

environment at Zengpi has nurtured an abundant growth of algae on the exhibited excavations. It was therefore difficult to observe the stratigraphy of the rockshelter. If radiocarbon dates are accurate, and if the stratigraphic context is certain, then pottery shards from the lower levels (≈ 10 ka) may be some of the oldest pottery in the World. It may take new work at the site to confirm these facts.

Archeologists and paleontologists are actively excavating and analyzing prehistoric cave sites throughout China. Many of these cave sites date to the middle Pleistocene, in direct contrast to the paucity of cave sites of this age in the United States. Middle Pleistocene cave sites in China frequently do not resemble caves, but are usually cave fills left as remnants on topographic high points. New work in China may provide a better understanding of the processes involved in the accumulation and natural preservation of cave sites of various ages.

SPELEOLOGY AND COMMERCIAL CAVES

Thousands of caves have been recorded or mapped in China during the last 20 years. Cave exploration and mapping in China is considered a business and not a sport. Therefore, most cave surveys are conducted by professionals, not laymen. Many caves

have been discovered during hydrogeological and engineering investigations. Mineral exploration in karst terrains has also increased the number of known caves. In addition, archeological and paleontological surveys have contributed to the speleological data base in China. To our knowledge, there has been no attempt to compile a systematic index to the caves of China.

Many commercial caves have been opened to the public. Usually, there is a slight admission fee, and tours are lead by trained guides. The commercial caves of China appear to be very popular with the general public, as indicated by the number of tourists that visit them. Ya Ling Cave, approximately 90 km west of Hangzhou, is fairly typical of most commercial caves that we visited in China. The commercial entrance and exit to Ya Ling Cave have been created by blasting openings into the cave wall and then constructing stone gateways (Fig. 3). The natural entrance of Ya Ling Cave has been closed, but in other commercial caves the natural entrance is still used. Extensive stone walkways and stairs have been constructed along the tour route; side passages that exit from the main chamber are not open to the public.

There are many spectacular speleothems in the cave, and it is quite comparable to many of the commercial caves in the United

States. Speleothems are illuminated by electric lamps of various colors, and the lights are turned off after the tours to guard against the growth of algae. Discussions by the tour leaders appear to focus on the imaginary shapes of the speleothems. Lions, dragons, and pagodas are frequent patterns pointed out by the tour guides.

Karst is an exceptional natural resource for China. It is not only of economic and utilitarian importance, but karst provides aesthetic scenery which adorns many of the landscapes of Chinese art. The further development of karst research in China will undoubtedly contribute to greater insights into the phenomena of this field of science.

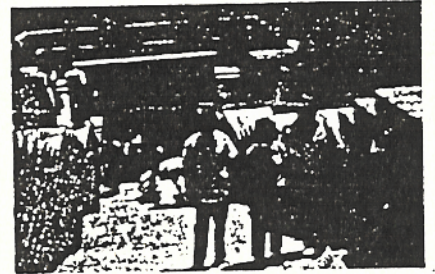


Figure 3. Commercial entrance to Ya Ling Cave, Zhejiang Province. Photo by R. W. Graham.

Romero, Aldemaro (1983)—Introgressive Hybridization in the *Astyanax fasciatus* (Pisces: Characidae) Population at La Cueva Chica. *The NSS Bulletin* 45: 81-85

INTROGRESSIVE HYBRIDIZATION IN THE *ASTYANAX FASCIATUS* (PISCES: CHARACIDAE) POPULATION AT LA CUEVA CHICA*

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INTRODUCTION

Hybridization in Fishes

STUDIES OF HYBRIDIZATION have contributed substantially to our understanding of evolutionary mechanisms. Natural and artificial fish hybrids, including intergeneric, have been reported for more than 50 families, mostly freshwater (Hubbs, 1955; Schwartz, 1981). This extensive hybridization apparently is due to the fact that external fertilization is common in these vertebrates (Bianco, 1982; Daget and Moreau, 1981; Hubbs, 1955; Whitmore, 1983).

