

on conflicts between water resource exploitation and environment protection (Qui Chagsi), whilst others consider conflicts between groundwater exploitation and industries such as quarrying for example (G. Michel). Other interesting papers include a discussion of the use and difficulties associated with creating underground storage reservoirs in karst areas in Yugoslavia (P. Milanović), legal problems of water abstraction and associated environmental problems in the U.S.A. (P. E. LaMoreaux), and the effect of catchment altitude on the hydrodynamic, physical and chemical behaviour of springs in Switzerland (Y. Lavanchy *et al.*). The large number of Chinese authors has resulted in hydrological and geomorphological descriptions of many previously undocumented karst areas in China. There is also a paper which lists uranium-series ages of speleothems in caves from eastern China (Zhao Shusen *et al.*).

Part 2 contains papers that are both more quantitative, and more wide ranging in their applications to karst aquifers. The section concerning modelling for instance not only contains research relating to mathematical modelling of spring response (Lin Min *et al.*), but also work which examines the similarity between flow through fissured and porous aquifers (S. Troisi *et al.*). Few of the modelling papers relate to environment protection, but applications of remote sensing to this task are discussed (J. Svoma), along with its use for locating water bodies (Liu Guangyao *et al.*). The tracing section includes more site specific work using dye tracers in Austria for example (R. Benischke *et al.*), and use of B, F, and Sr tracers in Israel (A. Arod). This section also contains research into geothermal resources (Zhang Zhenguo) and thermal mineral waters including their medicinal uses (Tan Kai'ou *et al.*). General pollution problems are examined (Z. P. Stevanović), along with models of contaminant transport (Yang Tianxing *et al.*), and protection strategy proposed for aquifers in the U.S.A. (M. S. Field). Other environmental problems discussed in part 2 include mine dewatering, leakage from karst reservoirs and surface collapse problems, all of which are dominated by examples from China. These include both description of problems encountered (Zou Chengjie) as well as their control and prevention (Tian Kaiming).

The paper that the proceedings are printed on is cheap, but the production is acceptable; however the small number of photographs included have not reproduced well. At only US\$20 for over 1,250 written pages, one cannot be too critical of the poor quality paper. Some of the diagrams are also poor, but this is a reflection on individual authors, as papers were submitted in a camera ready form to the publishers.

In summary this conference proceedings is recommended to all, but especially for libraries, and those interested in karst research in China.

SBORDONI, V. (ed.): Speciation and adaptation to cave life: gradual vs. rectangular evolution. *International Journal of Speleology* vol. 16(1-2), 1987, 68 pp.

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(reviewed by P. R. J. Chapman)

Valerio Sbordoni's introduction raised hopes that this collection of papers would take a new look at one of cave biology's longest running controversies, namely: 'are caves a cosy "twilight home" for elderly and infirm "living fossils" which can no longer survive the rough and tumble of the real world outside, or are they a kind of "Wild West Frontier" under constant pressure

from would-be settlers, where only the fittest and most adaptable survive?' The controversy is of more than academic interest to biospeleologists, because, if the former viewpoint prevails, their discipline is seen by the mainstream scientific establishment as a mere curiosity, whereas the latter interpretation suggests that caves should be a focal point for evolutionary research.

In fact, the aim of this symposium was to consider just one specific evolutionary issue: that of whether evolution happens by a process of gradual adaptation of species to meet the demands of their environment through natural selection (as suggested by classical 'neo-Darwinian' theory) or whether species suddenly appear and change rapidly, then remain almost unchanged for long geological periods (the 'rectangular evolution' or 'punctuated equilibria' model, based on observation of the fossil record).

The symposium kicks off with a paper (*The evolution of non-relictual tropical troglobites*) by Frank Howarth, doyen of the 'Wild West' school of biospeleology and long-time champion of lava tubes.

