ACTA CARSOLOGICA

36/1 · 2007

ACTA CARSOLOGICA
ISSN 0583-6050

Naslov uredništva / Editor's address:
Inštitut za raziskovanje krasa ZRC SAZU - Karst Research Institute ZRC SAZU
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Fax: +386 (0)5 700 19 99, e-mail: kranjc@zrc-sazu.si

Spletni naslov / Web address: http://carsologica.zrc-sazu.si

Distribucija in prodaja / Ordering address:
Založba ZRC/ZRC Publishing
Novi trg 2, P.O.Box 306, SI-1001 Ljubljana, Slovenia
Fax: +386 (0)1 425 77 94, e-mail: zalozba@zrc-sazu.si, http://zalozba.zrc-sazu.si

Sprejeto na seji uredniškega odbora 25. januarja 2007.

Cover photo: Cover montage by Will Pearce. Images courtesy of Horton H. Hobbs III, John Mylroie, Arthur N. Palmer, and Ira D. Sasowsky..

Cena / Price
Posamezni izvod / Single Issue
Individual / Posameznik: 15 €
Institutional / Institucija: 25 €

Letna naročnina / Annual Subscription
Individual / Posameznik: 25 €
Institutional / Institucija: 40 €

ACTA CARSOLOGICA

36/1
2007

SLOVENSKA AKADEMIJA ZNANOSTI IN UMETNOSTI
ACADEMIA SCIENTIARUM ET ARTIUM SLOVENICA
Razred za naravoslovne vede – Classis IV: Historia naturalis

ZNANSTVENORAZISKOVALNI CENTER SAZU
Inštitut za raziskovanje krasa – Institutum carsologicum

LJUBLJANA 2007

60 let / *years*

Inštitut za raziskovanje Krasa ZRC SAZU
Karst Research Institute at ZRC SAZU

ACTA CARSOLOGICA je vključena v / *is included into*: Current Geographical Contents / *Ulrich's* Periodicals Directory / COS GeoRef / BIOSIS Zoological Record.

ACTA CARSOLOGICA izhaja s finančno pomočjo / *is published with the financial support of*:
Agencije za raziskovalno dejavnost RS / *Slovenian Research Agency*, Slovenske nacionalne komisije za UNESCO / *Slovenian National Commission for UNESCO* in / *and Postojnska jama turizem d.d.*

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FOREWORD

Time occupies a curious place in science. In most of science, including karst science, "how" questions predominate. How are caves formed? How are caves eroded? How do animals survive in caves? How do animals come to lose their eyes and pigment in caves? But "when" questions have probably been asked from the very beginning of karst studies. Some of the fascination with time comes from the parent disciplines of biology and geology. The difference between "catastrophism" and "uniformitarianism" in geology is also a question of differences in time—rapid catastrophes versus slow, small changes. In biology, particularly in the late 19th and early 20th centuries, great controversies raged between the slow pace of evolution envisioned by Darwinians and the fast pace of evolution envisioned by neo-Lamarckians.

Questions of time have been especially fascinating in the karst sciences, probably because our senses tell us that caves (and cave animals) are very ancient. Caves are after all the dwelling place in mythology of ancient creatures—dragons especially. Of course our senses (and our mythology) can be deceiving, and perhaps caves and cave animals are not as old as they seem to be. Wide differences of opinion have persisted about the ages of both caves and cave animals—estimates at present that range between less than a million years to up to 100 million years! The time is ripe to examine time in karst.

The set of papers and abstracts in this volume is the result of a meeting, *Time in Karst,* of karst scientists in Postojna, Slovenia, in March 2007. Jointly sponsored by the Karst Research Institute ZRCSAZU of Slovenia and the Karst Waters Institute of the U.S.A., an international group of scientists came together to learn about and discuss time processes in karst from six perspectives:

- *The age of karst landscapes, including caves and other karst landforms*
- *The biogeographic history of cave animals, especially as it relates to the present and past distributions of cave animals*
- *Methods of determining the age of caves, especially geophysical ones*
- *Paleokarst and what it can tell us about age*
- *The sediment record*
- *The age of lineages of cave animals, especially using molecular clock techniques*

Both the Karst Research Institue ZRCSAZU and the Karst Waters Institute have a history of promoting both international and interdisciplinary cooperation, and they are pleased to form a partnership in this international, interdisciplinary endeavour.

The participation of many researchers in early stages of their careers was made possible by project SMART-KARST of the Karst Research Institute, ZRC SAZU, funded by the Marie Curie programme, sponsored by the European Commission. Many members of the Karst Research Institute ZRCSAZU and the Karst Waters Institute worked hard to make this meeting possible, including Drs. Daniel Fong, Franci Gabrovšek, Andrej Kranjc, Tanja Pipan, and Ira Sasowsky.

Tadej Slabe
David C. Culver

COBISS: 1.01

ON DENUDATION RATES IN KARST

O HITROSTI DENUDACIJE NA KRASU

Franci GABROVŠEK[1]

Abstract UDC 551.331.24:551.44

Franci Gabrovšek: On denudation rates in Karst

Paper presents a simple mathematical model, which enables study of denudation rates in karst. A vertical flow of water which is uniformly infiltrated at the surface is assumed. Denudation rate is calculated from the time needed to remove certain thickness of rock. This is done concretely on a limestone block dissected by a vertical array of fractures. It is shown that denudation rate increases with the thickness of removed layer and approaches an upper limit which is defined by the maximum denudation equations, which are based on assumption that all dissolution potential is projected into a surface lowering.

Keywords: karst, denudation rate, limestone dissolution, mathematical model.

Izvleček UDK 551.331.24:551.44

Franci Gabrovšek: O hitrosti denudacije na Krasu

V prispevku predstavim enostaven matematični model s katerim raziskujem dinamiko zniževanja kraškega površja. Predpostavim enakomerno napajanje s površja in vertikalno pronicanje vode. Denudacijsko stopnjo izračunam iz časa, ki je potreben za odstranitev določene debeline kamninskega sloja. Konkretno to naredim na primeru apnenca v katerem se voda pretaka v sistemu vertikalnih razpok. Hitrost denudacije narašča z debelino odstranjene plasti in doseže zgornjo mejo, ki je določena z enačbami, ki temeljijo na predpostavki, da se celoten korozivni potencial vode manifestira v zniževanju površja.

Ključne besede: kras, denudacijska stopnja, raztapljanje apnenca, matematični model.

INTRODUCTION

Uniform lowering or surface denudation is a dominant karstification process (Dreybrodt, 1988; Ford & Williams, 1989; White, 1988). **The denudation rate is defined as the rate (LT^{-1}) of lowering of a karst surface due to the dissolution of bedrock.** A common approach used to estimate the denudation rate is based on the presumed equilibrium concentration (or hardness) and the amount of water which infiltrates into the subsurface. It is summarized in the famous Corbel's equation (Corbel, 1959):

$$D_C\ (m/Ma) = \frac{(P-E)H}{1000\cdot\rho} f \qquad 1$$

The infiltrated water in mm/y is the difference between precipitation P and evapotranspiration E. H is the equilibrium concentration (Hardness) in mg/L of dissolved rock, ρ is the density of limestone in g/cm^3, f denotes the portion of soluble mineral in the rock, which will be 1 in this paper. The factor 1000 corrects for the mixture of units used in the equation.

There are more general equations of this kind like that of White (1984, this issue). For a Limestone terrain in a temperate climate all these equations give denudation rate of the order of several tens of meters per million years. Similar results are obtained from flow and concentration measurements in rivers which drain a known catchment area. From the measured data the total rock volume removed from the area in a given time period can be calculated. Dividing the removed volume by the surface of the area and the time interval gives the denudation rate.

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Received/Prejeto: 01.02.2007

Eq.1 implies that all dissolution capacity of water is used in the rock column, i.e. the solution at the exit of rock block is close to saturation. Among the many assumptions behind such estimations of the denudation rate I will address two of which at least one must be valid:

1. Most of the dissolution occurs close to the surface, i.e. within epikarst.
2. In the long term, the dissolution at depth is integrated into a surface denudation.

It is the intention of this paper to theoretically validate "maximum denudation" approach.

SURFACE LOWERING AND THE VOLUME OF DISSOLVED ROCK

Dissolution of any rock is not instantaneous, but proceeds at some finite rates. In conditions of diffuse infiltration through the karst surface and prevailing vertical flow, the concentration of dissolved rock in the infiltrating water will normally increase with the depth as schematically shown by color intensity in Fig.1.

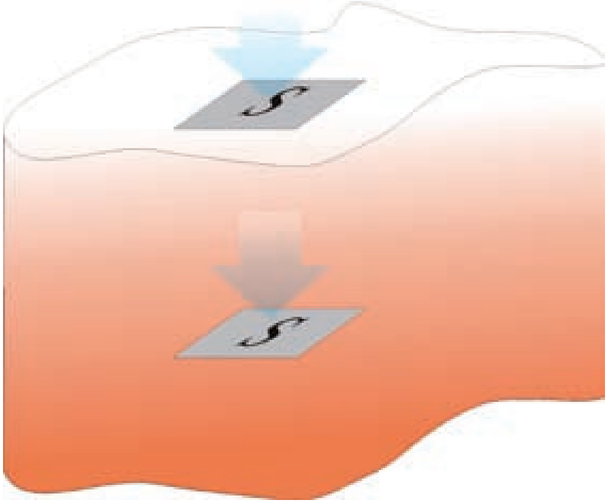

Fig. 1. Section of a terrain with a uniform surface infiltration of aggressive solution and prevailing vertical flow. Color intensity denotes that the concentration of dissolved rock increases with depth.

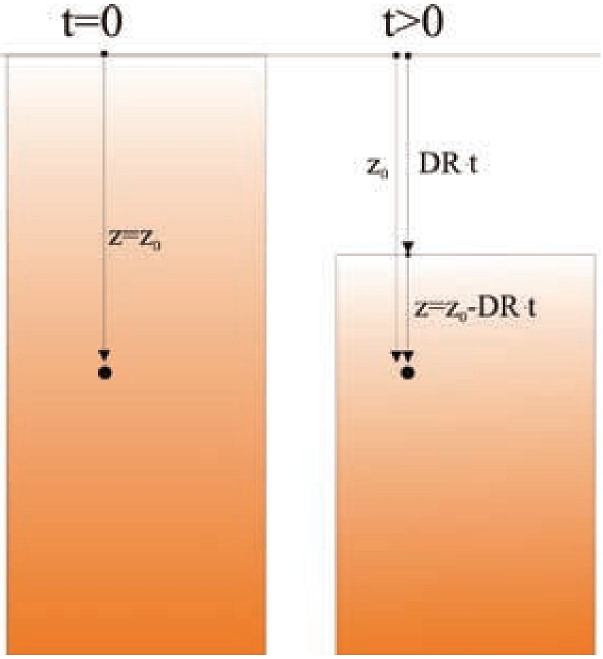

Fig. 2: Idealized profile through the rock column at time t = 0 (left) and t > 0 (right). The depth of the point which is at z_0 decreases in time due to the surface lowering.

Fig. 2 presents point at some depth z below the surface. The volume ΔV of rock dissolved **per unit surface area** S in time Δt between the surface and the point is given by

$$\Delta V / S = c(z) \cdot q \cdot \Delta t / \rho \qquad 2$$

where c(z) is the concentration of dissolved rock [M/L^3] at the depth z, q is the infiltration rate at the surface [L^3/(L^{2}T)] and ρ is the density of the rock [M/L^3].

Due to the surface lowering, the depth of the point is decreasing according to z(t) = z_0 – D·t, where z_0 is the depth at t = 0 and D is the denudation rate (Fig. 2). The volume of dissolved rock per surface area in time T above the point is then given by:

$$\Delta V / S\,(T) = \frac{q}{\rho}\int_0^T c\big(z(t)\big)\,dt = \frac{q}{\rho}\int_0^T c(z_0 - D\cdot t)\,dt \qquad 3$$

Introducing a new variable z=z_0 - D·t into the right hand integral in Eq. 3 gives:

$$\frac{\Delta V}{S}(T) = \frac{q}{D\cdot\rho}\int_{z_0 - DR\cdot T}^{z_0} c(z)\,dz \qquad 4$$

The complete volume of rock initially above z_0 is $z_0 \cdot S$. To remove this volume a time T_D is needed, where $z_0 = D \cdot T_D$. Using all this in Eq. 4, we obtain:

$$z_0 = \frac{q}{D\cdot\rho}\int_0^{z_o} c(z)\,dz \;=\; \frac{q\cdot T_D}{z_0\cdot\rho}\int_0^{z_o} c(z)\,dz \qquad 5$$

$$\frac{z_0}{T_D} = D = \frac{q}{z_0\cdot\rho}\int_0^{z_o} c(z)\,dz \qquad 6$$

As given, D is an average denudation rate, calculated from the time T_D needed to remove a layer of thickness z_0 from the rock column with initial a uniform porosity distribution in vertical direction. If a rock layer has a finite thickness, z_0 can be taken as the layer thickness, T_D the time needed to remove the complete layer and D an avarege denudation rate. It is easy to see that if the solution quickly attains equilibrium Eq. 6 gives maximum denudation rates:

$$D = \frac{q\cdot c_{eq}}{z_0\cdot\rho}\int_0^{z_o} dz = \frac{q\cdot c_{eq}}{\rho} = D_C \qquad 7$$

If this is not the case D will be below D_c, since integral with c_{eq} is maximal. In this case we rewrite Eq. 6 as:

$$D = \frac{D_c}{c_{eq}}\cdot\frac{1}{z_0}\int_0^{z_o} c(z)\,dz = \frac{\overline{c}\left[0,z_0\right]}{c_{eq}}D_C \qquad 8$$

With increasing layer thickness an average concentration within the layer increases and average denudation rates approach maximal.

CALCULATION OF THE CONCENTRATION PROFILE

The results given so far are valid for any “natural” c(z). To obtain some quantitative results we revert to a special case where the calcite aggressive water is infiltrating into a vertical fracture network. Therefore we need to couple the rate equation for limestone and flow of laminar film down a vertical fracture wall.

LIMESTONE DISSOLUTION RATES

Recently Kaufmann & Dreybrodt (2007) published the corrected rate equation with two linear regions and a non-linear region of dissolution kinetics:

$$R = \begin{cases} \alpha_1(0.3c_{eq} - c) & c < 0.3c_{eq} \\ \alpha_2(c_{eq} - c) & 0.3\,c_{eq} < c < 0.9c_{eq} \\ \beta(c_{eq} - c)^n & c > 0.9c_{eq} \end{cases} \qquad 9$$

The kinetic constants and rate orders are derived from theoretical and experimental results (Buhmann & Dreybrodt, 1985; Dreybrodt, 1988; Eisenlohr *et al.*, 1999; Kaufmann & Dreybrodt, 2007). Values depend on the temperature, p_{CO2} and laminar layer thickness and are given in Kaufmann & Dreybrodt (2007). We will use $\alpha_1 = 3\cdot10^{-4}$ cm/s and $\alpha_2 = 8\cdot10^{-6}$ cm/s, values which are valid at 10°C for the open system dissolution (Kaufmann & Dreybrodt, 2007). Nonlinear kinetics will not be discussed here. It is valid close to equilibrium and does not change the results substantially. c_{eq} depends on the p_{CO2}, temperature, the presence of the foreign ions and the nature of the system where dissolution proceeds (open, closed, intermediate) (Appelo & Postma, 1993; Dreybrodt, 1988). The calcium equilibrium concentration normally takes values between 0.5 mmol/l – 3 mmol/l, which in terms of dissolved calcite means 50—300 mg/l .

LAMINAR FLOW DOWN A SMOOTH VERTICAL WALL

Only rough assumptions can be made about the flow regime of infiltrated water. We assume a laminar film flow down the walls of vertical fractures. The velocity of such film is given by (Bird et al., 2002):

$$\overline{v} = \frac{g\delta^2}{3\upsilon}\;, \qquad 10$$

where δ is the film thickness, g gravitational acceleration and υ the kinematic viscosity. More suitable master variable is a flow density along the fracture walls q_f (cm^2/s). Applying $q_f = \overline{v}\delta$ we get:

$$\delta = \sqrt[3]{\frac{3q_f\,\upsilon}{g}} \quad \text{and } \overline{v} = q_f^{\;2/3}\left(\frac{g}{3\upsilon}\right)^{1/3} \qquad 11$$

THE COUPLING OF FLOW AND DISSOLUTION

To get the evolution of a concentration in a falling film, the mass balance for dissolved calcite must be coupled to the rate laws given in Eq. 9. In a small volume of water film with thickness *δ*, width *b*, length *dz* and concentration *c*, the mass balance requires:

$$\begin{aligned} &A\alpha_1(c_{app}-c)\,dt = V\,dc = A\delta\,dc\,; c < 0.3c_{eq} \\ &A\alpha_2(c_{eq}-c)dt = Vdc = A\delta dc\,; 0.3c_{eq} < c < 0.9c_{eq} \end{aligned} \qquad 12$$

where A is the surface of the water rock contact (b·dz). Integration of Eq. 12 gives the evolution of concentration in time as the film flows down the fracture wall:

$$c(t) = \begin{cases} 0.3\, c_{eq}(1-e^{-t/\tau_1});\; c < 0.3c_{eq} \\ c_{eq}(1-0.7\,e^{-t/\tau_2}); 0.3c_{eq} < c < 0.9c_{eq} \end{cases} \qquad 13$$

where $\tau_i = \delta/\alpha_i$. Note that τ_1 is more than an order of magnitude smaller than τ_2. The time domain can easily be converted into the space domain using $z = \bar{v}\cdot t$ and $q_f = \bar{v}\cdot\delta$

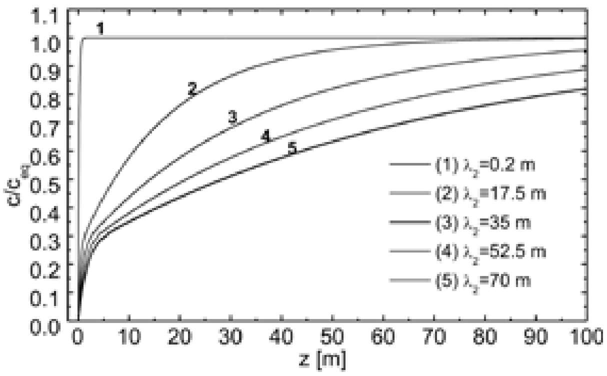

Fig.3: Concentration profile in a film flowing down a smooth vertical fracture and dissolving limestone walls. Values of λ2 are calculated from the fracture flow density obtained if the fracture spacing is 1 m and infiltration intensity is 0.114 mm/h, 10 mm/h, 20 mm/h, 30 mm/h and 40 mm/h for curves 1-5 respectively.

$$c(z) = \begin{cases} 0.3c_{eq}(1-e^{-z/\lambda_1});\; c < 0.3\, c_{eq} \\ c_{eq}(1-0.7\,e^{-z/\lambda_2});\; 0.3c_{eq} < c < 0.9c_{eq} \end{cases} \qquad 14$$

where $\lambda_i = q_f/\alpha_i$. Fig. 3 presents the evolution of saturation ratio c(z)/c_{eq} for different λ_2. For most reasonable scenarios, the first linear kinetics is active only close to the surface. Therefore, it will be integrated directly into the surface lowering (i.e. c(z= 0) = 0.3 c_{eq}).

SATURATION LENGTH λ AND THE FRACTURE FLOW DENSITY

Saturation length λ_2 controls the vertical evolution of concentration profile. It depends on the kinetic constant and the fracture flow density. To estimate the latter we assume that the rain falling to the surface with an intensity q is evenly infiltrated into a regular grid of fractures as shown on Fig. 4. The flow density in each fracture is proportional to the ratio between the surface of the infiltration area and the total breadth of the fractures draining the area. In a regular grid of fractures with fracture spacing d we obtain:

$$q_f = N\cdot q\cdot d\ , \qquad 15$$

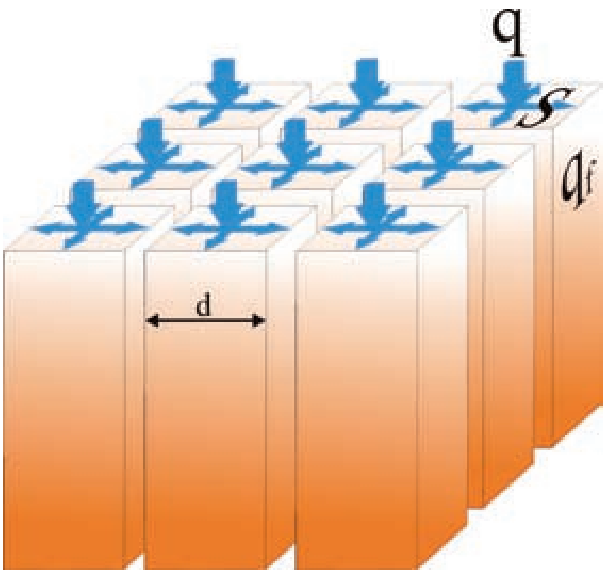

Fig. 4: Rain falling with intensity q [LT-1] is uniformly distributed into the fractures with flow density qf [LT-1] according to Eq.15.

where N depends on the geometry of fracture grid (e.g. ½ for a series of parallel fractures and ¼ for a square grid).

For thin films ($\delta < 0.005$ cm) the rates are controlled by conversion of CO_2 into H^+ and HCO_3- and therefore increase linearly with film thickness. Infiltration intensity below 3 mm/h into a series of fractures with d = 100 cm produces film thicknesses below 0.005 cm. Extremely low infiltration intensities (< 1 mm/h) and fracture spacing in the range of few centimeters result in film thicknesses in the order of 0.001 cm. This reduces the kinetic constant α approximately by a factor of 5. For thin films, the film thickness and α decrease with $q_f^{1/3}$. Consequently λ_2 is proportional to the $q_f^{2/3}$. This has limited consequences for the dissolved volume and denudation rate discussed in the next section.

In the early stages, the fracture flow is not expected to be in the form of a free surface film, but full fracture flow instead. The saturation lengths in that case would be smaller than those derived here. The evolution of such fractures is given in Dreybrodt *et al.* (2005).

RESULTS AND DISCUSSION

Inserting the concentration profile from Eq. 14 (second linear region only) into Eq. 7 gives:

$$\begin{aligned} D &= \frac{q \cdot c_{eq}}{\rho} \int_0^{z_0} (1 - 0.7 e^{-z/\lambda_2})\ dz = \\ &= \frac{qc_{eq}}{\rho} - \frac{0.7qc_{eq}}{\rho} \int_0^{z_0} e^{-z/\lambda_2}\ dz = \qquad 16 \\ &= D_c - 0.7 \cdot D_c \cdot \frac{\lambda_2}{z_0} \cdot (1 - e^{-z_0/\lambda_2}) \end{aligned}$$

Although it is a matter of a definition, the average denudation rate given in Eqs. 8 and 16 are not exactly what we are after. What we look for is the actual lowering of karst surface, which is given by dz_0 / dT_D. We will not go into mathematical details of derivation, but instead discuss its consequences on a plot of z_0(TD). Note that the $z_0(T_D)$ has no explicit form, but its inverse function does:

$$T_D(z_0) = \frac{z_0}{D_c - 0.7 \cdot D_C \cdot \frac{\lambda_2}{z_0}\left(1 - e^{-z_0/\lambda_2}\right)} \qquad 17$$

We will demonstrate the results on a characteristic data for a moderate climate with I=1000 mm/y and relatively bare karst area with c_{eq}= 1mmol/l or H = 100 mg/L. For $\rho = 2.5$ g/cm^3. D_C for this case is 40 m/Ma. We assume that the rain infiltrates into a parallel set of fractures with spacing d = 1 m.

Fig. 5a shows $z_0(T_D)$ for four different saturation lengths arising from different infiltration intensities. Yearly infiltration is 1000 mm/y for all curves. Therefore, the time period of dissolution is inversely proportional to the infiltration intensity. Dashed line shows the uniform lowering by D_C. We wee that all lines become practically parallel to maximum denudation line for $z_0 > 2\lambda_2$.The actual denudation rate becomes "maximal" when the removed thickness is larger than $2\lambda_2$. This is about the depth where the concentration reaches 90% of saturation. The slope of the dotted lines presents the averaged denudation rates for curve with $\lambda_2 = 70$ m.

Fig. 5b shows the averaged rate for the same scenarios as Fig. 5a. Red dashed red curve clearly shows the fast approach of the actual rate to maximal for $\lambda_2 = 52.5$ m.

Another interesting conclusion can be made from Fig. 5a. Different saturation lengths λ can also arise from different fracture spacing (see Eq. 15 for qf) . If we imagine a region with high fracture density within a region of low fracture density, the first will initially be denuded faster, but latter on both actual rates will become the same. Therefore the difference made at the onset will stay projected in the surface. This is shown by the double arrow between lines 3 and 4.

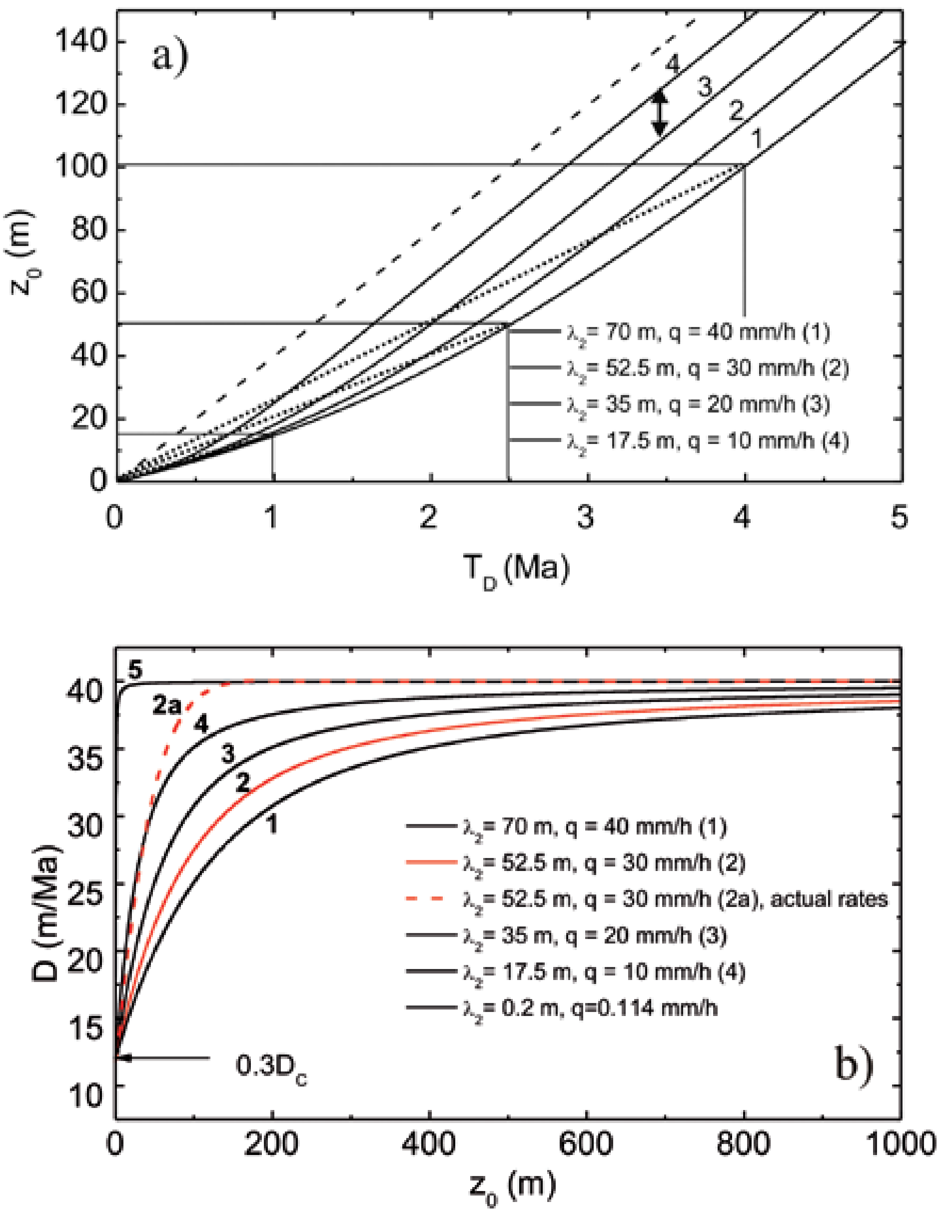

Fig. 5: a) The time dependence of removed thickness for several infiltration intensities. I=1000 mm/y, H = 100 mg/L, $\rho = 2.5$ g/cm^3, d = 100 cm, N = 2. Dashed line show the "maximum denudation" rate which is 40 m/Ma. Dotted lines present the time averaged denudation rates (Eq.16). Double arrow demonstrates the difference between the denuded thicknesses which is kept in time due to the initial rate differences.

b) Dependence of average denudation rates on the removed thickness for the same scenarios as in Fig. 5a. Dashed line presents the actual surface lowering for $\lambda_2 = 52.5$ m.

CONCLUSION

Denudation rate in a block with initially uniform porosity increases as the denudation proceeds and becomes maximum denudation (Eq.1), when the thickness of removed layer is about twice the typical saturation length. Initial differences arising from different saturation lengths remain imprinted in the surface.

If a soluble layer has a finite thickness, the average denudation rate increases with the thickness, i.e. denudation is more effective on thick rock layers.

The presented results are based on many assumptions which might not be valid. Nevertheless, it gives some theoretical validation of maximum denudation formulae and suggest some mechanisms that can cause irregularities in karst surface.

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COBISS: 1.01

VARIATION IN RATES OF KARST PROCESSES

SPREMENLJIVOST HITROSTI KRAŠKIH PROCESOV

Arthur N. PALMER[1]

Abstract UDC 551.44

Arthur N. Palmer: Variation in rates of Karst processes

The development of karst is not a linear process but instead takes place at irregular rates that typically include episodes of stagnation and even retrograde processes in which the evolution toward maturity is reversed. The magnitude and nature of these irregularities differs with the length of time considered. Contemporary measurements in caves show fluctuations in dissolution rate with changes in season, discharge, and soil conditions. Dissolution is sometimes interrupted by intervals of mineral deposition. Observed dissolution rates can be extrapolated to obtain estimates of long-term growth of a solution feature. But this approach is flawed, because as the time scale increases, the rates are disrupted by climate changes, and by variations that are inherent within the evolutionary history of the karst feature (e.g., increased CO_2 loss from caves as entrances develop). At time scales of 10^5-10^6 years, karst evolution can be interrupted or accelerated by widespread fluctuations in base level and surface river patterns. An example is the relation between karst and the development of the Ohio River valley in east-central U.S.A. At a scale of 10^6-10^8 years, tectonic and stratigraphic events cause long-term changes in the mechanism and style of karst development. For example, much of the karst in the Rocky Mountains of North America has experienced two phases of pre-burial Carboniferous karst, mineral accretion during deep burial from Permian to Cretaceous, extensive cave development during Paleocene-Eocene uplift, and stagnation and partial mineral deposition caused by late Tertiary aggradation. At such large time scales, it is difficult to determine rates of karst development precisely, if at all. Instead it is appropriate to divide the evolutionary history into discrete episodes that correlate with regional tectonic and stratigraphic events.

Key words: Karst evolution, dissolution rates, retrograde processes, paleokarst.

Izvleček UDK 551.44

Arthur N. Palmer: Spremenljivost hitrosti kraških procesov

Razvoj krasa ni lineareni proces, pač pa poteka s spremenljivo hitrostjo, značilna so tudi obdobja stagnacije in obdobja, ko je razvoj obrnjen v smeri manj zrele faze. Velikost in narava sprememb sta odvisni tudi od časovnega merila v katerem jih opazujemo. Današnja merjenja v jamah kažejo, da je hitrost raztapljanja odvisna od letnega časa, pretoka in pogojev v prsti. Raztapljanje je občasno prekinjeno z obdobjem izločanja. Izmerjene hitrosti raztapljanja lahko ekstrapoliramo v času in na osnovi tega sklepamo o rasti določene korozijske oblike. Vendar bomo pri tem storili napako, saj merjenja ne vsebujejo dolgočasovnih sprememb. Te so lahko posledica različnih dejavnikov, kot so klimatske spremembe in spremembe, ki nastanejo zaradi samega razvoja krasa (npr. uhajanje CO_2 zaradi odpiranja jamskih vhodov). V časovnem merilu 10^5-10^6 let razvoj krasa prekinjajo ali pospešujejo spremembe erozijske baze in spremembe površinskih vodotokov. Tak primer je povezava med razvojem krasa in doline reke Ohio v vzhodnem delu centralnih ZDA. V časovnem merilu 10^6-10^8 let tektonski in stratigrafski dogodki povzročajo dolgočasovne spremembe v razvoju krasu. Tak primer je kras v Skalnem gorovju v Severni Ameriki. Dvem fazam zakrasevanja v karbonu je sledil pokop in mineralna zapolnitev med permom in kredo. Temu je sledil obširen razvoj jam med paleocensko-eocenskim dvigom ter stagnacija in delna mineralna zapolnitev v poznoterciarni agradaciji. V tako velikem časovnem merilu je težko določiti hitrost razvoja krasa, če sploh. Primerneje je, da razvojno zgodovino razdelimo v obdobja, ki ustrezajo pomembnejšim regionalnim tektonskim in stratigrafskim dogajanjem.

Ključne besede: razvoj krasa, hitrost raztapljanja, procesi nazadovanja, paleokras.

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Received/Prejeto: 27.11.2006

INTRODUCTION

In any discussion of the age of karst, one must consider the rates of the genetic processes and how they vary with time. These are influenced by the length of time over which they have operated. Karst development undergoes large variations in rate and is commonly interrupted by periods of stagnation or even retrograde processes in which mass is accumulated instead of removed. This paper focuses on several field examples that illustrate these processes and the difficulty of quantifying them. These studies are still in progress and are used here only as points for discussion.

SHORT-TERM VARIATIONS IN DISSOLUTION RATE

One approach to interpreting karst history is to measure current rates of bedrock dissolution, for example by applying the mass balance, or by measuring rates of bedrock retreat with micrometers or standardized bedrock tablets. In the two following studies, empirical kinetic equations are applied. On the basis of prior dissolution experiments, field measurements of water chemistry are used to estimate dissolution or accretion rates at specific locations and times.

Field example: eastern New York State

Chemical measurements were made during 1985-1996 in streams of McFail's Cave, New York (Fig. 1; Palmer, 1996). Suitable data-loggers were not available for use in this flood-prone cave, so measurements were made randomly at every opportunity. Although statistically shaky compared to continuous or short-interval sampling, this approach allowed full chemical analyses.

The cave, in Silurian-Devonian limestones, consists of stream passages fed by dolines and ponors. Local soil P_{CO2} is 0.02-0.04 atm, but in this well-aerated cave the mean P_{CO2} of streams is only ~0.003 atm. Most measurements were made in the main passage and were correlated with discharge, but this location was not accessible during high flow. To provide broader coverage, additional measurements were made in similar passages with year-round accessibility. Chemical variations between sampling sites were negligible compared to variations with time. To allow extrapolation, the measurements were combined in a probability plot (Fig. 2), in which SI = log (IAP/K), IAP = $(\mathrm{Ca}^{2+})(\mathrm{CO}_{32-})$, and K = calcite solubility product.

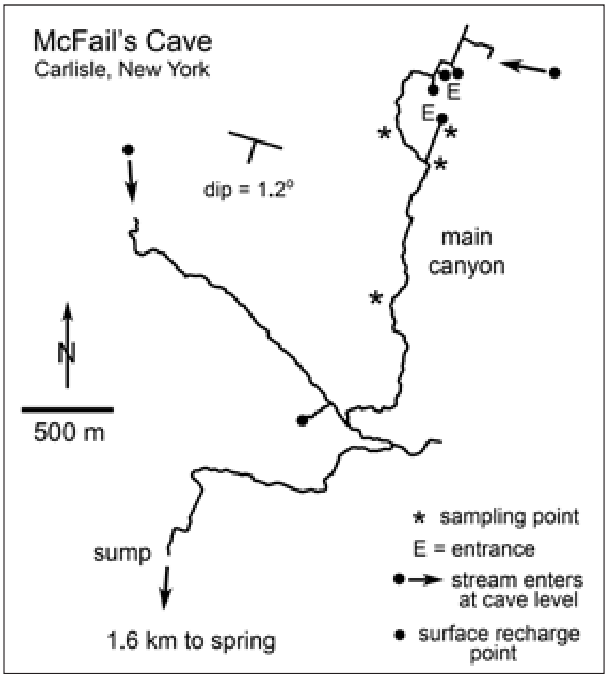

Fig. 1: Map of McFail's Cave, New York, showing location of sampling sites.

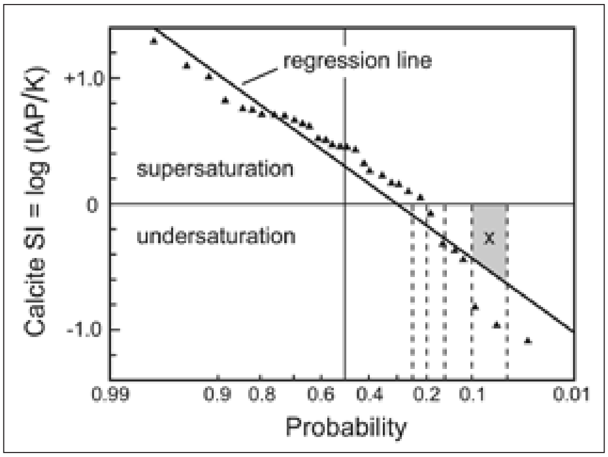

Fig. 2: Probability plot of calcite saturation index in McFail's Cave for the period 1985-1996, where SI = log(IAP/K). Data points are triangles; X = example of probability interval used in Table 1.

Although the passages involved are active canyons, the water is conspicuously supersaturated except during the highest 20-30% of flow. At low flow the calcite SI often exceeds +0.4 (~138% saturation). Calcite can precipitate at approximately SI > +0.2, so why does it not precipitate in the cave at those times?

During a particularly dry summer (1995), a conspicuous calcite layer did accumulate on the canyon floors. This coating averaged 0.3 mm thick with inclusions of clay and quartz silt (Figs. 3 & 4). It was limited to surfaces that remained water-covered during lowest flow and formed a continuous layer in areas of steep gradient (supercritical flow) but only discontinuous patches in ponded water.

Fig. 3: Main stream of McFail's Cave during the summer of 1995, with calcite coating on floor of canyon.

In mid-January, 1996, heavy rain fell on rapidly melting snow and produced a flood with a return period of ~50 years. The main cave entrance was covered by 5 m of water, and smaller inputs contained roaring waterfalls. The calcite SI of the water entering the cave averaged -1.9 (cf. Fig. 2). This sample is not included in the statistics, as it was not random, but obtained purposely at the flood peak, and it is not in the same class as the in-cave samples. However, it illustrates the high dissolutional capacity of extreme floodwater.

The rate of limestone removal can be estimated by

$$S = 31.56\,k\,(1 - C/C_s)_n / \rho \quad \text{cm/yr}$$

(Palmer, 1991), where S = rate of bedrock retreat, k = rate constant (mg-cm/L-sec), n = reaction order (dimensionless), C_s = calcite saturation concentration, C = actual concentration of dissolved calcite, and ρ = rock density (g/cm³). C/C_s is the saturation ratio, where 1.0 represents calcite saturation. From computer analysis, $C/C_s \sim (IAP/K)^{0.35}$. For the cave conditions (mean P_{CO2} = 0.003 atm and T = 8°C), laboratory measurements by Plummer *et al.* (1978) show that k ~0.01 and n ~2.2 at $C/C_s < 0.6$, and k ~0.05 and n ~4 at $C/C_s > 0.6$ in open-system turbulent flow. Bedrock density is ~2.7 g/cm³ in this low-porosity rock.

From chemical measurements during the winter and spring of 1996, it was predicted that the entire calcite coating of 1995 should have been removed by the time the cave became accessible in May. In fact, all but a few sheltered remnants of the calcite had been removed by then. Although mechanical abrasion may have aided the removal in places, the agreement between prediction and result is mild support for the validity of this approach.

Fig. 2 includes a best-fit regression line through the chemical data. Where this line extends below saturation, the probability scale was divided into 5% increments. From the mean SI in each increment, a net dissolution rate of 1.3×10^{-3} cm/yr was calculated for the period of study (Table 1). At that rate, the main cave stream would have deepened about 18 cm since the last glacial retreat in the region about 14,000 years ago. This is compatible with the presence of varved clays no more than a few centimeters above the lowest bedrock floors. The clay was deposited when retreating glaciers blocked the local surface river, flooding the valley and neighboring caves.

Probability range	***Mean C/C_s***	***Mean S (cm/yr)***	***Net annual entrenchment (cm)***
<0.05	~0.52	~0.017	~8.5×10^{-4}
0.05 – 0.10	0.65	0.0064	3.2×10^{-4}
0.10 – 0.15	0.74	0.0019	9.5×10^{-5}
0.15 – 0.20	0.88	8.8×10^{-5}	4.4×10^{-6}
0.20 – 0.25	0.89	7.4×10^{-5}	3.7×10^{-6}
0.25 – 0.30	0.95	2.1×10^{-6}	1.1×10^{-7}
		TOTAL:	**1.3×10^{-3} cm/yr** **13 mm/1000 yrs**

Tab. 1: Net dissolution rate in McFail's Cave canyons, 1985-1996,where the best-fit line in Fig. 2 falls below SI = 0. Entrenchment rates are calculated from the regression line, rather than from specific data points, and provide only a rough approximation.

At the estimated entrenchment rate, the 10 m depth of the main McFail's canyon would have required more than 700,000 years to form. This rate seems low for an active canyon with a gradient of 1.2 degrees, but it is

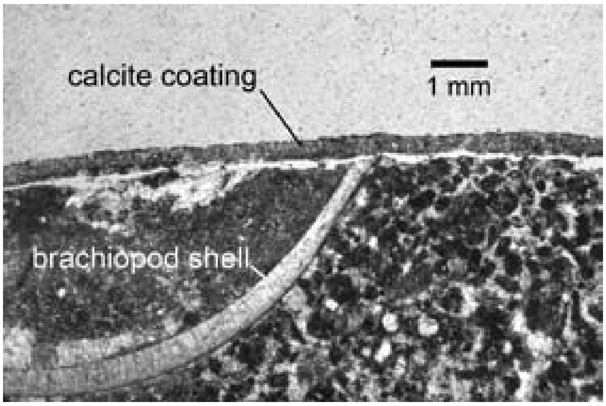

Fig. 4: Thin-section photomicrograph showing calcite crust on a limestone pebble from McFail's Cave (September, 1995).

compatible with U/Th speleothem dates. Related caves at the same elevation as McFail's contain speleothems dated up to 277 ka (Dumont, 1995; Lauritzen & Mylroie, 2000; Mylroie & Mylroie, 2004). Some speleothems were located near the cave floors, so the passages themselves are far older. But the entrenchment rate during this period must have varied because of climate changes and burial beneath glacial ice for several tens of thousands of years. (The only known glaciation in the area was Wisconsinan.) The coarse bedload in parts of the cave also suggests mechanical abrasion during high flow.

The entrenchment rate has probably decreased with time. When entrances were blocked by glacial sediment, or had not yet enlarged enough to form open holes, escape of CO_2 to the surface must have been severely limited and the mean aggressiveness would have been higher than it is today. Also, calcareous glacial deposits cause low-flow inputs to be saturated with calcite before they even reach the cave.

The main canyon of the cave has an entirely vadose origin because it extends exactly down the local dip of the strata, except where it is deflected by joints (Fig. 1). Therefore the canyon originated after surface rivers had entrenched below its level (currently about 300 m above sea level). Although the age of the landscape is difficult to determine from the surface, data from the cave can provide helpful information.

Mammoth Cave, Kentucky

Meiman & Groves (1997), Anthony & Groves (1997), and Groves & Meiman (2005) conducted a similar study in the main river passage of Mammoth Cave, Kentucky. They made a high-frequency record of water levels in monitor wells, combined with periodic measurements of water chemistry. To calculate dissolution rates, they used the kinetic equation described above. Because of thick sediment, cave enlargement rates could not be estimated precisely. However, the authors determined that during the highest 5% of flow, 38% of the mass was removed (vs. about 65% in McFail's). The difference is probably due, at least partly, to the lack of entrances near the sampling sites in Mammoth Cave through which CO_2 is lost, the higher carbonate content of soils in the New York karst, and the dominance of sinking-stream inputs to McFail's Cave during severe floods.

VARIATION IN KARST PROCESSES AT TIME SCALES OF 10^5–10^6 YEARS

The low-relief karst plateaus of Kentucky and Indiana, U.S.A., are developed on early Carboniferous carbonates and include extensive doline fields bordered by sinking streams. These include the Pennyroyal Plateau in Kentucky and the Mitchell Plain in Indiana. They are dissected to a maximum of 50-65 m by river valleys. Near rivers, inter-doline divides and residual flat areas lie 175-190 m above sea level, and up to a few tens of meters higher elsewhere. Although resistant beds form local flat areas, the overall surface is discordant to the strata. The surface is mantled in many places by residual, colluvial, and alluvial sediment up to 30 m thick, the surface of which is concordant with the erosion surface on nearby bedrock. In the Mitchell Plain the deposits are attributed to a widespread Tertiary rise in base level (Palmer & Palmer, 1975). On the Pennyroyal, Ray (1996) calls this relatively flat surface the Green River Strath and attributes it to fluvial processes.

Caves are common in the karst plains and in adjacent sandstone-capped uplands. Mammoth Cave, Kentucky, is the best-known upland example. Its highest passages correlate with nearby low-relief areas of the Pennyroyal (Fig. 5), and passage patterns and gradients show that the Pennyroyal was the source of the cave water (Palmer, 1981). These passages are mostly large canyons filled partly or completely with stream sediment (Fig. 6). Dating of these sediments by cosmogenic radionuclides gives ages up to 4 Ma (Granger *et al.*, 2001), but in areas bordering the Green River (the outlet for Mammoth Cave water), most samples date to ~2.2 Ma (see also Anthony & Granger, 2004, 2006). These passages record a history of slow Tertiary entrenchment interspersed with aggradation, and with a widespread rise in base level of more than 20 m at ~2.2 Ma. The fragmentary sediment surfaces at the same elevation in the Pennyroyal must be correlative. The cause of the widespread aggradation at

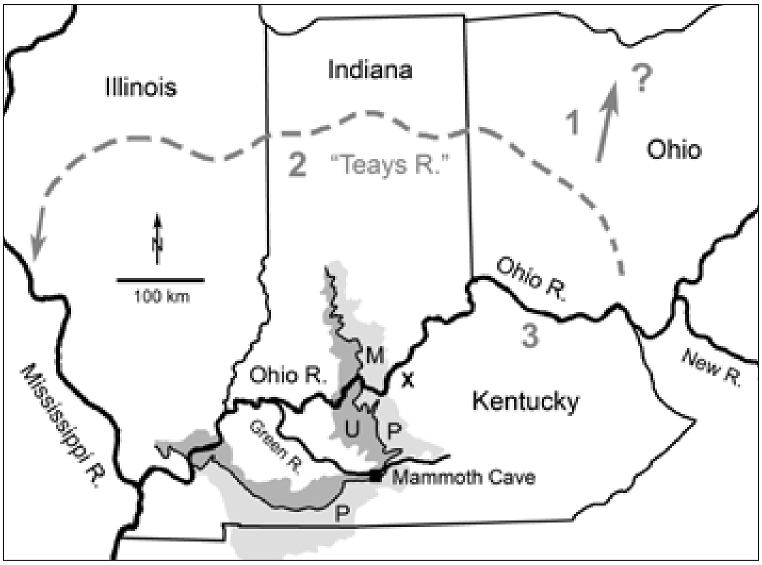

Fig.5: Location of Mammoth Cave and surrounding landscapes. M = Mitchell Plain, P = Pennyroyal Plateau, U = sandstone-capped uplands. X = pre-Pleistocene head of Ohio River. 1, 2, 3 = sequence of drainage from Appalachian Mountains. 1 is probable but entirely hypothetical. 2 = late Tertiary "Teays River," which is well known by its former valley, now filled with glacial sediment. 3 = course of the Ohio River since the early Pleistocene. After Palmer (1981); see also Granger et al., (2001) for explanation.

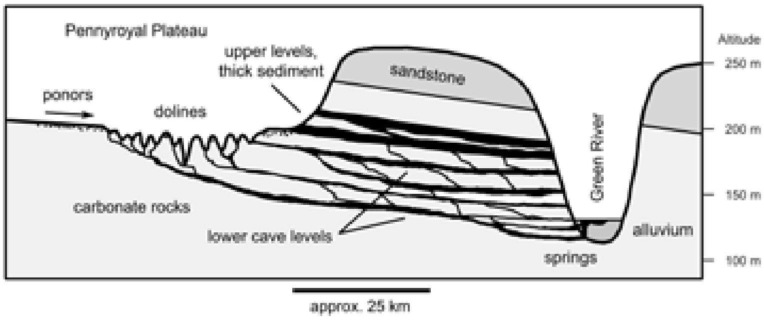

Fig. 6: Simplified cross section through the Pennyroyal Plateau and Mammoth Cave, Kentucky (after Palmer, 1981).

Fig. 7: Typical upper-level passage in Mammoth Cave with detrital sediment fill. This is a former tourist trail that is no longer open to the public. Sediment once filled the passage almost half-way but later subsided into an underlying passage. Note banks of remaining sediment on the left.

2.2 Ma is uncertain. It correlates roughly with the onset of widespread continental glaciation at higher latitudes, but it may relate more directly to a drying climate during the late Pliocene, which would have favored the accumulation of sediments in lowlands.

Pleistocene continental glaciers extended southward as far as northern Kentucky and caused much rearrangement of surface drainage. Initial entrenchment below the uppermost passages in Mammoth Cave may have been triggered by the establishment of drainage from the Appalachian Mountains westward to the Mississippi River, to form the so-called "Teays River" (Fig. 7; see Granger *et al.,* 2001). Later, the previously tiny Ohio River became one of the largest rivers on the continent when the Teays was diverted into it (Fig. 7). These shifts enhanced the rate of river entrenchment into the sediment-mantled plains of carbonate rock. Subsurface karst drainage developed and the surfaces became "sinkhole plains." Pleistocene cave passages formed at various levels as much as 60-70 m below the Tertiary passages. Again, caves provide clues to the interpretation of surface landscapes that cannot be discerned from surface observations alone.

Could the karst plateaus have retained vestiges of their original flat surface for 2 Ma without significant lowering? Although dolines extend deeply into them, nearly flat remnants of the sediment-covered and resistant bedrock surfaces remain at approximately the same elevations as the sediment in the upper-level passages of Mammoth Cave, which suggests that parts of the original surface have survived with little or no lowering.

What is the current karst denudation rate? Much of the Mammoth Cave area is drained by the Turnhole Spring basin, which has an area of 220 km^2 (Quinlan *et al.*, 1983). In this basin, Hess (1974) measured a mean-annual Ca content of ~60 mg/L and Mg of ~7.5 mg/L (see also Hess & White, 1993). These measurements represent a mean dissolved load of ~0.044 cm^3/L calcite and ~0.020 cm^3/L dolomite (with the simplifying assumption that dolomite = Mg and calcite = Ca – Mg, in moles/L). The annual precipitation is 1.26 m/yr, and about 2/3 of it lost to evapotranspiration, so a 220 km^2 basin would have a mean runoff of roughly 9 x 10^7 m^3/yr. The loss of carbonate rock is therefore about 6000 m^3/yr. Roughly half of the basin consists of exposed carbonates, so the denudation rate on that half is about 5.5 cm/1000 years. This figure corresponds to some of the lowest measured rates of carbonate denudation elsewhere (Ford & Williams, 1989, p. 112–117). Transport of solids is neglected, as is subsurface dissolution. The Mammoth Cave System represents a maximum porosity of about than 4%, even in areas of maximum passage density (Palmer, 1995).

When the denudation rate is extrapolated to 2 million years, it indicates an overall lowering of the soluble Pennyroyal surface of roughly 100 m. This is impossible, because it exceeds the total relief between the original surface and the Green River. There is no doubt that most of the surface has been lowered (Fig. 6), but there were evidently long periods of stagnation, especially at the beginning, when large parts of the surface were mantled with thick sediment. Most of the denudation is in the form of doline growth. Gams (1965) points out that corrosion accelerates in dolines as they grow, because of enhanced CO_2 production in their thickening soils. Apparently the rate of karst denudation is higher today than during the early Pleistocene.

KARST DEVELOPMENT AT TIME SCALES OF 10^7–10^8 YEARS

Karst that evolves throughout entire geologic periods or eras tends to do so in discontinuous steps in which lengthy episodes of stagnation exceed those of active karst processes. For example, certain karst areas of the Rocky Mountains and Black Hills (western U.S.A.) have undergone at least 7 different stages over the past 350 my but were actively forming only about 20% of that time. Jewel and Wind Caves in South Dakota are good examples (Fig. 8). With mapped lengths of 218 and 196 km, they are among the most complex caves in both pattern and diversity of geologic history. Each successive set of features was superposed on the previous ones, because each provided favorable sites for those that followed. Osborne *et al.* (2006) describe a similarly complex history in the Jenolan Caves of Australia.

The major stages of karst development in the Black Hills are outlined below (Palmer & Palmer, 1989, 1995):

1. Early Carboniferous carbonates of the Madison Formation were deposited on a low-gradient continental shelf. Interbedded sulfates were included in the middle and upper Madison.

2. Brecciation and early voids formed by dissolution and reduction of sulfates, plus production of sulfuric acid (Fig. 9). Sulfate rocks were almost completely removed.

3. A mid-Carboniferous karst formed throughout much of western North America (Sando, 1988). Surface features included fissures and dolines up to 30 m deep. Caves concentrated at 20-50 m below the surface along former sulfate zones and intersect earlier breccias and caves (Fig. 10). Comparison with modern caves suggests some freshwater-saltwater mixing dissolution.

4. The karst was buried by late Carboniferous detrital sediment, and most caves were completely filled. The sedimentary burial continued through the Cretaceous to a depth of

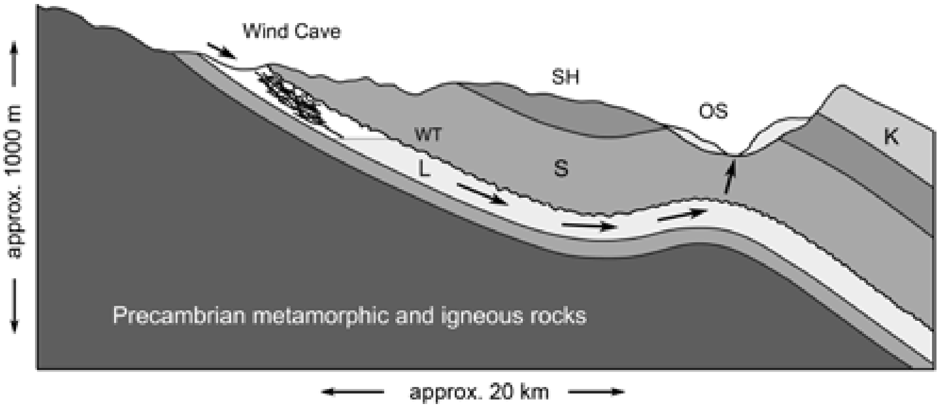

Fig. 8: Geologic setting of Wind Cave, South Dakota. L = Madison Limestone (early Carboniferous) underlain by thin Cambrian sandstone, S = late Carboniferous sandstone, SH = mainly shale, K = Cretaceous sandstone, OS = Oligocene sediment (mainly siltstone, widely eroded). The upper surface of the Madison is irregular paleokarst. WT = water table in lowest passage of Wind Cave. The cave extends only a few meters below the water table. Arrows show dominant flow pattern of today.

Fig. 9: Early solution voids and brecciation related to early Carboniferous sulfate-carbonate interactions in Jewel Cave, South Dakota. These are exposed by collapse of wall of a later cave. Height of photo is about 2 m.

at least 2 km. Buried caves and vugs, as well as voids in the Carboniferous sediment, were lined by white scalenohedral calcite about 1-2 cm thick (Fig. 11). Pre-burial voids can be recognized by this distinctive coating. Along faults, surfaces were coated by euhedral quartz up to a 5 mm thick.

Fig. 10: Mid-Carboniferous paleokarst, Bighorn Mountains, Wyoming. Caves in cliff were once filled with late Carboniferous sediment, but much of it has been removed by weathering and stream erosion.

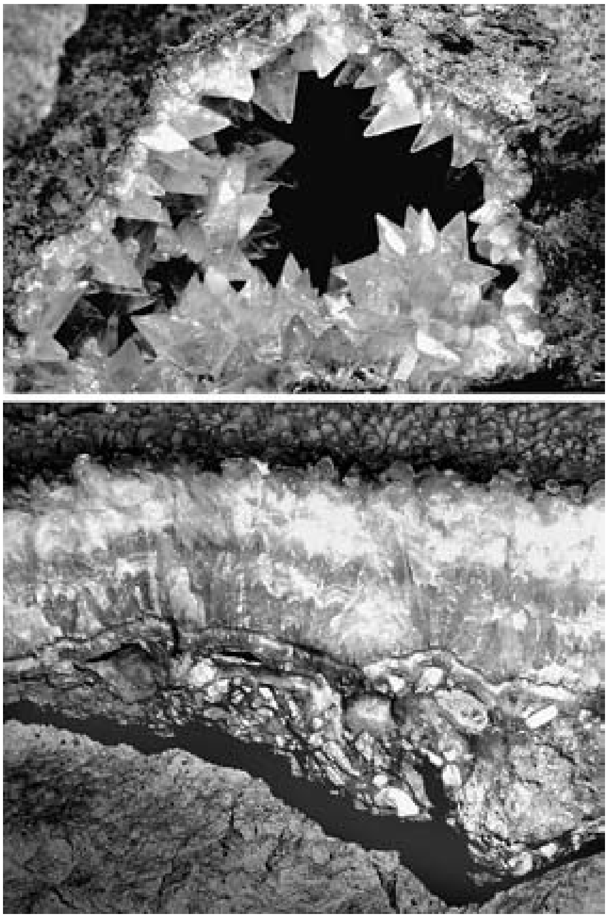

Fig. 11: Top: Scalenohedral calcite coating of Mesozoic age on walls of Carboniferous vug, Wind Cave (crystal length ~1.5 cm). Bottom: Rhombohedral calcite coating of late Tertiary age on weathered walls of an early Tertiary passage, Jewel Cave (maximum thickness of calcite = 15 cm).

6. The Black Hills and Rocky Mountains were uplifted by the Laramide orogeny (latest Cretaceous through Eocene; Fig. 8). The climate was more humid than today's, and the present topography above the caves was formed by the end of the Eocene. Enhanced groundwater flow enlarged earlier caves to their present form (Fig. 12). Their layout shows evidence for mixing between shallow and deep water (Palmer and Palmer, 1989), although Bakalowicz *et al.* (1997) suggest a purely thermal origin.

7. The caves drained and were exposed to subaerial weathering, which produced thick carbonate deposits in many passages.

8. Most of the Eocene landscape was buried by Oligocene sediments during a drying of the climate. Although much of this sediment has been removed by later

erosion, the Eocene landscape on the resistant Paleozoic-Mesozoic rocks has survived almost intact, as have the underlying caves, thanks to the present semi-arid climate.

9. Partial blockage of springs by Oligocene sediments caused a second phase of calcite coating (mainly rhombohedral) averaging 15 cm thick in Jewel Cave (Fig. 11) but thinner in Wind Cave. The earlier scalenohedral coating is still visible in pockets and vugs that were isolated from the cave development and exposed by later breakdown.

In this sequence there is little information about developmental rates. Instead, the karst history is portrayed as a series of discrete episodes, which span a wide range of processes, groundwater conditions, tectonic relationships, and levels of diagenetic maturity of the host strata. All effects have overlapped, and in some caves it is possible to stand in a single spot and distinguish every phase of their history.

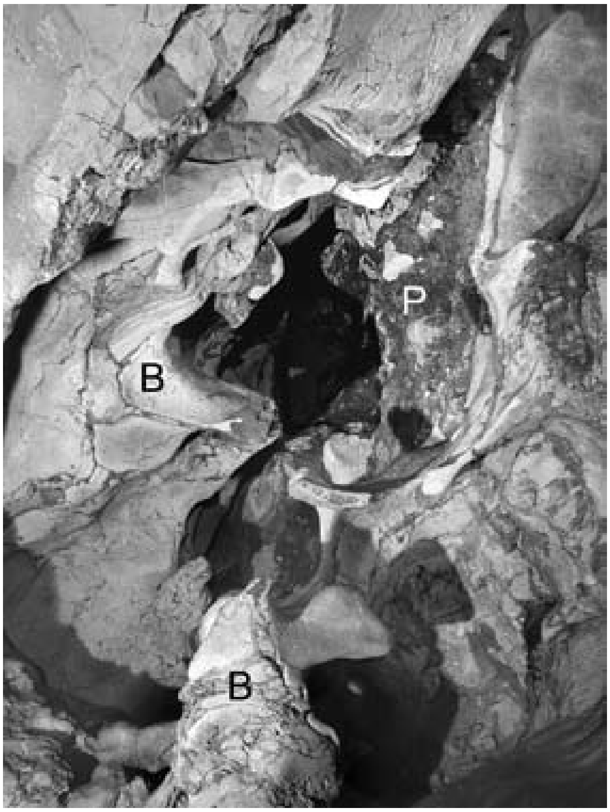

Fig. 12: Typical cave passage of Eocene age in Wind Cave, showing remnants of earlier breccia (B) and paleo-fill (P).Height of photo is about 2 m.

CONCLUSIONS

Karst processes operate at rates that vary considerably with time, and the magnitude of that variation is generally greater as the developmental time span increases. At every time scale, the developmental history of karst (at least in the examples described here) includes episodes of stagnation and of retrograde development when material is deposited instead of removed.

Modern measurements of the rates of karst processes can be extrapolated into the past, but this extrapolation becomes more suspect as the time span increases. Over the entire growth history of major cave systems (usually 10^6-10^7 years), many disruptions in rate are caused by changes in climate, base level, and river patterns. At time scales of 10^7-10^8 years, interpretation of evolutionary rates becomes difficult, and the history of karst is usually subdivided into discrete episodes, in the same manner as tectonic and sedimentary events.

As a karst feature develops toward maturity, it tends to undergo inherent changes in developmental rate. For example, a cave may decrease in enlargement rate as entrances open and enlarge, allowing greater rates of CO_2 loss. Rates of karst development may increase with time as dolines develop and enlarge, owing to greater exposure of soluble rock and accumulation of high-CO_2 soils in depressions.

It is impossible to interpret caves and karst without a solid understanding of their surrounding geology and physiography. But, despite uncertainties about their rates of development, karst features can provide more information about the surrounding landscape than vice versa.

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COBISS: 1.01

TIME SCALES IN THE EVOLUTION OF SOLUTION POROSITY IN POROUS COASTAL CARBONATE AQUIFERS BY MIXING CORROSION IN THE SALTWATER-FRESHWATER TRANSITION ZONE.

ČASOVNO MERILO RAZVOJA POROZNOSTI ZARADI KOROZIJE MEŠANICE V MEJNEM OBMOČJU SLADKOVODNIH LEČ V MEDZRNSKO POROZNEM KARBONATNEM OBALNEM VODONOSNIKU

Wolfgang DREYBRODT[1] & Douchko ROMANOV[2]

Abstract UDC 556.3:552.54:539.217

Wolfgang Dreybrodt and Douchko Romanov: Time scales in the evolution of solution porosity in porous coastal carbonate aquifers by mixing corrosion in the saltwater-freshwater transition zone.

Dissolution of calcium carbonate in the saltwater-freshwater mixing zone of coastal carbonate aquifers up to now has been treated by coupling geochemical equilibrium codes to a reactive-transport model. The result is a complex nonlinear coupled set of differential transport-advection equations, which need high computational efforts. However, if dissolution rates of calcite are sufficiently fast, such that one can assume the solution to be in equilibrium with respect to calcite a highly simplified modelling approach can be used. To calculate initial changes of porosity in the rock matrix one only needs to solve the advection-transport equation for salinity s in the freshwater lens and its transition zone below the island. Current codes on density driven flow such as SEAWAT can be used. To obtain the dissolution capacity of the mixed saltwater-freshwater solutions the calcium equilibrium concentration $c_{eq}(s)$ is obtained as a function of salinity by PHREEQC-2. Initial porosity changes can then be calculated by a simple analytical expression of the gradient of the spatial distribution s(x, y) of salinity, the distribution of flow fluxes q(x,y) and the second derivative of the calcium equilibrium concentration $c_{eq}(s)$ with respect to salinity s.

This modelling approach is employed to porosity evolution in homogeneous and heterogeneous carbonate islands and coastal aquifers. The geometrical patterns of porosity changes and the reasons of their origin will be discussed in detail. The results reveal initial changes of porosity in the order of several 10^{-6} per year. This places the time scale of cavern evolution to orders from several tens of thousands to a hundred thousand years.

Keywords: Calcite dissolution, mixing corrosion, saltwater-freshwater, mixing zone, coastal aquifer, evolution of porosity.

Izvleček UDK 556.3:552.54:539.217

Wolfgang Dreybrodt and Douchko Romanov: Časovno merilo razvoja poroznosti zaradi korozije mešanice v mejnem območju sladkovodnih leč v medzrnsko poroznem karbonatnem obalnem vodonosniku

Dosedanji modeli raztapljanja kalcijevega karbonata v območju mešanja sladke in slane vode temeljijo na združitvi geokemičnih ravnotežnih in reakcijsko transportnih modelov. Dobljeni sistem nelinearnih enačb zahteva veliko računske moči. Če je hitrost raztapljanja dovolj visoka in lahko predpostavimo, da je raztopina ves čas v ravnotežju glede na kalcit, rešimo problem z poenostavljenim modelskim pristopom. Začetno spreminjanje poroznosti v kamninski matriki določa advekcijsko tranportna enačbo, ki opisuje slanost v sladkovodni leči in prehodnem območju pod njo. Pri reševanju porabimo dostopne programske kode. Tokove nastale zaradi razlik v gostoti modeliramo s programom SEAWAT, topnost kalcita v mešanici sladke in slane vode v odvisnosti od slanosti pa izračunamo s programom PHREEQC-2. Začetno spreminjanje poroznosti lahko nato izračunamo z enostavnim analitičnim izrazom gradienta prostorske razporeditve slanosti s(x,y), razporeditve gostot toka q(x,y) in drugega odvoda ravnotežne koncentracije kalcija po slanosti.

Tak modelski pristop uporabimo pri računanju razvoja poroznosti v homogenih in heterogenih karbonatnih otokih in obalnih vodonosnikih. Podrobno so prikazani vzroki in geometrijski vzorci spreminjanja poroznosti. Rezultati kažejo, da je začetna hitrost spremembe poroznosti reda velikosti 10^{-6} na leto. To postavi časovno merilo razvoja jam v območje nekaj deset tisoč do sto tisoč let.

Ključne besede: Raztapljanje kalcita, korozija mešanice, območje mešanja sladke in slane vode, obalni vodonosnik, razvoj poroznosti.

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Received/Prejeto: 21.12.2006

INTRODUCTION

Carbonate islands consisting of porous rocks show typical karst features characterized by large dissolution chambers close to the coast, which have been created by mixing corrosion in the fresh-saltwater transition zone (Mylroie and Carew, 2000). Figure1 represents the basic concept. Due to meteoric precipitation a freshwater lens builds up, floating on the denser saltwater (Vacher, 1988) The transition from freshwater to seawater is not sharp. Depending on many factors, such as tidal pumping, periodicity of annual recharge, and the heterogeneity of the rock's properties in the aquifer it exhibits a transition zone. This zone can range from a few meters to half the depth of the lens. In this zone mixing between saltwater and freshwater activates mixing corrosion, which creates large chambers. These are called flank-margin caves. Figure 2 shows such a cave with its typical solutional features on its ceiling.

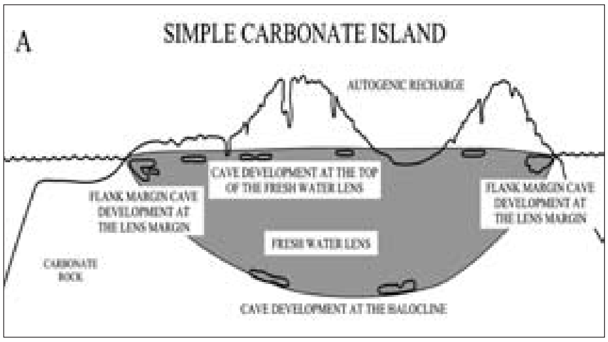

Fig. 1: Conceptual representation of a carbonate island from Mylroie and Carew (2000).

Fig. 2: Flank-margin cave.

When seawater mixes with a solution of H_2O-CO_2-$CaCO_3$ saturated with respect to $CaCO_3$ the mixture is no longer in equilibrium with respect to calcite. Depending on the chlorine concentration s, termed as chlorinity further on, of the mixture undersaturation or supersaturation may result. Figure 3 gives an example. It depicts the difference $\Delta c_{eq}(s) = c_{eq}(s) - c_{mix}(s)$ of the calcium concentration $c_{mix}(s)$ of the mixture and that of its corresponding equilibrium concentration $c_{eq}(s)$ as a function of s. This is the amount of calcium, which can be dissolved or precipitated, when the mixed solution is in contact with carbonate rock. The H_2O-$CaCO_3$-CO_2 solution used to calculate this data is in equilibrium with a partial pressure of CO_2 of 0.01 atm at a temperature of 20°C. The seawater also is at 20°C. The data in Fig. 3 were obtained by use of the code PHREEQC-2 (Parkhurst and Apello, 1999).

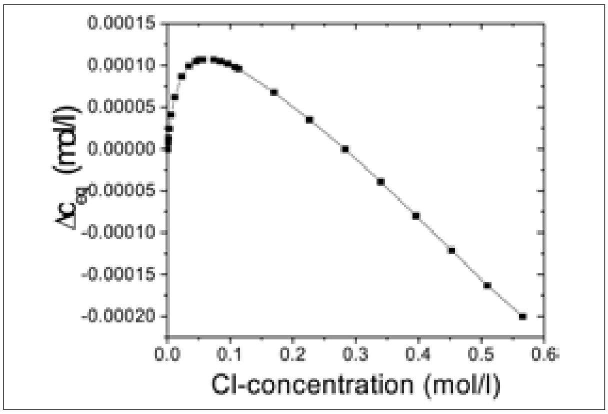

Fig. 3: $\Delta c_{eq}(s) = c_{eq}(s) - c_{mix}(s)$ as a function of chlorine concentration. The curve extends from pure freshwater (right) to pure seawater (left).

From Figure 3 it is evident that mixtures with low content of seawater, chlorinity s ≤ 0.3 mol/ℓ, can dissolve calcite, whereas mixtures with higher chlorinity may precipitate calcite. Renewed aggressivity due to mixing therefore occurs only at the freshwater side of the mixing zone where chlorinity is low. If one assumes that dissolution of calcite proceeds sufficiently fast the solution there will be saturated with respect to calcite.

