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CONTENTS

SPECIATION AND ADAPTATION TO CAVE LIFE: GRADUAL VS. RECTANGULAR EVOLUTION

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PART I

Introduction

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Science has much to do with conceptual keys, at least at the same extent as with empirical results. The adoption of different conceptual keys may result in drastically different interpretations of the same data, and the relatively young science of Biospeleology has already experienced this state of affairs. Are caves to be considered as refugia for ecological, biogeographic and phylogenetic relicts, i.e. « living fossils »? Or are they ecological scenarios promoting adaptive shifts in colonizing populations? Provided that different structurally reducing mutations may lead different cave fish populations to the same regressive phenotypic expression (Wilkens, 1971), what is the relative role of natural selection vs. genetic drift in shaping the regressive evolution of troglobites?

Some of these controversial issues have already received consideration in cave biology. A good example is provided by the recent publication of the Proceedings of a Symposium on Regressive Evolution (Culver, 1985).

One such issue in evolution, which might throw some stimulus and insight into the field of Biospeleology is represented by the well known theory of punctuated equilibria (Eldredge & Gould, 1972). Aside from the various controversies raised on the neodarwinian or non-darwinian matrix (Stebbins & Ayala, 1981; Newman et al., 1985) and on the rhetorical content (Lyne & Howe, 1986) of the theory, « punctuated equilibria » provide a possible interpretative framework for the remarkable morphological changes associated with adaptation and for speciation in cave habitats. How much gradual or punctuated are morphological changes associated with cave life? What is the appropriate time scale to detect relevant, « macroevolutionary » changes, in cave evolving animals? Do such changes occur only in short bursts during speciation? Is there any evidence for stasis?

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To stimulate answers, discussions, and perhaps new questions we promoted a Symposium on « Speciation and adaptation to cave life: gradual vs. rectangular evolution » as one of the international Symposia organized within the 51th Congress of the Unione Zoologica Italiana, in the hope it could be of interest not only for students of cave biology but also for zoologists and evolutionary biologists in general. The Symposium was co-organized by the Société de Biospéologie. Papers presented at the Symposium include a spectrum of contributions from review articles to tests of hypotheses and case studies relevant to the subject.

For editorial reasons the proceedings will appear in two separate issues of the International Journal of Speleology.

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The evolution of non-relictual tropical troglobites

Francis G. Howarth *

SUMMARY

The discovery of terrestrial troglobites living in caves on young oceanic islands with close epigean relatives living in nearby surface habitats offers unique opportunities to develop and test hypotheses concerning their evolution. Studies comparing the physiological ecology of troglobites with their epigean relatives suggest that troglobites are highly specialized to exploit resources within the system of interconnected medium-sized voids (mesocaverns) and only colonize cave passages (macrocaverns) with a stable, water vapor-saturated atmosphere. Few other animals can live in the mesocaverns. Rather than being relicts isolated in caves by the extinction of their epigean ancestral population, troglobites appear to evolve by a process called adaptive shift from species that are frequent accidentals in the mesocaverns.

INTRODUCTION

This symposium is timely, as within only the last two decades there has been a virtual revolution in our thinking on cave biology. This radical change was precipitated by the discoveries of significant troglobitic faunas in tropical caves, in lava tubes, in the smaller voids within fractured subterranean substrates (Howarth, 1983b; Juberthie, 1983), and continues with the recent discoveries in bad air caves (Howarth & Stone, in prep.). These discoveries open up whole new fields of biospeleological investigations and call into question the theories on cave animal evolution developed from the pioneering studies in temperate limestone caves. No longer can caves be considered a separate biotope from the voids in the surrounding rock. In fact, both an expanded conception of the subterranean biome and the formulation of a new synthesis on the evolution of cave species are now necessary (Howarth, 1983b).

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In spite of the fact that the most obvious characters displayed by troglobites appear to be reductive (i.e. loss of such conspicuously adaptive organs as eyes, wings, and body color), I believe that more might be learned from studying what they have gained in order to exploit their environment rather than from focusing only on what they have lost.

HAWAIIAN CAVES AND THEIR FAUNAS AS MICROCOSMS FOR EVOLUTIONARY STUDIES

The relatively young, isolated Hawaiian Archipelago, which arose from the sea floor by frequent volcanism, is an ideal location for studying the evolution and ecology of cave species and formulating a new synthesis. The islands, which are the emergent summits of mammoth submarine volcanoes, are separated from each other by deep straits 50 km or more wide. The eight main islands become progressively older as one moves northwest and range in age from 6 million years for Kauai to less than a million years for the youngest, largest and still volcanically active, Hawaii (Mac Donald et al., 1983). Each island or close group of islands is like a mini-continent, since its whole terrestrial biota is derived solely from across water colonists. Swarms of closely related species exploit different habitats, and some of the best examples of adaptive radiation anywhere (Simon et al., 1984; Carson & Templeton, 1984) are found in the Hawaiian Islands.

The Hawaiian cave animals also fit this pattern of adaptive radiation, and 43 species of terrestrial troglobites are now known (Table 1). They are not evenly distributed but, surprisingly, are most diverse on the younger islands, with 24 species known from Hawaii, 14 from Maui, 2 each from Molokai and Kauai, and 1 from Oahu. They evolved independently from different ancestors on each island, but at least 10 native radiating groups evolved cave species through parallel evolution on separate islands (Table 2). Such independently evolved communities, exploiting similiar resources and physical environments, offer unique opportunities to develop and test hypotheses about their evolution. Furthermore, many of these highly specialized cave species have close epigean relatives still extant living in nearby surface habitats. These provide species pairs for comparative studies on cave adaptation.

Three of the better studied examples (cixiid planthoppers, gryllid crickets and lycosid spiders) will illustrate this point. Within the cixiid genus *Oliarus,* there are about 80 endemic

Table 1 - Ecological roles and evolutionary relationships of the terrestrial troglobites of the Hawaiian Islands.

Taxa	Ecological Role	Extant native relatives*
Hawaii Island		
Haplophiloscia laevis (Isopoda)	scavenger	none known
Erigone stygius (Araneae)	predator	sympatric
Erigone sp. 1(?) (Araneae)	predator	sympatric ?
Lycosa howarthi (Araneae)	predator	parapatric
Oonops (?) sp.	predator	?
Tyrannochthonius howarthi (Pseudoscorpionida)	predator	allopatric
Lithobius (?) sp. 1 (Chilopoda)	predator	? parapatric
Dimerogonus (?) sp. 1 (Myriapoda)	fungivore	parapatric
Protanura hawaiiensis (Collembola)	omnivore	troglobite ?
Sinella yoshia (Collembola)	scavenger	troglobite ?
Caconemobius varius (Orthoptera)	omnivore	sympatric
Caconemobius sp. 1	omnivore	sympatric
Caconemobius sp. 2	omnivore	sympatric
Thaumatogryllus cavicola (Orthoptera)	omnivore	allopatric
Thaumatogryllus sp. 1	omnivore	allopatric
Anisolabis howarthi (Dermaptera)	predator	parapatric
Speovelia aaa (Heteroptera)	scavenger	none known
Nesidiolestes ana (Heteroptera)	predator	parapatric
Oliarus polyphemus (Homoptera)	sapsucker	parapatric
Oliarus sp. 1	sapsucker	parapatric
Oliarus sp. 2	sapsucker	parapatric
Schrankia sp. 1 (Lepidoptera)	root feeder	sympatric
Schrankia sp. 2	root feeder	sympatric
Unknown family (Lepidoptera)	root feeder	unknown
Maui Island		
Hawaiioscia parvituberculata (Isopoda)	scavenger	none known
Meioneta gagnei (Araneae)	predator	unknown
Tyrannochthonius sp. 1 (Pseudoscorpionida)	predator	allopatric
Lithobius (?) sp. 2 (Chilopoda)	predator	? parapatric
Dimerogonus (?) sp. 2 (Myriapoda)	fungivore	parapatric
Sinella sp. 1 (Collembola)	scavenger	troglobite
Caconemobius howarthi (Orthoptera)	omnivore	parapatric
Caconemobius sp. 2	omnivore	allopatric
Thaumatogryllus sp. 2 (Orthoptera)	omnivore	allopatric
Thaumatogryllus sp. 3	omnivore	allopatric
Oliarus priola (Homoptera)	sapsucker	parapatric
Oliarus sp. 3	sapsucker	parapatric
Mecyclothorax (?) sp 1 (Coleoptera)	predator	? parapatric
Schrankia sp. 3 (Lepidoptera)	root feeder	parapatric
Molokai Island		
Lithobius (?) sp. 3 (Chilopoda)	predator	? parapatric
Oliarus sp. 4 (Homoptera)	sapsucker	parapatric
Oahu Island		
Tyrannochthonius pupukeanus (Pseudoscorp.)	predator	allopatric
Kauai Island		
Spelaeorchestia koloana (Amphipoda)	scavenger	? allopatric
Adelocosa anops (Araneae)	predator	? allopatric

* «Sympatric» indicates that a related species (either troglobitic or troglophilic) occurs in caves with the listed species. «Parapatric» indicates that a related species occurs in neighboring habitats, and «allopatric» indicates that all related species are geographically isolated from the listed species.

Table 2 - Numbers of epigean, troglobitic and troglophilic species among the adaptively radiating native taxa that have independently invaded caves on more than one island. *

Taxa	No. of spp. Epigean	Hawaii	Maui	Island Molokai	Oahu	Kauai
Philosciidae	?	1 TB	1 TB	—	—	?
Linyphiidae	5	2 TB	1 TB	—	—	—
Lycosidae	10	1 TB	—	—	—	1 TB
Chthoniidae	—	1 TB	1 TB	—	1 TB	—
Lithobiidae	10	1 TB	1 TB	1 TB	—	—
Cambalidae	12	1 TB	1 TB	—	—	—
Entomobryini	?	1 TB	1 TB	—	—	—
Gryllidae						
Caconemobius	4	3 TB	2 TB	—	—	—
Thaumatogryllus	3	2 TB	2 TB	—	—	—
Cixiidae *Oliarus*	80	3 TB	2 TB	1 TB	—	—
Noctuidae *Schrankia*	12	2 TB, 3 TP	1 TB, 1 TP	1 TP	1 TP	1 TP

* TB = troglobitic; TP = troglophilic. Numbers of epigean native Hawaiian species appproximate.

Hawaiian species of which four or five separate lines have invaded caves (Howarth, 1986). Three troglobites, *O. polyphemus* Fennah and two undescribed species, occur allopatrically on Hawaii Island. *O. polyphemus* and one of the undescribed species are closely related to *O. inaequalis* Giffard, an epigean species in Hawaii Island rain forests (Fennah, 1973; Howarth, 1986). The other Hawaii Island troglobite is not closely related to *O. inaequalis.* Two unrelated cave species occur on Maui Island, *O. priola* Fennah and an undescribed species. One undescribed troglobitic species occurs on Molokai Island.

At least eight species of true crickets are restricted to Hawaiian caves. These belong to the Gryllidae and are not at all related to the continental cave crickets (Gurney & Rentz, 1978; Howarth, 1981). Members of the genus *Thaumatogryllus* belong to the native Hawaiian tree crickets, and the cave species prefer to forage on the ceiling. There are small-eyed and blind populations in caves on both Maui and Hawaii islands. The rock crickets, genus *Caconemobius,* prefer to forage on the floor and walls of caves. On Hawaii Island *C. varius* Gurney & Rentz and an undescribed sympatric species are closely related to each other and to *C. fori* Gurney & Rentz (Howarth, 1981). The latter species is restricted to young unvegetated lava flows on Hawaii Island (Howarth, 1979) and is thus parapatric to the cave species. The troglobitic *C. howarthi* Gurney & Rentz and an allopatric species in caves on Maui Island are closely related to an undescribed halophilic species, which lives on rocky seacoasts on all the main Hawaiian Islands.

The wolf or big-eyed hunting spiders, family Lycosidae, are among the best sighted spiders, and it would seem axiomatic that none would become cave-adapted (Gertsch, 1973). However, they are good long-distance dispersers, and Hawaii has a diverse and interesting epigean lycosid fauna. In lava tubes on Hawaii Island there lives the troglobitic small-eyed, big-eyed hunting spider, *Lycosa howarthi* Gertsch. But even more remarkable, there exists in a small area on the old island of Kauai another cave-adapted species, the rare no-eyed, big-eyed hunting spider, *Adelocosa anops* Gertsch, which, in spite of its appearance and cave adaptations, evolved independently from a different ancestor than did *L. howarthi*.

The ancestors of the Hawaiian cave animals were pre-adapted for cave-life and primarily inhabited two distinct epigean habitats: rain forests and wet rocky substrates. The *Thaumatogryllus* crickets, *Oliarus* planthoppers, *Nesidiolestes* thread-legged bugs, and *Schrankia* moths all have close relatives living in rain forest habitats. All known *Caconemobius* crickets occur only on wet rock habitats: new lava flows, sea coasts, cliff faces, and caves. The epigean lycosid spiders occur in both rain forests and rocky substrates. The ancestor of *Speovelia aaa* Gagne & Howarth remains unknown but probably was a sea coast species, like its congener, *S. maritima* in Japan.

Most of the troglobites are known from the youngest volcanoes on Hawaii Island, and they colonize new caves surprisingly fast. In fact, the most diverse cave with 11 troglobitic species is Kazumura Lava Tube, which is only 500 years old. A troglobitic *Caconemobius* cricket was collected in 1980 within a 6-year old lava tube in the 1974 Mauna Ulu eruption on Kilauea. *Oliarus polyphemus* inhabits a cave in the 1919 lava flow in Kilauea Caldera, even though the flow is still virtually unvegetated. The 100-year old Emesine Lava Tube already supports at least 7 troglobitic species. These observations support the hypothesis that troglobites can live in and disperse through the medium-sized voids (the mesocaverns) within young lava. The geological evidence also supports this as young lava has numerous suitable voids (MacDonald et al., 1983).

COMPARATIVE PHYSIOLOGICAL ECOLOGY OF HAWAIIAN TROGLOBITES

The almost universal observation that terrestrial troglobites display extreme sensitivity to relative humidity changes and, that cave populations are restricted to passages with stable air saturated with water vapor, provides a big clue to interpreting their

evolution (Howarth, 1980). In order to understand this rela-
tionship and answer the questions « How? » and « Why? », my
colleagues and I have been studying the climate of Hawaiian
caves and correlating that with the distribution and environ-
mental physiology of the troglobites and their surface relatives.

Charcoal Cave, at about 800 m elevation, on the south
slopes of Kilauea, Hawaii Island, was selected for more detailed
environmental studies. The large main passage, about 250 m
long, trends gently down slope from its single large entrance.
The large entrance allows the effects of surface climatic
events to enter the cave and affect a large portion of the
cave. Preliminary surveys showed that the distribution of cave
animals was dynamic and associated with the moisture supply
within the cave. In order to test this hypothesis, 3 weather
stations, each consisting of a recording hygrothermograph and
two piche atmometers were set 45 m, 110 m, and 185 m from the
entrance within the twilight, transition, and deep cave zones re-
spectively. As expected, the resulting data demonstrated the
dynamic nature of the cave environment and the relationship
between the environment and the distribution of troglobites
(Howarth, 1983a).

The climatic events within the cave are correlated with
events on the surface but with sometimes considerable tempo-
ral variation. Simple diffusion of water vapor is too slow to
significantly affect the cave environment. The major changes
in the relative humidity of the cave are precipitated by the
movement of air masses into and out of the cave both along
density gradients and pushed by surface winds. The effect of
the incoming air on the relative humidity within the cave de-
pends on its moisture content relative to that in the cave. The
relative humidity in the cave most commonly plummets at night
when the colder (and therefore drier) surface air sinks into the
cave. This is the tropical winter effect (Howarth, 1980). Incom-
ing surface air reaches the deep cave zone within minutes
but becomes saturated by evaporation from the moist walls
and falling water drops. The wave of unsaturation becomes
attenuated and takes one to two hours to move from the twi-
light zone station to the deep cave zone station. The more
water available the greater the attenuation and time lag. The
time lag and buffering are also greatly modified by the passage
size and shape.

