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Sensory adaptation

# Tunable colour vision in a mantis shrimp

Systems of colour vision are normally identical in all members of a species, but a single design may not be adequate for species living in a diverse range of light environments. Here we show that in the mantis shrimp *Haptosquilla trispinosa*, which occupies a range of depths in the ocean, long-wavelength colour receptors are individually tuned to the local light environment. The spectral sensitivity of specific classes of photoreceptor is adjusted by filters that vary between individuals.

Colour vision in mantis shrimps involves up to 16 types of visual pigment[1–3]. Spectral sensitivity is further tuned in an unusual way: transparent, coloured filters are placed in front of four classes of receptors[3–5]. Most mantis shrimp species occupy a narrow depth range, and the spectral properties of the filters vary with their characteristic depth. Species in shallow water with bright, broad-spectrum illumination have filters that tune some photoreceptors to very long wavelengths, with sensitivity peaking at wavelengths greater than 600 nm. As sea water selectively attenuates long-wavelength light[6], these receptors would be ineffective at depths exceeding 10 m. In deeper-living species, corresponding filters transmit shorter wavelengths, providing a better match to the prevailing light conditions[3,7]. Animals that live in either environment may thereby perceive colour throughout almost the entire spectral range of available light.

*H. trispinosa*, however, lives at depths ranging from barely subtidal to 30 m or more, and long-wavelength photoreceptor classes that are useful near the surface would not function in deep water. To meet this challenge, different individuals within the species could express different sets of visual pigments, or filters could vary between individuals. At Lizard Island, Australia, we collected adults of *H. trispinosa* at depths of 1 m and 15 m and characterized the visual pigments and filters in their retinae using microspectrophotometry[1,5]. Deep and shallow populations had



**Figure 1** Normalized, average absorption spectra (*n* = 2–9) of all filter classes in *H. trispinosa* retinae. The colour of each line represents how the filter class appears to the human eye. The spectral maxima of visual pigments in the receptors that underlie each filter class are (described using filter colours in the upper-left panel): yellow, 508 nm; orange, 537 nm; red, 539 nm; blue, 558 nm. **a,** Filters in adults from shallow water (1 m) and deep water (15 m). The two longer-wavelength classes, which appear red (thin arrows) and blue (thick arrows) in retinae of shallow-water individuals, absorb shorter wavelengths in deeper-living adults. **a,** Filters of newly settled post-larvae and of juveniles after 3 months in white or blue light.
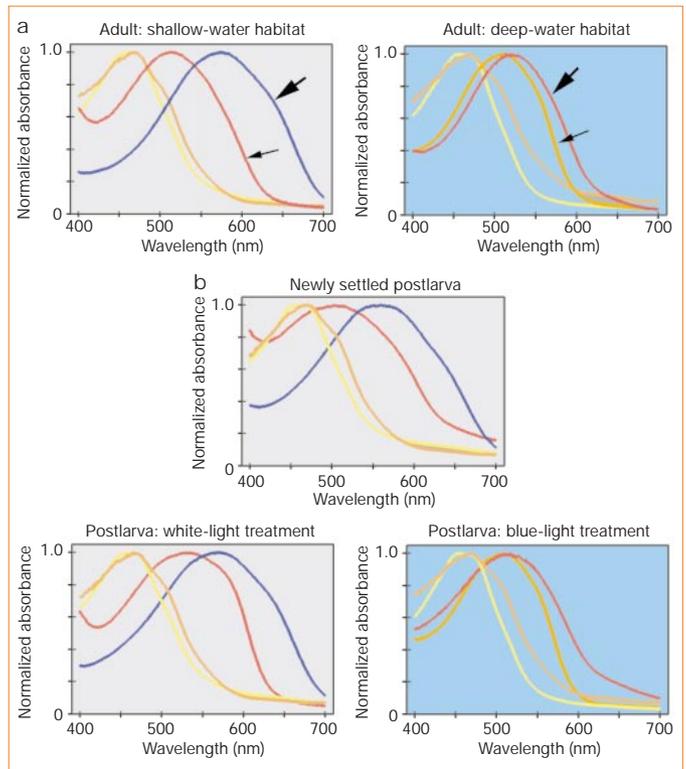
identical visual pigments (data not shown), but the filters that tune the long-wavelength receptor types (Fig. 1a, arrows) were significantly shifted towards shorter wavelengths in deeper-living animals. Thus, their underlying receptors could discriminate hues within the bluer spectrum present in deep water. We calculate that, despite a 96% reduction in illumination at wavelengths longer than 575 nm, the tuning of long-wavelength receptors of animals living at 15 m allows them to capture incident photons at 75% of the rate observed for surface dwellers.