Dissolution of minerals under such conditions is termed a gradient reaction (Phillips, 1991). Here we use this as a novel instrument to explain the evolution of porosity in carbonate islands. Dissolution rates of limestone are sufficiently fast, such that after mixing between saltwater and freshwater we assume saturation with respect to calcite in the entire lens.

After attaining equilibrium the local distribution of calcium concentration $c_{eq}(s(x,z))$ becomes stationary and exhibits gradients. Necessarily advection and diffusion must transport the dissolved limestone to the outflow of the aquifer.

DISSOLUTION IN THE MIXING ZONE

The advection term:

In Figure 4 we consider a volume element dxdydz at position (x,y,z), into which flow, with components q_x and q_z, enters perpendicular to dydz or dxdy. The flux q is defined by the volume of fluid per time unit entering through a unit of surface area and is given in [$cm^3/(cm^2s) = cms^{-1}$].

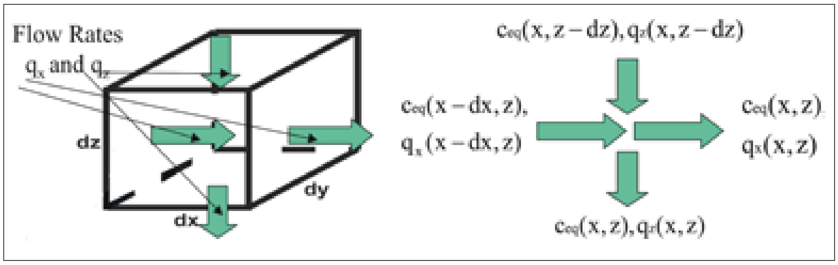

Fig. 4: Mass balance for the advection term.

The component q_x transports solution from the neighbouring elementary cell at position (x-dx, y,z) via the area dydz into the cell dxdydz. This solution has already attained equilibrium c_{eq}(s(x-dx,y,z)) at position x-dx. When it enters into the volume element dxdydz it must dissolve or precipitate limestone to adjust its calcium concentration to equilibrium c_{eq}(s(x,y,z)) at position x. On the other hand solution from the element dxdydz flows out into the neighbouring cell with flux q_x(x,y,z). Mass conservation requires that the amount of limestone dissolved per time unit in the element dxdydz must be equal to the difference of mass transported into the cell and that transported out of it. From this one finds

$$\frac{(q_x(x,z)\cdot c_{eq}(x,z) - q_x(x-dx,z)\cdot c_{eq}(x-dx,z))dydz}{dxdydz} = Q_x \qquad (1)$$

An analogue equation exists for Q_z the amount of limestone dissolved by the flux component q_z entering via the surfaces (dx,dy).

$$\frac{(q_z(x,z)\cdot c_{eq}(x,z) - q_z(x,z-dz)\cdot c_{eq}(x,z-dz))dxdy}{dxdydz} = Q_z \qquad (2)$$

Therefore

$$Q_{adv} = Q_x + Q_z = \vec{q}\cdot grad(c_{eq}(s(x,z)) + c_{eq}(s(x,z)\cdot div\vec{q} \qquad (3)$$

Because the flux q follows the Darcy law of incompressible fluids, $div(\vec{q})=0$.

$$Q_{adv} = \vec{q}\cdot grad(c_{mix} + \Delta c_{eq}) \qquad (4)$$

whereby we have replaced $c_{eq} = c_{mix} + \Delta c_{eq}\cdot c_{mix}$ is the calcium concentration resulting from the mixing of seawater and freshwater and is a linear function of Cl-concentration s.

$$c_{mix} = c_{fresh} + (c_{sea} - c_{fresh})\cdot\frac{s}{s_{sea}} \qquad (5)$$

Δc_{eq} is the increase of equilibrium concentration as given in Figure 3, s_{sea} is chlorinity of seawater.

The diffusion term:

Our mass balance so far, however, is incomplete because gradients of c_{eq} cause transport by diffusion. The rate Q_D of mass transport by diffusion is given by

$$Q_D = -\varnothing\cdot D\vec{\nabla}^2(c_{mix} + \Delta c_{eq}) \qquad (6)$$

where D = qd/Φ + D_m is the coefficient of dispersion. Φ is the porosity of the rock and d its grain size. (Phillips, 1991). Dm is the constant of molecular diffusion (10^{-5}cm s^{-1}).

The total rate:

The total dissolution rate Q_{tot} is then given by Q_D+Q_{adv}.

$$Q_{tot} = \vec{q}grad(c_{mix}) - \varnothing D\vec{\nabla}^2(c_{mix}) + \vec{q}grad(\Delta c_{eq}) - \varnothing D\vec{\nabla}^2(\Delta c_{eq}) \quad (7)$$

Due to the linearity of c_{mix} with salinity s (eqn. 5) one finds grad(c_{mix}) proportional to grad(s).

The distribution of salinity is governed by the advection-diffusion equation

$$\partial s/\partial t = \vec{q}grads - \Phi D(\vec{\nabla})^2 s = 0\,, \qquad (8)$$

because the distribution s is stationary. From the linearity of s with c_{mix} we have

$$\partial c_{mix}/\partial t = \vec{q}grad c_{mix} - \varnothing D(\vec{\nabla})^2 c_{mix} = 0\,, \qquad (9)$$

The total dissolution rate Q_{tot} is given by the master equation

$$Q_{tot} = \vec{q}grad(\Delta c_{eq}) - \varnothing D\vec{\nabla}^2(\Delta c_{eq}) \qquad (10)$$

Since Δc_{eq}(s(x,z)) is a function of local distribution s(x,z) by differentiating and using the chain rule, one finds using equation 8

$$Q_{tot} = -\varnothing(\mathrm{qd}/\varnothing + \mathrm{D_m})\cdot(\vec{\nabla}s(x,z))^2\,\frac{\partial^2\Delta c_{eq}}{\partial s^2} \qquad (11)$$

This master equation relates the amount of dissolved material per unit volume of the rock matrix [mol cm^{-3} s^{-1}]

to the gradient of salinity s, to the second derivative of $c_{eq}(s) = c_{mix}(s) + \Delta c_{eq}(s)$, and the flux q. $\partial^2 \Delta c_{eq} / \partial s^2$ can be obtained by differentiating twice the data set of Figure 3. This data set was obtained by using the program PHREEQC2 and calculating about 50 closely spaced points to avoid numerical errors, when differentiating twice. The result is shown in Figure 5.

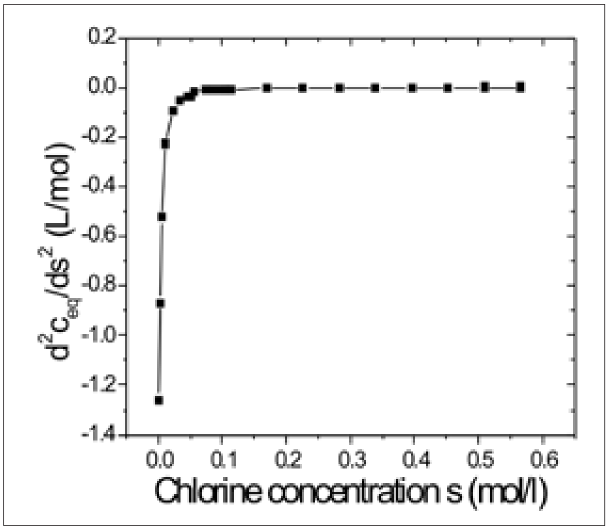

Fig. 5: Second derivative $\dfrac{\partial^2 c_{eq}}{\partial s^2}$.

The function $\left|\Delta s(\vec{x})\right|^2$ and the flow distribution $\left|\vec{q}(x)\right|$ can be obtained by the numerical hydrologic model SEAWAT, as will be shown in the next sections. To calculate the initial change of porosity it is sufficient to obtain the flux and salinity distribution of an island without considering calcite dissolution, because the time to establish a stationary state of the lens is in the order of 100 years. It is a good approximation to assume that during this time the change of porosity is insignificant.

Equation. 11 can be written in terms of the change of porosity as

$$\frac{\partial \phi}{\partial t} = \frac{M}{\rho} Q_{tot} = -\O D(\vec{\nabla} s(x,z))^2 \frac{\partial^2 \Delta c_{eq}}{\partial s^2} \frac{M}{\rho} \quad (1/\mathrm{s}) \qquad (12)$$

M = 100 g/mol is the molecular weight at $CaCO_3$, ρ=2.7 g/cm^3 is the density of compact $CaCO_3$. Q_{tot} the mass of $CaCO_3$ dissolved per time from a unit volume of the rock matrix is given in mol s^{-1} cm^{-3}. $\partial \phi / \partial t$ is the amount of volume dissolved per time from a unit volume of the rock matrix (cm^{3}s^{-1}/cm^3). By use of equation 12 it is now possible to construct a conceptual frame for the evolution of porosity. Tests of this approach on simple benchmark models have shown its reliability and have found agreement to experimental data (Romanov and Dreybrodt, 2006).

INITIAL CHANGES OF POROSITY IN A HOMOGENEOUS ISLAND.

To obtain the initial distributions of flux q and chlorinity s in the lens of a carbonate island we have used SEAWAT by USGS (Guo and Langevin, 2002). The modeling domain is shown in Figure 6. The island is a strip of 1 km width. Porosity Ø and the hydraulic conductivity K are uniform ($\O = 0.30, K = 10\, m/day$). The transversal dispersivity is a_T = d = 0.01 cm, the longitudinal dispersivity is a_l = 0.1 cm. Infiltration is $3 \cdot 10^{-3}$m/day =1.11m/year. This way the maximal depth of the lens is about 50 m below sea level. The lower border of the domain reaches down to 70 m. At that boundary an impermeable layer imposes no-flow conditions. The grid size in the domain is 1 m x 1 m in the part below sea level. In the part above sea level (2 m) the grid size is 0.2 m by 1 m. In its initial state when the island emerges out from the sea the entire aquifer is filled with seawater. When the island receives recharge from meteoric freshwater the lens builds up. A stable stationary lens is obtained after about 30 years. Fig.7 shows the results of the model run.

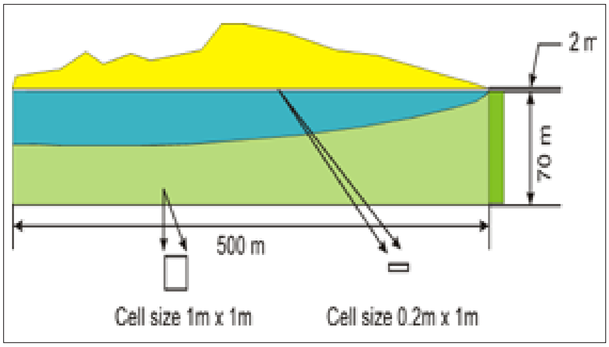

Fig. 6: Modeling domain of a carbonate island.

Figure 7a shows the freshwater lens (white), the transition zone and its distribution of Cl-concentration by a color code. From this distribution of chlorinity one can extract the scalar value $\left|\vec{\nabla} s(\vec{x})\right|^2$ and $\partial^2 c_{eq}(s(\vec{x})) / \partial s^2$. Figure 7b shows the chlorinity in units normalized to its maximum value along several horizontal sections as depicted in Figure 7a. The lowest section at -68 m is entirely in saltwater with maximum Cl-concentration. The section at -55 m extends through the almost horizontal base of

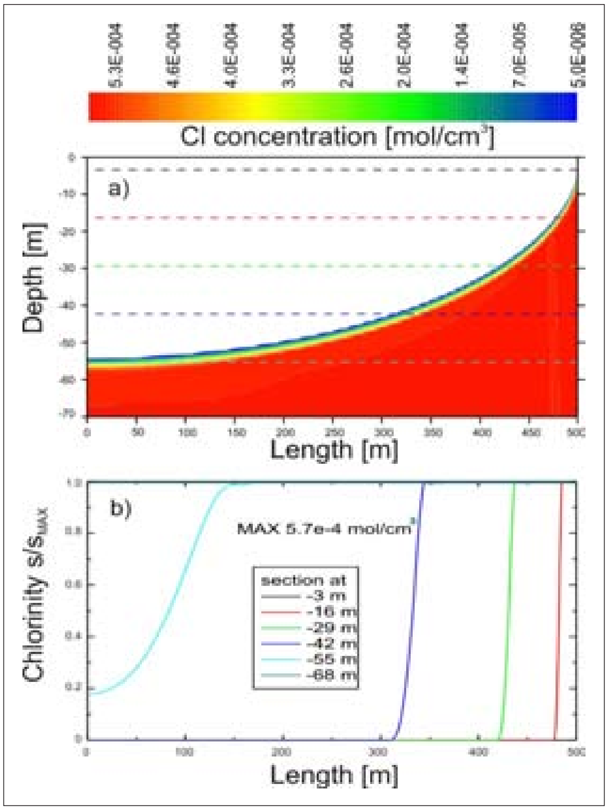

Fig. 7: Homogeneous island. a) Local distribution of chlorinity $s(\vec{x})$*. The white region designates the freshwater lens. b) chlorinity along horizontal sections as indicated in a).*

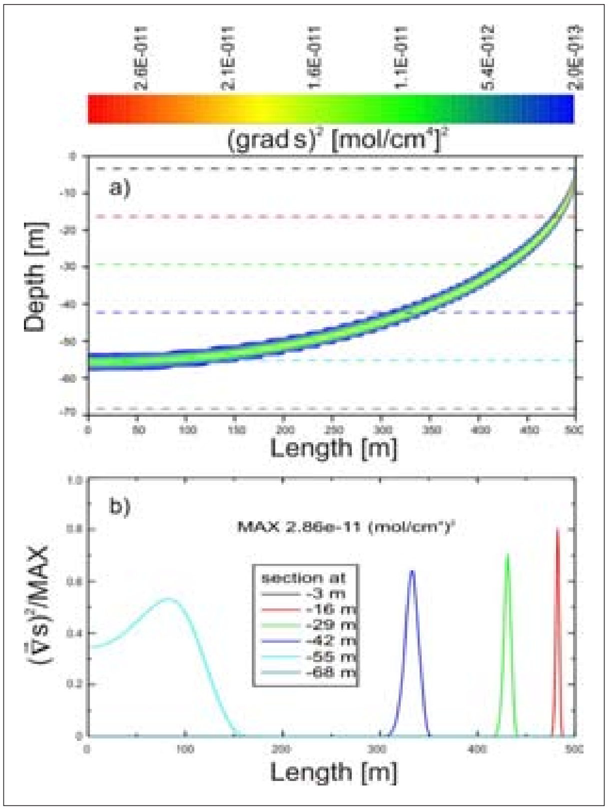

Fig. 8: Homogeneous island. a) Local distribution of the square of gradients $|\vec{\nabla}s(\vec{x})|^2$*, b) square of gradients along horizontal sections as indicated in a).*

the lens and shows a wide zone where the concentration raises to that of seawater. The upper sections cut through the mixing zone and there the rise in concentration from freshwater to seawater becomes steeper.

The square of the gradient $|\vec{\nabla}s|^2$ is shown by Figures 8a,b also normalized to its maximum value in Figure 8b. Figure 8a illustrates its local distribution, which exhibits large values only in the region of the transition zone. The horizontal distribution along horizontal sections is depicted in Figure 8b.

The second derivative $\partial^2 c_{eq}(s(\vec{x}))/\partial s^2$ obtained from the Cl-concentration in Figure 7a is given in Figure 9a. Its distribution is limited to that part of the transition zone with $0 < s < 0.03$ mole/ℓ. See Figure 5. This corresponds to a narrow fringe at the freshwater side of the transition zone with seawater content from zero up to about 4%. In any case creation of porosity is possible only in this restricted region. Figure 9b for completeness depicts some distributions of $\partial^2 c_{eq}(s(\vec{x}))/\partial s^2$ along horizontal sections.

To calculate the initial rate of change in porosity (conf. eqn 12) the Darcy fluxes q must be known. They are also obtained from the model run and shown in Fig 10. The flux is low in the center of the island $q \le 1$ m/year), but increases by orders of magnitude when the fluid moves coastward, where it becomes about 0.2 m/day at the outflow.

The dispersion coefficient $D = qd/Ø + D_m$ (conf. eqn. 11) depends on the flux q, but also on the coefficient of molecular diffusion $D_m=10^{-5}$ cm²/s. For low flux $q<10^{-4}$ cms^{-1} and particle diameters $d \le 10^{-2}$ cm dispersion is dominated by molecular diffusion. In the following scenarios we have used $d=10^{-2}$ cm, a realistic value in porous limestone. Therefore in the range of flux, which can be read from Figure 10b the dispersion coefficient in the center of the island is $D=10^{-5}$ cm²s^{-1}. It increases by about 60% of this value at the coast.

From the data given in Figures 7a, 8a, and 9a the initial porosity is obtained by use of eqn. 12. Figure 11 illustrates these results. Changes in porosity are restricted to a small fringe in the transition zone and are fairly even along it. They are in the order of 10^{-6} year^{-1}. This is sufficient to create substantial porosity within 100,000 years. At the outflow flank margin caves can develop in 10,000 years. One has to keep in mind, however, that the approximation as a homogeneous island is a high idealization. Any disturbances, which increase the width of the transition zone, will reduce the gradients of chlorinity and therefore on more realistic settings the initial porosity changes accordingly.

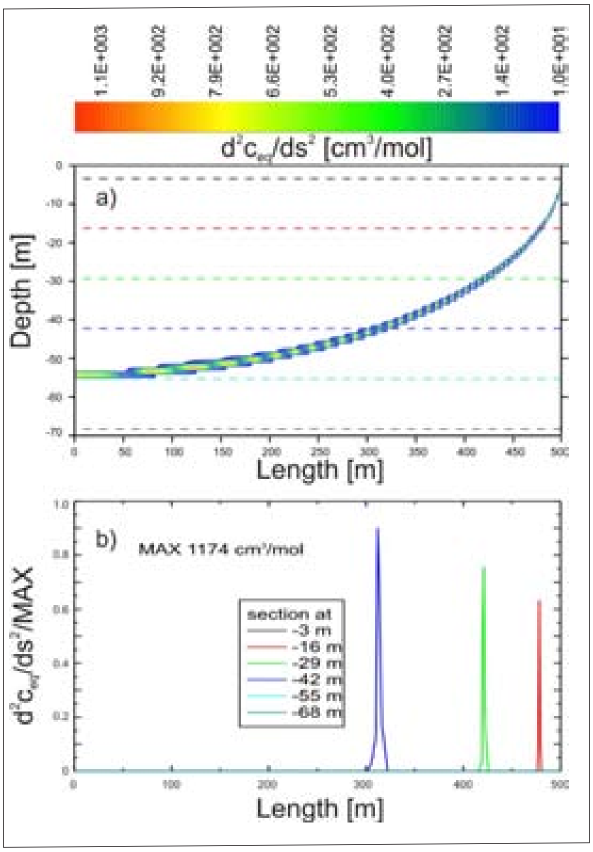

Fig. 9: Homogeneous island. Local distribution of the second derivative $\frac{\partial^2 c_{eq}}{\partial s^2}$*, b) second derivative along horizontal sections as indicated in a).*

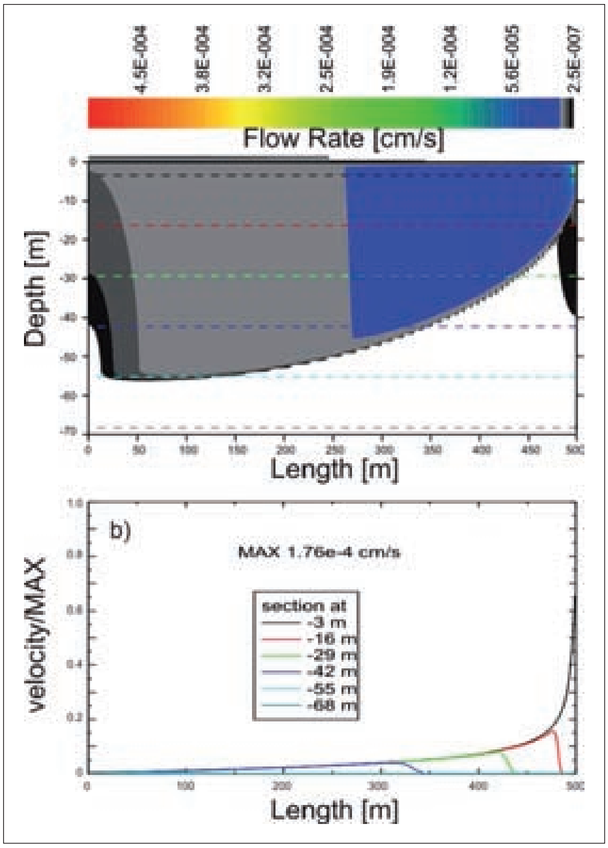

Fig. 10: Homogeneous island. a) Local distribution of flux b) flux along horizontal sections as indicated in a).

As we have stated already, the second derivative is restricted to narrow regions in the freshwater side of the transition zone. It exhibits significant values only at locations where the water contains between zero and 4% saltwater (see Figure 5). On the other hand the gradient in salinity is maximal at mixtures of about 50% seawater, because it arises from a diffusive process. In the region of maximal gradients, however, the second derivative is small. Vice versa in the region of high values of the second derivative, the gradients of salinity are low. This is illustrated in Figure 12. This figure is an overlay of the horizontal distributions (grads)^2 in Figure 8b (red curves), the second derivative in Figure 9b (green curves), and the initial porosity change in Figure 11b (black curves). All curves are normalized to their individual maximum values. Therefore their values are not comparable in this figure. What can be compared, are the locations. Evidently the curves for gradients and second derivative are well separated. The curves of porosity change are proportional to the product of the square of the gradient and the second derivative. Porosity change displays high values in between their maxima but close to the region of high values of the second derivative.

Figure 13 further illustrates this qualitatively. The red region depicts the locations of the modeling domain where (grads)^2 exhibits values $val \geq 10^{-2} val_{max}$· val_{max} is the maximal value. The green region shows these locations for the second derivative and finally the black region shows the locations of significant changes of porosity. These findings agree with those of Sanford and Konikow (1989) who also found that changes in porosity are restricted to regions where waters contain between 0.5% and 3% of seawater.

It should be noted here that any mechanism, which changes the sigmoid shape of the salinity distribution to a linear profile would enhance evolution of porosity dramatically. In this case salinity gradients become constant in the entire mixing zone and their value is at least one order of magnitude higher at the maximal value of the second derivative. One could speculate that tidal pumping and fluctuations of the water table due to seasonal changes of infiltration could cause such linear mixing zones. Present observations in boreholes give some evidence for such transition zones.

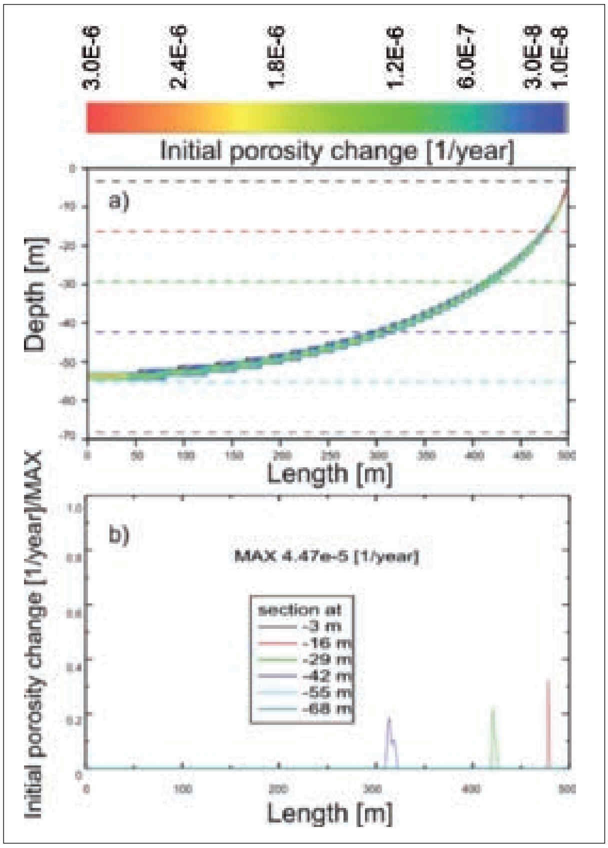

Fig. 11: Homogeneous island. a) Local distribution of initial change of porosity $\partial\phi/\partial t$. b) $\partial\phi/\partial t$ along horizontal sections as indicated in a).

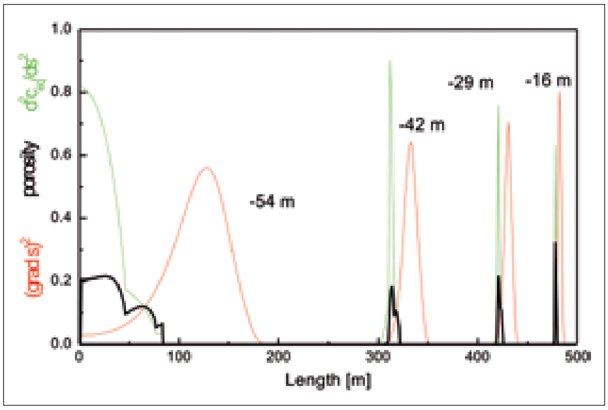

Fig. 12: Homogeneous island. (grads)² (red), $\frac{\partial^2 c_{eq}}{\partial s^2}$, (green), and) $\partial\phi/\partial t$ (black) along horizontal sections of the island. Numbers on the sets of curves give the depth of the section.

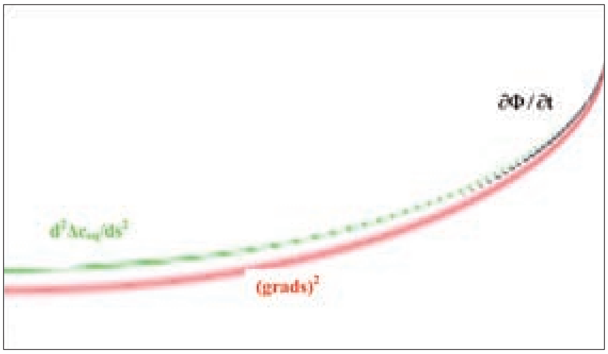

Fig. 13: Homogeneous island. Regions of (grads)² (red), of (green), and change of porosity (black).

INITIAL CHANGES OF POROSITY IN A HETEROGENEOUS ISLAND

A more realistic approach to nature can be taken by employing a geo-statistical distribution of hydraulic conductivities. Figure 14 shows such a distribution generated with the software of Chiang and Kinzelbach (1998). It covers conductivities of two orders of magnitude from about 380 m/day (red) down to 2 m/day (dark blue). Most of the aquifer is occupied by values between 10-200 m/day. Otherwise all previous boundary conditions are unchanged. The flow field is illustrated in Figure 15. Flux is unevenly distributed, because the heterogeneous distribution of conductivities distorts the pathways of fluid elements in comparison to the regular ones in a homogeneous island. Consequently the freshwater lens in Figure 16 shows a wide transition zone (compare to Figure 7a).

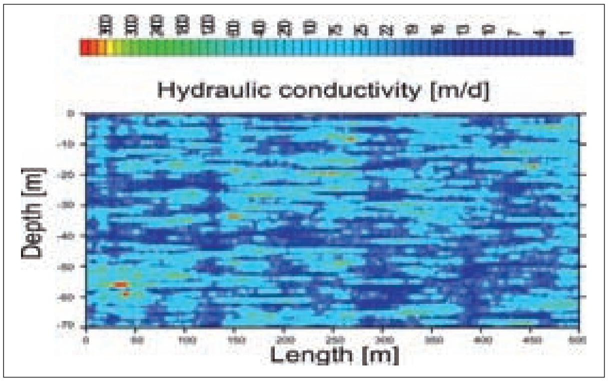

Fig. 14: Heterogeneous island. Statistical distribution of hydraulic conductivity in the modeling domain.

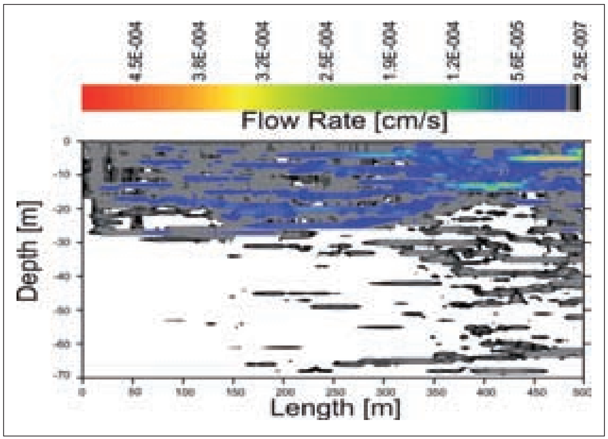

Fig. 15: Heterogeneous island. Local distribution of flux q.

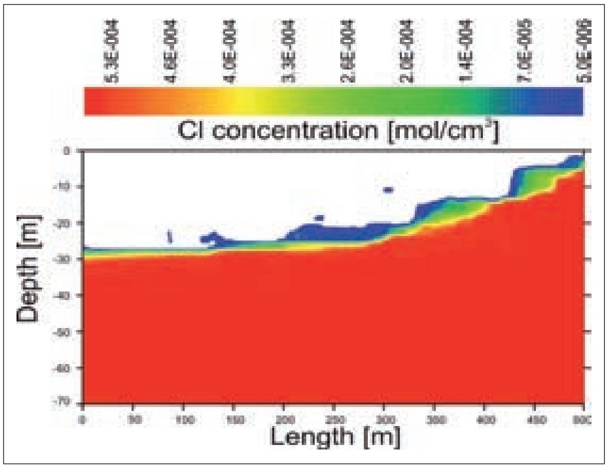

Fig. 16: Heterogeneous island. Local distribution of chlorinity $s(\vec{x})$*. The white region designates the freshwater lens.*

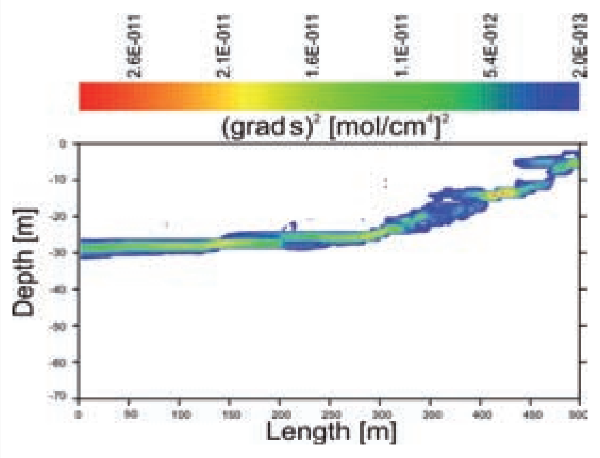

Fig. 17: Heterogeneous island. Local distribution of $\left|\vec{\nabla}s(\vec{x})\right|^2$.

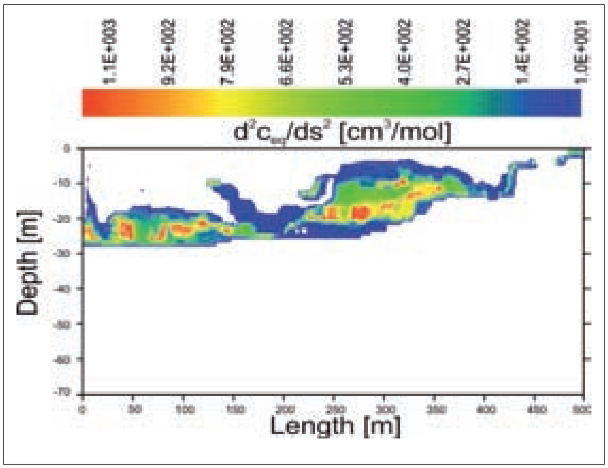

Fig. 18: Heterogeneous island. Local distribution of derivatives $\frac{\partial^2 \Delta c_{eq}}{\partial s^2}$.

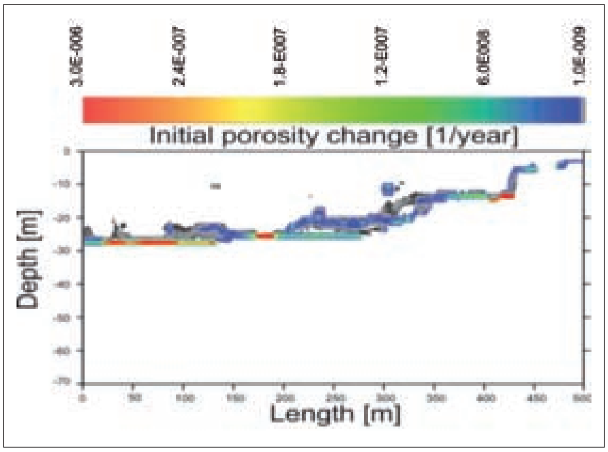

Fig. 19: Heterogeneous island. Local distribution of initial porosity change $\partial\phi/\partial t$.

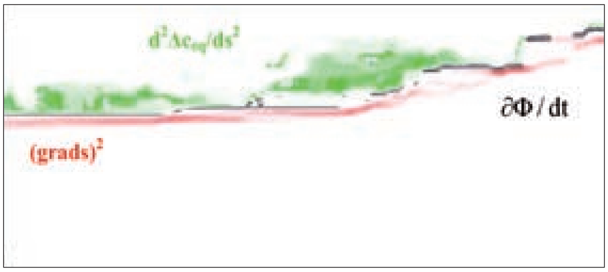

Fig. 20: Heterogeneous island. Regions of high values of (grads)^2 *(red),* $\frac{\partial^2 \Delta c_{eq}}{\partial s^2}$ *(green), and change of porosity (black) in the modeling domain.*

The square of the gradient is limited to the seawater side of the transition zone, as can be visualized from Figure 17. The region of 0-4% mixtures extends far into the freshwater lens. This can be also visualized from the second derivatives as shown in Figure 18.

Figure 19 illustrates the initial change of porosity, which exhibits high values of $3 \cdot 10^{-6}$ year^{-1} (red) at only a few locations close to the freshwater side of the transition zone. At some favorable locations (red and yellow) caves may evolve there in several 10,000 to 100,000 years.

This is further illustrated by Figure 20, which shows the regions of high values for (grads)^2 (red), d^2c_{eq}/ds^2 (green), and $\partial\phi/\partial t$ (black) in the modeling domain. Figure 21 depicts (grads)^2 (red), d^2c_{eq}/ds^2 (green), and $\partial\phi/\partial t$ (black) along selected horizontal sections.

In both figures we find that the regions of (grads)^2 (red), d^2c_{eq}/ds^2 (green) are well separated and porosity develops in between. Due to the heterogeneity, however, the patterns become complex.

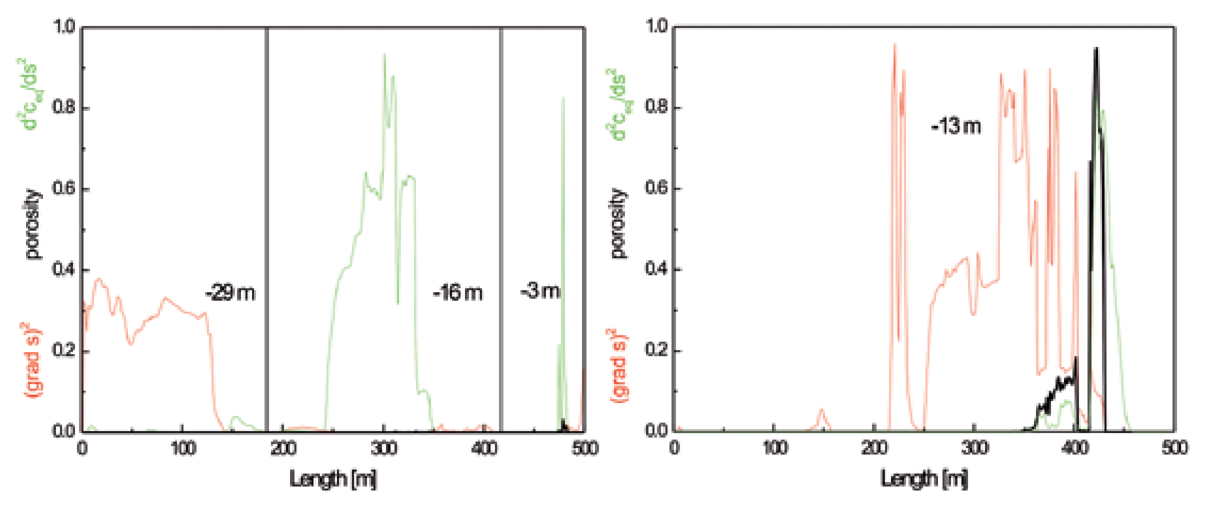

Fig. 21: a) Heterogeneous island. Distributions of (grads)^2 (red), $\frac{\partial^2 \Delta c_{eq}}{\partial s^2}$ *(green), and porosity change (black) along selected horizontal sections. Number on the sets of curves give the depth of the section.*

INITIAL CHANGES OF POROSITY IN SALTWATER TONGUES.

When impermeable strata underlay an island sufficiently close to its surface the freshwater lens cannot extend below this layer and a saltwater tongue intrudes from the coastland inward until it reaches the impermeable layer. From thereon the freshwater lens is truncated by this layer. In this situation mixing of waters is restricted to the transition zone of the tongue and one expects high dissolution rates in this region.

Fig. 22 shows the local distribution of chlorinity and the initial change of porosity using the statistical distribution in Figure 14 for the upper permeable part. The mixing zone exhibits a structure similar to that of the heterogeneous island at the corresponding locations. Porosity changes at the outflow are low, but we find values up to 10^{-6} 1/year land inward at various locations and also at the contact of the tongue with the impermeable rock.

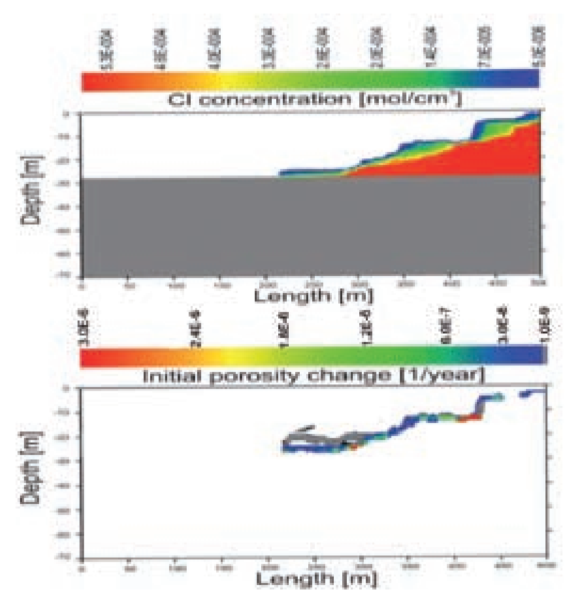

Fig. 22: Coastal aquifer with heterogeneous conductivity down to 29 m as used in Fig. 14. The strata below 29 m are impermeable (grey). Local distribution of Cl-concentration s(x) and initial porosity change $\partial\phi/\partial t$.

CONCLUSION

We have taken substantial steps in modeling the initial porosity changes in fresh water - saltwater mixing zones under various geological settings. We have demonstrated that the knowledge of the distribution of salinity and the amount of the flow velocity is sufficient to calculate the initial distribution of porosity changes. These are the first modeling results, which do not need scaling parameters for calibration as the models of Sanford and Konikow (1989), or more complex non-linearly coupled sets of differential transport- advection equations (Saaltink *et al.*, 2004). We now understand that in a stationary island high porosity can develop only if high salinity gradients exist in the region of low saltwater content to up to 3%. For the highly idealized scenarios of islands with homogenous hydraulic conductivity we find clear rules about the geometric distribution of porosity. These, however, are destroyed for islands with a statistical distribution of hydraulic conductivity. Each realization of a statistical distribution then will give different results, and a general standard scenario cannot be used as a tool. In heterogeneous settings porosity could occur at any place below the island and at favorable settings also flank-margin caves will arise. This explains why presence of these caves is not the rule, as it should be in homogeneous settings, where porosity develops only at the base and the outflow of the lens. In view of the restricted knowledge about the hydraulic properties and the initial porosity of the rock, which one necessarily has in carbonate platforms, detailed applied modeling at present, and most likely in the next decades will not be available.

On the other hand our findings give a firm basis for understanding the evolution of porosity on time scales of several ten to several hundred thousand years. Using an iterative procedure to implement changes of porosity and hydraulic conductivity in each time step will reveal the basic properties of processes involved in creating macro-porosity such as caves and conduits. Feed back mechanisms, which enhance dissolution in the regions of increased porosity and hydraulic conductivity could accelerate the evolution of porosity. Therefore time scales derived from the initial change in porosity represent upper limits only.

Further work into this direction is needed.

ACKNOWLEDGEMENT

We thank TOTAL S.A. for supporting this work.

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COBISS: 1.01

THE AGE OF KARST RELIEF IN WEST SLOVENIA

STAROST KRAŠKEGA RELIEFA V ZAHODNI SLOVENIJI

Andrej MIHEVC[1]

Abstract UDC 551.435.8 (497.4 Kras)

Andrej Mihevc: The age of Karst relief in west Slovenia

The age of a karst can be defined as the time when the karst rocks were uplifted out of the sea. The other view of the age of karst is to define the age of certain karst features or assemblages of karst features. On the Kras plateau there is a variety of forms that were formed at quite different times, but due to karst evolution, they coexist in today's relief. On the plateau, that is slowly rising, the hydrological zones in karst surface are moving downwards. Streams from the side ceased to flow on the karst and former leveled surface that was formed in conditions of high ground water is dissected by numerous dolines. Blind valleys are incised at the side and some of them show the influence of recent tectonics. The lowering of relief by corrosion exposes caves that have formed deep beneath the surface and creates unroofed caves that become a part of the surface topography. From the morphological comparison of the unroofed caves, blind valleys and levelled surfaces and by dating of the sediment and considering the age of tectonic phases we can reconstruct the evolution and estimate the age of the karst landscape.

Key words: karst, morphology, age, Kras, Slovenia.

Izvleček UDK 551.435.8 (497.4 Kras)

Andrej Mihevc: Starost kraškega reliefa v zahodni Sloveniji

Starost krasa lahko določimo s trenutkom, ko so bile kraške kamnine dvignjene iz morja. Drugi način opredelitve starosti krasa je z datiranjem reliefnih oblik ali skupin reliefnih oblik. Planoto Kras sestavlja vrsta zelo različnih reliefnih oblik, ki so nastale v različnem času, vendar so se zaradi posebnosti razvoja krasa ohranile in sobivajo v sedanjem reliefu. Na planoti, ki se počasi dviguje se hidrološke cone in kraško površje pomikajo navzdol. Vodotoki s strani so prenehali dotekati na kras in nekdanje v višini talne vode nastalo uravnano površje so razčlenile številne vrtače. Na robu krasa so vrezane slepe doline, nekatere od njih kažejo sledove tudi recentnih tektonskih premikov. Zniževanje reliefa zaradi korozije je razgalilo jame, ki so se oblikovale globoko pod površjem in ustvarilo brezstrope jame, ki so postale del današnje topografije površja. Z morfološko primerjavo brezstropih jam, slepih dolin in uravnav in datiranjem sedimentov ter upoštevanjem starosti tektonskih faz lahko rekonstruiramo razvoj reliefa in ocenimo starost kraške pokrajine.

Ključne besede: kras, morfologija, starost, Kras, Slovenija.

INTRODUCTION

The question about time, like velocity of processes or age of karst surfaces and caves is a very important issue in karst studies. The age and evolution of karst is also important when we study karst as a specific ecosystem. It can tell us when karst and especially the caves start to form in a given area and how the landscape is changing.

The first explanation of geomorphic evolution and the age of the karst in W Slovenia were made by geologists. To estimate the age they used geologic data – the age of last marine sedimentation and the tectonic evolution of Dinaric mountains and the Alps (Grund 1914).

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Received/Prejeto: 01.02.2007

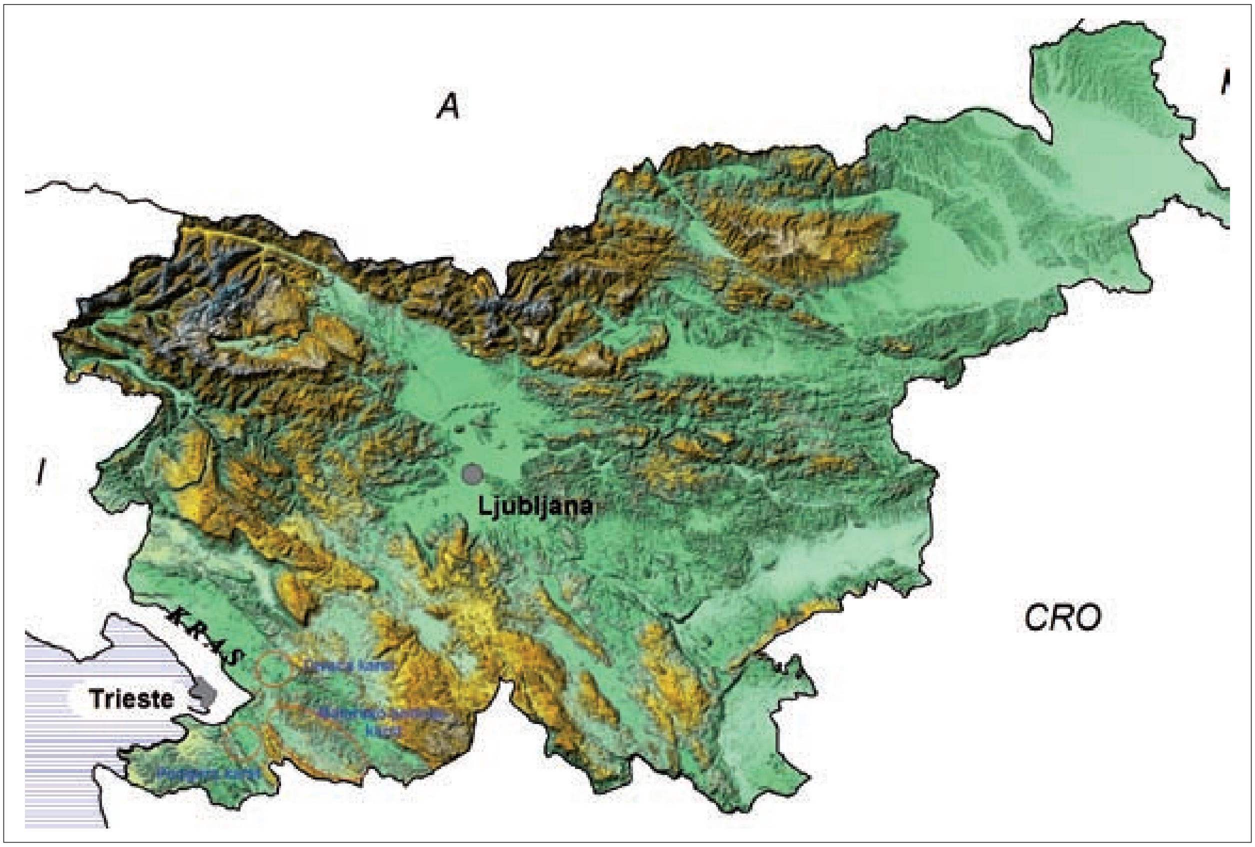

Fig. 1: The location of the Kras plateau and the study areas.

At first karstologists were focused on understanding karst processes and the evolution of karst features like dolines, poljes and corrosion plains. They were much influenced by the ideas of a geographic cycle promoted by Cvijić (1924). Karst evolution was divided into similar steps in the cycle but they also added a pre-karst phase of relief evolution with which they explained some morphological elements in karst.

The cyclic explanation of the karst evolution was later modified with climatic geomorphology (Roglič 1957, Radinja 1972). It emphasised the importance of climate on the morphological processes. This meant that some forms of relief, like conical hills and levelled surfaces were explained as a relicts from tropical climate. Because such a climate was present at the end of the Tertiary, these forms were determining the age of that relief features.

Another important climatic signal in the morphology of the Kras they estimate were the cold Pleistocene climates with periglacial processes in lower positions. Scree slopes, collapses in caves, fluvial deposits in contact karst areas and some finer sediment were explained as extremes of climate control and not normal karst phenomena. They were also used for determination of the age of features (Melik 1955, Gospodarič 1985).

Geomorphologists have abandoned the cyclic model of relief and are now paying more attention to structural elements in karst morphology like recent tectonic (Habič, 1982), field measurements and observations on karst denudation (Gams 1963), comparative studies of different karst features or types of karst, like contact karst (Gams 1962, Mihevc 1994), the study of dolines and collapsed dolines (Mihevc 2001) and new geomorphologic features like unroofed caves (Mihevc 1996, 2001, Slabe 1997) as an important remnants of former landscapes and a source of sediments. Flowstones in the caves were dated (Hajna 1991, Mihevc 2001) and paleomagnetic methods were used in cave and karst sediments (Bosak & al. 1999, 2004).

Very important data were provided by latest research on the plate tectonics. The tectonic evolution of the area is characterized since late Tertiary first by northward motion of Adria micro plate which caused contraction deformations. The contraction was exhausted at about 6 Ma ago and was followed by rotation accompanied with uplifts, folding and strike-slip basins formation. These events take place in two distinct phases (Vrabec & al. 2006, Fodor & al. 1998).

GEOMORPHIC EVIDENCES ON THE AGE OF KRAS

Kras is a low NW – SE trending longitudinal plateau along Trieste Bay (Adriatic Sea) between flysch Brkini hills on SE, Vipava Valley in NE, and the Soča River lowlands in NW. The plateau is about 45 km long and 14 km wide. The surface of the plateau is slightly tilted from 500 m a.s.l on SE towards NE where it ends at about 100 m above the Soča river.

The central part of Kras is built from highly permeable Cretaceous carbonate platform shallow marine limestone and less permeable dolomite. Eocene flysch that acts as an important impermeable barrier surrounds the carbonate massif.

The age of the karst of Kras plateau can be defined as the time when the karst rocks were uplifted out of the sea. For the most of Dinaric karst in Slovenia this occurred after the Eocene, since after that there is there is no evidence of younger marine sediments. As soon as the carbonate rocks were exposed, we can expect that the karst was formed, but there are no remnants of karst features from that time. Most likely denudation has destroyed them.

The other view on the age of karst is to define the age of those karst features for which we know how and when they were formed and which evolution was stopped long time ago. Such features are levelled surfaces, which evolve at the level of the karst water and blind valleys that were formed by alogenic rivers. We can compare them with evolution of fluvial relief and unroofed caves, which are caves exposed to surface by denudation.

On the Kras plateau there is a variety of forms that were formed at quite different conditions and time but due to peculiarities of karst evolution they coexist in today's relief. This can make the determination of the one age of a karst landscape difficult or impossible, but it tells us about the genesis of the landscape trough different phases.

Here we present the study of the part of the Kras, Divaški kras and Matarsko podolje and the edge of Podgorski kras from which there are some evidences about the evolution and age of Kras.

THE UNROOFED CAVES OF DIVAŠKI KRAS

The Divaški kras is tilted slightly towards NW at elevations between 450 and 400 m a.s.l, on the SE part of the Kras plateau. It is built up mostly by Cretaceous and Paleogene limestone. The karst features here are exceptional; there are the sinking of the Reka river into Škocjanske jame cave via large collapse dolines with and hundreds of dolines. The largest caves of the area are the 12,500 m long and 275 m deep Kačna jama and the 5800 m long and 250 m deep Škocjanske jame. The caves were formed by the Reka river which can be reached at a depth of 195 m in Škocjanske jame and 156 m a.s.l. in Kačna jama.

The main morphologic features of the area are collapsed dolines and dolines which together cover about 12% of the area. The collapsed dolines are connected with active water caves. The solution dolines cover less than 4% of the area. The rest of the surface (88%) is level. These points out the prevailing surface leveling process in the present conditions

In this levelled surface there are several large unroofed caves (Mihevc 1996). As such caves appear on the surface due to denudation, and we may call their remains denuded caves. A cave ceiling will be the first to be removed by denudation, which is why they are also called unroofed caves. They were first found and described in the Divača Karst. The unroofed caves share on the surface is small, only about 0.16% of the entire surface.

Three important unroofed caves have been found. The first is a 350 m long unroofed cave near Povir village at 400 m above the sea level. There is a remnant of a cave passage that was 6 m wide and over 5 m high. The entire volume of the passage has been filled by allochtonous fluvial sediments of clay, silicate sands and gravel with pebbles up to 25 cm in diameter.

The second is an unroofed cave near Divača on the slopes of doline Radvanj at the altitude of 390 - 415 m above sea level. It is exposed on the slope that dissects large cave passage, which is entirely filled with sediments. Similar sediments can be seen in the Divaška jama cave. This is a 600 m long cave, whose continuation towards 250 m distant unroofed cave is completely filled. The cave was also filled, but the sediment was later washed from it by the seepage water. Here we can see that a part of the unroofed cave that still exists as an underground cave.

The longest roofless cave is 1.800 m long remnant of caves whose passages were about 20 m large, and therein flew a great underground river. The cave was filled with fluvial sediments and massive flowstone. It is located

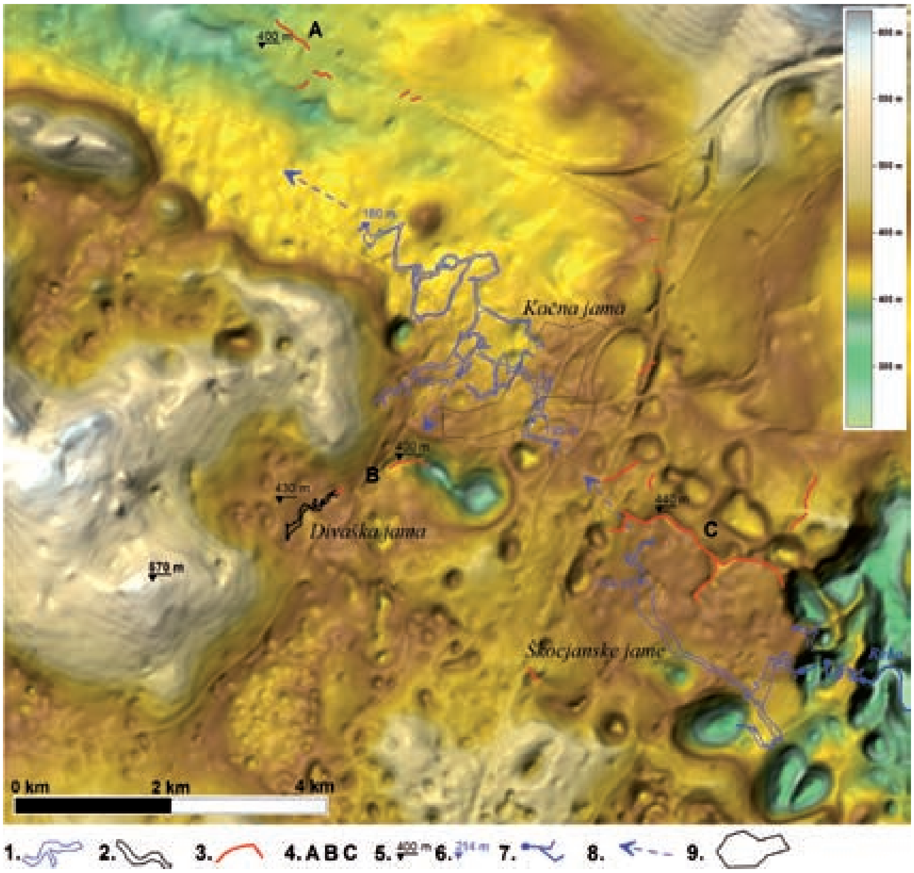

Fig. 2: The map of the Divača karst. On the levelled surface the large collapse dolines are dominating features, solution dolines are frequent, but they represent only small proportion of the surface. The outlines of the main caves and the main unroofed caves are marked. On the map made of DEM with 12.5 m grid the road cuts or causeways are also seen.

Legend: 1. Outline of the active river caves, 2. Divaška jama cave, 3. Unroofed cave, 4. Unroofed caves mentioned in the text: A: Unroofed cave near Povir, B: Unroofed cave in doline Radvanj, continuation of Divaška jama, C: Unroofed cave above Škocjanske jame, 5. Height of the surface, 6. Height of the water level in caves, 7. Reka river and ponors, 8. The supposed direction of water flow, 9. Outline of the town Divača.

partly above the Škocjanske jame, where the actual river bed in the cave is 230 m below the unroofed cave.

On the basis of the shape of walls and sediments we may reconstruct some evolution of the caves and later the surface. The caves are remnants of larger cave systems, which conducted waters from different sinking streams. Growth of speleothems in them was frequently interrupted by phases of erosion or backfill. The caves were afterwards filled up with fluvial sediments. The large pebbles in the caves testify the great gradient of the surface streams. Later all caves were filled with finer sediment, which could mean the lowering of the gradient in karst and aplanation. Later, the surface was tilted and uplifted which caused lowering of the karst water level.

The age of the unroofed caves can be established by comparative methods according the denudation rate of the surface. If we presume, that it is about 50 m/Ma (Gams 1962) and there was some 100 m - 200 m of rock removed from above the caves that they are at least 2 – 4 Ma old, and probably older (Mihevc 1996, 2001).

Similar time frames 1.6 – 1.8 Ma or/and 3.8 to 5 Ma were given also by paleomagnetic datation of clastic sediments (Bosak & al. 1998) and by the timing with tectonic phase that started at 6 Ma (Vrabec & al. 2006).

The age of the roofless cave can also be illustrated by the time, in which the water table in Kras lowered for 240 m, from about 400 m to 160 m a.s.l.

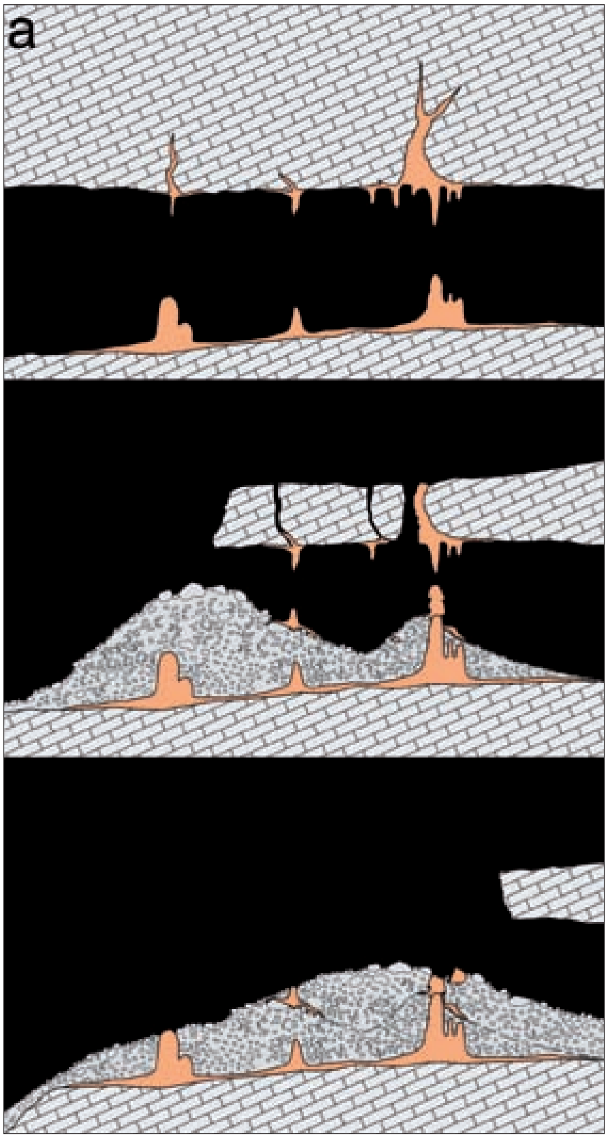

Fig. 3: Formation of the unroofed cave. The idealised drawing is representing actual cases of unroofed or partly denuded caves from the Divača karst, where probably more than hundred meters of the rock above unroofed caves were removed. The transformation of cave to the unroofed cave is here presented in three stages: a: Epiphreatic cave passage was formed deep below the surface, some flowstone was deposited after the cave became inactive; b: Surface approached the cave. At one side the slope cut the cave and made the entrance into the passage; from the horizontal surface former vadose shafts transformed into vertical entrance. Trough both entrances piles of boulders and scree deposited. c: Great deal of the ceiling dissolved, some collapsed and formed relief oblong depression of the unroofed cave ending in front of the entrance to the cave.

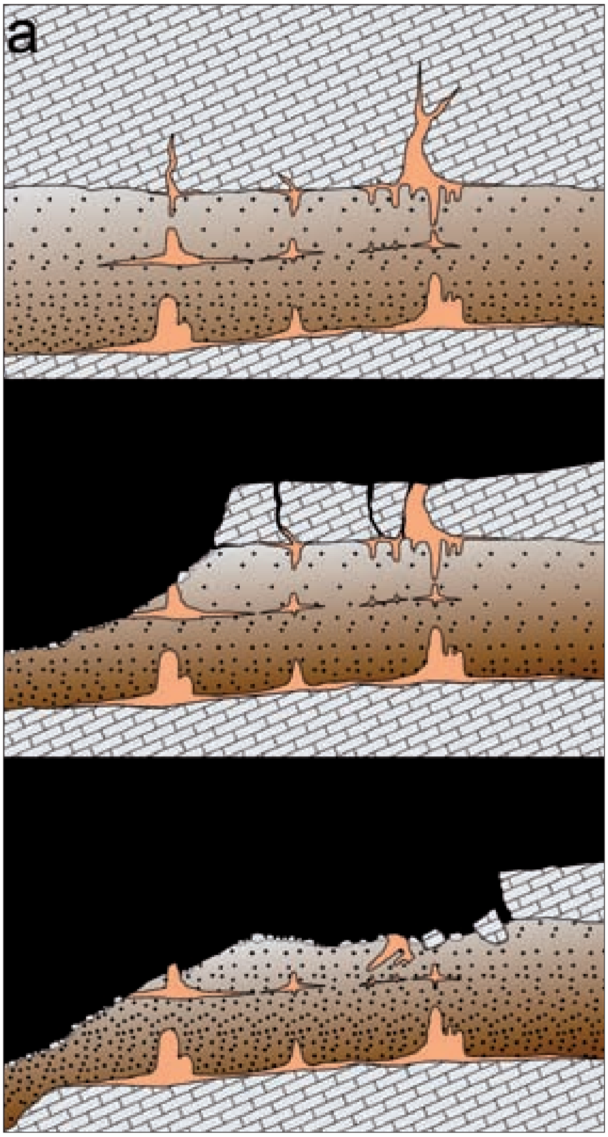

Fig. 4: Formation of the unroofed cave. The idealised drawings are representing the actual cases of unroofed or partly unroofed caves from the Divača karst which were completely filled with allogenic fluvial sediment.

The transformation is here presented in three stages: a: Cave passage was formed deep below the surface. There was alternation of the sedimentation of flowstone and allogenic sediments of the underground river. Towards the top of the profile sediments became finer. b: Surface approached the cave. At the side the slope cuts passage and exposed the cave sediments on the surface. c: After disintegration of the ceiling from the top oblong depression formed. In it there are alochtonous sediments and few blocks of limestone and some flowstone. The unroofed cave ends with steep limestone wall or slope from where the karst surface continues.

THE BLIND VALLEYS OF THE MATARSKO PODOLJE CONTACT KARST

Alogene rivers flowing to karst enhance the karstification process and form particular relief features. Phenomena and forms that develop at the contact of fluvial and karst relief are the result of the interaction of both morphological systems.

The Matarsko Podolje is a 25 km long and 2-5 km wide tilted karst surface. In longitudinal section it gently raises from about 490 m on NW to 650 m on SE side. The karst surface continues towards SE but from the highest point there is an abrupt change and relief lowers over the distance of 2 km for 200 m to Brgudsko podolje karst surface.

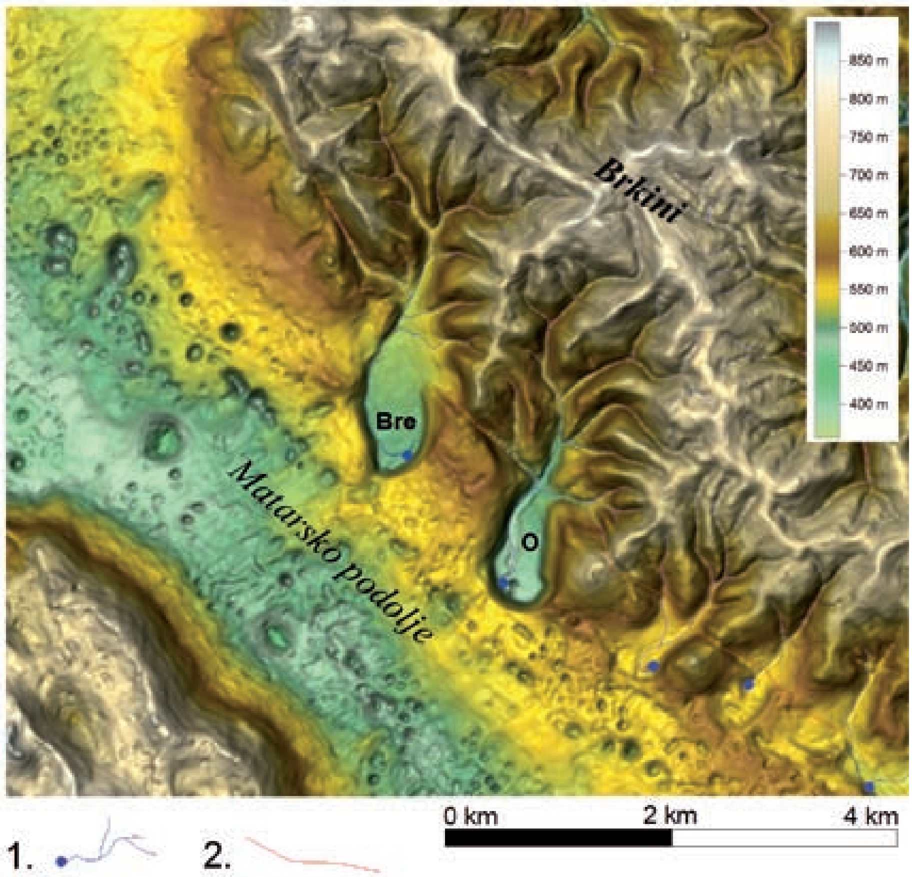

Fig. 5: Blind valleys Brezovica (Br) and Odolina (O) on the NW part of the Matarsko podolje karst. Blind valleys cut for about 50 m into the edge of the levelled karst surface where dolines and larger collapse dolines prevail. There are no traces of dry valleys or dry blind valleys.

Legend: 1. Sinking streams, 2. Boundary flysch – limestone.

From the flysch Brkini hills that are NE of podolje there are 17 sinking streams that formed a row of large blind valleys in the edge of the Matarsko Podolje. The bottoms of these valleys are situated between 490 to 510 m. As the valleys are incised in the border of the karst, uplifted towards SE, the blind valleys lying more to the south are deeper. The most NW lying, Brezovica and Odolina blind valley are cut for about 50 m only while the deepest is the last one, Brdanska dana on SE, deepened into limestone for 250 m.

The blind valleys started to cut into the corrosion plain with small transverse and longitudinal gradient as in the other case the fluvial valleys should develop in them. They should be preserved on karst as dry valleys. The corrosion plains along the ponors were controlled by the piezometric level this is why they are all at same altitude.

In the SE part where the uplift was stronger, the blind valleys show the disturbances caused by fast tectonic uplift and are preserved on the karst surface. Above the Račiška Dana blind valley there is a fossil one, on the bottom of which are some old sediment from flysch. This is now higher than the flysch hills where the sediment came from. The other case is the most SE blind valley Brdanska Dana. It developed in the SE edge of the Matarsko Podolje. The tectonic structure along which the Matarsko Podolje ends caused also the asymmetric development of the blind valley. The W side of the blind valley was uplifted and developed two fossil higher levels in the side of the blind valley.

The Brkini series of blind valleys offer enough data to follow the sequence of the morphological events and dominant factors which were decisive for the formation of the actual relief forms. The former shape along the ponors on the border of impermeable hills was karst corrosion plain. The water flowing on it had a modest gradient in karst and was capable of the aplanation of the surface only. The lowering of the piezometric level in the karst enabled the development of the relief depressions along the ponors. The deepening and the contemporaneous widening of the valleys followed the lowering of the karst water to the altitudes about 500 m.

The incision of blind valleys into the leveled surface probably started and continued trough the last tectonic phase that is 6 Ma before present. This is also accordance with the age of the cave sediments from Račiška pečina which were dated by paleomagnetic method and correlated with palaeontologic data to 3.5 Ma (Pruner & al. 2003).

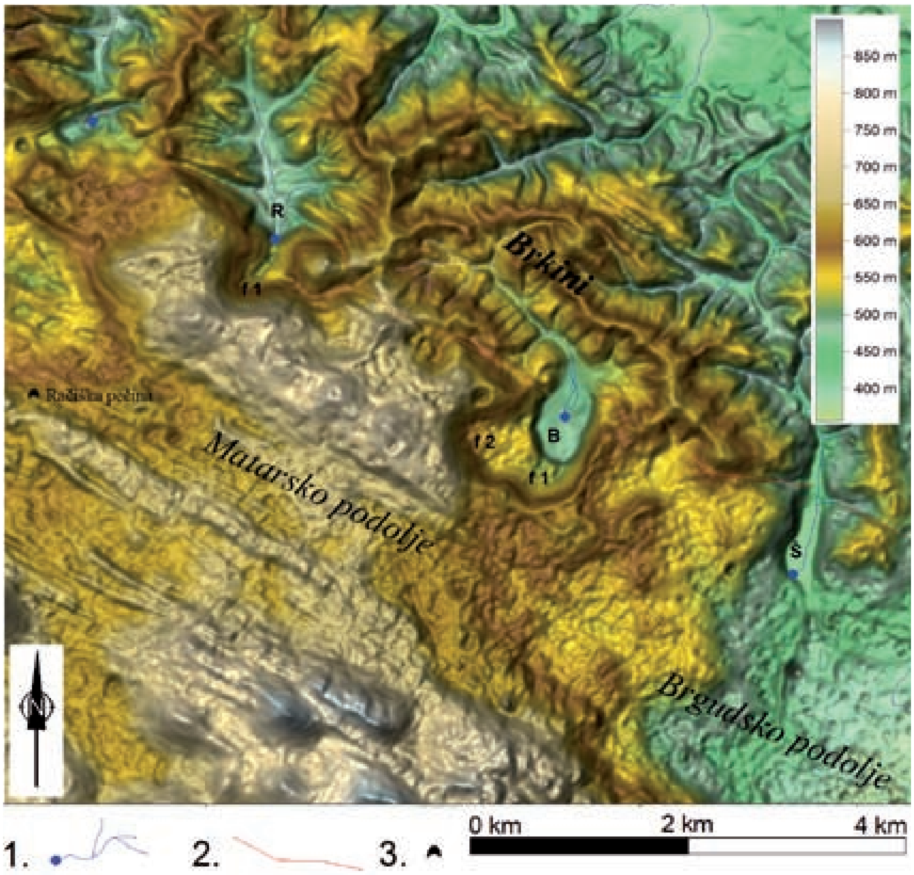

Fig. 6: Blind valleys Račiška dana (R) and Brdanska dana (B) with fossil blind valleys (f1, f2). These valleys developed in SE part of Matarsko podolje during the tectonic uplift. Uplift deformed older corrosion plain and created height difference between Matarsko and Brgudsko podolje. Further SE there is another blind valley (Š) which developed at the edge of Brgudsko podolje that was not uplifted. Račiška pečina cave that was once formed by sinking streams is at elevation about 600 m high above the recent ponors.