The potential evaporation rate at the 3 stations correlated
well with the degree of change in relative humidity. The rate
of potential evaporation at the deep cave station was only 36%
of the rate at the transition zone station and 8% of the rate
at the twilight zone station. Compared to the arid surface envir-
onment, the twilight zone was still quite humid. The potential

evaporation rate on the surface outside of the cave was at least 5 times the rate at the twilight zone station. During the period of study, specialized cave animals were found only beyond 165 m from the entrance. Thus the boundary between the transition zone and deep cave zone has a calculated potential evaporation rate of 0.16 cm^3 day $^{-1}$. The evaporation rate within the meso-caverns would be considerably less than this value. The boundary between the transition and deep cave zones is dynamic, and many troglobites migrate in response to the humidity changes. Most troglobites appear to exploit resources in caves only on temporary forays from their more humid retreats, unless the cave passage has an exceptional environment (see below).

We have also compared the water balance physiology of the cave spider *(Lycosa howarthi)* (Hadley et al., 1981) and crickets *(Caconemobius varius* and *C. howarthi)* (Ahearn & Howarth, 1982) with their close surface relatives. These studies corroborate the field studies and indicate that the cave species have adapted to a hydrating environment.

The relative rates of water loss by these epigean and cave species are clearly correlated with the availability of water in their respective environments. The cave spider and cricket, which live side by side in lava tubes, have almost identical permeabilities of 33.4 and 34.5 μg cm^{-2} hour^{-1} mmHg^{-1} (Hadley et al., 1981; Ahearn & Howarth, 1982). The surface spider, *Lycosa* sp., lives in the driest environment and loses water at 1/10 th the rate (3.1 μg cm^{-2} hour^{-1} mmHg^{-1}) of the cave species (Hadley et al., 1981). The 2 epigean crickets are intermediate, and significantly, the halophilic beach cricket, which rarely strays from its damp 98% RH littoral environment, loses less water than the cave species, indicating that the terrestrial cave environment is considerably more hydrating than marine environments (Ahearn & Howarth, 1982). These data suggest that there is selection pressure on terrestrial cave species to adapt to an atmospheric moisture content above the equilibrium humidity of insect hemolymph (i.e. 99.0-99.5% RH). They have become freshwater aquatic animals living in an aereal environment.

THE DISTRIBUTION OF TROGLOBITES WITHIN A « BAD AIR » CAVE

Recently, I have been comparing our Hawaii results with the ecology of both limestone caves and lava tubes in tropical north Queensland, Australia, (Howarth & Stone, in prep.). Here we have found a lava tube (Bayliss Cave) with a clear zonation

of troglophilic and troglobitic species correlated with abiotic environmental parameters, especially the concentration of CO_2. This zonation results from the location of the single constricted entrance at its upper end, passage configuration, and availability of moisture and organic matter.

Two constrictions trap the cave air into three compartments: an outer transition zone from the entrance to the Duckunder (where the passage height dips to 1.5 m) 345 m into the cave; a middle zone, 345-630 m from the entrance between the Duckunder and the Wall (a large dam of rocks across the passage); and an inner zone beyond the Wall. As the lighter warm cave air and water vapor rise towards the entrance, they become trapped by the Duckunder. The downward sloping cave acts as a trap for biogenically generated CO_2. The cave is mesotrophic to eutrophic with abundant living and dead tree roots, bat guano, dead animals, and washed in organic matter.

The distribution of the 51 species of terrestrial arthropods resident in the cave is clearly related to the environment. During our surveys in May and June, 1985 and 1986, a community composed almost entirely of troglobites occurred downslope of the Duckunder. Three-fourths of the 24 troglobitic species lived only in the middle and inner zones where the atmosphere was saturated with water vapor and where the elevated CO_2 concentrations (up to 200 times ambient) were approaching limiting values for surface and many troglophilic species. Most other tropical and temperate cave passages that I have studied resemble the transition zone upslope of the Duckunder, both in their abiotic environment and in the percentages and behaviors of troglobitic species. The environments of most lowland tropical caves are severely affected by the tropical winter effect and the presence of large or multiple entrances. In a few caves one can approach an environment similar to that near the Duckunder, and these often lower-level, dead end passages also contain a high diversity of troglobitic species (Howarth, 1980; Chapman, 1986). The long-term stable inner air mass in Bayliss Cave approaches equilibrium with the atmosphere of the surrounding mesocaverns. The occurrence of a community of troglobites in the "bad air" section of the cave supports the hypothesis that troglobites are specialized to exploit the resources in the medium-sized voids where gas mixtures, especially CO_2 and water vapor, are limiting for most surface species. The increased integumental permeability and the reduced metabolic rate observed in cave animals may be adaptations, respectively, to the hydrating environment (Ahearn & Howarth, 1982), and to the low O_2 and correspondingly high CO_2 concentrations in their environment (Howarth, 1983b; Hüppop, 1986).

ADAPTIVE SHIFT VERSUS ISOLATION HYPOTHESES IN TROPICAL TROGLOBITIC EVOLUTION

The initial studies in temperate regions indicated that the ancestors of troglobites became isolated in caves after local extinction of their surface populations by changing climates, especially those associated with glaciation (Barr, 1968; Sbordoni, 1982; Barr & Holsinger, 1985). Without this isolation it was assumed that immigration from surface populations would swamp any incipient adaptations to the cave environment. To their credit, biospeleologists were among the first to recognize the importance of extinctions in shaping evolution and ecology. Extinctions are finally getting their due in theoretical ecology and evolution (Fowler & MacMahon, 1982).

The discovery of terrestrial troglobites living sympatrically or parapatrically with their close surface relatives on young oceanic islands is, therefore, surprising and indicates that extinction of the surface population may not be a prerequisite of cave adaptation. If they are not relicts, how do the ancestors of troglobites initially become isolated in caves?

A big clue comes from the young Hawaiian lava tubes. When a large lava flow advances it often surrounds and leaves unscathed « islands » of older substrates isolated in the flow. These « islands », called *kipuka* in Hawaii, are a common phenomenon on the younger volcanoes. Young lava flows are veritable deserts to the rain forest animals living in the adjacent *kipuka,* such as the cixiid planthopper, *Oliarus inaequalis.* These rain forest animals cannot colonize lava flows until a mature rain forest develops. However, going underground within these young lava flows (such as Emesine Cave in the 1881 lava flow above 1500 m elevation on Mauna Loa), one discovers that the few scattered shrubs one metre tall on the surface have massive root systems at least 5 m deep in order to maintain themselves in the xeric surface environment (Gagne & Howarth, 1975; Howarth, 1986). Here is the rain forest, but until a rain forest species can survive, reproduce, and disperse underground, this resource remains entirely out of reach.

Over the millennia millions of transient subterranean populations became (and still are becoming) established. All but a few died out within a few generations. The major bottleneck for survival for many underground populations may have been the ability to locate mates and reproduce underground. Once a population could do this a large new habitat and food resource was opened up to it, and the population could expand rapidly. For a time backcrosses with its ancestors in boundary habitats could have added genetic variability for selection (e.g. Wilkens & Hüppop, 1986), but note that a change in mating

behavior, which may be one of the more important adaptive shifts necessary for successful colonization of the caves and mesocaverns, would also effectively isolate the incipient population underground.

Eruptions have been so frequent on Hawaiian volcanoes that new flows and caves are continuously created (MacDonald et al., 1983). These provide not only a large geographical area of cave habitat, but also a dynamic system of new habitats for colonization. Plant roots and other food resources penetrate much deeper into the young flows than in older substrates, so that more food is out of reach of the non-cave species. In fact, in many young cavernous substrates the evolving cave population may be larger than its parental epigean population, so that if swamping occurs it may be by the cave form (Howarth, 1980) rather than by the surface form, as envisioned by Barr (1968).

The subterranean habitat is so novel and the new selection pressures so strong that such new populations diverged morphologically, physiologically, and behaviorly from surface populations, and most have become genetically isolated from their ancestors and highly troglomorphic. The initial successful populations were probably each founded by an adaptive shift by only one or a few individuals, and, therefore, this model of cave adaptation fits both the evidence and the founder effect model of speciation (Carson & Templeton, 1984).

These *kipuka* and young lava flow environments are strikingly similar to periglacial, karstic, and montane terrains. In periglacial environments there are often islands of forests developing in protected sites separated by more-or-less barren ground. The extensive deposits of young moraines offer vast mesocavernous habitats for dispersing and evolving troglobites. The release and transport of organic debris trapped within the glacier may provide abundant food resources to periglacial underground habitats. In karst terrains barren rocky ground is often the norm, with leaf litter and vegetation restricted to cracks and sinkholes. In montane terrains the vegetation cover interdigitates with stone deserts on ridges, young rock slides, and rock outcrops. Shifting young talus slopes provide abundant mesocavernous habitats and dispersal routes between and among these vegetated islands.

In all of these cavernous terrains large amounts of organic food energy are continually being brought into the meso- and macro- cavernous voids by percolating groundwater, sinking streams, deeply penetrating roots, dispersing animals, and gravity. Wherever an interconnected mesocavernous system is well-developed, this organic material represents a significant exploitable resource which is largely out of reach to opportu-

nistic colonizing species, because they cannot cope with the inhospitable environment. It is this potential food resource that provides the driving force for the adaptive shift and evolution of cave species. Once an adaptive shift occurs, establishing a reproducing population underground, then it is both the effects of the strong new selection pressures (especially physiological and behaviorial) and the release from previously strong selection pressures that bring about the remarkable changes that we recognize as troglomorphy. The action of natural selection (including sexual selection) can be intense but is often seriously underestimated in evolutionary models (Carson & Templeton, 1984; Parsons, 1987).

In this adaptive shift model, troglomorphic populations may evolve parapatrically or narrowly sympatrically from their ancestors (Wilkens & Hüppop, 1986). However, we must consider evolution as two distinct, independent processes: adaptation, which is continuous with every generation, and speciation. Intuitively, most founder events and adaptive shifts would result in speciation; however, a speciation event may occur at any point during the divergence of two populations. All contingencies appear to be possible, from a speciation event (or even multiple speciation events) near the commencement of divergence, to the evolution of a highly troglomorphic population still capable of interbreeding with its epigean relative, as is the case with the fish, *Astyanax fasciatus* (Wilkens & Hüppop, 1986) or even with highly polymorphic species, such as *Plastosciara perniciosa* (Steffan, 1973).

The assumption that shrinking resources force a population to adapt to a new niche is based on a weak theoretical foundation. New populations and species evolve from a position of strength, since natural selection predicts that populations are becoming better and better adapted to their environment. Richer environments in terms of harvestable energy have a greater potential for colonization and evolution of new species.

In contrast to Wilkens (1986), I see no evidence for a linear relationship between time and degree of loss of any structure. In fact I find such an assumption to be an antithesis of evolutionary biology. For any adapting population the degree of phenotypic reduction of each character will be a function of several factors, including (1) time, (2) degree of pre-adaptation (that is, the character's starting point in the population), (3) its genetic repertoire (that is, the options the population's genotype allows), (4) the degree of positive, negative, and relaxed selection pressures on the structure, (5) degree of pleiotropic effects, (6) total number and interactions of the genes involved in the development of the structure, (7) founder effects, (8) effective population size (that is, deme effects), (9)

the mutation rate, (10) intensity of novel environmental stresses, (11) the genetic load (that is, the number of deleterious alleles the population already carries for the structure), (12) generation time, (13) genetic drift, (14) extrinsic and intrinsic stochastic events regulating population size, and (15) other genetic factors such as recombination rate, epistasis, transposons, and genetic contaminants. These factors are not mutually exclusive, and I may have missed some, but the important points are that there are many factors involved in the reduction of each structure and that each factor has an independent time component. Thus, a graph of reductive evolution in a population through time may be curvilinear and may have many plateaus, as each structure reduces to a point where positive selection pressures again become more important than reductive trends. Christiansen (1986) found both positive and negative correlations among reductive features in soil and cave Collembola, underscoring the fact that no one theory is likely to explain all reduction.

The three traditional models for explaining reductive evolution (1, the accumulation of neutral mutations, 2, pleiotropic effects, and 3, positive natural selection, especially for energy economy), are often assumed to be antagonistic to each other (Sket, 1986; Culver, 1982). In fact, these factors are probably not mutually exclusive, as reduction appears to be the result of the interaction and integration of a suite of evolutionary processes, including these three. The degree of reduction is correlated with the habitat; therefore, natural selection appears to mold and set the limits on the degree of reduction brought about by genetic processes.

Energy resources are not correlated with the degree of reduction (Poulson, 1986). For example, the food resources (i.e. roots of the native tree *Metrosideros polymorpha*) for both the cave cixiid *(Oliarus polyphemus)* and its close surface relative *(O. inaequalis)* on Hawaii Island are of the same quality and probably the same quantity within the feeding range of an individual; yet the two species show extreme differences in their degree of reduction (Fennah, 1973). The lava flow cricket, *Caconemobius fori,* shows no reduction yet it lives in an environment with far less visible energy than its close cave relatives (Howarth, 1981). Natural selection and thermodynamics dictate that economy of energy is built into evolutionary processes; i.e., all organisms evolve towards maximal utilization of their resources. Among polymorphic species, the richest food sources are often exploited by the most reduced forms (Steffan, 1973).

Even though cave environments are usually described as food poor (Barr, 1968; Poulson, 1986; Hüppop, 1986), the adapta-

tions for energy economy displayed by troglobites may be better understood by the spatial and temporal variability in the food supply, as well as its difficulty of exploitation, rather than the total amount. Within underground environments, especially within the mesocaverns, the behaviorial problems inherent in finding even rich food supplies are much more difficult than in most surface environments.

The loss of complex structures and systems under relaxed selection pressure is probably a much faster and more widespread phenomenon than was previously assumed. Recent genetics and molecular biological studies have demonstrated that removing a positive selection pressure from an organ or a gene will cause it to gradually disintegrate under mutation pressure (Carson et al., 1982). The more genes that are involved in a developmental process the faster the process will erode when selection is relaxed (Culver, 1982). Add to this the possibility of deleterious alleles already carried in the population, and the rate increases further. Even eyeless birds have been reported (Berger & Howard, 1968). Furthermore, among cave populations the mutation rate may increase dramatically due to the occurrence of high natural radiation levels underground. The high karyotypic variability in underground animals (Nevo, 1979) may reflect this phenomenon.

High stress environments may encourage more rapid evolutionary rates, not only from the more severe levels of natural selection but also from an increase of mutations, recombinations, and variability resulting from dysfunction of regulatory mechanisms caused by the stress itself (see review by Parsons, 1987). Organisms adapting to cave environments would be under more stress than their parental population especially since the cave environment would present a number of novel stressful parameters, and, therefore, they might be subject to higher evolutionary rates.

There is evidence for genes that act as regulators, keeping sections of the genome intact and providing some stability to the reproducing genome from generation to generation (Carson & Templeton, 1984; Parsons, 1987). However, these genes are subject to mutation and selection just as are other genes and chromosomes. Most mutations in this self regulating system would be deleterious and not survive. However, at certain points in the history of a population a destabilizing mutation is more likely to survive and lead to the evolution of new forms.

There are populations of Hawaiian species, often on the older islands, which show little variation and appear to be in a stasis stage. At the same time there are other populations — even of the same (!) species — which are in a state of explo-

sive change and are adapting to new habitats (Carson & Ohta, 1981).