A review of the literature reveals several generalizations frequently made concerning fish hybrids:

1) The characteristics of hybrids are phenotypically intermediate when com-

SUMMARY Results of morphological studies on a population of the characid *Astyanax fasciatus* at La Cueva Chica, San Luis de Potosí, Mexico, suggest that the current population is the result of introgression between a blind depigmented population at that cave locality and eyed pigmented fish from a nearby surface population. A synthesis of morphological data with previous breeding, electrophoretic, karyotypic, and behavioral information is made in order to assess how much and in what respects the cave population resembles other natural populations of hybrid fish. Current ideas on the relationship between genetic and phenotypic differentiation of cave populations from their surface ancestor are also discussed.

pared with those of the parents, although the degree of intermediacy has rarely been specified (Bianco, 1982; Hubbs, 1955; Mayden and Burr, 1980; Pethon, 1974);

2) Among hybrids, the sex ratio is skewed toward males (often about 4:1) (Bianco, 1982; Daget and Moreau, 1981; Hubbs, 1955; Pinto, 1982);

3) Hybridization is more likely to occur

when parental population sizes are substantially unequal (Bianco, 1982; Busack and Gall, 1981; Butcher, 1980; Cashner and Jenkins, 1982; Daget and Moreau, 1981; Rakocinski, 1980; Wallace and Ramsey, 1982; Whitmore, 1983);

4) Greater survival of hybrids occurs when the parental species and/or populations are closely related (Cashner and

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Jenkins, 1982; Dauble and Buschbom, 1981; Rakocinski, 1980; Wallis and Beardmore, 1980; Whitmore, 1983);

5) Hybrids are more successful when the environment of the contact zone between the parental populations is intermediate (Hubbs, 1955; Moore, 1977);

6) Hybridization is more likely to take place when overlap occurs both in spawning space and in spawning periods (Bianco, 1982; Dauble and Buschbom, 1981; Hubbs, 1955; Pethon, 1974, 1978, 1981; Rakocinski, 1980; Wallace and Ramsey, 1982).

Hybridization in Cave Animals

Because most related cave species are allopatric (geographically separated), hybrids among cave organisms or between cave and surface populations are rare (Allegrucci, *et al.*, 1982). Although hybridization between surface and cave fish populations has been suspected in at least three cases (*Caecorhamdia urichi* [Endler, 1982, pers. comm.]; *Poecilia sphenops* [Gordon and Rosen, 1962; Walters and Walters, 1965]; and *Lucigobius* spp. [Tomiyama, 1936]), the only well-known example is that of the characid *Astyanax fasciatus mexicanus*. This fish can be found as an eyed, pigmented, surface form and as a blind, depigmented, cave form; the latter was initially described by Hubbs and Innes (1936) as a new genus and species, *Anoptichthys jordani*. These forms interbreed under both natural and experimental conditions to produce fertile F₁ hybrids that are phenotypically intermediate and F₂ individuals (after F₁ × F₁) which range from an almost completely blind and depigmented form to an essentially eyed and pigmented one (Peters and Peters, 1973; Sadoglu, 1957). Electrophoretic and karyotypic

studies also indicate that blind cave and eyed surface forms are conspecific (Avisé and Selander, 1972; Kirby, *et al.*, 1977). These forms differ not only in morphology but, also, in behavior: contrary to the behavior of the eyed surface form, the blind cave one does not school, shows no circadian activity rhythm, and is not aggressive (Boucqquey, *et al.*, 1965; Breder, 1942; Breder and Gresser, 1941; Erckens and Weber, 1976). These behavioral differences can be seen among other cave fishes and their surface ancestors (Thinès, 1969).

Despite conspecificity of the cave and surface forms, their strong morphological and behavioral divergences and the phenotypic intermediacy of progenies resulting from crosses between these forms has led all authors concerned to refer to these progenies as hybrids (Breder, 1943; Peters and Peters, 1973; Sadoglu, 1957; Wilkens, 1969).

Hybridization between the surface and the cave populations has been reported for 9 of the approximately 30 caves supporting subterranean populations of *A. fasciatus* in the San Luis de Potosí area of east-central Mexico (Mitchell, *et al.*, 1977).