Legend: 1. Sinking streams, 2. Boundary flysch – limestone, 3. Cave Račiška pečina.

THE UNROOFED CAVES OF THE EDGE OF THE PODGORSKI KRAS

Podgora karst is small 5 km wide and long karst plateau, SW continuation of the Kras. Its surface is located at 500 to 450 m a.s.l. The plateau surface is leveled and dismembered only by numerous dolines. There is a sharp edge of the plateau and towards W in less than 1 km relief drops for 400 m. At the foot of the plateau there are recent karst springs of the rivers Rižana and Osapska reka at altitudes of about 50 m a.s.l.

In the Črnotiče quarry, that is located on the edge of the plateau, several caves were opened. Shafts with stalagmites and stalactites on the walls were filled by gravel as well as numerous bones of large Pleistocene mammals felt down to shafts.

There are also large remnants of horizontal caves. The largest, 150 m long partly unroofed passage with the diameter of more than 10 m was opened in the western part of the quarry. The passage was entirely filled by massive flowstones deposited over the fluvial sediments, layers of gravel and conglomerate mixed up with sand and clay layers. Sedimentary fill was 17 m thick at least.

In the cave calcareous tubes a serpulids were found both in sediments and still attached to the scalloped wall. They match the morphology of extant serpulid tubes of *Marifugia cavatica* (Mihevc 2000; Mihevc *et al.*, 2001a). Marifugia cavatica Absolon and Hrabe, 1930 is the only fresh-water species of the Serpulidae family and the only

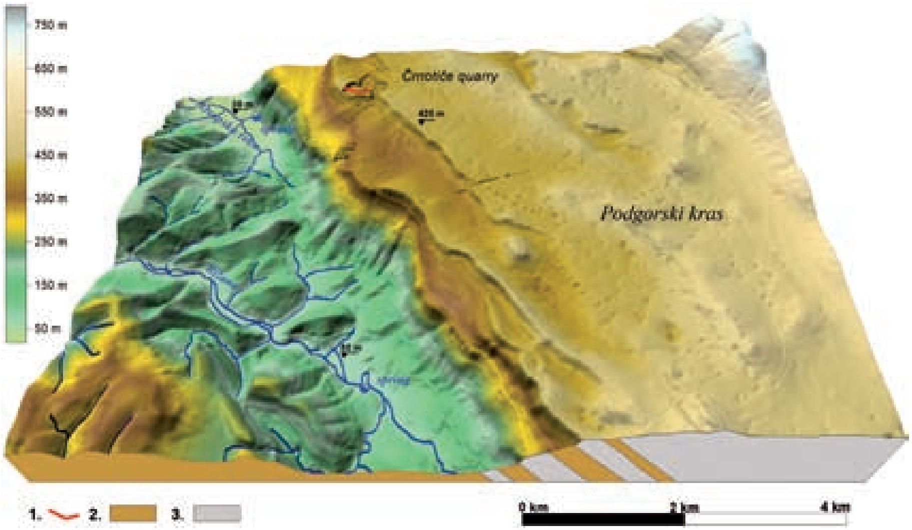

Fig. 7: DEM of the Podgorski kras. Levelled karst surface of Paleocene limestone and some intercalated flysch is in sharp contrast with fluvial relief that developed on Eocene flysch. At the foot of the karst there are the major karst springs where Marifugia cavatica still lives today. The fossil tubes were found in the large cave exposed in the Črnotiče quarry.

Legend: 1. Unroofed cave, 2: Flysch, 3: Limestone.

known tube worm inhabiting continental caves. Stable isotope analysis (Mihevc *et al.*, 2002) of fossil tubes from Črnotiče quarry site is comparable with stable isotope compositions of recent fresh-water species and greatly differs from those of marine serpulids. *Marifugia cavatica* is filter feeder with free-swimming larvae (Matjašič & Sket 1966). It is widely distributed within the Dinaric Karst and lives in springs of rivers Rižana and Osapska reka which are only few km and 370 m apart from the quarry.

Two profiles were analysed within the cave and dated back to 1.76 Ma (Črnotiče I) and 2.5–3.6 Ma (Črnotiče II site) (Bosak & al. 1999, Bosak & al. 2004).

Geomorphologic evolution of the plateau shows similarities to those of Kras and Matarsko podolje. Epiphreatic caves of the sinking rivers were filled with sediments; the surface was levelled and uplifted to present altitude. In the quarry there are several unroofed caves or remains old caves. The evolution of vertical shafts with dominance of later autochthonous fill resulted from younger vadose speleogenesis and Pleistocene sedimentation.

Fig. 8: The view of the unroofed cave in a quarry face. Lower part of the cave passage was filled with mostly laminated yellowish brown fluvial sediments. Upper part is filled with flowstone. The karst denudation already unroofed the cave, so that the flowstone is exposed to the surface. Tubes of Marifugia cavatica are on the scalloped walls in the lower part of the cave profile, which were protected by fine fluvial sediments.

CONCLUSIONS

Three different relief settings on the Kras, Matarsko podolje and Podgorski kras plateau show quite similar evolution. There are old caves present everywhere, which are now exposed by denudation. They were epiphreatic caves that were formed by sinking rivers, bringing allogenic sediments to caves. At the end of the morphogenetic phase all these caves were completely filled with fluvial sediments. This indicates the diminishing of the gradient in the whole area. After the caves were filled the three areas were levelled. Planation occurred in the similar conditions, most likely close to the level of the karst water.

Diminishing of the gradient which ended with planation could mean the same tectonic phase which ended at about 6 Ma ago. After that a new tectonic phase started. Three areas faced uplift and tilting for several hundreds meters. The uplift was stronger in the SE part of the area. Karst denudation was evenly lowering the surface, so the surface remained well preserved, dissected on central parts of karst with dolines, which represent few percent of total area only. The even denudation exposed former caves to the surface. Some of them are filled with sediments, from some sediments were washed away or were never filled.

On the edges of Matarsko podolje there were several sinking streams shaping blind valleys. Their incision was controlled by the piezometric level of the water in karst or the Matarsko podolje and by the tectonic uplift, they are getting deeper towards SE. Tilt of planation surface, different depth and asymmetric or fossil blind valleys are clear indicators of the recent tectonics.

Ages of sediments in the unroofed caves and the morphological datations are in accordance with the ages of main tectonic phases. From these data we can conclude that the oldest elements of the relief are the unroofed caves. The blind valleys are of same age even if they differ by the dimensions. The main process on the surface is even denudation and formation of dolines that form only small proportion of the surface.

The remains of tubes of *Marifugia cavatica* preserved in a quarry, high above the recent water caves indicate that the karst environment suitable for cave animals has been present for at least 6 Ma and that there was no interruption from the time of the formation of the caves in the Črnotiče quarry and drop of water table and/or tectonic uplift for at least 370 m.

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EVOLUTION AND AGE RELATIONS OF KARST LANDSCAPES

RAZVOJ IN STAROSTNI ODNOSI KRAŠKIH POKRAJIN

William B. WHITE[1]

Abstract UDC 551.44

William B. White: Evolution and age relations of karst landscapes

Any karst landscape is a work in progress. The observed evolution of the landscape is dictated by competing rate processes of surface denudation, stream downcutting, cave development, and tectonic uplift. Quantitative data on these processes, applied to two physiographic provinces of the Appalachian Mountains of eastern United States gives ages and time scales that are in agreement with previous geomorphic interpretation. The results are anchored, very loosely, by the few dates that have been established for cave sediments. Unfortunately, the measured rates vary over an order of magnitude as a result of local circumstances making regional interpretation a rough approximation at best.

Key words: fluviokarst, karst denudation, landscape evolution.

Izvleček UDK 551.44

William B. White: Razvoj in starostni odnosi kraških pokrajin

Vsaka kraška pokrajina je delo, ki napreduje. Razvoj pokrajine, ki ga je mogoče opazovati, je odvisen od medsebojno tekmujočih procesov površinske denudacije, vrezovanja površinskih tokov, razvoja jam in tektonskega dvigovanja. Številčni podatki o teh procesih, zbrani za dve fiziografski enoti v gorovju Apalači na vzhodu ZDA kažejo, da se starost in časovna skala ujemata s prejšnjimi geomorfnimi razlagami. Izsledke bolj ohlapno potrjuje nekaj podatkov, dobljenih za jamske sedimente. Žal pa so spremembe razmerja hitrosti zaradi lokalnih posebnosti v velikosti cele magnitude in je torej regionalna interpretacija v najboljšem primeru le grob približek.

Ključne besede: kraška denudacija, razvoj pokrajine.

INTRODUCTION: WHAT DO WE MEAN BY THE “AGE” OF A KARST LANDSCAPE?

By “landscape”, we usually mean some defined area of the earth’s surface as it exists at a single moment of time. Although most of the landforms remain constant on a human time scale, they are actually in the process of continuous evolution. In at least a microscopic way, today’s landscape is not quite the same as yesterday’s landscape. If the time scale is extended to thousands or millions of years, very large changes will have occurred to the landscape. Caves will have come and gone. A karst landscape, such as a doline plain, might superficially look the same but they wouldn’t be the same dolines. The land surface is continuously lowered by dissolution. Old dolines disappear and new dolines are formed.

Thus when we speak of the “age” of a karst landscape we must carefully specify both spatial scales and time scales. At the largest scales we can talk about global chemical erosion over geologic time (Gibbs *et al.,* 1999). We can talk about the general lowering of a karst landscape, the phenomenon generally called “karst denudation”. We can talk about the differential dissolution that produces surface karst landforms. We can talk about subsurface dissolution that produces caves. We can talk about the relative rates of landscape evolution on karstic and non-karstic rocks. We can talk about rates of tectonic uplift that provide the gravitational gradients that drive all of the processes. The observed landscape in any geo-

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Received/Prejeto: 20.12.2006

logic setting is the result of the interaction of all of these competing rate processes. As a result, "age" becomes a very slippery concept.

The objective of the present paper is to determine what constraints on the time evolution of karst landscapes can be extracted from known rates of the landscape processes. The discussion will be limited to fluviokarst. This means that consideration much be given to mass transport by surface streams on both carbonate and non-carbonate rocks as well as subsurface mass transport by dissolution. Illustrative examples are taken from the Appalachian Mountains of eastern United States. In the Appalachians are displayed two geologic settings: (1) The limestone valleys of the folded Appalachians where the karst surface is exposed across wide valley floors so that the disolutional dissection of the karst is primarily vertical and distributed across the surface. (2) The Appalachian Plateaus where the carbonate rocks are protected by clastic caprock and where the dissolutional attack is primarily by valley incision around the perimeter.

UNIFORM LANDSCAPE LOWERING: KARST DENUDATION

Setting aside the necessity for also removing insoluble residue, the evolution of a carbonate rock landscape can be considered to be a purely chemical process. The rock mass is taken into solution and carried away by the continuous flux of water that moves through the system. Any measure of the rate of carbonate removal can be recalculated as an average lowering of the karst surface, a quantity known as the karst denudation rate.

Various methods have been devised for the direct measurement of denudation rate (summarized by White, 2000). The rate of surface lowering can be measured directly on exposed rock surfaces using embedded reference pins and a precision micrometer (High and Hanna, 1970). The micrometer works best on bare rock surfaces. Most limestone dissolution takes place under a soil mantle. A technique to measure dissolution rates in soil is to bury carefully weighed plaques of limestone for a known time, then re-excavate and weigh them again (Gams, 1981).

On the scale of the entire drainage basin, it is possible to estimate denudation rate by a mass balance calculation using the volume of water leaving the basin and the concentration of dissolved carbonates contained in the water. The denudation rate is then given by

$$D_n = \frac{1}{N_L A}\frac{K}{\rho t_R}\int_{t_1}^{t_2} Q(t)\,H(t)\,dt \qquad [1]$$

In this equation, D_n is the denudation rate in $m^3km^{-2}yr^{-1}$ (numerically equivalent to the more common unit of mm/ka), A is the basin area in km^2, N_L is the fraction of the basin underlain by carbonate rocks, ρ is the density of carbonate rock in gcm^{-3}, t_R is the period of record in years, Q(t) is the instantaneous discharge in m^3s^{-1} (i.e. the hydrograph) and H(t) is the instantaneous (Ca + Mg) hardness in gcm^{-3} (i.e. the chemograph). The constant, K, contains unit conversions and has the value 10^{-12} for the units given. Because the mass balance equation requires continuous records of both discharge and hardness which are not often available, a variety of approximations have been proposed.

If the reaction between infiltrating water and carbonate rock at the base of the epikarst is assumed to reach equilibrium, the denudation rate can be calculated from first principles (White, 1984).

$$D_n = \frac{M_{cal}}{\rho\sqrt[3]{4}}\left(\frac{K_c\,K_1\,K_{CO_2}}{K_2\,\gamma_{Ca^{2+}}\,\gamma^2_{HCO_3^-}}\right)^{\frac{1}{3}} P_{CO_2}^{\frac{1}{3}}\,(P-E) \qquad [2]$$

In this equation, D_n is the denudation rate in mm/ka. Mcal is the molecular weight of calcite (or a weighted mix of the molecular weights of calcite and dolomite) and ρ is the rock density in gcm^{-3}. The K's are the usual equilibrium constants for carbonate reactions and the γ's are the activity coefficients. P-E (precipitation minus evapotranspiration) is the annual runoff in mm/yr

Many of the earlier measurements of karst denudation rates were reviewed and analyzed by Smith and Atkinson (1976). A selection of more recent data are displayed in Figure 1. The chosen examples include data from each of the three measurement methods described above and these give comparable results. The regional environments represented in Figure 1 include arid, alpine, northern, and temperate. Denudation rates vary by a factor of 5-10 within each group but the groups are almost completely overlapping. Local conditions at the sampling site, including soil cover, available water, and rock lithology, all contribute so that local site variation masks regional scale variations. There is also the question of how denudation rates have changed in response to climatic fluctuations of the Pleistocene. For the regional scale landscape evolution of interest in this paper, about the best that can be said is that exposed karst surfaces in the Appalachian Mountains would be lowered by dissolution at a rate of 20-30 mm/ka.

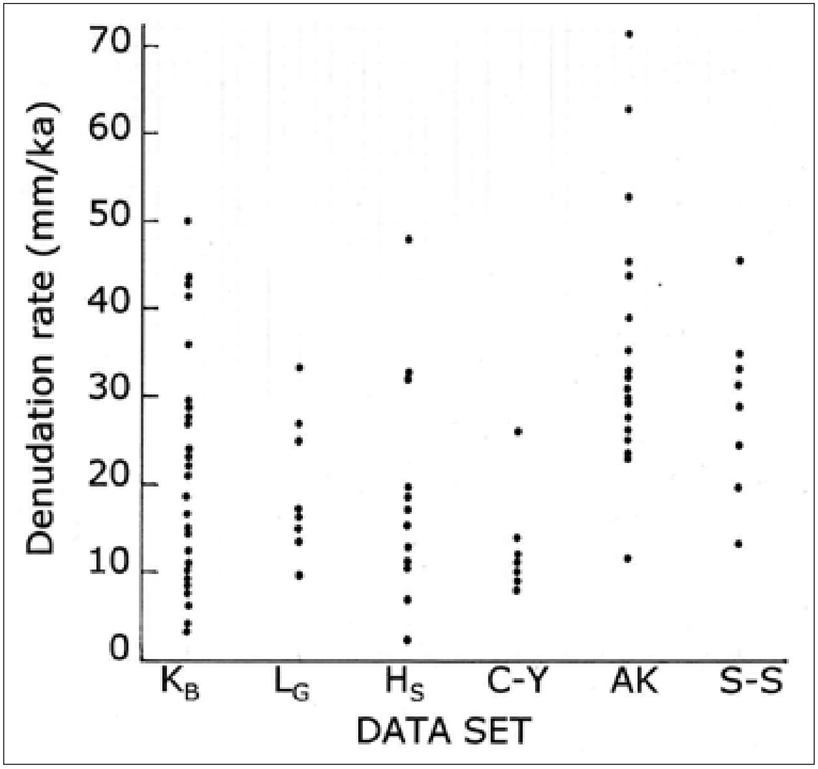

Fig. 1: Measured denudation rates. All data have been converted to units of mm/ka. K_R – Mt. Kräuterin, Austria (buried tablets) (Zhang et al., 1995). L_G – Logatec Doline, Slovenia (buried tablets) (Gams, 1981).
H_S – Hochschwab Massif, Austrian Alps (buried tablets) (Plan, 2005).
C-Y – Cooleman Plain and Yarrangobilly Caves area, New South Wales, Australia (microerosion meter) (Smith et al., 1995).
AK – southeastern Alaska (microerosion meter) (Allred, 2004). S-S – Saltfjellet-Svartisen area, northern Norway (mass balance) (Lauritzen, 1984).

RATES OF VALLEY DEEPENING

Regional rivers draining through areas of fluviokarst cut normal valleys in the clastic rocks that overlie, underlie, or border the karstic rocks and may appear as surface streams in valleys cut into the karstic rocks. Measurements of the downcutting rates of larger rivers are difficult because many of them, in their lower reaches, are at grade with a sediment load balanced against the discharge. Lowering of the bedrock channel can be very slow. A few data are given in Table 1. Lowering rates in the tectonically stable Appalachians fall in the same 20-30 mm/ka range as is found for denudation of karst surfaces. Only one example, the Bighorn Basin in western United States is a factor of ten higher and may represent a higher rate of tectonic uplift.

Small tributary streams that flow from surrounding non-karstic lands onto the karst and then sink at the contact with the soluble rocks seem to have a much higher rate of channel lowering. Some direct micrometer measurements in the beds of sinking streams are given in Table 2. Sinking stream waters are generally highly unsaturated so that sinking streams downcut rapidly into the carbonate rock at their sink points. Similar measurements at spring outlets produce much smaller numbers. The highest values yet reported were for a muskeg-draining stream in Alaska (Allred, 2004) where there is an implication that organic acids may also play a role.

Tab. 1. Downcutting Rate of Some Moderate-Size Rivers

Name and Location	***Rate (mm/ka)***	***Reference***
Bighorn River, Wyoming	350	Stock *et al.* (2006)
East Fork, Obey River, Tennessee	30	Sasowsky *et al.* (1995) Anthony & Granger (2004)
Green River at Mammoth Cave, Kentucky	30	Granger *et al.* (2001)
Juniata River, Newport, Pennsylvania	27	Sevon (1989)
New River at Pearisburg, Virginia	27	Granger *et al.* (1997)

Tab. 2. Downcutting Rate in Small Karst Streams

Name and Location	***Rate (mm/ka)***	***Reference***
Cataract Cave, southeast Alaska	137	Allred (2004)
County Clare, Ireland	500 400	High and Hanna (1970)
Muskeg Inflow Cave, southeast Alaska	1670 1080	Allred (2004))
Slate Cave, southeast Alaska	180	Allred (2004)
Yarrangobilly, NSW, Australia	200	Smith *et al.* (1995)

CAVE DEVELOPMENT IN FLUVIOKARST

Caves – here considered to be master trunk caves related to surface base-level streams – have a three-stage development. (1) The initiation phase is the evolution of an initial mechanical fracture to a critical-size protoconduit about one centimeter in aperture. (2) The enlargement phase takes the protoconduit up to the meters to tens of meters diameter of a typical cave passage. (3) The stagnation and decay phase is that period after the cave passage has been drained and abandoned by lowering base levels. As the stagnation phase progresses, entrances are developed and process of collapse, speleothem growth, and sediment infilling choke off the once continuous conduit. Deepening of surface valleys breaks the cave into fragments.

The initiation phase is almost purely chemical. Nearly saturated water percolates along alternative paths in the carbonate rock, slowly enlarging them. The initiation phase ends when one pathway becomes sufficiently large to permit critically undersaturated water to pass completely through the aquifer. As a result, the final layout of the conduit system is largely determined during the initiation phase. The initiation phase is particularly amenable to geochemical modeling and some very elegant models have been constructed (Dreybrodt *et al.,* 2005). The time scale for the initiation depends on assumed initial conditions but appears to be in the range of 10,000 to 20,000 years.

The enlargement phase is largely independent of outside factors. The rate of retreat of passage walls can be described by the Palmer-Dreybrodt equation (Palmer, 1991).

$$S = \frac{31.56\,k\left(1-\frac{C}{C_S}\right)^n}{\rho_R} \qquad [3]$$

S is the rate of wall retreat in cm/yr. Some calculations for passage

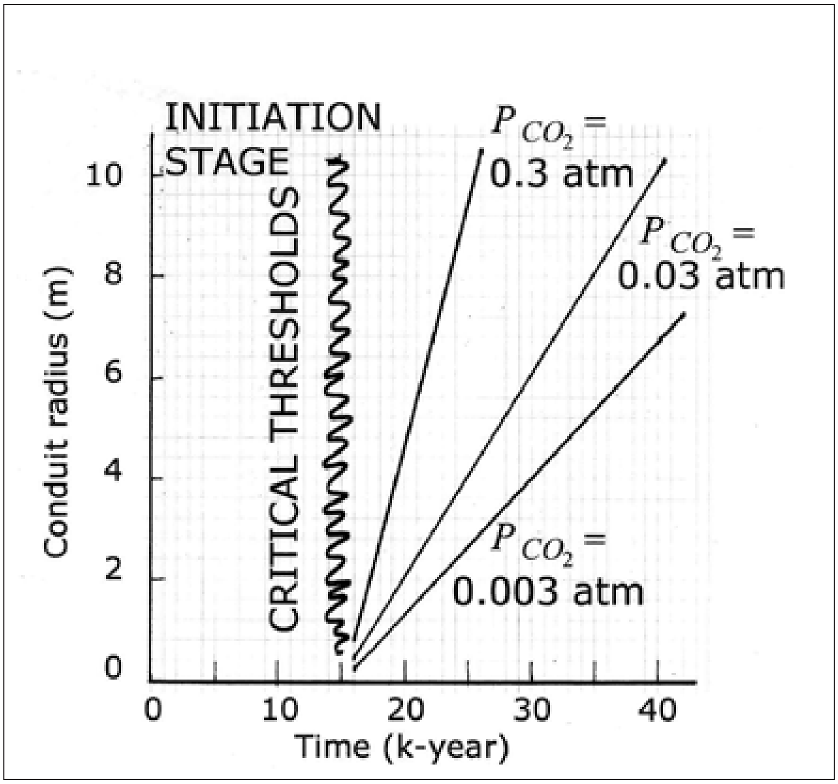

Fig. 2: Enlargement phase for typical conduits assuming various carbon dioxide partial pressures based on the Palmer-Dreybrodt equation.

enlargement are plotted in Fig. 2. The rate constant, k, was taken from Palmer (1991). The rock density, ρ_R was set equal to 2.65 g/cm^3. The reaction order, n = 1, in the fast dissolution regime. The only environmentally sensitive parameter is the saturation concentration of calcium carbonate which depends on the carbon dioxide partial pressure. Figure 2 shows the passage enlargement rates expected for a reasonable range of CO_2 pressures. Although the details are site-specific, even rough calculations suggest that 50,000 to 100,000 years are sufficient to allow a master cave to develop.

The relationship between hydraulic gradient, h_f/L, discharge, Q, and passage radius, R, is given by a form of the Darcy-Weisbach equation

$$\frac{h_f}{L} = \frac{f\,Q^2}{4\pi^2\,g\,R^5} \qquad [4]$$

Some maximum gradients that can be supported by a given size conduit are plotted in Figure 3 for a selection of discharges.

Because of the low hydraulic resistance of conduit systems, the elevation difference between the headwaters and the downstream reaches of surface streams can provide sufficient head to drive the cave-forming process. By this process of autopiracy, caves develop beneath surface valleys (or more often in the valley walls) and drain off the flow from the surface stream. Such caves generally have flatter gradients than the valleys that they underdrain.

Unlike karst surfaces or surface valleys which are continuously evolving, caves remain as fixed elevation markers and are the only features of the karst landscape for which the age is locked in. Caves may ride upward with tectonic uplift, but otherwise remain fixed as the surface landscape falls around them. This is the stagnation and decay phase in the cave's history and is the phase in which entrances are developed and the once-continuous conduit is fragmented as the surface lowers and valleys deepen. In terms of importance as biological habitat, the final stage is very important. Unfortunately, the details of the conduit decay of the conduit depends on local circumstances does not lend itself to numerical analysis.

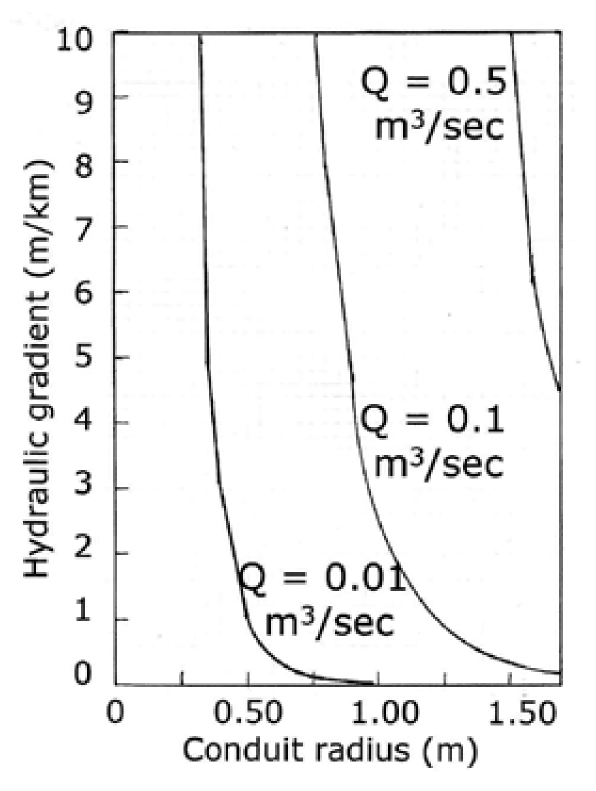

Fig. 3: Supportable hydraulic head as a function of conduit radius for various discharges. The Darcy-Weisbach friction factor, f = 100. The gravitational acceleration, g = 9.8 msec^{-1}.

AGE RELATIONSHIPS IN THE PLATEAU FLUVIOKARST SETTING

The Cumberland Plateau is the southern-most extension of the great Appalachian plateaus that extend from New York State into Alabama. The Cumberland Plateau in Tennessee and Alabama is an upland of low-dip Mississippian rocks. The plateau is capped with a highly resistant quartzite which provides a reference elevation at about 550 to 600 meters. The denudation of the resistant quartzite is very slow, 3-5 mm/ka, according to Anthony and Granger (2004). The plateau is bounded by a pronounced escarpment into which deep valleys (known locally as "coves") have been incised. At the base of the western escarpment is a karst surface known as the Highland Rim. The doline surface of the Highland Rim extends into many of the deeper coves. Mississippian limestones underlie the valley walls of the coves and much of the Highland Rim (Fig. 4).

The downcutting rate of one incised valley, that of the East Fork of the Obey River in north-central Tennessee was first calculated from magnetic reversals in the sediments of one of the caves in the valley wall (Sasowsky *et al.*, 1995). This number was revised when cosmogenic isotope dating of the same cave showed that

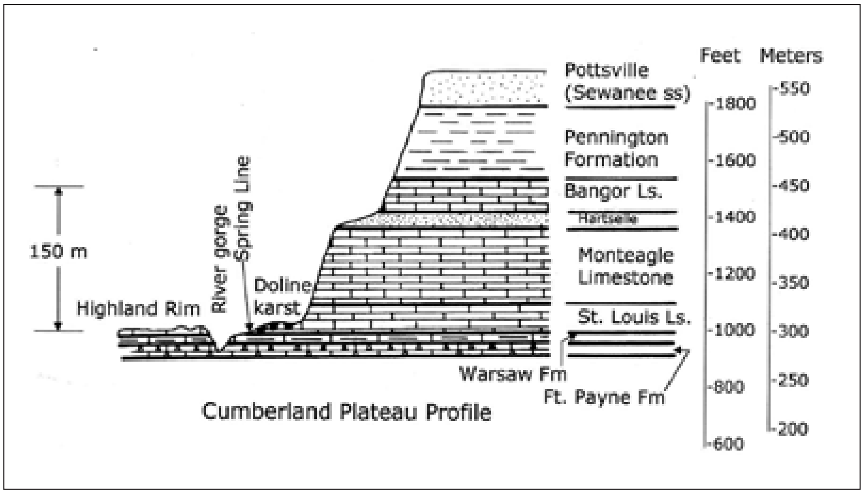

Fig. 4: Schematic cross-section through the western escarpment of the Cumberland Plateau. Thicknesses of individual beds are nominal values; bed thicknesses vary considerably over short distances (Milici et al., 1979).

the paleomagnetic measurements referred to an earlier reversal (Anthony and Ganger, 2004). The revised value of 30 mm/ka (Table 1) is similar the downcutting rate of other moderate size rivers and also very similar to the expected denudation rate.

The Highland Rim surface at the base of the western escarpment has nearly eroded to the bottom of the carbonate sequence. It all about 150 meters of limestone have been removed. If the Highland Rim is raised according to the 30 mm/ka denudation rate, approximately 5 million years ago, the erosion surface was at the top of the limestone. The sediments in Big Bone Cave were dated at 5.7 Ma (Anthony and Granger, 2004) and it was claimed that this date represents a time when the Cumberland River was flowing at the elevation of the Highland Rim.

AGE RELATIONSHIPS IN APPALACHIAN VALLEY FLUVIOKARST SETTING

The karst surfaces of the Great Valley and Valley and Ridge Provinces of the folded Appalachians are breached anticlines. Deep erosion along the anticlines has exposed the Ordovician and Cambrian limestones and dolomites which now form the valley floors. The more resistant quartzites on the flanks of the anticlines remain as long nearly-parallel ridges bounding the valleys (Fig. 5). Contemporary surface streams have downcut 50 to 75 meters into the valley surface. There must have been a time when the anticlines were first breached to expose the carbonate rocks to denudation. Figure 6 shows the sequence of events (without time scale) and includes the recognized erosion surfaces identified in central Pennsylvania.

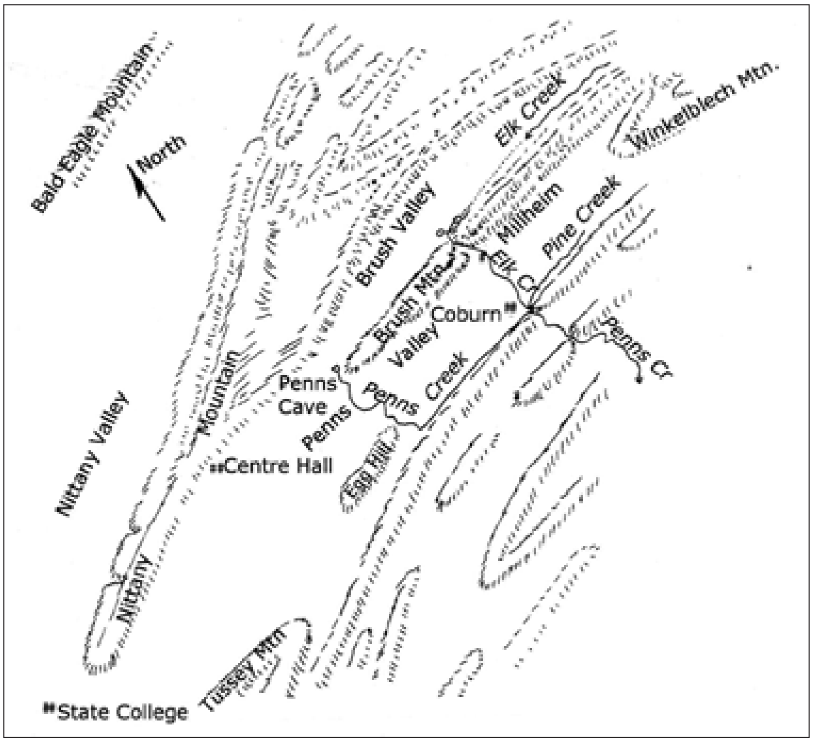

Fig. 5: Sketch showing topographic relations in central Pennsylvania. Ridges are supported by resistant quartzite; most of the valley floors are underlain by Cambrian and Ordovician carbonate rocks. After Deike (1961).

The Nittany Valley near State College, Pennsylvania is an interfluve area. Here are found residual soils

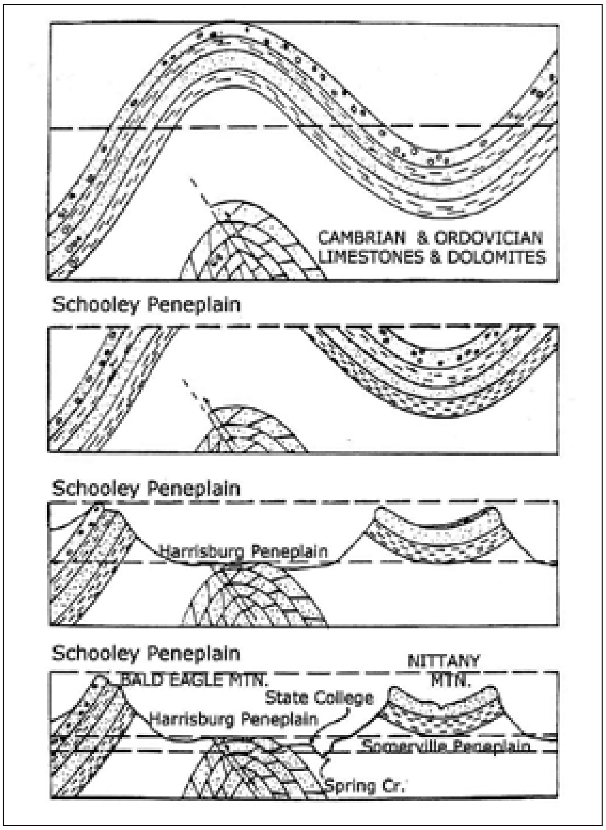

Fig. 6: The evolution of the Nittany Valley in central Pennsylvania showing traditional erosion surfaces. After Gardner (1980).

with thicknesses averaging 50 meters. On the assumption that these are let-down soils consisting of the insoluble residues from the dissolution of the carbonate rocks, a calculation based on insoluble residue content and bulk density suggests that more than 425 meters of carbonate rock were removed to accumulate this thickness of soil (White and White, 1991). On the (quite possibly unreasonable) assumption that the denudation rate has been 30 mm/ka, the removal of 425 meters of carbonates would require on the order of 14 million years, placing the beginning of what has been a uniform denudation process in mid-Miocene time. The present relief between the valley floor and the ridge tops is about 250 meters. The carbonate surface at the beginning of the denudation process would be 175 meters above the present-day ridge tops. However, the estimated denudation would not include the entire carbonate section so it does not represent the breaching of the anticline which must have taken place earlier.

The accordant ridge-lines of the folded Appalachians are often taken to represent the Schooley Peneplain. If these quartzite-topped ridges erode as slowly as similar rocks on the Cumberland Plateau, the limestone would have filled the valley to the level of the ridge tops only 8 – 9 Ma ago. The age of the Schooley Peneplain would be much less than many ages that have been assigned to it, some setting the age as far back as the Jurassic.

The valley floors which represent the Harrisburg Survey have been dissected by present day streams to produce an internal relief of about 60 meters. The caves of the Valley and Ridge Province are found within this interval. Some are inlet caves with high gradients due to the rapid downcutting of sinking streams. Others are fragments of base-level conduits. Given the observed rates of stream downcutting, the time span available for the development of these caves is 2 – 3 million years.

CONCLUSIONS

Although doline plains give the impression of stable erosion surfaces, denudation measurements suggest the rate of lowering is comparable to the rate of downcutting of surface valleys. The horizontal surface is maintained because of the internal drainage through the dolines. It is, therefore, problematic to attempt to assign and age to karst surfaces.

Cave development is very rapid compared with the evolution of the surface landscape. Caves in tectonically stable areas serve as better markers of temporarily stable pauses in base level lowering than do either surface streams or the elevations of karst "erosion surfaces". This conclusion has been suspected at least since the work of Davies (1960) but was given much stronger support by recent cosmogenic isotope dating (Granger *et al.,* 1963; Anthony and Granger, 1964). It is also supported by the present geochemical calculations and mass balance arguments.

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COBISS: 1.01

CAVE AND KARST EVOLUTION IN THE ALPS AND THEIR RELATION TO PALEOCLIMATE AND PALEOTOPOGRAPHY

RAZVOJ JAM IN KRASA V ALPAH V LUČI PALEOKLIME IN PALEOTOPOGRAFIJE

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Abstract UDC 551.435.84(234.3)

Philippe Audra, Alfredo Bini, Franci Gabrovšek, Philipp Häuselmann, Fabien Hobléa, Pierre-Yves Jeannin, Jurij Kunaver, Michel Monbaron, France Šušteršič, Paola Tognini, Hubert Trimmel & Andres Wildberger: Cave and Karst evolution in the Alps and their relation to paleoclimate and paleotopography

Progress in the understanding of cave genesis processes, as well as the intensive research carried out in the Alps during the last decades, permit to summarize the latest knowledge about Alpine caves. The phreatic parts of cave systems develop close to the karst water table, which depends on the spring position, which in turn is generally related to the valley bottom. Thus, caves are directly linked with the geomorphic evolution of the surface and reflect valley deepening. The sediments deposited in the caves help to reconstruct the morphologic succession and the paleoclimatic evolution. Moreover, they are the only means to date the caves and thus the landscape evolution. Caves appear as soon as there is an emersion of limestone from the sea and a water table gradient. Mesozoic and early tertiary paleokarsts within the alpine range prove of these ancient emersions. Hydrothermal karst seems to be more widespread than previously

Izvleček UDK 551.435.84(234.3)

Philippe Audra, Alfredo Bini, Franci Gabrovšek, Philipp Häuselmann, Fabien Hobléa, Pierre-Yves Jeannin, Jurij Kunaver, Michel Monbaron, France Šušteršič, Paola Tognini, Hubert Trimmel & Andres Wildberger: Razvoj krasa in jam v Alpah v luči paleoklime in paleotopografije

V članku predstavimo nova spoznanja o razvoju alpskih jam. Ta temeljijo na sintezi novih dognanj o procesih speleogeneze in rezultatih intenzivnih terenskih raziskav v Alpah v zadnjih desetletjih. Razvoj freatičnih delov jamskih sistemov poteka v bližini freatične površine, ki je vezana na položaj izvirov, ti pa so vezani na dno alpskih dolin. Torej je razvoj jam neposredno vezan na geomorfološki razvoj terena in poglabljanje dolin. Jamski sedimenti nosijo informacijo o zaporedju morfoloških in klimatskih dogodkov. Še več, določanje starosti jam in poteka razvoja površja, je možno edino z datacijo jamskih sedimentov. Razvoj jam se začne ob emerziji apnenca in vzpostavitvi hidravličnega gradienta. Mezocojski in zgodnje terciarni paleokras v območju Alp so dokaz starih emerzij. Hidrotermalni kras je očitno bolj razširjen, kot so domnevali v preteklosti. Te jame so bile pozneje preoblikovane z meteorno vodo, ki je zabrisala sledi zgodnjega hipogenega zakrasevanja. Ledeniki zavi-

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Received/Prejeto: 01.12.2006

presumed. This is mostly due to the fact that usually, hydrothermal caves are later reused (and reshaped) by meteoric waters. Rock-ghost weathering is described as a new cave genesis agent. On the contrary, glaciers hinder cave genesis processes and fill caves. They mainly influence cave genesis indirectly by valley deepening and abrasion of the caprock. All present datings suggest that many alpine caves (excluding paleokarst) are of Pliocene or even Miocene age. Progress in dating methods (mainly the recent evolution with cosmogenic nuclides) should permit, in the near future, to date not only Pleistocene, but also Pliocene cave sediments absolutely.

Key Words: Karst, Cave genesis, Alps, Glaciations, Messinian event, Paleoclimate, Paleotopography.

rajo procese speleogeneze in zapolnjujejo jame. Na razvoj jam vplivajo posredno, preko poglabljanja dolin in brušenja površja. Novejše datacije kažejo, da so številne jame v Alpah pliocenske ali celo miocenske starosti. Nove datacijske metode – predvsem metoda kozmogenih nuklidov – bodo omogočile absolutno datacijo sedimentov do pliocenske starosti.

Ključne besede: kras, geneza jam, Alpe, poledenitve, mesinska stopnja.

INTRODUCTION

Progress in cave exploration and cave genesis studies (Audra 1994, Jeannin 1996, Palmer 2000) permitted to recognize the potential of caves for the study of landscape evolution, valley deepening and thus erosion rates and climate changes (Häuselmann *et al.* 2002; Bini *et al.* 1997). Most of the information that is sheltered within the cave's morphology and sediments is no more available at the surface, mainly due to the intensive erosion, especially during the glaciations.

This article gives information about cave genesis and its potential for the reconstruction of the evolution and timing of the landscape: Part I presents the latest results concerning cave genesis and their link with the landscape. Part II deals with new concepts about early cave genesis, including pre-existing karst systems (paleokarst), hydrothermal karst, and pseudokarst. Many caves are older than the glaciations and glaciers generally are rather hindering cave genesis processes. Part III consequently presents evidences supporting a high age of many cave systems. In Part IV, ages obtained by different dating methods prove that karst genesis in the Alps started far before the Quaternary, as far as the Cretaceous.

SETTING

The Alpine belt extends from Nice (France) to Vienna (Austria) into seven countries (France, Switzerland, Italy, Liechtenstein, Austria, Germany and Slovenia). Karsts and caves are found in each country, the largest karst areas being located in periphery (Fig. 1). All massifs are dissected by deeply entrenched valleys which divide continuous structures into different physiographic units. Annual precipitation range from 1500 to more than 3000 mm.

The French Western Prealps consist of folded and thrusted massifs of mainly Cretaceous rocks. The elevation ranges generally between

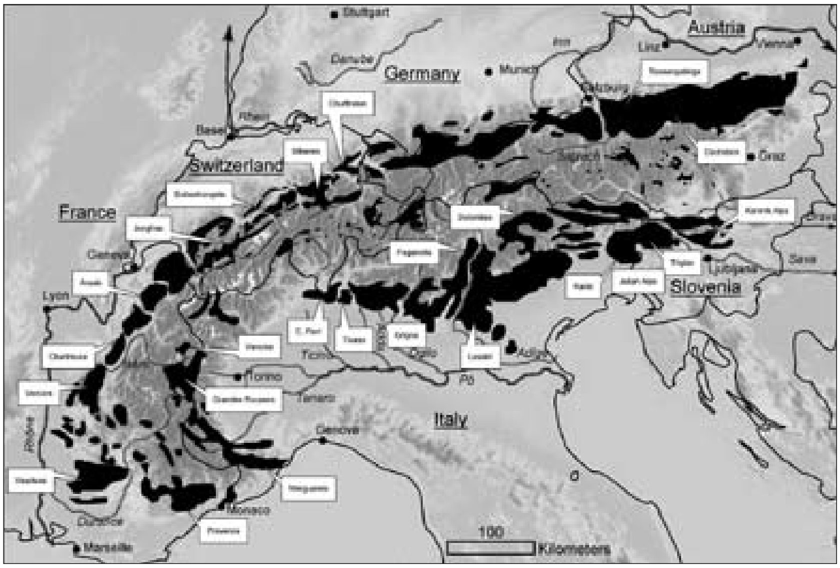

Fig. 1: Map of the alpine karsts (dark color) with location of the mentioned massifs (karst areas after: Buzio & Faverjon 1996; Mihevc 1998; Stummer & Pavuza 2001; Wildberger & Preiswerk 1997. Map: D. Cardis).

1000 and 2000 m. The Vercors displays a landscape of ridges and valleys, whereas the Chartreuse presents a steep, inverted relief.

The Central Swiss Alps harbors the highest alpine karst areas at Jungfrau (3470 m ASL). The Siebenhengste (2000 m ASL) and the Hölloch-Silberen (2450 m ASL) consist of nappes of Cretaceous and Eocene rocks.

The Italian Southern Alps are located to the south of the Insubric Line. The carbonate rocks range in age from Carboniferous to Cretaceous-Eocene. They are deformed and displaced by S-vergent thrusting and large scale folding. The elevation ranges from 200 m to 2400 m ASL.

The Northern Calcareous Alps in Austria are composed of a slightly folded succession of Trias limestones and dolomites with a thickness of more than 1000 m. Large plateaus extend from 1800 to 2200 m ASL.

In the Slovenian Alps, the Julian and the Kamnik Alps correspond to the roots of the Austrian nappes. Thus the landscape is often similar, with plateaus and narrow steep ridges dominated by high peaks reaching more than 2800 m ASL.

GENERAL CONCEPTS OF CAVE GENESIS

The basics of cave genesis are beyond the scope of this paper. The reader can refer to the most comprehensive and up-to-date work *Speleogenesis: Evolution of Karst Aquifers* (Klimchouk *et al.* 2000).

GENESIS OF CAVES AND MORPHOLOGY OF PASSAGES RELATED TO WATER TABLE POSITION

Water flowing into limestone corrodes and erodes the rock. Driven by gravity and geological structure, it flows down more or less vertically, until it reaches either the karst water table or impermeable strata. Then it continues flowing more or less horizontally towards the spring, collecting water from other lateral passages. Water flowing in the vadose (unsaturated) zone can only erode the floor of a gallery creating a meandering canyon. On the other hand, water flowing within the phreatic (saturated) zone corrodes over its whole cross-section, giving a rounded cross-section (Fig. 2). The morphologies that are preserved once the watercourses have been abandoned give information about the prevailing position of the phreatic zone during the genesis of the galleries.

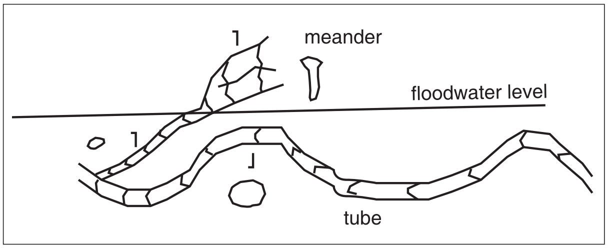

Fig. 2: An undulating phreatic tube is co-fed by a vadose meandering canyon, whose shape turns into a tube below the floodwater table. The arrow marks the transition from vadose to phreatic.

RECOGNITION OF CAVE GENESIS PHASES AND RELATION TO THE SPRING

Within the saturated zone, two geometric types of conduits prevail (Ford 1977, 2000): 1) the *water table caves,* represented by horizontal conduits located at the top of the saturated zone; 2) the *looping caves,* represented by vertically lowering and rising conduits, whose amplitude may reach as much as 300 m, or even more.

A "phase of cave genesis" corresponds to the network of active conduits related to a given (paleo)spring. As springs move together with valley bottoms, we usually find many different "phases of cave genesis" in a given karst region.

As described on figure 2 the transition between phreatic conduits (elliptical shape) and vadose ones occurs at the top of the epiphreatic zone, i.e. more or less at the top level reached by water during highwater stages. Due to headlosses, highwater level is inclined towards the outlet of the system, namely the karst spring (Jeannin 2001, Häuselmann 2003). Most of the time conduits are located within a given range of altitudes (sometimes more than 300 m) below the (inclined) water table limit. These conduits go up and down (hence their name: "loops") within this range and towards the spring. Sometimes main conduits of a given phase can be followed for kilometers and display a phreatic morphology all along. Sometimes the highest passages clearly show vadose entrenchment because they were located higher than the top of the epiphreatic zone, at least most of the time.

Reality is a little more complicated that exposed here (see Häuselmann *et al.* 2003 for instance), but the principle is the same. The main exceptions to this model, linking quite directly the phases of cave genesis to the (paleo)spring positions, i.e. valley bottom, occur when impervious barriers dam water somewhere inside the aquifer.

SUCCESSION OF CAVE GENESIS PHASES, CAVE LEVELS RECORDING BASE LEVEL CHANGES

If the spring lowers gradually, the cave system behind also adapts gradually by entrenchment to the new situation: no distinct phases exist. If the spring lowers in a stepwise manner, followed by a time of relative stability, the flowpath readjustment in the cave also occurs rapidly and a new cave genesis phase develops. Calculations show that, once a proto-conduit has been formed, caves may evolve very rapidly, in the order of 10'000 years, to reach penetrable size (Palmer 2000). Therefore, after a new entrenchment of a valley, pre-existing or newly created *soutirages* (Häuselmann *et al.* 2003) allow for the water to reach the spring level quite quickly and a new water table, i.e. phase of cave genesis is created (Fig. 3). Former conduits, perched in the vadose zone after the deepening of the karst system, are abandoned and remain dry (fossil passages). Provided that the cave genesis phases reflect the deepening of the valleys through time, they give information for the reconstruction of paleorelief. Equivalent information at the surface is usually no longer present, mostly due to river or glacier erosion.

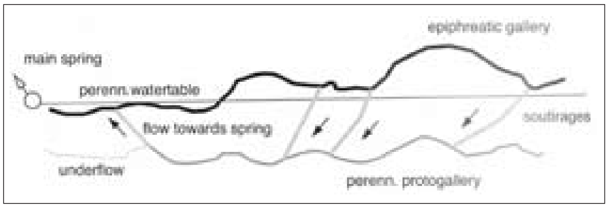

Fig. 3: Schematic flow system. Black = main (epiphreatic) gallery; light grey = soutirages (downward) and upflow (upward); dark grey = perennial phreatic conduit.

In some cases, the base level may rise again after a period of deepening (e.g. post-messinian infilling of the overdeepened canyons in the southern part of the Alps; Felber & Bini 1997). This caused a flooding of pre-existing karst systems and a reactivation of previously vadose or abandoned passages (Tognini 2001).

THE RELATION BETWEEN MORPHOLOGY, CLIMATE, AND SEDIMENTS

Cave morphology depends on the position of the epiphreatic water table. The size of the passage, however, depends (among others, mostly geological factors) on time and flow rate. Worthington (1991) puts forward that there is an "equilibrium size" of a phreatic passage for a given flow rate. After this size is reached, the passage hardly grows anymore, and a growth above this size is mainly dependent on an increase in flow rate, either by capturing another catchment, or related to an increase in precipitation. For example, in the Siebenhengste system, the size of the main conduits doubles between two phases (700 m and 660 m). This very probably corresponds to the capture of the Schrattenfluh catchment, which significantly increased the size of the catchment area (Fig. 4). Conversely, a reduction in the catchment area due to valley entrenchment produces rearrangement of the cave system. Newly formed passages will be smaller than in the previous phase.

Beside the size of the conduits, sediments also provide direct information about the flow velocities, i.e. discharge rates in the conduits. Grainsize distribution of cave sediments and conduit size make it possible to assess paleodischarge rates quite precisely.

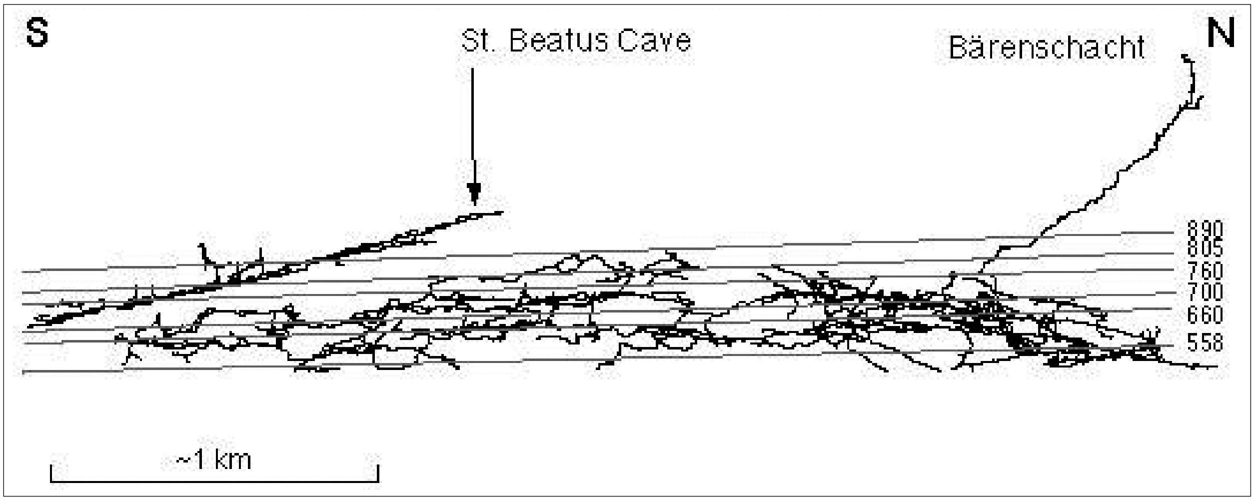

Fig. 4: N-S-projection of Bärenschacht and St. Beatus Cave with the recognized phases. The numbers are the elevations (in m ASL) of the corresponding spring. Phase 558 is the present one.

NEW CONCEPTS ABOUT CAVE GENESIS

THE INFLUENCE OF EARLY PHASES: PRE-EXISTING KARST SYSTEMS (PALEOKARST), HYPOGENIC KARST AND PSEUDOKARST

Syn- and post-sedimentary paleokarsts

"Paleokarst" are features that are not related to any present water circulation and completely obstructed. Since most of the caves (including fossil tubes) are related to present rivers and valleys, they are not considered as paleokarst.

Some paleokarsts have been formed during or immediately after the sedimentation of carbonate platforms (Upper Triassic, for example Calcare di Esino/Grigna; Dachsteinkalk/Northern Limestone Alps). Dolines, pockets and red paleosoils interfere within the cyclic sedimentation of the so-called loferitic succession. Under a premature diagenesis, dissolution and concretion produced evinosponges (Bini & Pellegrini 1998) and dolomite-filled fractures that contain iron oxides from paleosoils. In the Julian Alps, paleokarstic conduits have been filled with carbonate mud and later lithified, so that – presently – a paleoconduit is just a portion of somehow differently colored solid rock. Other paleokarst had been set up after the emersion of the limestone strata. They are fossilized by Jurassic sediments (Swiss Prealps, Julian Alps), Upper Cretaceous sandstone (Siebenhengste), Eocene sands (Vercors), or Miocene conglomerates (Chartreuse).

Those paleokarsts features may form highly porous discontinuities that may have guided the placement of later cave systems.

- Hydrothermal caves related to tectonic build-up

Some caves have a hydrothermal origin, which can be recognized after their typical corrosional cupolas originating from convection cells and their sediments like large calcite spar (Audra *et al.* 2002a; Audra & Hofmann 2004; Bini & Pellegrini 1998; Sustersic 2001; Wildberger & Preiswerk 1997). Those hydrothermal upflows are usually located near huge thrust and strike-slip faults. Such karstifications created well connected cave systems which later had generally been re-used by "normal" meteoric water flow after uplift above the base level. Since this change has mostly deleted the marks of their origin, they are only conserved when rapidly fossilized.

- Pseudokarst creating rock-ghosts (cave phantoms)

Models of apparent karst features created by processes other than pure dissolution are called pseudokarst. The phantomisation (rock-ghost weathering) was recently described as a major agent of karstification in impure limestones (Vergari & Quinif 1997). In such limestones flow remained guided by fractures but partially occurred in the matrix around the fracture. In a favorable context, warm and humid climate and long-term stability of the base level, this type of flow could dissolve the limestone cement, but impurities remained in place, in place, preserving the parent material tex-

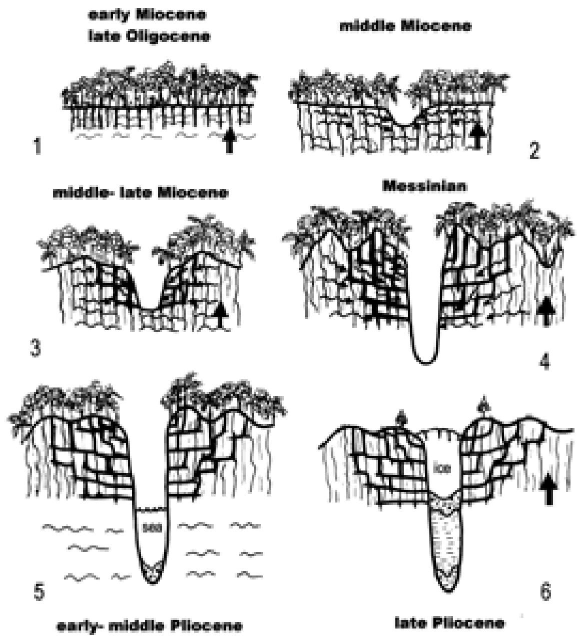

Fig. 5: Pseudoendokarst cave system in the marly-silicated Moltrasio Limestone of Mt. Bisbino, Lake of Como (Tognini 1999, 2001).

1 – Late Oligocene-Early Miocene: The tectonic structure was achieved during the neo-alpine phase. Uplift raised the area above sea level, producing a gentle relief dissected by valleys.

2-3 – Middle-Late Miocene: According to very long base level stability under warm and humid climate, deep soils develop. With very low gradient and water movements, weathering progressively penetrates deeply into the water-filled zone. Uplift gradually deepens the valleys.

4 – Messinian: Valleys dramatically entrench, water table lowers, inducing an active flow. The weathered rock-ghosts are eroded away by piping, causing the formation of cave systems, which extend progressively in size and complexity. Steep hydraulic gradients prevent a further weathering at depth. The present remnants of rock-ghosts mark the maximal depth (700 m) reached by weathering that corresponds to the present 500-600 m altitude. With a continuous entrenchment, pseudoendokarsts become perched and only "classical" cave system develop below.

5 – Early-Middle Pliocene: Pseudoendokarstic caves systems stopped developing.

6 – Late Pliocene-Quaternary: Sequences of erosion and deposition are developing (e.g. lacustrine caves sediments recording the presence of the Adda glacier close to the caves entrances; speleothem deposition is enhanced during interglacials).

tures and structures. Rock porosity increased up to 35%, causing a dramatic increase in hydraulic conductivity. This weathered material is called rock-ghosts, or phantoms. The downstream part of such systems, close to the surface, can be eroded by piping because of the absence of cement. This may produce caves (Tognini 2001). Some peculiar features may point out their different origin (weathered walls, regularly spaced 3D network, brisk change in passage morphology, dead-end at gallery terminations with conservation of the ghost of the weathered host-rock). After the piping event, the rock-ghosts remained perched on an unweathered rock, in which only "classical" karst processes adapted to the new base level began to be active.

COMPLEX RELATIONSHIPS TO GLACIERS

Some older theories supported a direct relationship between glaciations and genesis of cave systems through glacial meltwater. However, recent datings (U/Th, paleomagnetism) and fieldwork has clearly proven that many caves are older than the glaciations. The role of the glaciers seems to be mostly limited to valley deepening, base level rising during glacial periods and related sedimentation in the conduits (Audra 1994, 2004; Bini 1994; Häuselmann 2002). The genesis of new caves only takes place in certain contexts, where the glacial influence often is only indirect.

Glacial processes mainly fill caves

In the Alps, glaciers were temperate with flowing water. As valley bottoms were filled by ice, base levels raised all along the valleys. Furthermore, tills obstructed the preexisting springs. Therefore, a large glacier body may have raised karstwater level by several hundreds of meters, for instance 500 to 600 m in the Bergerhöhle/Tennengebirge (fig. 6). Such a rising karstwater level reactivated many older conduits, increasing drastically flow cross-sections and leaving only restricted flow velocities in each conduit. Fine-grained carbonate-rich sediments found in very many caves are good indicators of these stages. Since this carbonate flour could obviously not be dissolved by the natural aggressivity of the water, it implies that a chemical erosion of cave walls was very probably negligible. This is confirmed by old speleothems, preceding such phases, that are hardly dissolved (Bini *et al.* 1998). Mechanical abrasion in the flooded zone is also improbable because of the small flow velocity. Therefore, it must be postulated that the genesis of deep-seated cave conduits is not favored by glaciations (Audra 1994, 2001a; Bini *et al.* 1998; Maire 1990).

In contrast, interglacials induce the presence of vegetation and soil at the surface. Both elements greatly enhance the CO_2 content of the water (Bögli 1978), and reduce the amount of debris washed into the cave. So, water has a much higher initial acidity and can therefore enlarge caves (Audra 2004). During the same time, water from the fine fissures and matrix, which entered the system below the soil and epikarst, where pCO2 is high, is oversaturated with respect to calcite when it reached a (ventilated) cave passage. Therefore many speleothems formed. In some low valleys with flat bottoms, lakes filled the previously overdeepened valley and kept the water table high. Therefore, in spite of the sometimes considerable valley deepening by glaciers, the karst water table could never reach the total depth of the valley, blocking thus the genesis of deeper cave levels (Kanin). Nevertheless, in the South Alpine domain, the fluvial valley deepening may have allowed deep (and today submerged) karstification.

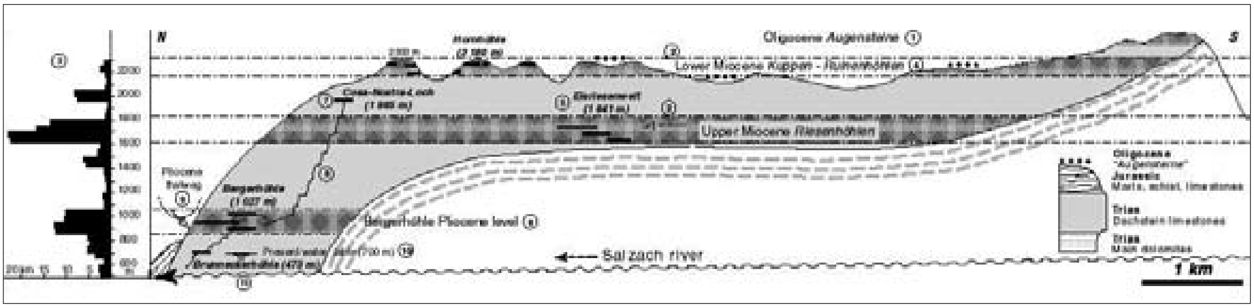

Fig. 6: The Cosa Nostra-Bergerhöhle system/Tennengebirge, Salzburg Alps (Audra et al. 2002b). To the left (3), relationship between cave passage altitude and old karst levels. Karst development began during the Oligocene beneath the Augensteine (1). During the Miocene, horizontal systems developed with alpine water inputs (2), showing different levels (3) related to successive phases of stability: Ruinenhöhlen (4) and Riesenhöhlen (e.g. Eisriesenwelt – 5). Following Pliocene uplift, alpine systems developed (e.g. Cosa Nostra-Bergerhöhle – 6). Horizontal tubes at the entrance correspond to a Miocene level (7). A shaft series (6) connect to horizontal tubes from Bergerhöhle-Bierloch (8), corresponding to a Pliocene base level (9). The present water table at 700 m (10) pours into Brunnecker Cave, which connects to the Salzach base level (11).

	Cave system	*Massif*	*Difference in heigh, horizontal cave levels / present base level (m ASL)*	*Dating*	*Allogenic fluvial pebbles*	*Old sediments - weathered soils - presently removed covers*	*Partly eroded catchment, large dimensions not related to present topography, truncated by erosion*	*Presumed age of the system*	*References*
France	Ch. du Goutourier	Dévoluy	2300 / 875 m	> 780 ka (paleomag.)		Tertiary weathered soils		Upper Miocene?	Audra 1996
	Gr. Vallier	Vercors	1500 / 200 m	Tertiary, Lower Pleistocene glacial varves (paleomag.)		Tertiary weathered soils	yes	Upper Miocene	Audra & Rochette 1993
	Réseau de la Dent de Crolles	Chartreuse	1700 / 250 m	> 400 ka (U/Th)		Cretac. sandstones	yes	Upper Miocene?	Audra 1994
	Gr. Théophile	Gdes Rousses	1900 / 1850 m	95 ka (U/Th)				Middle Pleistocene	Audra & Quinif 1997
	Gr. de l'Adaouste	Provence		Stratigraphic correlation		Miocene pebbles	Artesian	Tortonian	Audra & al. 2002
	Système du Granier	Chartreuse	1500 / 1000 m	> 1-1,5 Ma (^{234}U / 2^{38}U equilibr., paleomag.) 1,8-5,3 Ma (cosmonucleides)	Upper cretac. and oligo. limest.	- Cretac. sandstones - weathered soils	yes	Upper Miocene?	Hobléa 1999; Hobléa & Häuselmann 2007
Switzerland	Beatushöhle – Bärenschacht	Siebenhengste	890 / 558 m	> 350 ka (U/Th)				Pleistocene	Häuselmann 2002
	Siebenhengste	Siebenhengste	1900 / 558 m	4.4 Ma (cosmonucleides)				Pliocene	Häuselmann & Granger 2005
	Jochloch	Jungfrau	3470 m	Lower Pleistocene? (palynology)			practically no catchment today	Lower Pleistocene	Wildberger & Preiswerk 1997
	Ofenloch	Churfisten	655 / 419 m	> 780 ka (paleomag.)				Pliocene	Müller 1995
	Hölloch–Silberensystem	Silberen	1650 / 640 m	>350 ka (U/Th), <780 (paleomag)				Lower Pleistocene?	
Italy	Battisti	Paganella	1600 m	> 1-1,5 Ma (^{234}U / ^{238}U equilibr.)		Cherts from Eocene limestones	yes	Oligo-Miocene	
	Conturines	Dolomite	2775 m	> 1-1,5 Ma (^{234}U / ^{238}U equilibr.)			yes	Oligo-Miocene	Frisia & al. 1994
	Capana Stoppani, Tacchi-Zelbio	Pian del Tivano	900 / 200 m	> 350 ka (U/Th)	Boulders from glacial sinkholes		yes	Oligo-Miocene	Tognini 1999, 2001
	Gr. dell'Alpe Madrona	Mte Bisbino	1000 / 200 m	> 350 ka (U/Th)				Miocene	Tognini 1999, 2001
	Covoli di Velo Ponte di Veia	Mte Lessini		33-38 Ma (K/Ar)		yes		Eocene and Oligocene	Rossi & Zorzin 1993
	Gr. Masera	Lario	200 / 361 m	≈ 2.6 to 7.2 Ma (cosmonucleides)	Fluvial pebbles			Pliocene or older	Häuselmann unpub. Bini & Zuccoli 2004
	Gr. On the Road	Campo dei Fiori	805 / 300 m	> 1-1,5 Ma (234U / 238U equilibr)				Oligo-Miocene	Uggeri 1992
	Gr. Via col Vento	Campo dei Fiori	1015 / 300 m	> 350 ka (U/Th) Upper Plio. glacial sediments				Oligo-Miocene	Uggeri 1992
	Gta. sopra Fontana Marella	Campo dei Fiori	1040 / 300 m	Middle Pleistocene (micro-fauna)	Conglomerate with crystalline pebbles	Ferralitic soils	yes	Oligo-Miocene	Zanalda 1994
	Ciota Ciara – Cuitarun caves	Mte Fenara			Large miocene fluvial pebbles		yes	Oligo-Miocene	Fantoni & Fantoni 1991
Austria	Cosa Nostra-Bergerhöhle	Tennengebirge	1600-1000 / 500 m	> 780 ka (paleomag)	yes	Augensteine	yes	Miocene – Upper Pliocene	Audra & al. 2002
	Mammuthöhle	Dachstein	1500-1300 / 500 m		yes	Augensteine	yes	Miocene	Trimmel 1961, 1992; Frisch & al. 2002
	Eisriesenwelt	Tennengebirge	1500 / 600 m		yes		yes	Lower Pliocene?	Audra 1994
	Feichtnerschacht	Kitzsteinhorn	2000 / 1000 m	118 ka (U/Th)				Pliocene?	Audra 2001, Ciszewski & Recielski 2001
Slovenia	Poloska jama	Mt Osojnica	750 / 500 m				yes		
	Crnelsko brezno	Kanin	1400 / 400 m	> 780 ka (paleomag) Glacial varves					Audra 2000
	Snezna jama	Kamnik Alps	1600 / 600 m	1.8 to 3.6 or 5 Ma (paleomag)	yes	yes	yes	Miocene?	Bosak & al. 2002

Tab. 1: Synthesis of information about the quoted caves systems

As a conclusion, a warm climate induces passage growth and speleothem deposition, whereas a cold climate generally tends to obstruct the lower passages by sediments.

Glacial sediments covering older speleothems: cave systems may predate glaciations

Some cave sediments correspond to very old glaciations, according to paleomagnetic measurements that show inverse polarity: Ofenloch/Churfirsten (Müller 1995), grotte Vallier/Vercors (Audra & Rochette 1993), Crnelsko brezno/Kanin (Audra 2000). These sediments often overlie successions of alterites or massive flowstone deposits, which in turn prove the existence of a warm and humid climate, thus showing that the cave systems predate those glaciations. Some of the old speleothems are more or less intensely corroded by flowing water postdating their deposition.

Cave development and glacial activity

- ***Glacial abrasion at the surface and erosion in the vadose zone.*** At the surface, the glacial activity is without doubt responsible for the abrasion of a variable amount of bedrock (50-250 m), which has surfaced old conduits that previously were deeply buried. This is manifested by wide open shafts, cut galleries and arches. During glacial melt, meltwater disappeared into distinct sectors. As soon as fractures were connected to preexisting conduits, they enlarged quickly and thus formed the "invasion vadose shafts" (Ford 1977), which can reach several hundred meters of depth: Granier, Silberen, Kanin (Kunaver 1983, 1996). The effectiveness of such meltwater is mainly due to its velocity in the vertical cascades as well as their abrasive mineral load originating from bedrock and till material.

- ***Some new cave systems appeared in the intra-Alpine karst area due to glacial erosion.*** Thin limestone belts or marbles intercalated with metamorphic series were freed from their impervious cover by glacial erosion. Some caves are still in direct relationship with the periglacial flow, and act as swallowholes. Their morphology reflects the cascading waterflow and has a juvenile form: Perte du Grand Marchet/Vanoise, Sur Crap/Graubünden (Wildberger *et al.* 2001). At the Grotte Théophile/Grandes Rousses, U/Th datings evidenced that the cave was active at least along the two glacial-interglacial cycles that are marked by the sequence of passage-forming/filling with gravel/sinter deposition (Audra & Quinif 1997). Since cave development mainly occurred during interglacial, the effect of the glacier is only indirect, by eroding the impervious covers (Audra 2004).

- ***The lower phases of huge cave systems are indirectly generated by glacial valley-deepening.*** While the uppermost cave systems are often older than the glaciations *(infra),* the lower passages are often of Quaternary age, since they are related to valleys evidently deepened by glaciers. In this respect, glaciers are indirectly responsible for the creation of new cave passages (Siebenhengste, Chartreuse, Vercors). This strongly contrasts with the South Alpine domain, where valleys were deepened during the Messinian event. Here, glaciations contributed merely to the infilling of the preexisting valleys. Thus, most of the South Alpine cave systems are thought to be older than the glaciations.

