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Underwater Vision in Semi-Aquatic European Snakes

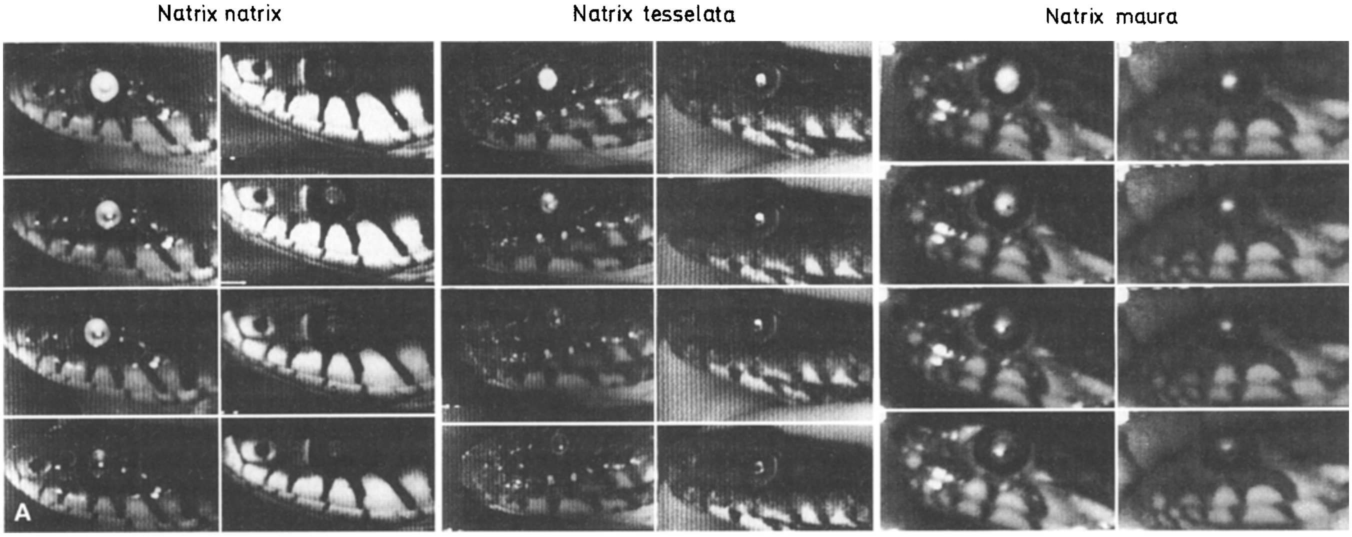
F. Schaeffel
Forschungsstelle für experimentelle Ophthalmologie, Augenklinik Abt. II, W-7400 Tübingen, FRG

U. Mathis
Institut für Biologie I (Zoologie), W-7800 Freiburg, FRG

Some snake species have entered the aquatic niche secondarily [1], and face the problem of poor underwater visual acuity because the refractive power of the anterior surface of the eye is lost as a result of the higher refractive index of water. There are a number of studies known from semi-aquatic birds (e.g., comorants [2], penguins [3]) and mammals [4] which examine the optical properties of eyes designed to focus in both air and water. Little is known, however, about underwater visual acuity in semi-aquatic snakes, although considerable differences in visual performance have been observed behaviorally [5]. Schaeffel and de Queiroz [6], in a comparative study of the optics of eyes in some north American species, found that the differences in underwater visual performance could be explained by the different ranges of ocular accommodation. Strikingly, there was an enormous variability in the ranges of accommodation among closely related species, with some species unable to focus underwater at all despite semi-aquatic living habits. Apparently, predation under water does not imply that good vision is preserved in both media. For instance, Fleishman et al. [7] showed that crocodiles do not focus underwater although they hunt mainly in water.

We have compared the capability to focus in both air and water in the three water snake species which are common in Europe, *Natrix natrix, N. tesselata,* and *N. maura.* The refractive state of the eyes of unrestrained snakes diving in an aquarium (approx. 80 × 40 × 30 cm) was recorded continuously using a recently developed technique, infrared photoretinoscopy [8]. Because of the use of infrared light, the measurements did not disturb the snakes' behavior. Measurements took place at a luminance of 2 – 5 lx.

