BÖHME, W., BISCHOFF, W. & T. ZIEGLER (eds.): HERPETOLOGIA BONNENSIS, 1997: 125-138

Anuran eye colouration: definitions, variation, taxonomic implications and possible functions

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Introduction

Different characters related to external eye morphology are commonly used to characterize anurans. Pupil shape, which can often be classified either as horizontal or vertical, is important in field identification of certain genera. The relation of eye diameter to tympanum diameter is often useful to distinguish between closely related species, but this seems mainly caused by the variability of tympanum diameter.

In contrast to morphometric characters, eye colouration is seldom used taxonomically, although the enormous relevance of life colour for frog determination has often been emphasized (e.g. DUELLMAN 1975: 31 and 32). This may be partly caused by the fact that taxonomists traditionally worked mainly with preserved specimens which had lost their characteristic colour patterns. Just in the last decades colour photographs of many anuran species have been published, potentially allowing the use of eye colouration as a taxonomic character.

In this paper we will describe and discuss eye colour patterns of anurans. Our observations and conclusions are mainly based on species from Madagascar but will be compared to published data referring to other anurans (the often similar patterns of urodeles and reptiles are not considered here). Since the eyes of the rhacophorine genus *Boophis* are extremely colourful and variable between species we will focus our analysis on this genus.

Material and methods

A large collection of colour photographs of Madagascan anurans, made between 1987 and 1995 and consisting of more than 200 different species, was screened 1) to find general pattern of eye colouration and 2) to compare eye colouration of closely related species. Comparisons of advertisement calls were used in most cases for the identification of sibling species, to exclude the possibility that specimens with similar morphology but different eye colouration are only colour morphs of a single species. Most photographs were made by using flashlight and Fuji 100 ASA colour slide films.

To test the general significance of observations we consulted colour photographs of frogs from different parts of the world, mainly those published by PASSMORE & CARRUTHERS (1995) for South Africa, BLOMMERS-SCHLÖSSER & BLANC (1993) for Madagascar, COGGER (1992) for Australia, MENZIES (1974) for New Guinea, LIM & LIM (1992) for Singapore, KARSEN et al. (1986) for Hong Kong, ZHAO & ADLER (1993) for China, NÖLLERT & NÖLLERT (1992) for Europe, BEHLER & KING (1979) for North America, RODRIGUEZ & DUELLMAN (1994) for South America. Colour pictures of most Madagascan species mentioned in the present text have been published in GLAW & VENCES (1994). Refer to this publication also for exact location of frog collecting localities in Madagascar.

Figure 1 defines the different parts of anuran eyes as they will be used in the following chapters. Definitions are based on *Boophis* eyes but generally also apply to other anurans and urodeles. However, it can not be excluded that some of our definitions do not correctly correspond with morphological nomenclature. For example we did not study whether 'iris periphery' as it will be used in this study is in fact structurally a part of the iris; it may also belong to the nictitating membrane or to another tissue type.

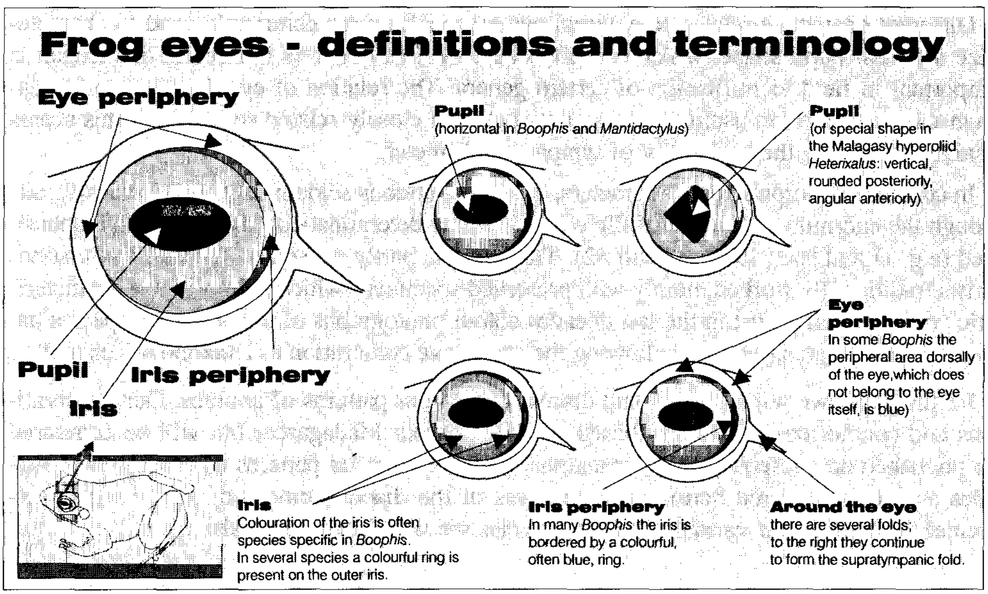

Fig. 1. Definitions of frog eye structures as used in the text.

Morphology and physiology of the amphibian eye

The pigments of amphibians are composed mainly of the following pigment cell types: Melanophores contain black or brown melanine, xantophores and erythrophores yellow, orange or red pigment. Iridophores do not contain real pigment, the silvery or golden colour is produced by physical effects (WINTER 1988). The epithelial layers of the iris contain iridophores and melanophores, in some anurans xanthophores are also present (DUELLMAN & TRUEB 1986). According to DUBOIS (1976) black eyes are caused by the absence of iridophores, a reduction of xanthophore numbers, and a dominance of melanophores.