I believe that one of the major events allowing the survivorship of genotypes decoupled from their stabilizing regulatory genes is the ecological release from previously strong selection pressures, such as often occurs with a founder event or adaptive shift. When the release leads to a J-shaped population curve many genotypes, including changes in stabilizing genes, that are normally suppressed can survive and reproduce. Release from the stabilizing genes allows greater phenotypic variability upon which the new selection pressures can act. This scenario fits the adaptive shift model of cave adaptation, as well as the observed phenomena associated with recent colonizers (for example, the increase in the frequency of host changes and other adaptive shifts, as well as population crashes and the appearance of apparent poor fitness among some populations undergoing rapid expansion). This scenario also fits the predictions of the modern synthesis, since it envisions natural selection molding successful genomes from the accumulating random mutations and recombinations.

The theoretical effects on evolution of founder events and population bottlenecks have received considerable attention, but the effects of the possibly equally important and related phenomenon of explosive population buildup after bottlenecks are less appreciated (see review by Carson & Templeton, 1984). Selection pressures favoring survival and reproduction among individuals in expanding populations, crashing large populations, and stable small populations are all very different; e.g. for crashing populations there are additional intense intraspecific competition and increased mortality factors. Thus, gene frequencies may change more dramatically and adaptive shifts may be more likely with fluctuating populations than with stable ones. Cave animals on Hawaii Island appear to have undergone frequent flush/crash population cycles after the initial founding event, as they were able to colonize young flows before they were extirpated from older ones. Thus, the colonization of caves on Hawaii Island agrees with the genetic model for speciation by founder effect outlined by Carson & Templeton (1984).

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The role of gradualism and punctuation in cave adaptation

David C. Culver *

SUMMARY

The theory of punctuated equilibrium, offers a potential explanation for the profound morphological changes that accompany isolation in caves. I consider three aspects of punctuation theory: the association of morphological change with speciation; periods of stasis; and the number of genes controlling a trait. If the evolution of cave organisms is associated with speciation, then speciose groups and cave species derived from other cave-limited species should show increased adaptation. Analysis of Kane and Barr's data on the subspecies of *Neaphaenops tellkampfi* and Holsinger's data on crangonyctid amphipods fails to provide any support for the hypothesis. If the evolution is characterized by long periods of stasis, then directional selection should be rare. An estimate of selection in a cave population of *Gammarus minus* indicates that directional selection is occurring. Third, if punctuation is important, characters associated with isolation in caves should be controlled by a single gene. Wilkens and others have found most characters in cave *Astyanax* to be controlled by between 3 and 7 genes. It is more useful to frame the question of evolutionary change accompanying cave invasion in terms of adaptive topographies. Several examples of its use are discussed, including assessing the role in selection in structural reduction, and the role of isolation in adaptation to cave life.

INTRODUCTION

In the past decade a forceful group of critics of neo-Darwinism have emerged. The initial impetus for the critique was the contention by some paleobiologists that the fossil record did not correspond to a model of gradual change in morphology, but rather consisted of long periods of no change (stasis) followed by short bursts of morphological change, termed punctuation by Eldredge and Gould (1972). An alternative mechanism to the gradual action of natural selection has been proposed: namely the idea that morphological change is primarily asso-

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ciated with speciation, often brought about by mutations of rather large effect. This theory, or more accurately this set of theories, has been the subject of considerable controversy (e.g. Charlesworth, Slatkin and Lande, 1982; Gould and Eldredge, 1986). It is not my purpose here to review the controversy, nor to determine how much of punctuated equilibrium theory is new and non-neo-Darwinian, rather it is my purpose to review several key ideas that have emerged in this controversy and ascertain their relevance to adaptation to the cave environment.

At the same time as the large controversy concerning punctuated equilibrium has been swirling about in evolutionary biology, there has been a smaller controversy in biospeleology, one that raises many of the same questions. The standard view of adaptation to cave life has been that adaptation requires (1) that cave populations are genetically isolated from surface ancestors, and (2) that structural reduction (eye and pigment loss) are at least indirectly selected for because the energy savings from such reduction can be used in the elaboration and size increase in extra-optic sensory structures such as antennae in arthropods and lateral line systems in fish. Both of the tenets have been challenged. Howarth (1980), with his adaptive shift theory, has questioned the role of isolation in adaptation; and Culver (1982) and Wilkens (1985) with the theory of neutral mutations, have questioned the role selection plays in structural reduction.

This paper has two main parts. First, three pivotal questions raised by the theory of punctuated equilibrium will be considered in light of available data on cave organisms. These questions are:

(1) Is morphological change in cave organisms associated with speciation?

(2) Are there periods of stasis in cave animals?

(3) Are adaptive traits controlled by a few genes of large effect?

The second main part of the paper will be a consideration of the potential that the concept of adaptive surfaces offers in clarifying questions concerning cave adaptation.

THE CONNECTION BETWEEN SPECIATION
AND MORPHOLOGICAL CHANGE

Perhaps the single most important characteristic shared by the various critiques of neo-Darwinism is that morphological change is almost invariably associated with speciation. If this hypothesis is true, then one prediction is that highly speciated groups should be more adapted to the cave envi-

ronment than species-poor groups. Table 1 summarizes two such comparisons for some cave amphipod species. One measure of adaptation to the cave environment is the increase in size of antennae relative to the body (Culver, 1982). More highly cave adapted species should have relatively longer antennae. In the Ozark Plateau of central United States, two genera of amphipods are commonly found in caves — the species-poor *Allocrangonyx* with less than a dozen species world-wide and only 2 in the Ozark (Holsinger, 1971) and the species-rich *Stygobromus* with more than 100 species world-wide and nearly a dozen species in the Ozark Plateau (Holsinger, 1967; 1987). Yet there is no significant difference in antennal-body ratios between the two genera in the Ozark (Table 1). An additional comparison using *Stygobromus* in different regions also has bearing on the question. All but two species of *Stygobromus* are known from North America, the other two known from deep lakes in Siberia (Holsinger, 1987). A comparison of species from deep lakes in the western United States with Siberian species from the same habitat fails to indicate any dif-

Table 1 - Maximum antenna 1/body length ratios for selected subterranean amphipod species. Data from Holsinger (1967; 1971; 1974; 1987)

SPECIES		RATIO
Ozark Plateau:		
Allocrangonyx hubrichti		.70
A. pellucidus		.65
	$\bar{x} =$	.67 $\pm$ .02
Stygobromus barri		.85
S. bowmani		.65
S. clantoni		.65
S. elatus		.65
S. heteropodus		.70
S. montanus		.75
S. ozarkensis		.90
	$\bar{x} =$	.74 $\pm$ .04
Deep Lakes:		
Stygobromus pusillus (Teletskoye)		.40
S. lacicolus (Tahoe)		.45
S. tahoensis (Tahoe)		.40

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ference in adaptation. Therefore, *Stygobromus* fails to provide
any support for the idea that speciation plays an important
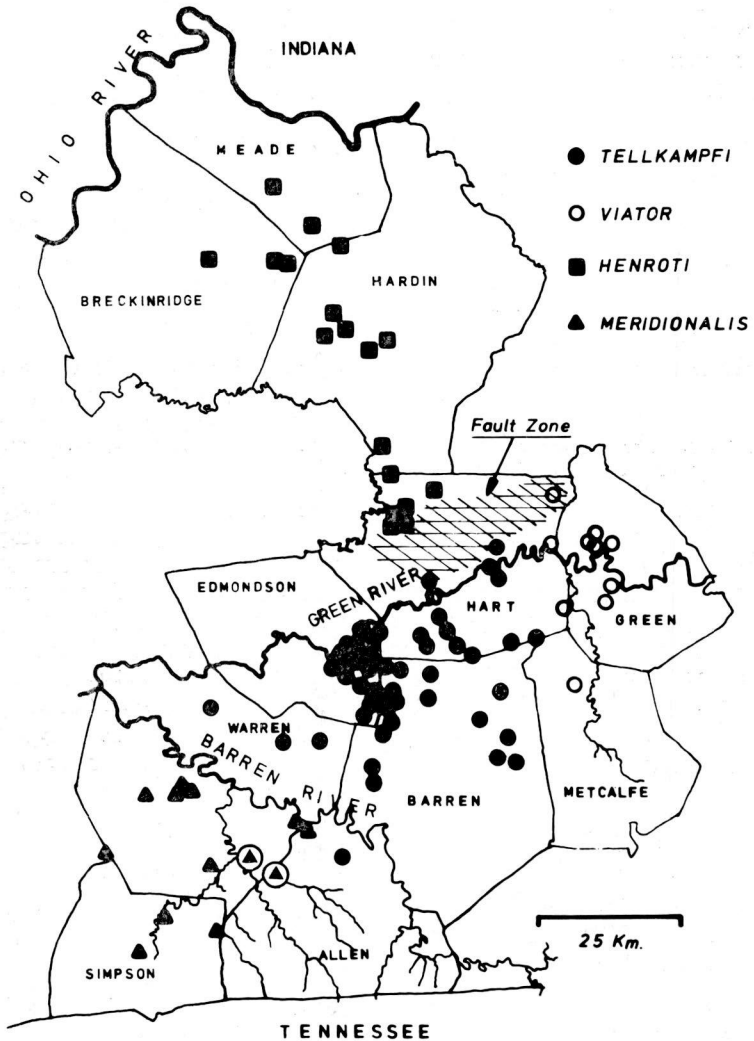role in morphological change in subterranean populations.

Fig.   1 - Distribution of the four subspecies of the carabid beetle *Nea-
          phaenops tellkampfi* in west central Kentucky. The triangles
          within a circle are hybrids between *meridionalis* and *tellkampfi*
          subspecies. Modified from Barr (1979).

Table 2 - Rogers' coefficients of genetic similarity (S) for the four subspecies of *Neaphaenops tellkampfi*. From Kane and Brunner (1986).

	tellkampfi	meridionalis	viator	henroti
tellkampfi	.963			
meridionalis	.730	.956		
viator	.737	.740	963	
henroti	.963	.748	.741	.975

Arguably the most thoroughly studied North American cave species from an ecological (Kane and Ryan, 1983), genetic (Kane and Brunner, 1986). and morphological (Barr, 1979) point of view is the carabid beetle *Neaphaenops tellkampfi*. According to Barr, *N. tellkampfi* originally invaded caves in the southern part of its range (Fig. 1), within the range of the subspecies *meridionalis*. Via subterranean dispersal it spread to the area occupied by the subspecies *tellkampfi,* and then to the areas occupied by the subspecies *henroti* and *viator*. Genetic distances between the subspecies, based on electromorphs of 9 loci, are as great as that between many species, except for *tellkampfi* and *henroti* (Table 2). If morphological change accompanies speciation, then *tellkampfi* should be more highly adapted than *meridionalis,* and *henroti* and *viator* should be more highly adapted than *tellkampfi*. But the four subspecies differ only in very subtle morphological ways (Barr, 1979), and none of these differences appear to be associated with adaptation to the cave environment. As with *Stygobromus, Neaphaenops tellkampfi* provides no support for the hypothesis that morphological change is associated with speciation.

THE EVIDENCE FOR STASIS

If for most of the phyletic history of a species there is no morphological change, such periods of stasis should be characterized by the absence of directional selection, no genetic variation for selection to act upon, or by strong stabilizing selection. Pearson (1903) first showed that multivariate statistics could be used to discern the effect of direct and indirect selection on characters. Recently Lande and Arnold (1983) have extended this work to show how multiple regression methods can be used to measure the effects of directional and stabilizing selection.

Ross Jones of Northwestern University has utilized Lande and Arnold's methodology in measuring some components of selection in a cave population of the amphipod *Gammarus minus*. Jones took advantage of the fact that male *G. minus* carry females (amplexus) for several weeks prior to fertilization. In a collection of nearly 300 individuals from Organ Cave, individuals in amplexus were assigned a fitness of 1 and individuals not in amplexus were assigned a fitness of 0. Thus he measured sexual selection and part of fecundity selection, but he did not measure differences in mortality. He measured head capsule length, eye facet number, and first antennal flagellar segment number. Eye facet number and antennal flagellar segment number were regressed on head length, and the residuals obtained were used for the multivariate analysis of selection parameters. This eliminates overall size effects from the two variables. Four parameters of directional selection were obtained:

(1) S, the selection differential, is the change in the mean of a character during an episode of selection, and estimates the effect of direct and indirect selection on a trait;

(2) i, the selection intensity, is the standardized S (i=S/S.D.), where S.D. is the standard deviation of the character;

(3) β, the selection gradient, is the partial regression coefficient of relative fitness on a character, and measures only the direct effects of selection on a trait; and

(4) β', the standardized selection gradient, is standardized β, calculated directly from the multiple regression model using standardized character measures (X'= (x-avg.X)/S.D.X)'.

Two parameters of stabilizing selection, here defined as selection causing changes in the variance of a trait, were obtained:

(1) λ, the stabilizing selection gradient, is the analog of β above and;

(2) λ', the standardized stabilizing selection gradient, is the analog of β' above.

More details on this technique can be found in Lande and Arnold (1983) and Endler (1986).

The results of the analysis are summarized in Table 3. For males, there was significant directional selection on head length and eye facet number, but not on antennal segment number. There was significant stabilizing selection on head length and antennae, but not on eyes. For females the pattern was the same except the stabilizing selection occurred on eyes and antennae, but not on head length. How are these data to be interpreted? First, selection on head length is probably meaningless because different aged individuals were

Table 3 - Estimates of directional and stabilizing selection for *Gammarus minus* in Organ Cave in January, 1986. Parameters are defined as follows (see text for details); S is change in mean of characters; i is change in mean of characters in units of standard deviations; β is the rate of change in fitness as a function of one character, holding all other characters constant; β' is the rate of change in fitness per one standard deviation of a character, holding all other characters constant; λ is the rate of change in fitness as a function of the variance of a character, holding all other characters constant; and, λ' is the rate of change in fitness per one standard deviation in the variance of a character.

	Selection Parameters					
	Directional				Stabilizing	
	Total		Direct			
	S	i	$\beta \pm$ SE	β'	$\lambda \pm$ SE	λ'
Males						
Head length	.0404*	.449	4.79 $\pm$ 1.19*	.43	−38.9 $\pm$ 11.6*	−.32
Eye	−.3149*	−.390	−.4469 $\pm$ .1327*	−.36	−.239 $\pm$ .163	−.16
Antenna[1]	.2468	2.38	.9027 $\pm$ 1.03	.09	−15.1 $\pm$ 6.5**	−.16
	$R^2 = .38$					
Females						
Head length	.052*	.337	2.88 $\pm$ 1.16**	.397	−10.01 $\pm$ 6.48	.19
Eye	−.192**	−.283	−.298 $\pm$ 18	−.202	−.633 $\pm$ .23**	−.29
Antenna[1]	.004	.041	.9027 $\pm$ 1.28	.111	−11.59 $\pm$ 6.84***	−.11
	$R^2 = .166$					

* Significant at the .01 level
** Significant at the .05 level
*** Borderline Significant; .1 > P > .05

present, and these values simply reflect that older in-
dividuals are larger. While head length at any specific age
is heritable (Fong, 1985), heritability of head length of a sample
of mixed ages, as is the case here, is low. Second, there is
significant directional selection against large eyed individuals
in both sexes. While the absence of detectable directional selec-
tion on antennae is surprising, there is clearly directional se-
lection occuring. Since eye facet number is highly heritable
(Fong, 1985) and selection is occurring, the mean phenotype is
changing. That is, the population is not in a period of stasis.
Third, stabilizing selection is also present, but may largely be
an artifact of the fact that many forms of directional selection,
such as truncation selection, reduce the variance as well as
change the mean. That is, except for male antennae, there is
no clear evidence for stabilizing selection in the sense that
both extremes of the distribution are selected against.

In sum, the data of Jones, even though preliminary, pro-
vide convincing evidence for directional selection. The multi-
variate techniques used hold exceptional promise not only
for the study of adaptation to cave life, but for the study of
adaptation in general.

ARE ADAPTIVE TRAITS POLYGENIC?

