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Amelanistic phenotypes in Western Palearctic water frogs from Poland
(Anura: Ranidae: *Rana*)

Amelanistische Phänotypen bei Wasserfröschen aus Polen
(Anura: Ranidae: *Rana*)

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KURZFASSUNG

Mutanten mit einem Melanindefizit (amelanistische und hypomelanistische Phänotypen) sind bei vielen Wasserfröschen der Gattung *Rana* (*Pelophylax*) sp. beschrieben worden. Diese Arbeit gibt einen kurzen Überblick über publizierte Fälle von Albinismus und unpublizierte Labordaten über 5 Froscharten (*R. ridibunda*, *R. lessonae*, *R. perezi*, *R. epeirotica*, *R. kurtmuelleri*) sowie den Hybriden *R. esculenta*. Das Phänomen des Albinismus wird in Licht der Hybridogenese diskutiert.

ABSTRACT

Colour mutants with a deficit of melanin pigment (amelanistic or hypomelanistic phenotypes) have been described in many species Anurans. Here we present a brief review of published accounts of albinism in water frogs *Rana* (*Pelophylax*) sp. and unpublished data from field observations and laboratory crosses for five species (*R. ridibunda*, *R. lessonae*, *R. perezi*, *R. epeirotica*, *R. kurtmuelleri*) and also the hybridogen *R. esculenta*. Albinism in the light of hybridogenesis is discussed.

KEY WORDS

Amphibia: Anura: Ranidae: *Rana* (*Pelophylax*) sp., *R. ridibunda*, *R. lessonae*, *R. perezi*, *R. epeirotica*, *R. kurtmuelleri*, *R. esculenta* amelanism, hypomelanism, hybridogenesis, experimental crosses, field surveys

INTRODUCTION

The number and spatial arrangement of three types of pigment cells called chromatophores determine the pigmentary pattern of amphibians. These include melanophores containing brown or black melanin pigment, xanthophores with yellow pteridines (carotenoids in some species), and iridophores containing reflecting platelets consisting of crystalline purines and/or pteridines (FROST-MASON et al. 1994). Mutant individuals ascribed as having a deficit of melanin, commonly referred to as "albinos", have been reported in a number of species of anurans (e.g., DUBOIS 1979; NISHIOKA & UEDA 1985; CORN 1986; FROST-MASON et al. 1994). In the absence of melanin, xanthophores and iridophores establish the pigmentation pattern and this usually results in a pale yellowish colour of the skin. We refer to mutant individuals as being amelanistic when no melanin is deposited in the melanophores and hypomelanistic when melanin deposition is substantially reduced. A frog is referred to as wildtype when the phenotype does not obviously deviate from common pigmentation patterns.

Here we present the results of experimental crosses and field observations in which Western Palearctic water frogs *Rana* (*Pelophylax*) sp. exhibiting amelanism or hypomelanism were found between the years 1963 and 2002. Most data on pigment defects was collected incidentally, as experimental crosses and fieldwork were conducted for other purposes (cf. BERGER 1988; RYBACKI & BERGER 2001). However, in view of the large number of frogs examined and unique mode of inheritance in some lineages of water frogs, we feel that a brief description of the instances is warranted.

The Western Palearctic water frogs consist of several Mendelian species and their associated hemiclonal hybrid lineages (review in GRAF & POLLS-PELAZ 1989). Mainland Europe harbours at least seven species: *Rana ridibunda* (PALLAS, 1771), *Rana lessonae* (CAMERANO, 1882), *Rana perezi* (SEOANE, 1885), *Rana epeirotica* (SCHNEIDER, SOFIANIDOU & KYRIAKOPOULOU-SKLAVOUNOU, 1984), *Rana bergeri* (GÜNTHER, 1985) *Rana shqiperica* (HOTZ, UZZELL, GÜNTHER, TUNNER & HEPPICH, 1987) and *Rana kurtmuelleri* (GAYDA, 1940). The common, central European hemiclonal hybrid between *R. ridibunda* and *R. lessonae* is known as *Rana esculenta* (LINNAEUS, 1758). Hemiclonal hybrids reproduce by hybridogenesis (SCHULTZ 1969; TUNNER 1974), a peculiar form of clonal inheritance. A chromosome set of one of the parental species is excluded before meiosis, the remaining set is endoreduplicated. Meiosis proceeds, however, its genetic consequences are nonexistent because the two homologues of each chromosome are sister-chromatid derived copies (TUNNER & HEPPICH-TUNNER 1991; GRAF & POLLS-PELAZ 1989). Central European populations of water frogs are by far the best studied and are commonly composed of *R. lessonae* and hemiclonal lineages of *R. esculenta*. The latter most often transmit an unrecombined *ridibunda* genome to its gametes while eliminating the *lessonae* genome. These lineages depend on *lessonae* gametes from syntopic *R. lessonae* in order to restore hybridity in each generation (the L-E system; UZZELL & BERGER 1975). Therefore, they mate with and coexist as sexual parasites of *R. lessonae*.