The iris of anurans can be dilated or contracted to control the size of the pupil and thus the amount of light that strikes the retina. Therefore a comparison of iris colouration is only possible in frogs with similar degree of dilatation. A specimen pictured in darkness will have a large (blackish) pupil, with the pigmented iris as only a small ring around. Another problem is that eyes are not always fully opened, especially during the day. In these cases the colouration of the outer iris area is not or only partly visible (e.g. in *Boophis viridis*).

According to the summary of DUELLMAN & TRUEB (1986), the retina of anurans and urodeles contains four types of receptor cells. These are two types of cones and two types of rods, and their relative numbers vary in relation to the amount of light to which the species normally is exposed. Rods are responsible for colour vision in mammals, and the presence of a second type of rods (green rods) is unique to anurans and urodeles among vertebrates. PENZLIN (1980), probably referring to relatively ancient literature, reported interspecific differences in amphibian colour recognition: no such ability was detected in *Alytes*, whereas *Rana temporaria*, *Triturus alpestris* and *T. vulgaris* could differentiate between red and blue. Few experimental data about colour vision in amphibians are available, but these indicate at least a limited distinction of different wavelengths of light (DUELLMAN & TRUEB 1986). Contrasting this opinion, ZWEIFEL (1992) states that no indication exists that anurans can distinguish colours.

Pattern and variation of eye colouration

Common eye colour combinations: Several main types of colour combinations in the iris can be distinguished in *Boophis* and other anuran genera (see also tab. 1):

I Iris with a blue ring

a) blue or turquoise outer iris area, inner iris area brown: *Boophis albilabris occidentalis*, *B. viridis* und *B.* sp.n. 3, and the microhylid *Platypelis pollicaris*. This colour pattern is also present in *Rhacophorus angulirostris* (see MALKMUS 1995 and a picture made by P. HOFFMANN in Borneo). In this latter species the bluish colour is present on the dorsal part of the iris, to a lesser extent on the ventral part of the iris, and not recognizable laterally.
b) blue outer iris area, inner iris area silvery: *Boophis erythrodactylus*, *B. rappiodes*, and the microhylid *Plethodontohyla* sp.n.

II Iris with a red or yellow ring

a) red or orange outer iris area, inner iris area beige or brown: *Boophis luteus*, *B. guibei*, *B. boehmei*, *B. miniatus*, *B.* sp.n. 4 and *B.* sp.n. 7, *Litoria chloris* from Australia.
b) yellow or whitish outer iris area, inner iris area brown: *Boophis madagascariensis*, *B.* cf. *burgeri*.

III Iris uniformly coloured

a) iris greenish: *Boophis microtympanum*, *B. laurenti*, many *Bufo viridis* and *B. calamita*.
b) iris reddish brown: *Boophis goudoti*, *B. pauliani*, *Stumpffia tridactyla* and many non-Madagascan species (e.g. *Bufo bufo*).

species	locality	iris colouration	iris periphery
B. madagascariensis	Andasibe	externally cream white, inside brown	white
	Andasibe	externally yellow, inside brown	???
	Ankeniheny	externally yellowish, inside brown	white
	An'Ala	externally yellow, inside brown	yellow
	Marojezy	externally yellowish, inside brown	white
	M.d'Ambre	golden to light brown	yellowish
B. brachychir	Benavony	silvery-grey	grey-white
B. sp. (cf. *brachychir*)	M.d'Ambre	red-brown	light green
B. reticulatus	An'Ala	externally golden-yellow, inside silvery-grey	light green
B. reticulatus	Ranomafana	externally golden-yellow, inside brown	light green
B. sp.n. 7 (cf. *reticulatus*)	An'Ala	externally red inside, golden-brown	light green
B. burgeri	Andasibe	externally yellow, inside red-brown	dark blue
B. cf. *burgeri*	Marojezy	above dark brown, externally silvery, inside brown	white
B. boehmei	Andasibe	externally red, inside beige	blue
	Ankeniheny	externally red, inside beige	blue
	Ranomafana	externally orange, inside brown	blue
	Andringitra	externally red, inside beige	blue
	Ambohitantely	externally red, inside brown	blue
B. goudoti	Andasibe	golden to red-brown	light green
B. cf. *rhodoscelis*	Ambohitantely	golden	blue
B. microtympanum (normal)	Ankaratra	green	grey
(yellow mutant)	Ankaratra	grey-green	???
B. cf. *microtympanum*	Andringitra	green	???
B. laurenti	Andringitra	green	???
B. tephraeomystax	Nosy Be	golden	grey
	Kirindy	golden	light grey
	Tolagnaro	golden	light grey
	Andasibe	golden	light grey
	Ranohira	golden	light grey
B. guibei	Andasibe	externally red, inside silvery-grey	???
B. sp.	Andrakata	golden	white
B. idae	Andasibe	golden or brown	light grey
B. sp.n. 8	Ambavaniasy	golden	light grey
B. sp.n. 9	Kirindy	golden	light grey
B. pauliani	Andasibe	copper	grey?
B. opisthodon	Nosy Boraha	golden	grey white
	Tolagnaro	golden	???
B. sp.n. 10	An'Ala	silvery, reticulated	???