If morphological change happens rather suddenly and in
conjunction with speciation, then these changes should be the
result of changes at only one or perhaps two loci, since the
simultaneous occurrence of many mutations all with small
effects in highly improbable. Wilkens (1985) has analyzed the
genetic basis of a series of traits in the cave fish *Astyanax
fasciatus*. All are polygenic except for melanin content of the
melanophore (Table 4), and the melanophore system as a
whole is polygenic. There is, however, some evidence that eye

Table 4 - Minimum number of loci involved in various traits of cave po-
pulations of *Astyanax fasciatus* (from Wilkens, 1985)

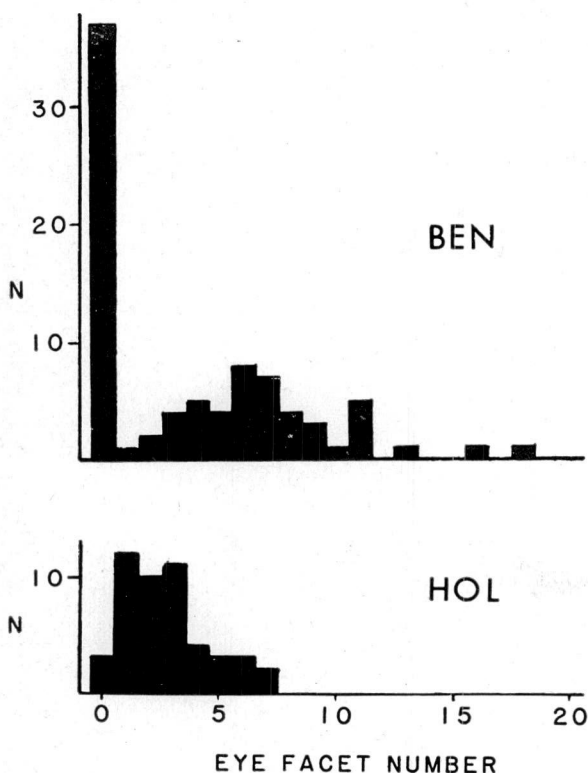| Character	Number of Loci
Eye Size	6-7
Melanophore Number	2-3
Melanin Content of Melanophore	1
Food Swimming Angle	3
Taste Buds	2-4

Fig. 2 - Frequency of distribution of ommatidia (lens numbers) of two
populations of the amphipod *Gammarus minus* from Benedict's
Cave (BEN) and The Hole (HOL) in Greenbrier Co.. West Vir-
ginia. For details see Culver (1987).

facet number in some populations of *Gammarus minus* is
controlled by a single gene while in others it is polygenic (Cul-
ver. in press). The evidence is this. In some populations the
distribution of eye facet numbers is unimodal and approxi-
mately normal, suggesting polygenic control. An example is The
Hole in Fig. 2. In other populations the distribution of eye
facet number is bimodal, suggesting control by a single gene
difference. An example is Benedict's Cave in Fig. 2. The data
in Fig. 2 are based only on phenotypes not genotypes, although
heritability of eye facet number is likely to be high (Fong, 1985).
In sum, neither *Astyanax* nor *Gammarus* provide overwhelming
support for single gene control of a trait.

AN ALTERNATIVE

There is little evidence to support a punctuationist view of cave adaptation. But this still leaves us with controversies concerning the causes of regressive evolution and the role of isolation in cave adaptation. There are at least two problems with the punctuationist view of cave adaptation. First, punctuation and stasis were originally used to explain sequences in the fossil record, sequences that generally involved the evolution of higher categories (genera, families, etc.). Cave adaptation rarely involves the origin of higher categories so that punctuational equilibria may be inappropriate for reasons of scale. Second, for the most part, punctuational equilibrium theory has not been formulated with any clear genetic basis.

A theory that is both at the appropriate scale and is at least implicitly genetic is the idea of an adaptive topography. Originally formulated by Wright (1932) in terms of gene frequencies, his basic idea was to let the x-axis and y-axis graph gene frequencies at two loci, and let the z-axis represent fitness. This creates an adaptive surface in which selection causes populations to move uphill to adaptive peaks. Provine (1986) has pointed out some ambiguities in the original formulation, but many of these problems disappear if the x-axis and y-axis are some measure of phenotype (see Simpson, 1944). A representative phenotypic adaptive topography is shown in Figure 3. Implicit in the phenotypic adaptive topography is that the characters are polygenically controlled, which allows for small changes in phenotype. Except for genetic constraints such as pleiotropy and linkage, populations will, as a result of selection, come to occupy peaks.

The neutralist-selectionist controversy is depicted in Figure 4, with the two phenotypic measurements being antennal size and eye size. If reduced characters, such as eyes, are selectively neutral, then the adaptive topography will be that depicted in the top frame, with the population coming to occupy a ridge as a result of selection for increased antennae. Only the accumulation of structurally reducing, selectively neutral mutations (see Culver, 1982) will cause the population to have reduced eyes. One prediction of this model is that species will likely evolve increased antennal size before reduced eye size. The selectionist model is depicted in the bottom half of Figure 4. In this case selection operates both to reduced eye size and increase antennal size. In this case, there is no reason to expect species to increase antennal size before decreasing eye size.

The role of isolation is depicted in Figure 5. In the top frames, the original adaptive peak of the epigean population

Phenotypic Adaptive Topographics

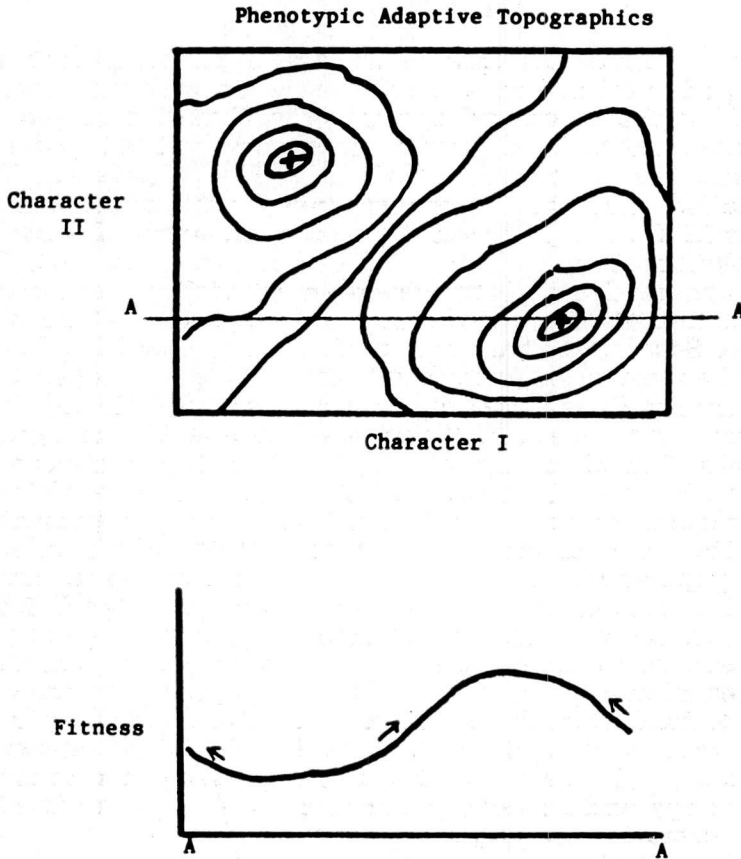Character II

Character I

Fitness

Fig. 3 - A sample phenotypic adaptive topography. Two morphological measurements (e.g., eye size and antenna size) are plotted on the x- and y-axis. The z-axis represents fitness. The lower frame is a slice through the adaptive topography. The arrows indicate direction that a population will move as a result of selection.

(large eyes and small antennae) disappears when the population is isolated in caves. The population then evolves in a straightforward manner to a small eyed, large antennae population, which is the cave adaptive peak. However, if isolation is not necessary, and the population invades the cave habitat but still retains contact with the surface population, then the epigean adaptive peak remains in addition to the new cave adaptive peak. This is depicted in the bottom frames of Figure 5. The problem now is that for cave adaptation to proceed, the population must cross the valley, an adaptive low.

D.C. CULVER

Neutralist

Antenna

Eye

Selectionist

Antenna

Eye
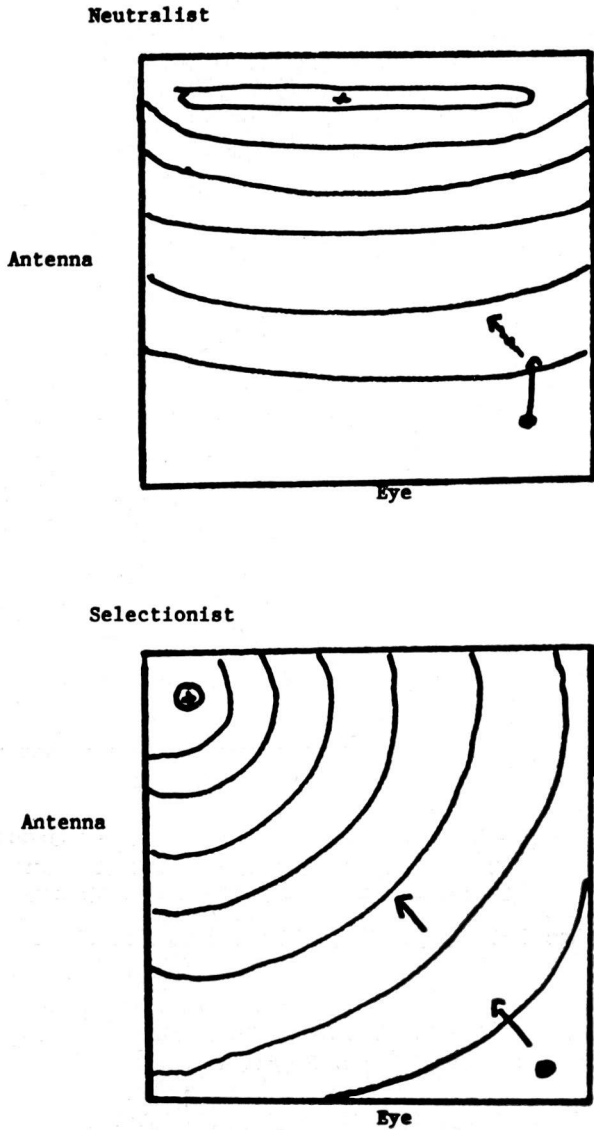
Fig. 4 - Hypothetical adaptive topographies for eye reduction in which no direct or indirect selection is involved (top panel) and in the case when selection for eye reduction is involved (bottom panel).
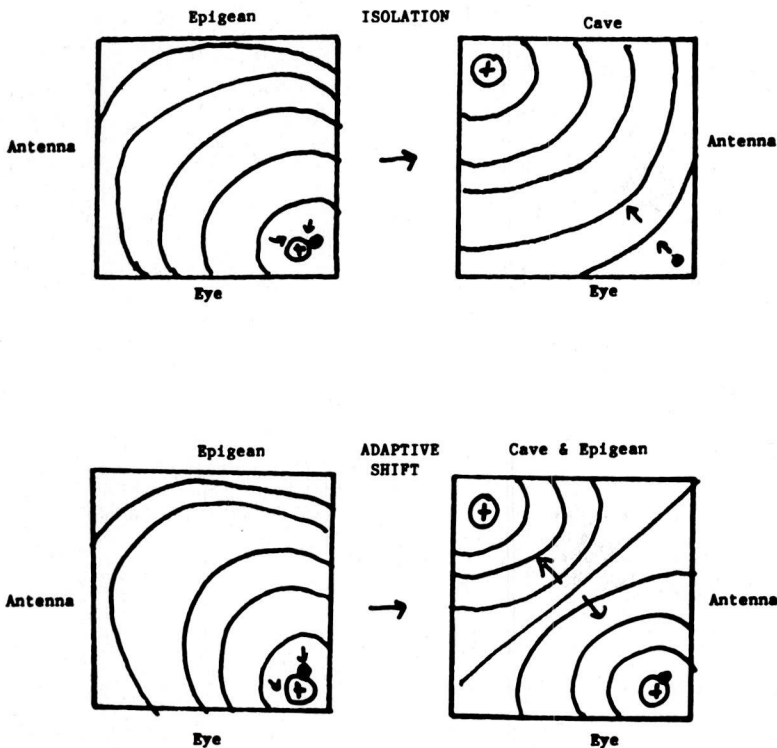
Fig. 5 - Hypothetical adaptive topographies in the case of isolation in caves (above) and in the case of adaptive shift without isolation (below).

Selection, by itself, will not result in a valley crossing, since selection acts to move a population toward a local peak (see Fig. 3). The problem of reaching a new adaptive peak is a problem that has occupied evolutionary theorists for decades, and brings us full cycle back to the question of punctuated equilibria. Wright's (1932) shifting balance theory suggested that the optimal conditions for reaching a new adaptive peak occurred in a subdivided population with extensive pleiotropy, with genetic drift playing an important role. Goldschmidt (1940), considered by some to be the intellectual father of punctuated equilibrium theory, argued that macromutations were the major source of new adaptive peaks. In this case, such a rare mutation is most likely in a very large population. Finally, Lande (1985) demostrated that in the case of phenotypic adaptive topographies, genetic drift in small population was the most likely means of a population evolving to a new adaptive peak.

These examples by no means exhaust the potential for adaptive topographies, but are intended to show that they are likely to be useful. If they are indeed useful, then a major effort needs to be made to measure fitness (see above), and to begin to construct some adaptive topographies.

ACKNOWLEDGEMENTS

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Genetic analysis of evolutionary processes

Horst Wilkens *

SUMMARY

Epigean and cave populations of *A. fasciatus* (Characidae, Pisces) differ in a series of morphological, physiological, and ethological features. The interfertility of these populations made possible a genetic analysis of organs characteristic of interspecific divergence.

The study of the regressive organs « eye » and « melanophore system » on the one hand and that of the constructively improved « gustatory equipment » and « feeding behaviour » on the other yielded identical principles of genetic manifestation: (1) All features have a polygenic basis with an at least di- to hexahybrid inheritance. (2) All polygenes have the same amount of expressivity. (3) After recombination of a minimum number of genes, discontinuous distributions (threshold effects) develop. (4) All features are independently inherited. (5) The genes responsible for a feature are unspecific. In the case of the eye this means that no « lens- » or « retina-genes » are analyzed; due to developmentally physiological interdependence within complex structures, only so-called « eye-genes » have as yet been described.

Because of the developmentally physiological interdependence of complex organs, the process of reduction proceeds as a diminution in size, that of constructive evolution as enlargement. In both cases different allometric correlations of the single structures can be found.

The convergent reduction of eyes in cave animals is caused by the loss of stabilizing selection which normally keeps the eye in its appropriate adapted form. It is not directional selection pressure, like f. ex. energy economy, but mutation pressure that causes eye reduction. By this, random mutations, which are mostly of deleterious character are accumulated.

The principles of regressive evolution are not restricted to the development of cave species. The absence of stabilizing selection regularly occurs during transitional evolutionary phases. These are f. ex. initial stages of speciation which may be observed when biotopes with little or no interspecific competition are colonized by an invader. Genotypic and phenotypic variability now arise and equilibria become punctuated, because stabilizing selection for a specific ecological niche which has once

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been acquired by the invading species is no longer acting. Examples include the evolution of species flocks in geologically young lakes or oceanic islands. Rapidly increasing variability now secondarily provides the material for directional selection which radiates such species into vacant niches. Genetic threshold effects as described above may accelerate this process. Variability will finally become lower again under the influence of inter- and intraspecific competition. A new equilibrium is attained.

INTRODUCTION

The concept of the theory of « Punctuated Equilibria » is that the history of life has been dominated by concentrated outbursts of rapid speciation rather than by slow, steady directional transformations (Newman et al., 1985; Lewin, 1986). Studying the explosive radiation of Cichlid fishes in the East African great lakes, especially that of Lake Victoria, Greenwood (1984) interprets the evolution of fish species flocks as an example of an extant punctuational phase.

The genetic analysis of the morphological changes has not yet been performed neither in the cichlids nor in any other examples of intralacustrine speciation. However, there are a lot of results from the study of the evolution of the different epi- and hypogean populations of the Mexican characin *Astyanax fasciatus*. It is the aim of this paper to demonstrate the similarity of these processes by applying the findings of the cave fish study.