The infrared photoretinoscope creates a light crescent in the pupil which results from infrared light reflected from the fundus. The position of the reflex indicates the sign of defocus relative to the camera (top of pupil: hyperopic, bottom of the pupil: myopic), and its size allows one to determine the amount of defocus [8]. By refracting from five different eccentricities [8], one obtains five differently sized light crescents in a row (Fig. 1A) which improve the precision of measurement. Refractions from the three species in air (left columns) and under water (right columns) are shown in Fig. 1A. As can be seen from the reflexes in the top of the pupils, the eyes of all species are moderately hyperopic in air. However, because the apparent hyperopia can be explained by the so-called small eye artifact of retinoscopy [9], it can be concluded that the snakes are actually properly focused in air. The striking observation is that, under water, almost no light is coming out of the pupil of *N. natrix,* whereas a refractive state similar to the one in air can be measured in the eyes of *N. tesselata* and *N. maura.* It can be shown [6] that the lack of a reflex in the eyes of *N. natrix* is the result of an enormous amount of hyperopic defocus which is beyond the range of measurement of the retinoscope. Here, the defocus is not directly measurable but it can be calculated from the spectacle radius of curvature. Figure 1C (upper two frames) shows examples of photokeratometric mesurements [10] of the spectacle radius of curvature in *N. natrix* (left) and *N. tesselata* (right). If this parameter is known, the loss of refractive power under water can be calculated for an eye lacking accommodative power to refocus under water. Figure 1B shows the action of an image-processing computer program which determines refractive state in digitized video images of the eyes. We found that *N. natrix* does not attempt to accommodate at all under water, whereas the two other species are properly focused in both media. The impressive range of accommodation is also illustrated by the lower frame in Fig. 1C, which shows a specimen of *N. tesselata* just emerging from diving. The snake is very myopic because it is still focused for sharp vision under water (note reflex in the bottom of the pupil, refraction about − 65 diopters). Refractions and pupillary constrictions under water are summarized in Fig. 2A and B, respectively. The two specimens of *N. natrix* became very hyperopic under water, whereas both *N. tesselata* and *N. maura* remained appropriately focused.



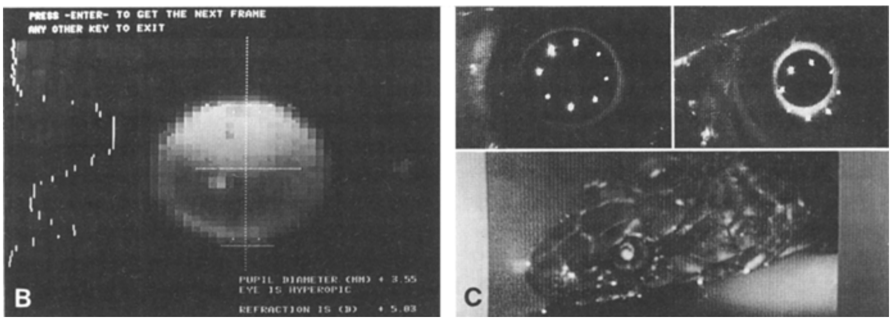


Fig. 1. A) Photoretinoscopic reflexes in the pupils of the three European water snake species. *Left columns:* refractions in air, *right columns:* refractions in water. Note that, under water, no light is coming out of the pupil of *N. natrix,* indicating a large amount of defocus. B) Output of a video-image-processing computer program (written in lattice C) which reads out pupil diameter and refractive state directly on the video monitor. C) Above: photokeratometric measurements of the spectacle radius of curvature. *N. natrix* (left) has a flatter spectacle than *N. tesselata* (right) as can be seen from the smaller diameter of the circular arrangement of infrared light reflexes. Below: *N. tesselata,* just emerging from under water. Because the snake is still accommodating for vision under water, it is very myopic (as indicated by the photoretinoscopic light reflex in the bottom of the pupil)

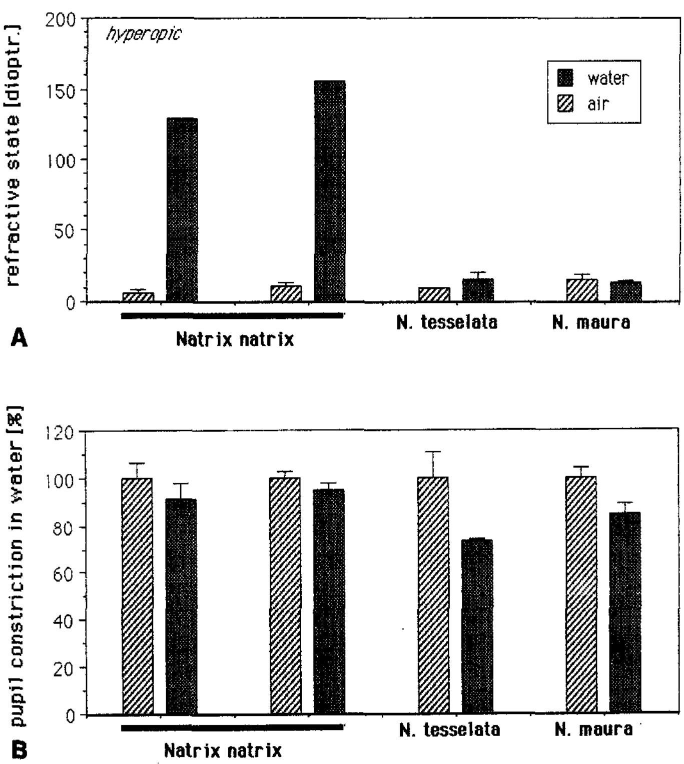


Fig. 2. A) Refractive states in air and water. Averages with standard deviations from 3 – 6 measurements are shown. Note that *N. natrix* becomes very hyperopic under water (two animals tested) whereas the other two species do not differ significantly in refractions in air and water due to their large ranges of accommodation. B) Pupillary constrictions under water. The pupillary constrictions are not strong enough to support an assumption of a mechanism of accommodation similar to the one found in diving birds, where the lens is squeezed through a strongly contricted pupillary aperture