MORPHOLOGIC AND TOPOGRAPHIC EVIDENCES FOR A HIGH AGE OF CAVE SYSTEMS

Some existing caves and karst features clearly correspond to a strongly different topography than today. They are therefore supposed to be older. In the following paragraphs, the position and morphology of caves are compared to today's landscape. Then cave sediment characteristics are presented and discussed. In a third part, links between caves and well-recognized paleotopographies are explained. All those indications are clear evidences for a high age of cave systems.

CAVE SYSTEMS VS. PRESENT TOPOGRAPHY

Perched phreatic tubes

Conduits with an elliptical morphology are sometimes perched considerably above the present base level (Tab. 1, 3rd column). They developed close to a paleo base level, long before today's valley deepening. At the Siebenhengste, the highest phases even show a flow direction opposite to the present one.

Caves intersected by current topography

Old perched caves are often segmented by a subsequent lowering of the surface. Two situations are usually found in the field:

- Old phreatic caves at the surface of karst plateaus, which have been eroded by glacial abrasion (Grigna, Dolomites, Triglav, Kanin, Tennengebirge…)
- Old phreatic caves along valley flanks, obviously cut by the lowering of the topography (Adda, Adige, Salzach, Isère): Pian del Tivano, Mt. Bisbino, Mt. Tremez-

zo, Campo dei Fiori (Southern Alps), Paganella (Dolomites).

Dimensions too large with respect to the present catchment and climate

The dimensions of some conduits are far too large compared to the present catchment area, thus proving that the older catchment areas had been much larger, but are now truncated by erosion (Eisriesenwelt/Tennengebirge (fig. 6); Antre de Vénus/Vercors; Snezna jama na Raduhi/Kamnik Alps, caves at Pokljuka and Jelovica plateaus at Julian Alps, Siebenhengste, Pian del Tivano, Campo dei Fiori/Southern Alps).

Spring location vs. present base level

If the position of a spring is not due to a geologic perching above an impervious layer, it has to be close to base level (see part I). However, in some cases springs did not lowered down to today's base level. In other cases springs are obviously located far below the base level. This can be explained by the following hypotheses:

- Some springs are perched, because the valley incision is very recent and rapid (Pis del Pesio/Marguareis).
- Others are presently submerged below the base level and hidden by alluvial fill or till (Emergence du Tour/Aravis; Campo dei Fiori). They were set into their place before the base level raised and they continue to function due to the high transmissivity of the sediment fill.

A specialty is given when old vertical vadose caves are suddenly stopped by the present water table, proving that the horizontal drains are at much greater depth and completely drowned. Typical vadose morphologies (speleothems, karren) are known in some drowned conduits (Grotta Masera, Grotta di Fiumelatte/Lake of Como; Fontaine de Vaucluse/Provence). Here, the spring location is adapted to the present base level, but the caves are proof that the base level may, in some cases, also rise. This is especially true for areas affected by the Messinian crisis (Bini 1994; Audra & al. 2004).

CAVE SEDIMENTS SHOWING EVIDENCE OF A REMOTE ORIGIN, DIFFERENT CLIMATE AND OLD AGE (tab. 1)

Old fluvial material

The presence of some caves sediments is inexplicable with the present waterpaths. Big rounded pebbles found in caves perched high up on top of cliffs mean that a valley bottom had to exist at this level. Afterwards, the valleys deepened so much that they are far below such perched massifs (Salzach/Salzburg Alps; Granier/Chartreuse). Often, gravels found in these caves have a petrography and mineralogy that is not found in the present rocks. They are issued either from caprock that has disappeared a long time ago (Fontana Marella, Campo dei Fiori) or from distant catchments, as proven by fluvial pebbles (Augensteine/Northern Limestone Alps in Austria), quartz sandstones (Slovenian Alps), fluvioglacial sediments (Lake of Como). Dating of fluvial pebbles by cosmogenic nuclides from the Grotta Masera (Como), yielded a probable age comprised between 2.6 to 7.2 Ma, showing a pliocene age, or maybe older (Häuselmann unpub.; Bini & Zuccoli 2004). In the Granier system, this method yields ages comprised between 1.8 to 5.3 Ma (Hobléa & Häuselmann 2007).

Record of climatic changes in subterranean sediments

Often, the analysis of the sediments evidences climate changes, with a change from biostatic conditions, marked by the rarity of allogenic sediments, towards rhexistatic conditions, with lots of allogenic sediments. These sediments come from the erosion of soils in a context of climate degradation and general cooling. They usually are interpreted to reflect the climatic change in the Pliocene, before the onset of the glaciations. Such sediments are present in most of the old cave phases, which therefore should be older than the end of the Pliocene: Grotte Vallier/Vercors; Tennengebirge (Audra 1994, 1995), Campo dei Fiori (Bini *et al.* 1997), Monte Bisbino (Tognini 1999, 2001). In the Dachstein-Mammuthöhle, which dates back to the Tertiary and shows a phreatic tube perched 1000 m above the Traun valley, flowstones grown during the interglacials interfinger with a series of debris-flow conglomerates of glacial origin (Trimmel 1992). In the Grotta di Conturines/Dolomites (2775 m ASL), the mean annual temperatures deduced from the ^{18}O of speleothems were between 15 and 25°, which implies that speleothemes deposited in a warmer climate within the Tertiary, probably also at a lower altitude than it is found today (Frisia *et al.* 1994). Furthermore, in many caves, either conduits or flowstones have been deformed by late Alpine tectonic movements: Grotta Marelli, Grotta Frassino/Campo dei Fiori (Uggeri 1992; Bini *et al.* 1992, 1993).

Dating results prove the antiquity of cave systems

The calculated age of old speleothems are regularly above the U/Th limits (700 ka, even 1.5 Ma according to the ^{234}U/^{238}U equilibrium (Bini e*t al.* 1997); Tab. 1). The paleomagnetic measurements often show inverse magnetism, sometimes with multiple inversion sequences, proving of a very old age of the cave sediments (Audra 1996, 2000; Audra & Rochette 1993; Audra *et al.* 2002b). The use of the new cosmonucleide method to date old quartz sediments also confirms this trend and yield ages reaching back to about 5 Ma (see the details for Siebenhengste example in this volume).

RELATIONS TO AN OLD TOPOGRAPHY

The geomorphologic approach, which uses external markers of old base levels (paleovalleys, paleoshelves with associated sediments) that are well dated, offers precious possibilities for the dating of karst systems. Sadly, correlations are almost impossible up-to-date due to the scarcity of such information. In the northern flank of the Alps, the glaciations often caused the remnants of an old topography to disappear. The southern Alps, less glaciated and better studied in this context, offer more possibilities, also thanks to the presence of guiding events like the Messinian incision and the following Pliocene marine highstand.

Old erosion surfaces

The identification of old erosion surfaces is a precious tool in geomorphology. Large surfaces often top the relief and cut across very old caves that are difficult to link to an old drainage system because of their fragmented character. The cave systems developing below those high surfaces are more recent, such as the stacked surfaces in the Vercors, of Eocene, infra-Miocene and Pliocene age (Delannoy 1997). Shelves along slopes, created by lateral corrosion of the rim of ancient depressions, have the same significance as perched valley bottoms. In Vercors, Pliocene caves could be associated on them, such as the Antre de Vénus and the Grotte Vallier (Delannoy 1997). In the area of Varese (Lombardy), the Oligo-Miocene surface that cuts across limestone, porphyritic rocks and granites, is dissected by the late Miocene valleys that had been deepened during the Messinian (Bini *et al.* 1978, 1994; Cita & Corselli 1990; Finckh 1978; Finckh *et al.* 1984).

Morphological and sedimentological evidences of prepliocene paleovalleys

A fluvial drainage pattern of Oligo-Miocene age, incised in the relief, predated the Alpine tectonic events of the late Miocene. The drainage originated in the internal massifs, cut through the calcareous border chains, and ended in alluvial fans in the molasse basins. In the border chains, perched paleovalleys are found more than 1500 m above the present ones (Salzburg Alps), as well as fluvial deposits coming from siliceous rocks (Augensteine/Northern Calcareous Alps; siliceous sands/Julian Alps (Habic 1992)), sometimes buried in caves near the valley slopes (Grotta di Monte Fenera/Piemont, Grotta Fontana Marella/Campo dei Fiori).

In the northern flank of the Alps, these valleys have been destroyed by the deepening of the hydrographic network, aided by the action of the glaciers. In the South, the old valleys have been deepened by the Messinian incision and filled by Pliocene sediments (Lake of Como/Adda, Varese, Tessin, Adige, Durance). As a consequence, the horizontal karstic drains that were linked to the old valleys had been truncated by slope recession, and are presently perched (Grotta Battisti/Paganella; Grotte Vallier/Vercors; Pian del Tivano, Monte Bisbino (Tognini 2001); Campo dei Fiori (Uggeri 1992)). The almost generally observed input of allogenic waters coming from impermeable rocks upstream, combined with a tropical humid climate with considerable floods, explains the giant dimensions of those caves.

AGE OF ALPINE KARSTIFICATION: FROM PALEOKARSTS TO RECENT MOUNTAIN DYNAMICS

PALEOKARST, A MILESTONE FOR OLD KARSTS

The study of paleokarsts is a separate domain. No cave system has survived in its integrality from the periods predating the Miocene. In the Northern Limestone Alps of Austria, the possibility that caves of the highest level (Ruinenhöhlen) may be relicts of an oligocene karstification has been discussed (Frisch *et al.* 2002). However, Paleogene paleokarsts are frequent, as evidenced by natural or artificial removal of their filling:

- In Siebenhengste, upper Cretaceous paleotubes and fractures are found in Lower Cretaceous limestone, filled with Upper Cretaceous Sandstone (Häuselmann *et al.* 1999).
- In many places, (Switzerland, Vercors, Chartreuse) vast pockets covering a karst relief and filling up some conduits can be observed.
- In Southern Alps, upper Eocene and lower Oligocene sediments have been found into large cavities infilled by basaltic intrusions (Covoli di Velo, Ponte di Veia/Monte Lessini) Their age could be determined by K/Ar datings (Rossi & Zorzin 1993).

In several regions (Vercors and Chartreuse, Monte Lessini), karstification is more or less continuous from the Eocene onwards. However, the tectonic and paleogeographic changes have only left dispersed paleokarsts. Since the Miocene on, several massifs emerged from the molasse basins, thus allowing a karstification that continues today.

ESTIMATION OF THE FIRST EXPOSURE ACCORDING TO MOLASSE PETROGRAPHY

The main phase of karstification begins when suitable rocks are exposed at land surface. Since the oldest remnants of karst are often eroded, it is possible to calibrate the beginning of the karstification by the foreland sediments (mainly the Molasse), which contain limestone pebbles eroded away at the surface. However, absence of evidence is not evidence of absence: sedimentary gaps are frequent, and a karst in biostatic conditions does not spread detritic elements towards the foreland. As a general rule, the Miocene molasse registered the beginning of the last big karstification phase, earlier in Italy, later in Switzerland:

- Upper Oligocene-Lower Miocene (30 to 20 Ma) in the Southern Molasse, based on dated fluvial sediments located in paleovalleys (Gelati *et al.* 1988).
- Lower Miocene (20 Ma) in the molasse south of Grenoble, corresponding to the erosion of the emerged anticlines of the Vercors and Chartreuse (Delannoy 1997).
- Lower Miocene (20 Ma) in the Austrian Nord-Alpine molasse, corresponding to the erosion of the Augensteine cover, which is of Upper and Middle Oligocene age (Lemke 1984; Frisch *et al.* 2000).
- Upper Freshwater Molasse in the Eastern Swiss basin (Hörnli fan, Middle Miocene 17-11 Ma) which contains pebbles of the first erosion of Helvetic nappes (Siebenhengste, Silberen, Speck 1953; Bürgisser 1980).

DATING THE YOUNGEST PHASES AND EXTRAPOLATION

The most generally applied dating method for cave sediments is U/Th. It makes it possible to date speleothems. In best cases, it allows for going back to as far as 700 ka – dating only the sediment contained within the cave and not the cave itself. The use of paleomagnetic dating makes it possible, in some scarce cases, to push back the datable range to 2.5 Ma. The use of cosmogenic isotopes (Granger *et al.* 2001) is the only recent method that opens new possibilities, having a dating range between 300 ka and 5 Ma. Another solution consists in dating lower cave phases that are supposed to be younger, and in progressively going up the phases towards the oldest cave systems, until reaching the limits of the used methods. From the calculated rate of valley deepening, one can then extrapolate the age of the uppermost phases. Of course, such an approach can only give a general idea about the age.

The lowermost phases of the Siebenhengste cave system, St. Beatus Cave and Bärenschacht, have been dated by U/Th. The following ages have been obtained: Phase 558 (youngest) began at 39 ka (max. 114 ka) and is still active today; Phase 660 was active between 135 and 114 ka; Phase 700 was active between 180 and 135 ka; and Phase 760 started before 350 ka and ended at 235 ka (Fig. 4). These age values indicate a general valley incision rate of 0.5 to 0.8 mm/a, with a tendency to slow down as the age gets higher. Extrapolation indicated an age of about 2.6 Ma for the oldest cave systems, at 1850 m ASL. Absolute cosmogenic dating yielded an age of 4.4 Ma for the oldest sediment, contained in the second-highest cave phase at 1800 m, showing a slower entrenchment in the older phases (Häuselmann & Granger 2005; see also this volume). Dating of the cave systems at Hölloch/Silberen gave maximal rates of valley incision in the range of about 1.5 to 3.5 mm/a.

RELATIVE UPLIFT RATES AND EROSION VOLUMES IN FORELAND SEDIMENTS

Uplift rates are generally calculated for long periods of time, taking the average of variable rhythms and integrating vast parts of the area, without taking into account block tectonics which can differ considerably from one massif to the other. In the same range, the estimated volume of the foreland basins only gives a global approach. Such results only may give a general frame for a validation. Modeling the fission-track measurements of the Swiss Central Alps (Reuss valley) give an average uplift of 0.55 mm/a (Kohl, oral comm. 2000) comparable to calculations of recent uplift (0.5 mm/a; Labhart 1992) and consistent with the rates inferred from dating in caves. Uplift is maximal in the central parts of the mountain chains, therefore the rocks are more deeply eroded in this area. As a consequence, the oldest caves had to have disappeared from the central zones, compared to the border chains where they are better preserved due to the slower erosion.

CONCLUSION

The examples mentioned above are distributed throughout the Alpine belt. Therefore, the conclusions drawn here are valid for Alpine Caves at least, but they may be applied to other cave systems also. The main following conclusions can be drawn from the above synthesis:

- In contrast to some earlier views, caves are not directly linked to glaciations. On the contrary, there is evidence that during glaciations caves are mainly filled with sediments, while they are enlarged during the interglacials. The main influence of glaciers upon cave genesis is the deepening of the base level valley, thus inducing a new cave genesis phase to be formed.

- U/Th datings, coupled with paleomagnetism, inferred a Lower Pleistocene to Pliocene age for several cave sediments. Fossil or radiometric datings of solidified cave fills (sandstone, volcanic rocks) gave ages reaching back to the Upper Cretaceous. It follows that caves are not inherent to the Quaternary period, but are created whenever karstifiable rocks are exposed to weathering. Due to later infill, however, most explorable caves range from Miocene to present age.

- We have shown that caves are related to their spring, which is controlled by a base level that usually consists of a valley bottom. So, the study of caves gives very valuable information about valley deepening processes and therefore about landscape evolution.

- Caves constitute real archives, where sediments are preserved despite the openness of the system. The study of cave sediments gives information about paleoclimates. Moreover, the combination of cave morphology and datable sediments allow to reconstruct the timing of both paleoclimatic changes as well as landscape evolution between the Tertiary and today. Differential erosion rates and valley deepenings can be retraced. Information of this density and completeness has disappeared at the surface due to the erosion of the last glacial cycles and the present vegetation.

- Correlations between well-dated cave systems can significantly contribute to the geodynamic understanding of the Alpine belt as a whole. The location of most cave systems at the Alpine border chains is very lucky: since they are dependent on base level (in the foreland), recharge and topography (towards the central Alps). They inevitably registered changes in both domains. Caves are therefore not only a tool of local importance, but may have a wide regional/interregional significance.

- The dating method by cosmogenic nuclides was recently applied in some French, Italian and Swiss alpine cave systems which partially contain pre-glacial fluvial deposits. The dated sediments yielded ages ranging between 0.18 and 5 Ma, which are consistent with other approaches. Advances in modern dating techniques (cosmogenic isotopes, U/Pb in speleothems) therefore open a huge field of investigations that will very significantly contribute to the reconstruction of paleoclimates and topography evolution along the last 5, possibly 15 to 20 Ma.

- The messinian event influenced cave genesis over the whole southern and western sides of the Alps by overdeepening valleys. However, the subsequent base level rising flooded those deep systems creating huge deep phreatic aquifers and vauclusian springs (Audra *et al.* 2004).

ACKNOWLEDGEMENTS

PH, PYJ and MM acknowledge the Swiss National Science Foundation for support of the Habkern Workshop (Grant No. 21-62451.00) and for research support (Grant No. 2100-053990.98/1).

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COBISS: 1.01

ASPECTS OF THE EVOLUTION OF AN IMPORTANT GEO-ECOSYSTEM IN THE LESSINIAN MOUNTAIN (VENETIAN PREALPS, ITALY)

POGLEDI NA RAZVOJ POMEMBNEGA GEO-EKOSISTEMA V GORAH LESSINI (BENEŠKE PREDALPE, ITALIJA)

Leonardo LATELLA[1] & Ugo SAURO[2]

Abstract UDC 551.442:574.4 (234.323.4)

Leonardo Latella & Ugo Sauro: Aspects of the evolution of an important geo-ecosystem in the Lessinian Mountain (Venetian Prealps, Italy)

The Grotta dell'Arena (476 V/VR), located in the Lessinian Mountain, at the elevation of 1512 m a.s.l., is a very important underground karst system. Although it is only 74 m long, several of the geological, geomorphological and environmental features of the High Lessinian underground karst are present in this cave. The Grotta dell'Arena shares some common geological and faunistic characters with other important and well known karst systems. This cave has also one of the highest number of troglobitic species in all Venetian Prealps and some of them possibly originated in the pre-Quaternary. From the geological point of view the cave is the expression of a contact karst, where different limestone types come in contact both stratigraphically and along tectonic structures. The Grotta dell'Arena is located at the stratigraphic contact between the "Calcari del Gruppo di San Vigilio" and the "Rosso Ammonitico" and it is very close to a fault plane putting in vertical contact the two above formations with the "Biancone", a kind of limestone closely stratified and densely fractured, very sensible to frost weathering. It is interesting to note the presence of a good number of species of Tertiary, or more generally pre-Quaternary, originate in the Grotta dell'Arena. This presence is possibly related to the geology of caves. In this paper the different kinds of underground karst systems in the Grottta dell'Arena and Lessinian Mountain, are analyzed and the relation with the cave fauna distribution are taken in consideration.

Key words: karst evolution, geomorphology, biospeleology, faunistic invasions, Venetian Prealps, Italy.

Izvleček UDK 551.442:574.4 (234.323.4)

Leonardo Latella & Ugo Sauro: Pogledi na razvoj pomembnega geo-ekosistema v gorah Lessini (Beneške Predalpe, Italija)

Jama Grotta dell'Arena (476 V/VR) v gorah Lessini, 1512 m n.m., je zelo pomemben podzemeljski kraški sistem. Čeprav je dolga le 74 m, vsebuje geološke, geomorfološke in okoljske elemente, značilne za kraško podzemlje Visokih Lessini. Grotta dell'Arena ima nekaj geoloških in favnističnih značilnosti skupnih z drugimi pomembnimi in znanimi kraškimi sistemi. Jama je med tistimi z največjim številom troglobiontskih vrst v vseh Beneških Predalpah, od katerih nekatere verjetno izvirajo izpred kvartarja. Z geološkega vidika predstavlja jama kontaktni kras, kjer so vzdolž stratigrafskega in tektonskega stika različni apnenci. Grotta dell'Arena je na stratigrafskem stiku med apnenci "Calcari del Gruppo di San Vigilio" in "Rosso Ammonitico" in je zelo blizu prelomne ploskve, vzdolž katere se vertikalno stikata omenjeni formaciji s formacijo "Biancone", to je vrsta drobnoplastovitega in gosto prepokanega, slabo odpornega apnenca. Zanimiva je prisotnost precejšnjega števila terciarnih oziroma splošneje predkvartarnih vrst. To je verjetno v zvezi z jamsko geologijo. V prispevku so podrobneje obravnavane različne vrste podzemskih kraških sistemov v sami jami Grottta dell'Arena kot tudi v gorah Lessini in tudi njihovi odnosi z razporeditvijo jamskega živalstva.

Ključne besede: razvoj krasa, geomorfologija, biospeleologija, invazija favne, Beneške Predalpe, Italija.

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Received/Prejeto: 21.12.2006

INTRODUCTION

The Grotta dell' Arena is registered with the number 476 in the Cadastre of the Caves of Veneto Region (the cave has been surveyed by A. Pasa in 1942, and GAS USV in 1972); the karst area is ML03 (Monti Lessini 03). The cave is 74 m long with a difference in elevation of - 22 m. It is located in the Lessinian Mountain district of Bosco Chiesanuova, in Malga Bagorno area. G.C: 11° 06' 02" E 45° 39' 56" N, elevation 1512 m a.s.l.

The Grotta dell'Arena is a significant kind of underground karst system in Lessinian Mountain in fact:

– it is a type of speleogenetic style in the morphodynamic context of the High Lessinians,

– several of the geological, geomorphological and environmental features of the High Lessinian underground karst are present in this cave and played a significant role in karst evolution,

– some of the best known karst systems in the Lessinian Mountain (Mietto & Sauro, 2000; Rossi & Sauro, 1977), such as the Abisso della Preta, the Covolo di Camposilvano, the Abisso del Giacinto, the Abisso dei Lesi, the Ponte di Veja, share some common characters with the Grotta dell'Arena,

– from the biospeleological point of view, this cave has one of the highest number of troglobitic species in all Venetian Prealps,

– several troglobitic species are endemic for the Grotta dell'Arena or the Lessinian Mountains and some of them possibly originated in the pre-Quaternary.

The Grotta dell'Arena is a large chamber, roughly elliptical in plane section, with a main diameter of about 50 m. The roof coincides mostly with bedding planes. The southern part of the floor is characterized by a large, asymmetrical, funnel-shaped depression, a kind of subterranean doline developed in the collapse debris.

The chamber is situated a few meters below the topographical surface; it is connected to the surface through

Gastropoda	**Opiliones**	**Diplopoda**	**Orthoptera**
Zospeum sp.	Ischyropsalis strandi	Lessinosoma paolettii	Troglophilus sp.
Anellida	**Copepoda**	**Collembola**	**Coleoptera**
Marionina n.sp.	Speocyclops cfr. infernus	Onychiurus hauseri	Orotrechus vicentinus juccii
Araneae	Lessinocamptus caoduroi	Pseudosinella concii	Orotrechus pominii
Troglohyphantes sp.	Moraria n. sp.	**Sincarida**	Italaphaenops dimaioi
Pseudoscorpiones	Elaphoidella n. sp.	Bathynella sp.	Lessinodytes pivai
Chthonius lessiniensis	**Isopoda**	**Amphipoda**	Laemostenus schreibersi
Neobisium torrei	Androniscus degener	Niphargus galvagnii similis	Halberrria zorzii
Balkanoroncus boldorii			

Tab. 1: List of the cave-dwelling species in the Grotta dell'Arena.

Fig. 1: The collapse depression called Arena.

Fig. 2: The large chamber in the Arena cave. In the foreground the debris blocks, in the background the inner "doline".

some narrow passages which start from an open collapse depression located on a slope, which resembles a Roman theatre (i.e. an "Arena", hence the name of the cave) (Fig.1, Fig. 2). The depression is the result of the collapse of part of the subterranean room.

To understand the significance of this cave it is necessary to:

– delineate the geological, geomorphological, and, in general, environmental characteristics of this cave,

– reconstruct the framework of the spatial and temporal evolution of the High Lessini karst,

– taking into account the climatic and environmental changes of the external environment surrounding the cave that occurred during the Pleistocene.

– analyse the phyilogeographical and taxonomical affinities of the troglobitic elements of its fauna.

THE ENVIRONMENTAL CONTEXT

The Grotta dell'Arena had been previously defined not as a distinct structure, but as a window on a subterranean space, that allows us to see only some features of a karst system (Castiglioni & Sauro, 2002). In fact, the subterranean environment is a much more complex system, mostly hidden to the human perception.

From the geological point of view the cave is expression of a contact karst, where different limestone types come in contact both stratigraphically and along tectonic structures (Capello *et al.* 1954; Pasa, 1954; Sauro, 1973, 1974, 2001). In particular, the limestone formations present here are:

– "Calcari del Gruppo di San Vigilio" of lower-middle Jurassic, about 60 m in depth, pure both oolitic and bio-sparitic/–ruditic, or reef limestones, relatively densely fractured,

– "Rosso Ammonitico", a condensed rock unit of middle- upper Jurassic age, about 30 m in depth, made up by nodular micritic limestone very resistant to erosion, crossed by widely spaced fractures,

– "Biancone", a chalk type unit, from the lower and middle Cretaceous, 100-200 meters in depth, made up by whitish marly limestone closely stratified and densely fractured, very sensible to frost weathering.

The Scaglia Rossa formation of the upper Cretaceous, and the Eocene limestone, which lie above the Biancone in the western and southern part of the plateau are not present in the studied area because they have been completely eroded. Below the "Calcari del Gruppo di San Vigilio" there is the formation "Calcari Grigi di Noriglio", of lower Jurassic, which is about 300 m in depth and outcrops in the slopes of the main valleys, a kind of fluvio-karstic canyons.

The Grotta dell'Arena is located at the stratigraphic contact between the "Calcari del Gruppo di San Vigilio" and the "Rosso Ammonitico" and it is very close to a fault plane putting in vertical contact the two above formations with the Biancone (Fig. 3). The cover rocks of the cave are made mostly by the massive beds of lower Rosso Ammonitico, whereas the inner cave is mostly developed inside the Calcari del Gruppo di San Vigilio. At the topographical surface, the line of the normal fault runs along

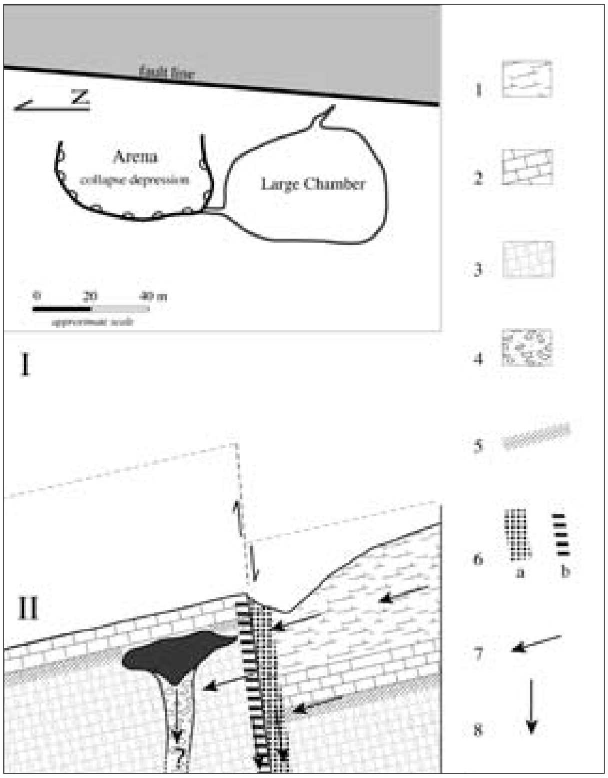

Fig. 3: Sketches of the Arena cave system:

I – Plan of the system; the grey corresponds to the Biancone rock unit.

II – Vertical model of the karst system. Legend: 1) Biancone formation, 2) Rosso Ammonitico, 3) Calcari del Gruppo di San Vigilio and Calcari Grigi, 4) debris pipe in the cave, 5) bedding plane karst zone at the contact Rosso Ammonitico- Calcari del Gruppo di San Vigilio, 6) fault plane karst zone, a) at the Biancone side, b) at the Rosso Ammonitico side, 7) lateral flow inside and from the Biancone aquifer, 8) vertical karst flow.

a small valley, a few meters to the east of the cave; the displacement of the fault is about 100 m.

From the geomorphological point of view, Biancone is dissected by a network of dry valleys, whereas Rosso Ammonitico generates a rocky landscape with large flat karren separated by corridors, or rock cities of large blocks.

From the hydrological viewpoint, the water circulates diffusely inside the dense network of discontinuities of the Biancone unit; the preferential flows is sub-parallel to the topographical surface and occurs mostly below the dry valley bottoms, but is also influenced by the structural setting; vertical losses occur along the fault and fracture zones. In contrast, water circulation is more concentrated and mostly vertical in the Rosso Ammonitico.

SPATIAL AND TEMPORAL EVOLUTION OF THE KARST SYSTEM

It is easy to understand that the Grotta dell'Arena results of different spatial and temporal processes which occurred as a consequence of several predisposing factors. In fact, the cave is at the same time, an example of lithological contact karst, of intra-stratal karst, of fault zone karst and of a subterranean hydrological transition from a dispersed and sub-horizontal water flow to a more concentrated and sub-vertical one.

The Grotta dell'Arena system is fed by a lateral water flow coming from the Biancone aquifer and crossing the fault zone, facilitated by the westward dipping of the strata. The speleogenesis of the cave has taken place in the lithological, tectonic and hydrological transition zone.

Each cave we visit represents a moment of a long history, it is like the picture of a movie. Surely the present aspect of this cave and of its collapsed part are the result of relatively recent processes, occurred mostly during the middle and upper Pleistocene. But the karst system of which the cave is expression has surely begun to develop much earlier.

Some caves, located in middle of the Lessinian plateau and in the Berici hills, are the result of the re-activation of old paleokarstic nets developed during the Paleogene (Rossi & Zorzin, 1989, 1991; Dal Molin *et al.* 2000); other caves with fillings from the early middle Pleistocene developed mostly during the lower Pleistocene. The Grotta dell'Arena chamber seems to be related with the second group.

The fault to the east side of the cave is a paleotectonic feature of Jurassic age, reactivated during the Cretaceous and later by the Alpine orogenesis during the Paleogene and the Neogene. The area where the cave is located probably emerged from the sea during the Oligocene, as the southern part of the Lessinian plateau. The erosion of the Eocene rock unit occurred during late Paleogene and early Neogene. The Scaglia Rossa formation was probably eroded during middle to late Neogene. At the beginning of the Quaternary these two formations disappeared completely in the area (remnants of Scaglia are still present in the western High Lessinian).

A model showing the sequence of landscapes developed in the different rocks by the erosion can be created, based on present-day landscapes of other parts of the Lessini Mountains, where the eroded geological formations are still present. Thus in the southwestern Lessinian Mountain (High Valpolicella) there is an active hydrographic network with gorges entrenched in both Eocene Limestones and in the Scaglia Rossa.

Here, the early morphogenesis, after the emersion and the uplift, has been mostly of the fluvial type, marked by the development of a network of valleys strongly controlled by the tectonic structure. So, a valley developed along the fault line. Following the incision of the Scaglia Rossa, the karst process begun to affect the fault zone. But, it is especially after the erosion of the Scaglia Rossa that the aquifer hosted in the Biancone started to feed a new underground karst system located near to the fault zone of which the Grotta dell'Arena is the present day expression.

From this simple model it is possible to infer that the evolution of the underground karst system started since Neogene, probably since middle- upper- Miocene. The transition from the fluvial environment to the karst environment has been accompanied by the development of a fluviokarstic milieu in the Biancone. In this milieu, which is still present, there is not surface runoff except during exceptional events, but there is a diffuse circulation inside the rock, for some aspects similar to that occurring below the river beds, inside the alluvial deposits (Fig. 4).

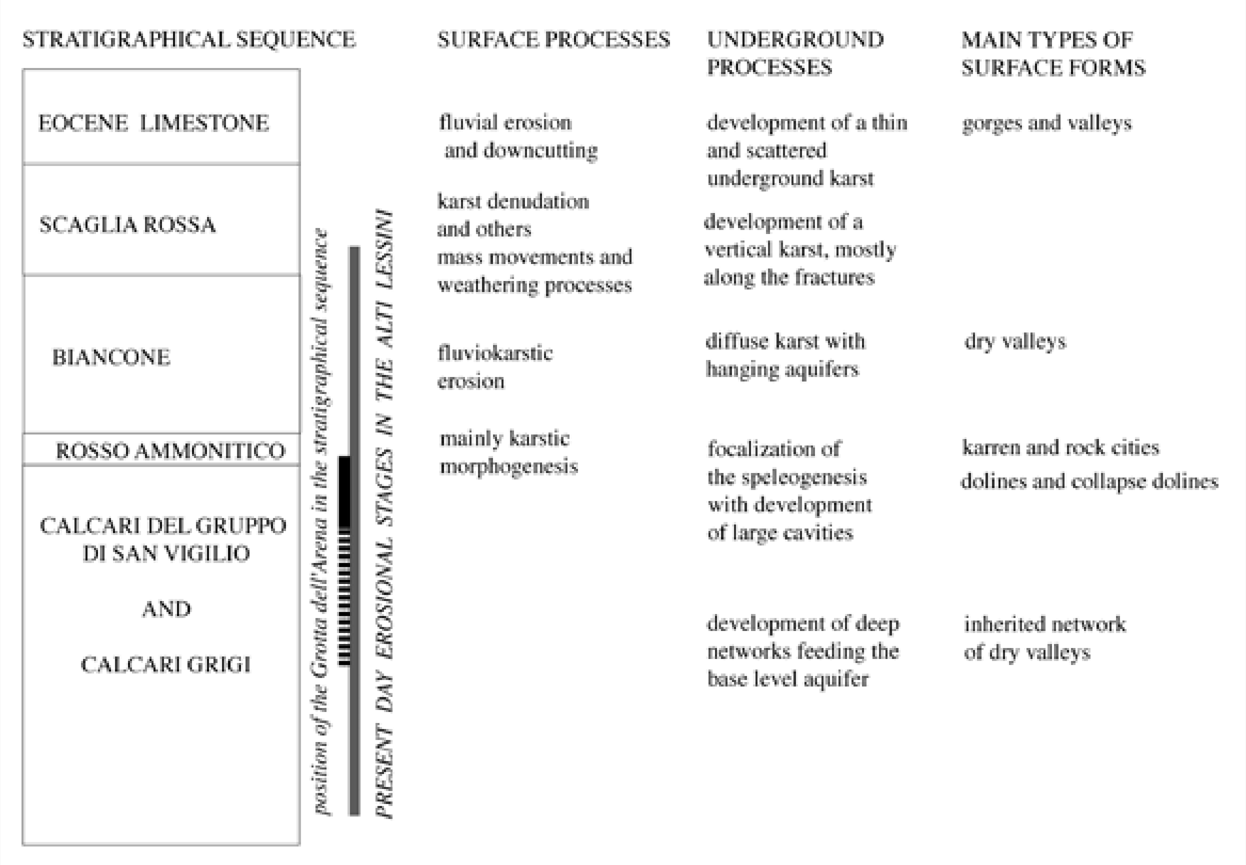

Fig. 4: Sketch of the morphological evolution of the alti Lessini according with the erosional stages reached by the relief (progressive erosion of the rock units).

THE CLIMATE AND ENVIRONMENTAL CHANGES DURING THE PLEISTOCENE

The Lessinian Mountain plateau was affected by the climatic and environmental changes of the Pleistocene. In the cave area there is no evidence of past development of local glaciers (the nearest local glacier was more than 1 km to the northwest). However, traces of strong periglacial processes, such as remnants of small rock glaciers, nivation niches, etc. are present (Sauro, 2002). During the last Würm sporadic permafrost was present in the area. The material resulting from the collapse of the Arena depression has been affected by cryoclastic processes, as shown by a large solifluction lobe located to the north side of the same hollow.

The climate and enviromental change occurred in the Pleistocene, affected the colonization of the subterranean environment by some actual troglobitic species and shaped the distribution of the species that colonized this environments before the Pleistocene.

THE CAVE FAUNA AT PRESENT

The cave fauna of the Grotta dell'Arena is characterized by the presence of high number of troglobitic and endemic species (Caoduro & Ruffo, 1998). Colonization of the cave by the troglobitic elements occurred in different times. Ancient elements of this fauna colonized the subterranean environments before the Pleistocene, and other species invaded the cave in different periods along the Quaternary.

Today, this cave has a high number of cave-adapted animals. Of the 43 taxa known for the cave, 24 could be considered eucavernicolous species (sensu Ruffo, 1955: eutroglophiles+troglobites). The specialization index (eutroglobites/ eucavernicolous), has a value of 0.91, this means that 91% of the cave species in the Grotta dell'Arena are troglobionts.

FINAL REMARKS

The subterranean karst of the alti Lessini is much more spatially developed than what is perceived by a speleologist. It consists not only in large pits and chambers but in a network of smaller cavities and fissures. In the two horizontal dimensions it is a kind of net, even if anisotropic, better developed along the fault zones and some bedding planes. In the vertical dimension the anisotropy is even greater, and the thickness overpasses one thousand of meters.

In the time dimension, this karst network has evolved progressively, even with different speeds influenced by the changes of the morphostructural setting and of the external environment. The karst morphogenesis occurred as result of the co-occurrence of various favourable conditions.

The hydro-geological condition of the alluvial deposits of the water courses of the early erosional stage, during middle Neogene, are no present here nowadays, but there are situation for some aspects similar both below the valley bottoms of the Biancone and in the diffuse net of karst fissures developed inside this rock unit. This diffuse aquifer is in contact with the more typical karst aquifer of the limestone of the Jurassic rock units.

Likewise, some of the larger karst pockets developed in the Eocene limestone, may have had some connections with the karst cavities in the Scaglia, and, along the main fault structures or volcanic structures, also with the karst voids in the Jurassic rock units.

Here, sudden and sharp changes of conditions of the underground environments have not occurred during the late Neogene and the Pleistocene. Even the abrupt climatic changes of the Pleistocene have had a limited influence on the underground environments, according with the large thickness reached by it before the end of Neogene.

It is interesting to note the presence of a good number of species of Terziary, or generally pre-Quaternary, origin in the Grotta dell'Arena. The most important relict species are: *Balkanoroncus boldorii* (Beier, 1931), *Lessinocamptus caoduroi* Stoch, 1997, *Italaphaenops dimaioi* Ghidini, 1964 and *Lessinodytes pivai* Vigna Taglianti e Sciaky, 1988 (Casale & Vigna Taglianti, 1975; Vigna Taglianti & Sciaky, 1988; Gardini, 1991; Galassi pers. com.).

The presence and distribution of these species inside the caves of Lessinia (particularly the terrestrial species) has been usually related to certain environmental characteristic like temperature, humidity, air circulation etc. However, on the basis of the actual knowledge (Latella & Verdari, 2006), it appears that all these species are present in caves with a large range of temperatures, altitude and morphology. All these caves are developed inside, or in contact with, the Biancone or Scaglia (Cretaceous limestone) formations. It is likely that the geomorphology of the cave plays an important role not only in shaping the historical distribution, but also the actual presence, of cave animals in Lessinian area.

ACKNOWLEDGMENTS

We are grateful to Sandro Ruffo for the helpful discussions and for the reading of the manuscript. We also thanks Augusto Vigna Taglianti for the informations regarding Trechinae, Diana Galassi for the informations on Copepoda and Beatrice Sambugar for the Anellida.
Thanks to Cristina Bruno for the linguistic review.

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COBISS: 1.01

HISTORICAL BIOGEOGRAPHY OF SUBTERRANEAN BEETLES – "PLATO'S CAVE" OR SCIENTIFIC EVIDENCE?

ZGODOVINSKA BIOGEOGRAFIJA PODZEMELJSKIH HROŠČEV – »PLATONOVA JAMA« ALI ZNANSTVENI DOKAZ?

Oana Teodora MOLDOVAN[1] & Géza RAJKA[1]

Abstract UDC 595.76:551.44
591.542

Oana Teodora Moldovan & Géza Rajka: Historical biogeography of subterranean beetles – "Plato's cave" or scientific evidence?

The last two decades were particularly prolific in historical biogeography because of new information introduced from other sciences, such as paleogeography, by the development of quantitative methods and by molecular phylogeny. Subterranean beetles represent an excellent object of study for historical biogeography because they are the group with the best representation in the subterranean domain. In addition, species have reduced mobility, display different degrees of adaptations to life in caves and many specialists work on this group. Three processes have shaped the present distribution of the tribe Leptodirini (Coleoptera Cholevinae) in the world: dispersal, vicariance, and extinction. Therefore, three successive stages can be established in the space-time evolution of Leptodirini: (1) dispersal from a center of origin in the present area(s); (2) dispersal, extinction and vicariance among the present area(s); and (3) colonization and speciation in the subterranean domain. The Romanian Leptodirini, especially those from Western Carpathians is examined with respect to these processes. Their pattern of distribution in different massifs and at different altitudes is discussed, with possible explanations from a historical biogeographic point of view.

Key words: Historical biogeography, cave beetles, Leptodirini, Romania.

Izvleček UDK 595.76:551.44
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Oana Teodora Moldovan & Géza Rajka: Zgodovinska biogeografija podzemeljskih hroščev – jama »Platonova« ali znanstveni dokaz?

Zadnji dve desetletji sta bili za historično biogeografijo še posebej bogati, predvsem zaradi številnih novih informacij in dognanj paleogeografije, razvoja kvantitativnih metod ter molekularne filogenije. Podzemeljski hrošči so odličen model za proučevanje historične biogeografije, saj spadajo v tisto skupino organizmov, ki je v podzemlju najpogosteje zastopana. Hrošči iz podzemlja imajo zmanjšano mobilnost, razvili so številne načine prilagoditev na življenje v tem habitatu. S to skupino organizmov se ukvarjajo številni raziskovalci po svetu. Na trenutno razširjenost vrst rodu Leptodirini (Coleoptera Cholevinae) so vplivali trije procesi: disperzija, vikarianca in izumiranje. V prostorsko-časovnem razvoju Leptodirinov se lahko pojavijo tri zaporedne faze: (1) razširjanje iz izvornega mesta na sedanje/a poročje/a, (2) razširjanje, izumrtje in vikarianca med sedanjimi območji, ter (3) kolonizacija in speciacija v podzemeljskih habitatih. S tega vidika smo proučevali Leptodirine iz Romunije, s poudarkom na vrstah iz zahodnih Karpatov. V prispevku je opisan vzorec razširjenosti hroščev v različnih gorskih predelih ter na različnih nadmorskih višinah. V razpravo smo z vidika historične biogeografije vključili tudi verjetno interpretacijo.

Ključne besede: zgodovinska biogeografija, speleobiologija, Leptodirini, Romunija.

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Received/Prejeto: 04.12.2006

INTRODUCTION

The Greek philosopher, Plato (428-348 BC), in his book, The Republic, tells about Socrates teaching lessons of wisdom. One of these is about human beings kept in a cave with one source of artificial light coming from behind. The idea of the allegory is that we might have a wrong perception about what is reality, or, that most people live in a world of ignorance because they rely only on their narrow experiences and rely on their own truths. Another possible interpretation of Plato's allegory is that we might be wrong if we consider concepts and perceived objects on the same level. Historical biogeography is a science based on concepts and suppositions and there is no direct evidence available in the attempt to build credible scenarios about past and present animal distributions. However, development of this science on circumstantial evidence ensures better understanding of the objects under study.

Biogeography studies geographic distribution of organisms. This simple definition describes an extremely complex science. Geology, geography and various branches of biology define a discipline that is continuously developing. The Swiss botanist de Candolle (1820) was the first to speak about ecological and historical biogeography as separate branches of biogeography. They differ mainly in what concerns spatial and temporal scales. Historical biogeography reports on evolutionary processes over millions of years, mostly on a global scale (Crisci 2001). Pleistocene glaciations are sometimes collectively considered a separate or intermediary branch between historical and ecological biogeography. The last two decades were particularly prolific in papers on historical biogeography due largely to new information introduced from other sciences, such as paleogeography, by the development of quantitative methods (Morrone & Crisci 1995) and by the development of molecular phylogeny.

Morrone & Crisci (1995) and Crisci (2001) define the biogeographic processes that modify the spatial distribution of taxa and recognize nine basic approaches to historical biogeography: (1) Identification of the centers of origin, or the existence of "Eden" where different lineages of all living beings moved from by dispersal to the present areas; (2) Panbiogeography, which plots the distribution of different taxa on maps, connecting their distribution areas together with lines; (3) Phylogenetic biogeography and (4) Cladistic biogeography, both assuming correspondence between taxonomic relationships and area relationships; (5) Parsimony analysis of endemicity that classifies areas by their shared taxa; (6) Event-based methods; (7) Phylogeography; (8) Ancestral areas; and (9) Experimental biogeography.

The evolution of subterranean animals is a process that can be presumed but not directly proven. The origin, migration and colonization of the subterranean realm can be explained by a multitude of arguments and indirect evidences which support or falsify the proposed hypotheses. The role of historical biogeography is to explain the way subterranean animals gain their present distribution, using available data from biology and other sciences. Through this process, we can gain a new insight into the mechanisms of colonization that have affected some of the extreme areas or habitats which exist in the subterranean domain. Chronologically, the history of a taxonomic group (like the beetles), or of a phyletic lineage must begin with its origin. To understand present distribution patterns and why some areas were colonized and others were not, we must first establish temporal and spatial reference points.

SUBTERRANEAN COLEOPTERA EXAMPLES IN HISTORICAL BIOGEOGRAPHY

There are several reasons why subterranean beetles represent an excellent object of study for historical biogeography:

1. They are the best represented group in the subterranean karst environment or domain, with many species inhabiting caves and the mesovoid shallow substratum (also called MSS, see Juberthie *et al.* 1980);

2. Most species are terrestrial and therefore have reduced mobility; and while they are not limited to limestone/karst areas, most taxa inhabit caves;

3. A group whose representatives that display different degrees of adaptations to life in caves. Some of the lines have endogean and hypogean species, of which the last is more or less adapted to subterranean environment.

4. They are a well known group, with many specialists studying various aspects of their biology, including taxonomy, adaptations, behavior and molecular phylogeny.

Two families encompass most of the world's subterranean beetles, the Trechinae (predator Carabidae) and the Cholevinae (detritivorous and saprophagous Leiodidae). Our example is from one of the best represented subterranean tribe of Cholevinae, the Leptodirini (former Bathysciini). According to ecological biogeography, Leptodirini are presently distributed in caves, MSS, and other dark and humid habitats, such as litter and moss, mostly in the Palearctic region.

For historical biogeography the life of the tribe Leptodirini begins in the Paleozoic. The present distribution of Leptodirini can only be explained through Wegener’s theory of continent drift and the dispersal, vicariance and extinction processes. Dispersal was the main concept in biogeography before Wegener and it explains the area of a population by the mechanisms of migration and crossing over geographical barriers. Extinction means the death of local populations, species or even supraspecific taxa, and its role in biogeography has not always been recognized. Vicariance represents the splitting of an ancestral population into several subpopulations, which will later evolve into species through isolation. These three processes have shaped the present distribution of Leptodirini, and three successive stages can be established in the space-time evolution of this group:

I. Dispersal from a center of origin in the present area(s);

II. Dispersal, vicariance, and extinction among the present area(s);

III. Colonization and speciation in the subterranean domain.

I. According to Giachino & Vailati (1998) the ancestral family of Oricatopidae inhabited the southern part of the Gondwana supercontinent (Fig. 1). Descending from this family, ancestors of Leptodirini and other tribes migrated at the end of Paleozoic to the what is now the south of Eurasia on the microplates that broke off from Gondwana. Thus, Eurasia was colonized by the ancestors of Leptodirini 120–150 Ma ago. More recently, 50-65 Ma ago, the group dispersed from northeast, through the central south of Asia, up to eastern Eurasia and then toward the west, along the Mediterranean basin. Epigean individuals successively migrated at the surface, and they were probably pre-adapted to low, constant temperatures and high humidity. Jeannel & Leleup (1952) provide excellent examples for preadaptated ancestors of pselaphid beetles, after studying high altitude (2000-2900 m) beetles on Mount Kivu (Congo). At this level, the species are exclusively humic inhabitants, deepened at few centimeters in humus, where proper conditions, such as constant temperature (10°C) and high humidity, are fulfilled. They also described a species with similar adaptations to those inhabiting caves, and also found deeper, under the humus.

II. The second phase of evolution of the group probably happened before the Miocene, and possibly in the late Oligocene. The dispersal of beetles was from Asia, along the Miocene Alpine chain, whose remains are the Cantabric chain, Pyrenees, Central French Massif, Alps, Dinarides, Balkans, Pindus chain, Peloponnesus chain, and Pontic Alps. Afterwards, some species colonized the Apennines, Jura, Carpathians, Rodops, Taurus, Caucasus and Mediterranean inlands (Giachino *et al.* 1998). Due to major geological and geographical transformations of the landscape, extinction and vicariance alternated during the next periods. A large and continuous distribution area of epigean and probably endogean ancestors of Leptodirini that migrated from east was then fragmented, even before the colonization of the subterranean domain. New paleogeographic data about the evolution of the Paratethys from Late Eocene to Pliocene has been recently published (Steininger & Rögl 1985, Popov *et al.* 2004), and it appears that paleoconfiguration of the Paratethys shaped the distribution of Leptodirini in Europe.

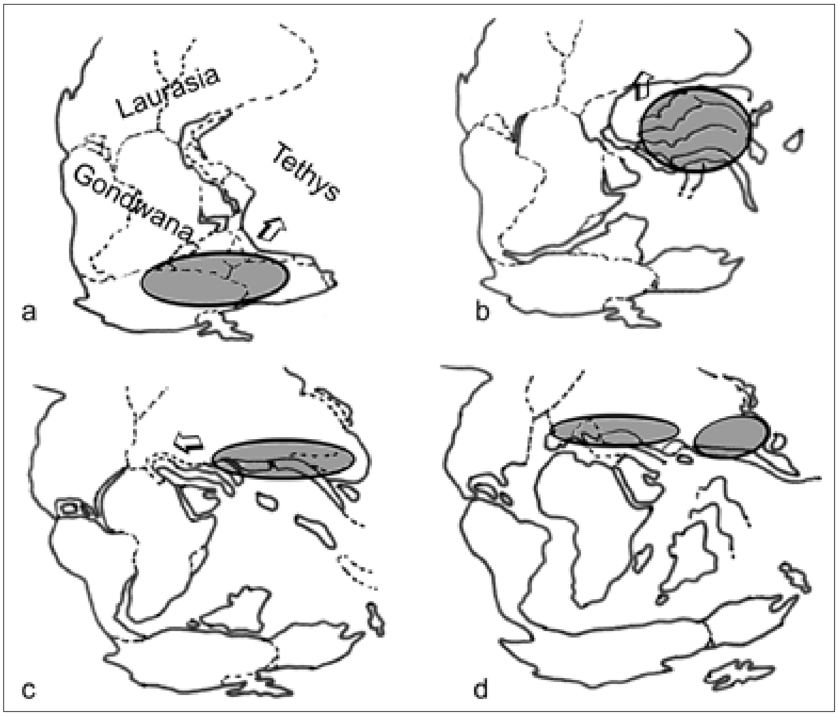

Fig. 1: Historical biogeography of ancestors of Leptodirini, which migrated from Gondwana (a) together with continental microplates (b), up to Eurasia (c), from there dispersed west to the Mediterranean region (d) (modified from Giachino et al. 1998): areas covered by Leptodirini are represented by grey ellipses.

III. The third stage is represented by colonization and speciation in the subterranean domain. Two scenarios were proposed for explaining the mechanisms of underground colonization by epigean and endogean representatives of various groups of fauna (Holsinger 2000, 2005):

(1) The climatic-relict model, in which preadapted or adapted animals were "forced" or constrained by climatic fluctuations to find refuge in caves. The best documented are the Pleistocene glacial-interglacial periods. Eventually, surface ancestors of these successful colonizers went extinct. This model not only fits temperate climate regions, but also any region that has previously sustained drastic climatic changes.

(2) The adaptive-shift model is mostly applied to lava tubes and tropical karst regions. Proposed by Howarth (1981), it explains the active colonization by preadapted ancestors and exploitation of new and empty niches to avoid competition. In this model, adaptation to the new environment does not depends on physical isolation from surface ancestors, as is necessaryin the previous model.

In our opinion, colonization of the subterranean domain is an active process, as is the case of empty niche colonization anywhere on Earth. Climatic changes have made important contributions in shaping the distribution areas and breaking off gene flow with surface relatives. Climatic changes can also interrupt energetic flow between surface and subterranean environments, leading to extinction of populations on one or both sides. This apparently happened in parts of the world directly affected by or covered by Pleistocene glaciers.

Bellés (1991) enumerates three reasons for cave colonization:

1. Survival, when external stress determines animals to find refugee in caves;
2. Opportunism or colonization of an empty space;
3. Convenience or escaping surface competition which uses the same trophic resources.

Peck (1980), Vailati (1988) and Juberthie (1988) proposed scenarios for cave colonization by beetles in the family Leiodidae from North America and Europe. Juberthie's model uses complex data from studies on the ecology, ethology, genetics, tectonics, paleoclimate and geology of species from the *Speonomus delarouzeei* complex (Leiodidae: Cholevinae: Leptodirini). These species inhabit the MSS and caves on Mount Canigou in the French Pyrenees. The history of this complex begins with the first glacial period (2.3 Ma), when high altitude species separated from those at low altitude in the Mediterranean climate. The two species, S. brucki and respectively S. delarouzeei are characterized by different mating behavior, by reproductive isolation and by genetic distance. There are also differences in fecundity and egg development speed at different temperatures. Thus, depression of temperature during glaciation selected cold resistant genotypes at 1000 m altitude, where annual mean temperature in caves is today 8-10°C, while *S. delarouzeei* remained at low altitude at temperatures of 14°C. During glacial periods, the forest belt displaced several hundred meters downslope on Mount Canigou and was replaced by steppe vegetation. Cracks, voids, MSS and even caves formed during these periods, while filling happened during interglacial periods. At altitudes between 500 and 1000 m two other species, S. emiliae and S. charlottae, inhabit subterranean habitats. *S. emiliae* lives in the MSS at 720 m altitude and is presumed to be the ancestor of *S. brucki,* and probably populated caves and MSS at different altitudes. *S. emiliae* migrated together with the forests during glacial periods through cracks and MSS down to the present altitude. The isolation of this species and *S. brucki,* which formed a population at high altitude, happened by infilling of the MSS and related cracks and crevices. Similar mechanism acted in a previous period for separating *S. charlottae* from ancestors of *S. brucki.*

By comparing cuticular hydrocarbons (pheromones that act at short distance or by contact) of species of the *S. delarouzeei* complex, Moldovan (1997) and Moldovan *et al.* (2003) obtained a different composition in the mountain species *S. brucki* and the Mediterranean species, *S. delarouzeei:* shorter chains in the first one and longer in the second. *S. emiliae,* at an intermediate altitude, displays a mixture of short and long molecules in the cuticular hydrocarbon cocktail. The result can be explained by temperature influence on cuticular hydrocarbon composition. A small variation in temperature can change hydrocarbon composition even from the first generation (Toolson *et al.* 1990). For subterranean beetles, adaptation to a new climate can rapidly change the pheromone composition, thus representing an important mechanism of isolation that acts prior to mating. Climate changed the distribution of populations on the slope of Canigou Mountain through migrations of ancestral populations. Consequently, composition in cuticular hydrocarbons changed and preceded genetic mutations. Hydrocarbon changes become stable if climate is maintained over long periods of time, eventually causing isolation of populations and genetic mutations. Therefore, speciation of subterranean inhabitants can occur without the existence of physical barriers as proposed in Juberthie's model.

REFERENCE MARKS IN HISTORICAL BIOGEOGRAPHY OF ROMANIAN LEPTODIRINI

With its geographic position in eastern Europe, Romania is very rich in subterranean fauna for a non-Mediterranean country. This is due to the special features defined as follows (Moldovan *et al.* 2005):

1. The geographic position of the country, with climatic and fauna influences from various regions;
2. The reduced total surface of limestone; karst areas are distributed along the Carpathians and in Dobrogea, covering only 2% of the surface of Romania (Onac & Cocean 1996);
3. The high number of caves/surface units; even if the covered surface is so small, the speleological potential is high, with almost 12,000 caves discovered prior to 1989 (Goran 1989);
4. The distribution of caves at low altitude, with 27% of karstic rocks at altitudes below 500 m and 47% up to 1000 m a.s.l. (Bleahu & Rusu 1965);
5. The patchy distribution of limestone, with small outcrops scattered especially in western and southern regions. From an ecological point of view Romanian karst forms small continental islands between non-karstic rocks, which act as natural barriers to migration of subterranean organisms. Each area represents an island to its inhabitants, which in turn leads to isolation and promotes evolution and formation of new species. The discovery of the MSS has added new insights into the availability of subterranean habitats, but it can explain only short distance migrations between geographically close areas.

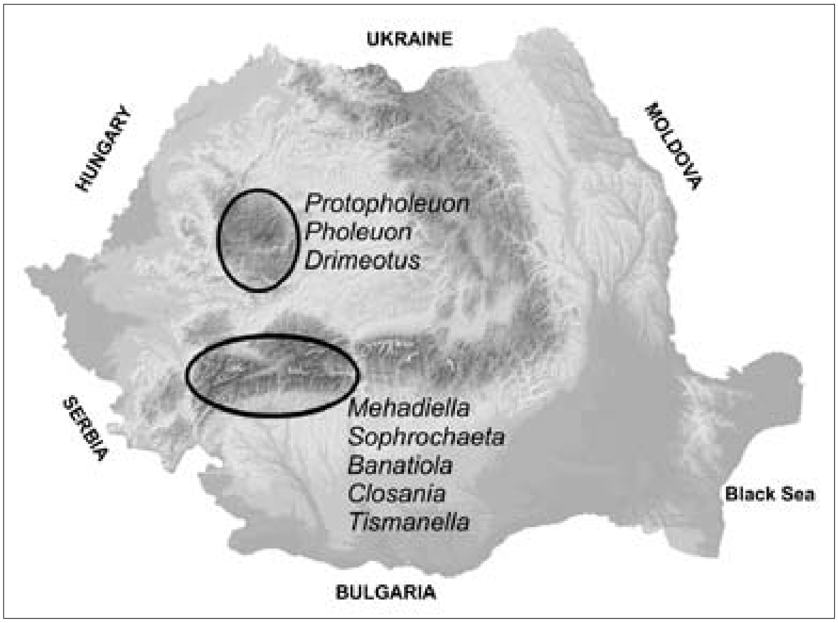

Fig. 2: Genera of Leptodirini distributed in the Western and Southern Carpathians of Romania.

The above-mentioned features explain the fragmentation of the initial distribution area of surface ancestors of cave animals and speciation processes. It also explains the high number of genera and species for a country at 45° northern latitude. Other countries at the same latitude are much poorer in species (e.g., Austria - 2 species, Switzerland – 1 species), even though their limestone areas in these countries are larger.

Romanian Leptodirini is represented by 8 genera and 6 subgenera with 50 species and 46 subspecies, composed of 1 epigean, 10 endogean and 85 strictly cavernicolous taxa. Concerning the distribution of subterranean beetles, the Romanian Carpathians can be divided in three geographical units: Western, Southern and Eastern Carpathians. The last unit has few caves and no representatives of Leptodirini. More than half of the karst surface of the country belongs to the Western unit (the Apuseni Mountains). This region also has the highest degree of speciation with 63 taxa in the genera *Drimeotus, Pholeuon* and *Protopholeuon*. These species inhabit caves and the MSS. More genera but fewer species are found in the Southern Carpathians: the epigean monospecific *Mehadiella*, and the 34 taxa of subterranean *Banatiola, Sophrochaeta, Closania* and *Tismanella* (Fig. 2).

The origin of Romanian Leptodirini is strictly linked to dispersal of ancestral lineages that inhabited the Alpine Miocene chain and to a Paratethys evolution. Jeannel (1924, 1931) and Decu & Negrea (1969) suggested a Dinaric origin for the Romanian Leptodirini, based on morphological similarities, and especially on features of the male genitalia. This theory explains the colonization of the Apuseni Mountains through the Bohemian massif, and direct colonization of the Southern Carpathians from the Dinarides. Differences between the two phyletic lineages (Western *Drimeotus* and Southern *Sophrochaeta)* justified this hypothesis, which is also supported by new paleogeographic data (Steininger & Rögl 1985, Popov *et al.* 2004). When these different waves of colonization occurred is questionable, because direct Dinarides-Carpathians connection is either very old or too recent.

Migration of Asian ancestors of Cholevinae was not possible until the Upper Oligocene-Early Miocene, when a Dinarian-Pelagonian-

Anatolian landmass was formed, and linked to the rest of Europe by the recurring Slovenian corridor. This was the first connection between the Dinarides and Carpathians and lasted until Lower Badenian (16 Ma) when the Central Paratethys was flooded. It provided the possibility of populating the Southern Carpathians by Dinaric lineages, which was also at the time of Carpathian system development (Fig. 3). In Upper Ottnangian (17-18 Ma), the basin of the Paratethys was profoundly altered and a connection between the Alps and the Carpathians was established. The first Alps-Bohemian Massif-Carpathians connection provided conditions for the Apuseni Mountains colonization through the Bohemian massif. In Lower Badenian (15-16 Ma) a major transgression temporarily interrupted the connection between the Carpathians and the Bohemian Massif. Later, in Middle Badenian (14-15 Ma), the connection was definitively established. A connection between the Dinarides and the Carpathians was also established during the Messinian crisis (5-6 Ma) but cannot explain the processes of Southern Carpathian colonization and speciation. Subterranean beetles are less mobile, even if they can migrate over relatively short distances through the non-calcareous MSS. Supposing that epigean and edaphobiont forms migrated and colonized this region, it is improbable to admit that adaptation to deep subterranean habitats and speciation could have occurred in such a short period of time.

In conclusion, the Dinaric origin of subterranean Romanian beetles can be explained by a first migration wave of a Dinaride lineage over the Southern Carpathians and a later one through the Bohemian massif of a lineage that colonized the Apuseni Mountains. Both lineages are morphologically linked to Dinaric species, with some peculiar features in the *Drimeotus* western lineage. An additional migration from the southwest during the Messinian crisis also could have been possible but only for species less adapted to caves. The next step in the evolution of the Apuseni beetles was subterranean domain colonization. The processes and mechanisms that could have driven the subterranean colonization were presented in the previous section.

We also analyzed spatial distribution of species and subspecies of the Drimeotus phyletic lineage to obtain information which can be corroborated with available taxonomic and molecular data. Romanian Leptodirini offer good material for studying speciation and vicariance processes, because it involves insular distribution, which is different from the large, continuous limestone surfaces such as those of the Dinarides and the Pyrenees, where speciation has occurred in the absence of geographical barriers. The Apuseni Mountains are inhabited by three genera *(Protopholeuon, Pholeuon* and *Drimeotus),* belonging to the *Drimeotus* phyletic lineage (Fig. 4). The lineage is monophyletic (Bucur 2003) and suggests a common ancestor, probably epigean. *Protopholeuon*, which is monospecific, inhabits the Metaliferi Mountains, while the other two genera have larger distribution. Most species of *Pholeuon* and *Drimeotus* occur in the Padurea Craiului and the Bihor mountains. *Pholeuon* also

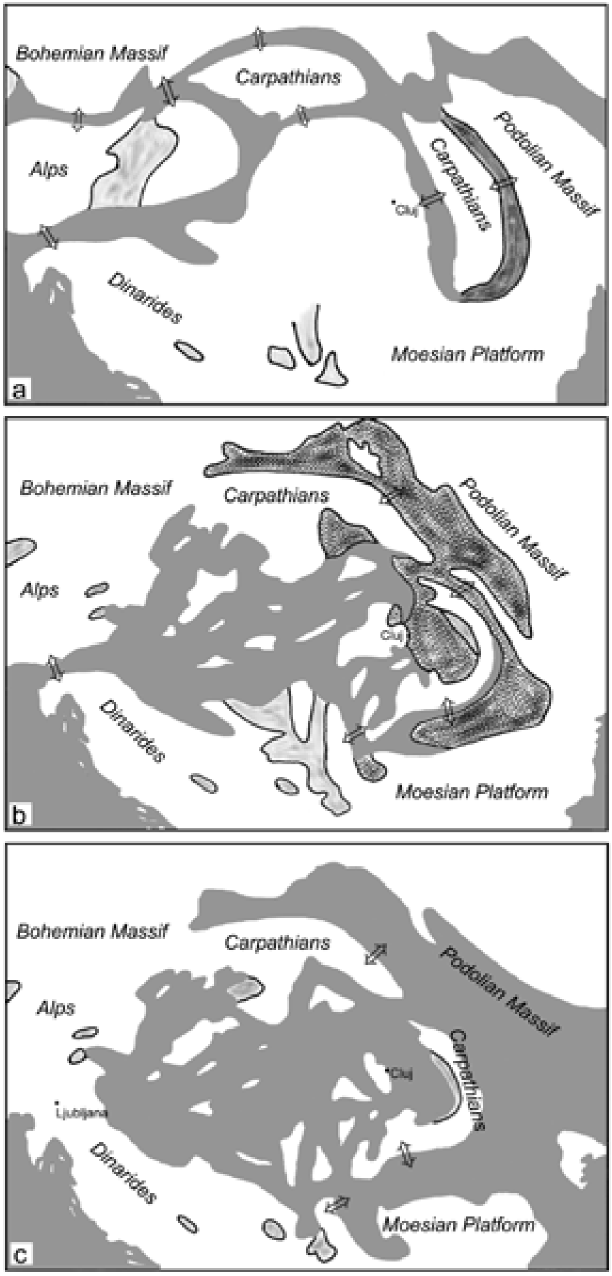

Fig. 3: Evolution of the Paratethys in Upper Ottnangian (a), Middle Badenian (b) and Lower Badenian (c) (Cluj is located in North-Western Romania) (simplified after Rögl & Steininger 1984): grey – marine realms, dark grey – evaporitic basins, light grey – important areas with fluvio-terrestrial sedimentation and/or lignite formation, white – continental realms, ⇔ - basins narrowed post-sedimentation by tectonic processes.

has sub-genera in the Codru-Moma unit, while *Drimeotus* is in the Metaliferi and the Trascau Mountains. Each mountain is inhabited by a different sub-genus. It is possible that future searches will enlarge the distribution of *Drimeotus* also in Codru-Moma. (The first and last specimen of Drimeotus in the Metaliferi was found as recently as 2001 in a cave well known for *Protopholeuon* and this was after several trapping episodes where *Protopholeuon/ Drimeotus* ratio was 150/1.)

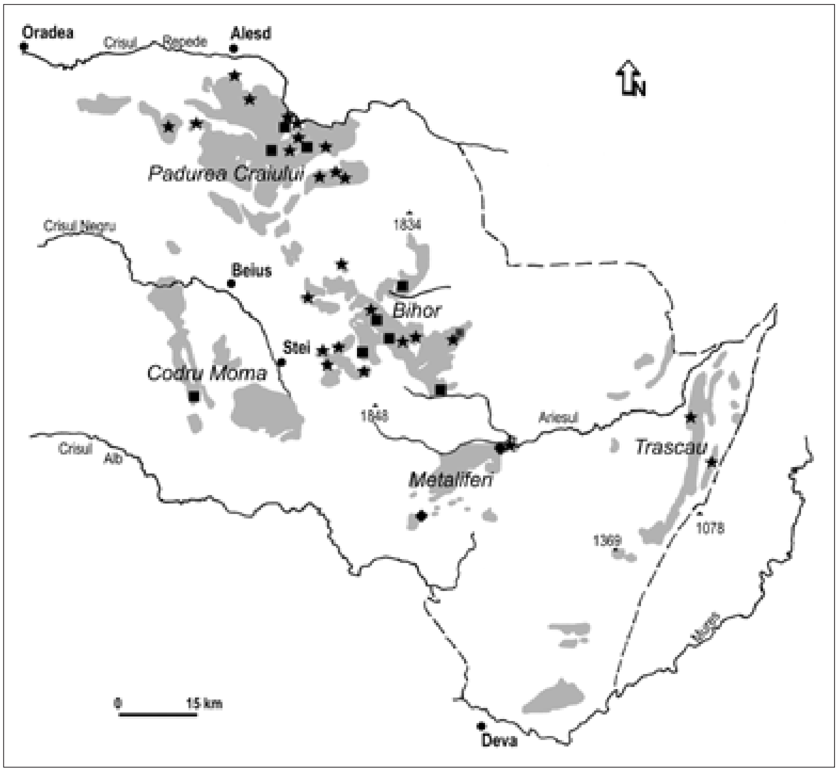

Fig. 4: Distribution of Leptodirini in the Western Carpathians (Apuseni Mountains): ★ - Drimeotus, ■ - Pholeuon, ◆ - Protopholeuon, grey areas - karst.

Comparing the largest geographical units in the Apuseni, Padurea Craiului and Bihor, the number of species and subspecies of less adapted *Drimeotus* and the more adapted *Pholeuon* is different between genera and between units. *Drimeotus* (20 species and 12 subspecies) has higher specific diversity in both units and lower subspecific diversity than *Pholeuon* (6 species and 20 subspecies). This can be explained by the difference in adaptation and different histories of the two genera. *Pholeuon*, very adapted, is less mobile and very few individuals were found in MSS or under rocks. Preadapted ancestors of *Pholeuon* colonized deep subterranean environment in the entire area and since then small modifications have occurred. Lacking competition, infra-generic differentiation of *Pholeuon* is slow. *Drimeotus*, less adapted and relatively mobile between limestone areas, is under stronger climatic and biologically stronger selective pressures, which explains larger distribution areas and higher specific diversity. There are also differences between the Padurea Craiului and the Bihor *Drimeotus*, with more than two-thirds of the species in the first mountains. In Padurea Craiului the climate is warmer and less humid, with caves at lower altitude than in Bihor. Therefore, migration and gene flow between populations inhabiting different limestone areas or caves are limited and speciation is stronger. The more humid and colder Bihor Mountains allows superficial migrations and gene interchange between geographically close populations.

The altitudinal distribution of Leptodirini was first discussed by Jeannel (1952), who mentioned the presence of the same genus and even same species at the surface at 1500 m altitude, under the rocks at 1000 m, and strictly cavernicolous at 500 m. A sound analysis of the distribution published by Decu (1980) emphasizes the lack of correlation between body size and altitude. We found different results, given in Table 1. For *Drimeotus*, correlation between altitude and body length or relative length of antennae is negative for Padurea Craiului samples, and positive for Bihor samples. An approach that links geography to morphology is the kriging method, which uses a topographic representation of the data sets. Using the Golden Software Surfer 8 we obtained the maps in Fig. 5. As one can see, the vectors define centers of origin at about 500-700 m altitude. Ancestors of the *Drimeotus* lineage probably inhabited superficial habitats between 500 and 1000 m altitude. Colonizing caves at lower or higher altitude induced body increase, a process explained by lack of competition and/or decrease of temperature. Body growth, as a result of cave colonization, is not only known for subterranean beetles. The *t* test showed no significant difference in body length between populations of Padurea Craiului and Bihor. The same test on the relative length of antennae gives shorter antennae in Bihor than in the Padurea Craiului samples. This can be due to the fact that the higher Bihor Mountains are inhabited by populations less confined to cave, compared to the Padurea Craiului. *Pholeuon* has the same tendencies as *Drimeotus*, with a negative correlation of body length and altitude in Padurea Craiului and a positive correlation in Bihor, and the antennae length decrease with altitude.