MORPHOLOGY OF EPIGEAN AND CAVE POPULATIONS OF *A. FASCIATUS*

The very common epigean fish *Astyanax fasciatus* has developed a series of cave populations in Mexico. These populations diverge from their epigean ancestor by a large number of features, which have been subjected to regressive or constructive evolutionary processes (Mitchell et al., 1977).

The most obvious is the reduction of eyes and melanin pigmentation. The well-developed eye of the epigean fish has been reduced to a tiny rudiment in the cave form (fig. 1). Lens and visual cells are reduced during ontogeny. In a few eyes a retinal rudiment consisting of ganglionic, inner nuclear, and plexiform layers may be developed. In others even these have vanished (Peters & Peters, 1966; Wilkens, 1970 a).

The light phenotype of the cave fish is caused by the reduction of the melanophore system. For this a lower number
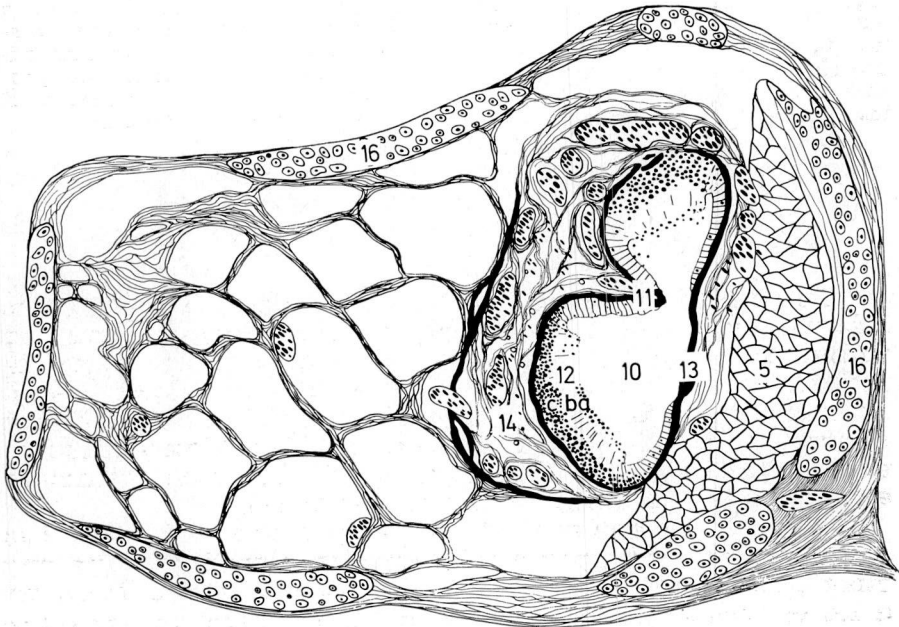
Fig. 1 - The eye rudiment of *A. fasciatus* (Population Cueva de El Pa-
          chón)
          1 = epidermis
          2 = lumen of connecting duct between eye ball and body surface
          3 = cornea conjunctiva
          4 = cornea propria
          5 = ligamentum annulare
          6 = anterior eye chamber
          7 = lens capsule
          8 = cristalline lens
          9 = campanula halleri
         10 = vitreous body
         11 = processus falciformis
         12 = retinal rudiment (a = ganglionic, b = inner plexiform, c =
              inner nuclear, d = visual cells)
         13 = pigmentary epithelium
         14 = chorioidea
         15 = optic nerve
         16 = sclera

of melanophores, less melanin content, and loss of the ability
of the morphological colour change are responsible (fig. 2)
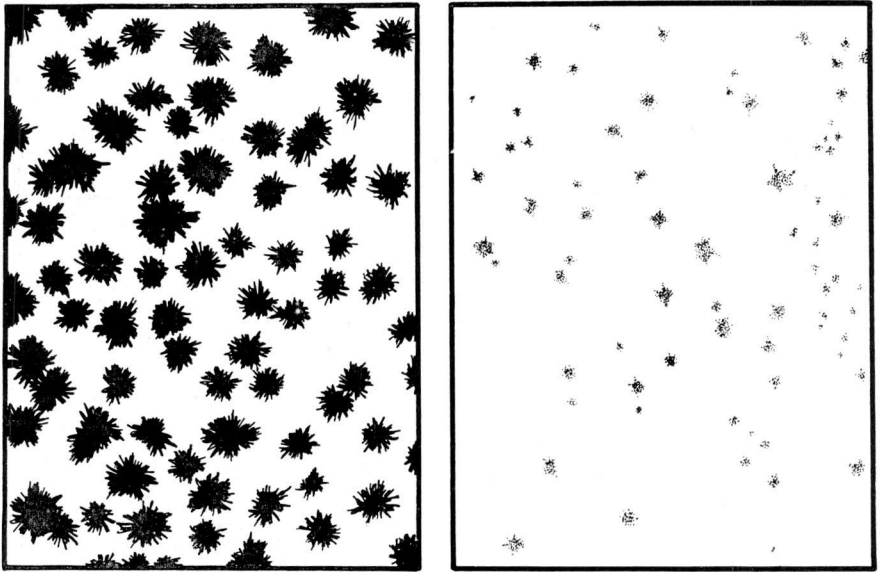(Wilkens, 1970 b).

Fig. 2 - The melanophore system of epigean and hypogean *A. fasciatus*.
In the cave population (right) the number of melanophores as
well as their melanin content are reduced.

Contrary to the regressive organs eye and melanophore
system, the gustatory equipment and the feeding behaviour
are constructive adaptations to the cave biotope. The gusta-
tory equipment of the epigean fish consists of an area of
taste buds on the tips of the chin and lips. The area covered
by these organs has been extended considerably especially
on the ventral side of the head of the cave fish. Additionally,
in one population the density of taste buds seems to have
increased (Schemmel, 1967).

However, an appropriate and successful use of the im-
proved gustatory equipment is only possible by an additio-
nal alteration of feeding behaviour. Without optic orientation
epigean individuals feed in an 80⁰ angle to the bottom and
are not very successful in food finding (Hüppop, this issue).
Contrary to this, cave specimens feed in an angle of 55⁰. By
this they can more efficiently use the gustatory apparatus while
steadily swimming in close contact to the bottom searching
for food (Schemmel, 1967; 1980).

GENETICS

The divergences between epigean and cave populations have a genetic basis. Its analysis has been made possible by the interfertility of these forms (Sadoglu, 1956). Although eyes and melanophore system on the one hand are phylogenetically old organs, and gustatory equipment and feeding behaviour on the other are recently improved features, no fundamental differences of genetic manifestation were discovered. The principles of genetic manifestation of these features can be summarized in five points (Wilkens, 1980; 1984).

(1) All four features display polygenic inheritance. It is based on at least two factors regarding the gustatory equipment and up to at least six factors regarding the eye.

(2) All polygenes on principle show the same amount of expressivity. This can be concluded from the intermediate manifestation and from normal distribution of features in the F_1 - and F_2 - crossings (figs. 3, 4, 5, 6).

(3) A further common characteristic of all the polygenic systems in *A. fasciatus* is an alteration of the gene expressivity, called threshold effect (Rieger et al., 1968). Due to this phenomenon a discontinuous enlargement of a feature can be observed as described before (figs. 3, 4, 5, 6). The sudden enlargement only develops after a certain number of polygenes has been recombined. The threshold effect may increase the amount of manifestation considerably: the eye size f.ex. is discontinuously enlarged by about 17% (fig. 7).
It is characteristic of the features eye size, taste bud density and feeding behaviour that the threshold effect cannot be influenced by environment. The melanophore system diverges from this. In this organ the increase of colour cells is manifested only over dark not over light underground. Thus it is influenced by the environment. The threshold effect in this feature delivers the genetic basis of a common adaptation in fish, the morphological colour change.
The threshold effect described before is probably a very common principle of genetic manifestation.
In many examples monogenic inheritance may turn out to be based on the fact that one single polygene of high expressivity is acting while all other polygenes responsi-
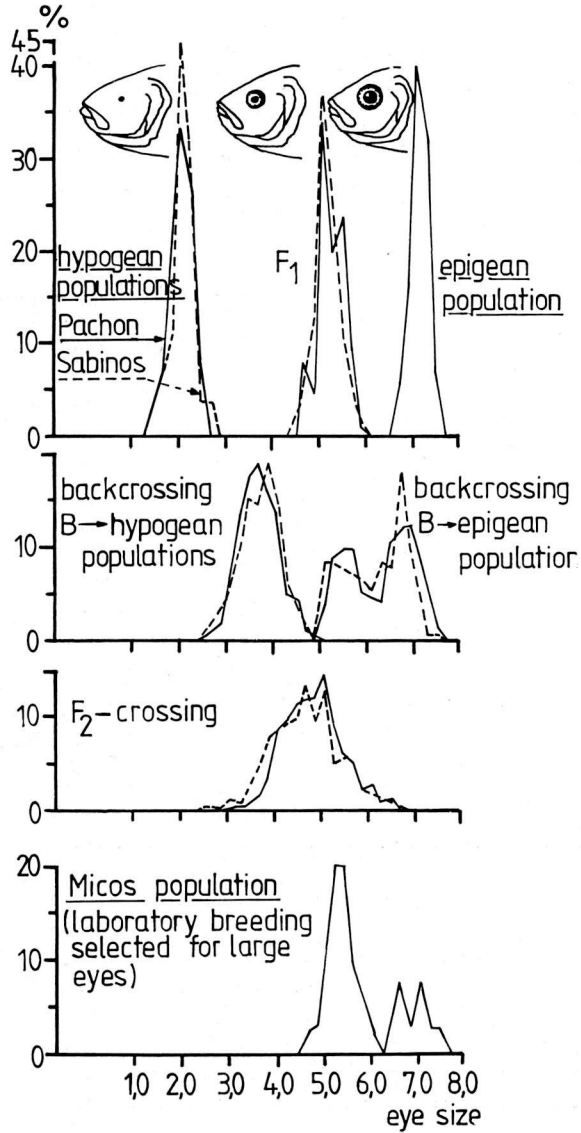
Fig. 3 - Distribution of eye size of different *A. fasciatus* populations and their crossings (Wilkens, 1970a, 1976, 1980).
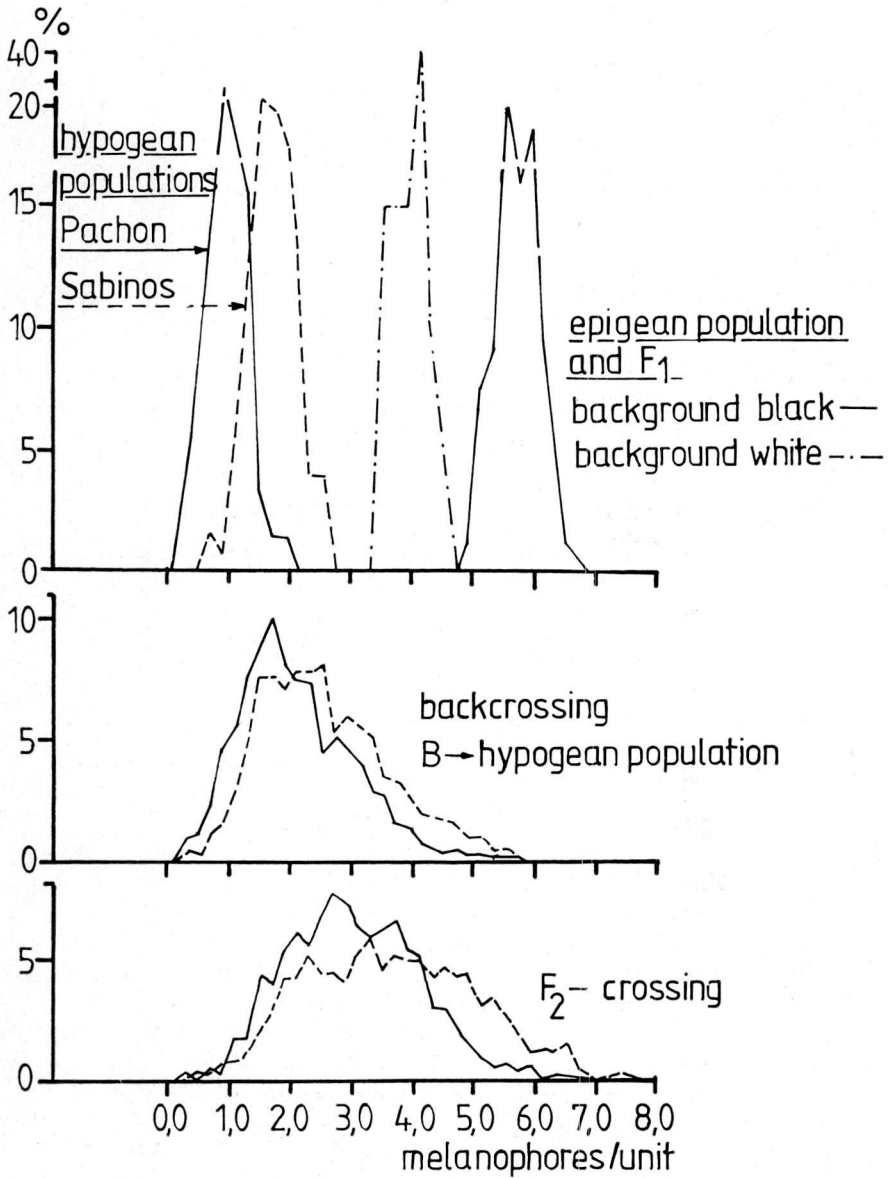
Fig. 4 - Distribution of melanophore densities of different *A. fasciatus* populations and their crossings (Wilkens, 1970c).
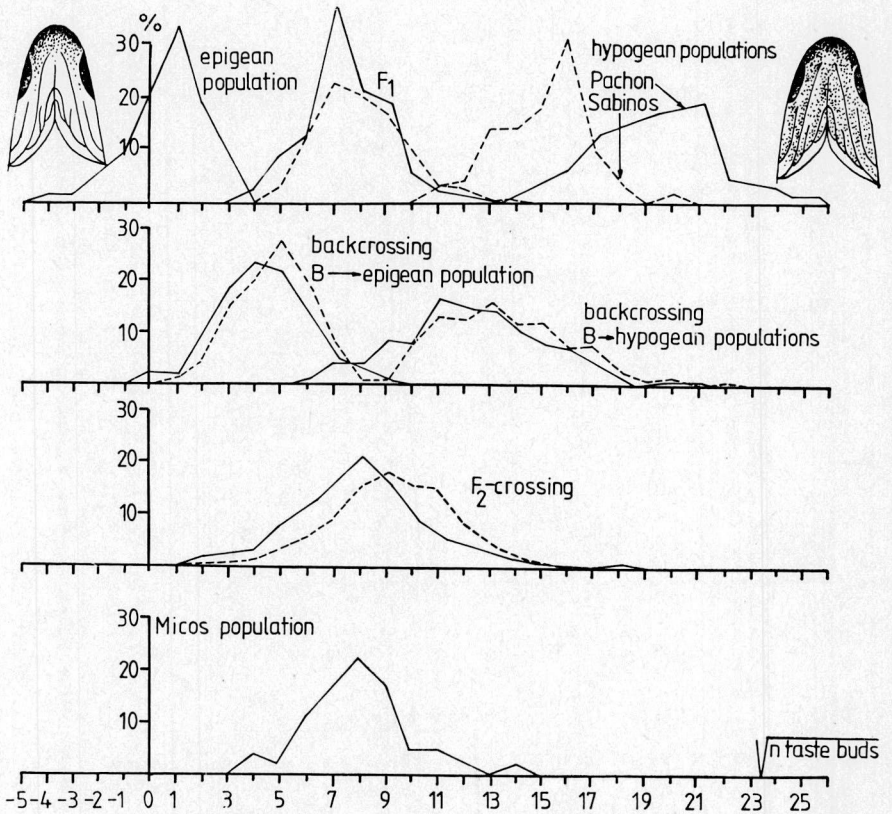
Fig. 5 - Distribution of taste bud density of various *A. fasciatus* popula-
tions and their crossings (Schemmel, 1974).

