etal anomalies affecting the axial skeleton of *Tht* heterozygotes (see Figure 4). This mutation was mapped to chromosome 5 (Beechey and Searle 1980) and was further shown to be noncomplementary with a novel insertional mutation *usd*^{TgN370Rpw} that causes defects in the vertebrae of the distal tail (Schrick et al. 1995). When both alleles are present in the same mouse, they lead to a more severe defect in vertebrae at the tip of the tail than does either mutation by itself, suggesting that *usd*^{TgN370Rpw} and *Tht* might be alleles (Schrick et al. 1995). It should now be possible to clone the gene using the *usd*^{TgN370Rpw} transgene insertion and study its aberrant expression in the *Tht* and *usd*^{TgN370Rpw} mutant mice.

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Inheritance of Body Coloration in the Lyretail Toothcarp (*Aphyosemion australe* Cyprinodontidae)

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The lyretail toothcarp (*Aphyosemion australe*) exhibits two body colorations. These are a brown coloration characteristic of *A. australe* and an orange color variant sometimes referred to as the golden lyretail. Segregation patterns observed in the offspring from 11 different matings support the hypothesis that body coloration in *A. australe* is controlled by two autosomal loci acting in a complementary fashion, with dominance at both loci required for the expression of the brown phenotype.

Egg-laying toothcarps in the genus *Aphyosemion* (Cyprinodontidae) exhibit a variety of coloration patterns and body markings (Axelrod and Vorderwinkler 1962; Paysan 1975). The lyretail toothcarp (*Aphyosemion australe*), one of the more common African "nonannual" toothcarps, exhibits two distinct body color phenotypes. Characteristically this species exhibits shades of brown on the epaxial and hypaxial regions of the body with small red spots (Mills 1993). A color variant of *A. australe*, which arose among aquarium stocks of *A. australe* and is sometimes referred to as the golden lyretail, is distinctively orange in color with varying intensities of red spotting on its flanks. Natural populations of this species are almost exclusively comprised of individuals exhibiting the brown phenotype.

As a result of an extensive use of *A. australe* in my laboratory for comparative studies on the regulation and divergence of isozyme loci, I had the opportunity to ascertain the nature of the inheritance of body coloration in the lyretail toothcarp. The present communication reports on these findings.

Materials and Methods

Healthy adults of *A. australe* exhibiting either the brown coloration pattern characteristic of this species or its orange color variant were obtained from Mid-Atlantic Distributors, Inc. (Springfield, Virginia), and maintained in 20 gal capacity holding tanks at 26°C. Sexually mature pairs exhibiting the brown and orange phenotypes were selected at random and placed in 5 gal capacity breeding tanks. All fry were

obtained from natural matings under conditions described by Axelrod and Vorderwinkler (1962). Subsequent to each spawning, the parentals were removed from the breeding tank. After leaving their eggshells, fry from each mating were placed in their own 5 gal rearing tank and allowed to develop until their phenotype could be visually determined. Parental and selected F_1 fishes of both phenotypes were subsequently used in a series of 31 matings, and the phenotypic data from all progeny were recorded and subjected to chi-square analysis.

Results and Discussion

Probable genotypes, observed phenotypic frequencies, expected ratios, and probability of fit for *A. australe* analyzed for the inheritance of the brown and the orange (golden lyretail) phenotypes are given in Table 1. All P, F_1, and F_2 individuals conformed to either the brown or orange phenotype. Parentals exhibiting the brown coloration (A1, A2, A3, and A4) were scored as homozygous dominants, since all matings involving these individuals resulted in that phenotype (matings 1–6, 13, 14, 17, 18, 23, 24). Parentals exhibiting the orange phenotype (H1, H2, and H3) were scored as homozygous recessives, as all matings between these fishes resulted in all orange fry (matings 7–11). In addition, reciprocal matings between orange and brown parentals always resulted in brown progeny (matings 17 and 18). Further, crosses between these F_2s resulted in a satisfactory fit to a 9 brown : 7 orange ratio of F_2 progeny (matings 19–22), commensurate with a modified 9:3:3:1 ratio resulting from dominant complementary gene action (i.e., *A B* is required for the brown phenotype). Backcrosses of brown parentals consistently bred true (matings 13, 23, 24), while backcrosses of orange parentals resulted in a satisfactory fit to the expected 1 brown : 3 orange ratio (matings 25–28).

Complementary gene action as the mode of inheritance of body coloration in *A. australe* is also supported by matings employing F_1 fry presumed to be homozygous recessives (N2). Matings between N2 fishes and heterozygotes (N3 and N4) resulted in a satisfactory fit to the expected 1:3 ratio (matings 29–31), while N2 × N2 matings and backcrosses of orange parentals (matings 15 and 16, respectively) resulted in the expected orange fry.