Tab. 1: Linear regression (y) and coefficient of determination (R^2) at Drimeotus (13 populations) and Pholeuon (6 populations) from the Padurea Craiului and the Bihor Mountains (Western Carpathians): BL Body length, AL/BL antenna/body lengths ratio.

	Altitude (m)		
	0-499	**500-999**	**> 1000**
Drimeotus			
BL	$y = -0.0003x + 4.4511$ $R^2 = 0.0096$	$y = 0.0004x + 4.1025$ $R^2 = 0.2337$	$y = 0.0007x + 3.5404$ $R^2 = 0.3301$
AL/BL	$y = -8E\text{-}05x + 0.5969$ $R^2 = 0.1077$	$y = 3E\text{-}05x + 0.5327$ $R^2 = 0.0195$	$y = 0.0001x + 0.4088$ $R^2 = 0.2449$
Pholeuon			
BL	$y = -0.0001x + 3.9152$ $R^2 = 0.0239$	$y = 0.0031x + 2.142$ $R^2 = 0.7849$	$y = 1E\text{-}04x + 4.6179$ $R^2 = 0.0150$
AL/BL	$y = -1E\text{-}04x + 0.8619$ $R^2 = 0.2445$	$y = -0.0002x + 0.9593$ $R^2 = 0.7847$	$y = -0.0001x + 0.9044$ $R^2 = 0.2529$

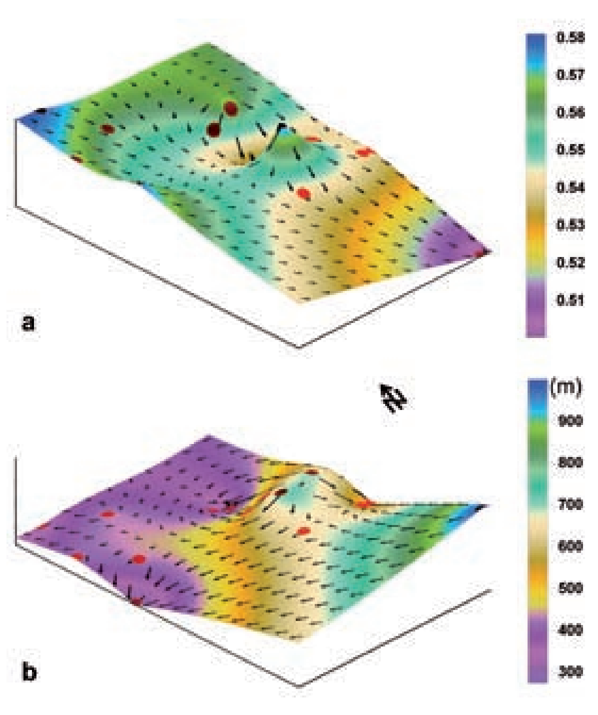

Fig. 5: Antennae relative length (a) and altitude (b) variations in geographical coordinates for 15 populations of Drimeotus s. str. (red dots) of Padurea Craiului Mountains, in 3D and vectorial overlayed representations.

Mantel's test (XLSTAT 2006.5 software) was also used to correlate geographic distance with morphological features, such as body and relative antennae lengths. Mantel's test is a regression in which variables are matrices summarizing pairwise similarities among sample locations. Geographic distance was used as a predictor variable, and morphological features of populations belonging to *Drimeotus* and *Pholeuon*, from the Padurea Craiului Mountains, as dependant distance matrices. For $\alpha = 0.01$, the test gives strong correlation for *Drimeotus* samples (Fig. 6) and no correlation for *Pholeuon*. For the moment, we cannot explain this result, although presumptions can be formulated.

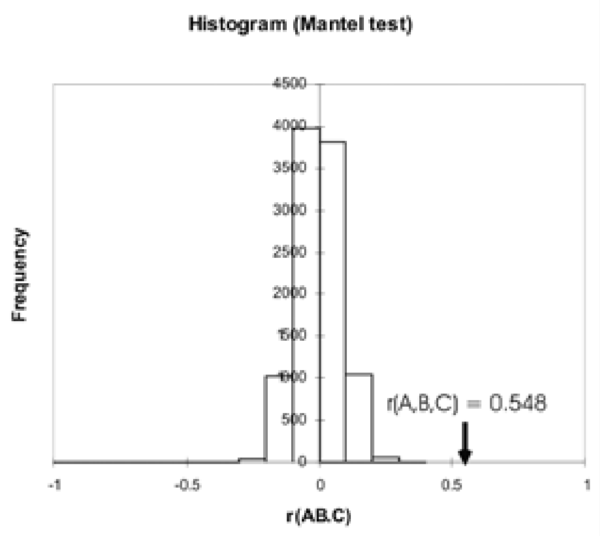

Fig. 6: Histogram representing results of the Mantel test on representatives of Drimeotus s. str. from Padurea Craiului.

CONCLUSIONS

Plato’s allegory still raises questions in historical biogeography of cave beetles, but new scientific acquisitions will also enhance the chances for a more objective view in explaining the history of one group or another and what shaped their present distribution.

We have only presented few results and further research must take into consideration more populations and the surface of the populated area, as in insular studies. In caves, as well as on oceanic islands, the number of endemics can be related to the size of the area. Studies of Barr (1985) and Culver *et al.* (1973) applied the insular theory of McArthur & Wilson to karst areas, which have the characteristics of continental islands separated by non-calcareous “seas”. Thus, the number of subterranean species is strongly correlated with the surface of the limestone.

The recent interest in biogeographic studies has resulted from conservation necessities, especially in the last decade. For example, the concept of habitat fragmentation became one of the priority themes of conservation researches. The concept is considered ambiguous, and empirical studies demonstrate a wide variety of direct and indirect effects, even with opposing implications (Haila 2002). The effects of habitat fragmentation are considered extremely dangerous for species and population preservation, and are often mentioned when establishing protection areas for rare and vulnerable species.

From a biospeleological point of view, habitat fragmentation represents one of the main mechanisms that enhanced speciation processes in reduced areas (at least for terrestrial fauna). This idea, different from the conservationist concern, can be extremely useful in solving protection problems. Unfortunately, none of the main contributions in conservation biology mentions caves and cave fauna as examples of survival in small, fragmented areas.

ACKNOWLEDGEMENTS

We are grateful to John Holsinger and David Culver for valuable suggestions, our colleagues Gheorghe Racovita and Tudor Tamas for useful discussions, and Andrej Mihevc, Liviu Buzila and Alexandru Imbroane for advice and maps.

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COBISS: 1.01

WHAT DOES THE DISTRIBUTION OF STYGOBIOTIC COPEPODA (CRUSTACEA) TELL US ABOUT THEIR AGE?

KAJ NAM POVE RAZŠIRJENOST STIGOBIONTSKIH CEPONOŽNIH RAKOV (CRUSTACEA: COPEPODA) O NJIHOVI STAROSTI?

David C. CULVER[1] & Tanja PIPAN[2]

Abstract UDC 595.3-15
591.5:595.3

David C. Culver & Tanja Pipan: What Does the Distribution of Stygobiotic Copepoda (Crustacea) Tell Us About Their Age? Geographic distribution of stygobionts is often used to estimate age of a group by assuming vicariant speciation with little or no subsequent dispersal. We investigated the utility of using distributional data for Slovenian stygobiotic copepods by assuming that dispersal is a way to measure age of a species. We list some species of Copepoda that, on the basis of their range and frequency of occupancy within their range, should be older. Body size is not predictor either of range or frequency of occupancy.

Key words: Speleobiology, Copepoda, stygobionts, dispersal biogeography.

Izvleček UDK 595.3-15
591.5:595.3

David C. Culver & Tanja Pipan: Kaj nam pove razširjenost stigobiontskih ceponožnih rakov (Crustacea: Copepoda) o njihovi starosti?
Ob predpostavki, da je nastajanje novih vrst posledica vikariance, brez naknadne disperzije, se za ocenjevanje starosti živalskih skupin pogosto uporablja geografska razširjenost stigobiontov. Ob domnevi, da je disperzija merilo za določanje starosti vrst, smo proučevali primernost podatkov o razširjenosti stigobiontskih kopepodov v Sloveniji. Na osnovi analize obsega naselitve in pogostosti naseljevanja znotraj območja smo v prispevku priložili seznam nekaterih vrst ceponožnih rakov, ki naj bi bile evolucijsko starejše. Telesna velikost ne določa obsega naselitve in pogostosti pojavljanja.

Ključne besede: speleobiologija, Copepoda, stigobionti, disperzijska biogeografija.

INTRODUCTION

The distribution of stygobionts has often been used to infer the age of a fauna. The general procedure has been to assume that little or no migration has occurred, and that the extant distribution represents the site of original colonization and isolation in subterranean habitats. The vicariance biogeographic view, now dominant in modern biogeography (e.g., Crisci, Katinas, and Posadas 2003) largely supplanted the old idea of centers of origin with species dispersing out from this central place (Matthew 1915). Given the reduced opportunities for dispersal of subterranean animals, it is not surprising that there have been a number of studies that show a correspondence between ancient shorelines and current distributions, especially Tethyan and Paratethyan distributions (Culver and Pipan in press). In some cases, it has been possible to match distributions to historical events and to obtain support from molecular clock data (see Verovnik, Sket, and Trontelj 2004). However, not all subterranean dis-

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Received/Prejeto: 27.11.2006

tributions can be explained solely by vicariance. A particularly interesting example is the cirolanid isopod *Antrolana lira* Bowman. In general, subterranean cirolanids are found near to marine shores (Botosaneanu, Bruce, and Notenboom 1986), suggesting a marine ancestor with vicariant isolation. But, *A. lira* is found in caves in the Appalachian Valley of Virginia and more than 200 km from not only the present ocean shore, but from any ocean dating back at least to the Paleozoic (Holsinger, Hubbard, and Bowman 1994).

In this contribution, we take a dispersalist rather a vicariance view of subterranean biogeography. We consider a model of colonization and isolation as follows. A species colonizes and is isolated in a subterranean site. As adaptation occurs, the species occupies more sites in the vicinity of the colonization. That is, the frequency of occupancy of subterranean sites increases. In the next stage, the species expands its range, with a high occupancy of suitable sites in its range. Finally, as other species also evolve, the original species may be out-competed or it may become specialized in response to competition. In this scenario, it will then occupy a lower frequency of sites within its range. Thus, we can rank the ages of species in increasing age as follows:

1. Species with small ranges and occupying few (sometimes only one) sites
2. Species with small ranges but occupying a high frequency of sites within its range
3. Species with large ranges and occupying a high frequency of sites within its range
4. Species with large ranges and occupying a low frequency of sites within its range.

We examine this hypothesis using distributional data of subterranean copepods from Slovenia (see Pipan 2005), and make assess the utility of this approach.

METHODS AND MATERIALS

From information in Pipan (2005) and Culver, Pipan, and Schneider (in press) we generated list of stygobiotic copepods from seven Slovenian caves, with information on ranges, frequency of occupancy of well-sampled caves, and average body size. Ranges were categorized into three groups:

1. Slovenian endemics
2. Balkan endemics
3. European endemics
4. Cosmopolitan species

To measure frequency of occupancy, we used data from Pipan (2005), which was intensive enough that it is likely that most species were found (Pipan and Culver in press). Body sizes were taken from original species descriptions and direct measurement by TP. Data were available for 37 species.

Analysis was done by grouping ranges into two categories (Small—categories 1 and 2 and Large—categories 3 and 4), frequency of occupancy into two categories (Low—1 to 3 caves and High—4 to 7 caves), and size into two categories (Small—less than the overall mean of 0.61 and large—greater than or equal to the overall mean of 0.61). The resulting 2X2 contingency tables were analyzed for independence using Fisher's Exact Test in JMP™ (Sall, Creighton, and Lehman 2005).

RESULTS

Available data for the 37 species of stybobiotic copepods are shown in Table 1. In Table 2, all species are categorized into four groups based on range and occupancy. There was no significant difference between observed and expected although there was a small excess of species with large ranges that were also found in a high frequency of caves. Those species hypothesized to be the oldest (large ranges, low occupancy) were:

- *Acanthocyclops kieferi*
- *Acanthocyclops venustus stammeri*
- *Diacyclops clandestinus*
- *Dicyclops languidoides*
- *Elaphoidella elaphoides*
- *Morariopsis scotenophila*

The group hypothesized to be the next oldest are those with large ranges and high occupancy:

- *Elaphoidella jeanneli*
- *Bryocamptus balcanicus*
- *Acanthocyclops venustus*
- *Parastenocaris nolli alpina*

Tab. 1: Stygobiotic copepod species found in seven well-sampled caves in Slovenia. See Pipan (2005) and Culver et al. (in press).

Species Name/Taxonomic Authority	**Mean Body Size**	**No. Caves Occupied**	**Range**
Acanthocyclops kieferi (Chappuis, 1925)	0.73	2	3
Acanthocyclops venustus (Norman & Scott, 1906)	1.07	1	3
Acanthocyclops venustus stammeri (Kiefer, 1930)	1.07	5	3
Bryocamptus balcanicus (Kiefer 1933)	0.40	4	3
Bryocamptus borus Karanovic & Bobic, 1998		1	2
Bryocamptus pyrenaicus (Chappuis, 1923)	0.80	7	3
Bryocamptus sp.		2	1
cf. Stygepactophanes sp.	0.35	3	1
Diacyclops charon (Kiefer, 1931)	1.00	7	2
Diacyclops clandestinus (Kiefer, 1926)	0.40	3	4
Diacyclops hypogeus (Kiefer, 1930)	0.50	2	1
Diacyclops languidoides (Lilljeborg, 1901)	0.80	3	4
Diacyclops slovenicus (Petkovski, 1954)	0.68	3	1
Echinocamptus georgevitchi (Chappuis, 1924)	0.70	1	2
Elaphoidella cvetkae Petkovski, 1983	0.75	4	2
Elaphoidella elaphoides (Chappuis, 1924)	0.60	1	3
Elaphoidella franci Petkovski, 1983	0.64	1	1
Elaphoidella jeannelli Chappuis, 1928	0.60	4	3
Elaphoidellakarstica Dussart & Defaye (1990)		1	1
Elaphoidella sp. A		2	1
Elaphoidella sp. B		2	1
Elaphoidella stammeri Chappuis, 1936	0.62	4	1
Maraenobiotus cf. brucei	0.60	1	1
Metacyclops postojnae Brancelj, 1990	>0.61	1	2
Moraria sp. A		2	1
Moraria sp. B		1	1
Moraria stankovitchi Chappuis, 1924	0.55	2	2
Morariopsis dumonti Brancelj, 2000	0.39	2	1
Morariopsis scotenophila (Kiefer 1930)	0.49	3	4
Nitocrella sp.	0.50	2	1
Parastenocaris cf. andreji	0.40	2	1
Parastenocaris nolli alpina (Kiefer, 1938)	0.42	5	3
Parastenocaris sp. A	0.40	2	1
Parastenocaris sp. B	0.40	4	1
Parastenocaris sp. C	0.40	2	1
Speocyclops infernus (Kiefer 1930)	0.47	6	2
Troglodiaptomus sketi Petkovski, 1978	0.88	3	2

We investigated whether there was a body size bias for occupancy or range size. Smaller copepods might be able to disperse more easily but they may also be more subject to the vagaries of water movement in epikarst (Pipan and Culver 2006). In any case, there was no relationship between frequency of occupancy and body size and no relationship between range and body size (Table 3).

Tab. 2: Number of species of stygobiotic copepods in categories of large and small range and high and low frequency of site occupancy. Numbers in parentheses are the expected numbers. Observed and expected numbers do not significantly differ (p=0.21, Fisher's Exact Test).

	High Occupancy	*Low Occupancy*
Large Range	4 (2.4)	5 (6.6)
Small Range	6 (7.6)	22 (20.4)

Tab. 3: Number of species of stygobiotic copepods in categories of high and low frequency of site occupancy (A), large and small range (B) and body size. Numbers in parentheses are the expected numbers. Neither association was statistically significant (p=0.71 for A, p=0.71 for B, Fisher's Exact Test).

A.

	High Occupancy	*Low Occupancy*
Large Body Size	5 (4.3)	8 (8.7)
Small Body Size	5 (6.7)	12 (11.3)

B.

	Large Range	Small Range
Large Body Size	5 (4.5)	8 (8.5)
Small Body Size	5 (5.5)	11 (10.5)

Finally, we investigated the taxonomic position of the putative older species, i.e., those with larger ranges. Of the ten species listed above, five are cyclopoids and five are harpacticoids. There is an excess of large ranged cyclopoids but the difference was only significant at p~0.10 (Table 4). *Acanthocyclops* is especially noteworthy. All three stygobiotic species *(A. kieferi, A. venustus, and A. venustus stammeri)* had large ranges. In contrast none of the three species of Moraria *(M. stankovitchi, sp. A, and sp. B)* have large ranges. The lone calanoid species *(Troglodiaptomus sketi)* also has a small range.

Tab. 4: Relationship between range and taxonomic group (Cyclopoida vs. Harpacticoida). Expected numbers are given in parentheses. The relationship was marginally significant (p~0.10, Fisher's Exact test).

	Large Range	Small Range
Cyclopoida	5 (2.8)	5 (7.2)
Harpacticoida	5 (7.2)	21 (18.8)

DISCUSSION

We have created a list of copepod species that, according to the hypothesis outlined in the introduction, should be older than other stygobiotic copepod species discussed in this study. Unfortunately, we know of no detailed phylogeny that would allow for such a comparison but we think that it would make for a very interesting study to do so. What is known about copepod phylogeny is that the Cyclopoida seem to be a more recent group than the Harpacticoida, accoding to the phylogeny of Huys and Boxshall (1991). The fact that cyclopoids are over-represented among species with large ranges (Table 4) contradicts the hypothesis put forward. Of course, just because cyclopoids as a group are younger does not mean that the species are all younger than harpacticoids. Alternatively, it may be that harpacticoids are in general being outcompeted by cyclopoids, and this has resulted, not only in reduction in occupancy frequency, but also in range contraction.

We think that examination of the kinds of distribution patterns (range size and occupancy) discussed here will yield interesting results. This analysis would enrich phylogeography studies as well as provide additional hypotheses about the origin and evolution of subterranean groups.

ACKNOWLEDGEMENTS

The authors were supported by funds from the Center for Subterranean Biodiversity of the Karst Waters Institute and the Ministry of Higher Education, Science, and Technology of the Republic of Slovenia.

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COBISS: 1.01

HOW TO DATE NOTHING WITH COSMOGENIC NUCLIDES

KAKO DATIRATI PRAZNINE S KOZMOGENIMI NUKLIDI

Philipp HÄUSELMANN[1]

Abstract UDC 539.16:552.5(494)

Philipp Häuselmann: How to date nothing with cosmogenic nuclides

A cave is a natural void in the rock. Therefore, a cave in itself cannot be dated, and one has to resort to datable sediments to get ideas about the age of the void itself. The problem then is that it is never very certain that the obtained age really is coincident with the true age of the cave. Here, we present the use of a method which couples sedimentary and morphologic information to get a relative chronology of events. Datings within this relative chronology can be used for assessing ages of forms, processes, and sediments, and the obtained dates also fix some milestones within the chronology, which then can be used to retrace, among other things, paleoclimatic variations. For many cave systems, the dating limits of the most widely used U/Th method on speleothems are too low (350 to max. 700 ka) to get ages that inform us about the age of the cave. The recent use of cosmogenic nuclides on quartz-containing sediment permits to push the datable range back to 5 Ma. While the theoretical background is explained elsewhere (Granger, this volume), we concentrate on the Siebenhengste example (Switzerland).

Key words: relative chronology, cosmogenic nuclides, cave dating methodology, Siebenhengste.

Izvleček UDK 539.16:552.5(494)

Philipp Häuselmann: Kako datirati praznine s kozmogenimi nuklidi

Jame predstavljajo praznino v kamninski masi in jim kot takim ne moremo določiti starost. Zato z datiranjem jamskih sedimentov sklepamo tudi o starosti jame, pri čemer seveda ne moremo trditi, da je dobljena starost tudi prava starost jame. V članku predstavimo metodo pri kateri z združitvijo sedimentarnih in morfoloških izsledkov sklepamo o relativni kronologiji dogodkov. Datiranje v oviru relativne kronologije lahko uporabimo za določevanje starosti različnih oblik, procesov in sedimentov. Dobljene rezultate pa lahko uporabimo kot pomembne mejnike v kronologiji, npr. pri intepretaciji klimatskih sprememb. Veliko jam je starejših od zgornje meje starosti (350 do 700 ka), ki jo lahko določimo z uran-torijevo metodo, ki je zelo razširjena. V zadnjem času se zato uveljavlja metoda datacije s kozmogenimi nuklidi, ki omogoča datiranje dogodkov do starosti 5 Ma. Ker je teoretično ozadje te metode predstavljeno drugje (npr. Granger v tej številki), se tu omejimo le na uporabo metode v jamskem sistemu Siebenhengste (Švica).

Ključne besede: relativna kronologija, kozmogeni nuklidi, metodika datiranja jam, Siebenhengste.

INTRODUCTION

For many cave scientists, it might not be evident that a cave does not exist - only the surrounding rock gives existence to the void called cave. Therefore, a cave cannot be dated by conventional methods (Sasowsky 1998), but one has to use datable sediments. In karstic caves, the age of the surrounding rock gives a maximal age of the cave, while the sediments found within the cave give variable ages from today (in the case of still active speleothems) up to the last stages of speleogenesis (in the case of specific sand deposits dated by cosmogenic nuclides) and therefore to the age of nothing itself.

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Received/Prejeto: 11.12.2006

This paper contains two parts. In the first part, the concept of relative chronology is explained. The link between morphology and sediment succession leads to a relative chronology of erosional and depositional events. Any dating of sediment with the purpose of studying the age of nothing basically requires such a relative chronology, which places the obtained data into a timeframe.

In the second part, the dating of sandy cave sediments with cosmogenic nuclides is briefly presented. Especially when dealing with sands, a relative chronology is very important to date only meaningful sediments. The theoretical background is only very briefly presented, and the reader is referred to Granger (this volume) for more thorough information. The Siebenhengste example, the use of the relative chronology, and the obtained results are presented in more detail.

THE CONCEPT OF RELATIVE CHRONOLOGY

INTRODUCTION

Geologists and other scientists are usually aware of the laws of stratigraphy, which say that a younger sediment overlies an older one. These laws are the base of a relative chronology. This chronology is normally used to assess the correctness of an obtained age - the numerical value has to be concordant with stratigraphy, or the dated age may not be correct. Most of the time, this principle is used with stalagmites, where the obtained ages must be older at the base and younger at the top (e.g. Spötl *et al.* 2002).

Morphological indications, on the other hand, also give chronological information. A keyhole passage informs us that a phreatic phase was followed by a vadose one. Successions of speleogenetic phases are found in many cave systems. While some of them indicate base level rises (Audra *et al.,* 2004), most of them indicate a downcutting of the regional base level (uplift, valley deepening, e.g. Ford & Williams 1989; Rossi, Cortel & Arcenegui 1997). This in itself is also a chronological information: the oldest cave passages are on top, the youngest ones near the present baselevel.

The difficulty now is to connect the sediments of several, basically independent, sedimentary profiles and to link them with the morphological succession of the cave passages. Thus, the sedimentary profiles are not independent from each other, and a relative chronology of erosional and depositional events over the whole cave can be made.

EXAMPLE

Figure 1 shows a real situation encountered in St. Beatus Cave (Switzerland):

To the right side is a typical keyhole passage which proves that a phreatic initiation of the ellipse on top was followed by a canyon incision. In the middle part of the figure, the meander gradually disappears and is replaced by a more or less elliptic passage that continues towards the left side of the figure. We see therefore a transition of a vadose feature into a phreatic one, and thus an old water level. In the profile to the right, we observe flowstone deposition that was truncated by the river incising the meander. Therefore, the flowstone predates the canyon, but postdates the initial genesis of the elliptic passage to the right. The meander changes into an elliptic passage, thus the two forms are contemporaneous. Consequently, the older flowstone disappears in the area of this transition. Within all the passages, silts were deposited. They are younger than the meander incision, and younger than the passage to the left, and prove of an inundation of the whole cave. Stalagmites grow on the silts and are partially still active. This example can be written as a table (Tab. 1).

Phreatic genesis of top ellipse	
	Water level lowering
Deposition of flowstone	
Erosion of flowstone	
Erosion of meander	
	Water level lowering
Silt deposition	
Stalagmite growth	

Tab. 1: Chronology of erosional and depositional events (Fig. 1)

This table is a first relative chronology that links the sediments and the morphology of the cave.For practical reasons, the table presenting the chronology of events in a large cave system is not rewritten with each sedimentary succession found. Instead, the single sedimentary sequence is coupled with morphology, and is written as a column in the table. The next sedimentary sequence, again coupled with morphology, is written as another column. Thus, the above example would then look like Table 2.

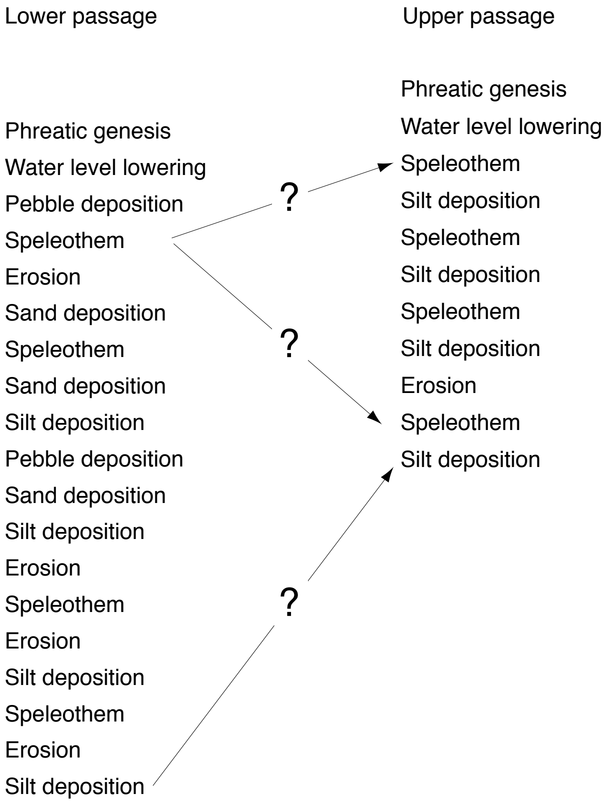
Sequence at left	Sequence at right
	Phreatic genesis of top ellipse
	Water level lowering
Phreatic genesis	Deposition of flowstone
Phreatic genesis	Erosion of flowstone
Phreatic genesis	Erosion of meander
Water level lowering	
Silt deposition	Silt deposition
Stalagmite growth	Stalagmite growth

Tab. 2: Chronological table with columnar writing of Fig. 1

EXPANSION

If we continue up- and downstream of that profile, we find several other morphological indications and sedimentary successions, each of them having a link with our initial profile - until we encounter the next paleo-water-level and thus the next morphological change. There, the links have to be established again. The table thus slowly grows and gets more complete.

Of course, the example presented above is an ideal case. Often, the passages lack some information, thus making it difficult to establish an unambiguous chronological table. Table 3 give an example: here, the upper passage lacks incision of a canyon. Therefore, it is not clear whether the sediments found in the upper passage were all deposited while the lower passage was still in its initial genesis, or whether the sediments can be partly correlated. In this case, a relative correlation of the sediments by observation only is not possible: some absolute dates have to be obtained. Of course, these ages have to be in stratigraphic order of both the sediment succession and the morphologic indications. The above example had been dated by U/Th on speleothems. The resulting table is presented in Table 4. Here, the speleothems with roughly the same age have been grouped together. Then, laminated silt deposits that are thought to be a product of glacial damming (Bini, Tognini & Zuccoli 1998; Audra *et al.*, this volume), are parallelized, inferring that the whole cave was flooded in such conditions. Of course, some uncertainties still persist.



Lower passage	Upper passage
	Phreatic genesis
Phreatic genesis	Water level lowering
Water level lowering	Speleothem
Pebble deposition	Silt deposition
Speleothem	Speleothem
Erosion	Silt deposition
Sand deposition	Speleothem
Speleothem	Silt deposition
Sand deposition	Erosion
Silt deposition	Speleothem
Pebble deposition	Silt deposition
Sand deposition	
Silt deposition	
Erosion	
Speleothem	
Erosion	
Silt deposition	
Speleothem	
Erosion	
Silt deposition	

Tab. 3: A more complicated example from St. Beatus Cave

Lower passage	Upper passage
	Phreatic genesis
	Water level lowering
	Speleothem (>350 ka)
Phreatic genesis	Silt deposition
Water level lowering	
Pebble deposition	
Speleothem	Speleothem (337 ka)
Erosion	
Sand deposition	
Speleothem (235 ka)	
Sand deposition	
Silt deposition	
Pebble deposition	
Sand deposition	
Silt deposition	Silt deposition
Erosion	
Speleothem (180 ka)	
Erosion	
	Speleothem (114 ka)
Silt deposition	Silt deposition
	Erosion
Speleothem (91 ka)	Speleothem (99 ka)
Erosion	
Silt deposition	Silt deposition

Tab. 4: The more complicated example, dated and expanded

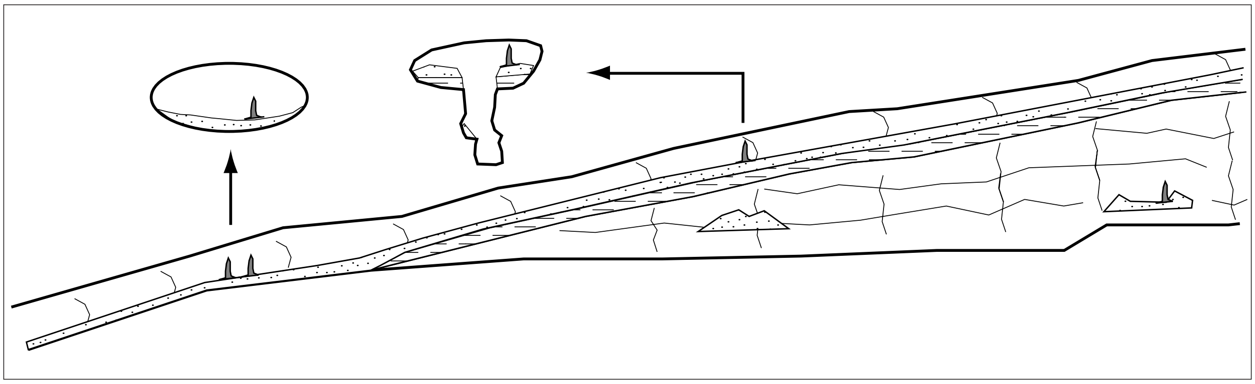


Fig. 1: Schematic section through a part of St. Beatus Cave (Switzerland), showing the relationship between sediments and morphology.

WHY A RELATIVE CHRONOLOGY?

The huge advantage of such a table of relative chronology is that it offers more control on the correct stratigraphic order than single sections, in ideal cases also the cave genesis can be dated, and last but not least, when having parallelized all the sedimentary sequences, it is possible to make a synthetic and dated sediment profile of the whole cave, which can then be used to get information on climatic variations and the presence or absence of glaciers damming the cave's exit (Häuselmann 2002).

DATING WITH COSMOGENIC NUCLIDES

INTRODUCTION

Cosmogenic nuclides are generated by the interaction of cosmic rays (mainly protons, neutrons, and muons) with atoms in the Earth's atmosphere and lithosphere. The production rate of cosmogenic isotopes depends on the intensity of the cosmic rays, which is subject to change. The atmosphere then absorbs most of the primary rays and thus causes production rates to depend on elevation. Finally, the geometry of the sample location (and eventual snow or soil cover) also has its effects. The radioactive nuclides most widely used for dating purposes are ^{10}Be and ^{26}Al produced in Quartz.

THE PRINCIPLE AND POSSIBILITIES OF BURIAL DATING

Burial dating of cave sediments is a relatively new technique that indicates the time sediment has been underground (Granger, Fabel & Palmer 2001). It relays on the radioactive decay of the nuclides that were previously accumulated when the sediment was exposed at the surface. Whereas the intensity of the cosmic rays may vary with time, the ratio of produced ^{10}Be to ^{26}Al remains always approximately 1:7. The ^{10}Be/^{26}Al ratio can thus be calculated from the production rates and radioactive decay. If a sample that contains ^{10}Be and ^{26}Al is washed underground to sufficient depth to be shielded from further radiation, the nuclide concentrations diminish. Since ^{26}Al has a half-life of 720 ka, opposed to the one of ^{10}Be of 1.34 Ma, the ratio of 1:7 is gradually lowered. Measurement of that ratio therefore gives a direct indication of the time the sample remained underground.

Of course, several prerequisites have to be fulfilled in order to get a burial age:

- First of all, the sediment must contain quartz that was irradiated sufficiently prior to burial. The grain size should be minimally fine sand (otherwise the cleaning process also eliminates the quartz), but may reach pebble size without problem.
- Then, burial should ideally be 20-30 m below the surface to be sufficiently shielded from radiation.
- In order to make a measurement meaningful, the stratigraphic relationship of the sampled sand with the passage and other sediments should be clearly established - the relative chronology is needed.

Burial dating has a range from about 100'000 years up to 5 Ma. After that time, the amount of remaining isotopes is usually too small to be measured accurately (Granger & Muzikar 2001). It is one of only a few radiometric methods that date lower Quarternary and Pliocene deposits. It is of great interest for cave dating, first because many old caves were created in the Pliocene or even earlier, and second because caves are very effective at shielding the sediment from further cosmic ray bombardment. As with other cave-dating methods, burial dating may also be used to date the age of the passage,

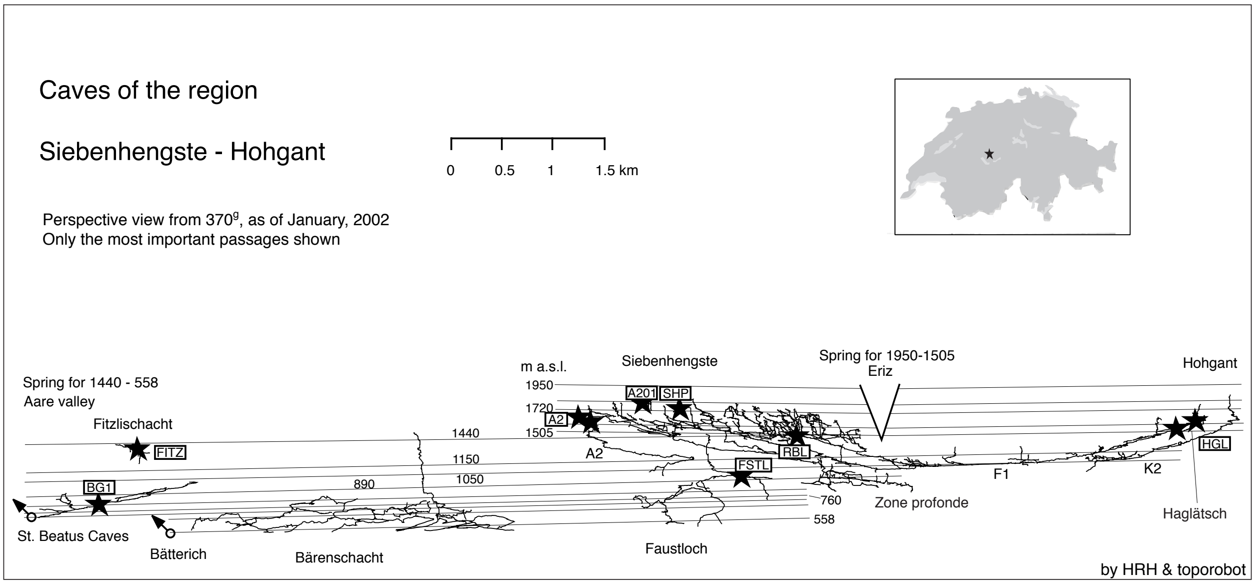


Fig. 2: Projection (370 degrees) of the Siebenhengste caves with the speleogenetic phases. Stars indicate sampling places for cosmogenic dates. From Häuselmann & Granger (2005), modified.

thus indicating valley deepening rates and evolution of the surface outside the cave.

THE SIEBENHENGSTE EXAMPLE

We used burial dating to date the old passages of the Siebenhengste cave system in Switzerland. The Siebenhengste region is situated in the north-western part of the Alps, adjacent to the molasse basin. From Lake Thun, the mountain range extends to the Schrattenfluh, 20 km away. The cave region is one of the longest and deepest worldwide, with the Réseau Siebenhengste-Hohgant having 154 km length and -1340 m depth. The caves comprise 14 different speleogenetic phases, which can be related to paleo-valley bottoms (Jeannin, Bitterli & Häuselmann 2000). The highest and oldest five phases (at presumed spring elevations of >1900, 1800, 1720, 1585, and 1505 m a.s.l.) had their springs in the Eriz valley (Fig. 2). The next phase, at 1440 m, shows a change in flow direction of 180°. The spring was then located in the area of Lake Thun. The influence of today's Aare valley (the site of Lake Thun today) therefore became predominant. All subsequent springs (at 1145, 1050, 890, 805, 760, 700, 660, and 558 m a.s.l.) drained towards the Aare valley.

In the area between Lake Thun and Hohgant, a total of 23 sites were selected for sampling (see Fig. 2: stars indicate sites). Selection was made on the basis of a relative chronology, and care has been given to ensure that either the oldest possible sediment, or a series in stratigraphic order, was sampled. Due to the limited amount of time in which sampling could be done, the relative chronology is incomplete (Tab. 5), although the main events were retraced. 21 samples were analysed (Häuselmann & Granger 2005). The results show a great diversity of ages, ranging from 118 ka up to

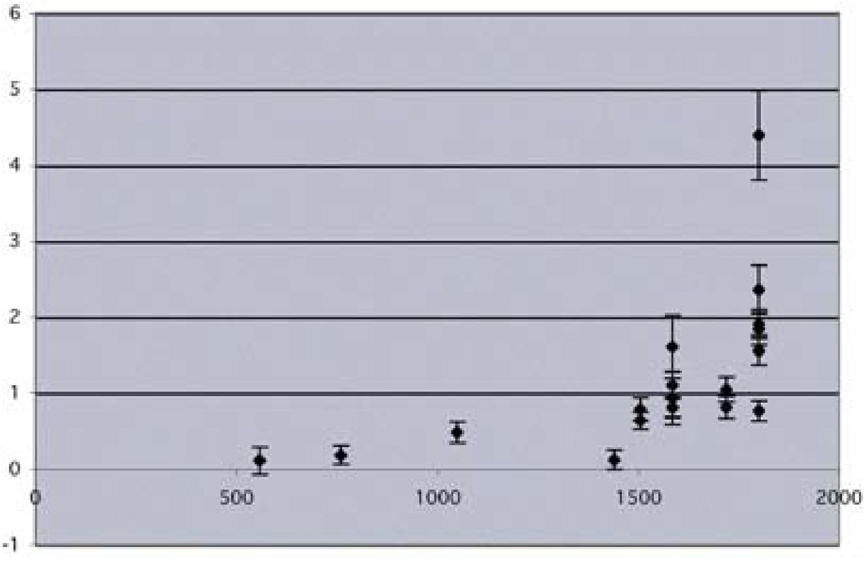


Fig. 3: Plot of ages (vertical) versus altitude (horizontal).

bold = morphologic event (a **Ø** denotes phreatic genesis, a **v** vadose enlargement), *italic* = dated event

A201	ShP low	SHP up	Haglätsch	A2TR	A2CHU	A2NS	RBL	L18	Faustloch	Beatus	Age	Interpretation
1800Ø	**1800Ø**	**1800Ø**										**1800Ø**
	SHP 7	Sediment								*4.39*		
	Erosion	**Erosion**										
	SHP2										*2.35*	
	SHP 3											
	Silt											
			1720Ø	**1720Ø**								**1720Ø**
	Flowst.	Flowst.										
	Silt	lake	Silt									
	Erosion	**Erosion**	**Erosion**									
	Flowst.											
	Sand											
	Erosion											
A201	*SHP5*										*1.9-1.84*	
	Sand	Sand										
	Silt		Silt									
			1585Ø		**1585Ø**	**1585Ø**		**1585Ø**				**1585Ø**
	Erosion	**Parag.?**										
Flowst.	Flowst.											
Silt												
Flowst.												
Erosion												
lake												
	SHP1	*SHP6*	*HGLP*								*1.54-1.60*	
	Flowst.	Flowst.	Flowst.									
		Erosion	**Erosion**	**Canyon**								
					Paragen. epiphreatic							
			HGLS					*L18*			*1.04-1.09 (.93?)*	
								Silt				
							1505/1440Ø					**1505/1440Ø**
								Flowst.				
	SHP4		*HGLT*	*A2TR*	*A2CHU*	*A2NS*	*RBL2*				*0.78-0.80 (.93?)*	
								Erosion				
							RBL1				*0.63*	
									1050Ø			**1050Ø**
									1050v	**890Ø**		**890Ø**
									Flowst.			
									flooding			
									FSTL		*0.47*	
										805Ø		**805Ø**
										760Ø		**760Ø**
										BG23	*0.23*	
										BG1	*0.18*	
										BG20	*0.16*	

Tab. 5: Relative chronology of events around the Siebenhengste

4.4 Ma (Tab. 6). The surface sample (MWA) has a burial age of 106 ± 176 ka. Thus, the value is indistinguishable from zero, and we may assume that the sample was never buried. The sample from St. Beatus Cave (BG1) has an age of 182 ± 122 ka. Its true value, bracketed by U/Th

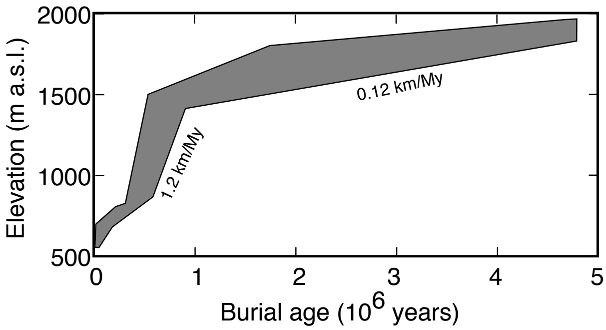
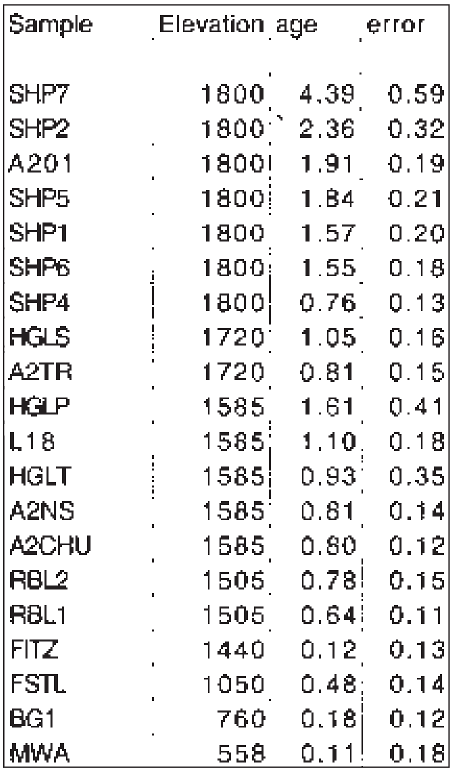


Fig. 4: Rate of valley lowering in the Siebenhengste. Only maximum and minimum ages are displayed; however the valley deepening rates as well as the knickpoint at ~800 ka are easily visible.

ages, should be between 160 and 235 ka, which is again the case. These values indicate that the method yields young ages where expected.

A difficulty for dating with cosmogenic nuclides is mobility of the sediment. For instance, recent sand can be transported into a fossilized cave by a flood and then be deposited. Our results show that this process happens: for any speleogenetic phase, there is a range of ages observed (Fig. 3). However, Fig. 3 also indicates that the re-mobilization and re-deposition of old sediments is rarely observable: if this would be the case, we would expect a random distribution of ages throughout the phases. However, the maximum age decreases with the next lower phase. We can thus construct a gradual valley lowering with time which is represented in Fig. 4. We see a knickpoint in the line connecting the ages: this knickpoint occurs at around 800 ka and 1500 m. This point reflects a dramatic increase in valley deepening rate and coincides with the change in flow direction from Eriz to the Aare valley.



Sample	Elevation	age	error
SHP7	1800	4.39	0.59
SHP2	1800	2.36	0.32
A201	1800	1.91	0.19
SHP5	1800	1.84	0.21
SHP1	1800	1.57	0.20
SHP6	1800	1.55	0.18
SHP4	1800	0.76	0.13
HGLS	1720	1.05	0.16
A2TR	1720	0.81	0.15
HGLP	1585	1.61	0.41
L18	1585	1.10	0.18
HGLT	1585	0.93	0.35
A2NS	1585	0.81	0.14
A2CHU	1585	0.80	0.12
RBL2	1505	0.78	0.15
RBL1	1505	0.64	0.11
FITZ	1440	0.12	0.13
FSTL	1050	0.48	0.14
BG1	760	0.18	0.12
MWA	558	0.11	0.18

Tab. 6: Results of dating.

CONCLUSIONS

A relative chronology of events, albeit incomplete, coupled with burial age dating by cosmogenic nuclides, permitted to obtain a continuous history of valley incision in the Alps. Such data cannot be obtained in the same precision with other methods or at the surface. The results presented here are the first cosmogenic dates for an Alpine cave system in a glacially influenced area. The results indicate an onset of karstification in the Siebenhengste before 4.4 Ma, that is in the Pliocene or even earlier. Together with U/Th dates obtained earlier (Häuselmann 2002), the history of the Siebenhengste cave system and its surrounding environment can be traced back over a huge time span.

The construction of a complete relative chronology is very time-consuming, but can be extremely rewarding given the information one can extract from the cave. If speleogenetic phases, which are related to the overall geomorphic evolution of an area, can be expanded by such relative chronologies as well as absolute dates, the rate, duration, and extent of valley deepenings can be assessed, and a paleoclimatic history can be drawn as well.

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COBISS: 1.01

UPPER CRETACEOUS TO PALEOGENE FORBULGE UNCONFORMITY ASSOCIATED WITH FORELAND BASIN EVOLUTION (KRAS, MATARSKO PODOLJE AND ISTRIA; SW SLOVENIA AND NW CROATIA)

ZAKRASELA PERIFERNA IZBOKLINA POVEZANA Z RAZVOJEM ZGORNJEKREDNO-PALEOGENSKEGA PREDGORSKEGA BAZENA; KRAS, MATARSKO PODOLJE IN ISTRA (JZ SLOVENIJA IN SZ HRVAŠKA)

Bojan OTONIČAR[1]

Abstract UDC 551.44.551.7(497.4-14)
552.541.551.7(497.4-14)

Bojan Otoničar: Upper Cretaceous to Paleogene forbulge unconformity associated with foreland basin evolution (Kras, Matarsko Podolje and Istria; SW Slovenia and NW Croatia)

A regional unconformity separates the Cretaceous passive margin shallow-marine carbonate sequence of Adriatic Carbonate Platform from the Upper Cretaceous and/or Paleogene shallow-marine sequences of synorogenic carbonate platform in southwestern Slovenia and Istria (a part of southwestern Slovenia and northwestern Croatia). The unconformity is expressed by irregular paleokarstic surface, locally marked by bauxite deposits. Distinctive subsurface paleokarstic features occur below the surface (e.g. filled phreatic caves, spongework horizons…). The age of the limestones that immediately underlie the unconformity and the extent of the chronostratigraphic gap in southwestern Slovenia and Istria systematically increase from northeast towards southwest, while the age of the overlying limestones decreases in this direction. Similarly, the deposits of synorogenic carbonate platform, pelagic marls and flysch (i.e. underfilled trinity), deposits typical of underfilled peripheral foreland basin, are also diachronous over the area and had been advancing from northeast towards southwest from Campanian to Eocene. Systematic trends of isochrones of the carbonate rocks that immediately under- and overlie the paleokarstic surface, and consequently, of the extent of the chronostratigraphic gap can be explained mainly by the evolution and topography of peripheral foreland bulge (the forebulge). The advancing flexural foreland profile was the result of vertical loading of the foreland lithospheric plate (Adria microplate) by the evolving orogenic wedge. Because of syn- and post-orogenic tectonic processes, and time discrepancy between adjacent foreland basin deposits and tectonic ("orogenic") phases it is difficult to define the exact tectonic phase responsible for the evolution of the foreland complex. According to position and migration of the subaerially exposed forebulge, distribution of the foreland

Izvleček UDK 551.44.551.7(497.4-14)
552.541.551.7(497.4-14)

Bojan Otoničar: Zakrasela periferna izboklina povezana z razvojem zgornjekredno-paleogenskega predgorskega bazena; Kras, Matarsko podolje in Istra (JZ Slovenija in SZ Hrvaška)

V jugozahodni Sloveniji in Istri so kredna karbonatna zaporedja Jadranske karbonatne platforme pasivnega obrobja Jadranske mikroplošče ločena z regionalno diskordanco od zgornjekrednih in paleogenskih karbonatnih zaporedij sinorogene karbonatne platforme. Razgibano paleokraško površje, ki diskordanco označuje, je lokalno prekrito z boksitom. Pod površjem se pojavljajo različne podpovršinske paleokraške oblike, med drugim večje zapolnjene freatične jame in diskretni horizonti drobnih prepletajočih se kanalčov. Starost apnencev neposredno pod paleokraškim površjem in obseg stratigrafske vrzeli v jugozahodni Sloveniji in Istri sistematično naraščata od severovzhoda proti jugozahodu, nasprotno pa starost apnencev, ki paleokraško površje pokrivajo v tej smeri upada. Preko obravnavanega območja so med campanijem in eocenom od severovzhoda proti jugozahodu napredovala tudi sedimentna zaporedja sinorogenih karbonatnih platform (karbonatne kamnine Kraške grupe) ter pelagičnih laporjev in fliša, ki predstavljajo sedimente podhranjenega predgorskega bazena. Sistematične trende izohron karbonatnih kamnin, ki ležijo neposredno pod in nad paleokraškim površjem in posledično razpona stratigrafske vrzeli lahko v veliki meri razložimo z evolucijo in topografijo periferne predgorske izbokline. Napredujoči fleksurni predgorski profil je nastal zaradi vertikalne obremenitve predgorske litosferske plošče (Jadranske mikroplošče) z nastajajočim orogenim klinom. Zaradi sočasnih in postorogenih tektonskih procesov ter časovnega neskladja med sedimenti sosednjih predgorskih bazenov in med različnimi tektonskimi (»orogenimi«) fazami tega dela zahodne Tetide v kredi in paleogenu, je opredelitev tektonske faze, ki je neposredno odgovorna za evolucijo obravnavanega predgorja otežena. Glede na položaj in migracijo periferne iz-

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Received/Prejeto: 01.02.2006

related macrofacies and orientation of tectonic structures, especially of Dinaric nappes, and Dinaric mountain chain I suggest that the foreland basin complex in western Slovenia and Istria was formed during mesoalpine ("Dinaric") tectonic phase due to oblique collision between Austroalpine terrane/Tisia microplate and Adria microplate when probably also a segmentation of the foreland plate (Adria microplate) occurred.

Key words: forebulge unconformity, paleokarst, chronostratigraphic gap, flysch, Adriatic Carbonate Platform, synorogenic carbonate platform, foreland basin, Adria microplate, Dinaric orogene, Cretaceous, Paleogene, SW Slovenia, Istria.

bokline, razporeditev makrofaciesov podhranjenega predgorskega bazena ter usmerjenost tektonskih struktur, predvsem Dinarskih pokrovov, in Dinarskega gorstva v celoti domnevam, da je nastal predgorski sistem v zahodni Sloveniji in Istri med mezoalpidsko (»Dinarsko«) tektonsko fazo, kot posledica bočne kolizije med Avstroalpidskim terranom in/ali Tisa mikroploščo ter Jadransko mikroploščo, pri čemer je verjetno prišlo tudi do segmentacije Jadranske mikroplošče.

Ključne besede: diskordanca, paleokras, kronostratigrafska vrzel, fliš, Jadranska karbonatna platforma, periferna predgorska izboklina, sinorogena karbonatna platforma, predgorski bazen, Jadranska mikroplošča, Dinarski orogen, kreda, paleogen, jugozahodna Slovenija, Istra.

INTRODUCTION

Plate tectonics theory had a crucial impact on our understanding of sedimentary basins, and consequently, of carbonate sedimentary systems. Plate tectonics determines not only the gross architecture (dimension and shape) and lithological/structural characteristics of carbonate platforms (Bosellini, 1989), but also their evolution and the longevity. Those characteristics are largely defined by specific geotectonic setting in which certain carbonate platform begin to grow. Carbonate platform(s), which colonize certain area through longer or shorter period of geologic history, constantly change its/their position in relation to the equator and plate boundaries and pass through different phases of the Wilson cycle. The sedimentary and diagenetic character of the carbonate platform(s) constantly change(s) during this journey and at a stretch, the platform evolution may be stoped. In this case, the area formerly inhabited by the carbonate platform may fall under conditions which are not favourable for considerable carbonate production. In one scenario it may immediately after the deposition or later in the geologic history be uplifted, subaerially exposed and karstified. Similarly as the plate tectonics governs the sedimentary evolution of the carbonate platforms, it may also determins their diagenetic evolution, including karstification. The gross architecture, lithological/structural caharacteristics, and the evolution and the longevity of the uplifted area with subaerially exposed carbonate platform are mainly dependent on its geotectonic position regard to plate boundaries, former geodynamics and consequently topography of the area, especially of the carbonate platform. Although important for the appearance of the karstic landscape, the effects of other variables, such as climate and ground water level, may be just superimposed on the geotectonically predisposed framework.

Each karstic landscape carries its specific geotectonic signature which can be read from and explained with specific evolution of karstic features and a karst system as a whole. In addition, studies of sedimentary successions of rocks that under- and overlie the (paleo-) karstic surface and that of the adjacent sedimentary basins as well as the general geologic conditions of the region may significantly improve our knowledge on geodynamics of the uplifted area.

The paper documents an example of paleokarst that occurred during the uplift of the Adriatic Carbonate Platform (sensu Vlahović *et al.,* 2005) in the distant foreland region of the evolving collision related orogenic belt between the Adria microplate (sensu Stampfli *et al.*, 1998) and the Austroalpine terrane and/or Tisia microplate (sensu Neugebauer *et al.,* 2001) in the Late Cretaceous and the Early Paleogene.

The study is based on 36 geological profiles from the karstic regions of southwestern Slovenia, both Slovenian and Croatian part of Istria peninsula and the area between Trieste bay and Italian-Slovenian border in northeastern Italy (Figs. 1, 2). To get a whole picture of conditions that dominated the region during the emersion period, I expend the area of interest to synorogenic carbonate platform that onlap the paleokarstic surface and to siliciclastic flysch regions of afore mentioned areas and the adjacent regions of western Slovenia and northeastern Italy (along the border between Italy and Slovenia).

The aim of this work is to show the causes of the uplift and subaerial exposure of the northwestern part of the Cretaceous Adriatic Carbonate Platform in Late Cretaceous and Early Paleogene. The data presented here were provided mainly from the studies of paleogeographic and topographic extent of the emersion, stratigraphy of the carbonate successions that immediately under- and

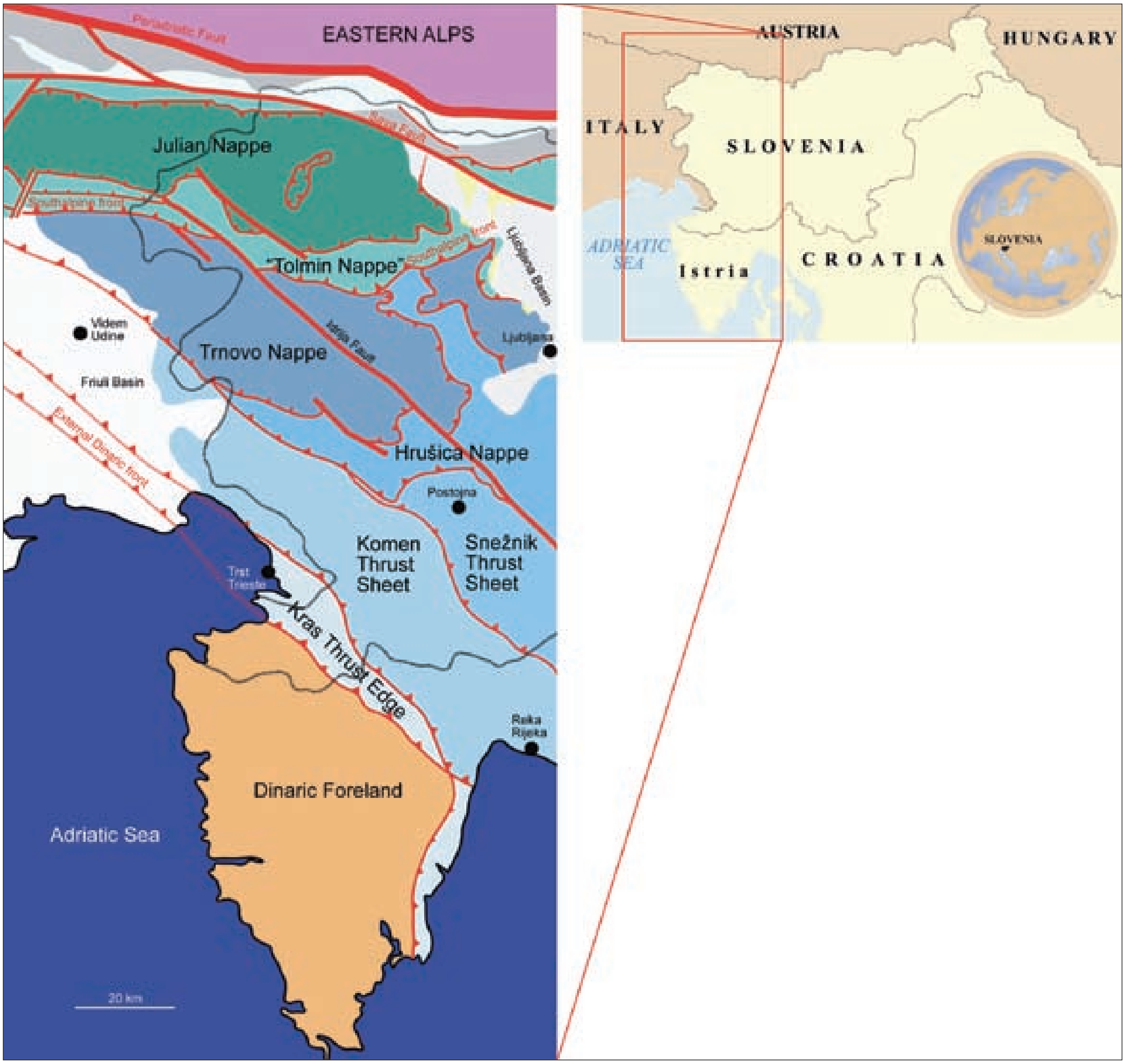

Fig. 1: Geographical position and simplified geological map of the western Slovenia and Istria showing major structural elements (modified from Placer, 1999).

overlain the paleokarstic surface, stratigraphy and sedimentology of the onlapping synorogenic carbonate platform and adjacent deeper marine basin as well as from regional geotectonic and general geologic situation. The time of the uplift is correlated with events on the adjacent plate boundaries of the western Tethian domain (traditional "orogenic phases") and global eustatic curve.

GEOLOGY OF THE AREA

The geology of southwestern Slovenia and Istria has been studied from the late 19th century on. Since that time also a regional unconformity which separates shallow-marine carbonate successions of different Cretaceous formations from shallow-marine limestones of the Upper Cretaceous/Lower Paleogene Liburnia Formation or Eocene

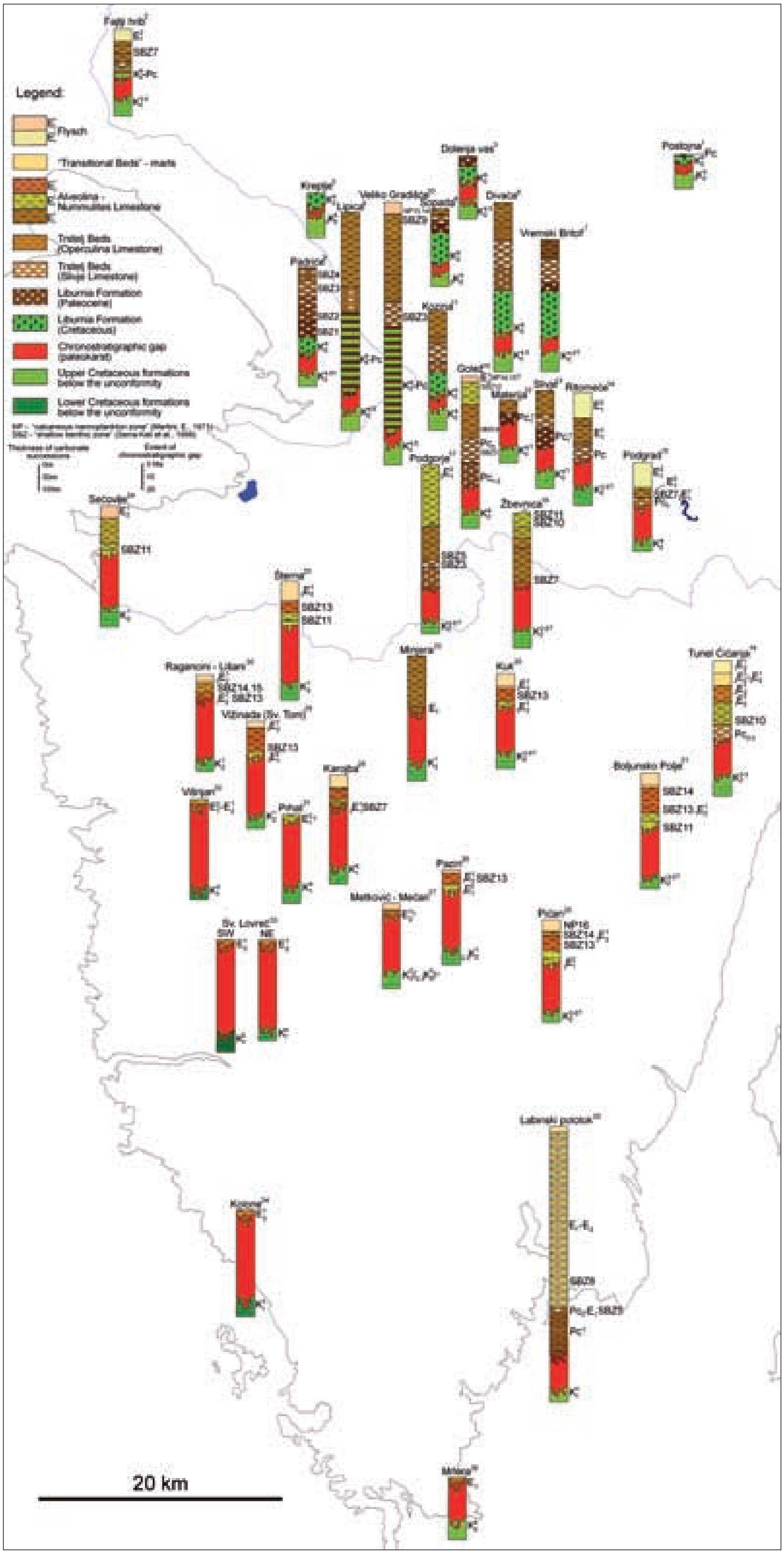

Fig. 2: Simplified lithostratigraphic columns of Cretaceous to Eocene successions in southwestern Slovenia and Istria (NW Croatia and SW Slovenia), with one column from NW Italy. Authors of original geological columns are listed below:

1) Šribar (1995); Rižnar (1997), 2) Drobne (1977, 1979), 3) Drobne et al. (1988, 1996); Šribar (1995); Jurkovšek et al. (1996), 4) Jurkovšek et al. (1996), 5) Drobne (1981); Jurkovšek et al. (1996), 6) Jurkovšek et al. (1997), 7) Hamrla (1959); Drobne (1977, 1979); Pavlovec et al. (1991), 8) Hamrla (1959, 1960); Jurkovšek et al. (1996), 9) Brazzatti et al. (1996), 10) Hamrla (1960); Drobne et al. (1991); Jurkovšek et al. (1996), 11) Hamrla (1959); Buser & Lukacs (1979); Delvalle & Buser (1990); Jurkovšek et al. (1997); this study, 12) Drobne (1977); Delvalle & Buser (1990), 13) Delvalle & Buser (1990); Šribar (1995); Buser & Radoičić (1987), 14) Šikić et al. (1972); Drobne (1977), 15) Drobne (1977); this study, 16) Drobne (1977, 1981); Hottinger & Drobne (1980); Drobne & Pavlovec (1979); Drobne et al. (1991); Turnšek & Drobne (1998); this study, 17) Drobne (1977), 18) Šikič et al. (1972); Drobne (1977), 19) Biondić et al. (1995), 20) Šikić et al. (1972); Drobne (1977), 21) Šikić et al. (1968); Drobne (1977), 22) Pleničar et al. (1969); Drobne (1977); Gabrić et al. (1995), 23) Pleničar et al. (1969); Drobne (1977), 24) Hamrla (1959); Pleničar et al. (1973); Drobne (1977); Velić & Vlahović (1994); Matičec et al. (1996), 25) Šikić et al. (1968); Drobne (1977); Hottinger & Drobne (1980); Drobne et al. (1991), 26) Matičec et al. (1996), 27) Tarlao et al. (1995), 28) Buser & Lukacs (1972); Drobne (1977); Hottinger & Drobne (1980); Matičec et al. (1996), 29) Polšak & Šikić (1973); Drobne (1977), 30) Drobne et al. (1991), 31) - 34) Matičec et al. (1996), 35) Šikić et al. (1968); Magaš (1973); Šikić et al. (1973); Šikić & Polšak (1973); Höttinger & Drobne (1980); Otoničar et al. (2003), 36) Polšak (1970); Drobne (1977); Matičec et al. (1996).

Alveolina-Nummulites Limestone has been known. The Liburnia Formation, Alveolina-Nummulites Limestone and intermediate Trstelj Beds represent the Kras Group (Košir, 2003) (Fig. 3), which corresponds to the lower unit of the underfilled peripheral foreland basin stratigraphy (i.e. the lower unit of the "underfilled trinity" of Sinclair, 1997). Thus the unconformity represents a megasequence boundary and typically separates the underlying passive margin carbonate succession from the overlying deposits of the synorogenic carbonate platform at periphery of the foreland basin (Košir & Otoničar, 2001). The synorogenic carbonate platform was finally buried by prograding hemipelagic marls (i.e. the middle unit of the "underfilled trinity" of Sinclair, 1997) and deep-water clastics (flysch) (i.e. the upper unit of the "underfilled trinity" of Sinclair, 1997) (Fig. 3). Because the name of the carbonatre platform that overlie the unconformity has not been defined yet, I will use in this paper only the general geodynamic term – i.e. the synorogenic carbonate platform.

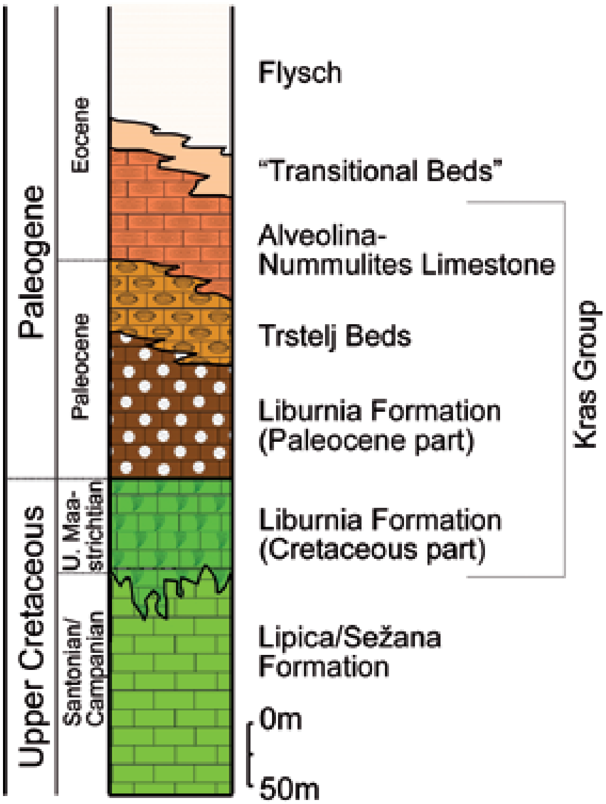

Fig. 3: Generalized stratigraphic column of Upper Cretaceous-Eocene succession in the Kras (Karst) and Matarsko podolje regions, SW Slovenia, showing major lithostratigraphic units (modified from Košir, 2004).

The unconformity is expressed by an irregular paleokarstic surface, locally marked by bauxite deposits. Although the unconformity has been repeatedly mentioned, no systematic study of paleokrast has been performed. Relatively numerous papers on biostratigraphy, especially on the carbonate successions of the Kras Group, have been published (see list of references attached to Fig. 2), yet not more than few attempts on explanation of the sedimentology of the paleokarstic deposits and onlapping beds have been done (Otoničar, 1997; Debeljak *et al.*, 1999; Durn *et al.*, 2003). Only occasionally, the geotectonic conditions under which the paleokarst (uplift) evolved have been briefly mentioned (Košir & Otoničar, 2001; Otoničar & Košir, 2001; Durn *et al.*, 2003).

Tectonically, the discussed area corresponds to three macrotectonic units, the Southern Alps, the Ex-

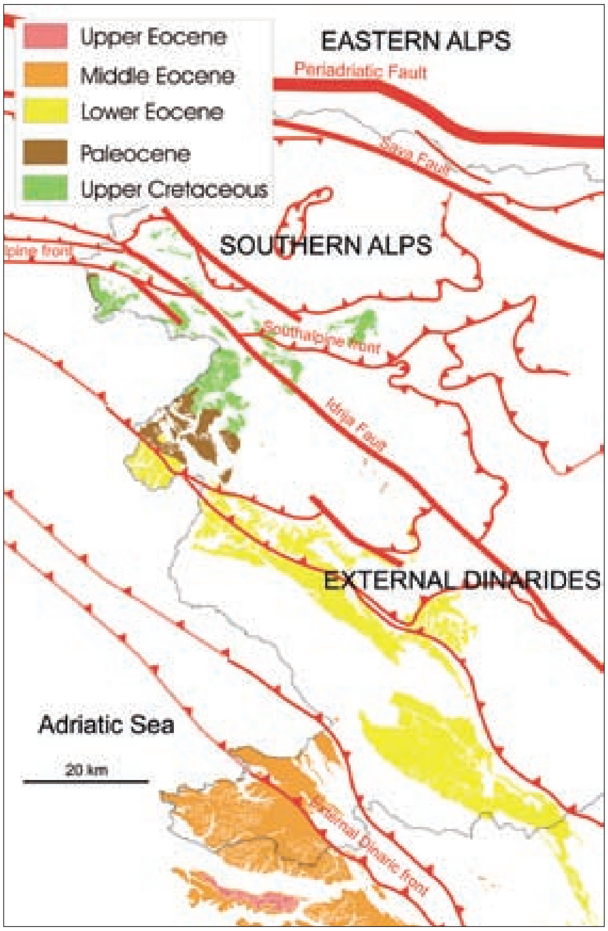

Fig. 4: Illustrative geological map showing distribution of flysch deposits and major structural elements in western Slovenia. The map is based mainly on data from basic geological maps of Yugoslavia, 1:100.000, sheets Beljak & Ponteba (Jurkovšek, 1986), Udine-Tolmin & Videm (Udine) (Buser, 1986), Kranj (Grad & Ferjančič, 1974), Gorica (Buser et al., 1968), Postojna (Buser et al., 1967), Trst (Pleničar et al., 1969) and Ilirska Bistrica (Šikić et al., 1972). Copyright: Geološki zavod Slovenije (Geological survey of Slovenia), 2002 – All rights reserved.