Tab. 1. Eye colouration in the genus *Boophis.* Species are listed according to species groups (see GLAW & VENCES 1994): *B. albilabris*-group, *B. luteus*-group, *B. rappiodes*-group, *B. difficilis*-group, *B. goudoti*-group, *B. microtympanum*-group, *B. tephraeomystax*-group.

species	locality	iris colouration	iris periphery
B. a. albilabris	Benavony	externally copper, inside brown	no periphery
	Marojezy	externally golden, inside brown (copper)	no periphery, upper margin green
	Anjanaharibe	externally copper, inside brown	no periphery, upper margin green
	Andasibe	externally copper, inside brown	no periphery, upper margin green
	An'Ala	above silvery, rest dark grey	no periphery
	Ambatolahy	uniformly orange	grey-white
B. a. occidentalis	Isalo	externally blue, inside brown	blue
B. l. luteus	Ifanadiana	externally red, inside beige	blue
	Andasibe	externally red, inside beige	blue
	Tolagnaro	externally red, inside beige	???
B. l. septentrionalis	M.d'Ambre	externally yellow, inside silvery	blue-grey
B. elenae	Vohiparara	externally white, inside pink-red	blue?
	Andasibe	externally white, inside red to brown	blue
B. englaenderi	Marojezy	externally golden, inside red-brown	blue-grey
B. jaegeri	Nosy Be	externally silver-grey, inside brown	blue
B. andreonei	Benavony	externally yellow, inside silver-grey	grey
B. cf. *andreonei*	Marojezy	externally golden, inside silvery	blue
B. ankaratra	Ankaratra	externally silvery or golden, inside red-brown	blue
	Andringitra	externally silvery, inside red-brown	blue
B. albipunctatus	Nahampoana	externally yellow, inside red-brown pattern	blue
	Andasibe	externally yellow, inside red-brown pattern	blue
B. sibilans	Andasibe	externally yellow, inside silvery with red-brown	blue
B. cf.*sibilans*	Ranomena	externally golden-yellow, inside brown pattern	blue
B. andohahela	Andohahela	externally golden-yellow, inside copper	blue
B. rappiodes	Andasibe	externally blue, inside silvery	blue
	Nahampoana	externally blue, inside silvery	blue
B. sp.n. 1	Andasibe		
B. erythrodactylus	Mandraka	externally blue, inside silvery	blue
B. mandraka	Mandraka	white with brown reticulation	blue
B. cf. *mandraka*	Ranomena	uniformly silvery/externally silvery inside brown	blue
B. viridis	Andasibe	externally black, blue in the middle, centrally brown	blue
B. difficilis	Andasibe	externally black/blue, inside silvery	blue-grey
B. sp.n. 2	Nahampoana	silvery-grey	blue
B. miniatus	Tolagnaro	externally red, inside silvery	blue-grey
B. sp.n.3 (cf.*miniatus*)	Andasibe	externally black/turquoise,cream(middle),inside brown	turquoise
B. majori	Andringitra	golden-yellow	light grey
	Vohiparara	golden-yellow	blue
B. sp.n. 4	An'Ala	above yellow or orange, inside silvery	blue
	An'Ala	above and below yellow, inside silvery	blue
	An'Ala	above and below orange, inside silvery	blue
	Mandraka	externally orange, inside silvery-beige	blue
B. blommersae	M. d'Ambre	silvery-golden	light grey-green
B. marojezensis	Marojezy	above yellow, below silvery, inside brown	light green
B. sp.n. 5	Marojezy	above orange, inside silvery	blue
B. sp.n. 6	Andasibe	above blue, inside silvery with reticulations	blue

c) iris red: not known from *Boophis*, but present in several neotropical hylids: *Agalychnis callidryas* and other species of this genus; most species of *Duellmanohyla* (CAMPBELL & SMITH 1992); *Ptychohyla legleri* (see picture in WEIMER et al. 1993a, but compare with CAMPBELL & SMITH 1992); one colour morph of *Eleutherodactylus caryophyllaceus* (see picture in WEIMER et al. 1993b); also visible in a specimen of *Phyllomedusa tarsius* from Tarapoto, Peru (SCHLÜTER 1987, cover photograph).

d) iris silvery or golden: *Boophis* cf. *rhodoscelis*, *B. idae*, *B. opisthodon*, *B.* sp.n. 9, *B. tephraeomystax*, *Mantidactylus argenteus*, many *Heterixalus* and many non-Madagascan species.

IV Iris with reddish or brownish ornamentations

a) irregular reticulations: *Boophis mandraka*.

b) symmetrical or regular markings: *Boophis albipunctatus*, *B. sibilans*, *B.* sp.n. 1, *B. marojezensis*, *B. elenae*.

V Iris dorsally light, ventrally darker: see section iris colour and body colour.

If inner and outer iris area are differently coloured, the inner area is generally less colourful (in most cases silvery, beige or brown). Red iris colour in the genus *Boophis* is present in most species groups: *B. luteus*-group: *B. luteus*; *B. difficilis*-group: *B. miniatus*, *B.* sp.n. 3; *Boophis goudoti*-group: *B. boehmei*, *B.* sp.n. 7; *B. tephraeomystax*-group: *B. guibei*.

Beside the colour of the iris itself, the colour of the iris periphery, especially its posterior part, is an important feature (see tab. 1). Species of the *Boophis luteus*- and *B. rappiodes*-group always have a blue or grey iris periphery, whereas the *B. tephraeomystax*-group has an indistinct and inconspicuously coloured, never blue, iris periphery.

Intraspecific geographic variation of eye colouration: In most *Boophis* species we did not observe important colour differences in the iris or iris periphery of specimens from different localities (see tab. 1). However, there are minor differences in the iris colouration of *Boophis luteus* from Tolagnaro (southeastern Mad.) versus Andasibe and the Ranomafana area (central eastern Mad.). Specimens from both latter localities are characterized by additional reddish pigment on the iris. Comparable patterns are also present in the eye of *Boophis boehmei* from Andringitra and lacking in specimens from Andasibe, Ranomafana and Ambohitantely.