ble for the manifestation of a feature remain hidden be-
cause of too little structural difference.
An example for this is delivered by the sex determination
within the toothcarp genus *Xiphophorus* (Kosswig, 1964;
Kosswig & Oktay, 1955). Here the transition from a merely
polygenic *(X. helleri)* to a monogenic *(X. maculatus)* me-
chanism is clearly developed. The species X. *cortezi* is cha-
racterized by an intermediate stage with both modi side
by side (Zander, 1965; 1986). In this form one of the male
determining polygenes manifests high expressivity and de-
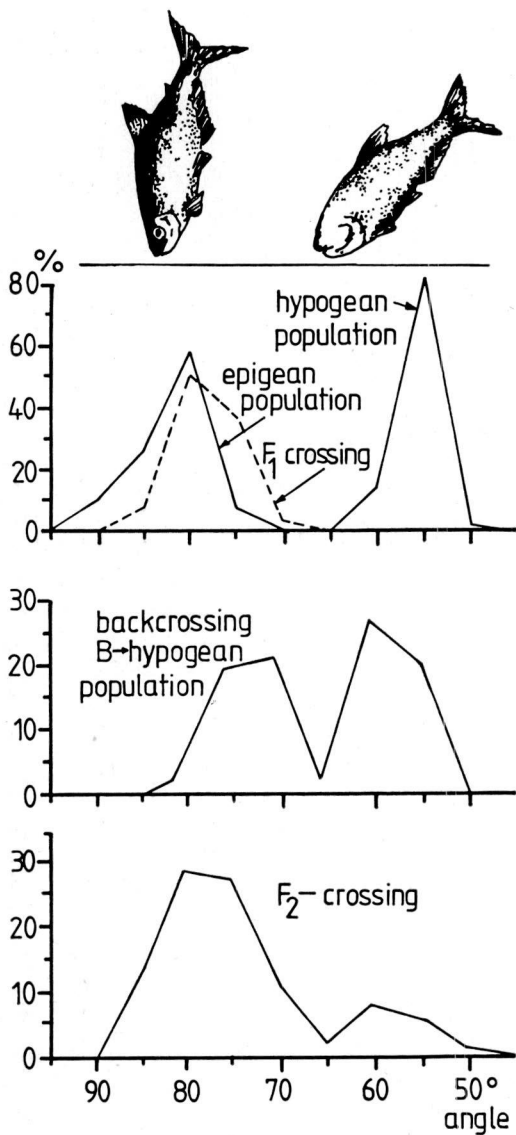livers the basis of an apparently monogenic mechanism
(Wilkens, 1980).

Fig. 6 - Distribution of feeding behaviour of various *A. fasciatus* populations and their crossings (Schemmel, 1980).
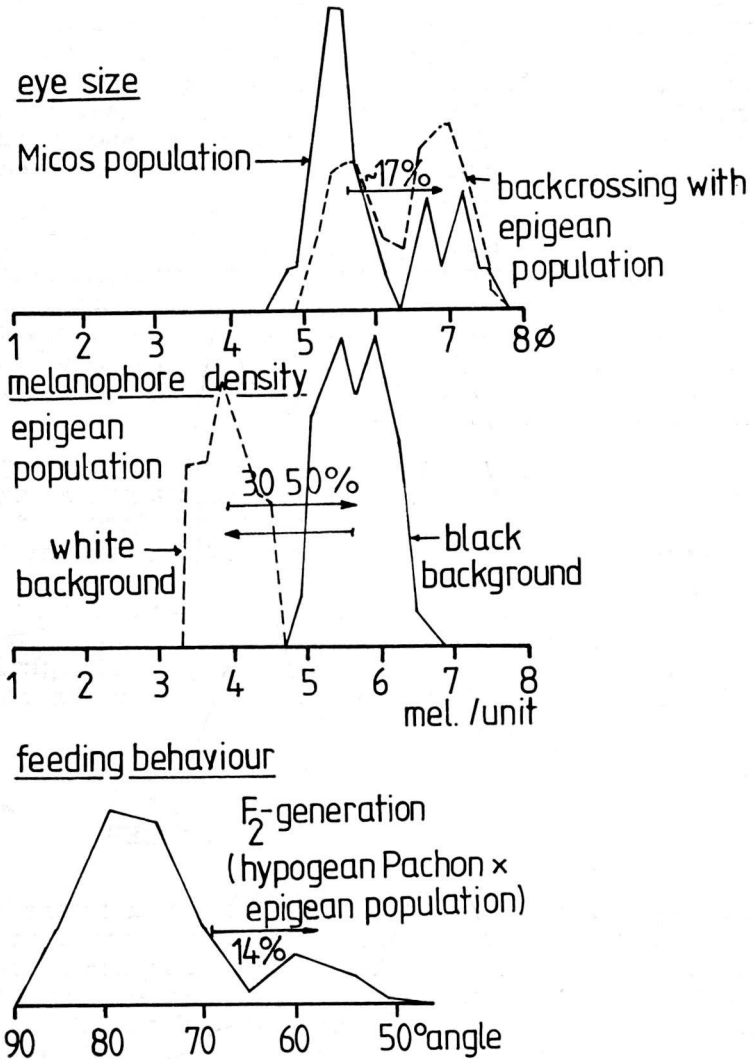
Fig. 7 - The threshold effect. After recombination of a minimum number of polygenes, which are responsible for the formation of a specific structure, gene expressivity changes. A structure may be improved by a considerable amount in one step (Wilkens, 1980).

Phenotypic sex determination delivers a further example for the general validity of the threshold effect as a common principle of genetic manifestation. In *Bonellia viridis* (Echiurida), larvae which attach to a female proboscis will become male. Contrary to this, those which do not come in contact will become female specimens. This phenomenon is completely comparable to the morphological colour change of *A. fasciatus*, in which the threshold effect can also be suppressed environmentally.

(4) It is characteristic of the genetic manifestation of the complex features, which were studied in *A. fasciatus*, that the polygenic systems being responsible for their formation do not show linkage but inherit separately. Even gustatory equipment and feeding behaviour, which are functionally correlated to some degree, are inherited independently from each other (Schemmel, 1967; 1980).

(5) It is characteristic for all features studied that no polygenes responsible for specific single features can be analyzed. In the case of the eye for example no « lens- » or « retina-genes » have as yet been separated. Therefore the term « eye-gene » was coined. « Eye-genes », « melanophore-genes », « taste-bud-genes » have a quantitative character and determine size respectively density. This method of manifestation is caused by the developmentally physiological interdependence of the single structures of complex organs (Wilkens, 1970 c; 1971).

EVOLUTION OF COMPLEX FEATURES

The developmental constraints within complex organs have been confirmed experimentally in the chicken eye (Coulombre, 1969). Ocular morphogenesis is regulated by the following main factors: (1) The size of the eye is determined by the dimension of the contact area of the optic vesicle with the surface ectoderm. Whenever it is smaller than normal a microphthalmic eye results. (2) The lens size is responsible for the accumulation of vitreous substance within the eye. It furthermore influences the normal growth and expansion of the superficial coats of the eye (pigmentary epithelium, chorioid coat, sclera). (3) The growth of the neural retina is relatively independent of any specific influence from other tissues. The neural retina influences the development of the pigmentary epithelium as well as the orientation and shape of the lens.

Similar regulatory mechanisms are characteristic of the eye of *A. fasciatus*. The first anlage of this organ in the cave fish is much smaller than in epigean individuals (Cahn, 1958). The neural retina seems to grow rather independently (fig. 8a, b). The pigmentary epithelium will flatten after the sensory cells are reduced. Further insight was gained by calculating allometric correlations, which reflect developmental constraints between different tissues. Also in the *A. fasciatus* eye the lens obviously plays a dominant role. Its size is correlated with that of the eye ball as well as with that of the pupillary opening (fig. 9). It is worth noting that in all crossings the formative influence of the lens on eye size is less effective than in the epigean fish. This can be concluded from the fact that hybrid eye size only increases negatively allometrically in correlation to this organ (Wilkens, 1970 c).

In hybrid eyes as well as in those of the variable Micospopulation the degree of differentiation is correlated to the eye size. The larger an eye is, the better it is developed. In the F_1-crossing between two extremely reduced cave populations individuals are found which have larger eyes. These may even develop structures like a lens capsule, which are never observed in the adult parental specimens (fig. 10) (Wilkens, 1971).

It seems in particular to be the relative size of an eye in comparison to body length that determines the degree of differentiation. This is clarified by similar tendencies of allometric correlation which are developed in eyes, the sizes of which have quite different causes (Wilkens, 1970 c). As could be examplified in the case of the lens of the crossings between the epigean and cave forms of *A. fasciatus* a positive allometric correlation is developed during individual ontogenetic growth as well as between eyes of different individuals the eye sizes of which are based on a different number of « eyegenes ». This principle also holds true for the observation that larval cave fish eyes are better differentiated than those of adult specimens (Cahn, 1958; Peters & Peters, 1973).

On account of developmentally physiological interdependence within complex organs no genes responsible for example for the formation of structures like retina or lens could as yet be determined for the eye. Although such genes probably exist, their loss by mutation will not only influence one specific organ but, on account of the developmental constraints, the whole eye. The phenotypic result is a smaller eye, which still possesses all typical single structures. From this it can be concluded that structural reduction quite generally will proceed as a process of diminution in size. Studies in cave animals have also shown that an important part of constructive adaptation may be the enlargement of relevant features.
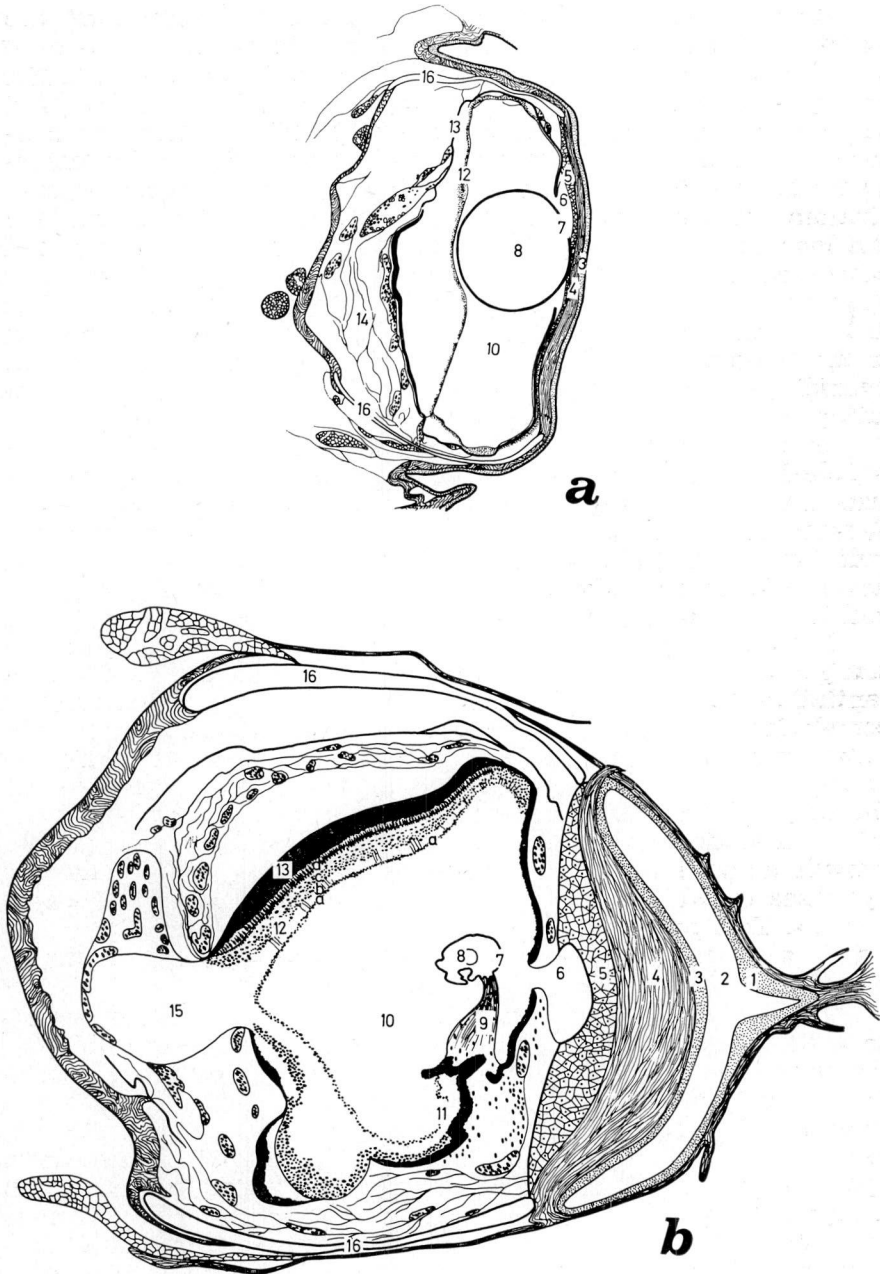
Fig. 8 - Even in large hybrid eyes the neural retina may secondarily de-
differentiate during late ontogeny (a). In others a rather well-de-
veloped retina is combined with a tiny lens rudiment (b). Thus a
considerable developmental independency of this organ is proven
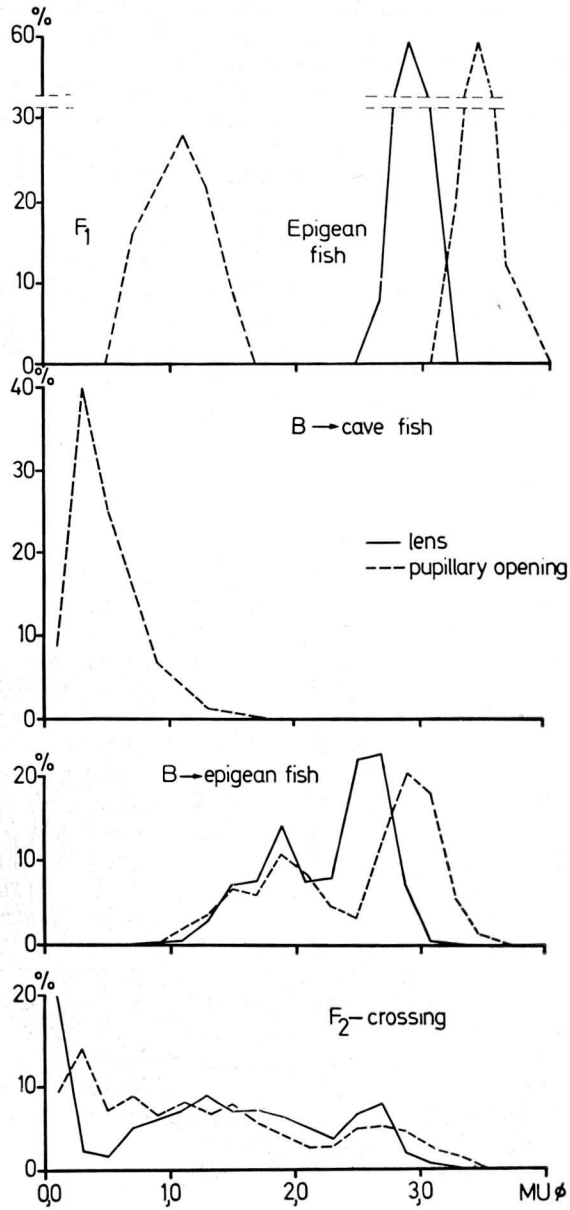(explanations fig. 1).

Fig. 9 - Correlation of lens and pupillary opening sizes in the crossings between epigean and cave *A. fasciatus* (Standard length 2,5 cm).