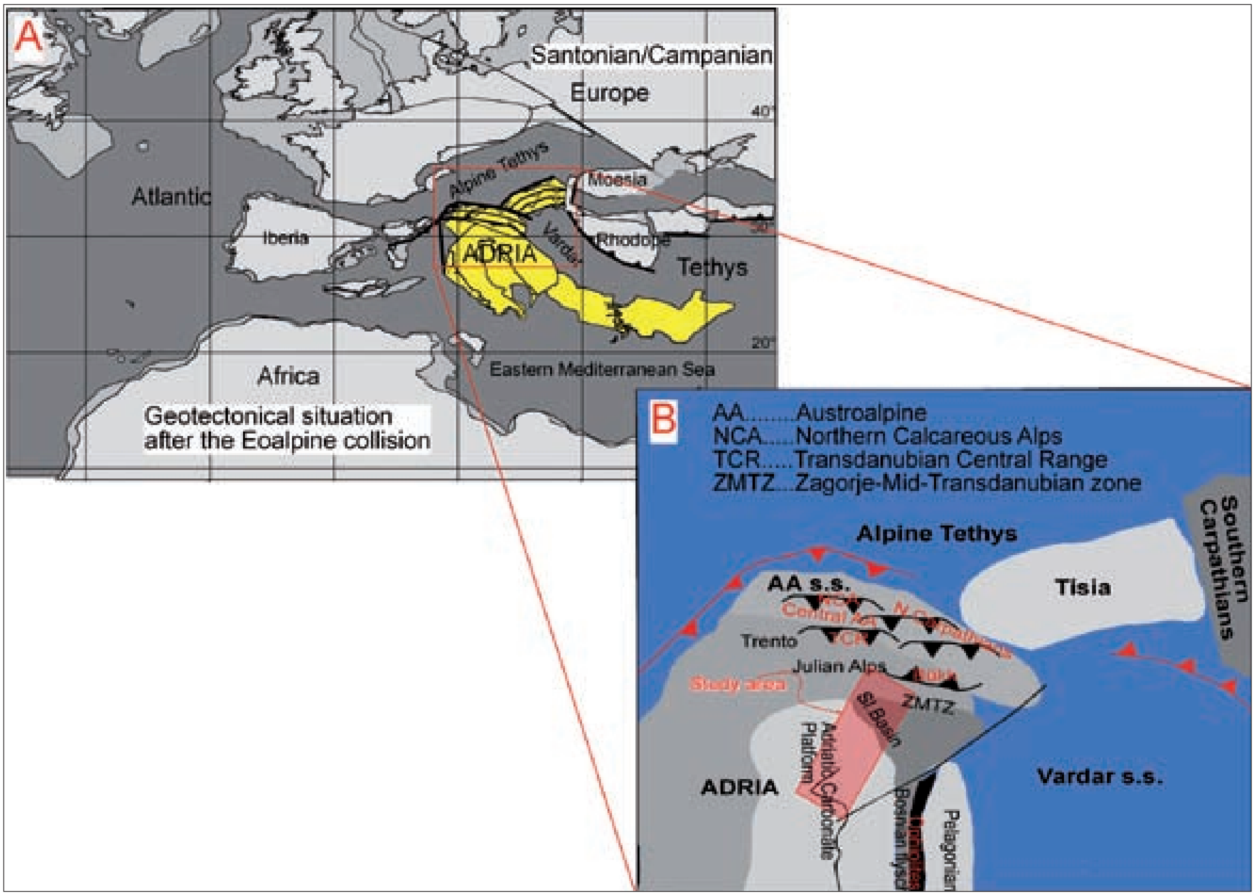

Fig. 5: A) Paleogeographical map showing major geotectonic units at Santonian-Campanian boundary in western Tethys and central Atlantic (modified from Neugebauer et al., 2001). B) Geotectonic and paleogeographic units of Adria microplate and adjacent areas.

ternal Dinarides and the Dinaric foreland (Placer, 1999) (Fig. 1). While the flysch-related sediments can be followed across the all three units (Fig. 4), the unconformity and the overlying carbonate successions of the Kras Group correspond to the most external thrust unit of the Dinaric fold and thrust belt – the northwestern External Dinarides in southwestern Slovenia, Italian part of the Kras plateau and northeastern Istria, and to more stable foreland domain of the Dinaric mountain belt in other parts of Istria (Figs. 1, 2).

The nappe structure of northwestern part of the External Dinarides comprises five successively lower and younger thrust units from northeast to southwest: Trnovo Nappe, Hrušica Nappe, Snežnik Thrust Sheet, Komen Thrust Sheet and Kras Thrust Edge (Placer, 1981, 1999, 2002) (Fig. 1).

The External Dinarides and the Dinaric foreland correspond to the northwestern part of the Cretaceous Adriatic Carbonate Platform and the Upper Cretaceous-Eocene synorogenic carbonate platform which occupied northeastern part of the Adria microplate s.s. (Fig. 5). In the Cretaceous the area of present day Southern Alps was a part of deeper marine realm which comprised the Slovenian Basin formed in the Middle Triassic (Cousin, 1981; Buser, 1989) and the area of former Julian Carbonate Platform which was drowned in the Lower and Middle Jurassic (Cousin, 1981; Buser, 1989).

The geologic and paleogeographic situation started to change severely in the Late Cretaceous (see below). It is important to note, that the described region is recently confined from the north side by the Periadriatic fault zone, from the west by the deposits of the Southern Alpine Molasse Basin and from the south and southwest by the Adriatic Sea and its sediments (Fig. 1).

To understand the mechanisms that governed the uplift and emersion, regional geotectonic conditions of the wider area of the Late Cretaceous-Early Paleogene Western Tethys were taken into consideration.

During the Mesozoic, the area between Eurasia and Gondwana or the western part of the extensive Tethys bay of the Pangea was occupied by more or less uniform Adria microplate surrounded by smaller tectonic units or terranes (Fig. 5). With regard to major geotectonic events, the extent and shape of Adria microplate was changing constantly through the geologic history. The results of these events (e.g. tecto-sedimentary successions or cycles) could be correlated between geographically and geologically distant parts of the Adria microplate.

After substantial Permian to Middle Triassic and Triassic/Jurassic extensional tectonics, the Adria domain became encircled by oceanic bays and dissected by numerous deepwater basins and drowned carbonate platforms (Fig. 5). It is considered that since Early Jurassic the Adriatic Carbonate Platform had been isolated by deeper marine realms (Vlahović *et al.,* 2005).

At the Middle/Late Jurassic boundary compressional tectonic regime prevailed over the peri-Adriatic region. It was caused by the beginning of closure (subduction) of the adjacent oceanic bays of the Western Tethys. During the Late Jurassic and Cretaceous gentle broad-scale positive and negative lithospheric deflections periodically occurred on the Adriatic Carbonate Platform. The deflections were expressed by coexistence of karstic areas and somewhat deeper marine intra-platform basins (Tišljar *et al.,* 1995; 1998; Vlahović *et al.,* 2005). Distinctive deflections correspond to period of ophiolite emplacement [e.g. the Late Jurassic/Early Cretaceous obduction of ophiolite suite of the Dinaric Tethys on the E margin of the Adria microplate (Pamić *et al.,* 1998; 2000)] and distant collisions [e.g. the mid-Cretaceous Eoalpine orogenesis in the Pelso/Austroalpine/Tisia domain (Faupl & Wagreich, 2000; Neugebauer *et al.,* 2001)]. Topographic disunity over the platform gave rise to irregular facies distribution and thickness of carbonate successions of different parts of the platform.

Significant interruptions of carbonate successions are also related to global eustatic oscillations and/or oceanic anoxic events, but they are mainly superimposed on tectonically induced changes of relative sea-level.

Thus before the beginning of the uplift of northern part of the Adriatic Carbonate Platform in the Late Cretaceous and the synchronous onset of flysch sedimentation in the area north and north-eastern of the platform, the whole region was already topographically distinctly heterogeneous. Flysch started to deposit in deeper marine basin with partly inherited bathymetry from former deeper marine domain of Slovenian Basin and drowned Julian Carbonate Platform (Fig. 5). Deeper marine realms with more or less uninterrupted sedimentation had still encircled the carbonate platform from its western and southwestern side (Vlahović *et al.,* 2005) (darker grey area on Fig. 5).

Later tectonic activity which shortened the area and displaced different parts of the region, prevent more accurate interpretation of geotectonic conditions at those time. Namely, except the substantial shortening of the region due to different "thrusting" phases of Alpine orogeney, the area north from the Periadriatic Fault Zone was displaced for at least 100 km eastward during the Miocene (Ratschbacher *et al.,* 1991; Frisch *et al.,* 1998; Vrabec & Fodor, 2006), in some estimates up to 500 km (Haas *et al.,* 1995). It should be noted that western Istria (i.e. Dinaric Foreland on Figure 1) experienced significant counterclockwise rotation most likely between the end of Miocene and the earliest Pliocene (Márton et al., 1995; Márton, 2006).

PALEOKARST

In the investigated area both surface and subsurface paleokarstic features occur. In places the paleokarstic surface is denoted by surface karst forms like karrens, dolines and depressions of decimetric amplitude (Fig. 6a). Pedogenic features and enlarged root-related channels characterize the upper part of the vadose zone, the epikarst. Vadose channels, shafts and pits penetrate up to a few tens of meters bellow the paleokarstic surface, where they may merge with originally horizontally oriented phreatic cavities. The latter comprise characteristics of caves forming in fresh/brackish water lenses. At least some of them may be defined as flank margin caves (Fig. 6b, 6c). In extensive outcrops, the remains of such caves can be followed as much as few hundreds of meters along strike. In one case a breccia body which was defined as paleokrastic cave related deposit (Otoničar *et al.,* 2003), is so extensive that was used even as mappable unit for Basic geologic map of Yugoslavia 1:100.000 (see Magaš, 1965). The cavities are usually irregular and elongated in shape, and could be up to few tens of meters long and up few meters high (Fig. 6b). Depending on locality, the phreatic cavities were found in different positions regarding to the paleokrastic surface, the lowest one some 75 meters below it. The cavities had been subsequently partly reshaped and entirely filled with sediments and flowstones in the upper part of the phreatic, epiphreatic and vadose zones (Figs. 6b, 6c). Similarly, the vadose channels and voids are also filled by sediments and flowstones, but they usually differ from these of phreatic cavities in higher content of noncarbonate material, lower δ13C values of carbonate material and more distinctive pedogenic modification. The denudation had frequently exposed filled paleokarstic subsurface cavities on the paleokarstic surface, where they may be identified only by the remains of their fill (Otoničar

Fig. 6: A) Paleokarstic surface is locally denoted by small scale depressions (motorway road-cut at Kozina village, SW Slovenia). Note colour contrast between Upper Cretaceous shallow marine limestone of the Lipica Formation and dark grey palustrine limestone of the Liburnia Formation. Hammer for scale is about 30 cm high. B) Horizontally oriented cave of irregular shape largely filled with reddish-stained calcareous mudstone/siltstone (Podgrad, Matarsko Podolje, SW Slovenia). The maximal height of the cave is approximately 4 meters. The cave deposits are artificially marked by reddish transparent colour on the photograph. C) Breccia body represents a part of filled roofless paleokarstic phreatic cave at Koromačno in Istria, NW Croatia. (1,8 m tall geologist for scale in the upper right corner) D) Excavated paleokarstic cavity (vadose shaft?) originally filled with bauxite (Minjera, Istria, NW Croatia).

et al., 2003) (Fig. 6c). The internal sediments and flowstones often occur as grains in deposits that cover the paleokarstic surface or fill subsurface paleokarstic cavities of different generations. Paleokarstic surface with its depressions as well as subsurface channels and voids are often covered and filled by bauxite deposits which were locally exploited (Fig. 6d) (Gabrić *et al.,* 1995).

Certain limestone lithofacies of immediate cover of the unconformity are commonly locally confined, suggesting highly irregular topography of the karstic surface before the beginning of transgression. In places it is clear that the incipient transgression involved gradual increase of groundwater table and, eventually, ponds or "blue holes" were formed in karstic depressions (Durn *et al.*, 2003). In the Kozina site (southwestern Slovenia) during the "blue hole" stage of the transgression, a paleokarstic pit was filled by coarse grained breccia with vertebrate remains, mainly dinosaurian and crocodilian bone fragments and teeth (Debeljak *et al.*, 1999, 2002). Generally, the cover sequence (i.e. the Liburnian Formation of Maastrichtian and early Paleogene age) is characterized by restricted, marginal marine and palustrine lithofacies, which frequently show pedogenic modifications.

EVOLUTION OF THE PERIPHERAL BULGE (THE FOREBULGE)

Besides the research on paleokarst related phenomena, the study of sedimentary successions of the host rock in which the paleokarstic features occur and those that overlie the paleokarstic surface is of crucial importance to understand the uplift of substantial part of the Adriatic Carbonate Platform above the sea-level in the Late Cretaceous and Paleogene. To explain the mechanisms that govern the uplift, regional and global geotectonic and eustatic conditions were taken into consideration, too.

STRATIGRAPHY

The age of the limestones that immediately underlie the unconformity and the extent of the chronostratigraphic gap in southwestern Slovenia and Istria systematically increase from northeast towards southwest (Figs. 2, 7a, 7b), while the age of the overlying limestones decrease in this direction (Figs. 2, 7c). In western part of Istria the orientation of the isochrones is slightly different and

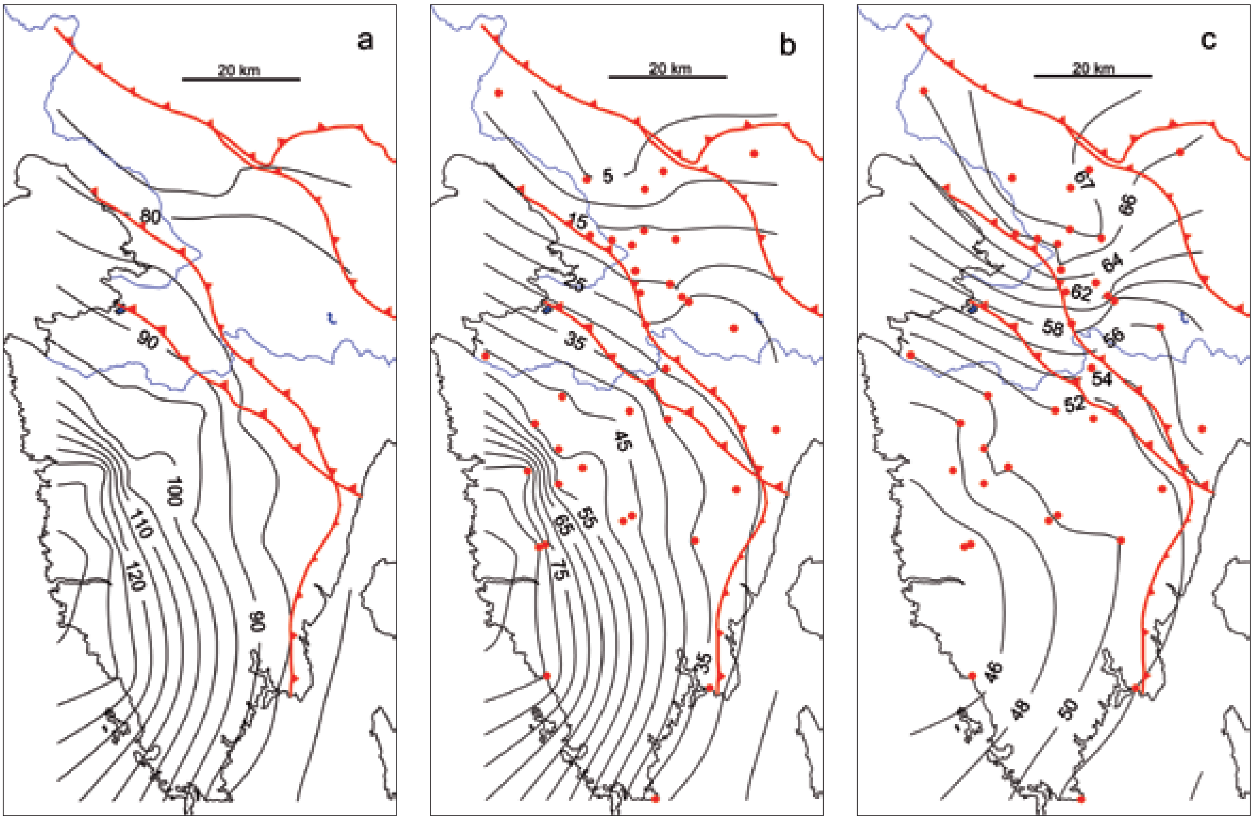

Fig. 7: A) Isochrones of carbonate rocks that immediately underlie the unconformity. B) Isochrones of the extent of the chronostratigraphic gap. C) Isochrones of carbonate rocks that immediately overlie the unconformity. Isochrones in all figures are in Ma. Major structural elements of the area (see Fig. 1) and positions of the geological profiles used in the research (see Fig. 2) are also shown in the figures.

shows a dome-like topography of the forebulge. The isochrones represent a statistic result acquired by kriging in Surfer programme version 8.00 (© Golden Software, Inc.). The data were provided from 36 geological profiles from the karstic regions of southwestern Slovenia, both Slovenian and Croatian part of Istria peninsula and the area between Trieste bay and Italian-Slovenian border in northeastern Italy (Figure 2 and red dots on Figures 7a, 7b, 7c).

The youngest rocks below the unconformity belong to mid-Campanian and occur in the central and northeastern part of the Kras (Karst) plateau (the Komen thrust sheet) (Fig. 1) (Jurkovšek *et al.,* 1996) and close to Postojna (the Snežnik thrust sheet) (Fig. 1) (Šribar, 1995; Rižnar, 1997) in southeastern Slovenia, while the oldest one, Valanginian and Hauterivian in age, crop out in the western part of Istria (Matičec *et al.,* 1996) (Figs. 2, 7a).

The beds that cover the unconformity correspond to different ages, litofacies, members and formations. As mentioned afore, the age trend of the immediate cover is opposite to that of the footwall. In this case the oldest rocks occur in southwestern Slovenia and belong to the youngest stage of the Late Cretaceous - the Maastrichtian. Towards southwest, progressively younger deposits onlap the paleokarstic surface (Figs. 2, 7c). However, the youngest strata that onlap the unconformity don't fit exactly with the oldest one immediately below it. With regard to described situation, the chronostratigraphic gap increases considerably from few Ma on the Kras plateau (southwestern Slovenia) to more than 80 Ma in western Istria (Figs. 2, 7b).

The lithofacies of the lower part of the cover sequence (The Liburnian formation) frequently show features typical of subaerial exposure surfaces, including calcrete, pseudomicrokarst, brecciated horizons and karstic surfaces. Locally, the lowermost subaerial exposure surface of the Liburnija Formation, which shows karstic topography of decimetric amplitude, and the main paleokarstic surface form a composite unconformity. Sporadically, thin coal beds and seams occur in the lower part of the sequence. Although the stratigraphy of the Kras Group, "Transitional Beds" and Flysch (Fig. 3) shows overall deepening of the basin, prominent subaerial exposure surfaces also occur in carbonate successions of Trstelj Beds and Alveolina-Nummulites Limestone (Košir & Otoničar, 1997; Košir, 2003). Much thicker successions of paralic sediments with more frequent unconformities and marsh related sediments occur in southwestern Slovenia and northeastern Istria in comparison with other parts of Istria, yet local variation can be significant (Figs. 2, 8). In western Istria, where the chronostratigraphic gap is the most extensive, the foraminiferal limestones frequently lie directly on the paleokarstic surface (Matičec at al., 1996). The thickness of the Kras Group generally decreases from northeast toward southwest, although also in this case significant deviations may occur (Figs. 2, 8).

The point where the unconformity pinch-out towards the foreland basin occurs somewhere between the northeastern part of the Kras plateau on the Komen Thrust Sheet and some 10 km (approximately 25 km in original position – see Placer, 1999) distant Mt. Nanos on the Hrušica nappe (Fig. 1). From this point on towards the foreland basin, the uplift of the forebulge didn't take place because the area was so close to the orogene that experienced only a subsidence. Here, the sedimentary succession of the Adriatic Carbonate Platform gradually passes into progressively deeper-marine carbonate succession of synorogenic carbonate platform. Namely, on the Mt. Nanos at Campanian-Maastrichtian boundary, the deepening of the shallow marine carbonate platform without any evidence of preceding emersion is documented (Šribar, 1995).

Further towards the northeast, in the Julian Alps (the eastern part of the Southern Calcareous Alps) and in the most northern part of recent Dinaric mountain belt in western Slovenia and northeastern Italy (the Trnovo Nappe), the turbiditic siliciclastic sediments (flysch) started to deposit in Campanian and Maastrichtian over the rocks of different lithology, age and origin (Pavšič, 1994). Flysch often overlies deeper marine pelagic marls of "scaglia" type and alodapic carbonates, which were receiving the material from Adriatic Carbonate Platform. It is important to note that in this part of western Slovenia deep-marine basin existed before flysch or above mentioned deeper marine pelagic marls started to deposit. However, the oldest pelagic marls (pre-flysch deposits) which overlie the Upper Cretaceous shallow marine carbonates of the northeastern margin of the Adriatic Carbonate Platform also belong to Maastrichtian. Similar as I stated for chronostratigraphic gap, the pelagic marls and flysch deposits are also diachronous over the area. From northeast toward southwest, successively younger strata onlap the pre-foreland basin deposits (Fig. 4).

The successions of pelagic marls and especially siliciclastic flysch were periodically interrupted by deposition of calcarenitic and calcruditic beds/megabeds, locally even of olistostrome character. Those beds were supplied by turbiditic currents from the fault-related escarpments of distorted and seismically active marginal areas of former Adriatic Carbonate Platform (Skaberne, 1987; Tunis & Venturini, 1987) and later also from outer parts of synorogenic carbonate platforms (distally steepened ramps?) (Fig. 9).

The synorogenic carbonate and siliciclastic deposits of other parts of External Dinarides (e.g. Dalmatia) are

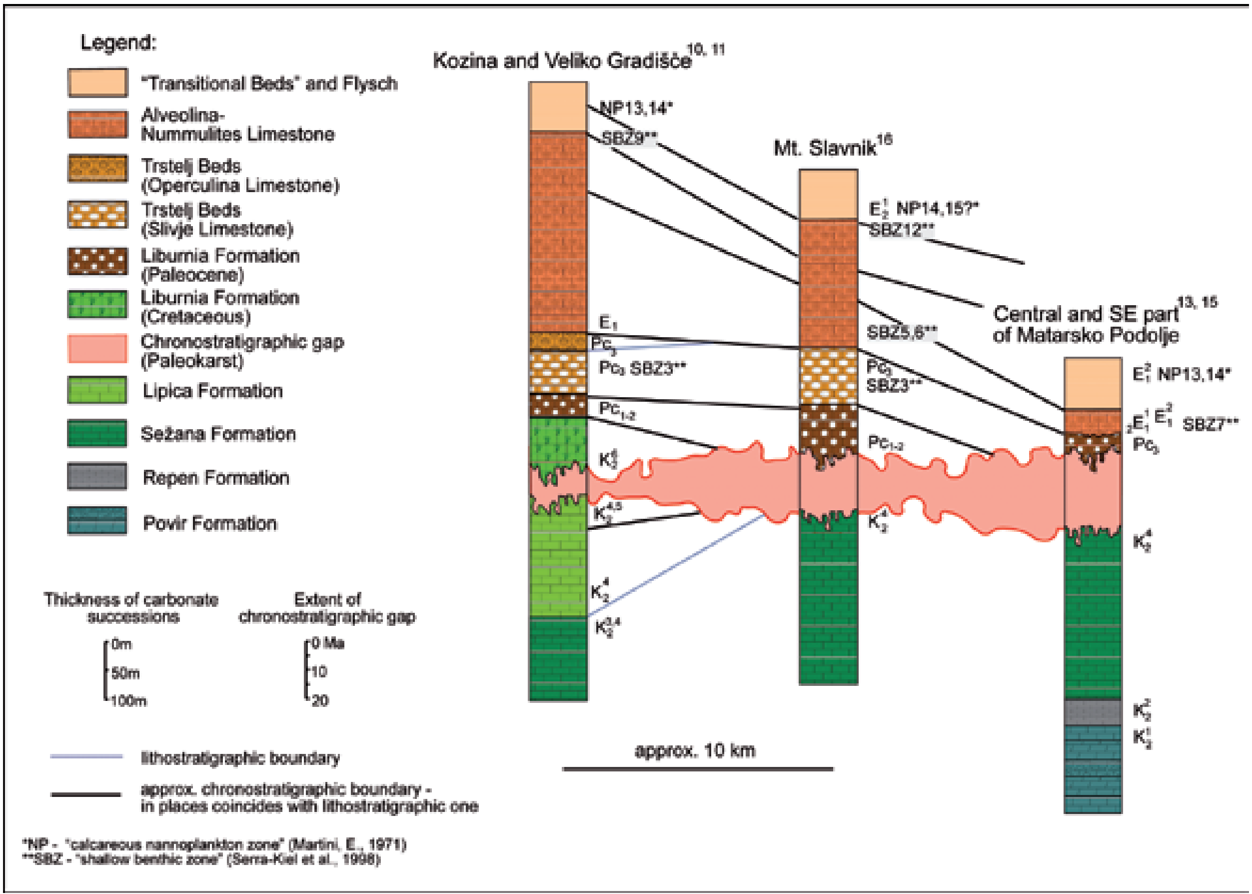

Fig. 8: Lithostratigraphic columns for three adjacent sites in Matarsko Podolje and Mt. Slavnik (SW Slovenia). Note significant variations in thickness of lithostratigraphic units and in time span of stratigraphic gap.

younger than these described here. They started to deposit not before Eocene (Marjanac & Ćosović, 2000) and probably represent deposits of different foreland system or at least of different segment of the one described here.

DISCUSSION

Systematic trends expressed by isochrones showing the age of the carbonate rocks that immediately under- and overlie the paleokarstic surface (Figs. 7a, 7c), and consequently, the extent of the chronostratigraphic gap (Fig. 7b), can be explained mainly by the evolution and topography of peripheral foreland bulge (the forebulge) (Fig. 9).

When the foreland continental lithospheric plate is vertically loaded by the fold and thrust belt, it responds with flexure. In front of the evolving orogen an asymmetric foreland basin is formed; the deepest part of the basin (the foredeep) is located adjacent to the orogenic wedge (Fig. 9). Because of the isostatic rebound on vertical loading of the lithosphere, the opposite side of the basin (opposite to the orogenic wedge) is instantaneously upwarped and the bulge with subtle relief is formed, the peripheral bulge or the forebulge. The bulge is especially well expressed in early, flysch stage of the foreland basin evolution (Crampton & Allen, 1995). While the wavelength of the deflection is approximately the same for both, foreland basin and peripheral bulge, the amplitude of the basin subsidence is typically much greater as the uplift of the bulge (Crampton & Allen, 1995; Miall, 1995). If the conditions are suitable, synorogenic carbonate platforms with distinctive ramp topography may colonise the gentle slope of the forebulge toward the foredeep (Dorobek, 1995).

Significantly, as the whole complex of the orogenic wedge advances forelandward, the flexural profile produced by the orogenic wedge advances with it. Topography of the forebulge is controlled by numerous factors, among which the rigidity of the foreland lithospheric plate and the rate of emplacement of the load are the most important (Allen & Allen, 1992; Dorobek, 1995; Miall, 1995). An expected maximal height of the forebulge above the sea level (if the foreland plate is at or close to sea-level prior to flexural loading) would be in the range of up to a few tens to few hundreds meters (Crampton &

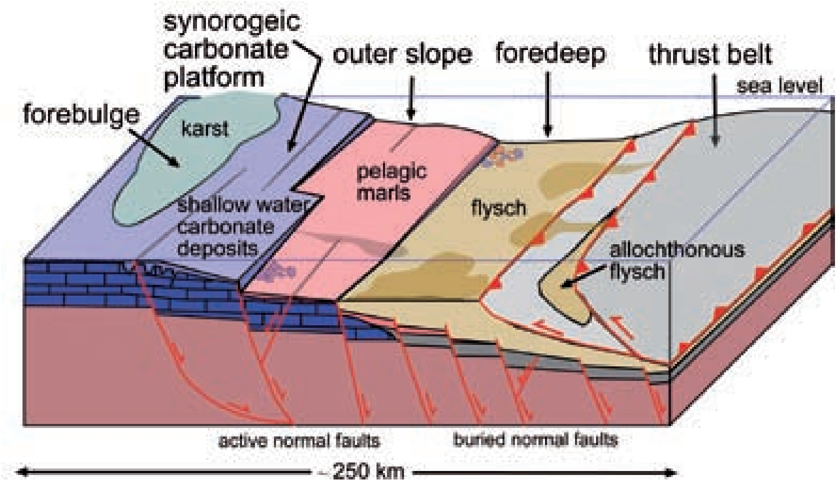

Fig. 9: Schematic block diagram of foreland basin complex showing the position of the orogenic wedge, foredeep and forebulge with distribution of macrofacies belts before plate convergence ended (modified from Bradley & Kidd, 1991).

Allen, 1995; Miall, 1995). According to topography of the forebulge, the rate of erosion (see White, 2000) and the style of migration of the orogenic wedge, the area of maximal denudation should occur in the central part of the region, which is over-passed by the bulge (Crampton & Allen, 1995). In addition, non-flexural deformations (e.g. reactivation of pre-existing heterogeneities, enhanced deflections because of horizontal in-plane stresses…) and inherited topography may significantly influence the evolution and topography of the forebulge (Allen & Allen, 1992; Dorobek, 1995; Miall, 1995; Crampton & Allen, 1995).

On Mt. Nanos (Hrušica Nappe; Fig. 1) shallow water rudist limestone of the Adriatic Carbonate Platform gradually passes over limestone with orbitoidiform larger foraminifera into pelagic marls without any emersion at the base of the deepening sequence – the erosional gap reduces to conformity. The age span of this transition falls within a period of the shortest documented chronostratigraphic gap between the northeastern part of former Adriatic Carbonate Platform and the overlying synogenic carbonate platform (Fig. 2), which extends from mid-Campanian to Late Maastrichtian. Maastrichtian in age are also the oldest pelagic marls which in places directly overlie the Upper Cretaceous shallow water carbonates of former northeastern margin of the Adriatic Carbonate Platform. Although the oldest turbiditic siliciclastic flysch was deposited in a basin with inherited deeper marine bathymetry (former Slovenian Basin) its Campanian and Maastrichtian age could be correlated with other incipient foreland related deposits and phenomena. With regard to these criteria and trends of unconformity related isochrones elsewhere (Figs. 2, 7a, 7b, 7c), I suggest that northern part of the Adriatic Carbonate Platform had thrived more or less prosperously till the end of Campanian, when an initial uplift of the forebulge occurred. The carbonate sediments that had originally been deposited till that time, and are now missing in carbonate successions immediately below the unconformity, had been erased during the paleokarstic period by the karstic denudation processes.

According to topography of the forebulge and advancing nature of the foreland geodynamic complex as a whole, the most extensive denudation is expected in the central area over which the forebulge migrates. The western part of Istria, where the chronostratigraphic gap is the largest and the beds immediately below the unconformity are the oldest (Fifs. 2, 7a, 7b), most probably corresponds to this zone. However, in an ideal conceptual/mathematical model of the forebulge unconformity, the amount of erosion should remain more or less constant over vast area in the central part of the region over-passed by the bulge, and decreases on its distal slope towards back-bulge basin (Crampton & Allen, 1995). Instead, in western Istria the isochrones of the beds underlying the unconformity show distinctive condensation compared to situation in northeastern Istria and southwestern Slovenia (Fig. 7a). I suggest that this is not the result of rapid increase of the amount of footwall eroded but rather of denudation of primarily much thinner Cretaceous carbonate successions in western Istria. Namely, in this part of Istria the carbonate successions are relatively thin (Matičec *et al.,* 1996), partly because of repeating emersions throughout the Cretaceous (Velić *et al.,* 1989) and partly because of reduced accommodation space of Cretaceous shallow marine environments. Evidence of considerable Late Jurassic and Cretaceous land areas in the vicinity of western Istria (probably offshore form its recent west coast), came also from dinosaur record (footprints and bones) (Della Vecchia *et al.,* 2000; Mauko & Florjančič, 2003; Mezga *et al.,* 2003) and distribution of sedimentary facies of the adjacent peritidal to deeper marine environments of intraplatform basins (Tišljar *et al.,* 1995; 1998). Why was the area of western Istria beeing preferentially uplifted during the Cretaceous is still questionable, but the reasons for deflections should be searched at adjacent plate boundaries where their reorganisation and different collision-related events and processes (see Faupl & Wagreich, 2000; Neugebauer *et al.,* 2001) produced horizontal in-plane stresses that may be transmitted many hundreds of kilometers inboard of actual collision (Zeigler *et al.,* 1995).

It is also possible that the central zone of the forebulge and the slope towards back-bulge basin in their final position occurred offshore of recent Istrian west coast. However, we should be aware that the Late Cretaceous Adriatic Carbonate Platform was surrounded from the western side by deeper marine interplatform basins (Vlahović *et al.,* 2005) what might considerably affected the appearance of the forebulge and the back-bulge area.

Although the "abnormal thickness" of denuded stratigraphy in western Istria is mainly the result of previous sedimentary history, some uncertainties may also arise from differential uplift/subsidence of certain parts of the forebulge. Evidence for differential subsidence along reactivated ancient tectonic structures is for example well documented in carbonate successions of the Kras Group, where the thickness of chrono- and lithostratigraphic units may vary considerably over short distances (Figs. 2, 8).

In conclusion I suggest that the denudation exposed the oldest carbonate rocks in the western Istria partly because of specific evolution (migration) and topography of the forebulge and partly because of primarily thinner carbonate successions in this part of Istria compared to more northeastern parts of the investigated area.

The rate of transgression over the paleokarstic surface is expressed by the isochrones of the strata that onlap the unconformity (Fig. 7c). While the large scale diachronism of the onlapping strata shown in Figure 7c is the result of specific large-scale topography and migration of the forebulge as a whole, local smaller scale spatial differences in the onlap pattern (not observable in Figure 7c) are due to shorter oscillations of relative-sea level and deposition over topographically irregular paleokarstic surface (e.g. dolines, shafts… – a "blue hole phase" of the transgression). The pattern of the isochrones shown in Figure 7c suggests that the transgression during its earlier stages (southwestern Slovenia and northeastern Istria) was slower compared to its later stages (western Istria). Although subsequent tectonic deformations, such as tectonic shortening, faulting and rotation, substantially affected the area, the rate of the onlap in southwestern Slovenia and northeastern Istria is estimated to about 2-3 km/Ma while in southwestern Istria to about 4-5 km/Ma. We should be aware that some apparent anomalies, especially at terminations of the isochrones may be the result not only of later tectonic deformations of the area but also of limited number of data points which are not uniformly distributed, spatially confined area of the investigation along the strike of the forebulge and defectiveness of statistic method (kriging) used. Slightly different orientation of the isochrones in western part of Istria compared to those in southwestern Slovenia and northeastern Istria (Figs. 7a, 7b, 7c) may also be the result of different sydepositional or synorogenic orientation of the prevailing stresses (see Marinčić & Matičec, 1991; Matičec *et al.,* 1996) during the Cretaceous and Paleogene and later counterclockwise rotation of the area (see Márton *et al.,* 1995 amd Márton, 2006). In spite of all that, the reasons for different stratigraphic pinch-out rate are many sided and may arise from differential rheologic and structural characteristics of the foreland plate itself, events at collision zone and adjacent plate boundaries, sublithospheric processes and external reasons like eustatic sea-level oscillations and climate changes. In our case it is difficult to determine the exact reason for the increasing rate of the onlap in Lower Eocene, not only because different processes may lead to the same result, but also because they can act simultaneously.

Long term sea-level fall (i.e. second-order cycle of Haq *et al.,* 1987) may for example slow-down the onlap rate and vice-versa long term sea-level rise may increase the onlap rate. If we observe the eustatic curve for the Cretaceous and Paleogene (Haq *et al.,* 1988) we can notice that the rate of the onlap is in relatively good agreement with mid-Campanian to Late Paleocene second-order fall and Early Eocene rise of the sea-level. However, the foreland basin should progressively widen and pinch-out migration rate would increase also if, for example, the orogenic wedge loaded a progressively stronger elastic lithosphere (Allen & Allen, 1992).

Although not all local variations of relative sea-level oscillations and so the onlap rate could be identified from isochrones in the Figure 7c, they could be observed in the field. Namely, the subaerial exposure surfaces that periodically interrupt the carbonate sedimentation of the Liburnia Formation reflect relative sea-level falls. Short term falls (i.e. third-order cycles of Haq *et al.,* 1987), which were documented in Late Maastrichtian, Late Paleocene and Early Eocene (Haq *et al.,* 1988), could cause these unconformities.

On the other hand, a few other processes may influence the rate of the onlap. The forebulge should increase in height and migrate toward the orogenic wedge over time if the foreland lithosphere behaves viscoelastically even when the load is unchanging (Tankard, 1986). However, estimations for time constants of the viscous relaxation of stresses are longer than actual amount of time available for the forebulge migration (Allen & Allen, 1992; Dorobek, 1995). Variation in onlap rate may reflect also changes in sediment supply, or within the orogenic wedge, such as the formation of a new thrust complex (Crampton & Allen, 1995) or transition from passive to active thrusting phase. An increase in compressive in-plane stress produced during convergence also might enhance uplift of the forebulge and causing shoreline regression along its flank (Allen & Allen, 1992; Dorobek, 1995).

Evidence of short term sea-level oscillations could also be recognized from the specific evolution of the paleokarst, especially phreatic caves. If the majority of lenticular caves with irregular walls and discrete horizons of spongework or swisse-cheese like vugs on young carbonate islands originated at/in fresh/brackish water lenses (see Mylroie & Carew, 1995), then in our case the major part of the cavities had been emplaced in the vadose zone prior to submergence and burial. Namely, the caves are frequently completely filled with deposits originated in vadose zone, like flowstone and bauxite, or they had been opened to the paleokarstic surface by complete denudation of the roof (i.e. roofless caves of Mihevc, 2001). If the water-level is stagnant and the forebulge migrates, than in the conceptual sense only those phreatic cavities developed below that forebulge flank that facing towards back-bulge basin should be uplifted in the vadose zone before subsidence. On the contrary, phreatic caves developed below the flank facing the foreland basin and the advancing orogenic wedge should suffer nothing but subsidence and subsequent burial. Theoretically it is possible that because of the advancing character of the forebulge, caves formed in different sides of the forebulge may occur in the same karstic profile. Phreatic cavities developed below the flank facing towards the back-bulge region should be uplifted and modified in the vadose zone. Subsequently, after the crest of the forebulge migrates over the back-bulge flank, the "back-bulge" phreatic caves should re-immerge into phreatic zone, but this time below the flank facing towards the foreland basin. It is important to note that frequently observed multiphase modifications of originally phreatic caves could also be the result of the same causes of relative sea-level oscillations that govern the onlap character of the beds that overlie the unconformity (e.g. relaxation of the viscoelastic bulge, formation of a new thrust complex, increase of horizontal in-plane stress, eustatic sea-level fall…).

The carbonate platform was subsequently re-established and finally buried by prograding deeper-marine clastics (pelagic marls and flysch) of the migrating foreland basin (Fig. 9). As it has been already discussed, shallow-water carbonate successions that cover the unconformity may yield a considerable amount of information about relative sea-level oscillations and geodynamics of the forebulge.

Paralic/shallow-marine successions with frequent unconformities and palustrine deposits of the Liburnia Formation (Fig. 3) are usually much thicker in southwestern Slovenia and northeastern Istria than in central and western Istria (Fig. 2). There the paleokarstic surface is frequently directly overlain by foraminiferal limestones (Matičec at al., 1996). The general trend of thickness and the rate of transition from shallow to deep marine environments (drowning) (Fig. 2) are in good agreement with the rate of the onlap (Fig. 7c) and should be the result of the same processes that caused the differentiations in the onlap pattern. I suggest that the anomalies in thickness and facies distribution that could be in places quite distinctive may arise from reactivation of inherited geological structures due to the approaching orogenic wedge.

It has been discussed already, that the orogenic phases could be recognised from structural and stratigraphic data even in areas that are located at some distance from the source of tectonic activity at plate boundaries (e.g. collision and orogenesis). Because of later tectonic deformations it is sometimes difficult to define the exact tectonic phase which affects the area and the actual source of tectonic activity.

In our case, the structural and stratigraphic data indicate the evolution of migrating synorogenic foreland basin complex, which should be the result of collision processes and the evolution of the advancing orogenic wedge (see e.g. Allen & Allen, 1992; Crampton & Allen, 1995; Miall, 1995). At first sight it seems normal to link the foreland complex to tectonic phase that generated structures by mainly NE-SW compression (mesoalpine phase of some authors; see Doglioni & Bosellini, 1987) and gave rise to Dinaric mountain belt during its final stages. However, the Dinaric orogenic belt of which final uplift occurred during the Oligocene-Miocene (Vlahović *et al.,* 2005) is supposed to be the result of collision between Tisia and Adria microplates with onset of collision during the Eocene (Pamić *et al.,* 1998; Pamić, 2002), what is also the age of the oldest synorogenic deposits of the "coastal" part of the External Dinarides (Marjanac & Ćosović, 2000). On the contrary, although the nappe structures of western Slovenia and Late Cretaceous – Paleogene compressional deformations of northeastern Italy indicate NE-SW or ENE-WSW compression, and so "Dinaric" orientation of prevailing regional stress, the oldest foreland basin deposits in these regions are much older than those of other parts of the External Dinarides and belong to the latest stages of Late Cretaceous (Pavšič, 1994; Doglioni, 1987; Doglioni & Bosellini, 1987). As it is shown on Figure 4 the age distribution of flysch deposits indicates the advancing nature of foreland basin from northeast towards southwest what is in accordance with "Dinaric" orientation of the prevailing regional stress. While south of Zagreb-Zemplen fault line, the remnants of oceanic lithosphere (i.e. ophiolite melange) as well as subduction and collision related rocks of Internal Dinarides (i.e. the Sava-Vardar zone by Pamić et al, 1998), which could be linked to closing processes of the Vardar Ocean and collision between Tisia and Adria (Pamić, 2000) are widespread, north of Zagreb-Zemplen line no such rock has been found so far. It seems possible that in central Slovenia, in prolongation of the Sava-Vardar zone, such rocks have been buried by Tertiary sediments and Southern Alpine nappes. In addition, on the NNE side the nappe structure of Western Slovenia was cut from its "root zone" by Periadriatic fault. The "root zone" should be displaced for at least 100 km eastward during the Miocene (Ratschbacher *et al.,* 1991; Frisch *et al.,* 1998; Vrabec & Fodor, 2006).

Although, the structural and sedimentary features of eoalpine tectonic phase which culminated in mid-Cretaceous orogeny in the Austroalpine domain (Faupl & Wagreich, 2000) and also affected the central and western part of the Italian Southern Alps (Doglioni, 1987; Doglioni & Bosellini, 1987) mostly pre-date the foreland related features and sediments described here, it should be noted that in Istria Tertiary tectonic cycle (from Eocene on) display distinctively different orientation of the prevailing stress than Mesozoic one (Marinčić & Matičec, 1991; Matičec *et al.,* 1996).

In conclusion, the foreland basin complex in western Slovenia and Istria was probably formed during mesoalpine ("Dinaric") tectonic phase, although some influences of eoalpine tectonic phase could be important in earlier stages of its evolution. The time discrepancy and also the exact orientation of prevailing regional stress are probably the result of oblique collision between Adria and Tisia microplates (and/or Austroalpine terrane?) and/or segmentation of the foreland plate (see Ricci-Lucchi, 1986; Allen & Allen, 1992).

Oligocene to recent tectonic events especially in Dinarides and Apennines, and conter-clockwise rotation of Adria importantly modified the area formerly occupied by the forebulge, but this is already beyond the scope of this paper.

CONCLUSIONS

In spite of all structural and depositional heterogeneities and subsequent tectonic deformation of the area the paleokarstic unconformity marked by distinctive surface and subsurface paleokarstic features exhibits characteristics typical of a forebulge unconformity:

1) From northeast towards southwest the unconformity cuts progressively older units which are onlapped by progressively younger shallow water carbonates; the chronostratigraphic gap progressively increases.

2) Deepening upward sequences of synorogenic ramp-like carbonate systems overlie the unconformity. In marginal parts of the former Adriatic Carbonate Platform towards the foreland basin, a deepening upward sequence is documented also without intermediate unconformity – here the sequence is conformable because the orogenic wedge was so close that the area experienced only subsidence and forbulge uplift had no taken place.

3) The foreland basin with siliciclastic turbiditic flysch deposits was developing synchronously with the forebulge and synorogenic carbonate platforms. It was also advancing synchronously in the same direction as they were forebulge and synorogenic carbonate platforms. The stratigraphy overlying the unconformity (i.e. underfilled trinity) representing subsidence in underfilled peripheral foreland basin.

4) Evidence of contemporary seismic activity arises from periodic carbonate resediments (megabeds, olistostromes) find in siliciclastic flysch successions. They were supplied by turbiditic currents from the fault related escarpments of the forebulge slope (reactivated ancient faults). Besides flexural upwarping because of the isostatic rebound on vertical loading of the foreland lithosphere, other smaller scale flexural and non-flexural deformations significantly influenced the evolution and appearance of the forebulge (incuding its diagenesis and karstification), lithofacies distribution and thickness of the carbonate successions above the unconformity. At least some influence of eustatic sea-level oscillations cannot be excluded.

5) The subaerially exposed area and the facies belts of progressive forelandward advancing shallow-marine, pelagic, and turbiditic depositional environments ahead of the orogenic front are roughly parallel to the Dinaric mountain chain. However, the Dinaric foreland-related system supposedly began to evolve during the Eocene when Tisia and Adria microplates began to collide what is much later comparing to Late Cretaceous onset of foreland basin evolution and forebulge uplift in western Slovenia and Istria. In Istria the orientation of the prevailing regional stress during Cretaceous tectonic cycle differs significantly from Eocene one. I suggest that the foreland basin complex in western Slovenia and Istria was probably formed during mesoalpine ("Dinaric") tectonic phase, due to oblique collision of Adria and Tisia microplates (and/or Austroalpine terrane?) and segmentation of the foreland plate.

ACKNOWLEDGMENTS

Most of this work was performed as part of doctoral dissertation at University of Ljubljana. I am grateful to David Culver for English correction of an earlier version of the manuscript and Adrijan Košir for constructive reviews.

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A REVIEW OF COALESCED, COLLAPSED-PALEOCAVE SYSTEMS AND ASSOCIATED SUPRASTRATAL DEFORMATION

MEDSEBOJNO ZDRUŽENI PORUŠENI PALEOKRAŠKI JAMSKI SISTEMI IN DEFORMACIJE NAD NJIMI LEŽEČIH PLASTI – PREGLED

Robert G. LOUCKS[1]

Abstract UDC 551.44

Robert G. Loucks: A Review of Coalesced, Collapsed-Paleocave Systems and Associated Suprastratal Deformation

Coalesced, collapsed-paleocave systems and associated suprastratal deformation appear to be prominent diagenetic/structural features in carbonate sections at/near composite unconformities. The basic architecture of the system can be divided into two sections. The lower karsted section, where high-density cave formation took place, is preserved as massive breccias commonly displaying a rectilinear pattern in map view. The overlying suprastratal deformation section is characterized by large, circular to linear sag structures containing faults and fractures. Regional distribution of coalesced, collapsed-cave systems commonly appears as large-scale (hundreds to thousands of square kilometers in area), rectilinear patterns with areas of concentrated, coalesced breccias separated by relatively undisturbed host rock. This pattern may reflect development of the paleocave system along fracture swarms.

Collapsed-paleocave systems are large, complex features that show broad-scale organization. The complete paleocave system may need seismic data or large, mountain-scale outcrops to define their architecture and distribution.

Key Words: Paleocaves, Paleokarst, karst, suprastratal deformation, cave systems.

Izvleček UDK 551.44

Robert G. Loucks: Medsebojno združeni porušeni paleokraški jamski sistemi in deformacije nad njimi ležečih plasti – pregled

Medsebojno združeni porušeni paleokraški jamski sistemi in deformacije nad njimi ležečih plasti predstavljajo izrazite diagenetsko/strukturne oblike karbonatnih zaporedij v bližini sestavljenih geoloških nezveznosti. Osnovno zgradbo posameznega sistema lahko razdelimo na dva dela. Spodnji zakraseli del, kjer je gostota jam velika, je ohranjen v obliki masivnih breč, ki pogosto kažejo v tlorisu vzorec sestavljen iz ravnih odsekov. Za deformirane plasti, ki prekrivajo porušene jamske sisteme, so značilne velike skledaste do škatlaste uleknine, ki jih sekajo prelomi in razpoke. Regionalno gradijo združeni paleokraški jamski sistemi tega tipa vzorec velikega merila (zajemajo območja velika stotine do tisoče kvadratnih kilometrov), sestavljen iz ravnih odsekov in vključuje območja zgoščenih združenih brečastih teles, ločenih z relativno neprizadeto prikamnino. Tak vzorec lahko kaže na razvoj paleokraškega jamskega sistema vzdolž razpoklinskih con. Porušeni paleokraški jamski sistemi predstavljajo velike kompleksne pojave, ki odražajo organiziranost velikega merila. Za opredelitev zgradbe in razprostranjenosti popolnega paleokraškega jamskega sistema teh dimenzij potrebujemo podatke seizmičnih raziskav ali izdanke dimenzij gorovja.

Ključne besede: pelokraški jamski sistemi, paleokras, deformacije, jamski sistemi.

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Received/Prejeto: 27.11.2006

INTRODUCTION

At several composite unconformities in the stratigraphic record, carbonate sections display extensive karsting that leads to multiple development of cave systems (Esteban, 1991). These cave systems underwent extensive collapse and mechanical compaction with burial. Deformation of the overlying strata is associated with burial collapse of the cave system. The effects of this suprastratal deformation can be noted 700+ m up section above the karsted interval.

This review will describe the evolution of cave systems during burial and what the characteristics of the cave systems are at different stages of burial. Also the characteristics of suprastratal deformation will be described. Paleocave systems have been investigated by several authors including Lucia (1968, 1995, 1996), Loucks and Anderson (1980, 1985), Kerans (1988, 1989, 1990), Wilson *et al.* (1991) Wright *et al.* (1991), Candelaria and Reed (1992), Loucks and Handford (1992), Lucia *et al.* (1992), Kerans *et al.* (1994), Hammes *et al.* (1996), Mazzullo and Chilingarian (1996), McMechan *et al.* (1998), Loucks (1999, 2001, 2003), Loucks *et al.* (2000, 2004), Loucks and Mescher (2001), McMechan *et al.* (2002), and Combs *et al.* (2003). The review will mainly synthesize material from these studies.

CLASSIFICATIONS OF CAVE PRODUCTS AND FACIES

Loucks (1999) and Loucks and Mescher (2001) produced classifications of cave products and cave facies. Loucks (1999) used a ternary diagram (Fig. 1) to show the relationships between crackle breccias, mosaic breccias, chaotic breccias, and cave sediments. Crackle breccias are highly fractured rock, with thin fractures separating the clasts and only minor displacement existing between the clasts. Mosaic breccias show more displacement than crackle breccias, but the clasts can still be fitted back together. Chaotic breccias are composed of mixtures of clasts that have been transported vertically by collapse or laterally by fluvial or density-flow mechanisms. Clasts show no inherent association with their neighbors. Chaotic breccias grade from matrix-free, clast-supported breccias; through matrix-rich, clast-supported breccias; to matrix-rich, matrix-supported breccias. Cave-sediment fill can consist of any material, texture, or fabric.

Loucks and Mescher (2001) proposed a classification of six common paleocave facies (Fig. 2): (1) Undisturbed strata, which are interpreted as undisturbed host rock. In this facies bedding continuity is excellent for tens of hundreds of meters. (2) Disturbed strata that are disturbed host rock around the collapsed passage. Bedding continuity is high, but it is folded and offset by small faults. It is commonly overprinted by crackle and mosaic brecciation. (3) Highly disturbed strata, which is collapsed host rock adjacent to or immediately above passages. (4) Coarse-clast chaotic breccia that is interpreted as collapsed-breccia cavern fill produced by ceiling and wall collapse. It is characterized by a mass of very poorly sorted, granule- to boulder-sized chaotic-breccia clasts approximately 0.3 to 3 m long that form a ribbon-to tabular-shaped body as much as 15 m across and hundreds of meters long. It is commonly clast

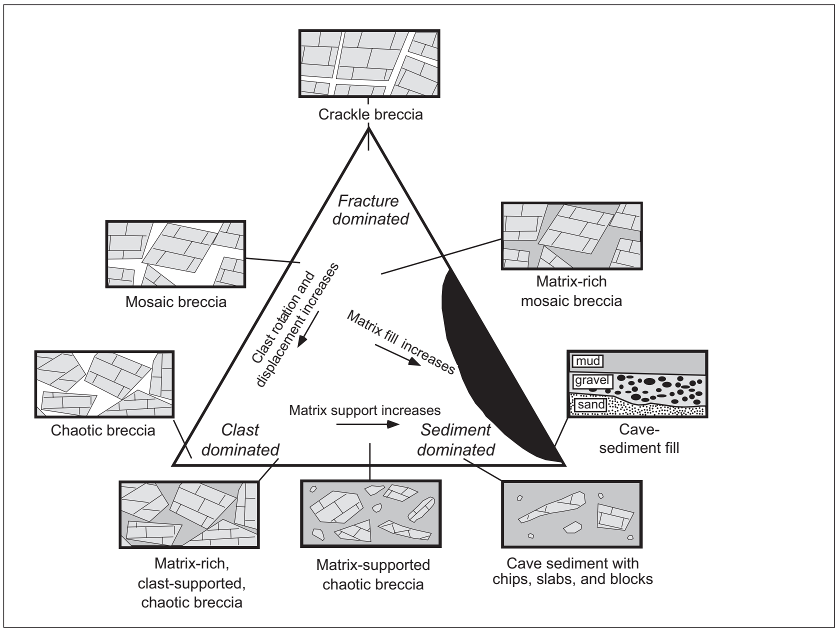


Fig. 1: Cave-sediment fills and breccias can be separated into three end members: crackle breccia, chaotic breccia, and cave-sediment fill. Modified from Loucks (1999) and reprinted by permission of the AAPG whose permission is required for further use."

supported, but can contain matrix material. (5) Fine-clast chaotic breccia interpreted as laterally (hydrodynamically) sorted, transported-breccia cavern fill. Characterized by a mass of clast-supported, moderately sorted, granule- to cobble-sized clasts with varying amounts of matrix. Clasts can be imbricated or graded. Resulting bodies are ribbon- to tabular-shaped and are as much as 15 m across and hundreds of meters long. (6) Cave-sediment cavern fill that can be carbonate and/or siliciclastic debris of any texture or fabric and commonly displaying sedimentary structures.

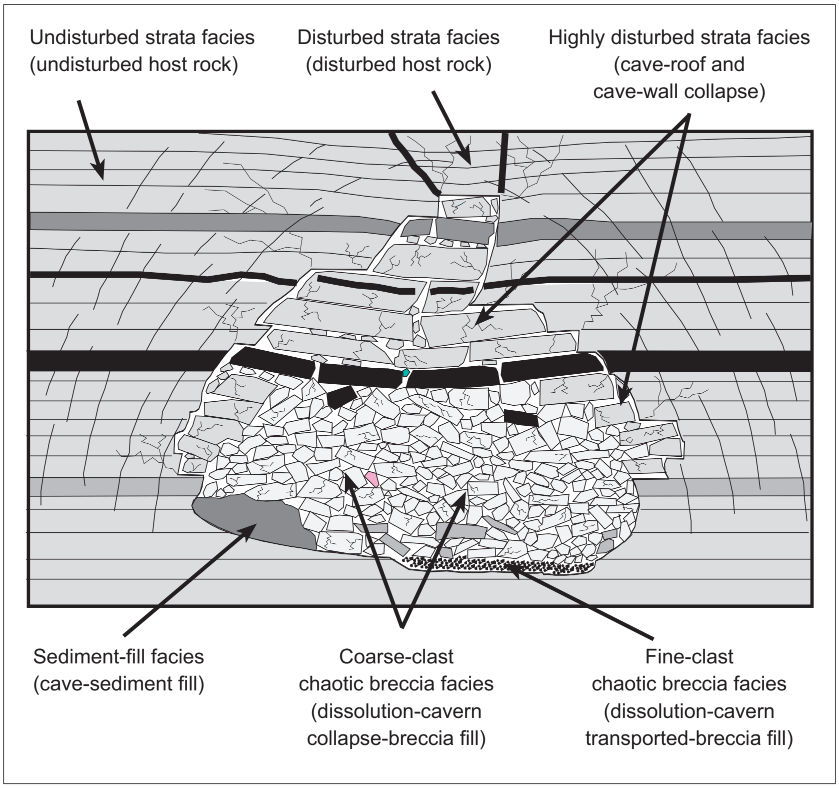


Fig. 2: Six basic cave facies are recognized in a paleocave system and are classified by rock fabrics and structures. Modified from Loucks and Mescher (2001) and reprinted by permission of the AAPG whose permission is required for further use."

EVOLUTION OF CAVE PASSAGES

Knowledge of the processes by which a modern cave passage forms at the surface and evolves into a collapsed paleocave passage in the subsurface is necessary to understand the features of paleocave systems. Loucks (1999) described this evolutionary process (Fig. 3), and the review presented here is mainly from that investigation.

A cave passage is a product of near-surface karst processes that include dissolutional excavation of the passage, partial to total breakdown of the passage, and sedimentation in the passage (Fig. 4). During later-burial cave collapse, mechanical compaction takes place.

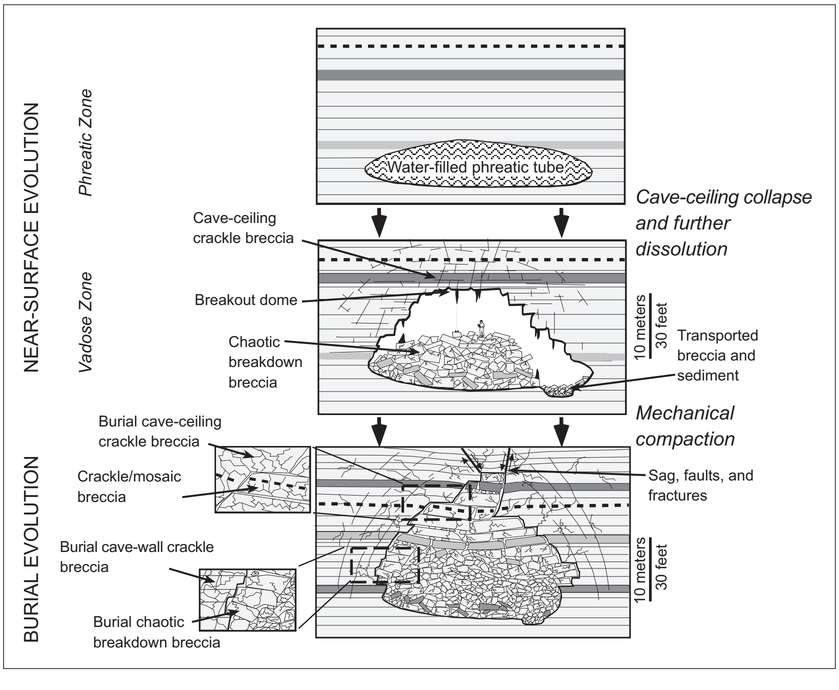


Fig. 3: Schematic diagram showing evolution of a single cave passage from its formation in the phreatic zone of a near-surface karst environment to burial in the deeper subsurface. Modified from Loucks (1999) and reprinted by permission of the AAPG whose permission is required for further use."

Initial passages form in phreatic and/or vadose zones (Fig. 3). Passages are excavated where surface recharge is concentrated by preexisting pore systems, such as bedding planes or fractures (Palmer, 1991), that form a continuous link between groundwater input, such as sinkholes, and groundwater output, such as springs (Ford, 1988). Cave passages are under stress from the weight of overlying strata. A tension dome, or zone of maximum shear stress, is induced by the presence of the passage or cavity (White, 1988). Stress is relieved by collapse of the rock mass within the stress zone. This collapse produces chaotic breakdown breccia on the floor of the cave passage (Figs. 3 and 4). The associated stress release around the cavity produces crackle and mosaic breccias in the adjacent host rock.

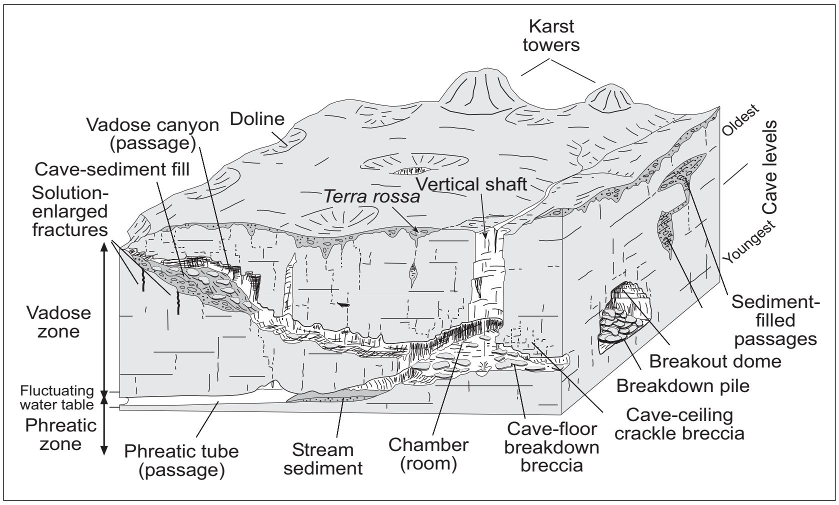


Fig. 4: Block diagram of a near-surface modern karst system. The diagram depicts four levels of cave development (upper-right corner of block model), with some older passages (shallowest) having sediment fill and chaotic breakdown breccias. Modified from Loucks (1999) and reprinted by permission of the AAPG whose permission is required for further use."

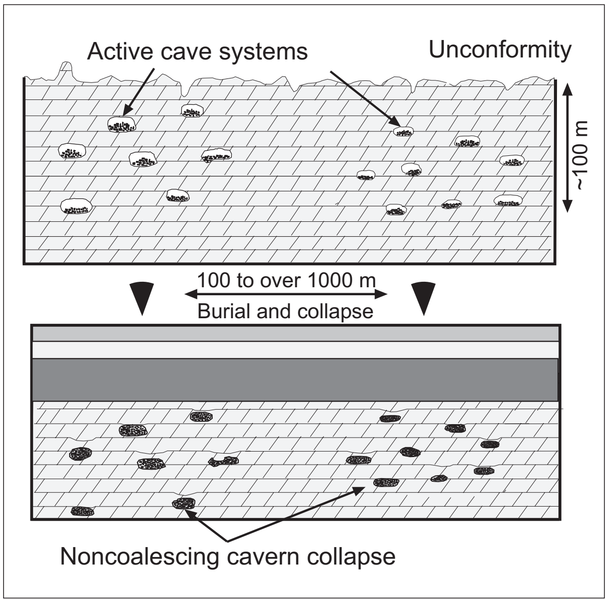
As cave-bearing strata are buried, extensive mechanical compaction begins, resulting in collapse of the remaining void (Fig. 3). Multiple stages of collapse occur over a broad depth range. Meter-scale bit drops in wells (indication of cavernous pores) are not uncommon down to depths of 2,000 m and are observed to occur to depths of 3,000 m (Loucks, 1999). The collapsed passages become pods of chaotic breccia (Fig. 3). The areal cross-sectional extent of brecciation and fracturing after burial and collapse is greater than that of the original passage because the adjacent fractured and brecciated host rock has become part of the brecciated pod. Sag features, faults, and fractures (Fig. 3) occur over the collapsed passages.

EVOLUTION OF COALESCED, COLLAPSED-PALEOCAVE SYSTEMS

A coalesced, collapsed-paleocave system can be divided into two parts: (1) a lower section of strata that contains collapsed paleocaves and (2) an upper section of strata that is deformed to varying degrees by the collapse and compaction of the section of paleocave-bearing strata (Fig. 5). The deformed upper section of strata is termed *suprastratal deformation* (Loucks, 2003) and is discussed in a later section.

Cave systems are composed of numerous passages. If the areal density of passages is low, the collapsed cave system will feature isolated, collapsed passages (noncoalescing paleocave system; Fig. 6). If the cave system has a high density of passages, as is common at composite third-order unconformities (Esteban, 1991; Lucia, 1995;

Fig. 6: Schematic diagram showing burial and collapse of low-density cave system (noncoalescing, collapsed-cave system) and reprinted by permission of the AAPG whose permission is required for further use."



Loucks, 1999), then upon burial and collapse the system can form large-scale, coalesced, brecciated and fractured breccia bodies upon burial and collapse that are the amalgamation of many passages and intervening disturbed host rock (coalescing paleocave system; Fig. 5). The bodies are hundreds to several thousands of meters across, thousands of meters long, and tens of meters to more than 100 m thick. Internal spatial complexity is high, resulting from the collapse and coalescence of numerous passages and cave-wall and cave-ceiling strata.

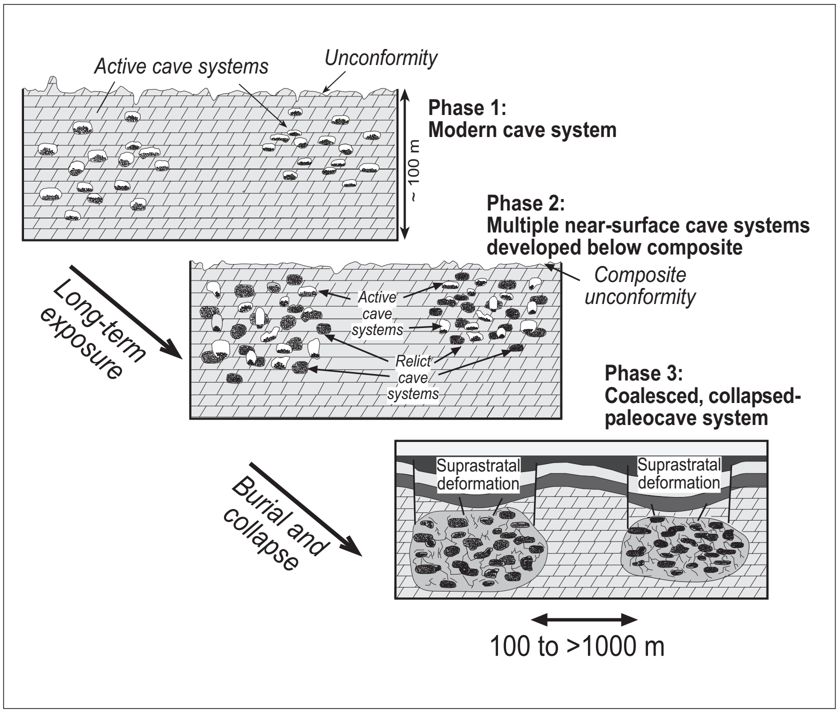


Fig. 5: Schematic diagram showing the stages of development of a coalesced, collapsed-paleocave system. Modified from Loucks et al., (2004) and reprinted by permission of the AAPG whose permission is required for further use."

SUPRASTRATAL DEFORMATION

Collapse and compaction of cave systems provide potential for development of large-scale fracture/fault systems that can extend from the collapsed interval upward to more than 700 m (Kerans, 1990; Hardage *et al.,* 1996a; Loucks, 1999, 2003; McDonnell *et al.*, in press). These fracture/fault systems are not related to regional tectonic stresses.

Large-scale suprastratal deformation occurs above the collapsed-cave system. As the cave system collapses during burial, overlying strata will sag or subside over the collapsed area. This phenomenon is well documented in mining literature (Kratzsch, 1983; Wittaker and Reddish, 1989). Kratzsch (1983, p. 147) presented a diagram (Fig. 7) that shows the stress field above a collapsed mine passage and associated subsidence. The overlying stress field widens from the edges of the excavation, and the overlying strata are under compression directly over the excavation. Near the edges of the excavation, between a vertical line extending from the edge of the cavity and the limit line, strata are under extension (tension). Within this zone of stress the overlying strata have the potential to sag, creating faults and fractures for some distance upward, depending on the mechanical properties of the strata and the thickness of the beds within the strata. Fig. 8 is a scatterplot showing a number of examples of the magnitude of subsidence over coal mines. The graph indicates that subsidence is recorded at horizons more than 800 m above the cavity. These data indicate the magnitude of the effect that the collapse of a cavity can have on overlying strata.

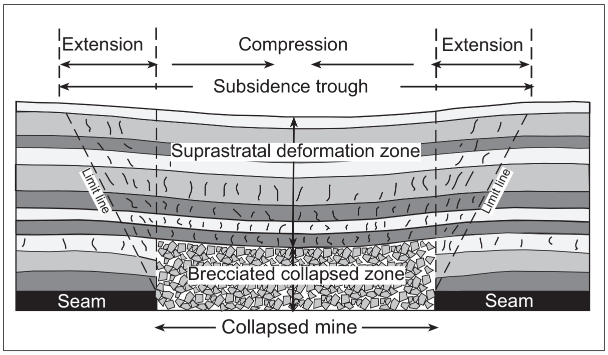


Fig. 7: Diagram of a collapsed mine showing collapsed breccia zone and suprastratal deformation. The center of the subsidence trough is under compression, whereas the wings are under extension. Modified from Kratzch (1983).