Most reports of amelanistic or hypomelanistic water frogs pertain to solitary individuals or siblings. In 1879 PAVESI (after DUBOIS 1979) described several specimens of adult water frogs from Italy with "complete" or "partial albinism". ROSTAND (after DUBOIS 1979) was the first to report pigmentless water frog eggs and also found a "partially albinotic" tadpole. Taxon designation of these early accounts is uncertain (HOTZ 1983; GÜNTHER & PLÖTNER 1995). OGIELSKA-NOWAK (1985) and GÜNTHER (1990) described pigmentless eggs of *R. esculenta*. GÜNTHER (1990) also managed to rear albinotic froglets from these eggs. TUNNER (1979) obtained a "semi-albino" tadpole of the *ridibunda* phenotype whose parents were *R. esculenta* exhibiting typical pigmentation. The long-term presence of amelanistic tadpoles of *R. lessonae* has been documented in the Czech Republic (DANDOVÁ et al. 1995; KOTLÍK & ZAVADIL 1997). There have been a few other reported instances of hypomelanism in adult *R. ridibunda* (GABRIEL 1987; MIKULÍČEK et. al. 2001).

MATERIALS AND METHODS

A total of 1495 experimental crosses between several species of water frogs and their hybrids were conducted following standard procedures (BERGER 1988; BERGER et al. 1994) between the years 1963 and 2002. These crosses were designed for various purposes and some results have been published elsewhere (e.g., BERGER 1976; BERGER & ROGUSKI 1978; BERGER & BERGER 1992) while still much remained unpublished. Eggs, tadpoles and frogs were reared either in controlled or comparable conditions, therefore, the induction of mutant phenotypes by environmental factors or disease can be ruled out.

Field surveys of water frog populations have been conducted in Poland since 1963. The results of these surveys and a description of methods used have been published in RYBACKI & BERGER (1994, 2001). A total of 11,170 adult frogs and numerous larvae were examined from 152 localities in Poland. Only two natural populations harboured anomalously pigmented individuals. A gravel pit near Poznań-Naramowice was sampled once (dip-netted for larvae) in 1968. Amelanistic tadpoles were discovered in this locality. In 1974 a large clay pit near Fabianowo revealed two hypomelanistic individuals. This locality was repeatedly sampled for adult water frogs during that year and yielded a total of 3000 adult *R. ridibunda*.

RESULTS

All instances of amelanism and hypomelanism are reported in table 1. Eggs, larvae and adults of amelanistic water frogs are shown in figure 1.

Experimental crosses

Only *R. esculenta* females laid amelanistic eggs. Two of these females (nos. 2 and 4, table 1) came from backcrosses involving a *R. lessonae* female and a *R. esculenta* male, the other six originated from mixed *lessonae-esculenta* populations (L-E system) inhabiting the environs of Poznań, Poland. The eggs were completely white and hence lacked melanin altogether. These females also produced wildtype eggs in the same batches, although in different proportions (table 2 and fig. 1A). In some egg batches it was difficult to distinguish between the two because a few individual eggs had an intermediate phenotype, these were regarded as wildtype. The number of pigmentless eggs ranged from 18 to 4775 per clutch (0.4 to 98.5%, respectively). The eggs of *R. esculenta* fell into 3 size categories – small, medium and large (BERGER & UZZELL 1980; BERGER 1995). All mutant eggs were medium-sized.