The first indication that introgression (*i.e.*, stabilization of backcross types) between surface and cave forms was taking place was presented by Breder (1943). He compared specimens of *A. fasciatus* from La Cueva Chica collected from 1936 to 1942, and, based on changes in phenotypic ratios (eyes and pigmentation), he concluded that a recent invasion of eyed and pigmented fish through a subterranean connection with surface waters was changing the genetic structure of the cave population. Further studies support the cave/surface connection hypothesis (Mitchell, *et al.*, 1977).

The aim of this paper is: a) to give further evidence that introgression between cave and surface populations of *A. fasciatus* has occurred at La Cueva Chica, and that it has occurred rapidly in evolutionary time; b) to compare the characteristics observed in this introgressed population with those commonly attributed to hybrid fishes; and c) to discuss the implications of introgression regarding our present knowledge of the evolutionary biology of cave organisms.

MATERIAL AND METHODS

One hundred individuals of *A. fasciatus* were collected during May 1983 in pool II (*sensu* Breder, 1942) of La Cueva Chica. Pool II was chosen for this study because: a) almost all previous information about the morphology of this cave population comes from material collected at that pool (Álvarez, 1946; Breder, 1942, 1943; Hubbs and Innes, 1936); b) this population is comparatively large for that of a cave organism, (Mitchell, *et al.*, 1977); and c) this pool is the most remote of all from the surface, eyed *A. fasciatus* and is isolated from the rest of the pools during the dry season, restricting gene flow.

Norelco red-infrared 125-watt lamps were used for collecting in caves, since preliminary studies had shown that these fish do not react to such light (Romero, *in litt.* a). All fish were randomly caught by netting, and their standard lengths were immediately measured using calipers read to the nearest 0.1 mm. Sex was determined using sexually dimorphic characters described by Álvarez (1946), Kosswig (1964), and Wiley and Collette (1970). To make comparisons with data previously published, I used Breder's (1943) qualitative criteria for eye condition and pigmentation. Immature individuals (< 35

EYE CONDITION (% of the population)					
Year	N	Sunken			"Normal"
		Blind	Covered	Uncovered	
1936	90?*	100	0	0	0
1939	90?*	100	0	0	0
1940	38	85	6	0	9
1942	28	61	4	21	14
1983	100	4	83	9	4

PIGMENTATION (% of the population)						
Year	N	Intermediate				
		None	Little	Moderate	Considerable	Full
1936	90?*	100	0	0	0	0
1939	90?*	100	0	0	0	0
1940	38	90	2	6	2	0
1942	28	53	11	11	0	25
1983	100	0	28	31	37	4

* Estimate drawn from Breder's (1943) comment, "something less than 100."

Pigmentation	EYE				
	Normal	Sunken		retina	
		Reduced but external	retina visible	not visible	Absent
Full	0	0	0	4	0
Considerable	0	5	18	10	4
Moderate	2	2	18	9	0
Little	2	2	15	9	0
None	0	0	0	0	0

Table 2. (above) Crosstable of distribution of features in the individuals collected in 1983 (N = 100).

Table 1. (left) Phenotypic conditions in the fishes from La Cueva Chica; 1936 to 1942 data from Breder (1943); 1983 data, this paper.

mm) were impossible to sex and were not included in the 100 individuals used for the present study. Fifty four fish were retained for behavioral studies; the rest were returned to the pool.

RESULTS

My results and those of Breder (1943) are presented in Table 1; they suggest that introgression has occurred since 1940. Table 2 shows that none of the 100 individuals collected in 1983 has the morphological attributes of the parental populations (*i.e.*, either totally blind and depigmented or displaying full eyes and pigmentation simultaneously). Table 3 gives the sex ratio of the individuals collected in 1983, plus the sex ratios obtained in previous studies by other authors at this and other localities for cave and surface forms. The hybrid population at La Cueva Chica contains fewer males than females, as is the case for most populations of *A. fasciatus*.

Table 3. Sex ratios for different cave and surface populations of *A. fasciatus*. Data from Mitchell, *et al.* (1977) unless otherwise indicated.