Applying the above concept of stress fields over cavities to the collapse of a cave passage during burial suggests that similar stress fields will develop. As the cave passage collapses, it has the potential to affect a considerable number of overlying strata. Within a cave system, numerous passages will collapse with burial. Each passage will develop a stress field above it, and these stress fields will interact to create a larger, combined stress field. This concept was presented by Wittaker and Reddish (1989; p. 47), who detailed instances in which multiple mining excavations are collapsing. The stress field above a collapsing cave system will be complex because the different cave passages do not collapse and compact uniformly over time. As local areas collapse, different stress fields will develop, producing fractures and faults related to that individual stress field. Resulting suprastratal deformation will show variable fracture and fault patterns within an overall subsidence sag. A unique circular fault pattern above collapsed cave systems is recognized by cylindrical faults (Hardage *et al.*, 1996a; Loucks, 1999; McDonnell *et al.*, in press).

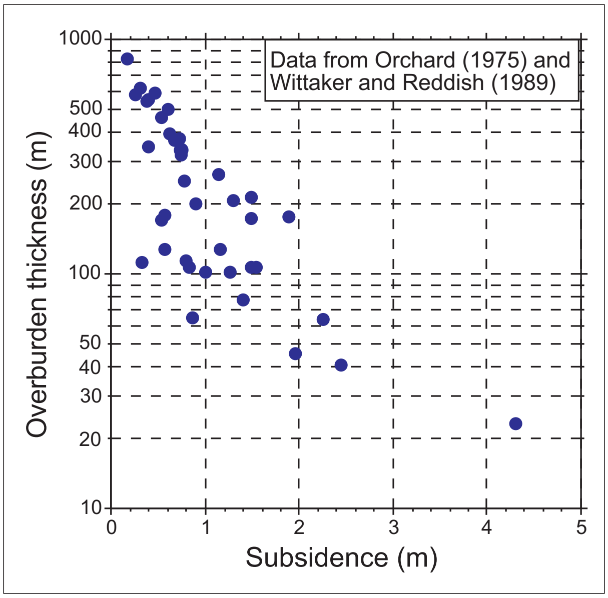


Fig. 8: Scatterplot showing thickness of overburden that can be affected by mine collapse. Graph shows a trend of greater subsidence with less overburden.

MEGASCALE ARCHITECTURE PATTERNS OF COALESCED, COLLAPSED-PALEOCAVE SYSTEMS

Coalesced, collapsed-paleocave systems are megascale diagenetic/structural features that can affect more than 700 m of section and be regional in scale. As discussed earlier, the karsted section reflects the coalescing of collapsed breccias that formed by collapse of passages and associated disturbed host rock. The vertical extent of the breccias commonly affects the upper 100 m of section (Loucks and Handford, 1992; Loucks 1999) and as much as 300 m of the total section (Lucia, 1996). The intensity of brecciation can vary throughout the affected interval. Kerans (1990), Loucks (1999), Loucks *et al.*, 2004), and many others have published descriptions of collapsed, brecciated paleocave zones. Fig. 9 shows examples of cave facies from the Lower Ordovician Ellenburger Group in central Texas (Loucks *et al.*, 2004).

The regional pattern of the collapsed paleocave system is commonly rectilinear (Loucks, 1999). This rectilinear pattern is probably an artifact of the original cave system developing along an early-formed fracture system. In a detailed study of a paleocave system in the

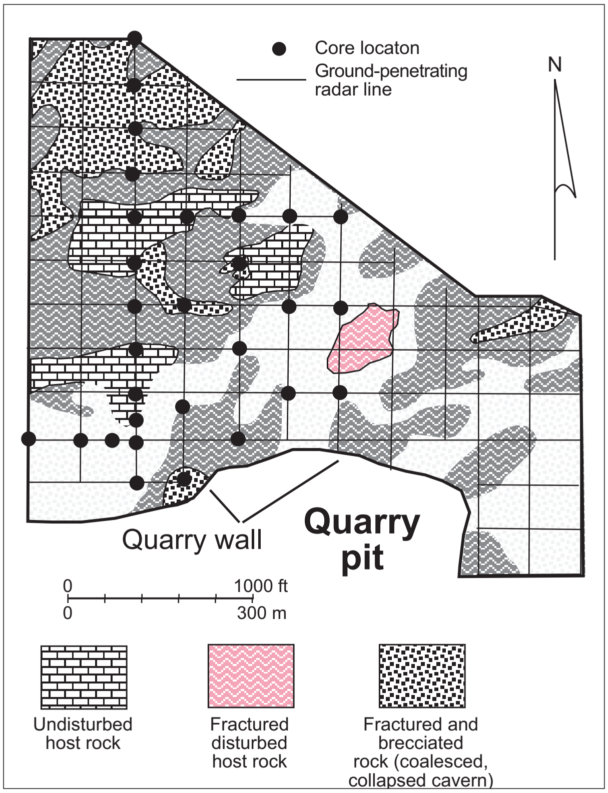


Fig. 10: Slice map through a collapsed-paleocave system in the Lower Ordovician Ellenburger Group in central Texas. Modified from Loucks (2004) and reprinted by permission of the AAPG whose permission is required for further use."

Lower Ordovician in central Texas, Loucks *et al.* (2004) presented maps (Fig. 10) and cross sections of the three-dimensional, fine-scale architecture of a coalesced, collapsed-paleocave system. The coalesced, collapsed-passage breccias range in size to as much as 350 m and are separated by disturbed and undisturbed host rock ranging in size up to 200 m. Lucia (1995) also presented a map of brecciated collapsed passages (Fig. 11) from outcrops in the Franklin Mountains of far west Texas, which displays a crude rectilinear pattern.

This rectilinear pattern can be seen on seismic data as well. Loucks (1999) presented seismic-based maps from Benedum field in West Texas that display a rectilinear pattern of sags and circular faults induced by collapse of the Ellenburger paleocave system below (Fig. 12). A similar rectilinear pattern is evidenced on seismic data in Boonsville field (Fig. 13) in the northern Fort Worth Basin in Texas (Hardage *et al.*, 1996a; McDonnell *et al.*, in press). In both the Benedum and Boonesville datasets, suprastratal deformation affects up to 700 m of section above the karsted interval (Figs. 12 and 13).

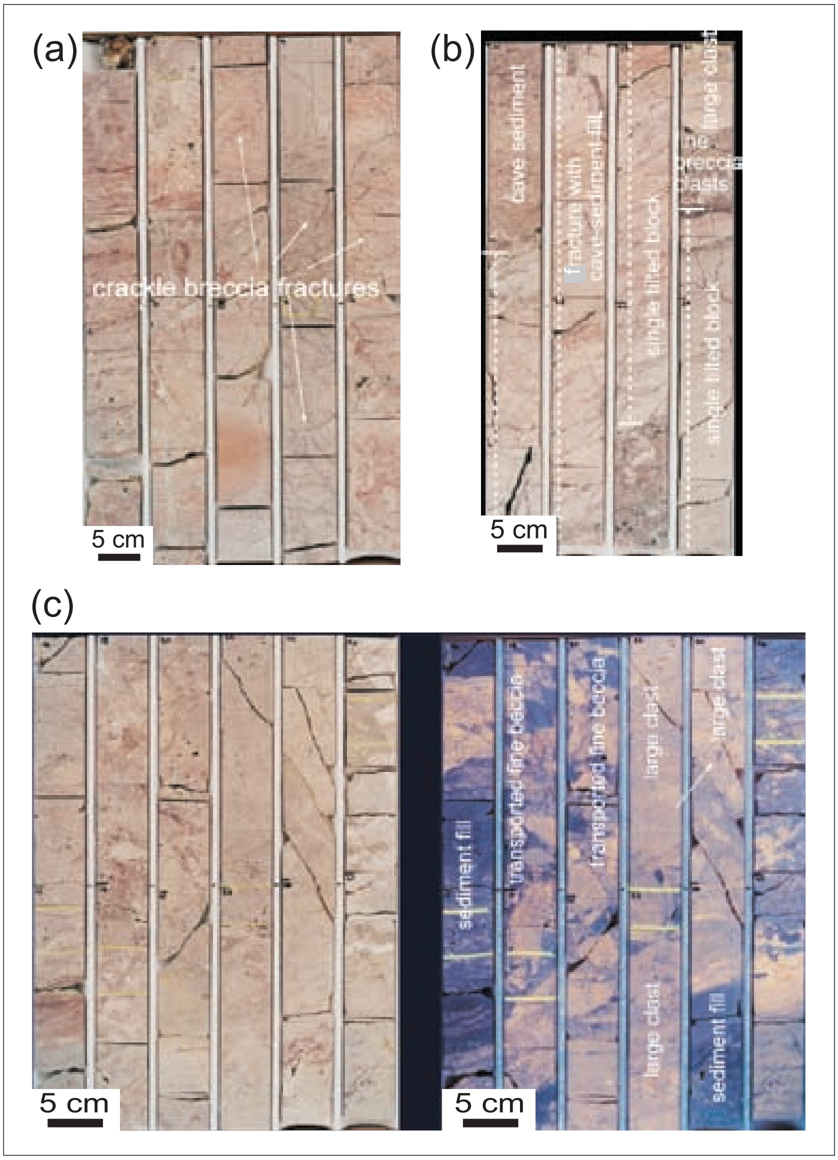


Fig. 9: Representative cores from paleocave facies. (a) Crackle-fractured disturbed host rock. (b) Collapsed chaotic breccia with large slabs and cave-sediment fill. (c) Transported chaotic breccias in carbonate cave-fill matrix. Sample on right is under UV light. Samples from Lower Ordovician Ellenburger Group in central Texas. Modified from Loucks (2004) and reprinted by permission of the AAPG whose permission is required for further use."

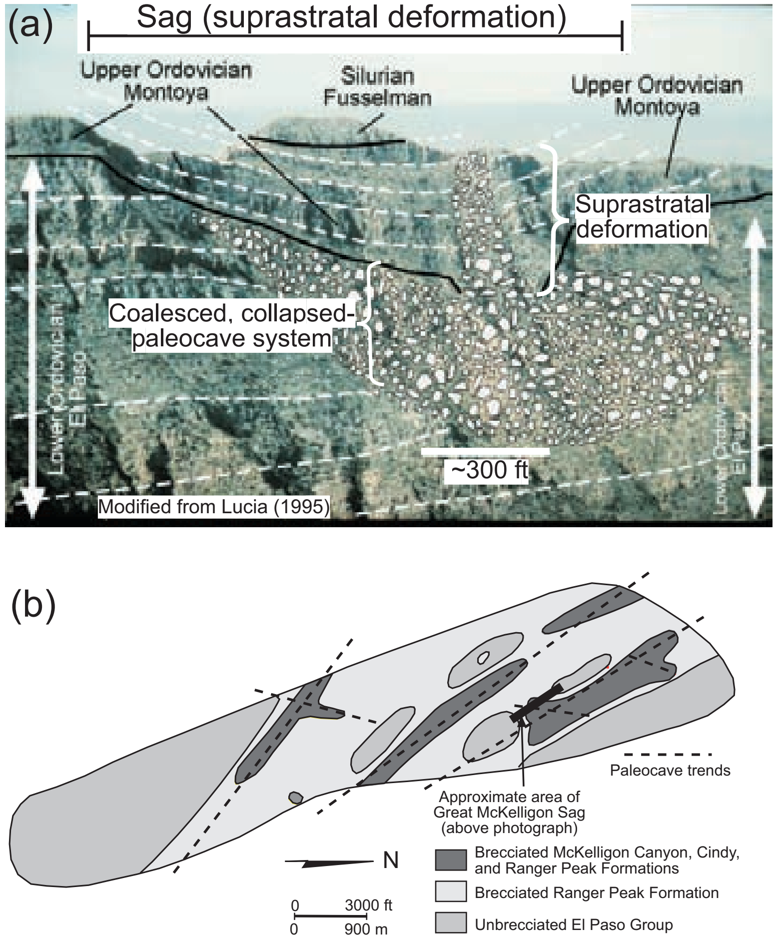


Fig. 11: (a) Photograph of the Great McKelligon Sag in the Franklin Mountains of far West Texas. Photograph and general interpretation are from Lucia (1995) but have been modified by current author. This outcrop is an outstanding example of a collapsed-paleocave system with associated overlying suprastratal deformation. (b) Map produced by Lucia (1995) of several paleocave systems within the Franklin Mountains. Paleocave trend lines are by current author.

CONCLUSIONS

Coalesced, collapsed-paleocave systems are megascale diagenetic/structural features that can affect more than 700 m of section and be regional in scale. The architecture of the complete system can be divided into the lower collapsed zone, where the dense system of caves formed and collapsed with later burial, producing a complex zone of brecciation. The upper, suprastratal deformation section formed during the collapse of the karsted section. The overlying strata were generally lithified, but the sag also affected concurrent sedimentation patterns (Hardage *et al.*, 1996b). The deformation in the deformed suprastratal zone consists of normal, reverse, and cylindrical faults and fractures (Loucks, 1999; McDonnell *et al.*, in press). It is important to emphasize that large-scale structural features can develop above karsted zones and not be related to regional tectonic stresses.

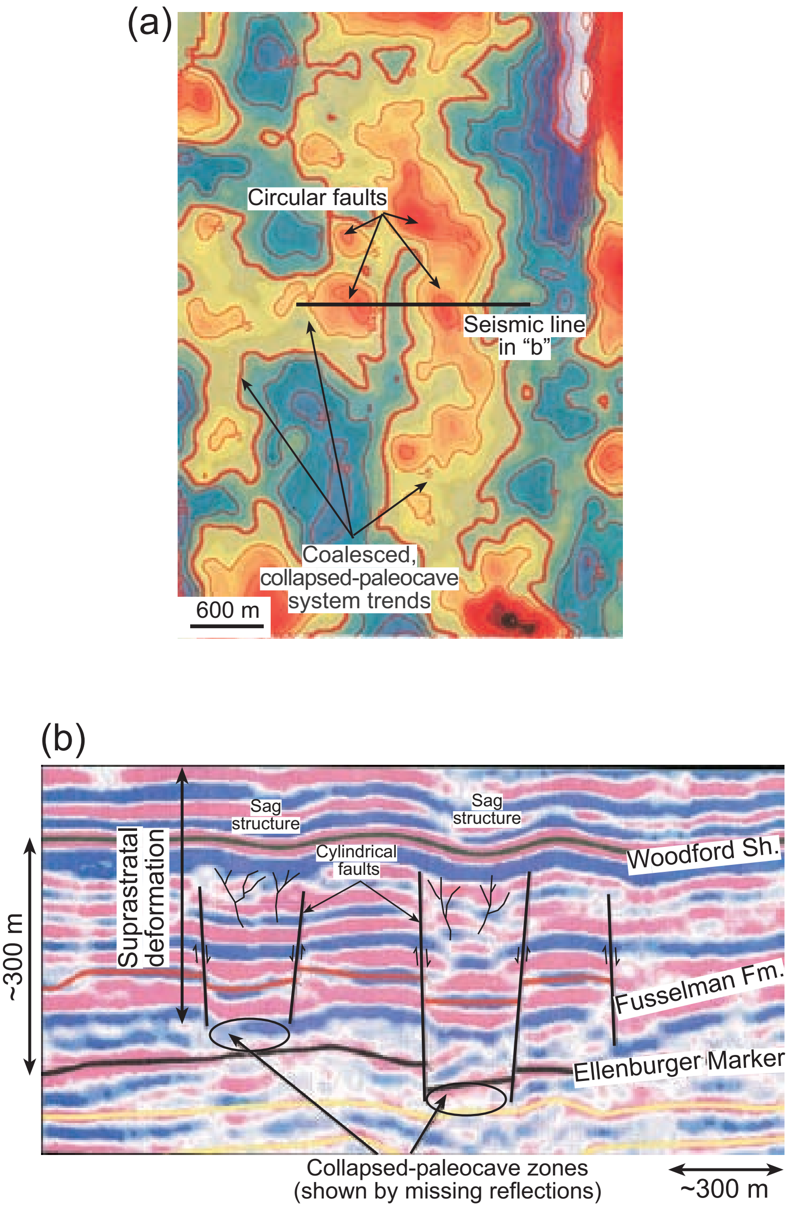


Fig. 12: 3-D seismic example over an Ellenburger paleocave system from Benedum field in West Texas. (a) Second-order derivative map in the Fusselman interval displaying sag zones produced by Ellenburger paleocave collapse. (b) Seismic line showing missing sections (collapse in Ellenburger section), cylindrical faults, and sag structures. Suprastratal deformation is >1,000 ft thick in this section. Modified from Loucks (1999) and reprinted by permission of the AAPG whose permission is required for further use."

Coalesced, collapsed-paleocave systems and associated suprastratal deformation are complex systems, and large-scale outcrops or datasets are necessary to define them. However, with the model presented in this paper, individual data points can lead to recognition that the system is a coalesced, collapsed-paleocave feature.

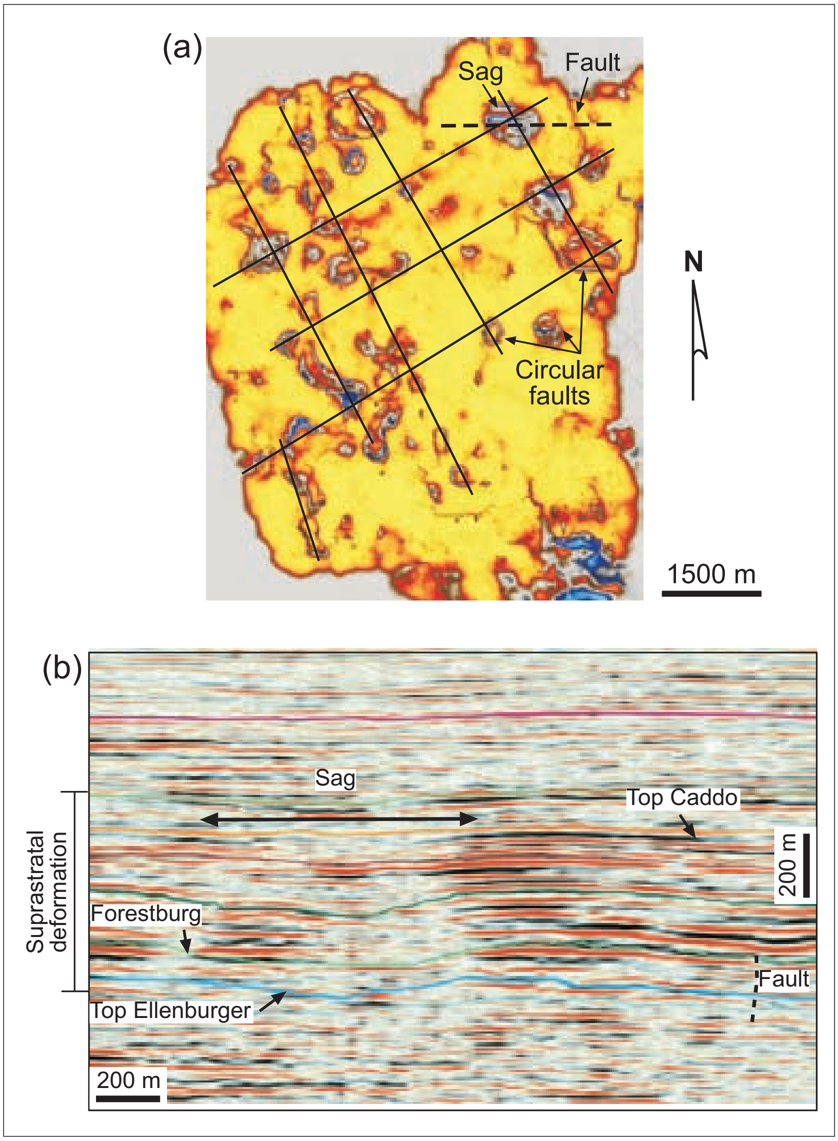


Fig. 13: Suprastratal deformation sag features in post-Lower Ordovician Ellenburger strata in Fort Worth Basin in north Texas. (a) Curvature map at Mississippian Forestburg Limestone horizon displaying sag features and faults produced by collapse in the Ellenburger interval. From McDonnell et al. (in press). (b) 3D seismic line at 1:1 scale showing sag features produced by paleocave collapse in the Ellenburger section. Line-of-section location is shown by dashed line in Fig. 13a.

ACKNOWLEDGEMENTS

I would like to express my appreciation to Angela McDonnell for reviewing this manuscript. Lana Deiterich edited the text. Published with the permission of the Director, Bureau of Economic Geology, John A. and Katherine G. Jackson School of Geosciences, The University of Texas at Austin.

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THE WORLD'S OLDEST CAVES: - HOW DID THEY SURVIVE AND WHAT CAN THEY TELL US?

NAJSTAREJŠE JAME NA SVETU: KAKO SO SE OHRANILE IN KAJ NAM LAHKO POVEDO?

R. Armstrong L. OSBORNE[1]

Abstract UDC 551.44(091)

R. Armstrong L. Osborne: The world's oldest caves: - how did they survive and what can they tell us?

Parts of an open cave system we can walk around in today are more than three hundred million years old. Common sense tells even enthusiasts like me that open caves this old should not still exist, but they do! Their survival can be partly explained by extremely slow rates of surface lowering, but this is not sufficient by itself. Isolation by burial and relative vertical displacement by faults are probably also required. Now one very old set of caves have been found, are there more of them? What can they tell us?

Key words: speleology, oldest cave, survival of old caves.

Izvleček UDK 551.44(091)

R.A.L. Osborne: Najstarejše jame na svetu: kako so se ohranile in kaj nam lahko povedo?

Deli odprtega jamskega sistema, po katerem se lahko danes sprehajamo, so stari več kot 300 milijonov let. Zdrav razum celo takemu navdušencu, kot sem jaz, pove, da tako stare odprte jame ne morejo obstajati, a vendar so! Da so se ohranile, je lahko deloma vzrok v izredno počasnem zniževanju površja, toda to samo po sebi ni dovolj. Jama je morala biti najbrž tudi zasuta in s tem odrezana od sveta, potreben pa je bil tudi relativen navpičen premik ob prelomih. Zaenkrat je bil najden en sam niz zelo starih jam, ali jih je morda še več? Kaj nam lahko povedo?

Ključne besede: speleologija, najstarejša jama, ohranitev starih jam.

INTRODUCTION

In June 2004, when I last spoke here at Postojna about dating ancient caves and karst I found it difficult to not to reveal the exciting discovery which this paper follows (see Osborne, 2005). My collaborators and I had been convinced since mid 2001 that sections of Jenolan Caves in eastern Australia had formed 340 million years ago. We had to ensure that our story was published and that we could convince others. The issue was not whether the dates themselves were correct, but did the evidence really mean that the caves containing the clays were of such a great age. This took four years of intensive work on the clays and additional dating.

Now after the publication of the results (Osborne *et al,* 2006), and the following media interest; it seems appropriate to reflect on the significance and implications of the survival of Early Carboniferous open caves.

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Received/Prejeto: 27.11.2006

THE POTENTIAL FOR CAVES/SECTIONS OF CAVE TO HAVE A GREAT AGE

Despite many years of working on palaeokarst, I initially found the Early Carboniferous (340 Ma) K-Ar dates for unlithified clays in Jenolan Caves incredible (Figure 1).

Fig. 1: Plastic illite–bearing clay, mustard yellow, in the River Cave, Jenolan Caves, NSW Australia. The < 2μm fraction of this clay was K-Ar dated by Osborne et al., (2006) at 357.30 ± 7.06 Ma.

As I pointed out in 2004 (Osborne, 2005), some Permian landforms do survive relatively intact in Australia. Even a Late Carboniferous age would not have been too surprising, as a Late Carboniferous landsurface has been exhumed at Jenolan from below the overlying Permo-Triassic Sydney Basin.

An Early Carboniferous age seemed challenging for two main reasons:

1 The 340 Ma age sits in the middle of the accepted timing for the last folding event in the area (350-330 Ma). Not only the caves, but also the relatively undeformed and well-lithified caymanite deposits they intersected had to be younger than this event. The clay dates upset the accepted chronology for the area and suggested that the last folding was older than previously thought.

2 The 340 Ma age is older than the accepted emplacement age for the adjacent Carboniferous granites (320 Ma). The plateau surface adjacent to the caves intersects granite plutons. Why didn't the process that exposed the plutons wipe out the ancient caves?

My opponents believed that while other landforms in Australia were old, the caves were not. They argued that there was no demonstrably old sediment in the caves. I have already discussed this argument elsewhere (Osborne, 1993a, 2002, 2005). The Early Carboniferous clays from Jenolan are the first evidence for ancient sediments in Australian caves accessible to humans, but they make the problem of the survival of ancient caves even more difficult, because they are so very old.

If we think about the geological history of karstification at Jenolan then the formation of caves in the Carboniferous should not be surprising. The best dates for the Jenolan Caves Limestone put it in the Latest Silurian (Pridoli, 410-414 Ma)(Pickett, 1982).

As well as telling us about the 340 Ma event, the K-Ar clay dating indicated that the limestone underwent a pre-tectonic period of cave development in the Early Devonian before 390 Ma when the caves were filled with the unconformably overlying volcaniclastics. There was also a post-tectonic period of ancient speleogenesis before a marine transgression filled the second generation of caves with lime-mud and crinoidal debris. I suspect if we had announced a third-phase of lithified palaeokarst some 340 million years old at Jenolan, there would have been little reaction, although the problem of its survival and the problem with the timing of folding would have been the same as the problems with our relict sediments.

It would not be surprising for limestone anywhere in the world to have undergone speleogenesis some 70 Ma after its deposition. The development of a modern cave in Late Cretaceous limestone is hardly unusual.

So, what is the problem? I suspect that while geomorphologists think surface lowering will destroy old caves, many geologists expect that:

1 open caves fail relatively quickly by breakdown (by analogy with mines and quarries)

2 palaeokarst caves only survive because they are filled with rock; the rock supports the roof preventing destruction due to breakdown.

3 cave sediments become lithified quickly, so old unlithified relic sediments cannot exist

These ideas are refuted by the findings of palaeokarst workers, surface cavers and the oil industry so I will not expand on them here, rather I will concentrate on geomorphological challenges to the survival of 340 million year old caves.

HOW COULD THEY SURVIVE?

WHY CAVES MAY SURVIVE LONGER THAN SURFACE LANDFORMS

Landforms are always under threat from the processes of weathering, incision and surface lowering. Weathering in the normal sense of the word is irrelevant in karst since, except in the case of Nadja's incomplete solution (Zupan-Hajna, 2003), carbonate weathering results in almost total removal of the rock mass. Incision may re-activate or expose ancient caves, but will rarely affect enough of the rock mass to lead to the destruction of ancient caves. It is surface lowering that is the greatest threat to ancient caves and the main process that leads to their late stage modification into unroofed caves. What processes may protect caves from surface lowering?

Protection by the rock mass

Since caves form below the surface, there is a thickness of rock between them and the zone where surface lowering is progressively removing the surface of the Earth. This means that caves have a head start in survival compared with surface landforms of the same age. Caves unroofed at the surface are always substantially older than the surface in which they are exposed.

Isolation and "karst resistance"

Not a lot happens once a cave space enters the vadose zone, there may be breakdown or speleothem deposition, but many cave openings just sit there, inactive while the water is directed through active conduits at a lower level.

The "god" that protects cave walls

Apart from speleothem and lithified sediments that may outlive all of the cave they formed in (Figure 2), it is the walls of a cave that survive the longest, right up to the very last stage of an unroofed cave (Figure 3).

Why don't the cave walls fail and simply fall into the void beside them and why don't they allow the whole cave to fill with speleothem during its siesta in the vadose zone? Some process must protect cave walls from failure and penetration by potentially lethal vadose flow. I am indebted to Andrej Mihevc for the concept of a '"god" that protects cave walls'. I am sure this god is a useful addition to the karst panoply.

Three factors are probably important for the survival of cave walls, particularly in teleogenic karsts: -

- rock strength
- Slow and gentle cave excavation, leading to gradual stress release (caves are not mines or tunnels)
- Degassing and precipitation from seeping water makes cave walls self-sealing

Fig. 2: Speleothem, exposed on surface above Dip Cave, Wee Jasper, NSW, Australia. Cave entrance can be seen top of photo. This speleothem has outlived all of the cave it formed in.

Some cave walls do fail for a variety of reasons. We can observe this in many breakdown chambers and it is possible to recognise the sources of the weakness in the walls that resulted in their failure.

Lack of substantial entrances

Some caves, e.g. cryptokarst caves of thermal /hydrothermal origin, may have no entrances or very poor connection to the surface. If there is no entrance or surface connection then surface processes cannot get in and modify the cave.

Entrance Blockages

It is very easy for cave entrances to become blocked. Prograding entrance facies talus cones reaching the ceiling, talus from the surface or breakdown, growth of flowstone masses, logs, vegetation and biogenic deposits such as guano piles can all easily block cave entrances. With a small amount of vadose cementation, these blockages can become effectively permanent and the cave can become isolated.

Fig. 3: Looking towards the surviving cave wall from the floor of an unroofed cave, Trieste Carso, Italy.

Protection by filling

If a cave is filled with easily removed material, it is possible for the cave to remain "fossilized" for a geologically significant time and then become exhumed. If the fill is impermeable to vadose seepage, it will not become cemented. Even if it is cemented, if the fill contains minerals that are unstable when exposed to oxygen-rich vadose water it can be removed from the cave with little effect on the enclosing walls.

Protection by cover/burial

Cover by sediments, volcaniclastics or lava flows can protect not only the caves, but also surface karst landforms. For the process to be effective, the cover must be removed without a great effect on the underlying older karst. It helps if the cover consists of relatively weak rock or of rock that is easily weathered. An outstanding example of this process is the burial by Permian basalt and later exhumation of the Shinlin karst in southern China.

DENUDATION RATES

Both biblical prophets and geomorphological pioneers predicted a flat future, the "rough places a plain" of Isaiah 40:4 and the peneplanation of W. M. Davis. While peneplanation may be out of favour, surface lowering is a real phenomenon. The problem for survival of old caves is that even with the slowest rates of surface lowering most Mesozoic and all Palaeozoic caves should have been destroyed, except those that have been deeply buried and later exhumed following tectonic movements.

In some parts of Australia, extremely low denudation rates apply. Wilford (1991) reported rates as low as 0.5 metres per million years in the Officer Basin of Western Australia over the last hundred million years.

Surface lowering rates in the eastern Australian highlands, where Jenolan Caves are located, are said to range between 1-10 metres per million years (Bishop 1998). If this is so, then the limestone exposed at the surface today in these areas was between 65 and 650 metres below the surface at the end of the Mesozoic. While these rates are slow by world standards, they are not slow enough to account for the survival of extremely old features.

Surface lowering and early incision may be slower than we think

Studies of past erosion rates in the Shoalhaven Catchment in eastern Australia by Nott *et al.,* (1996) show that we must approach incision and denudation with some care. Their relevant findings are that:

- summit lowering and scarp retreat were insignificant when compared to the process of gorge extension
- the rate of summit lowering was 250 times less and the rate of scarp retreat was 15 times less than the rate of headward advancement of gorges
- stream incision in the plateau upstream of the erosion head is very slow compared to the rate of gorge extension
- there was "insignificant lowering of the interfluves throughout the Cainozoic" (Nott *et al.,* 1996, p 230)
- "Over the long term, the highlands…will become considerably more dissected well before they decrease substantially in height or are narrowed" (Nott *et al.,* 1996, p 224)

The stream incision rate is important when we consider the age of relict caves. If incision rates early in the history of the landscape are much slower than at later stages, present incision rates will lead us to seriously underestimate the age of relict caves located high in the sides of valleys.

If lowering of interfluves, i.e. surface lowering, is much slower than incision, scarp retreat and nick-point recession then plateau karst, high level caves and surface caves exposed on hilltops could be very much older than we have previously thought. In dissected terrains the caves will not just be *as old as the hills,* but considerably older.

TECTONIC PROCESSES ARE NECESSARY FOR EXTREME SURVIVAL

Low denudation rates, low relief and low rainfall, the Australian trifecta, can only go so far to preserve old landforms. Stephen Gale recognised this point: "Although low rates of denudation are an important factor in ensuring the survival of ancient landscapes, this alone is inadequate as an explanation of the maintenance of landforms over ten and even hundreds of millions of years" (Gale, 1992, p 337). Gale went on to discuss how denudation needed to be localized if old landsurfaces were to survive. One way the landsurface can be isolated from surface lowering is through the relative adjustment of adjacent blocks by faulting.

The Fault-Block Shuffle

The problem at Jenolan is the elevation of the old caves relative to the adjacent plateau surface. The plateau surface to the south of Jenolan Caves exposes and intersects post-tectonic Carboniferous granites, thought to be 320 million years old. Figure 4 is a cartoon drawn to explain in simple terms how the caves may have survived.

The caves must have been relatively close to the surface when the cupolas formed and the volcanic ash that formed our old clays entered them (Step 1 in Figure 4).

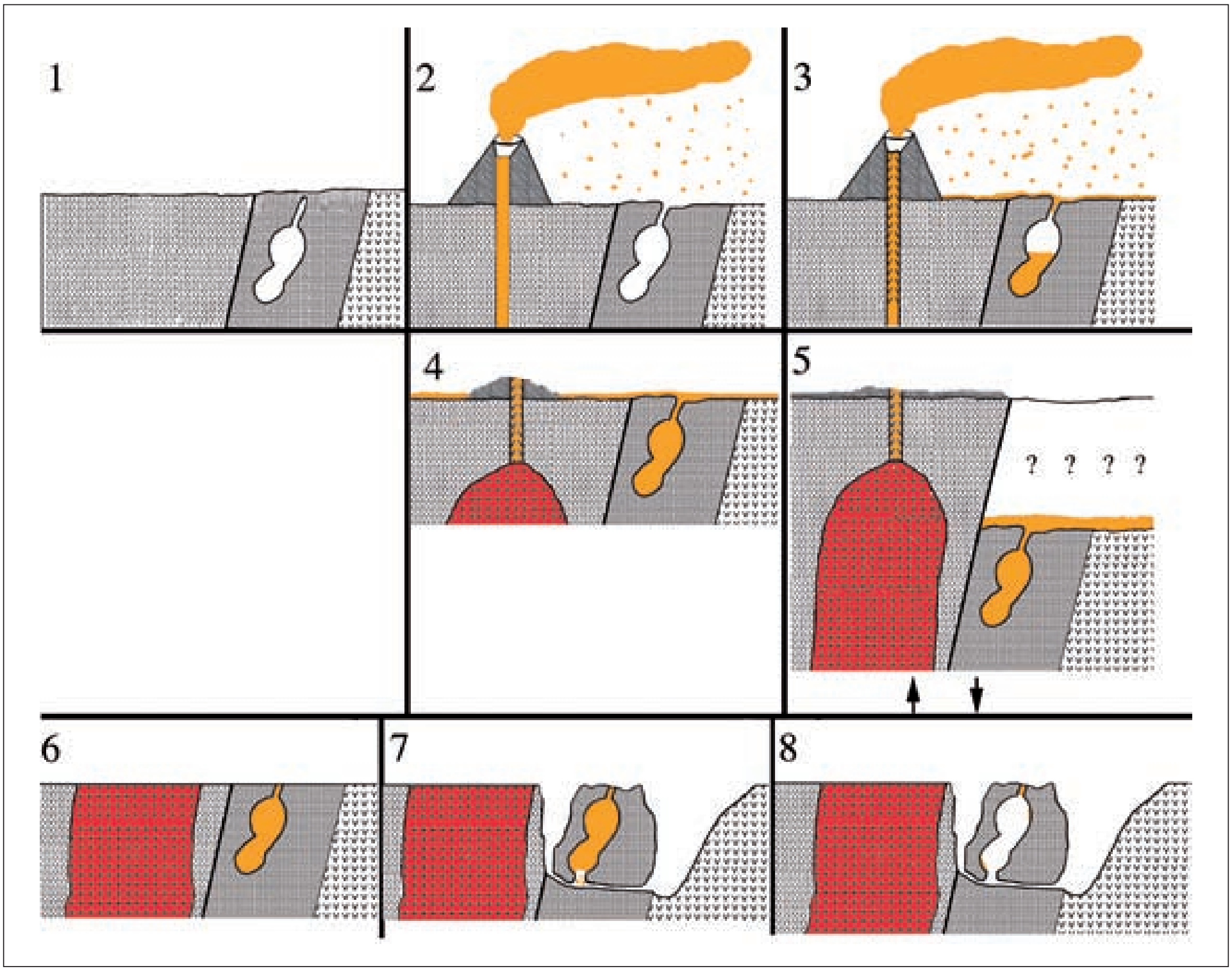

Fig. 4: Cartoon of postulated events at Jenolan Caves to explain the survival of caves with Carboniferous clays

1 *Cave excavated by thermal processes following folding of limestone*
2 *Volcano erupts; tephra falls to ground and enters caves.*
3 *Fine tephra begins to fill caves and reacts with water in caves to produce clay minerals. These clays have been dated at 340 million years.*
4 *Volcano stops and begins to be eroded. The caves are full of clay. Granite intrudes the rock near the caves (? 320 Ma).*
5 *The rock mass containing the granite moves up along the fault, while the rock mass containing the caves moves down.*
6 *Late Carboniferous: At least 8 kilometres thickness of rock is eroded away, probably partly by glaciation. This cuts off the top of the granite and brings the cave back close to the surface.*
7 *Late Mesozoic: Valleys erode into the surface and a new stream cave forms below the level of the filled cave. The clays, still soft, are undermined. They fall down and are carried way by the stream.*
8 *Today: Almost all of the 340 million year old clay has now been removed from the caves, small remnants are found and dated.*

Even if the granites did form close to the surface, something between hundreds of metres and a few kilometres of rock must have been removed from the plateau surface to expose the granite. This amount of surface lowering should have removed any older caves, particularly those shallow enough to fill with surface-derived sediment.

For the caves to survive there must have been a relative change in elevation between the mass of rock intruded by the granite and the mass of rock hosting the caves (Step 5 in Figure 4) before significant regional denudation took place.

For the sake of simplicity and because the history is not well understood, several steps have been left out in Figure 4 between Step 6 and Step 7. In the Late Carboniferous, the upper sections of the present valleys were incised and fluvial caves formed. These filled with glaciofluvial sediment and the whole landscape was buried under the Sydney Basin.

In the late Mesozoic, the Sydney Basin was stripped back and the valleys re-juvenated. New fluvial caves formed below the level of the old filled ones (Step 7 in Figure 4). Underhand stoping has now removed most of the old clay and only tiny remnants of clay remain in the caves.

WHERE ARE THE OTHER OLD CAVES?

When speaking here in 2004 (Osborne, 2005) I suggested a number of characteristics of localities where one might expect to find very old caves, interestingly Jenolan has only some of these. So how might we recognize “funny old caves” and ancient cave sediments?

“ABNORMAL CAVES” AND “ABNORMAL” SECTIONS OF “NORMAL” CAVES

My work on palaeokarst in caves and on non-fluvial cave morphology frequently takes me to caves that others regard as unusual. The Carboniferous clays from Jenolan are found in cupolas and other non-fluvial sections of the caves. Interestingly, these same sections of cave also intersect caymanite palaeokarst.

Fieldwork on non-fluvial morphology in Europe during 2005 took me to Belianska Cave in Slovakia and Račiška pečina in Slovenia. Co-incidentally, (or not) these are the same localities where Pavel Bosak and co-workers have found the oldest relict cave sediments in Europe (see Bella *et al.,* 2005 & Bosák *et al.,* 2005).

Non-fluvial caves, the *per ascensum* caves of Ford (1995), are characterised by being isolated from or poorly integrated with the modern hydrological system. Some have no natural entrances, while others have poor connection or secondary breakdown entrances. This gives them a head start in the survival stakes when compared with fluvial caves. Generally odd caves may survive longer than normal ones.

THE OLDEST CAVES ARE NOT ALWAYS AT THE TOP

When I first discovered the caymanite deposits in Jenolan Caves in the 1980s, I could not understand why they were intersected by cave passages at low levels in the limestone mass, not by (older) high-level passages. I did not realize then that while level in the landscape is a good indicator of the age of fluvial caves, it has little to do with the age

Fig. 5: Palaeokarst sandstone filling spar-lined tube intersected by more recent cave in the entrance area of Lucas Cave, Jenolan Caves, NSW, Australia. The strongly cemented sandstone is younger than the plastic clay shown in Figure 1.

of non-fluvial caves. In fluvial caves you look to the top for the old sections of cave, but in non-fluvial caves, you must look high and low.

RECOGNISING OLD SEDIMENTS

How can we recognise very old relict sediments in caves? The old clays at Jenolan were not found by looking for old material, we were originally looking for unusual minerals. The clays that looked different contained larger than normal amounts of illite and so we were able to date them. After the first old date, samples were chosen strategically, to get the maximum amount of chronological information from the minimum number of samples. This was only possible because there were existing palaeokarst and cave morphology stratigraphies to test (Osborne, 1999).

Unconsolidated Relict Sediments May Be Older than Lithified Palaeokarst Deposits

In my last presentation here, I raised the idea of the *lithification trap:* the idea that strongly lithified cave deposits and palaeokarsts may be *younger* than some unconsolidated or uncemented cave sediments (Osborne, 1995). This makes sense if we think about flowstone growing over mud and recognise that cementation, rather than compaction is the main agent of lithification in caves. Above ground geologists often find this idea conceptually challenging.

At Jenolan Caves, a crystal-lined cave passage is filled with strongly cemented sandstone (Figure 5). We have no problem with the sandstone being younger than the crystal, but stratigraphy suggests that this sandstone is younger than the unconsolidated clay shown in Figure 1.

WHAT CAN THEY TELL US?

GEOLOGICAL HISTORY OF THE CAVES

During the 1980s and 1990s, the aim of my research on palaeokarst was to show that speleogenesis and karstification in eastern Australia had a *geological* history (Osborne 1984, 1986, 1991b, 1993 a & b, 1995, 1999). That is, palaeokarst deposits intersected by *"modern" accessible* (open) caves indicate repeated periods of cave development at the same locality over periods of hundreds of millions of years. Cavities filled with strongly lithified palaeokarst deposits represented the older periods of cave development.

The discovery of 340 million year old clays in open accessible caves at Jenolan (Osborne *et al.,* 2006) demonstrated something significantly different. The open caves themselves, not just cavernous karsts, can have developmental histories extending over geologically significant periods of time (i.e. hundreds of million years).

Not much happens during the life of an old cave; they just snooze like an old pet cat. Sometimes dramatic events above, below or beside the cave may wake it from its slumber and leave their mark for us to find in the future.

GEOLOGICAL HISTORY FROM THE CAVES

Much has been said about the *potential* of the stratigraphic, geomorphic and climatic record in caves. Even the most generous previous estimates for the age of caves (not palaeokarst) suggested that such evidence would be limited largely to the younger end of the Cainozoic, and might perhaps in places like eastern Australia with old landscapes extend to the late Mesozoic. The survival of Palaeozoic open caves presents a new vista of using caves as a source of geological information. Both ancient caves and palaeokarst deposits could contain records of "missing sequences" for which there is no other record. While there has been significant progress in reading the ancient record of palaeokarst, lack of suitable dating techniques and a lack of expectation make geological history from the caves an open and uncultivated field.

Evidence for Global Events

Cave sediment research, particularly in the UK and Australia, began with a focus on a geological problem of global significance. Today we call it the Pleistocene extinction. The protagonists at the time saw it in terms of the "deluge" and the extinction or not of "antediluvian" faunas (see Osborne 1991a). Caves were an obvious focus for this research as Pleistocene vertebrate fossils occur in great abundance in the red earths of caves throughout the globe.

If the surface of some interfluves dates back to the Mesozoic, then ancient caves have the potential to contain evidence of the K-T boundary. What signal should we expect to find in the caves from the K-T event and how would we recognise it? Commentators have suggested that the K-T event involved dramatic changes in the pH of meteoric water, with strongly acidic rain falling from the sky. If this were sustained it should have left an imprint of extreme surface karstification and enhanced vadose and fluvial speleogenesis. Given how effectively caves have trapped Pleistocene loess, we might also expect to find iridium-rich silt in caves that were open at the K-T boundary. I don't know if anyone has looked, but perhaps they should.

Caymanites & unknown transgressions

Lazlo Korpas has been able to make great progress in understanding the evolution of the karst of Hungary by dating caymanites, because these contain fossils and they correlate with magnetostratigraphy (Korpas, 1998, Korpas *et al.,* 1999). Caymanites provide very useful evidence for marine transgressions (Korpas, 2002).

Caves intersect caymanites in at least six karst areas in eastern Australia. None of the caymanites have been directly dated. The 340 Ma old caves at Jenolan intersect caymanites, indicating a minimum age. The eastern Australian caymanites indicate one or more marine transgressions, probably in the Early Carboniferous for which there is no other geological evidence.

Volcaniclastic cave sediments/palaeokarst

Given the close physical relationship between stratovolcanoes and carbonate terrains in island arcs and active margins, volcaniclastic cave sediments and palaeokarst deposits should be common in both modern and ancient island arcs and active margins. There seems, however, to be scant reference to such deposits in the literature. Perhaps this is due to the concentration of karstological effort on Tethyan karsts.

Volcaniclastic cave sediments and palaeokarst deposits should be expected to occur around the Pacific rim, particularly in volcanically active island arcs e.g. Indonesia, Philippines, Malaysia, Japan, New Zealand and in southern Europe (Mts Etna and Vesuvius). They should also be expected where I work in the early Palaeozoic island arc environments of the Tasman Fold Belt of eastern Australia. While andesitic and silicic stratovolcanoes are likely to be the most common sources of tephra for volcaniclastic deposits in caves and karst depressions, basaltic tephra can also fill caves.

Five volcaniclastic palaeokarsts and volcaniclastic relict sediment deposits, including the 340 million year old clays, have now been recognised in eastern Australia (Table 1). It seems likely that more will be recognised, given that many of the cavernous Palaeozoic limestones are overlain by volcaniclastics.

Tab. 1: Volcaniclastic Palaeokarst and Relict Cave Sediments in eastern Australia

Type	*Likely Age*	*Karst Area*	*Chemistry*	*Reference*
Pk	? Tertiary	Crawney Pass	Basaltic	observed by author
Pk	Mid Devonian	Jenolan	Silicic	Osborne *et al.* 2006
R	Early Carboniferous	Jenolan	Silicic	Osborne *et al.* 2006
Pk	Mid Devonian	Wombeyan	Silicic	Osborne, 1993
Pk	?	Wellington	Silicic	Osborne in prep

Pk = palaeokarst
R= relict cave sediment

SPECULATION

We still know very little about extremely ancient caves. There are good prospects for making new geological discoveries in very old caves. All we have to do is identify funny old sediments in funny old caves, ascertain their meaning and find ways to date them. This sounds easy, but it is not.

The Jenolan team consisted of a karst geologist, a dating guru (essential so there is no argument about the technical aspects of the dates) and two mineralogists. It took six frustrating years and a sponsor with deep pockets to get the work completed and published.

A new world of geology of and from ancient caves awaits those with a stout heart, a thick skin, a good sponsor and eyes for caves and sediments that don't seem quite right; something like the qualifications for Antarctic explorers.

ACKNOWLEDGEMENTS

This paper was presented at the Time in Karst symposium at the Karst Research Institute, Postojna, Slovenia in March 2007. The University of Sydney Overseas Travel Grant Scheme and Top-Up funding for the Faculty of Education and Social Work supported attendance at the symposium. This paper arises from the dating of clays at Jenolan Caves (Osborne *et al.,* 2006). Many thanks are due to my co-workers, Horst Zwingmann, Ross Pogson and David Colchester.

Final corrections to the Jenolan Clay paper were made in Europe in the second half of 2005. I wish to thank colleagues in the Czech Republic, Hungary, Slovakia and Slovenia for their assistance and support. Work on Belianska Cave with Pavel Bella, Peter Gazik, Jozef Psotka and Stanislav Pavlarčik assisted in developing the ideas presented here. Other inspiration came when Karel Žác showed me the caves of the Bohemian Karst and Lazlo Korpas showed me his caymanite sequences and well-dated unconsolidated old sediment. Andrej Mihevc engaged in lively discussions about surface lowering, the "god that protects cave walls" and the origins and survival of Račiška pečina. Penney Osborne read the drafts.

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COBISS: 1.01

CLASTIC SEDIMENTS IN CAVES – IMPERFECT RECORDERS OF PROCESSES IN KARST

KLASTIČNI SEDIMENTI V JAMAH – NEPOPOLNI ZAPIS KRAŠKIH PROCESOV

Ira D. SASOWSKY[1]

Abstract UDC 552.517:551.7
Ira D. Sasowsky: Clastic sediments in caves – imperfect recorders of processes in karst
Clastic sediments have played an important role in deciphering geologic history and processes since the inception of the discipline. Early studies of caves applied stratigraphic principles to karst deposits. The majority of cave deposits are breakdown and alluvium. The alluvial materials have been successfully investigated to determine ages of caves, landscape evolution, paleoenvironmental conditions, and paleobiota. Rapid stage changes and the possibility of pipe-full flow make cave deposits different than surface deposits. This and other factors present difficulties with interpreting the cave record, but extended preservation is afforded by the "roofing" of deposits. Dating by magnetism or isotopes has been successful in many locations. Caves can be expected to persist for 10 Ma in a single erosive cycle; most cave sediments should be no older than this.

Key words: clastic sediments, paleoclimate, sedimentology, stratigraphy, dating.

Izvleček UDK 552.517:551.7
Ira D. Sasowsky Klastični sedimenti v jamah – nepopolni zapis kraških procesov
Že od nekdaj so klastični sedimenti pomembno orodje pri razbiranju geološke zgodovine. V zgodnjih študijah so uporabili načela stratigrafije tudi pri raziskovanju jamskih sedimentov . Glavnino jamskih sedimentov sestavljajo podori in aluvij. Raziskave aluvija so se uspešno izkazale pri dataciji jam, določanju razvoja površja, paleookolja in paleontologije. Zaradi možnega tlačnega toka in hitrih sprememb stanj, so jamski sedimenti drugačni od površinskih. To, poleg ostalih dejavnikov, predstavlja težave pri interpretaciji zapisov, ki jih hranijo jame. Po drugi strani pa je obstojnost jamskih sedimentov daljša zaradi zavetja, ki jim ga nudi jama. Po vsem svetu poznamo številne uspešne datacije jamskih sedimentov z magnetizmom ali izotopi. Jame znotraj erozijskega cikla vzdržijo do10 milijonov let, zato naj jamski sedimenti ne bi bili znatno starejši.

K**ljučne besede:** klastični sedimenti, paleoklima, sedimentologija, stratigrafija, datiranje.

INTRODUCTION

Geology is undeniably a science of history, and since the earliest practice of the discipline, that history has been revealed in clastic sedimentary deposits. William Smith, for example, created maps of the sedimentary rocks in England in the late 1700's, and established a relative chronology of their deposition using stratigraphic position and fossils. It has been natural, therefore, that karst scientists examine clastic deposits in caves, in order to explore geologic time. In doing so, they are in large part applying the same principles and techniques developed by classical stratigraphers. An early example of this was a study by Kukla and Ložek (1958) examining the processes of cave sediment deposition and preservation. In the present day, work such as that by Granger *et al.* (2001) and Polyak et. al. (1998) builds upon those classical techniques and applies laboratory methods to develop absolute chronolo-

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Received/Prejeto: 24.01.2007

gies. These chronologies in turn have allowed insight to such processes as river incision, water-table lowering, and landscape/climate linkages.

This paper is a brief evaluation of clastic sediments as they apply to deciphering historical processes and events in karst terrane. Advantages and problems of working with these unique deposits are presented. For purposes of this paper, the "age" of a given cave sediment refers to the time of deposition of the material in the cave.

MATERIALS AND PROCESSES

The processes that result in clastic sedimentation in caves are quite varied. Reviews and details including classification of deposits are presented in several texts (White, 1988; Ford and Williams, 1989; Sasowsky and Mylroie, 2004). A perspective is given here.

A useful broad-level classification is genetic, and based upon whether the clastic material originated within the cave (autogenic) or was carried in from the surface (allogenic). The former class is mainly bedrock breakdown (incasion), but encompasses fine grained sediments sourced from insoluble residue during phreatic enlargement, collapse of secondary mineralization (speleothems), and so forth. Allogenic sediments include alluvium, windblown material, animal feces, fossil matter, till, etc.

In practice, the most commonly occurring materials by far are bedrock breakdown and alluvium. Consequently, autogenic cave sediments are mainly limestone. Allogenic sediments are usually resistant siliciclastics, because carbonates do not typically persist in the fluvial environment.

There is no satisfying overall term for the clastic deposits found in caves. The word "soil" has been applied to the fine grained deposits, but this is a misnomer by most definitions, and is not recommended. Cave fill and cave earth have also been used. Regolith seems applicable in spirit, but, because this material does not strictly "….form(s) the surface of the land ...." (Jackson, 1997) some may object to such usage.

BREAKDOWN

The collapse of cave bedrock walls and ceilings results in material that is angular, and ranges in size from sand to boulders. It is possible many times to visually fit larger blocks to their point of origin on the adjacent cave walls and ceilings. The process of breakdown is not a common occurrence on human timescales. Only a few cases of present-day natural failure have been documented. For example, in Mammoth Cave, Kentucky only one large collapse was noted in 189 years of mining and tourism (May *et al.*, 2005). However, on geologic timescales, the process is pervasive and evident in most caves. Failures occur along existing planes of weakness (joints, faults, bedding planes). Causes of collapse can include removal of underlying support (particularly loss of buoyancy caused by the transition from phreatic to vadose conditions), removal of overlying arch support, cryoclastism (wedging by ice), and secondary mineral wedging (White and White, 2003). Triggering by earthquakes has also been observed, for example in Sistem Zeleške Jame-Karlovica (personal communication, F. Drole). Davies (1951) published an early analysis of expected collapse parameters in the cave environment. This was expanded on by White (1988, p. 232) to evaluate stability of ceilings relative to limestone bed thickness. Greater spans can be maintained by thicker beds. Jameson (1991) provides a comprehensive overview and classification of breakdown.

Breakdown is frequently most prolific at 1) the intersections of cave passages, presumably due to the greater span lengths present at such points, and 2) where the cave is close to the surface, due to lack of thinning of the span and resulting decreased competency. In evaluations of causes for passage terminations (White, 1960) it was noted that many cave passages ended in breakdown blockage (referred to by explorers as "terminal breakdown").

Although pervasive, breakdown has not found significant utility for deciphering earth history in karst terranes.

ALLUVIUM

Alluvium enters caves by sinking stream, and occasionally by colluvial mechanisms. The transport processes are for the most part similar to those in surface channels. The full range of sediment sizes are seen, structures such as cross-bedding and pebble imbrications develop, and cut-and-fill stratigraphy is possible. However, there are two important differences exhibited for stream flow in caves when compared to most surface channels. First, channel width is severely constrained by bedrock walls. This promotes rapid stage increase during flooding, akin to that of slot canyons in surface streams (Fig. 1). Second,

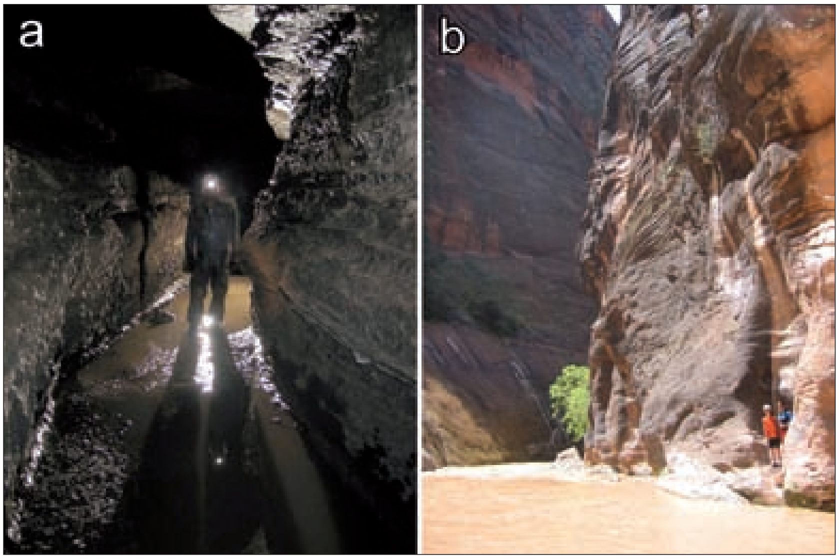

Fig. 1: Subterranean stream channels are typically narrow, and have no floodplain (a). This leads to rapid stage changes. Similar conditions in the surface environment are only seen in slot canyons such as the Virgin River, Utah, USA (b).

because the channel is roofed over, it is possible to have confined (pipe-full) rather than open channel flow. Taken in conjunction, the results of these two conditions are the likelihood of high flow velocities, and the possibility of upwards phreatic flow. A striking example of rapid stage change is seen in Hölloch, Switzerland, where rises of 250 m in a single flood have been recorded (Wildberger and Preiswerk, 1997; Jeannin, 2001). Cases of phreatic lifts are seen in many cave systems. In Castleguard Cave (Rocky Mountains, Canada) a seasonally active lift of 9 m is observed (Schroeder and Ford, 1983). In that situation well-rounded cobbles are accumulated at the base, where they reside until communition reduces them sufficiently to allow transport up the lift tube.

The composition of the alluvium reflects the source of the material, as well as some other factors. It is interesting to note that a high proportion of clay sized material found in cave alluvium is actually fine-grained silica, not a clay mineral (White, 1988). The residuum found on the surface of many karst terranes frequently contains high amounts of clay and chert. The clay results from insoluble residues of the weathered limestone. The chert behaves in a very persistent way, being found throughout cave passages.

INFORMATION REVEALED

In the investigation of clastic sedimentary deposits, either cave related or not, answers are sought to such questions as: How old? What was the paleoenvironment? What was the flow direction? What organisms were present? These in turn allow an understanding of geologic history, environments of deposition, past climates, and potential for sedimentary deposits to act as mineral and fuel reservoirs.

In the case of cave studies, it is primarily the first question which has been addressed. Caves can only be numerically dated by the deposits that they hold, and this age is usually reported as a minimum value. Alluvial materials are considered superior to speleothems in this undertaking, because they are emplaced much earlier in the existence of the cave. Once a date has been obtained, subsequent inferences such as rates of river incision, denudation, and so forth, can then be made based upon the relation of the cave to the landscape. Dating has been accomplished by radiocarbon, magnetism, and cosmogenic isotopes.

Paleoenvironmental information is revealed through studies of sedimentary structures and sequences, as well as via analyses of clay mineralogy and environmental magnetism. Paleohydrology can be deduced using traditional stratigraphic indicators such as cross-bedding, pebble imbrication, etc. Fossil deposits of organisms are actually rather rare within caves – most cave depsits are barren of these materials. Significant deposits are known, though, and many excavations made in caves (particularly in the entrance facies) serve as irreplaceable records of terrestrial fauna.

LIMITS ON TIMESCALE

Caves are erosional landforms, which have a limited period of existence. Excluding those caves which have been subjected to burial, this places a practical limit on their duration as potential recorders of nearby processes. In any case, the cave sediments can be no older than the cave they are emplaced in (Sasowsky, 1998). Therefore, the ultimate limit on preservation of sediments within a cave is the persistence (lifetime) of the cave in the environment.

In most limestone terranes epigenetic processes occur, with dissolution taking place both at the surface (forming pavements, dolines, etc.) and in the subsurface (forming caves). As base level lowers, denudation of the upland surfaces is also occurring and uppermost caves are eventually breached and destroyed. In certain settings examples of various states of decay can be seen in the landscape, and the sedimentary fills of breached (unroofed) caves may even be observed (e.g. Šušteršič, 2004). In settings such as the Appalachian Valley and Ridge, hundreds of meters of carbonate have been denuded from anticlinal valleys (White, 1988), and one may imagine extensive systems of caves which have been obliterated with no remaining trace.

Bounds on the expected lifetime of an epigene cave may be evaluated by considering the two main controlling factors: initial depth of formation and rate of land surface lowering (denudation, Fig. 2). Although caves may form at any depth, a practical limit of 300 m is reasonable, and the majority of caves are much shallower (Milanovic, 1981). Note that this "depth" is not correlative to the frequently reported mapped depth of caves, which refers to the maximum vertical extent of survey. In the context of the present evaluation, depth is the position below surface (thickness of overlying rock) at a given point in the cave. Denudation rates can be quite variable, and tend to correlate with rainfall (White, 1988, p. 218). Envelopes of expected cave persistence can be constructed (Fig. 2) using these 2 parameters. Based upon this calculation, epigene caves would usually exist in the erosive environment for up to 10 Ma.

In practice, dating has not yet resulted in identification of caves this old within the present erosional cycle. Paleomagnetic dating has been used back to 4.4 Ma (Cave of the Winds, Colorado, USA; Luiszer, 1994). Cosmogenic isotope dating has documented cave sediments as old as 5.7 (±1.1) Ma (Bone Cave, Tennessee, USA; Anthony and Granger, 2004). The absence of older values may be a consequence of limitations of dating methods, or reflect the relative dearth of older caves in the environment, or both. The challenges of paleomagnetic dating include absence of fine-grained sediments, lack of uninterrupted sedimentation, and uncertainties of correlation with the global magnetic polarity scale. Cosmogenic dating is constrained by the absence of quartzose sediments, uncertainties in parent isotope values, and the cost/effort of analyses.

If consideration is extended beyond the present erosional cycle, filled and buried caves (paleokarst) are found in the rock record. Such materials have been recognized in many places, and the fills described in some detail (e.g. Loucks, 1999). Interest has been strong in the context of exploration for minerals or petroleum. These deposits also represent a potential trove of information on far past hydrologic and environmental conditions because of their capacity to preserve.

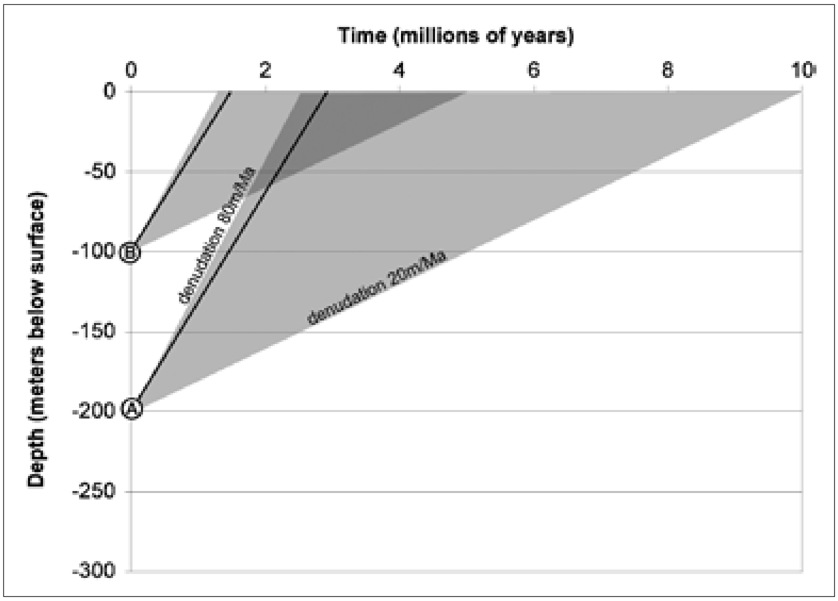

Fig. 2: Theoretical persistence of caves in an erosional environment. The length of time that a given cave will exist depends upon the initial depth of formation (position on y-axis) and the denudation rate (slope of line). Gray regions envelope a range of reasonable denudation pathways for two examples. In case A, a cave formed at 200 m depth, the expected lifetime is 2.5 to 10 Ma. For a cave formed at 100 m depth (case B), the lifetime is reduced to 1.25 to 5 Ma. Solid sloping lines are the average denudation rate, 69 m/Ma, for 33 major drainage basins (calculated from data in Summerfield and Hulton, 1994).

RESOLUTION, CONTINUITY, AND VERACITY

Stratigraphers have traditionally examined marine or paralic sediments because of their resolution, continuity, and veracity. Compared to terrestrial deposits, marine/paralic strata are much more laterally and vertically extensive, they are of economic interest, and they potentially function as continuous recorders for long periods of time. Terrestrial deposits are of interest though, particularly because they contain information about the on-continent setting. Within the terrestrial environment lacustrine deposits and fluvial terraces have seen the greatest attention as recorders of Cenozoic paleo-conditions. Lakes probably represent the highest quality records in the terrestrial environment – their environment many times is one of high preservation potential. Lacustrine deposits can be sampled by coring; duplication of cores can serve as a quality control; accumulation rates can be rapid; sediment properties are well tied to local environmental conditions; and spatial variability is usually well understood. Terraces tend to preserve a partial record of the fluvial environment, depending upon regional uplift or down-cutting of the stream.

In comparison, most caves contain spatially irregular deposits that can be affected by factors such as plugging of swallets, extreme flow events, and back-flooding. Hydrologic complexity is common (Bosák *et al.*, 2003), even more so than surface fluvial environments. Analysis of the paleohydrology of the depositional setting through cave passage morphometry is usually necessary, and may be quite time consuming if detailed maps are not available. Stratigraphic sections may be discontinuous, and require compilation. Caves are difficult sampling locations, due to logistics, remoteness, lack of light, and constraints on sampling equipment transport.

Nevertheless, the cave environment is one that provides some advantages in recording the history of a region. The greatest advantage is that of potential preservation. Because caves are "roofed over" deposits are likely to be protected (at least on intermediate time scales), from

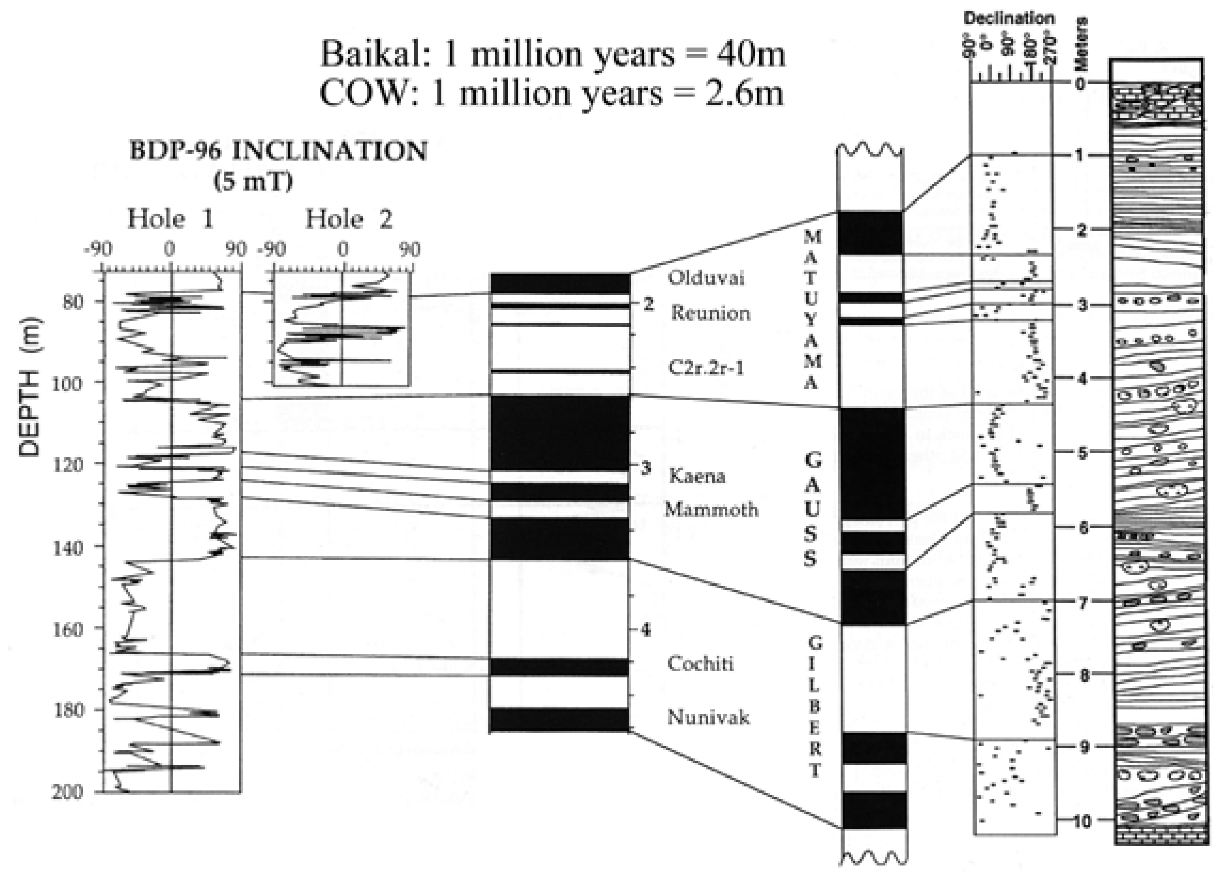

Fig. 3: Comparison of sedimentary records from Lake Baikal, Russia (3 columns on left), and Cave of the Winds, USA (3 columns on right). Baikal data used with permission from King and Peck, 2001. Cave of the Winds data used with permission from Luiszer, 1994.

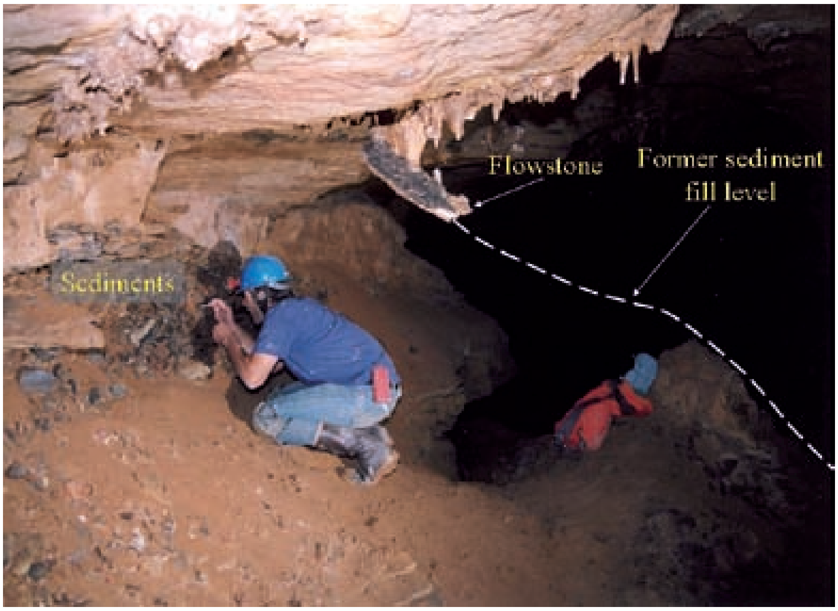

Fig. 4: Episodic infilling and removal of sediments is commonly observed in caves. In this section of Windy Mouth Cave (West Virginia, USA) a diamict was almost completely removed after being covered with flowstone. The conduit is presently dry.

surficial erosion. This is particularly germane for the fluvial deposits. Weathering and erosion of surface fluvial terraces is commonplace. In the cave, such materials may sit undisturbed for years. For example, in Xanadu Cave, Tennessee, USA, a pristine, non-indurated fluvial deposit that is greater than 780 ka was sampled (Sasowsky, *et al.*, 1995). Although rare, in exceptional settings the quality of the cave record may approach that of lakes (Fig. 3). Conditions amenable to this are stable recharge configuration, diffuse recharge, minimal variation of discharge, and deep circulation. In Figure 3 two exceptional records are compared. The Lake Baikal record was constructed from cores taken on watercraft. In that setting, about 40 m of sediment accumulate in 1 Ma. In contrast, at Cave of the Winds the accumulation rate is slower by more than an order or magnitude.

