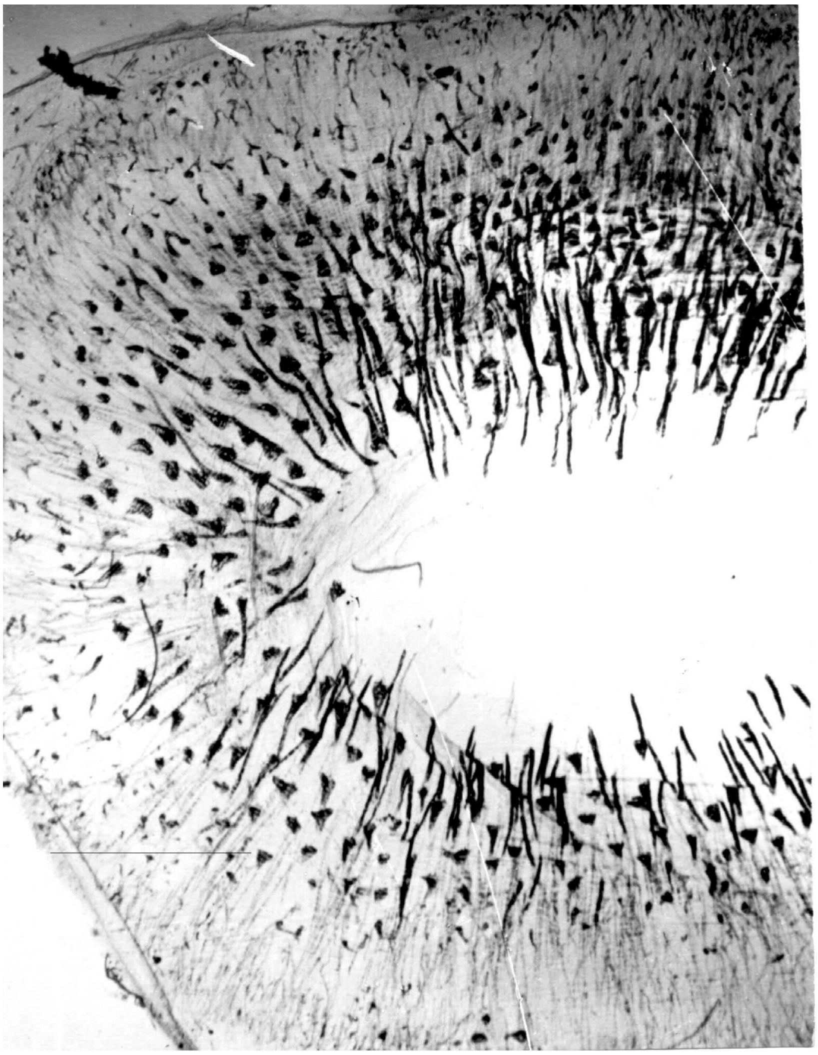

Fig. 5 Corneal color filter of Hemilepidotus at initial stage of transition from a dark-adapted state to light adaptation. Bar = 1 mm.

common among different daytime-active animals, aquatic and terrestrial (snakes and geckoes, squirrels and primates), vertebrates and invertebrates (squids and spiders). Its functional role concerns (i) the gain in visual resolution due to a decrease of the negative effect of chromatic aberration in camera eyes, and (ii) the absorption of the predominantly blue light, scattered in the media outside and inside the eye and

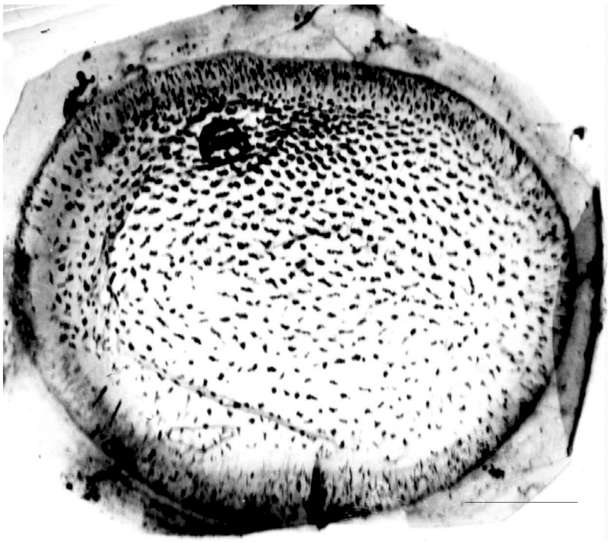

Fig. 6 Corneal filter of Hemilepidotus in a light-adapted state. Bar = 1 mm.

superimposed upon the image, thus decreasing its contrast. It is easy to imagine that the ability of changing the coloration may be of adaptive value in broadening the range of comfortable illumination levels.