We investigated whether the occurrence of different filter sets can be influenced by conditions during development. Newly metamorphosed postlarvae of *H. trispinosa* live in shallow water and have filters like those of shallow-water adults (Fig. 1b). We reared postlarvae under laboratory lighting, either in blue light lacking wavelengths longer than 550 nm or under broad-spectrum white fluorescent light. After 3 months, individuals reared in white light retained the filter classes of shallow-living adults, whereas the filters of the blue-light group were characteristic of deep-water populations (Fig. 1b).

To our knowledge, this is the first demonstration in any species of a tunable colour-vision system that responds directly to the light environment. The response involves precise changes in a unique system of spectral filters. Although some fish, amphibians and crustaceans vary their spectral sensitivity by changing their visual-pigment chromophores, this is controlled by environmental temperature or photoperiod[8,9]. Sensitivity also changes ontogenetically in some fish[10], perhaps by hormonal control. In mantis shrimps, tuning could be regulated by the overall level of illumination, which decreases with depth, or could be controlled by the spectral quality of incident light.

Colour vision in *H. trispinosa* is influenced to a surprising extent by developmental conditions. Individuals living at different depths have different colour perception and may rely on different biological signals to compensate for this. In any case, these mantis shrimps express an impressive degree of phenotypic plasticity in tailoring their visual systems to their habitats. We suspect that intraspecific variation in visual function may be widespread among species that occupy variable light environments.

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# Lungfish dental pattern conserved for 360 Myr

Lungfish, the closest living relatives of four-limbed animals, are unique in that adults lack marginal teeth and have to rely on palatal dental plates for crushing food. We have discovered that an identical pattern of tooth development is used to shape these plates in the hatchlings of fossil and living lungfish species that are separated by 360 million years (Myr) of evolution, even though the adults have very different dental forms; the same pattern is also evident in the transient marginal dentition, despite being functional only until the juvenile stage. This remarkable finding indicates that developmental programming for dentition in lungfish is uniform, unique and conserved for all tooth fields.

Adult lungfish have extensive, continuously growing tooth plates on the palate and the inner side of the lower jaws, which are formed without shedding any teeth. This type of dentition is developed and maintained through continual addition of new teeth labially and dentine from within. In this way individual teeth, arranged in radial rows, are consolidated into dental plates without loss through shedding[1]. This is in contrast to the conventional marginal linear rows of teeth that form the osteichthyan dentition (including tetrapods), in which tooth shedding usually occurs through lingual development of new teeth in each position, with loss of the old tooth. The specialized dentition unique to lungfish is one

example of a strongly conserved structure that is retained through constraints in developmental patterning.
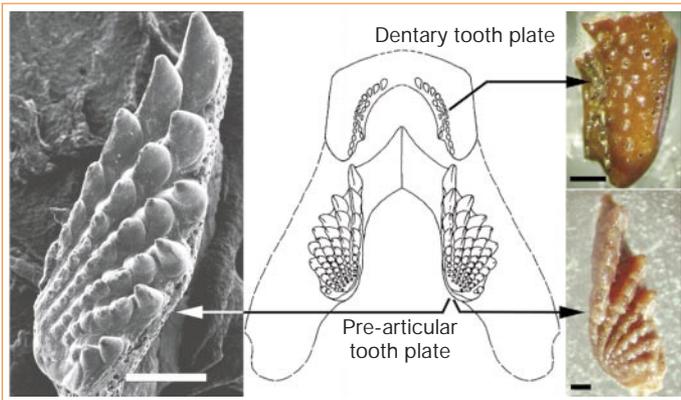
This type of development is shown clearly in the lower jaws of hatchlings of the extant *Neoceratodus* and the Late Devonian *Andreyevichthys*, two lungfish taxa that are separated by 360 Myr. Superbly preserved growth series of *Andreyevichthys* have been uncovered in central Russia[2]. These include not only thousands of specimens, but also the earliest hatchling stages, the only such examples in the current fossil record.