Hawaii's Big Island (Howarth's main study site), first emerged from the depths of the Pacific ocean less than a million years ago and its most active volcano, Kilauea, still produces new lava caves almost daily. All Hawaii's terrestrial cave species must have arrived on the island in geologically recent time, have successfully colonized above-ground habitats and from there have moved underground. Many of them are so highly specialized for a particular cave lifestyle that they can no longer survive in the outside world (they have no protection against solar radiation or drying atmospheres), yet often their parent, or sibling species live alongside them still. These are not 'living fossils' by any stretch of the imagination, but are good illustrations of evolution in action today.

In the core section of his paper (titled 'Adaptive shift versus isolation hypothesis . . .') Howarth addresses the problem of how terrestrial animals establish colonies in caves and how those colonies then acquire the distinct genetic identity which marks them as 'cave-evolved species'. Among the plum pudding of ideas are scenarios which might be seen as models for the speciation process as it may occur in all young caves when they first become available for colonization:

The first involves innumerable separate attempts by a poorly-preadapted out-of-cave species to exploit the rich food resources within caves and mesocaverns. Most fail, because the individuals concerned lack the necessary equipment to establish a cave population (can't breed in the dark, can't tolerate a hydrating atmosphere . . .). However, every once in a while, a mutant individual turns up whose offspring inherit the genetic equipment they need to make the crucial *adaptive shift* (perhaps changing from a visual-dependent to a visual-independent courtship pattern) which enables them to settle the cave. Starting with a tiny gene pool, the incipient cave species now quickly spreads through the subterranean environment. The conditions it faces—of release from stabilizing genes during the initial period of population expansion and of stress and intensifying selection pressures resulting from later flush/crash population cycles—conspire to encourage a profound and rapid reorganization of the genotype. This may (but not always does) confer reproductive isolation (if the initial adaptive shift had not already done so), and so may result in the appearance of a new cave-evolved species.

A second scenario applies to better preadapted species which can easily establish widespread populations in cave as well as in non-cave habitats. Previous authors have argued that in such cases gene swamping will occur of the incipient cave population's gene pool by the larger out-of-cave one, and that the only way the former can become 'cave-evolved', is for the

latter to be exterminated (e.g. by major climatic-ecological change, such as desertification or glaciation). Howarth argues that the subterranean biotope of young lava flows, such as in his Kilauea study site, is so rich and extensive, that a successful *cave* population, is likely to be *larger* than its surface-dwelling counterpart, and any gene swamping will work the other way! Hence the species can become cave-evolved without the need for extermination of the surface population. This is an exciting idea and this reviewer eagerly awaits some evidence to support it.

The weakness of Howarth's paper is that his evolutionary arguments are entirely based on inferences drawn from the present distribution patterns and taxonomic relationships of Hawaiian cave animals. The species complexes which he tantalisingly describes cry out for the kinds of detailed genetic study which have been lavished on Hawaiian *Drosophila* fruit flies, as well as on Horst Wilkens's cave fish (see below).

In *Genetic analysis of evolutionary processes*, Horst Wilkens explains how Mexican cave fish may have lost their eyes. According to him, this is an inevitable result of chance. Out-of-cave fish live in a world where the rules specify an optimum eye size for a particular species in a particular job, or 'niche'. If they have been in this niche a long time, the whole population will have reached a point of evolutionary equilibrium, where each of its members shares a similar set of eye-developing genes. Cave rules don't mention eye size (irrelevant in absolute darkness), so a move to cave-dwelling 'punctuates' the evolutionary equilibrium for this feature. Now any old eye mutation can accumulate in the settler population, which soon becomes very polymorphic for eye size. A number of independent and unspecific genes control the normal development of a baby fish's eye and a random change in any one of them is far more likely to impair rather than enhance its performance. Relaxed selection therefore results in progressively smaller and less functional eyes. Eventually, eyes disappear entirely, throughout the population. This marks a new equilibrium point and the fish are now committed to groping around in dark caves for the rest of their evolutionary span.