Geographic variation of iris colouration seems to occur also in neotropical frogs, but in it can not always be excluded that differences actually refer to (still unrecognized) different species or are due to misidentifications. WEIMER et al. (1993b) figured two colour morphs of *Eleutherodactylus caryophyllaceus* from Costa Rica. Both morphs show extremely different iris colouration. A specimen of *Phyllomedusa tarsius* figured in RODRIGUEZ & DUELLMAN (1994) shows a distinctly reticulated iris, whereas a specimen from Tarapoto (Peru) has a dark red iris (see SCHLÜTER 1987: cover photograph).

Altitudinal variation of iris colour was found in *Hyla lancasteri* (TRUEB 1968: 293). Few examples (*B. luteus*: Tolagnaro, near sea level, versus Andasibe, ca. 900 m) indicate that such variation could be present also in *Boophis*. The differences in *B. boehmei* (see above) can clearly not be explained by altitudinal variation, since the localities Andringitra and Ambohitantely are at similar altitude.

Eye colour variation within a population: In several anurans body colouration differs substantially within a population whereas eye colouration shows relatively low variability. This is especially remarkable in an undescribed *Boophis* (*B.* sp.n. 3) in which several different body colour morphs occur. Eye colour variation within a population mainly concerns colour intensity but not general pattern. The outer iris area and iris periphery of *B. madagascariensis* from Andasibe vary from nearly white to orange-yellow. In an undescribed *Boophis* species from An'Ala the outer iris area varies from yellow to orange, in *B. elenae* from Andasibe pigment in the inner iris area is red or red-brownish. Intrapopulational iris colour variation is often correlated to dorsal body colouration (see next section).

Iris colour and body colour: Obvious relationships between iris colour and dorsal body colour exist between individuals of a population as well as between different species. Some specimens of *Boophis* cf. *mandraka* (from Ranomena) have a uniformly pale green back and a uniformly silvery iris, whereas other specimens with brown pigments on the back have also brown pigments in the iris. At Andasibe there are specimens of *Boophis idae* with a silvery back and a golden iris beside specimens with a brownish back and a golden-brownish iris. *Boophis microtympanum* has a predominantly green back and a green iris. A flavistic mutant of *B. microtympanum* from Ankaratra (with a yellow instead of green back) had a grey-green instead of a metallic green iris as found in normal specimens. Another example can be found on the photographs in PASSMORE & CARRUTHERS (1995): The iris of a greenish morph of *Hyperolius argus* (from Richards Bay) has a greenish iris, a brown-backed morph from the same locality has a brownish iris. Two morphs of *Hyla leucophyllata* occur at Iquitos (Peru): A dark morph with largely dark iris and a lighter reticulated morph with a light iris (RODRIGUEZ & DUELLMAN 1994). Another correlation will be described in the section "Obligatorily black-eyed species".: Black eyes are often associated with aposematic body colouration.

In several anuran families a correlation between colourations of dorsal body and iris can be observed when related species are compared. The common toad (*Bufo bufo*) has a brown or reddish-brown back and a copper iris, whereas *Bufo calamita* and *Bufo viridis,* with a partly greenish back, have also a greenish iris. Males of *Rana lessonae* are predominantly yellow with a golden iris during the breeding period, whereas *Rana ridibunda* has more dark colour on dorsum and iris. Other examples are obvious in frogs of South Africa (see photographs in PASSMORE & CARRUTHERS 1995): A brown-backed *Kassina maculata* shows a brown iris, that of a more yellow-backed *Kassina senegalensis* a more golden iris. The iris of the five *Heleophryne* species largely reflect their dorsal colouration. The same is true for the pictured specimens of *Hyperolius horstocki* and *H. tuberilinguis*. The iris of the tree bark-like coloured *Boophis* sp.n. 10 from An'Ala has a colour very similar to the neighbouring skin. The same is true for *Hyla marmorata* from Peru (see photograph in RODRIGUEZ & DUELLMAN 1994).

In other groups such relationships between dorsum and iris colouration are completely lacking. Among the green species of the *Boophis luteus*-group none has a greenish iris. One adult flavistic specimen of this group (probably *B. sibilans*) with a yellow instead of green back had a normally coloured iris.

In many terrestrial (and some scansorial) species, the eye is concealed in a blackish head-side or in a completely dark lateral colouration. In such species the dorsal part of the iris contains light pigment whereas the ventral part is darker. This pattern, already mentioned by DUELLMAN & TRUEB (1986), can be found in many Madagascan species as *Aglyptodactylus madagascariensis*, *A.* sp.n. 1, *A.* sp.n. 2, several *Mantella*, in different subgenera of *Mantidactylus* (e.g. *M. depressiceps, M. luteus, M. aerumnalis*). As far as can be judged from photographs it occurs also in South African and Australian species as *Arthroleptella hewitti*, *Anhydrophryne rattrayi*, *Strongylopus wageri*, *Mixophyes* sp., *Philoria loveridgei*, *Taudactylus acutirostris*, *Litoria brevipalmata* (see PASSMORE & CARRUTHERS 1995, COGGER 1992).

An exceptional correlation between body and eye colouration exists in specimens with reduced or absent pigmentation, classified as "albino" or "semi-albino". KLEMZ & KÜHNEL (1986) give a table with a lot of published cases of albinism in anurans. Comparing the pictures in GABRIEL (1987), KARBE & KARBE (1988), MALKMUS (1993), and DANOVA et al. (1995), we can distinguish between albinos with translucent reddish eyes, semi-albinos with pigmentless body and normally pigmented eyes, and light yellowish, 'flavistic', specimens with normally pigmented eyes (often the iris in these specimens is somewhat lighter). Although the reddish-eye-forms have been quoted to have a pigmentless iris, in several pictures rests of the iris pigmentation are still recognizable (KARBE & KARBE 1988). The translucent reddish colour is most probably caused by the blood vessels in the retina.