In conclusion, the data presented here supports the hypothesis that body coloration in *A. australe* is controlled by two autosomal loci acting in a complementary fashion, with dominance at both loci required for the expression of the brown phenotype. It is interesting to note that a similar mode of inheritance has been observed for the blue and obliterative trunk colorations in the three-spot gourami (*Trichogaster trichopterus* Pallas; Frankel 1992).

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Table 1. Probable genotypes (PG), expected ratios, and probability of fit for matings among brown and orange lyretail toothcarp

Mating no	Parents ♀	(PG)		♂	(PG)	Phenotypic frequencies Brown	Orange	Expected ratio	*P*
1	A1	(*AABB*)	×	A1	(*AABB*)	33 (N1)	0	1:0	—
2	A2	(*AABB*)	×	A2	(*AABB*)	30	0	1:0	—
3	A3	(*AABB*)	×	A3	(*AABB*)	25	0	1:0	—
4	A4	(*AABB*)	×	A4	(*AABB*)	37	0	1:0	—
5	A1	(*AABB*)	×	A2	(*AABB*)	39	0	1.0	—
6	A4	(*AABB*)	×	A1	(*AABB*)	25	0	1:0	—
Sum of F_1 offspring from cross type *AABB* × *AABB*						189	0	1:0	—
7	H1	(*aabb*)	×	H1	(*aabb*)	0	23 (N2)	0:1	—
8	H2	(*aabb*)	×	H2	(*aabb*)	0	30	0:1	—
9	H3	(*aabb*)	×	H3	(*aabb*)	0	35	0:1	—
10	H1	(*aabb*)	×	H2	(*aabb*)	0	28	0.1	—
11	H2	(*aabb*)	×	H1	(*aabb*)	0	32	0:1	—
Sum of F_1 offspring from cross type *aabb* × *aabb*						0	148	0:1	—
12	N1	(*AABB*)	×	N1	(*AABB*)	36	0	1:0	—
13	N1	(*AABB*)	×	A1	(*AABB*)	30	0	1:0	—
14	A2	(*AABB*)	×	N1	(*AABB*)	32	0	1:0	—
Sum of F_2 and backcross offspring from cross type *AABB* × *AABB*						98	0	1:0	—
15	N2	(*aabb*)	×	N2	(*aabb*)	0	34	0:1	—
16	H1	(*aabb*)	×	N2	(*aabb*)	0	31	0:1	—
Sum of F_2 and backcross offspring from cross type *aabb* × *aabb*						0	65	0:1	—
17	A1	(*AABB*)	×	H1	(*aabb*)	25 (N3)	0	1:0	—
18	H3	(*aabb*)	×	H3	(*AABB*)	32 (N4)	0	1:0	—
Sum of F_1 offspring from cross types *AABB* × *aabb* and *aabb* × *AABB*						57	0	1:0	—
19	N3	(*AaBb*)	×	N3	(*AaBb*)	14	10	9:7	.90–.75
20	N4	(*AaBb*)	×	N4	(*AaBb*)	21	14	9:7	.50–.25
21	N3	(*AaBb*)	×	N4	(*AaBb*)	16	13	9:7	>.90
22	N4	(*AaBb*)	×	N3	(*AaBb*)	23	15	9:7	.75–.50
Sum of F_2 offspring from cross type *AaBb* × *AaBb*						74	52	9:7	.75–.50
23	A1	(*AABB*)	×	N3	(*AaBb*)	36	0	1:0	—
24	N4	(*AaBb*)	×	A3	(*AABB*)	33	0	1:0	—
Sum of backcross offspring from cross types *AABB* × *AaBb* and *AaBb* × *AABB*						69	0	1:0	—
25	N3	(*AaBb*)	×	H1	(*aabb*)	9	25	1:3	.90–.75
26	H3	(*aabb*)	×	N4	(*AaBb*)	10	27	1:3	.90–.75
27	N3	(*AaBb*)	×	H1	(*aabb*)	4	23	1:3	.25–.10
28	H3	(*aabb*)	×	N4	(*AaBb*)	11	26	1:3	.75–.50
29	N3	(*AaBb*)	×	N2	(*aabb*)	8	28	1:3	.75–.50
30	N2	(*aabb*)	×	N4	(*AaBb*)	6	20	1:3	.90–.75
31	N2	(*aabb*)	×	N4	(*AaBb*)	12	29	1:3	.75–.50
Sum of F_2 and backcross offspring from cross types *AaBb* × *aabb* and *aabb* × *AaBb*						50	178	1:3	.50–.25

Fish designated (A) are brown parentals; fish designated (H) are orange parentals; fish designated (N) are first-generation offspring and exhibit either the brown or orange phenotype.