How widespread is this phenomenon among fishes? Up to now it has been found in more than 100 species belonging to 16 families from 4 orders of bony fishes (see Table 1). A survey of representatives having variable corneal coloration shows that the evolutionary younger systematic groups of *Perciformes, Scorpaeniformes* and *Tetraodontiformes* dominate among them. These are diurnal sublittoral species, living under the favorable light conditions of shallow water that prevails during a considerable part of the day. No doubt, many new species will be added in future to the current list.

No less interesting is the zoogeographical aspect of the question. Table 1 demonstrates the global distribution of findings, including coastal waters of the Pacific and Indian Ocean; the White Sea and Kamchatka in the North and Australian waters in the South; rivers and lakes of South America and Africa, etc. It would be of interest to conduct a corresponding investigation among fishes of the same ecological group inhabiting European coastal waters of the Atlantic Ocean and the Mediterranean Sea, where many species from several families represented in our Table are known to exist. Both the intensity of corneal coloration due to specialized corneal chromatophores, and the range of its change in response to changes of ambient illumination, differ markedly among species. Fish expressing only slightly this phenomenon (either because of a small number of corneal chromatophores, or because their restricted specialization), may nevertheless be of great comparative interest. They may throw light upon consecutive steps of evolution which led to the presently known most specialized fishes. Despite differences between corneal chromatophores and dermal pigment cells as to their external morphology and the control of the intracellular movements of the pigments, they have much in common in their ultrastructure. We can suppose that they have common precursor cells in ontogenesis.

Table 1. *Fish with changeable corneal coloration: a list of species and their findings. Taxonomy is given after Lindberg (1971).*

ORDER/Family	Species	Locality	Reference
CHANNIFORMES			
Channidae	*Channa gachua* *C. punctatus* (Bloch) *C. striatus* (Bloch)	Fresh waters of tropical Africa, Indo-Malasian Archipelago and East Asia	Muntz (1982)
PERCIFORMES			
Bathymasteridae	*Bathymaster derjugini* Lindberg *B. coeruleofasciatus* Gilbert & Burke	Kunashir	Herald (1961)
Stichaeidae	*Alectrias cirratus* Lindberg *Chirolophis japonicus* Herzenstein *Ernogrammus hexagrammus* (Schlegel), *Kasatkia memorabilis* Soldatov et Pavlenko, *Opistocentrus dybowskii* Steindachner, *O. ocellatus* Tilesius *O. zonope* Jordan & Snyder *Stichaeus grigorjevi* Herzenstein *S. nozawae* Jordan & Snyder *S. punctatus* Fabricius	Peter the Great Bay (Japan Sea)	Herald (1961)
Pholidae	*Pholis fasciatus* (Bloch & Schneider)	Peter the Great Bay (Japan Sea)	Herald (1961)
Zoarcidae	*Neozoarces steindachneri* Jordan & Snyder	Peter the Great Bay (Japan Sea)	Herald (1961)
Blennidae	*Salarias fasciatus* (Bloch)	South-China Sea	Herald (1961)
SCORPAENIFORMES			
Hexagrammidae	*Hexagrammos lagocephalus* (Pallas), *H. octogrammus* (Pallas) *H. stelleri* Tilesius *Pleurogrammus azonus* Jordan & Metz	Peter the Great Bay (Japan Sea)	Kondrashev and Gnybkina (1987); Lindberg (1971)
	Hexagrammos decagrammus (Pallas) *Ophiodon elongatus* Girard	USA, Pacific coast	Herald (1961)
	Pleurogrammus monopterigius (Pallas)	Kunashir	Herald (1961)

ORDER/Family	Species	Locality	Reference
.... cont. *SCORPAENIFORMES* *Cottidae*	*Alcichthys elongatus* Steindachner *Argyrocottus zanderi* Herzenstein *Bero elegans* Steindachner *Hemilepidotus gilberti* Jordan & Starks *Myoxocephalus brandti* Steindachner *M. joak* Cuvier & Valenciennes *M. polyacanthocephalus* Pallas *M. stelleri* Tilesius *Porocottus allisi* (Jordan & Starks)	Peter the Great Bay (Japan Sea)	Herald (1961)
	Cottus amblystomopsis (Schmidt) *Gymnacanthus detrisus* Gilbert & Burke *Porocottus tentaculatus* (Kner)	Kunashir	Herald (1961)
	Cottus (Enophrys) bubalis Euphrasen	England coasts	Lythgoe (1975)
	C. bairdi Girard *C cognatus* Richardson	USA, New York	Heinermann (1984)
	C. beldingii Eigenmann & Eigenmann *C. perplexus* Gilbert & Eigenmann	USA, Oregon	Herald (1961)
	C. gobio (L.)	Europaean fresh waters	Herald (1961)
	C. kessleri Dybowski *Paracottus kneri* (Dybowski) *Procottus jeittelesi (*Dybowski) *Batrachocottus baicalensis* (Dybowski*)*	Baikal	Herald (1961)
	Cottus vicei *Enophrys diceraus* Pallas *Gymnacanthus galeatus* Bean *G. pistilliger* Pallas *Melletes papilio* Bean	Kamchatka	Herald (1961)
	M. scorpius (L.)	White Sea	Herald (1961)
Hemitripteridae	*Hemitripterus villosus* Pallas	Peter the Great Bay (Japan Sea)	Herald (1961)
Agonidae	*Agonomalus proboscidalis* (Valenciennes*)* *A. jordani* Schmidt *Podothecus gilberti* (Collett) *Tilesina gibbosa* Schmidt	Peter the Great Bay (Japan Sea)	Herald (1961)
Blepsiidae	*Blepsias cirrhosus* Pallas	Peter the Great Bay (Japan Sea)	Herald (1961)
Cyclopteridae	*Cyclopterus lumpus* L.	White Sea	Herald (1961)
	Eumicrotremus pacificus Schmidt	Peter the Great Bay (Japan Sea)	Herald (1961)