E y e c o l o u r d i f f e r e n c e s b e t w e e n m a l e s a n d f e m a l e s : There are still many Madagascan frog species in which females or their life colouration are unknown. In those cases in which photographs of both sexes are available we found no significant differences in the colour of iris or iris periphery between males and females. In the European *Rana lessonae* males in the breeding season have a more yellowish dorsal body colouration and a golden iris, whereas females have more dark pigment on body and iris.

Since it is currently nearly impossible to determine juveniles of Madagascan frogs, we can not treat intraspecific iris colour differences between juveniles and adults, which probably exist especially in *Boophis*.

E y e c o l o u r a t i o n a n d h a b i t s : Colourful eyes are mainly found in arboreal-nocturnal frogs of the tropics, which often share a "typical" treefrog habitus. Arboreal anurans have generally relatively larger eyes than aquatic or fossorial species (DUELLMAN & TRUEB 1986), and large eyes are especially evident in treefrogs. Two treefrog groups, the family Hylidae and the rhacophorine frogs, show the greatest diversity in eye colouration. Most *Boophis* species with colourful eyes occur primarily or exclusively in rainforest habitats. The same seems to be true for treefrog groups in other tropical regions.

B l a c k e y e s :

– Black eyes as rare mutations : Eyes with a blackish iris have been described as rare mutations in different anuran families (also known from urodeles): **Discoglossidae:** *Alytes obstetricans* (GALAN et al. 1990); **Bufonidae:** *Bufo bufo* (DUBOIS 1969), *Bufo viridis* (ENGELMANN & OBST 1976); **Hylidae:** *Hyla meridionalis* (DELCOURT 1963, after DUBOIS & VACHARD 1971); *Hyla cinerea* (CAIN & UTESCH 1976); **Ranidae:** *Rana clamitans* (RICHARDS

& Nace 1983), *Rana cyanophlyctis* (Dubois 1976), *Rana esculenta* (Boulenger 1897, Dubois 1968, 1979), *Rana graeca* (Boulenger 1898, after Dubois & Vachard 1971), *Rana lessonae* (Dubois 1979; Danova et al. 1995), *Rana nigromaculata* (Richards et al. 1969), *Rana pipiens* (Richards & Nace 1983), *Rana ridibunda* (see Dubois 1979), *Rana sylvatica* (Richards & Nace 1983), *Rana temporaria* (Rostand 1953, after Dubois & Vachard 1973), *Rana tsushimensis* (Richards et al. 1969).

Some of these variants were kept in captivity and not found to be more fragile or less healthy than those with normal eye colouration (Dubois 1979). Own unpublished observations on a partially albinotic "black eyed" specimen of *Alytes obstetricans* confirm this view. This specimen which was described and illustrated in Galan et al. (1990) was held in captivity by us for several years. During that period it did not show obvious differences in vitality to normal-eyed specimens held in the same terrarium. These observations suggest that black eye mutations can survive in wild populations under certain conditions.

– Obligatorily black-eyed species : There are several species of anurans, urodeles and snakes with obligatorily blackish eyes which may have their origin in mutations of normal eyed ancestors. We classify these species into three groups:

1. Black eyes in not aposematically coloured species are seldom observed. They are common in the genus *Nyctimystes* which occurs mainly in New Guinea (Menzies 1974, Cogger 1992, Martens 1992). The single Australian species (*N. dayi*) also has black eyes (Cogger 1992). A black iris is also typical for *Phyllomedusa boliviana* which shows a special behaviour that can be interpreted as deathfeigning (Köhler et al. 1995). Both genera *Phyllomedusa* and *Nyctimystes* are nocturnal rainforest treefrogs of the family Hylidae with vertical pupils and a reticulated translucent eyelid, whereas the Black-eyed Litter Frog (*Leptobrachium nigrops*) from Singapore (Lim & Lim 1992) and *Vibrissaphora boringii* from China (Zhao & Adler 1993) are terrestrial.

2. Aposematically coloured terrestrial species in which the body colouration is largely or completely uniform yellow, orange or red with a very contrasting largely black iris. Among these are: *Mantella aurantiaca* from Madagascar, the neotropical dendrobatids *Dendrobates pumilio* and *Phyllobates terribilis*, the brachycephalid *Brachycephalus ephippium* from South America, males of the bufonid *Bufo periglenes* (however, the latter has not a completely black iris). Exceptions are found in the bufonid *Atelopus zeteki* and the Madagascan microhylid *Dyscophus antongili*. These species have also a yellow or orange-red body colouration but the iris is light.

3. Aposematically coloured and black-eyed species in which the body is yellow, orange or red with black. Among anurans this is known from the Madagascan *Mantella baroni*, *M. cowani*, *M. laevigata*, several neotropical dendrobatids (e.g. *Dendrobates leucomelas*, *D. ventrimaculatus*), some specimens of the African microhylid *Phrynomantis bifasciatus* and the Australian myobatrachid *Pseudophryne corroboree* (some light pigment is still visible in the less aposematically coloured *P. dendyi*, see Cogger 1992). On the other hand, other aposematically coloured amphibians (e.g. several *Atelopus*) do not have uniformly black eyes.