Eggs (both amelanistic and wildtype variants) were artificially fertilized with *R. ridibunda*, *R. lessonae* or *R. esculenta* sperm. The development of the progeny from all crosses was similar (with one exception, see below). Amelanistic eggs and embryos remained devoid of pigment until larval stage 25 (GOSNER 1960) after which they began to gradually darken, accumulating melanin. All metamorphosed froglets from these crosses had normal pigmentation. One of the tadpoles (from female no. 2, table 2) showed signs of impeded development and remained pigmentless until death after 103 days.

In 1984 a hypomelanistic tadpole was discovered in progeny from a homotypic *R. perezi* cross. This individual retained its anomalous pigmentation and completed metamorphosis.

During crossing experiments in 1999, a tadpole exhibiting hypomelanism (the retina had a pigmented epithelium) and arrested development (it lived for 1.5

Table 1: Gross developmental stage of all amelanistic and hypomelanistic *Rana* (*Pelophylax*) spp. found in our experimental crossings between the years 1963 and 2002. Taxon refers to the inferred phenotype of the mutant individuals (see results), tadpoles to larvae after stage 25 (GOSNER 1960; free-swimming). a - amelanistic individual(s), h - hypomelanistic individual(s), – (dash) - wildtype, † - death shortly after metamorphosis.

Tabelle 1: Grobe Zuordnung zu Entwicklungsstadien aller amelanistischen und hypomelanistischen *Rana* (*Pelophyllax*) spp., die zwischen 1963 und 2002 in unseren Kreuzungsversuchen gefunden wurden. Taxon bezieht sich auf die ermittelten Phänotypen der mutierten Individuen (vergl. Ergebnisteil), Larven auf Kaulquappen nach dem Stadium 25 (GOSNER 1960, freischwimmend). a - amelanistische(s) Individuen (Individuum), h - hypomelanistische(s) Individuen (Individuum), – (Strich) - Wildtyp, † - Tod kurz nach Beendigung der Metamorphose.

Taxon	Developmental Stage / Entwicklungsstadium Eggs / Eier	 Tadpoles / Larven	 Adults / Adulte
Rana esculenta	a	-	-
Rana esculenta	a	-	-
Rana esculenta	a	-	-
Rana esculenta	a	-	-
Rana esculenta	a	-	-
Rana esculenta	a	-	-
Rana. esculenta	a	-	-
Rana esculenta	a	-	-
Rana perezi	-	a	a
Rana kurtmuelleri / Rana lessonae	-	h	†
Rana epeirotica	-	a	a
Rana ridibunda	?	a	†
Rana ridibunda	?	?	h

Table 2: Number of amelanistic eggs laid by several *R. esculenta*. Year – year in which amelanistic eggs were laid; SVL – snout-vent-length of female; Wildtype – number of eggs with typical pigmentation; n, % – number and percent of amelanistic eggs in clutch.

Tabelle 2: Zahl der amelanistischen Eier, die von einigen *Rana esculenta* gelegt wurden. Jahr – Jahr in dem die amelanistischen Eier gelegt wurden; SVL – Kopf-Rumpf-Länge des Weibchens; Wildtype – Zahl der Eier mit typischer Pigmentierung; n, % – Zahl und Prozent amelanistischer Eier des Geleges.

Female no. / Year Weibchen Nr. / Jahr	SVL (mm)	Total no. of eggs Eizahl gesamt	Egg pigmentation / Eipigmentierung Wildtype	amelanistic n	 %
1 / 1964	76.0	?	?	65	?
2 / 1966	63.0	2474	2337	137	5.5
3 / 1975	82.0	5579	5559	20	0.4
4 / 1976	61.0	1358	1340	18	1.3
5 / 1977	81.5	5553	5493	60	1.1
6 / 1977	80.0	3125	2188	937	30.0
7 / 1982	83.0	4070	60	4010	98.5
8 / 1999	80.5	5000	225	4775	95.5

years) was found in the progeny of a female *R. kurtmuelleri* and male *R. lessonae*. This tadpole had 214 wildtype siblings that metamorphosed after 50-70 days.