These findings confirm assumptions that developmental contraints and interactions impose limits on the evolution of complex features (Alberch, 1980; 1982).

It is a fact of general evolutionary importance that, additionally to the enlargement or diminution of complex structures, the allometric regressions may change. Due to a reduced number and a different recombination of genes this occurs in the hybrid eyes of epigean and cave *A. fasciatus*. In the epigean form both lens and pupillary opening as well as eye ball size show isometric correlations. In the crossings, however, the correlation of lens and eye ball becomes positively allometric, that of lens and pupil negatively allometric. In the phylogenetically young Micos population, which is characterized by variable eye sizes, an intermediate stage is developed.
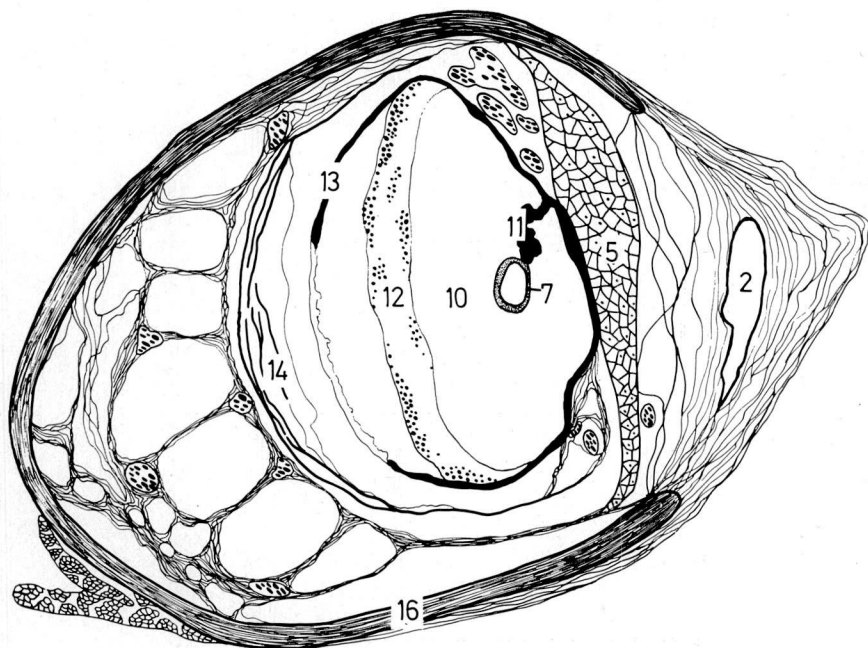

Fig. 10 - In some F₁-hybrids between extremely reduced cave populations eyes may develop which are larger and better differentiated than in the parental generation (explanations fig. 1).

MODE OF REGRESSIVE EVOLUTION

It is a common evolutionary phenomenon that features which have lost their biological function are reduced. In many cases the process of reduction is promoted by directional selection. However, there are cases like the eye and pigment regression in many cave animals which are characterized by the fact that directional selection no longer acts. After the loss of stabilizing selection which normally keeps the eye in its appropriate adapted form by eliminating negative mutants, the deleterious mutations can accumulate. Eye and pigmentation now reduce by mutation pressure, because the number of such mutations is higher than those which improve an existing system.

In haemophilia for example stabilizing selection without medical help still eliminates negative mutations immediately, because they become lethal. Due to the mortality new negative mutations are necessary to account for the constant frequency of haemophilia, which can be observed in the human population (Haldane, 1935). Actually one third of all casualties develop in families which before never did show haemophilia. These casualties therefore must be based on new mutations.

Until today the molecular nature of the negative mutations responsible for structural reduction has not been analyzed. However, molecular genetics of other features has provided insight. Studies of the bleeding disorder in man, haemophilia A, show that it is caused by defects in factor VIII, a component in the blood coagulation pathway. Gitschier et al. (1985) found that this disease is caused independently by 7 different mutations: 4 point mutations and 3 different partial deletions in the factor VIII gene. Also the clinically identical Tay-Sachs-disease of 2 different human populations turned out to be caused by different mutations (Myerowitz & Hogikyan, 1986).

As a main objection against the theory of accumulation of random mutations, which is forwarded here, energy economy is thought by many authors (e.g. Sket, 1985) to play an important role as the directional selection force in structural reduction. Recent studies reveal that the cave fish have developed other and more efficient strategies against the at least temporary food scarcity of the cave biotope. By these they probably are able to spare much more energy than by eye reduction. The most important are adaptations like the increase of egg yolk content and lower metabolic rates (Hüppop, 1985; 1986 a, b; Poulson, 1985). Further proof for the theory of mutation pressure is delivered by ethological features like aggressive and schooling behaviour. Both are optically triggered and thus are not displayed in the epigean *A. fasciatus* when kept under cave conditions. Although there was no possibility for any kind of

directional selection based on energy economy to reduce these non-manifested features, they show genetically based reduction (Burchards et al., 1986; Parzefall, 1985). The same is true for the circadian clock (Erckens & Martin, 1982; Lamprecht & Weber, 1985), which is reduced in the cave populations of *A. fasciatus* and in other troglobites.

After suggesting that several scientists had not done proper work, Bannister (1984)* recently supported the theory originally advanced by Heuts (1951), that characters of cavernicolous animals may be the result of neoteny. He examplified his assumption by the external observation that "the eyes in the adult »cave fish *Garra barreimiae*« are identical to those in the juvenile; they have not degenerated, they just have not developed further". Unfortunately the histological data have not been presented. As in all cave fish studied, they would have revealed the ontogenetic regression of this eye. As has been shown by Cahn (1958) in the *A. fasciatus* cave populations the first eye anlage is not only smaller but there are structures like the lens and parts of the retina which are reduced during the further ontogeny. Others like the ligamentum annulare or the processus falciformis relatively increase in size (Wilkens, 1970 a).

GENERAL IMPORTANCE OF REGRESSIVE EVOLUTIONARY PRINCIPLES

The principles of regressive evolution as described before also have general validity for constructive evolution. The lack of stabilizing selection occurs not only in biologically functionless features of cave animals, but can also be observed during transitional evolutionary phases (Wilkens et al. 1979; Wilkens, 1986).

Examples for this are delivered by the evolution of species flocks in geologically young lakes or in islands. These biota are characterized by depauperate faunas, which are caused by a geographically isolated position or — in the case of lakes — by an unusual ionic composition of the water (Ladiges, 1968; Wilkens, 1986). Lakes like the great East African lakes, the Laguna de Chichancanab (Yucatan) or the Cuatro Cienagas (Chihuahua) characterized by intralacustrine fish speciation deviate from the normal chemical freshwater composition (fig. 11). Invading fish species can find here various niches not claimed by other fish. Thus stabilizing selection for the relevant adap-

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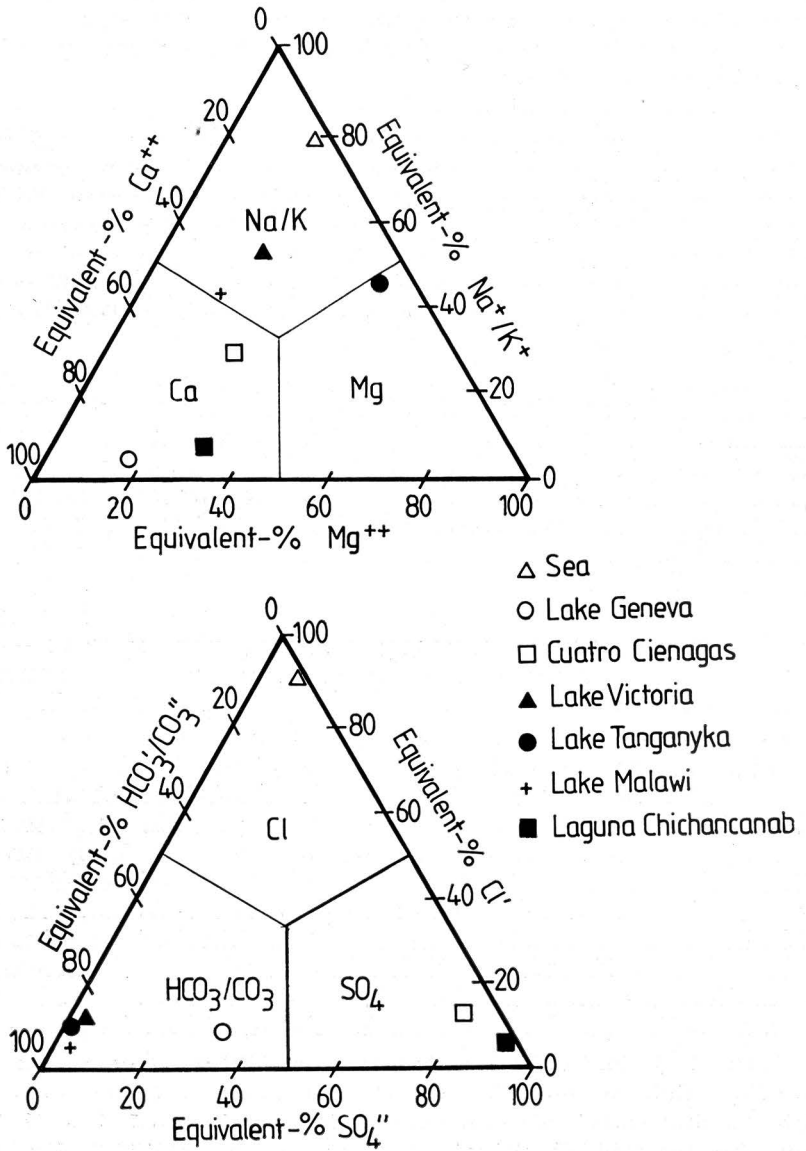* The confusing and, to a large part unjustified, critique shall be refuted in another paper.

Fig. 11 - Ionic composition of lakes with species flocks in comparison to the sea and Lake Geneva (modified after Grimm, 1986).

tations of the specific niche which the invading species once had acquired is lost. By this equilibria become punctuated. Variability arises and may persist, because there are no competing species in the niches which are taken advantage of the developing species flock.

For example, variability of shape arises. It is caused by random mutations which may provoke genetically based heterochronic changes in development and slight alterations of growth rates of the single structures of complex organs. In East African Lake Victoria haplochromine cichlids, the relative sizes and shapes of many of these fish lie in simple allometric relationships with one another and very often the differences between species are extrapolations of those within species (Greenwood, 1984).

Such variability is « allowed » as long as, and to the extent that, the viability of an individual is not influenced. Observations in the above mentioned cichlid species flock show that general body form develops only a little diversity (fig. 12) (Grenwood, 1984; Strauss, 1984). However, because empty trophic niches were available developing cranial and dental differences could persist. Those are the main features in the speciation of these fishes (fig. 13).

Based on Lack's (1947) studies of Darwin's finches of the Galapagos Islands, Kosswig (1948 a) showed that — although already adapted to several new niches — some of them are still characterized by little specialization to the food they live on and by structural variability of their bills.

The arising variability is not only restricted by viability. As has been shown before, developmental constraints also play an important role. Theoretically possible evolutionary pathways in many cases are family specific. They are limited as concerns the direction and the number (Kosswig, 1948 b; Alberch, 1980; 1982). In respect to specialized pharyngeal characters the molariform morph of *Cichlasoma minckleyi* of the Cuatro Cienagas (Chihuahua) for example resembles the mollusc crashing cichlids of East Africa more closely than its conspecific papilliform morph (Liem & Kaufman, 1984).

The only difference between the colonization of the niche-rich lakes or islands on the one hand and the cave biotope on the other is that the latter only offers one vacant niche which closely resembles that of the epigean ancestor. Thus variability is only « allowed » to those few features which have become functionless. Contrary to this, there is strong directional selection pressure on those which are most important for survival under extreme environmental conditions, as they are characteristic of the cave biotope.
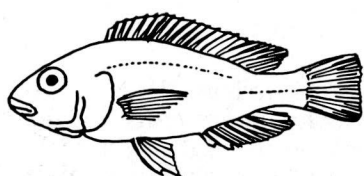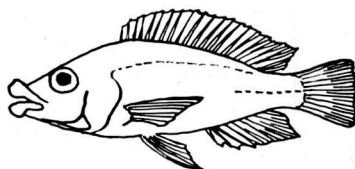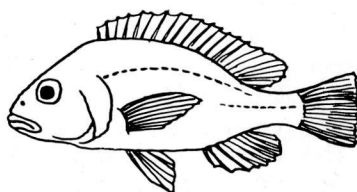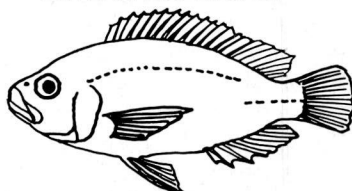
bottom feeder   insectivore
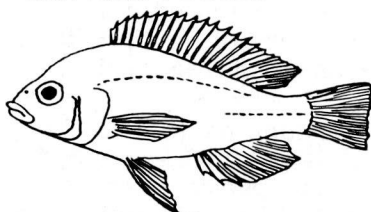
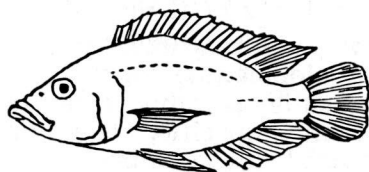mollusc eater   detritus eater

mollusc eater   paedophage

piscivore   piscivore
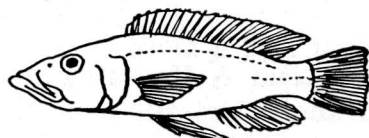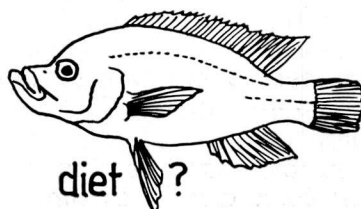
piscivore   diet ?

Fig. 12 - Body form in various Lake Victoria haplochromines (Greenwood, 1984).
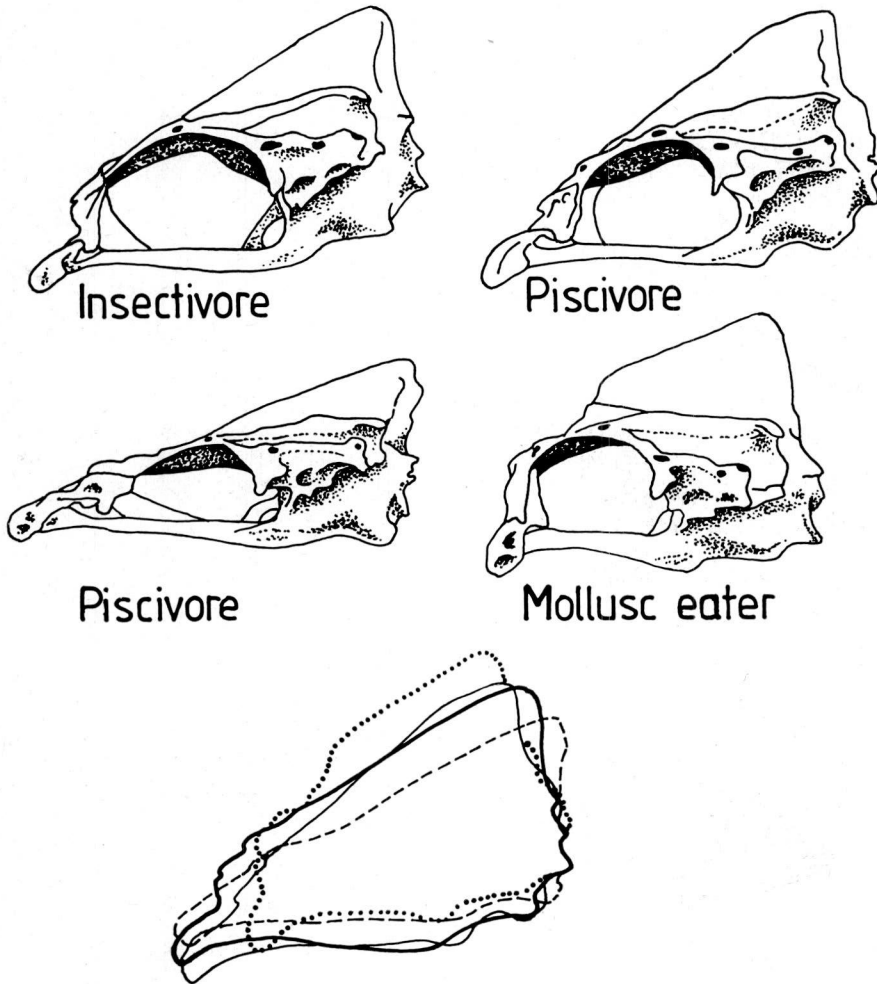
Fig. 13 - Skull form in various Lake Victoria haplochromines (Greenwood, 1984).