Eye colouration and taxonomy

S i b l i n g s p e c i e s w i t h d i f f e r e n t e y e c o l o u r p a t t e r n : Within *Boophis* several species are morphologically very similar to each other and can mainly be distinguished by advertisement calls. These species can be considered as sibling species. The majority of these siblings in *Boophis* can clearly be distinguished by iris colouration: *B. a. albilabris* – *B. a. occidentalis*; *B. madagascariensis* – *B. brachychir*; *B. elenae* – *B. l. luteus* – *B. l. septentrionalis*; *B. miniatus* – *B.* sp.n. 3; *B. reticulatus* – *B.* sp.n. 7; *B. rappiodes* – *B.* sp.n. 2; *B. jaegeri* – *B. andreonei*; *B. majori* – *B. marojezensis* – *B.* sp.n. 4. In contrast, only a few sibling species of the speciose mantelline genus *Mantidactylus* (*M. depressiceps* – *M. tornieri*; *M. aglavei* – *M. fimbriatus*) can be clearly distinguished by iris colouration. Only single examples are available for other Madagascan genera: The mantelline *Mantella baroni* has distinctly black eyes, whereas the similar *M. pulchra* has light iris pigments; the arboreal microhylid *Plethodontohyla* sp.n. has a bluish outer iris area which is brownish in the sibling species *P. notosticta*. No species of the hyperoliid treefrog genus *Heterixalus* can be identified by eye colouration.

This clearly demonstrates that the availability of eye colouration as taxonomic character strongly depends on the group under consideration. However, single examples of diagnostic eye colouration between closely related species seem to be widespread among anurans.

T a x o n o m i c i m p l i c a t i o n s : Evidence from *Boophis* supports the assumption that larger differences in eye colouration occur mainly between taxonomically different forms. Within frog populations we observed relatively low variability of this character, and few examples of geographic variation do exist. Judging from our current knowledge, eye colour patterns can therefore be a rather reliable taxonomic character, especially in groups with large interspecific variability of eye colour pattern. Larger differences in eye colouration between different "morphs" of a species (e.g. in *Eleutherodactylus caryophyllaceus*, see WEIMER et al. 1993b) may indicate that different taxa are involved. They should be used as stimulation to search for additional (e.g. bioacoustic) differences, but descriptions of new taxa should not be based exclusively on eye colouration. Considering the low number of diagnostic morphometric characters in anurans, more interest should be focused on the comparative investigation of life colouration.

Possible functions of eye colouration

Except for those examples in which iris pigments are integrated into a cryptic body colour (e.g. the terrestrial species with a light dorsal streak on the iris, or examples like *Hyla marmorata*), any statement on the function of eye colouration remains speculative. In the following we will discuss pros and contras of four alternative hypotheses.

A l t e r n a t i v e 1 – Eye colouration without any significance : Correlations between body and iris colouration (see section "Iris colour and body colour") demonstrate that iris colouration can not be always explained by structures and functions of the iris itsself. They can be interpreted as an effect of pleiotropy, indicating a partly common pigment controlling system for eye and body. They could also be used as argument to deny a separate functional significance of iris colour. However, at least two strong arguments stand against such a 'neutralist' approach. If colourful eye pigments had no adaptive importance,

– differences in pigmentation would be expected to increase with phylogenetic distance. However, strong differences in iris pigmentation are especially found in closely related syntopic sibling species.

– a random distribution of eye colours through ecological frog types would be expected. In contrast to this expectation colourful eye patterns evolved convergently in different anuran groups with similar habits (arboreal and nocturnal).

Alternative 2 – Eye colouration with physiological significance : It can be argued that the iris may be the place of some specialized physio-chemical reactions (and the colour a by-product of these processes). The iris could also be considered as a kind of 'waste pit' for chemical agents which accumulate during certain metabolic activities.

It can not be excluded that light not only reaches the retina through the pupil, but also through the iris. This iris-filtered light may provide some special (unknown) informations, especially during the day when the pupil is largely closed. Such a hypothetic physiological function of iris pigments is in agreement with the fact that some combinations of iris colour pattern have evolved convergently in different anuran groups. However, this fact can also be explained by other hypotheses. We are not aware of any other data which could confirm a physiological or waste pit function of eye colouration, which, in contrast, applies with a certain probability to several other animal pigmentations such as the regular ornaments of mollusc shells; in many species these are covered by the periostracum in life, and therefore can not have any function in communication.

Alternative 3 – Eye colouration with function in prey/predator relationships : Prey of small and medium sized arboreal frogs are mainly rather small arthropods, and it seems extremely unlikely that eye pigmentation could play any role in attracting such prey or distracting it while the frog approaches. A possible function as antipredator adaptation remains as the only conceivable function of colourful eye pattern in interspecific communication.

Before discussing this subject we first will have a look to the so-called "eyespots" which are common on the wings of butterflies and can also be found in the inguinal region of several terrestrial frogs. Leptodactylids of the genera *Pleurodema* and *Physalaemus* have large inguinal glands and assume a defence posture lowering the head and elevating the pelvic region, thereby presenting the glands to the predator (DUELLMAN & TRUEB 1986). Similar spots (without gland-like elevation) occur in the Madagascan microhylid *Plethodontohyla ocellata.* Such ocelli-like markings have been interpreted as "eyespots" with the suggestion that the broad pelvic region with elevated "eyes" gives the image of a much larger organism (DUELLMAN & TRUEB 1986). The interpretation of eyespots as an antipredator mechanism seems convincing at least in some species as *Pleurodema cinereum* which show exact imitations of eyes with a dark pupil. On the other hand the eyespots of *Physalaemus nattereri* (figured in DUELLMAN & TRUEB 1986) are uniformely dark and could be interpreted as imitations of black eyes.

If the ocelli-like markings in the inguinal region of these frogs are really imitations of eyes, it would be easy to imagine that real eyes can also have an impact on predators. This seems probable for the black eyes of the non-aposematically coloured species of *Nyctimy-*

stes, *Phyllomedusa* and *Leptobrachium* as well as for the strongly contrasting black eyes in light aposematically coloured species (e.g. *Mantella aurantiaca*). It is also possible (but not very probable) for certain types of colourful eyes.