In the year 2000, 110 hypomelanistic tadpoles hatched from wildtype eggs and maintained their mutant phenotypes after metamorphosis. Unfortunately, the total number of eggs of the mother was unknown. These frogs seem to lack melanin in the integument (fig. 1C), however, a ring of pigmented epithelium is present in the retina. Morphologically, they resemble *R. epeirotica*, in which the callus internus is very small (Berger & Czarniewska 2002). They do not seem to possess any other developmental abnormalities and have reached sexual maturity. These individuals are currently involved in crossing experiments.

Field surveys

The Poznań-Naramowice locality was inhabited by a pure *R. esculenta* population (Berger & Berger 1992). In 1968 a total of 638 tadpoles were caught of which 214 were morphologically *R. ridibunda*. Among these, 7 exhibited a deficit of melanin pigment (fig. 1B) and perished after metamorphosis. They were all female and curiously, lacked eyes. The *R. ridibunda* phenotype, female sex, and low viability point at intrahemiclonal *R. esculenta* parents (Berger & Uzzell 1977; Binkert et al. 1982).

In 1974, two hypomelanistic males of *R. ridibunda* were captured in a large clay pit near Fabianowo where a total of 3000 *R. ridibunda* were collected during the same year.

DISCUSSION

Our results and the published accounts inform of melanin deficits in five Mendelian species of waterfrogs (*R. ridibunda*, *R. lessonae*, *R. perezi*, *R. epeirotica*, *R. kurtmuelleri*), in progeny from crosses between some of these species, and in crosses in which one or both of the parents was the hybridogen *R. esculenta*.

Numerous authors have assumed pigment deficits to be determined by a single recessive gene in the homozygous condition (see Nishioka & Ueda 1985; Corn 1986). However, breeding experiments have revealed that genetically independent stock of albinotic *Rana nigromaculata* Hallowell, 1861 "1860" differ from each other in the locus of the mutant allele (Nishioka & Ueda 1985; Sumida & Nishioka 2000). The biochemical pathway leading to melanin synthesis involves several linear steps (Frost-

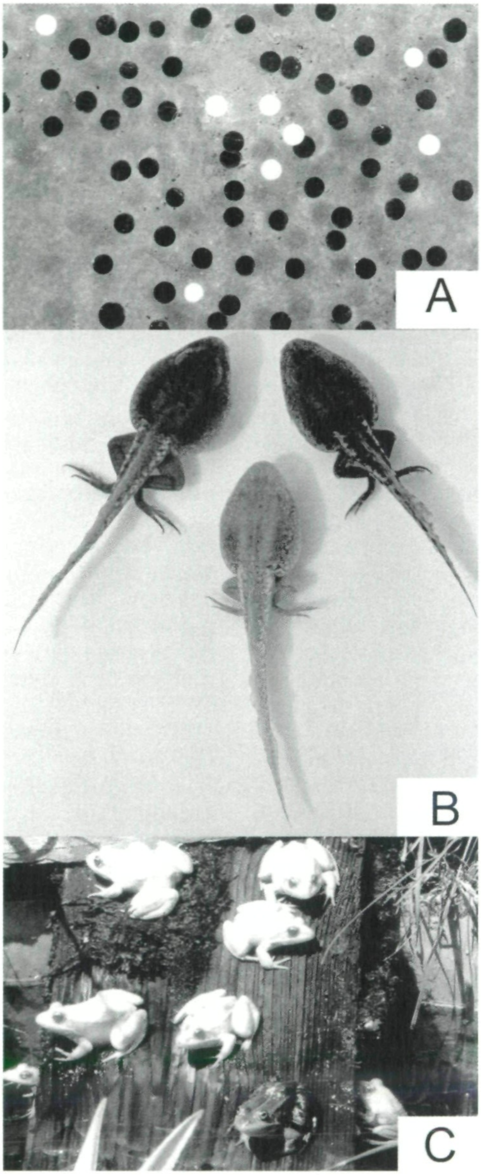

Figure 1: A - Amelanistic eggs of *Rana esculenta* among pigmented ones from female no. 2 (see table 1), in the lower left corner a large, probably diploid egg; photo by Z. PNIEWSKI.
B - Progeny of a homotypic *Rana esculenta* cross. Tadpoles are of the *ridibunda* phenotype, a hypomelanistic one between two pigmented individuals; photo by Z. PNIEWSKI.
C - Amelanistic individuals of *Rana epeirotica* and a waterfrog exhibiting typical pigmentation; photo by E. BIEGAŃSKI.