Uprising variability in species flocks delivers the material for directional selection which radiates such species into free niches. It will finally lower again under the influence of intra- and interspecific competition. Genetic threshold effects as described before may play an important role in accelerating this process. Finally a new static equilibrium is attained. Besides the spectrum of available free niches the number of

developing species is determined by ethological characteristics of the ancestral species. In cichlids, homogamy is probably responsible for the overwhelming number of forms (Kosswig, 1963; Dominey, 1984).

Even the time necessary for these processes is comparable. In the Lake Victoria cichlids, previously referred to the genus *Haplochromis* (Greenwood, 1984) a time of about 750.000 years is assumed for their speciation. The evolution of most cave populations of *A. fasciatus* originally described as an own genus « Anoptichthys » also started during Pleistocene.

Species flocks deliver examples of extant punctuational phases (Greenwood, 1984). As has been shown, the evolution of species flocks can be explained by the same developmentally physiological and genetical principles as that of cave animals. These are polygenetically based differences, slight alterations of allometric correlations and loss of stabilizing selection for certain features. Punctuational events therefore are not contradictive, but are also subjected to gradual change.

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Food-finding ability in cave fish
(Astyanax fasciatus)

Kathrin Hüppop *

SUMMARY

When competing under cave similar conditions, such as darkness and food scarcity, cave fish find much more food than their epigean relatives. The cave fish not only react much faster to food but also their food-finding ability is four times higher compared to that of the epigean fish. Several morphological and ethological alterations in the cave fish, described by other authors, seem to be responsible for this adaptation to the cave conditions.

INTRODUCTION

It is generally held that food scarcity in caves often acts as a forceful selective agent. Besides an efficient food utilization and a reduced food demand, because of reduced activity and/or reduced metabolic rate which results in greater resistance to starvation, a higher food-finding efficiency is an obviously adaptive response to environments poor in food (Culver, 1982, 1985; Mitchell, 1969; Peck, 1973; Poulson, 1963, 1964; Poulson & White, 1969). For example, the cave crayfish *Orconectes inermis* is better able to detect live prey compared to the epigean *Orconectes limosus* (Cooper, 1969), and the cave salamander *Proteus anguineus* shows a higher performance in prey detection than the closely related epigean salamander *Necturus maculosus* (Durand et al., 1981, 1982). Similarly the cave salamander *Haideotriton wallacei* and the spring cavefish

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Chologaster agassizi both have a relatively high feeding suc-
cess (Peck, 1973; Hill, 1969). Sensory improvement in compensa-
tion for the absence of vision has been shown in all the cave
animals investigated.

The characid fish *Astyanax fasciatus* (Cuvier, 1819) is wi-
despread in South and Middle American freshwaters and also
inhabits several limestone caves in North Mexico, Tamaulipas
and San Luis Potosi states (Michell et al., 1977). It represents a
special case: epigean and hypogean fish of this species are
completely interfertil (Sadoglu, 1956) although they are clear-
ly separable with regard to several morphological features. In
a few caves the hypogean fish live associated with epigean
ones, which sometimes are washed into the cave by floodings.
In such cases interbreeding seems to occur in caves where food
is abundant, as in the Chica cave, where food is provided by
bat guano (Avise & Selander, 1972; Mitchell et al., 1977; Wil-
kens, 1972). In caves where food is scarce, e.g. the Micos cave,
hybridization does not occur. Epigean fish washed into a cave
with little food look undernourished within a short time and
seem to be unable to compete with the cave fish (Mitchell et
al., 1977; Wilkens & Burns, 1972). In the Micos cave epigean
fish have very low condition factors compared to different kinds
of cave fish and also in comparison to epigean fish caught at
the surface (Wilkens & Hüppop, 1986). The condition factor,
i.e. the relationship of body mass and body lenght, is a good
measure of the nutritional state of a fish.

Besides having reduced eyes and a reduced melanophore
system based on the loss of function in darkness, the hypogean
A. fasciatus can be separated from their epigean relatives by
several adaptive features. These are the enlarged and predo-
minantly ventrally spread gustatory areas in the skin cove-
ring the head (Schemmel, 1967, 1974) and the difference in the
angle of the body when searching for food (Schemmel, 1981).
The aim of this investigation was to compare the efficiency
of the cave fish in finding food with that of the epigean
ones under cave similar conditions (food scarcity, darkness).
Former observations on food-finding efficiency of hypogean *A.
fasciatus* were made only with the hybrid and not food restric-
ted fish from the Chica cave (Glaser, 1968; Thines et al., 1966).

MATERIAL AND METHODS

Six epigean fish from the Rio Teapao and six hypogean
fish from the Pachon cave, three females and three males
each, were taken randomly out of groups that had been held

for at least one and a half years in the laboratory. The fish were transferred to a 200 l aquarium, maintained at a temperature of 25 °C in a dark and silent room. The fish were allowed to acclimatize to the cave similar conditions for about two weeks and were fed every other day. Disturbance was held to a minimum and all handlings and observations during the experiments were made with an infrared-night-sight apparatus.

After acclimations twenty experiments with twenty pieces of beef-heart muscle each (about 10 mm³ in size) were made every other day. This rate of feeding kept the fish hungry enough to search intensively for food. The single pieces of meat were carefully put into the water where they sank to the bottom immediately. The next piece of food was not given until the former one was found and eaten by a fish. This made it easy to observe whether an epigean fish or a hypogean one found and ate the food. After all twenty pieces of food were eaten, the fish were fed with beef-heart and with dry food ad libitum, enabling the epigean fish to finally find enough food as well.

RESULTS

About 80% of all food particles were found and eaten by the cave fish, whereas the epigean fish were successful at finding only 20% (Fig. 1). Furthermore, the epigean fish did not improve: food-finding was not higher at the end of the experiments than at the beginning. If habituation to the cave conditions took place it happened in the first weeks during the acclimation time, and was obviously insufficient.

Neither the epigean nor the hypogean fish responded to the food pieces as they sank to the ground. Only if direct contact near the mouth occurred, did the fish snap and try to catch it. However, when a piece of food laid on the ground there was a clear difference in behaviour between the epigean fish and the hypogean fish. The latter reacted to the presence of the piece of food already after 5 to 10 seconds. After one cave fish began to search, the other cave fish followed within a few seconds. They searched for it exclusively on the ground swimming at an angle of about 45° subtended to the ground as described by other authors (Glaser, 1968; Schemmel, 1967, 1980; Thinès, 1955). The epigean fish, on the other hand, not only reacted very slowly to the food but also showed little propensity to search for the food on the bottom. Often all six cave fish were looking for food on the ground before any epigean
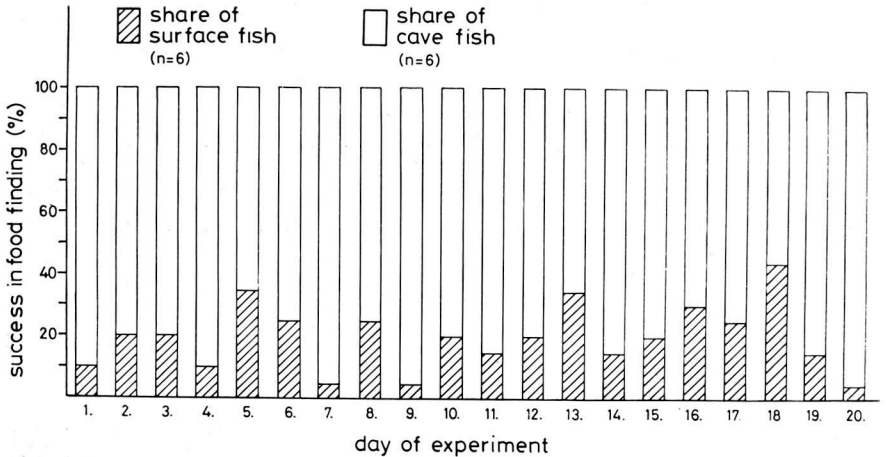
K. HUPPÖP

Fig. 1 - Food-finding success in cave-fish and in surface fish (*Astyanax fasciatus*), when competing under cave similar conditions.

fish showed a reaction. Only a coincidental approach towards the piece of food to a distance of less than 3 to 5 cm released food searching behaviour in the epigean fish. They then swam at a very steep angle (see also Schemmel, 1967, 1980). However, food searching was not very successful since the movements were excited and violent. The epigean fish could often not find the food particles, after having pushed them away while rotating around their body axis. Once the epigean fish started to look for food, they did it exclusively on the ground like the cave fish. Therefore they could find enough food at the end of each experiment when food was given ad libitum. The same behaviour has been observed in artificially blinded fish (Schemmel, 1967, 1980; Thinès & Capon, 1975). Epigean fish can find food in total darkness, but they need much more time compared to the cave fish.

DISCUSSION

For cavernicoles with epigean ancestors that forage nocturnally food scarcity rather than the darkness is the main selection factor for the evolution of a superior ability to locate food (Cooper, 1969). For cavernicoles with diurnal ancestors,

as *A. fasciatus,* both factors act together as important selective agents. The epigean fish usually take up floating food particles by optic orientation from the open water and almost never take up food from the ground. Since optic orientation is not possible in darkness, the cave fish evolved a more efficient food searching behaviour: they search only on the ground, as do most of the nocturnal feeders. This behaviour is supported by the morphological and ethological alterations mentioned above which enable the cave fish to preferentially register and localize food lying on the ground (see also Schemmel, 1967). They are also able to feed at the surface, another twodimensional area.

The fact that the cave fish reacted much faster to food does not imply an improvement in tasting ability, that is a lowering of tasting thresholds. Earlier investigations have never shown this (Breder & Rasquin, 1943; Humbach, 1960). Little is known of the nasal organ, however, no improvements in cave fish seem to exist (Breder & Rasquin, 1943; Schemmel, 1967). Chemicals may bring more and different informations to cave fish than to epigean ones which normally feed by optic orientation, independent of threshold effects. The same holds for disturbances caused by food particles dropping into the water. Additionally, my results may support earlier findings (Lüling, 1954) that characteristic food searching movements of the cave fish on the ground cause specific water turbulences. It might be possible that these turbulences contain more information for cave fish than for epigean ones. As a consequence, the cave fish, stimulated by the characteristic turbulences after one cave fish released them, would be searching for food on the ground long before the epigean fish. This would increase the possibility that a cave fish and not an epigean fish finds the food.

Intensive food searching behaviour on the ground as an adaptive trait in cave fish has also been observed in the hypogean form of *Poecilia sphenops,* and is possibly related to morphological alterations of the mouth, the belly, and the caudal peduncle (Gordon & Rosen, 1962; Walters & Walters, 1965). The hybrid Chica cave fish of *A. fasciatus* also show this form of food searching (Thinès et al., 1966). However, the Chica cave is rich in food and the observations were not quantitatively compared to the pure epigean fish. If the Chica cave fish are really better in food finding than epigean ones, this adaptation would be a compensation for the loss of vision only.

In food scarce caves where cave fish and inwashed epigean fish may occur together, as in the Micos cave (Mitchell et al., 1977; Wilkens & Hüppop, 1986) the cave fish have an advantage when competing with the epigean fish. The inferiority of the

epigean fish under cave similar conditions, which is accelerated by their higher metabolic rate and their higher body mass loss during starvation (Hüppop, 1985, 1986), explains their undernourished appearance in such caves.

ACKNOWLEDGEMENTS

RESUME'

Quand ils se trouvent en compétition dans des conditions identiques à celles existant dans les grottes, telle la rareté de la nourriture et l'obscurité, les poissons cavernicoles trouvent beaucoup plus de nourriture que leur parents épigés. Non seulement ils réagissent plus vite pour se nourrir mais aussi leur possibilité pour trouver leur nourriture est quatre fois supérieure à celle des poissons épigés. Plusieurs modifications morphologiques et éthologiques propres aux poissons cavernicoles, décrites par d'autres auteurs, semblent être responsables de cette adaptation aux conditions du biotope souterrain.

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BOOKS AND NEWS

MATTHEWS, Peter G. - Australian Karst Index 1985. 492 pages.
1985. A $35.00 (+ $17.00 postage and packing). Australian Spe-
leological Federation, 66 Frogmore Crescent, Park Orchards,
Victoria 3114, Australia.

Within the past twenty years there has been an extraordinary
number of cave studies and surveys in Australia. Expeditions
to the Bungonia area; Wombeyan Caves; the seemingly limitless
Nullarbor Plain; the deep caves of Tasmania; the abundant
towers of Chillagoe in northern Queensland all have resulted
in finding hundreds of new caves. Fortunately for later workers,
Australian speleologists for the most part are keen documentors,
so that most of the new caves studied were reasonably accurately
mapped and given precise geographic coordinates. As a result
records of these caves are to be found in the files and publi-
cations of the many Australian caving societies.

From 1968 on the Australian Speleological Foundation felt the
need to maintain an accurate record of all these caves. Because
of a desire to preserve this invaluable record of its nation's
heritage, the Australian government granted $14,000 to ASF
to initiate a computer database of Australian karst. After a
series of vicissitudes worthy of a book itself, ASF under the
editorial leadership of Peter Matthews, has produced this volu-
me which lists and describes every known cave in Australia
that had been surveyed by 1985.

A rather complex numbering system locates each case by
state, then by well known cave areas within each state, then
by grid reference to previously existing topographic survey
sheets. A short description is given for each cave; number
and type of entrance; significant historical, biological, paleon-
tological and archeological data; difficulty of access and/or
exploration; owner (if known) and references to the cave in
available publications.

The amount of data is awesome and represents the efforts
of dozen of Australian cavers. Several cross indexes permit
regional location of information pertaining to just about every
known cave and rock shelter in Australia. Instructions are

included that enable those with access to the computerized data base to obtain printouts of data in various formats.

Those using the karst index for the first time are advised to read carefully the many pages of instruction and explanation. Even for one who has never been to Australia, this karst index can serve as a valuable tool and model in developing similar listings for other countries. (Brother G. Nicholas)

McCLURG, David R. - Adventure of Caving. A Practical Guide for Advanced and Beginning Cavers. 1986. 332 pp. D & J Press, 1610 Live Oak, Carlsbad, N.M. 88220.

This is a rather personalized account of techniques useful in the successful exploration of caves. Roughly halft the volume pertains to methods essential to explore a cave properly. The other half of the volume applies to rigging caves and the many techniques for getting into and out of vertical caves. It is this latter section that reflects the author's skills and experience, as dozens of various devices developed for ascending and descending are analyzed. Even the types of clothing to be worn is discussed in some detail. The main lesson to be learned is that cave safety is a complicated and demanding skill. When one considers all the things that can go wrong on a cave trip, particularly in vertical caves, it becomes apparent that a great deal of preparation is needed to assure a safe return. The author emphasizes many of the practical steps to be taken, utilizing diagram and photograph to make his point. Comparisons are made of the differences in techniques, particularly rappelling and prusiking, to enable individuals to select those techniques best suited to one's specific needs. An appendix list sources of equipment and other volumes dealing with cave survival and cave science. (Brother G. Nicholas)

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Book: JAKUS, L. 1977. Morphogenetics of karst regions. Akadèmiai Kiadò, Budapest.
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