In poisonous species Müllerian Mimicry should be expected and would predict a strong convergence of eye colour patterns in syntopic species. This convergence is clearly not found in *Boophis*. A possible explanation is that *Boophis* species are probably not particularly poisonous. Thus, predators could potentially learn that they are edible; different eye colours of related species would be interpreted as a mechanism to prevent habituation of the predator (apostatic selection). However, the same argument would also predict high intraspecific variability of eye colour which is not found.

In species with an aposematic body colouration which includes black parts, the (black) eyes are concealed in these black parts; thus they do not break up the contrast, enhancing the effect of the general pattern. Many of these species have been demonstrated to be poisonous (e.g. the frog genera *Dendrobates* and *Mantella*, the urodele *Salamandra salamandra*, the snake genus *Micrurus*), and it can be assumed that the distinctly contrasting pattern constitute a strong signal to predators.

In cryptically coloured species in which iris colour is similar to body colour, and in terrestrial species with darker head side or flanks (see section "Iris colour and body colour") eye colouration most probably functions enhancing the concealing effect of body colouration.

Alternative 4 – Eye colouration as visual reproductive isolating mechanism : It can be hypothesized that eye colour is an important optical signal to recognize conspecific mates and/or rivals. In territorial species such a mechanism would save time and energy by avoiding superfluous battles with non-conspecifics. The obvious advantage of improved mate recognition is to avoid hybridization which often results in unviable offspring. Gull species from the arctic region mainly recognize their mates by the colouration of the area around the eye (SMITH 1967). A striking example of iris colour differences as probable reproductive character displacement is also found in Asian turtles (MOLL et al. 1981). Frogs normally use their advertisement calls as primary premating isolation mechanism, but additional visual mate recognition can be assumed for species with colourful iris pigmentation. The fact that closely related and syntopic sibling species often strongly differ by eye colour supports such a function.

The largest problem for this hypothesis is that most frogs (as well as geckos and snakes) with colourful eyes are nocturnal, often living in the deep darkness of dense forest. The low amount of available light probably does not allow colour-vision at night. Additionally the pupil of nocturnal frogs is enlarged at night and the colourful iris is reduced to a narrow margin along the border of the pupil, thus probably not recognizable. However, during or after heavy rain several *Boophis* species display diurnal activity and start calling long before sunset. The same is true for Nicaraguan *Agalychnis callidryas* (pers. observations). Diurnal calling activity from arboreal positions is generally extremely rare in frogs, probably because of predation by birds. During the day visual recognition of conspecifics could therefore partly replace the acoustic communication. To test this hypothesis it should be studied to which extent male arboreal rainforest frogs conquer and defend calling territories before sunset, and how many females approach their breeding water bodies and are clasped by males during the day.

References

BEHLER, J.L. & F.W. KING (1979): The Audubon Society Field Guide to North American Reptiles & Amphibians. – Alfred. A. Knopf, Inc., New York, 744 pp.

BLOMMERS-SCHLÖSSER, R.M.A. & C.P. BLANC (1993): Amphibiens (deuxième partie). – Faune de Madagascar, **75**(2): 385-530 + 20 planches.

BOULENGER, G.A. (1897): The tailless Batrachians of Europe. I. – London.

— (1898): The tailless Batrachians of Europe. II. – London.

CAIN, B.W. & S.R. UTESCH (1976): An unusual color pattern of the green tree frog, *Hyla cinerea*. – Southwest. Nat., **21**: 235-236.

CAMPBELL, J.A. & E.N. SMITH (1992): A new frog of the genus *Ptychohyla* (Hylidae) from the Sierra de Santa Cruz, Guatemala, and description of a new genus of Middle American strean-breeding treefrogs. – Herpetologica, **48**(2): 153-167.

COGGER, H.G. (1992): Reptiles & Amphibians of Australia. – Fifth Edition, Reed books, Chatswood, 775 pp.

DANOVA, R., KOTLIK, P. & V. ZAVADIL (1995): Ein Fall von Albinismus beim Kleinen Wasserfrosch. – Salamandra, **31**(1): 57-60.

DUBOIS, A. (1968): Sur deux anomalies de la grenouille verte (*Rana esculenta*). – Bull. Soc. linn. Lyon, **37**(7): 316-320.

— (1969): Sur un crapaud commun aux yeux noirs. – Bull. Soc. linn. Lyon, **38**(4): 105-106.

— (1976): Deux *Rana cyanophlyctis* du Nepal aux yeux noirs (Amphibiens, Anoures). – Bull. Soc. linn. Lyon, **45**: 303-307.

— (1979): Anomalies and mutations in natural populations of the *Rana "esculenta"* complex (Amphibia, Anura). – Mitt. Zool. Mus. Berlin, **55**: 59-87.

DUBOIS, A. & D. VACHARD (1971): Sur une anomalie pigmentaire de la grenouille verte (*Rana esculenta*) et de quelques autres amphibiens anoures et urodeles. – Bull. Soc. linn. Lyon, **40**: 40-52.

DUELLMAN, W.E. (1970): The hylid frogs of Middle America. – Monog. Mus. Nat. Hist. Univ. Kansas, **1**: 1-753.

DUELLMAN, W.E. & L. TRUEB (1986): Biology of Amphibians. – New York (McGraw-Hill), 670 pp.

ENGELMANN, W.-E. & F.J. OBST (1976): Partielle Pigmentlosigkeit bei *Bufo viridis viridis* (Amphibia, Anura, Bufonidae). – Zool. Abh. Mus. Tierk., Dresden, **34**: 39-41.