Abb. 1: A - Amelanistische Eier von *Rana esculenta* zwischen pigmentierten des Weibchens Nr. 2 (vergl. Tab. 1). In der linken unteren Ecke ein großes, wahrscheinlich diploides Ei; Photo Z. PNIEWSKI.
B - Nachkommen einer homotypischen *Rana esculenta* Kreuzung. Die Quappen sind vom *ridibunda*-Phänotyp. Ein hypomelanistisches zwischen zwei pigmentieren Individuen. Photo Z. PNIEWSKI.
C - Amelanistische Individuen von *Rana epeirotica* and ein Wasserfrosch mit typischer Pigmentierung. Photo E. BIEGAŃSKI.

MASON et al. 1994) and a mutation in genes affecting any protein involved may lead to the same phenotype, i.e. a deficit or complete absence of melanin deposition. Disrupting the structure and/or differentiation of melanosomes may also produce an albino phenotype. Tyrosine is the precursor of melanin and growth hormones, developmental defects or retarded growth in amphibians accompanied by amelanism may be attributed to defects in tyrosine synthesis (CHILDS 1953; BROWDER 1972). Two larvae (i.e. the tadpole from the *kurtmuelleri/lessonae* cross and the one from *R. esculenta* no. 2, see results) and also a group of tadpoles from the *R. esculenta* population in Poznań-Naramowice seem to be of this type. Other individuals apparently had unhindered development. It is obvious that the pigmentation mutants we examined had a diverse genesis.

The gametes of most central European *R. esculenta* contain only the *ridibunda* component because of segregation of entire genomes during hybridogenesis (GRAF & POLLS-PELAZ 1989). Evidence exists that this clonally transmitted genome accumulates deleterious mutations through a Müller's ratchet mechanism (BERGER 1976; VORBURGER 2001; GUEX et al. 2002). In our material, *R. esculenta* most often laid abnormally coloured eggs. Only *ridibunda* alleles are expressed in oocytes of *R. esculenta* (UZZELL et al. 1980; HOTZ 1983) and any mutation disrupting the development of pigmentation would be apparent at this stage. Larvae originating from amelanistic eggs began to produce melanin after stage 25. This is understandable, as after fertilization male genomes with a homologous wildtype allele controlling melanin synthesis may effectively mask the mutation present in the female-derived genomes. It is well known that larval melanin is synthesized de novo in melanophores (EPPIG 1970; OGIELSKA-NOWAK 1985).

The proportions of different phenotypes of oocytes observed in particular *R. esculenta* females (table 2) can be explained in several ways. In theory, all oocytes should be identical in genetic composition because hybridogenesis leads to the clonal inheritance of one of the parental genomes. However, a small amount of introgression between the two genomes has been documented (GÜNTHER & LÜBCKE 1979; UZZELL 1982) and therefore, recombination between the *lessonae* and *ridibunda* constituents may account for phenotypic heterogeneity of oocytes in *R. esculenta* ovaries. Another possibility is that a high mutation rate in primordial oogonial cells may contribute to the different proportions of wildtype/mutant eggs in ovaries. Finally, hybridogenesis may be imperfect in some individuals, which would ultimately lead to diversified gametes. This is evidenced by the genetic mosaicism of *R. esculenta* ovaries. Eggs of different ploidy level and genomic constitution appear in clutches (BERGER & ROGUSKI 1978; BERGER & UZZELL 1980; BERGER 1995). This aspect of *R. esculenta* reproduction is in need of further study.

Unfortunately, our results are too anecdotal to extract genetic conclusions. However, they show that a phenomenon of relatively high selective disadvantage in terms of predator avoidance (CHILDS 1953) can be fairly regularly produced in captive conditions. Also, maintaining amelanistic waterfrog lineages may prove worthwhile as they provide a readily detectable morphological marker that can help in elucidating many questions concerning the reproductive biology of this group of amphibians.

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