Cave Populations	(male:female)
Cueva Chica**	42:58
Cueva Chica*	3:6
Los Sabinos*	5:5
Pachon	10:12
Pachon*	6:9
Montecillos	5:4
Arroyo	8:7
Curva	6:7
Tigre	9:15
Jos	6:18
Palma seca	6:17
Tinaja	4:20
TOTAL	110:178
Surface Populations	
Tamesi	12:13
Arroyo	11:10
Panuco	8:15
TOTAL	31:38

*After Álvarez, 1946.

**This paper.

DISCUSSION

The identification of F₁ and/or backcross individuals is the basis for assessing introgressive hybridization (Whitmore, 1983). One of the reasons why introgression has been rarely reported in fishes is the difficulty in identifying these hybrid classes (Rakocinski, 1980). However, both the clear-cut morphological differences between the cave and surface forms of *A. fasciatus* and the detailed descriptions of F₁ and backcross generations from breeding studies on this

fish allow hybrid identification and, consequently, introgression assessment. The data in Table 2 show that: a) no parental forms were found in the current hybrid population; and b) most (if not all) individuals collected correspond to the descriptions of the F₁ and backcrossed individuals obtained in the laboratory. These data strongly indicate that the *A. fasciatus* population at La Cueva Chica is the result of introgression.

The data in Table 1 suggest that introgression took place in about 40 years (or less). Lack of hybrids and of eyed, pigmented individuals in the first two collections (1936 and 1939) and the absence of parental forms in the last one (1983) support such a contention. Unfortunately, there is little reliable information on the rate of introgression in natural fish populations. The introgression described here could have taken place long before the last collection (1983). *A. fasciatus* reaches sexual maturity at the age of six months, so it could produce up to two generations per year. Recent data on natural hybrid cichlids on Madagascar, for example, show that introgression can take place in less than 20 years (Daget and Moreau, 1981).

Generalizations on Fish Hybrids

1) *Intermediacy of hybrids.* Experimental studies have shown that hybrids between the blind form from La Cueva Chica and the eyed form from nearby surface populations are not precisely intermediate in their morphological and behavioral features. Wilkens (1969, 1970), for example, showed that eye size and the number of melanophores and their melanin content is slightly skewed to the surface population characteristics in both F₁ and F₂ generations. Boucquoy, *et al.*, (1965) found that F₁ hybrids display a rhythmic pattern of activity similar to that of the surface form, while the F₂ (after test-cross) shows the same arrhythmic time-regulation of activity as does the cave form. Schemmel (1980) showed that the angle of erection for bottom-feeding in F₁ and F₂ generations is closer to that of the surface form. Romero (*in litt.*, a), indicated that the level of photoresponses among natural hybrids is closer to that of surface populations than to that of blind, depigmented *A. fasciatus* from both natural and artificially bred cave populations.

Lack of exact intermediacy for various characteristics in the F₁ and F₂ hybrids of this characid is consistent with recent results of careful studies which suggest that other fish hybrids rarely are exactly intermediate in their characteristics, when compared with their parental populations (Bao and Kallman, 1982; Kerby, 1979; May, *et al.*, 1980; Neff and Smith, 1979; Ross and Cavender, 1981; Sutton, *et al.*, 1981; Wallace and Ramsey, 1982).

2) *Skewed sex ratio.* Table 3 does not provide support for the contention that hybrid populations of fish necessarily display sex ratios skewed toward males. Previous data on sex ratios for other surface and cave populations of *A. fasciatus* (including data for the original blind population of La Cueva Chica) suggest that the sex ratio in most populations, including the current population at La Cueva Chica, is skewed toward females (usually 2:3). A binomial test (95% probability) demonstrated no significant difference between surface and cave populations (excluding La Cueva Chica, 1983 data) and between either of these two sets of data and the 1983 La Cueva Chica data. These results indicate that neither adaptation to the cave environment nor hybridization between surface and cave populations changes the observed sex ratios in these populations.