GABRIEL, M. (1987): Ein albinotischer Seefrosch *Rana ridibunda* PALLAS, 1771 aus Sibenik, Jugoslawien (Anura: Ranidae). – Salamandra, **23**(4): 280-281.

GALAN, P., VENCES, M., GLAW, F., FERNANDEZ ARIAS, G. & M. GARCIA-PARIS (1990): Beobachtungen zur Biologie von *Alytes obstetricans* in Nordwestiberien. – herpetofauna, **12**(65): 17-24.

GLAW, F. & M. VENCES (1994): A Fieldguide to the Amphibians and Reptiles of Madagascar. 2nd edition, including mammals and freshwater fish. – Köln (Vences & Glaw Verlag), 480 pp. + 48 colour pages.

KARBE, B. & D. KARBE (1988): Fund eines adulten Albino-Grasfrosches *Rana temporaria* LINNAEUS, 1758 in Overath, Oberbergisches Land (Anura: Ranidae). – Salamandra, **24**(4): 316-317.

KARSEN, S.J., LAU, M.W. & A. BOGADEK (1986): Hong Kong Amphibians and Reptiles. – Urban Council Hong Kong, 136 pp.

KLEMZ, C. & K.-D. KÜHNEL (1986): Ein Beitrag zum Albinismus beim Moorfrosch *Rana arvalis* NILSSON, 1842. – Salamandra, **22**(2/3): 190-195.

KÖHLER, J., IBISCH, P.L., DIRKSEN, L. & W. BÖHME (1995): Zur Herpetofauna der semihumiden Samaipata-Region, Bolivien. 1. Amphibien. – herpetofauna, **17**(98): 13-24.

LIM, K.K.P. & F.L.K. LIM (1992): A Guide to the Amphibians and Reptiles of Singapore. – Singapore Science center, 160 pp.

MALKMUS, R. (1993): Ein Albino des Grasfrosches *Rana temporaria* LINNEAUS, 1758 aus dem Spessart, Nordwestbayern. – herpetofauna, **15**(85): 17-18.
— (1995): Kopfseitenflecken bei beiden Geschlechtern von *Rhacophorus angulirostris* AHL, 1927 (Amphibia: Rhacophoridae). – Salamandra, **31**(4): 245-246.
MARTENS, H. (1992): Froschlurche aus Papua-Neuguinea. – herpetofauna, **14**(79): 18-24.
MENZIES, J.I. (1974): Handbook of common New Guinea Frogs. – Wau Ecology Institute Handbook No. 1, Wau, Papua New Guinea, 75 pp.
MOLL, E.O., MATSON, K.E. & E.B. KREHBIEL (1981): Sexual and seasonal dichromatism in the Asian River Turtle *Callagur borneoensis*. – Herpetologica, **37**(4): 181-194.
NÖLLERT, A. & C. NÖLLERT (1992): Die Amphibien Europas. – Stuttgart (Franck-Kosmos Verlag), 382 pp.
PASSMORE, N.I. & V.C. CARRUTHERS (1995): South African Frogs. A Complete Guide. – Revised edition, Southern book publishers, Witwatersrand University Press, 322 pp.
PENZLIN, H. (1980): Lehrbuch der Tierphysiologie (3. Auflage). – Stuttgart (Gustav Fischer Verlag), 569 pp.
RICHARDS, C.M. & G.W. NACE (1983): Dark Pigment Variants in Anurans: Classification, New Descriptions, Color Changes and Inheritance. – Copeia, **1983**: 979-990.
RICHARDS, C.M., TARTOF, D.T. & G.W. NACE (1969): A melanoid variant in *Rana pipiens*. – Copeia, **1969**: 850-852.
RODRIGUEZ, L.O. & W.E. DUELLMAN (1994): Guide to the Frogs of the Iquitos Region, Amazonian Peru. – The University of Kansas Natural History Museum, Special Publication No. 22, 80 pp. + 12 plates.
ROSTAND, J. (1953): Sur l'anomalie "iris brun" chez *Rana esculenta* L. et chez *Rana temporaria* L. – C. r. Acad. Sci., **237**: 762-764.
SCHLÜTER, A. (1987): Die Froschlurche an einem Stillgewässer im tropischen Regenwald von Peru. – herpetofauna, **9**(50): 17-24 (title photograph).
SMITH, N.G. (1967): Visual isolation in gulls. – Scientific American, 94-102.
TRUEB, L. (1968): Variation in the Tree Frog *Hyla lancasteri*. – Copeia, **1968**(2): 285-299.
WEIMER, R., FEICHTINGER, W., BOLANOS, F. & M. SCHMID (1993a): Die Amphibien von Costa Rica. Herpetologische Eindrücke einer Forschungsreise. Teil 1: Einleitung, Hylidae (1). – Sauria, **15**(2): 3-8.
— (1993b): Die Amphibien von Costa Rica. Herpetologische Eindrücke einer Forschungsreise. Teil III: Leptodactylidae (1). – Sauria, **15**(4): 19-24.
WINTER, H.G. (1988): Färbung und Zeichnung. – In: KLEWEN, R.: Die Landsalamander Europas, Teil 1. – Die Neue Brehm Bücherei, Wittenberg Lutherstadt (A. Ziemsen Verlag), pp. 54-55.
ZHAO, E. & K. ADLER (1993): Herpetology of China. – Society for the Study of Amphibians and Reptiles, Oxford (Ohio), 522 pp., 48 plates, 1 map. Contr. Herpetol. 10.
ZWEIFEL, R.G. (1992): Frösche und Kröten. – In: COGGER, H.G. & R.G. ZWEIFEL (eds.): Reptilien und Amphibien, Hamburg (Jahr-Verlag), pp. 76-105.

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