Kathrin Hüppop (*Food-finding ability in cave fish*) fed bits of beef heart to pet groups of Wilkens's blind cave fish and of their eyed surface relatives in a darkened laboratory. Though they do not seem to have a particularly improved sense of taste, the cave fish searched the bottom of their tank more quickly and efficiently than the others and got more grub!

David Culver, in *The role of gradualism and punctuation in cave adaptation* mounts an ineffectual attack on some aspects of punctuation theory, then presents "an alternative" which turns out to be a mathematical model which may prove useful in predicting the direction in which selection is likely to operate on a species, providing its present 'fitness' (whatever that might be) can be measured. A single example of Culver's arguments should suffice here: On the basis of measurements showing that one highly speciated group of amphipods does not have significantly longer antennae than another less speciated group, he argues that morphological change is not necessarily 'almost invariably associated with speciation'. The logic, or indeed the point of this argument (as of the rest of Culver's dreadful paper) entirely escaped this reviewer.

In his introduction, Sbordoni posed several key questions, including: '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?' The answers would seem to depend on where researchers are based. Howarth in his relatively new Hawaiian

caves sees the evidence of explosive speciation and rapid 'macroevolutionary' change happening under his very nose. Wilkens, working with his rather older Mexican cave fish can still discern traces of what seems to have been a punctuation event when the fish first entered their cave. Finally, Culver in his ancient North American caves, well stocked with ecological, biogeographic and phylogenetic relicts sees only the end results of a vast period of change, and doubts that things were ever any different from the way they appear now.

It seems that today's punctuated equilibria may give rise to tomorrow's 'living fossils', Hawaii may become Kentucky, but we may have to wait a while . . .

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(reviewed by T. C. Atkinson)

As we in U.B.S.S. are well aware, small but high-quality journals are the backbone of scientific speleology. We like to believe that our own *Proceedings* is one such. Generally such journals are either based around a local or national speleological society. Their contents reflect their parent society's traditional strengths and often have strong local flavour. This is not to accuse such journals of parochialism. If I want to determine the state of scientific understanding of the southern British caves, it is to the U.B.S.S. *Proceedings* or perhaps *Cave Science* that I would naturally turn.

The *International Journal of Speleology* is published by the Speleological Society of Italy. It is produced to a very high editorial standard and printed on glossy paper. In production style it is like a cleaner and slimmer *Proceedings*. From the title and composition of the editorial board, it is evidently the editors' intention to provide an international forum which scientific speleology needs. To judge by the provenance of the latest double issue, they have succeeded. There are papers from the USA (2), Japan (1), France (1) and Italy (2). Five are in English, one in French and most written in the clear, economical style which is needed for an international journal. It is a pity, however, that several of the topics reported are rather slight. There is a short report of diatomaceous speleothems from a cave in pyroclastic rocks in Japan, and an equally brief account of pollen and gastropods found in speleothems in Georgia. Both of these papers are interesting, but one hungered for larger contributions. A third story, of stratigraphic sections in caves in Indiana, was too long and out of place in an international journal. It properly belongs in the *National Speleological Society Bulletin* or a local geological journal in the U.S.A.

The remaining papers are longer and of wide interest. Bernard Gèze discusses the origin of the term 'estavelle' and shows that its meaning has changed since it was coined 130 years ago. It originally meant an overflow spring which functioned only in flood when a lower main spring to which it was connected was surcharged. Through misreadings of early texts, 'estavelle' has now come to mean an opening which alternately functions as a spring and sink for surface water. Gèze points out that the type site, La Source de l'Estavelle in Languedoc, France, never was an estavelle in the modern sense and that it has now ceased to flow at all because of groundwater abstraction nearby. He proposes a new type site, at Inversac near Sète on the Languedoc coast. Logically, but I suspect quixotically, he suggests that the term 'estavelle' be abandoned and 'inversac' be substituted. Alas, language does not work like that! The remaining two papers from Italy are straightforward summaries