This discovery allowed us to compare the Devonian form with similar developmental stages of *Neoceratodus*. Although the dental plates in adult *Neoceratodus* are non-toothed surfaces for crushing, they develop from toothed rows[3], with new teeth being added labially to each row of the tooth plate as in adult *Andreyevichthys*[3] (Fig. 1, left arrow).
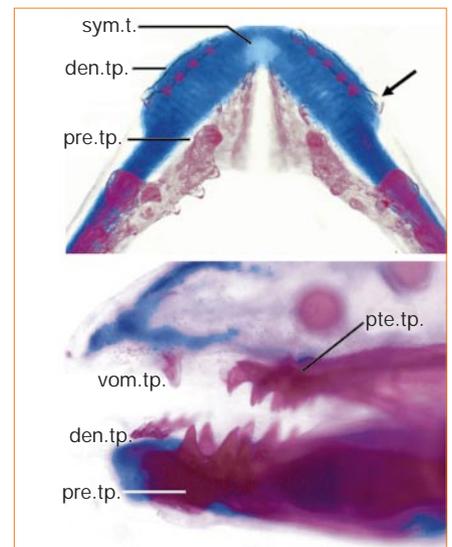
In addition, hatchlings of both taxa develop a marginal dentition, in which the feeding mode is different[4] from that in the adults. This marginal dentition is also organized in both taxa as small tooth plates and is quite unlike that in other osteichthyans. Each marginal set is formed from several rows of joined teeth in the Devonian form (Fig. 1, top right) and from paired single rows in the extant lungfish (Fig. 2). This provides substantial evidence that in lungfish the mode of dentition patterning is consistent in each tooth field, whether marginal or palatal, and that it is unique and specialized. This suggests that it is evolutionarily distinct from that of all other osteichthyans.

We also observed a pattern of selected dental loss through resorption of the marginal dentition from hatchlings to juveniles. In *Neoceratodus* the sequence of loss starts medially, first with the single symphyseal tooth, after which those on the dentary are resorbed, one tooth at a time, until the mar-



**Figure 2** Tooth plates of the extant *Neoceratodus forsteri*. Images show whole mounts of a hatchling at stage 56, stained red for bone and dentine, and blue for cartilage. Top, occlusal view of lower jaw in which resorption of dentary teeth has begun to occur (one medial tooth from left side). The symphyseal tooth has been completely lost, as shown by the pale blue region. Arrow shows addition of new teeth, which are not yet attached, at the postero-lateral ends of the dentary. Bottom, lateral occlusal view of head, showing the upper and lower tooth plates and the smaller, marginal plates supported by cartilage. In the later stages of ontogeny, the dentary tooth plate is completely resorbed. Material couresy of J. Joss. Abbreviations: den.tp., dentary tooth plate; pre.tp., pre-articular tooth plate; pte.tp., pterygoid tooth plate; sym.t., symphyseal tooth position; vom.tp., vomerine tooth plate.

ginal tooth plates are lost. Almost the same pattern of loss occurs in *Andreyevichthys* because the marginal tooth plates and the dentary bone of hatchlings subsequently disappear. The hatchling dentition is represented by dozens of dentary tooth plates, but none have been found among the thousands of juvenile and adult specimens.

Our results indicate that a specific developmental mechanism for programmed loss was preserved in these two lungfish throughout 360 Myr of evolutionary history. Early, more basal lungfish[3] have palatal and lingual tooth plates, whereas marginal bones have separate teeth; some later taxa also develop and retain marginal tooth plates as adults[5], indicating that this programme of development and loss evolved within lungfish, perhaps during the Late Devonian period.

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**Figure 1** Dorsal views of dentary and pre-articular tooth plates in the Late Devonian *Andreyevichthys epitomus*. The diagram shows a reconstructed outline of the lower jaw in occlusal view and the relative positions of the two types of plate. As in the extant lungfish (Fig. 2), the dentary tooth plate (top right; PIN 1302; arrow originates from and points to the centre of the radiating rows)



Dentary tooth plate

Pre-articular tooth plate

is completely resorbed during early ontogeny, and the dentary bone is lost, whereas the pre-articular tooth plate (left and bottom right; PIN 1328, 1548) continues to add new teeth. Both comprise radial rows of teeth. Left, scanning electron micrograph of the pre-articular plate, taken at an angle to show the new teeth at the labial end of each row (arrowhead). Six tooth rows can be seen, all showing a gradation from small, worn medial teeth to larger new teeth; rows 1–4 have 10 teeth, row 5 has 6 teeth and row 6 has 5 teeth. Material courtesy of N. Krupina. Scale bars, 500 μm.