ORDER/Family	Species	Locality	Reference
TETRAODONTIFORMES *Balistidae*	*Balistapus undulatus*(Mungo Park) *Rhinecanthus rectangulus* (Bloch & Schneider)	Indian Ocean	Muntz (1973)
	Hemibalistes chrysopterus (Bloch & Schneider) *Melichthys vidua* Solander *M. buniva* Lacepede *Rhinecanthus aculeatus* (L.)	South-China Sea	Kondrashev and Gnyubkina (1967); Kochetov (1991)
Aluteridae	*Amanses (Cantherines) pardalis* Rueppel, *Monocanthus chinensis* (Osbeck)	most species from South-China Sea	Herald (1961)
	M. mylii Bory de Saint Vincent *Osbeckia scripta* (Osbeck) *Pervagor melanocephalus* (Bleeker) *Oxymonacanthus longirostris* (Bloch & Schneider)	Australia	Shand (1988)
Tetraodontidae	*Arothron aerostaticus* Jenyns *A. hispidus* L. *A. meleagris* (Shaw) *A. immaculatus* (Bloch & Schneider) *Canthigaster cinctus* (Solander) *Gastrophysus sceleratus* (Gmelin) *G. spadiceus* Richardson *Lagocephalus inermis* (Temminck & Schlegel)	South-China Sea	Herald (1961)
	Arothron citrinellus Guenther	South-China Sea Indian Ocean	Herald (1961) Muntz (1973)
	Arothron manilensis (De Proce)		
			Muntz (1976)
	A. nigropunctatus (Bloch et Schneider)	Australia South-China Sea	Shand (1988) Herald (1961)
	A. stellatus (Bloch et Schneider)		
	Canthigaster valentini (Bleeker)	Indian Ocean	Muntz (1973) Shand (1988)
	Carinotetraodon somphongsi (Klausewitz)		
	Chelonodon patoca (Hamilton-Buchanan)	South-East Asia & Africa	Lythgoe (1975); Haas (1959)
	Chonerhinos amabilis Roberts (=*Ch. naritus* Weber & Beaufort = *Ch. modestus* Weber & Beaufort)	Indonesia	Herald (1961)
	Chonerhinos modestus (Bleeker)		

ORDER/Family	Species	Locality	Reference
.... cont. *Tetraodontidae*	*Colomesus asellus* (Muller-Troschel)	brakish water, South America;	Hass (1959); Lythgoe (1975); Roberts (1982)
	Fugu (Takifugu) chrysops (Hilgendorf)		Appleby and Muntz (1979); Bhattacharjee and Nag (1990)
	F. exascurus (Jordan & Snyder) *F. niphobles* (Jordan & Snyder)	Pacific coasts of S-E Asia	Masuda *et al.* (1975); Fujita and Shinohara (1986); Masuda *et al.* (1984) Fujita and Shinohara (1986); Masuda (1984) Shand (1988
	F. pardalis (Temminck & Schlegel) *F. poecilonotus* (Temminck & Schlegel) *F. rubripes* (Temminck & Schlegel) *F. vermicularis* (Temminck & Schlegel) *F. xantopterus* (Temminck & Schlegel)	Pacific coasts of S-E Asia	Fujita and Shinohara (1986); Masuda (1984) Shand (1988)
	Sphaeroides nephalus *S. testudineus*	Florida	[Herald (1961) - color photo]
	Sphaeroides lunaris (Bloch) *Tetraodon cutcutia* (Hamilton-Buchanan) *T. erythrotaenia* (Bleeker) *T. fahaka* (L.) *T.leiurus brevirostris* (Benl) *T. mbu* Boulenger *T. miurus* Boulenger *T. palembangensis* Bleeker (=*T. steindachneri* Dekkers) *T. pustulatus* Murray	freshwater species of tropical S-E Asia, Indo-Malayan Archipelago and Africa	Appleby and Muntz (1979)
	T. schoutedeni Pellegrin *T. fluviatilis* (Hamilton-Buchanan) (= *T. nigroviridis* De Proce)		Herald (1961) Kondrashev, S.L. and Gnyubkina, V.P. (1987); Appleby and Muntz (1979)

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