3) *Disproportionate size of parental populations.* Given the nature of the connection between the cave and surface waters (subterranean and physically impossible to explore), it is difficult to ascertain how frequently and in what numbers surface individuals may invade. The level of introgression may fluctuate through time.

4) *Close relationship of parental species.* Electrophoretic (Avisé and Selander, 1972), karyotypic (Kirby, *et al.*, 1977), and morphologic studies (Hubbs and Innes, 1936; Álvarez, 1946) show that the La Cueva Chica population and the nearby surface population are genetically very similar, and that they differ morphologically only in those characters related to cave-dwelling. This is consistent with the view that close relationship can be considered to be a facilitating factor for rapid introgression.

It has been proposed that there is more genetic than morphological differentiation between related cave and surface species and/or troglotic populations (Culver, 1982 p.95). This is largely based on Barr's (1968) contention that cave adaptation involves considerable reorganization of the genotype, which is, in turn, an application of Mayr's (1970) genetic revolution of the founder principle to the evolution of cave organisms.

5) *Hybrid success and intermediacy of the environment at the contact zone.* Although introgression has taken place in the native environment of one of the parental populations, the intermediate-environment hypothesis cannot be rejected, because: a) eyed, pigmented populations of *A. fasciatus* can be found in many caves not occupied by blind forms in the San Luis de Potosí area (Mitchell, *et al.*, 1977; Romero, *in litt.* b), in the cenotes of Yucatán (Hubbs, 1938), and in a cave in northern Mexico

(Reddell, 1982), and as facultative cavernicoles in Costa Rica (Romero, 1984a, b); and b) the high adaptability of this fish allows it to survive in many different kinds of environments (Bussing, 1976; López, 1978). In consequence, although La Cueva Chica does not represent an 'intermediate' environment for facilitating introgression, it is clear that caves are not unusual habitats for eyed, pigmented *A. fasciatus*. Mitchell, *et al.*, (1977), also suggested that hybridization might be favored by availability of abundant food resources.

6) *Overlap in reduced spawning space and spawning periods.* The physically constricted habitat in La Cueva Chica, whose waters are subdivided into several pools (especially during the dry season), facilitates contact among the individuals occupying the pools (Breder, 1942). Although there is little information on spawning behavior of these fish under natural conditions, no strong differences have been found in laboratory studies other than those related to the lack of vision in the cave form (Breder and Rosen, 1966). As for all characids, fertilization is external in *A. fasciatus*, and crosses between the cave and the surface forms are readily obtained under experimental conditions (Sadoglu, 1979). Even hybrids between cave

A. fasciatus and two other characids (*Ctenobrycon spilurus* and *Moenkhausia oligolepis*) have been reported (Kauffeld, 1954), suggesting that cave *A. fasciatus* display the spawning behavior common to this fish family. The reduced space in La Cueva Chica facilitates close contact between the cave and the surface forms, and, given the apparent lack of any reproductive isolating mechanism between these forms, there is a high probability of hybridization under these conditions. This is further supported by the fact that eight other hybrid cave populations of this fish have been described (Mitchell, *et al.*, 1977).

However, the introgression here described, as well as the breeding, electrophoretic, karyotypic, and behavioral studies mentioned above for the *A. fasciatus* population of La Cueva Chica, does not support such a generalization. In fact, all seem to indicate that typical cave features (e.g., blindness, depigmentation, larger number of taste buds, and behavioral modifications) can appear before any major differences in electrophoretic, karyotypic, or reproductive barriers arise between the cave and surface populations. It should not be forgotten that comparative morphological studies of cave and surface populations of

this fish species have shown that no significant meristic or morphometric differences exist between the forms, except for the cave-dwelling attributes (Álvarez, 1946; Peters and Peters, 1973; Wilkens, 1969). Similar conclusions have been reached when related but ecologically distinct fish species are studied from a genetic viewpoint (Avisé and Selander, 1972; Avisé, *et al.*, 1975; Bell, *et al.*, 1982). More extensive comparisons among obligatory cave organisms, their surface ancestors, and their hybrids will yield additional information about the correlation between phenotypic and genetic changes during the evolution of cave adaptations.

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