In many settings caves appear to undergo episodic filling and excavation (Fig. 4). In certain cases this may be locally controlled by catastrophic storms (e.g. Doehring and Vierbuchen 1971). However, the presence of broadly similar deposits/incisions within many caves in a region supports the idea that cave clastic materials reflect regional paleoclimatic conditions. These deposits hold much information that will be revealed with continued advances in conceptual frameworks and improved laboratory methods.

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COBISS: 1.01

ANALYSIS OF LONG-TERM (1878-2004) MEAN ANNUAL DISCHARGES OF THE KARST SPRING FONTAINE DE VAUCLUSE (FRANCE)

ANALIZA DOLGOČASOVNEGA (1878-2004) POVPREČNEGA LETNEGA PRETOKA KRAŠKEGA IZVIRA FONTAINE DE VAUCLUSE (FRANCIJA)

Ognjen BONACCI[1]

Abstract UDC 556.36(44)

Ognjen Bonacci: Analysis of long-term (1878-2004) mean annual discharges of the karst spring Fontaine de Vaucluse (France)

Statistical analyses have been carried out on a long-term (1878-2004) series of mean annual discharges of the famous karst spring Fontaine de Vaucluse (France) and the mean annual rainfall in its catchment. The Fontaine de Vaucluse is a typical ascending karst spring situated in the south-eastern region of France. The spring has an average discharge of 23.3 m^3/s. The average annual rainfall is 1096 mm. Its catchment area covers 1130 km^2. Using the rescaled adjusted partial sums (RAPS) method the existence of next five statistically significant different sub-series was established: 1) 1878-1910: 2) 1911-1941; 3) 1942-1959: 4) 1960-1964; 5) 1965-2004. The different spring discharge characteristics during this long period (1878-2004) can be caused by natural climatic variations, by anthropogenic influences, and possibly by climate changes. At this moment it should be stressed that objective and scientifically based reasons for different hydrological behaviour in five time sub-periods could not be found.

Keywords: karst hydrology, mean annual discharges, annual catchment rainfall, karst spring, Fontaine de Vaucluse, France.

Izvleček UDK 556.36(44)

Ognjen Bonacci: Analiza dolgočasovnega (1878-2004) povprečnega letnega pretoka kraškega izvira Fontaine de Vaucluse (Francija)

V prispevku predstavim statistično analizo časovne vrste povprečnega letnega pretoka in letnih padavin v zaledju slavnega izvira Fontaine de Vaucluse v Franciji. Fontaine de Vaucluse je tipični kraški izvir pri katerem voda priteka iz velike globine. Nahaja se v jugovzhodni Franciji. Povprečni pretok izvira je 23,4 m^3/s. Povprečna količina letnih padavin v zaledju, ki meri 1130 km^2, je 1096 mm. Z uporabo metode umerjenih delnih vsot (RAPS) smo določili pet statistično pomembnih različnih podobdobij: 1) 1878-1910: 2) 1911-1941; 3) 1942-1959: 4) 1960-1964; 5) 1965-2004. Vzrokov za različne pretoke preko celotnega obdobja (1878-2004) je lahko več; npr. klimatske spremembe in antropogeni vplivi. V tem trenutku moramo poudariti, da objektivne znanstvene razlage za različne hidrološke značilnosti v petih podobdobjih še ne poznamo.

Ključne besede: hidrologija krasa, povprečni letni pretok, količina letnih padavin, kraških izvir, Fontaine de Vaucluse, Francija.

INTRODUCTION

The Fontaine de Vaucluse represents one of the most famous and most important karst springs on the Earth. It is located in the south-eastern karst region of France (Figure 1), about 30 km eastward of the town of Avignon. It represents the only flow exit from the 1500 m thick karst aquifer of Lower Cretaceous limestone (Blavoux *et al.,* 1992b). The karst system of the Fontaine de Vaucluse is characterised by an approximately 800 m unsaturated zone. Emblanch *et al.,* (1998) and Emblanch *et al.,* (2003) stressed important role of this zone for the transformation of rainfall into runoff. The Fontaine de Vaucluse karst spring catchment area is estimated to be 1130

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Received/Prejeto: 27.11.2006

km^2 (Cognard-Plancq *et al.*, 2006a; 2006b). The average catchment altitude is 870 m a. s. l. The average annual air temperature of the catchment is 9,6 °C.

Fig. 1: Location map of karst spring Fontaine de Vaucluse.

The Fontaine de Vaucluse is typical ascending karst spring (Michelot & Mudry 1985; Blavoux *et al.*, 1991/1992; 1992a). Its limestone channel ranges in diameter from 8 to 30 m (Mudry & Puig, 1991). The lowest depth reached by diver was -308 m below the gauging station datum of 84.45 m a. s. l. This depth is still not at the bottom of the ascending karst channel.

The maximum water level measured at the gauging station was 24.10 m above the datum, the minimum was a few centimetres below the datum. The rate of the maximum discharge of the spring has never been precisely measured, but it is estimated that it cannot exceed 100 m^3/s (Blavoux *et al.*, 1991/1992; 1992a). Cognard-Plancq *et al.* (2006b) state that maximum spring discharge varies between 100 and 120 m^3/s. This surmise identifies a karst spring with limited discharge capacity (Bonacci 2001). The historical minimum discharge is 3.7 m^3/s (Blavoux *et al.*, 1991/1992).

Every karst aquifer has complex hydrodynamic behaviour. The Fontaine de Vaucluse karst system responses to rainfall quite rapid in comparison with the large recharge area. The peak of hydrograph occurred 24 to 72 hours after the rainfall events. The spring water level and discharge recessions are slow, which can be explained by the existence of a large storage capacity of the aquifer (Cognard-Plancq 2006b).

The primary objective of the investigation was to define sub-periods with different hydrological behaviour of the Fontaine de Vaucluse karst spring during 127 years period (1878-2004), analysing time series of mean annual spring discharges. It should be the first step in explanation of this extremely important and interesting phenomenon.

ANALYSIS OF CATCHMENT ANNUAL RAINFALL TIME SERIES

The climate in the catchment is Mediterranean. Rainfall distribution over the year as well as over the large spring catchment is irregular. Intensive and significant rainfall events occurred during autumn and spring, while summer and winter are generally dry. Interannual fluctuations of rainfall on the catchment are very high.

In order to define an historical homogeneous catchment rainfall database Cognard-Plancq *et al.*, (2006b) used six rainfall gauging stations. The mean elevation of these stations is 445 m a. s. l., while the mean elevation of the spring catchment is 870 m a. s. l. Transformation of the measured monthly rainfall to the altitude of 870 m a. s. l. was made. The average annual catchment rainfall in the 1878-2004 period is 1096 mm, while the minimum and maximum observed values were 641 mm (1953) and 1740 mm (1977) respectively.

Data series with linear trend line of the annual rainfall on the Fontaine de Vaucluse catchment for the period 1878-2004 are presented in Figure 2. The increasing trend of the catchment rainfall of 1.045 mm per year is not statistically significant but should not be neglected in further analyses.

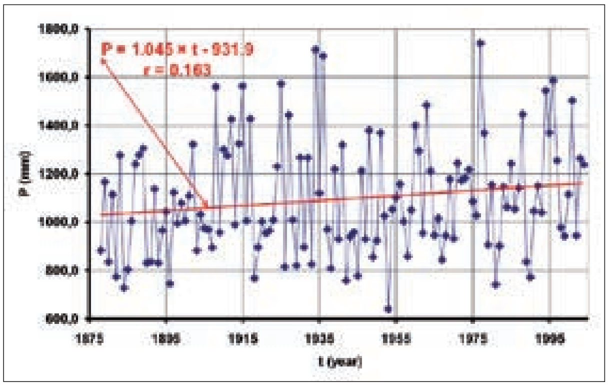

Fig. 2: Time data series of annual rainfall P at the Fontaine de Vaucluse catchment with trend line for the period 1878-2004.

ANALISIS OF MEAN ANNUAL DISCHARGES TIME SERIES

Data series with linear trend line of the mean annual spring discharges Q for the period 1878-2004 are presented in Figure 3. The decreasing trend of the mean annual discharges of 0.0468 m^3/s per year is not statistically significant. The average annual catchment discharge in the 1878-2004 period was 23.3 m^3/s, while the minimum and maximum observed values were 7.61 m^3/s (1990) and 53.4 m^3/s (1915) respectively.

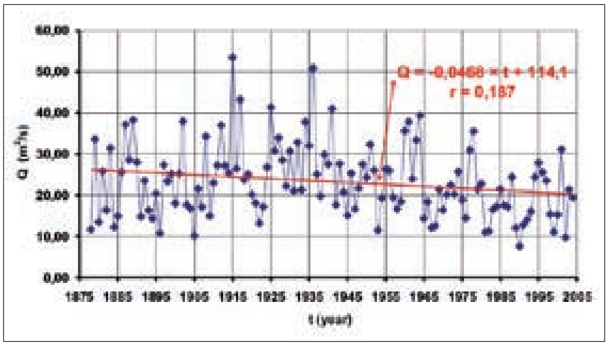

Fig. 3: Time data series of mean annual discharges Q at the Fontaine de Vaucluse karst spring with trend line for the period 1878-2004.

It should be stressed that annual catchment rainfall during the same period has an increasing trend. In Figure 4 linear regression between the mean annual the Fontaine de Vaucluse discharges Q and the Fontaine de Vaucluse catchment annual rainfall P is shown. The linear correlation coefficient is only 0.713, which is relatively low. A special problem is that the regression line cut abscissa line at 222 mm of annual rainfall P, which is relatively low value. Explanation of so unusual rainfall-runoff relationship can be found in fact that accuracy of discharges and rainfalls are not very high, and maybe the value of catchment area of 1130 km^2 is not precisely defined.

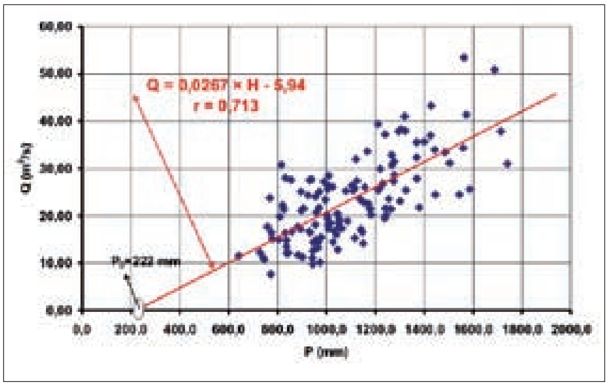

Fig. 4: Linear regression between the mean annual the Fontaine de Vaucluse discharges Q and annual the Fontaine de Vaucluse catchment rainfall P.

It should be stressed that determination of exact catchment area in karst is one of the greatest and very often unsolved problems. This may be the case with the catchment of the Fontaine de Vaucluse spring. The weak relationship between runoff and rainfall means that some others factors (probably: air temperature, groundwater level, interannual rainfall distribution, changes of catchment area during the time, preceding soil wetness, anthropological influences, climate change etc) have influence on it.

A time series analysis can detect and quantify trends and fluctuations in records. In this paper the Rescaled Adjusted Partial Sums (RAPS) method (Garbrecht & Fernandez 1994) was used for this purpose. A visualisation approach based on the RAPS overcomes small systematic changes in records and variability of the data values themselves. The RAPS visualisation highlights trends, shifts, data clustering, irregular fluctuations, and periodicities in the record (Garbrecht & Fernandez 1994). It should be stressed that the RAPS method is not without shortcomings. The values of RAPS are defined by equation:

$$RAPS_k = \sum_{t=1}^{k} \frac{Y_t - \overline{Y}}{S_Y}$$

where $\overline{Y}$ is sample mean; is standard deviation; n is number of values in the time series; (k=1, 2…,n) is counter limit of the current summation. The plot of the RAPS versus time is the visualisation of the trends and fluctuations of Y_t.

Time data series of Rescaled Adjusted Partial Sums (RAPS) for mean annual spring discharges in the period 1878-2004 are given in Figure 5. Therefore, the total data

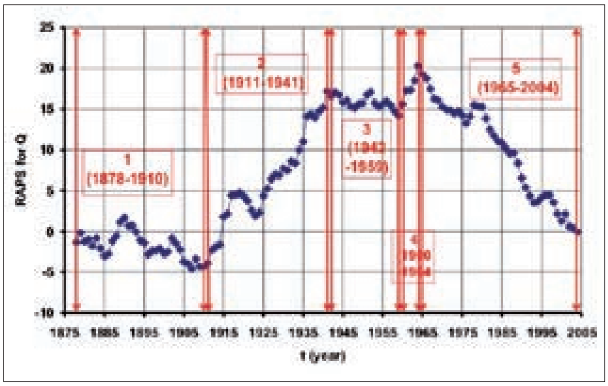

Fig. 5: Time data series of the Rescaled Adjusted Partial Sums (RAPS) for mean annual discharges Q for the period 1878-2004 with designated next five sub-periods: 1) 1878-1910; 2) 1911-1941; 3) 1942-1959; 4) 1960-1964; 5) 1965-2004.

series was divided into next five subsets: 1) 1878-1910; 2) 1911-1941; 3) 1942-1959; 4) 1960-1964; 5) 1965-2004. Cognard-Plancq *et al.,* (2006a; 2006b) defined the same five stationary sub-periods using different methodology.

Five time data sub-series of the Fontaine de Vaucluse karst spring mean annual discharges Q with trend lines for five defined sub-periods are shown in Figure 6. In order to investigate statistically significant differences between the averages of five time sub-series for Q and P the t-test was used. The neighbouring averages of discharges for all five sub-series are statistically significant at the 5 % and even more 1 %. At the same time the neighbouring sub-series averages of the catchment rainfall are not statistically significant.

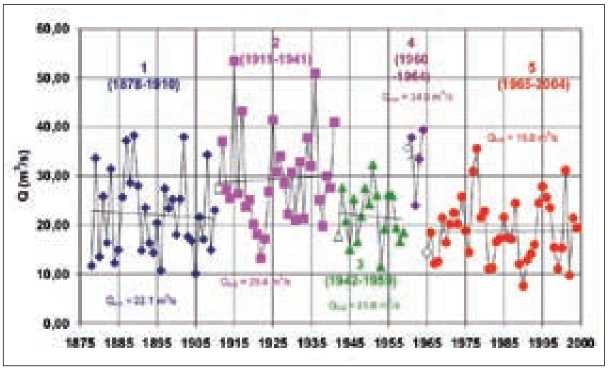

Fig. 6: Five time data sub-series of the Fontaine de Vaucluse karst spring mean annual discharges Q with trend line for five defined sub-periods.

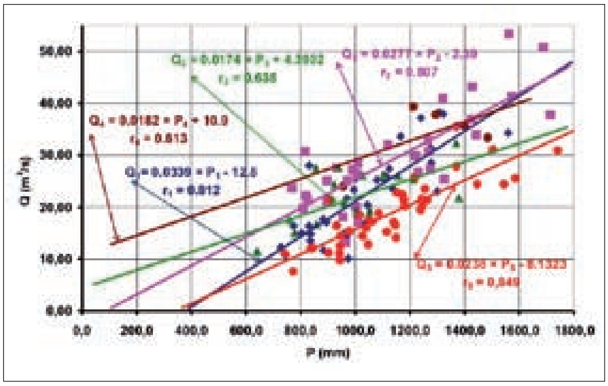

Fig. 7: Linear regressions between mean annual discharges Q and annual catchment rainfall P defined for five different sub-periods.

Figure 7 shows five linear regressions between mean annual discharges Q and annual catchment rainfall P defined for five different sub-periods. It can be seen that linear correlation coefficients for all sub-series, except for third (1942-1959) and fourth (1960-1964) ones are higher than the linear correlation coefficient for whole time series.

CONCLUSION

The rescaled adjusted partial sums (RAPS) method established existence of next five statistical, and hydrological significant different time sub-series: 1) 1878-1910: 2) 1911-1941; 3) 1942-1959: 4) 1960-1964; 5) 1965-2004. Variations in the Fontaine de Vaucluse karst spring hydrological regime during relatively short period of 127 years are very strong and cannot be neglected. Anthropogenic impacts are probably the main cause of such behaviour of the mean annual spring discharges time series analysed, but the natural pattern of drought and wet years is also possible. Land-use changes and overexploitation of surface water and groundwater at the spring catchment on hydrological regime of the Fontaine de Vaucluse spring certainly exists. Their exact quantification during analysed period is extremely questionable due to missing of many parameters. Strict division of natural and anthropogenic influences on the hydrological regime is hardly possible.

The significant changes of spring discharge characteristics during 127 years long period (1878-2004) can be caused by natural climatic variations, by anthropogenic influences, and possibly by climate changes. It is extremely hard, but at the same time extremely practically and theoretically important, to find correct and scientifically based explanation of this phenomenon.

Cognard-Plancq *et al.,* (2006a) consider that rainfall-runoff data have shown the large impact of climatologic variations on the hydrogeological system. They conclude that the underground storage zone is an important influence on karst spring outflow, which depends on rainfall amount over 2 or 3 previous years. Investigations made in this paper do not confirm this statement.

Correct answers on many questions dealing with changes in hydrological-hydrogeological regime of the Fontaine de Vaucluse karst spring cannot be done using only annual data. Some processes can be explained measuring and analysing climatologic, hydrologic, hydrogeological and geochemical interactions in shorter as well as larger time increments. The problem is that most of parameters required for these analyses were not monitored in the past.

More accurate and precise delineation and definition of the Fontaine de Vaucluse spring catchment should be done. It is possible that its catchment area changes as a function of groundwater level. This means that groundwater level measurements in deep piezometers should be organized across the catchment. The second task which should be considered in further analyses is detailed analysis of influence of rainfall distribution during the year on the spring runoff. This can have very strong influence on the relationship between rainfall and runoff, especially in karst areas.

It can be stated that main dilemmas about variations of mean annual discharges of the Fontaine de Vaucluse karst spring during 127 years long period have not been solved. They should be explained using number of different procedures and climatic as well as other indicators, and performing further detailed measurements and analyses. The paper presents the need for interdisciplinary analyses incorporating several approaches and techniques. For the sustainable development and the protection of such valuable water resource it is very important to establish prerequisites for the definition of a causes and consequences of its hydrological changes.

ACKNOWLEDGEMENT

The author thanks to Anne-Laure Cognard-Plancq and Christophe Emblanch from Laboratoire d'Hydrogéologie, Faculté des Sciences, Université d'Avignon et Pays de Vaucluse 84000 Avignon, 33 Rue Louis Pasteur, France, which kindly provide me with data analysed in this paper.

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TIMING OF PASSAGE DEVELOPMENT AND SEDIMENTATION AT CAVE OF THE WINDS, MANITOU SPRINGS, COLORADO, USA

ČASOVNO USKLAJEVANJE RAZVOJA JAMSKIH PROSTOROV IN SEDIMENTACIJA V JAMI CAVE OF THE WINDS, MANITOU SPRINGS, COLORADO, ZDA

Fred G. LUISZER[1]

Abstract **UDC 551.3:551.44:550.38 550.38:551.44**

Fred G. Luiszer: Timing of Passage Development and Sedimentation at Cave of the Winds, Manitou Springs, Colorado, USA.

In this study the age of the onset of passage development and the timing of sedimentation in the cave passages at the Cave of the Winds, Manitou Springs, Colorado are determined. The amino acid rations of land snails located in nearby radiometrically dated alluvial terraces and an alluvial terrace geomorphically associated with Cave of the Winds were used to construct an aminostratigraphic record. This indicated that the terrace was ~ 2 Ma. The age of the terrace and its geomorphic relation to the Cave of the Winds was use to calibrate the magnetostratigraphy of a 10 meter thick cave sediment sequence. The results indicated that cave dissolution started ~4.5 Ma and cave clastic sedimentation stopped ~1.5 Ma.

Key words: Cave of the Winds, Manitou Springs, magnetostratigraphy, aminostratigraphy, land snails.

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Fred G. Luiszer: Časovno usklajevanje razvoja jamskih prostorov in sedimentacija v jami Cave of the Winds, Manitou Springs, Colorado, ZDA

Članek se osredotoča na začetek razvoja jamskih prostorov in časovno sosledje sedimentacije v jami Cave of the winds, Manitou Springs, Kolorado. V bližini jame se nahajajo aluvialne terase, ki so bile datirane z radiometrično metodo. Z geomorfološko metodo so bile povezane z jamo Cave of the Winds. V teh aluvialnih terasah so bili najdeni fosilni ostanki kopenskih polžev, na katerih so bile opravljene datacije z aminokislinami, ki so pokazale starost ~ 2 Ma let. Starost aluvialnih teras in njihova geomorfološka povezava z jamo Cave of the Winds, sta služila kot izhodišče za natančnejšo časovno umestitev 10 metrov debele sekvence jamskih sedimentov, ki so bili magnetostratigrafsko opredeljeni. Raziskava je pokazala, da se je raztapljanje v jami pričelo pred ~4.5 Ma leti, medtem ko se je odlaganje klastičnih sedimentov prenehalo pred ~1.5 Ma let.

Ključne besede: Cave of the Winds, Manitou Springs, ZDA, magnetostratigrafija, aminostratigrafija, kopenski polži.

INTRODUCTION

Cave of the Winds, which is 1.5 km north of Manitou Springs (Figure 1), is a solutional cave developed in the Ordovician Manitou Formation and Mississippian Williams Canyon Formation. Commercialized soon after its discovery in the1880s it has been visited by millions of visitors in the last 125 years. As part of an extensive study (Luiszer, 1997) of the speleogenesis of the cave the timing of passage development and sedimentation needed to be determined. The task of dating the age of caves has always been an enigma because dating something that has been removed is not possible. Sediments deposited in the cave passages, however, can be dated, which then can be used to estimate the timing of the onset of cave dissolution and when the local streams abandoned the cave.

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Received/Prejeto: 13.12.2006

A specially constructed coring device was utilized to core several locations in the cave. The natural remnant magnetization (NRM) of samples taken from the cores were use to construct a magnetostratigraphic record. This record by itself could not be used to date the age of the sediments because sedimentation in the cave stopped sometime in the past and part of the record was missing.

An alluvial terrace, which overlies the Cave of the Winds, is geomorphically related to the cave. The age of the alluvial terrace, which had not been previously dated, can be used to determine the age of the youngest stream deposited sediments in the cave. An abundant number and variety of land snails were found when this alluvium was closely searched. Biostratigraphy could not be used to determine the age of the terrace because all of the snail species found were extant, however, the amino acid rations of the snails collected from this terrace and nearby radiometrically dated terraces were used to construct an aminostratigraphy that was used to date the alluvium. Once the age of the terrace was determined the age of the youngest magnetic chron of the magnetostratigraphic record could be assigned thus enabling the dating of cave dissolution and sedimentation.

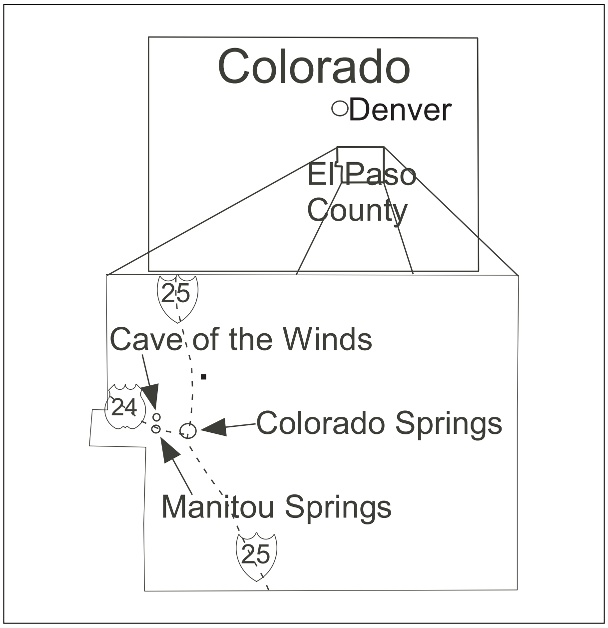


Fig. 1: Location of study area.

FIELD AND LABORATORY PROCEDURES

Amino Acid Dating

Snails were collected from outcrops of the Nussbaum Alluvium, and from younger radiometrically dated alluvia (Fig. 2) for the purpose of dating the Nussbaum Alluvium by means of amino-acid racemizatio.

Approximately 50 kg of sandy silt was collected at each site. To minimize sample contamination, washed plastic buckets and fresh plastic bags were used. The samples were loaded into containers with a clean metal shovel and with minimal hand contact. In the lab, the samples were disaggregated by putting them in buckets filled with tap water and letting them soak overnight.

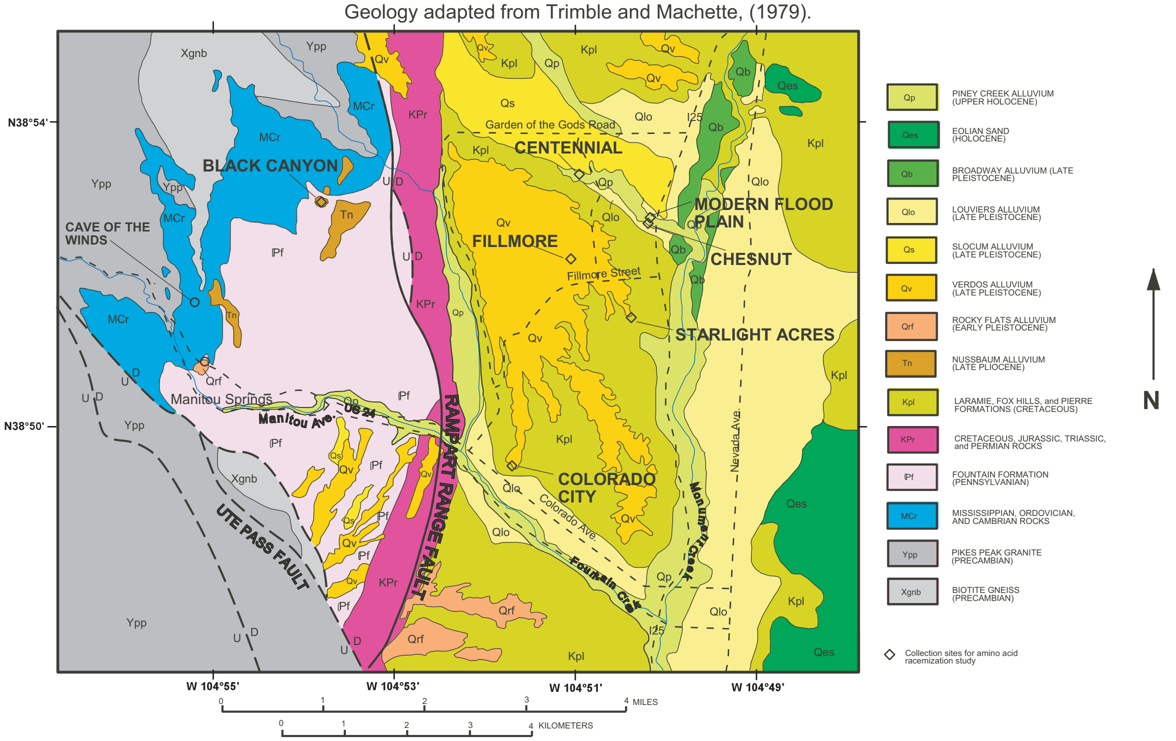
The samples were then washed with tap water through 0.5-mm mesh scree. Following air drying, the mollusks were hand picked from the remaining matrix by means of a small paint brush dipped in tap water. The mollusks were then identified. Only shells that were free of sediment and discoloration were selected for further processing. These shells were washed at least five times in distilled water while being sonically agitated. The amino-acid ratios were determined on a high-performance liquid chromatograph (HPLC) at the Institute of Arctic and Alpine Research (University of Colorado, Boulder).

Paleomagnetism

A coring device was used to sample the cave sediments at six cored holes in the Grand Concert Hall (Fig. 3). The core samples were obtained by means of a coring device in which a hand-powered hydraulic cylinder drives a stainless-steel, knife-edged barrel down into the sediments. Up to 40 cm of sediment could be cored each trip into the hole without sediment distortion. Samples were also collected from hand-dug pits at Mummys Alcove and Sniders Hall (Fig. 3). Additionally, samples were collected from a vertical outcrop in Heavenly Hall (Fig. 3). The pits and outcrops were sampled for paleomagnetic study by carving flat vertical surfaces and pushing plastic sampling cubes into the sediment at stratigraphic intervals ranging from 3.0 to 10.0 cm. The samples were oriented by means of a Brunton compass.

The core barrel and all pieces of drill rod that attached to the barrel were engraved with a vertical line so that the orientation of the core barrel could be measured with a Brunton compass within ±2°. A hand-operated hydraulic device was used to extract the sediment core from the barrels. As the core was extruded, a fixed thin wire sliced it in half, lengthwise. Plastic sampling cubes were then pushed into the soft sediment along the center line of the flat surface of the core half at regular intervals

Figure 2. GEOLOGY MAP OF COLORADO SPRINGS AND MANITOU SPRINGS AREA
with locations of snail collection sites.
Geology adapted from Trimble and Machette, (1979).



(generally ~5.0 cm). The samples at Sniders Hall, Mummys Alcove, and Hole 1 were taken with 3.2 cm^3 sampling cubes; all other samples were taken with 13.5 cm^3 cubes.

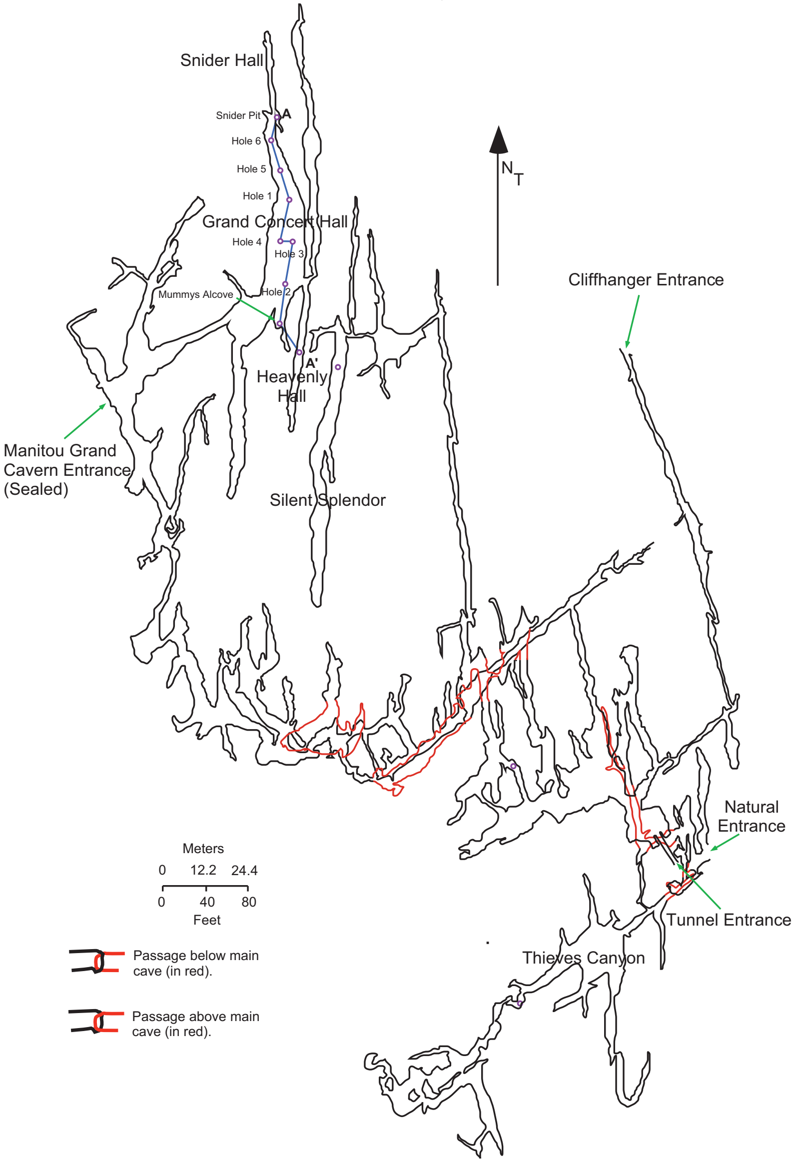
In the lab, the NRM (Natural Remanent Magnetization) of all samples was initially measured. Subsequently, the samples were subjected to alternating-field (A. F.) demagnetization and remeasured. All samples were first demagnetized at 10, and then at 15 millitesla (mT). Some samples at the bottom of Hole 5 that displayed aberrant inclinations and declinations were additionally demagnetized at fields up to 30 mT. All remanence measurements were made on a Schonstedt SSM 1A spinner magnetometer with a sensitivity of $1X10^{-4}$ A/m. Repeat measurements indicate an angular reproducibility of ~2° at an intensity of 1X10-6 A/m^2.

Age Of Cave Passages

Because Cave of the Winds is an erosional feature, its exact age cannot be determined. However, geologic and geomorphic features related to the cave can be used to bracket the age of incipient and major cave development. Solution breccia in the Manitou Formation indicate that there may have been some Middle Ordovician to Devonian cave development (Forster, 1977). Sediment-filled paleo-caves and paleo-sinkholes at Cave of the Winds indicate Devonian to Late Mississippian karst development (Hose & Esch, 1992). Subsequent Cenozoic dissolution along some of these paleokarst features has resulted in the formation of cave passage (Fish, 1988). Between the Pennsylvanian and Late Cretaceous, about 3000 m of sediments, which contain abundant shale beds, were deposited over the initial cave. Very little, if any, cave development could take place during this period of deep burial under the thick blanket of the nearly impervious rock.

The Laramide Orogeny, beginning in the Late Cretaceous (~75 Ma, Mutschler *et al.,* 1987), was associated with the uplift of the Rocky Mountains. The uplift, which included the Rampart Range and Pikes Peak, caused the activation of the Ute Pass and Rampart Range Faults (Morgan, 1950; Bianchi, 1967). In the Manitou Springs area, movement on the Ute Pass Fault resulted in the folding, jointing and minor faulting of the rocks (Hamil, 1965; Blanton, 1973). The subsequent flow of corrosive water along the fractures related to the folding and faulting would produce most of the passages in Cave of the Winds and nearby caves. Uplift during the early Laramide Orogeny increased the topographic relief in the Manitou Springs area, resulting in the initiation of erosion of the overlying sediments and also increased

Figure 3. Map Of Cave Of The Winds, Manitou Springs, Colorado showing locations of samplings sites.
Modified from Paul Burger, 1996



the local hydraulic head. The erosion of some of the impervious shale along with the increased hydraulic head may have initiated some minor water flow through the joints and faults, causing incipient dissolution. However, in the first 25 m. y. of the Laramide Orogeny, erosional stripping almost equaled uplift (Tweto, 1975) resulting in a subdued topography with a maximum elevation of about 1000 m (Epis and Chapin, 1975). It was unlikely, therefore, that a large hydraulic head existed--a necessary hydraulic head that would have had to be present to force through the rock the large volumes of water needed for development of a large cave system.

A Late Miocene-Early Pliocene alluvial deposit on the Rampart Range, 18 km northwest of Manitou Springs, indicates renewed Miocene-Pliocene uplift, which in some places was up to 3000 m (Epis and Chapin, 1975). At the same time, movement along the Ute Pass Fault caused redirection of Fountain Creek from its former position near the above-mentioned alluvial deposit to its present position (Scott, 1975). Valley entrenchment along the Ute Pass Fault by Fountain Creek, in conjunction with uplift, created the hydraulic head needed to drive the mineral springs, the mixing zone, and limestone dissolution (Luiszer, 1997). It is likely, therefore, that the age for the onset of major dissolution at Cave of the Winds is probably Late Miocene-Early Pliocene (7 Ma to 4 Ma).

Age Of Cave Fill

Sedimentation in the cave appears to have been contemporaneous with passage development. There are a few problems in proving this chronology. One is the lack of datable materials in the sediments, such as fossils or volcanic ashes. Preliminary study of the sediments indicated that magnetic reversal stratigraphy (magnetostratigraphy) might be useful in dating the sediments. The use of this method, however, presents another problem: it requires that the polarity sequence be constrained by at least one independent date.

The Nussbaum Alluvium, which crops out east of the cave and is ~20 m higher in elevation, is apparently related to coarse sediments present at the top of sediment sequences in Cave of the Winds. If an age can be assigned to the Nussbaum Alluvium and the relationship of the Nussbaum Alluvium to the coarse sediments in the cave deciphered, then an independent date can be assigned to at least one polarity reversal in the cave. The age of the Nussbaum Alluvium will be dealt with first, because the age of the Nussbaum Alluvium is poorly constrained. Various authors have assigned that range from Late Pliocene to early Pleistocene (Scott, 1963; Soister, 1967; Scott, 1975). For the purpose of correlating the Nussbaum Alluvium with a paleomagnetic reversal, a more accurate date of the Nussbaum Alluvium was needed. This problem was solved by aminostratigraphy.

Aminostratigraphy

Most amino acids exist as two forms: L- and D-isomers (Miller & Brigham-Grette, 1989). In a living organism, the amino acids are L-isomers. After the death of an organism, the amino acids racemize, which is the natural conversion of the L-isomers into D-isomers. Eventually the amino acids in the dead organism equilibrate to a 50/50 mixture of L- and D-isomers. The amino acids used in the present study are D-alloisoleucine and L-isoleucine (A/I). These amino acids are somewhat more complex, because L-isoleucine actually changes to a different molecule, D-alloisoleucine. This reaction, similar to racemization, is called epimerization (Miller and Brigham-Grette, 1989).

The rate at which this reaction takes place is a function of temperature. For example, if the burial-temperature history for a group of mollusks of different ages has been the same, the ratio of the two amino acids – alloisoleucine and isoleucine (A/I) – in the mollusk shells can be used for relative dating and in some cases, absolute dating (Miller and Brigham-Grette, 1989). Because temperature controls the rate of racemization, the temperature history of buried fossils must be considered before using A/I to derive ages.

Solar insolation, fire, altitude, and climate can effect the burial temperature of fossils. Diurnal or seasonal solar heating of fossils buried at shallow depths may accelerate racemization and increase the apparent age of the samples (Goodfriend, 1987; Miller and Brigham-Grette, 1989). Therefore, samples should be obtained from depths that exceed 2 m (Miller and Brigham-Grette, 1989). During the intense heat associated with a fire, racemization can also be greatly accelerated. For example, charcoal, which has a ^{14}C age of ~1500 years, found with snails at Manitou Cave suggests that the snails were exposed to a forest fire before being transported into the cave. If so, the A/I of the snails may be anomalously high for their age.

The altitude of the collection site can also affect racemization rates. For example, snails in this study were collected at altitudes between 1890 and 2195 m above sea level. Because of the normal adiabatic effect, the highest site averages about 1.7° C less than the lowest site. Another temperature variable is long-term climate change. For example, the Nussbaum Alluvium has probably been exposed to episodes of higher or lower temperatures for much longer periods of time than the younger alluvia. Because post-depositional thermal histories are impossible to ascertain, the burial temperature for all alluvia in this study are assumed to be the same.

Mollusks Results

In all, over 10,000 mollusks, which included one species of slug, one species of clam, and 24 species of snail, were identified and counted. The tabulated number for each species is the number of shells that could be identified. For example, the Louviers site had ~3,000 snails that could not be identified because they were too small (juvenile) or broke. Because of the small weight of the individual snails (0.3 to 5.0 mg) in relation to the 30 mg necessary for testing, only abundant species that occurred at multiple sites could be used for the amino-acid study. The species chosen for the Nussbaum (Black Canyon) were *Vallonia cyclophorella* and *Pupilla muscorum* and from the Verdos, *Vallonia cyclophorella* and *Gastrocopta armifera* (Table 1). All of the alloisoleucine and isoleucine (A/I) ratios of the snails along with laboratory identification numbers are tabulated in Table 2A. Table 2B contains the average and standard deviation of the A/I of selected snails from each site.

Discussion Of A-I Ratios

The epimerization rates of the four species used in this study are very similar. This is indicated in Table 2A by the comparable A/I values of different snail species at the same sample location. Moreover, shell size did not appear to greatly affect the A/I. For example, the average *Gastrocopta armifera* shell weighs 5 mg; the *Vallonia cyclophorella* 1 mg; yet, the A/I for these shells from Manitou Cave are similar (Table 2A).

The snails from the Verdos Alluvium, which include the Starlight, Fillmore, and Colorado City sites (Locations on Fig. 2), were used to test the A/I reproducibility of samples from one site and to compare the A/I from the different sites. Extra effort was put into assuring that the amino acid ratios of snails from Verdos Alluvium were as accurate as possible, because any errors in their A/I determination would greatly amplify the inaccuracies of the extrapolated age of the Nussbaum Alluvium (Fig. 4). Therefore, the Starlight site was sampled three times and the Fillmore site, twice. Although each of the two sub-sites at Colorado City were sampled twice, the scarcity of *Vallonia cyclophorella* and *Gastrocopta armifera* necessitated combining all snail shells of similar species from the entire site and from both sampling trips. One Starlight-site sample (Table 2A, Lab # AAL-5768) was excluded from the final curve fitting because it had an anomalously high ratio as compared to the others from that site. The snails that made up this sample (AAL-5768) may have been from an older reworked alluvium or there may have been a problem with their preparation or analysis.

The data from the Colorado City site were also excluded from the final curve fitting, primarily because the A/I of the two species were very different from each other

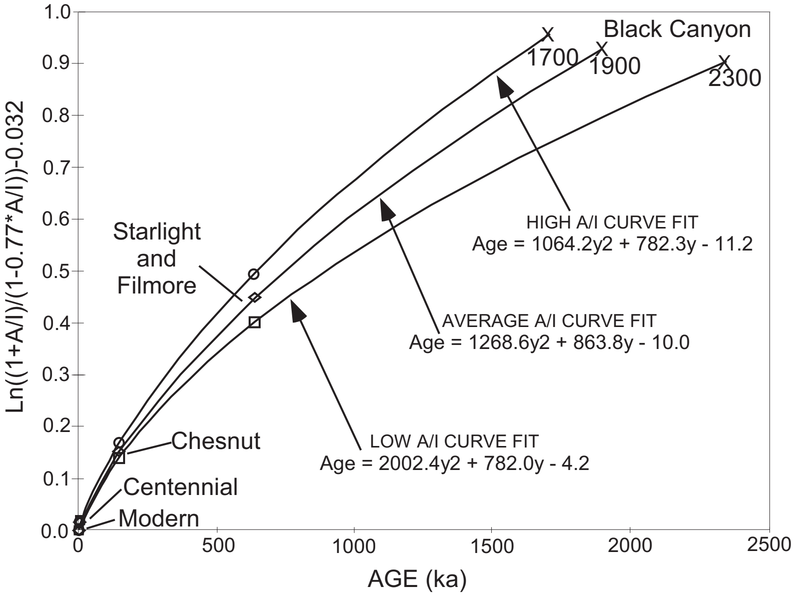


Figure 4. The A/I of snails from the Starlight and Filmore (Verdos Alluvium), Chesnut (Louviers Alluvium), Centennial (Piney Creek), and Modern Flood Plain sites are used for curve fitting. The diamonds represent the curve fit of the average A/I. The circles and squares represent the curve fits of +/- one standard deviation of the A/I. The A/I of the snails from the Black Canyon site with the appropriate equations are used to extrapolate the age of the Nussbaum Alluvium (1.9+0.4/-0.2 Ma).

and both A/I were much lower than those from the Starlight and Fillmore sites. Their low A/I would indicate that the Colorado City site may actually be either the Slocum or Louviers Alluvium. The anomalously low ratios, of course, could also be the result of contamination from modern shells or organic material.

Determination of anomalously high or low ratios would be impossible without multiple sampling. Taking one sample per site would have been useless for this study. Two samples per site was acceptable when the A/I ratios were about the same for both species. With 12 samples from the Verdos Alluvium, it was quite appropriate to discard the highest and lowest ratios.

Age Of The Alluvia

The higher A/I of the snails from Black Canyon site, which is mapped as Nussbaum Alluvium, indicates that it is older than the other alluvia (Table 2A). Furthermore, by ascertaining the ages of the younger alluvia, plotting those against their relative A/I ratio, and fitting a curve to the resultant plot, a equation can be derived that can be used to calculate the approximate age of the Nussbaum Alluvium.

Snails from the modern flood plain (Fig. 2) were used to ascertain the A/I ratio of modern snails. About 50% of the snails at this site were alive when collected. The live snails were not analyzed because the flesh, which may have different amino-acid ratios than the shells, might have contaminated the shell A/I ratios. Empty shells were used for analysis and assumed to be about one year old. There is a possibility that the modern shells were reworked from older sediments such as the Piney Creek Alluvium. However, the abundant live snails mixed with the dead snails of the same species suggests that all snail specimens were contemporaneous.

The Piney Creek Alluvium site (Fig. 2) has been mapped as Piney Creek and Post-Piney Creek (Trimble and Machette, 1979). Charcoal collected from the Piney Creek site (location on Fig. 2) was ^{14}C dated at 1542 ± 130 years old (Table 3) indicating that the site should be mapped as Post-Piney Creek Alluvium. The snails collected at Manitou Cave, which have relatively high A/I ratios, were initially thought to be about the same age as dated deposits at Narrows Cave. Narrows Cave is located ~0.4 km north of Manitou Cave contains flood deposits intercalated with flowstone that has been dated and found to have a maximum uranium-thorium age of 32 ± 2 Ka (Table 3). They were thought to be the same age because the snails at Manitou Cave and the deposits at were both deposited by paleo-floods and both had similar heights above Williams Canyon Creek. However, charcoal associated with the snails in Manitou Cave was ^{14}C dated with an age of 1552 ± 75 years (Table 3). Apparently, either young charcoal mixed with old snails during the paleo-flood or the snails were affected by a forest fire that induced anomalously high A/I ratios. This conflicting evidence made it necessary to exclude the Manitou Cave data from the curve fitting.

The Louviers Alluvium site was mapped by Trimble and Machette (1979). Elsewhere in Colorado the Louviers has been dated at 115 Ka by Machette (1975). Szabo (1980) gave a minimum age of 102 Ka and inferred that the maximum age was ~150 Ka. The Fillmore, Colorado City, and Starlight sites are all mapped as Verdos Alluvium (Trimble and Machette, 1979), which, in the Denver area, contains the 640-Ka Lava Creek B ash near its base (Sawyer *et. al.,* 1995; Izett *et. al.,* 1989; Machette, 1975). Because the Lava Creek B ash gives the maximum age for the Verdos Alluvium,

Tab. 1: Species identified, their location, and amount of shells counted.

	Modern Flood Plain		*Centennial*		*Manitou Cave*		*Chesnut*		*Filmore (Verdos)*		*Starlight (Verdos)*		*Colorado City*				*Black Canyon (Nussbaum)*	
													East (Verdos)		*West (Verdos)*			
Carychium exiguum (Say)											8	3	105	35	18	5		
Cionella lubrica (Muller)					20	3	1	0			2	1						
Columella alticola (ingersoll)							4	0					1	0				
Derocerus spp.											1	0			4	1		
Discus whitneyi					4	1	4	0										
Euconulus fulvus (Muller)					16	2	20	2					2	1				
Fossaria parva (Lea)							19	2			3	1	8	3	10	3		
Gastrocopta armifera (Say)	1	0	1	0	47	7	5	1	38	7	17	7	5	2				
Gastrocopta cristata Pilsbry	1	0							1	0	15	6	19	6	10	3		
Gastrocopta holzingeri (Sterki)	6	2					6	1			96	39	37	12	3	1		
Gastrocopta pellucida (Pfeiffer)	1	0			193	27			3	1			6	2	3	1	136	28
Gastrocopta procera (Gould)	6	2			5	1			35	6	5	2	14	5	3	1		
Gyraulus parvus (Say)													2	1	53	13		
Hawaiia minuscula (Binney)	23	6	43	5	82	12	134	14	84	14	12	5	20	7	12	3	26	5
Oreohelix spp.					28	4												
Oxyloma spp.							20	2			6	2	5	2				
Physa spp.													1	0	10	3		
Pisidium casertanum (Poli)													13	4	200	50		
Pupilla muscorum (Linne)	70	18	174	22	20	3	4	0	2	0	9	4	12	4	2	1	52	11
Pupoides albilabris (C.B. Adams)									7	1	4	2	8	3				
Pupoides hordaceous (Gabb)																	133	28
Pupoides inornata Vanatta	35	9	7	1	1	0			130	22	3	1	6	2	9	2	7	1
Stagnicola spp.															10	3		
Succinea spp.			4	1					45	8					3	1		
Vallonia cyclophorella (Sterki)	250	64	579	72	197	28	381	39	240	41	60	24	20	7	32	8	123	26
Vertigo gouldi and ovata			1	0	4	1	390	39										
Zonitoides arboreus (Say)	1	0			96	14	1	0			7	3	20	7	15	4	6	1
TOTAL	394	100	809	100	713	100	989	100	585	100	248	100	304	100	397	100	483	100
	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%

Tab. 2A: Alloisoleucine and isoleucine (A/I) ratios of snails.

Sample Location	*Species*	*Lab Number*	*Results*			*Average*	*Standard Deviation*
Modern	P	AAL-5990	0.020	0.022		0.021	0.001
Modern	V	AAL-5989	0.021	0.020		0.021	0.001
Centennial	P	AAL-5970	0.023	0.021		0.022	0.001
Centennial	V	AAL-5969	0.024	0.032		0.028	0.004
Manitou Cave	G	AAL-5993	0.042	0.056	0.051	0.050	0.006
Manitou Cave	P	AAL-5992	0.039	0.044	0.041	0.041	0.002
Manitou Cave	V	AAL-5991	0.043	0.069		0.056	0.013
Chesnut	GO	AAL-5972	0.106	0.124		0.115	0.009
Chesnut	V	AAL-5971	0.106	0.103		0.105	0.002
Colorado City	G	AAL-5986	0.154	0.210	0.163	0.176	0.025
Colorado City	V	AAL-5985	0.076	0.083		0.080	0.004
Fillmore 1	G	AAL-5976	0.279	0.274		0.277	0.003
Fillmore 1	V	AAL-5975	0.298	0.275		0.287	0.012
Fillmore 2	G	AAL-5988	0.239	0.233		0.236	0.003
Fillmore 2	V	AAL-5987	0.283	0.270		0.277	0.007
Starlight	P	AAL-5768	0.423	0.414	0.420	0.419	0.004
Starlight	V	AAL-5767	0.276	0.317	0.296	0.296	0.017
Starlight 1	G	AAL-5974	0.302	0.322		0.312	0.010
Starlight 1	V	AAL-5973	0.307	0.231	0.224	0.254	0.038
Starlight 2	G	AAL-5978	0.292	0.298		0.295	0.003
Starlight 2	V	AAL-5977	0.246	0.244		0.245	0.001
Black Canyon	P	AAL-5766	0.502	0.531	0.543		
					0.529	0.526	0.015
Black Canyon	V	AAL-5765	0.545	0.545	0.546		
			0.544	0.515	0.576	0.545	0.018

V = Vallonia cyclophorella P = Pupilla muscorum G = Gastrocopta armifera
GO = Vertigo gouldii and Vertigo ovata

the inferred maximum age of ~150 Ka was assigned to the Louviers Alluvium. The interpolated age of the Nussbaum Alluvium, therefore, represents its maximum age.

Tab. 2B: Average values and standard deviation of A/I ratios of selected snails from each site.

	Average - standard deviation	*Average*	*Average + standard deviation*
Modern Flood Plain	0.020	0.021	0.022
Centennial	0.021	0.025	0.029
Chesnut	0.103	0.110	0.117
Filmore and Starlight	0.249	0.275	0.301
Black Canyon	0.523	0.536	0.549

Parabolic Curve Fitting

Ages and A/I data (Table 2B) from four of the younger alluvia, together with A/I data from the Nussbaum, were used to extrapolate the age of the Nussbaum. Various authors have applied linear and parabolic curve fitting to amino acid data for both interpolation and extrapolation of age (Miller & Brigham-Grette, 1989). Mitterer & Kriausakul (1989) have employed the parabolic function ($y=x^2$) with good results. Applying the generalized parabolic equation ($y=A+Bx+Cx^2$) to my data resulted in a better curve fit than the specialized parabolic function ($y=x^2$). Use of the specialized parabolic function assumes that the A/I ratio starts at 0.0 and that at an initial age near zero, the racemization rate is infinitely large. The data from my study area suggest that both of these assumptions are invalid (Table 2B and Fig. 4).

Ignoring the A+Bx terms appears to have little effect on curve fitting of relatively young snails (<100 Ka). The generalized parabolic function, however, was used in this study because the age of the Nussbaum Alluvium is extrapolated 3 to 4 times beyond the oldest calibration point. Parabolic-curve fits for the average ratio with error bars of one standard deviation indicate an extrapolated age for the Nussbaum Alluvium of 1.9 +0.4/-0.2 Ma (Fig. 4).

Tab. 3: Uranium-thorium and ^{14}C dates.

	^{14}C Age (years B.P.)	*Lab. Number**
Centennial site	1495 ± 130	GX-15992
Manitou Cave	1505 ± 75	GX-15993
**Krueger Enterprises Inc.*		
*Uranium-thorium Age** (years B.P.)*		
Narrows Cave	32,000 ± 2,000	
***Dan Muhs, U.S.G.S., 1990, per. comm.*		

Extrapolating a date that is 3 to 4 times more than the maximum calibration date is a practice generally frowned up. I believe that by carefully collecting and handling samples, obtaining precise analysis of the amino acids, acquiring the best age determinations of the younger deposits, and curve fitting with the generalized parabolic function, I have ameliorated problems usually associated with such extrapolation. The 1.9-Ma date for the Nussbaum Alluvium is appropriate only for the unit mapped in the Manitou Springs area; it may not be correlative with the type section in Pueblo, Colorado. The date, 1.9 +0.4/-0.2 Ma, which is the most accurate date available for the Nussbaum Alluvium, was used to calibrate the magnetostratigraphy of the sediments in Cave of the Winds.

Magnetostratigraphy

Rocks and unconsolidated sediments can be magnetized by the magnetic field of the earth (Tarling 1983), acquiring natural remanent magnetization (NRM). A type of NRM in sediments is detrital remanent magnetization (DRM), which is formed when the magnetic grains of a sediment, such as magnetite or hematite, are aligned with the earth's magnetic field during or soon after deposition (Verosub, 1977). The DRM of a sediment has the same orientation as and its intensity is proportional to, the earth's magnetic field (Verosub, 1977).

The magnetic field of the earth has reversed many times in the past (Tarling, 1983). Polarity time scales have been constructed by compiling the reversals and the radiometrically derived dates of the rock in which the reversals are preserved, (Mankinen & Dalrymple, 1979; Harland *et. al.,* 1982; Hailwood, 1989; Cande and Kent, 1992).

There are several ways to use this time scale to date sediments. By assuming that the top of a sediment section starts at the present and sedimentation has been uninterrupted, such as in deep ocean basins, it is a simple matter of counting the reversals and correlating them with the polarity time scale. Because of erosion or a hiatus in deposition, however, the top of many sediment sections will have an older age that must be ascertained by some other technique before reversals in the section can be correlated with the polarity time scale.

Another way of dating sediments is by pattern matching. If the sedimentation rate of an undated section is constant or known and there are many reversals (5-10), the polarity record can be matched to the pattern of the polarity time scale to provide dating. This is possible because the timing of reversals is apparently random (Tarling, 1983). Therefore, the timing of a sequence of reversals is seldom repeated. Both of these techniques mentioned here were used to refine the age of the sediments at Cave of the Winds.

Paleomagnetic Results

All the paleomagnetic data from Hole 6 are presented to give an example of all the raw data from all sampling sites and how the samples responded to demagnetization (Table 4). Inspection of the complete data set revealed that all samples responded very similarly to demagnetization. The complete data set of sites included in this study as well as other miscellaneous sites not used in this study are available from the author on computer storage disks. Sample depth and magnetic declination after 15-mT AF demagnetization from each site were used to correlate the magnetic polarity within and between the Grand Concert Hall and nearby Heavenly Hall (Fig. 5). An exception to use of the 15-mT-AF demagnetization is Hole 5, where samples from 6.5 to 10.0 m were subjected to 20-, 25-, and 30-mT-AF demagnetization. The higher fields were applied in an attempt to remove secondary overprints. Even with the increasing demagnetization,

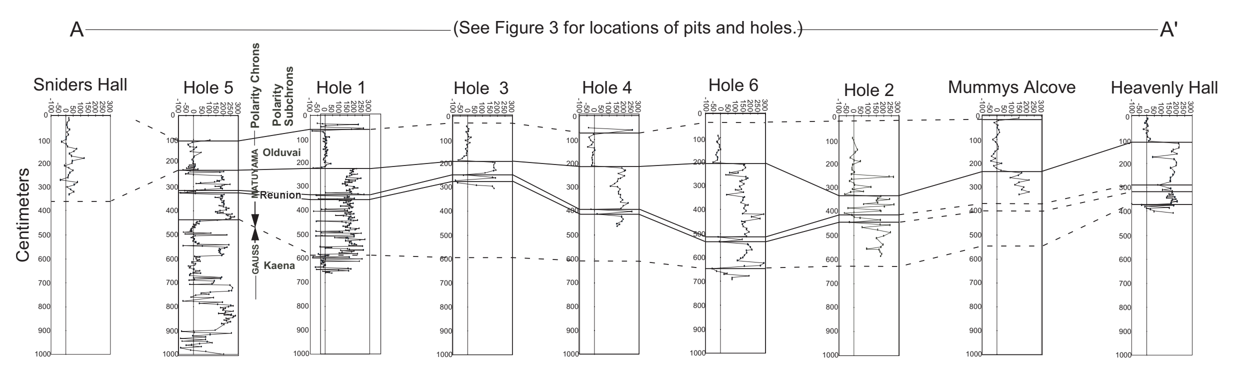


Figure 5. Cross-section and correlation of the magnetic declination of sampled pits and cored holes from the Grand Concert Hall and Heavenly Hall.

Tab. 4: Complete Paleomagnetic results of Hole 6, Grand Concert Hall

Sample Number	*Depth cm*	*Natural*			*10 mT*			*15 mT*		
		Dec.	*Inc.*	*Int.*	*Dec.*	*Inc.*	*Int.*	*Dec.*	*Inc.*	*Int.*
11	80	-10	62	1.2E-4	-21	55	5.4E-5	-14	58	4.7E-5
12	93	-30	45	1.5E-4	-7	54	6.8E-5	-16	52	5.0E-5
13	105	-11	52	2.0E-4	-4	52	1.2E-4	-9	60	1.1E-4
14	118	-23	27	1.5E-4	-23	26	1.1E-4	-24	24	9.7E-5
21	121	-14	44	1.8E-4	-21	40	1.2E-4	-20	39	9.6E-5
22	131	-11	46	2.7E-4	-7	39	1.7E-4	-6	40	1.5E-4
23	141	-0	41	1.4E-4	-13	34	7.2E-5	-7	37	6.6E-5
24	151	4	42	3.2E-4	3	38	2.1E-4	2	38	1.8E-4
31	154	-11	40	3.8E-4	-15	32	2.1E-4	-14	34	1.9E-4
32	163	-27	40	2.2E-4	-21	38	1.4E-4	-24	36	1.3E-4
33	172	-24	41	2.6E-4	-29	36	1.8E-4	-30	35	1.6E-4
34	182	-17	40	2.5E-4	-19	38	1.7E-4	-20	37	1.6E-4
41	184	-18	38	4.4E-4	-18	40	3.1E-4	-18	39	2.9E-4
42	194	-15	41	1.8E-4	-24	42	1.1E-4	-20	36	9.6E-5
43	204	-17	58	1.4E-4	-45	62	4.7E-5	-50	64	3.4E-5
44	213	165	-32	1.1E-4	162	-28	9.9E-5	162	-29	9.1E-5
51	216	115	11	7.0E-5	149	-9	6.1E-5	156	-11	5.7E-5
52	226	155	-29	9.5E-5	165	-36	1.0E-4	168	-35	9.2E-5
53	236	-14	52	7.4E-5	144	75	1.4E-5	149	59	1.1E-5
54	246	30	50	1.3E-4	54	30	5.5E-5	62	30	5.0E-5
61	249	81	47	6.7E-5	114	14	4.6E-5	119	3	3.7E-5
62	257	-2	51	1.2E-4	34	41	2.3E-5	36	16	1.0E-5
63	264	176	58	2.7E-5	164	-7	2.3E-5	170	-16	2.3E-5
64	271	177	-18	5.0E-5	184	3	6.4E-5	183	3	6.2E-5
71	273	-12	88	6.7E-4	169	-9	4.7E-5	172	-8	4.5E-5
72	281	203	14	3.9E-5	142	12	7.4E-5	144	8	7.0E-5
81	283	127	-11	1.2E-4	131	-19	9.6E-5	131	-18	8.6E-5
82	294	150	-17	6.4E-5	156	-21	6.2E-5	158	-24	5.2E-5
83	305	93	16	5.4E-5	130	-16	5.2E-5	128	-17	4.5E-5
84	316	59	30	2.2E-5	140	-34	2.2E-5	142	-38	2.0E-5
91	319	28	62	7.2E-5	82	47	2.2E-5	100	29	1.7E-5
92	329	85	67	4.5E-5	148	5	3.8E-5	154	-2	3.5E-5
93	339	-2	53	5.5E-5	41	61	1.4E-5	41	56	1.3E-5
94	349	17	75	6.3E-5	140	34	2.5E-5	162	26	2.2E-5
101	352	101	-26	5.4E-5	159	15	4.5E-5	153	3	4.1E-5
102	362	81	76	5.2E-5	131	33	2.0E-5	150	17	1.5E-5
103	372	67	79	7.7E-5	139	-1	2.6E-5	137	-6	3.2E-5
104	382	178	11	4.7E-5	179	-16	4.7E-5	186	-21	4.7E-5
111	385	170	24	5.5E-5	165	-3	4.9E-5	165	-2	4.5E-5
112	396	159	-12	3.7E-5	156	-30	3.5E-5	157	-29	3.3E-5
113	407	184	-10	3.9E-5	174	-32	4.8E-5	172	-32	4.5E-5

Sample Number	*Depth cm*	*Natural*			*10 mT*			*15 mT*		
		Dec.	*Inc.*	*Int.*	*Dec.*	*Inc.*	*Int.*	*Dec.*	*Inc.*	*Int.*
121	420	-37	-30	2.4E-5	-70	-57	1.2E-5	-49	-54	1.0E-5
122	431	228	52	2.5E-5	214	25	1.4E-5	208	18	1.1E-5
123	439	-44	55	3.1E-5	249	16	1.1E-5	266	16	1.1E-5
124	451	126	3	2.1E-5	145	-32	2.2E-5	142	-36	1.9E-5
131	453	211	7	1.6E-5	136	-38	9.8E-6	164	-55	9.8E-6
132	463	172	37	1.5E-5	144	-43	2.4E-5	147	-40	1.9E-5
133	472	69	-21	9.3E-6	149	-46	1.6E-5	152	-50	1.6E-5
134	481	263	19	5.4E-6	167	-32	1.3E-5	177	-28	1.2E-5
141	484	115	8	1.9E-5	183	-35	1.4E-5	174	-40	1.1E-5
142	493	189	-6	7.2E-5	188	-19	5.8E-5	192	-22	5.1E-5
143	503	176	62	2.1E-5	158	23	9.6E-6	163	20	8.2E-6
144	512	68	35	1.3E-5	186	-36	6.3E-6	175	-36	6.6E-6
151	514	-19	40	3.4E-5	-39	15	8.3E-6	-15	15	5.9E-6
152	525	41	70	4.7E-5	139	66	1.8E-5	146	60	1.6E-5
153	535	-6	46	8.1E-5	-4	33	3.3E-5	-7	36	2.6E-5
154	545	189	33	1.2E-4	185	21	1.1E-4	182	21	1.1E-4
161	547	173	57	2.8E-5	186	2	2.4E-5	187	-0	2.4E-5
162	558	208	7	2.6E-5	200	-28	3.8E-5	201	-28	3.2E-5
163	568	10	68	1.7E-5	206	-25	9.1E-6	211	-33	1.1E-5
171	570	146	73	4.4E-5	175	27	2.9E-5	173	31	2.7E-5
172	580	255	54	10.0E-6	190	-46	1.5E-5	176	-43	1.6E-5
173	591	131	63	4.3E-5	161	14	2.1E-5	160	10	2.2E-5
174	601	39	67	2.2E-5	148	14	6.4E-6	150	2	7.4E-6
181	603	92	52	7.9E-6	163	-18	6.4E-6	135	-31	4.9E-6
182	613	2	69	2.6E-5	152	87	1.2E-5	113	78	8.2E-6
183	624	-44	19	2.1E-5	-69	-45	1.7E-5	-67	-53	1.4E-5
184	634	-16	5	1.6E-5	267	-55	1.1E-5	-86	-59	8.6E-6
191	636	106	60	2.0E-6	112	-37	3.0E-6	160	1	1.4E-6
192	646	-38	7	2.3E-5	-54	-26	1.8E-5	-55	-40	1.2E-5
193	657	2	47	2.6E-5	-4	19	5.7E-6	-26	-27	3.0E-6
194	667	14	64	4.3E-5	42	63	1.6E-5	45	61	1.1E-5
201	669	8	45	4.5E-5	25	43	2.5E-5	24	45	1.6E-5
202	677	22	84	5.0E-5	183	84	2.6E-5	192	80	1.8E-5
203	685	48	52	3.3E-5	74	50	1.7E-5	78	44	1.2E-5
204	692	25	48	1.9E-5	56	25	6.3E-6	78	-17	1.6E-6

however, the declination of the deeper samples at Hole 5 have greater variability than those of shallower samples (Fig. 5). Additionally, the polarity results from Hole 5 are shown in Fig. 6, which also shows the correlation with the known paleomagnetic record and stratigraphy of the cave sediments.

Criteria For Reversal Assignment

Sequences of samples that had an average declination of ~0.0° and an average inclination of ~35.0° were assigned to normal polarity. The ideal inclination for DRM in the Manitou Springs area should be ~60°. The low values recorded at Cave of the Winds are considered to be the

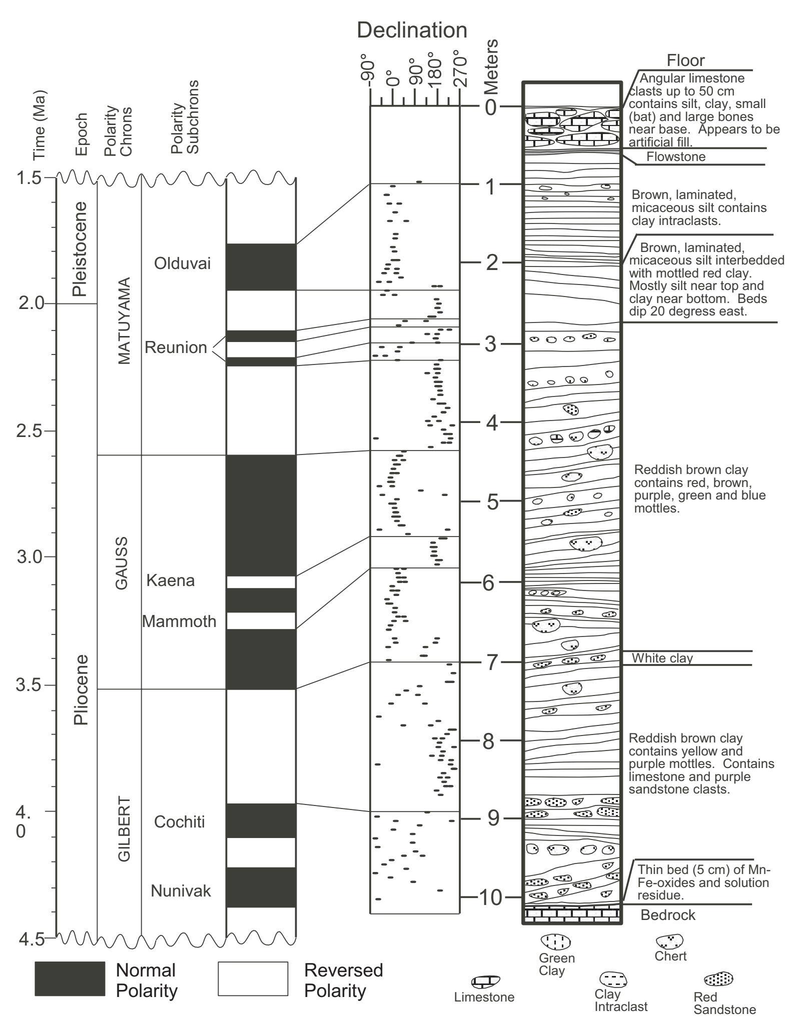


Figure 6. Paleomagnetic correlation and stratigraphy of Grand Concert Hall Hole 5. Paleomagnetic time scale adapted from Harland and others (1982).

result of inclination error resulting from sediment compaction (Verosub, 1977). Sequences of samples that had an average declination of ~180° were assigned a reversed polarity. In most cases, inclinations of these samples were variable, ranging mostly between -35.0° and +10.0°. Because of this variability, the sample declinations were used to determine reversals (Fig. 5). These anomalous inclinations appear to be related to post-depositional acquisition of remanent magnetization.

Effects Of Post-Depositional Remanent Magnetization On Sediments

Most post-depositional remanent magnetization (PDRM) is the result of realignment of the magnetic particles during compaction and especially dewatering, both of which can take place thousands to millions of years after deposition (Verosub, 1977). A possible explanation of the variability of the inclination of the reversed samples is that these samples were compacted and dewatered during a normal polarity interval, overprinting a normal component. The dewatering and compaction may have occurred rather quickly following rapid draining of the water in the cave passages related to downcutting by Fountain Creek. Mud cracks present in the top two meters of the sediments at the Grand Concert Hall combined with their mostly normal polarity (Fig. 6) indicate that this is a plausible explanation. Further micro-sampling and precision analysis would be necessary to ascertain the mechanism responsible for the difference in the inclinations.

Chemical remanent magnetization (CRM) may also be a contributing factor to the inclination anomalies. Alteration and oxidation of iron-bearing minerals in the sediments may contribute to the CRM. This could only be a factor in the top two meters of coarse sediments (Fig. 6), which contain unaltered minerals; because the general oxidizing conditions and neutral to slightly alkaline pH of percolating cave waters through these sediments would preclude mobilization or precipitation of iron oxides. The underlying soil-derived clays, which have already undergone prolonged oxidation before being deposited in the cave, are chemically stable and would not be vulnerable to CRM.

Paleomagnetic Correlation

Because there are no independent dates on the cave sediments, correlation of the magnetic polarity record of the Cave of the Winds sediments with the accepted polarity time scale is difficult. It requires matching the sequence of known polarity events with the Cave of the Winds record. The age of the Nussbaum Alluvium, which is apparently related to the uppermost coarse cave sediments, however, can be used to help constrain the paleomagnetic correlation. The relationship of the Nussbaum Alluvium to the detrital sediments in Cave of the Winds will be discussed in detail.

As discussed previously, the clay is deposited in the cave below the phreatic-vadose interface where sediment-laden streams enter water-filled passages. The

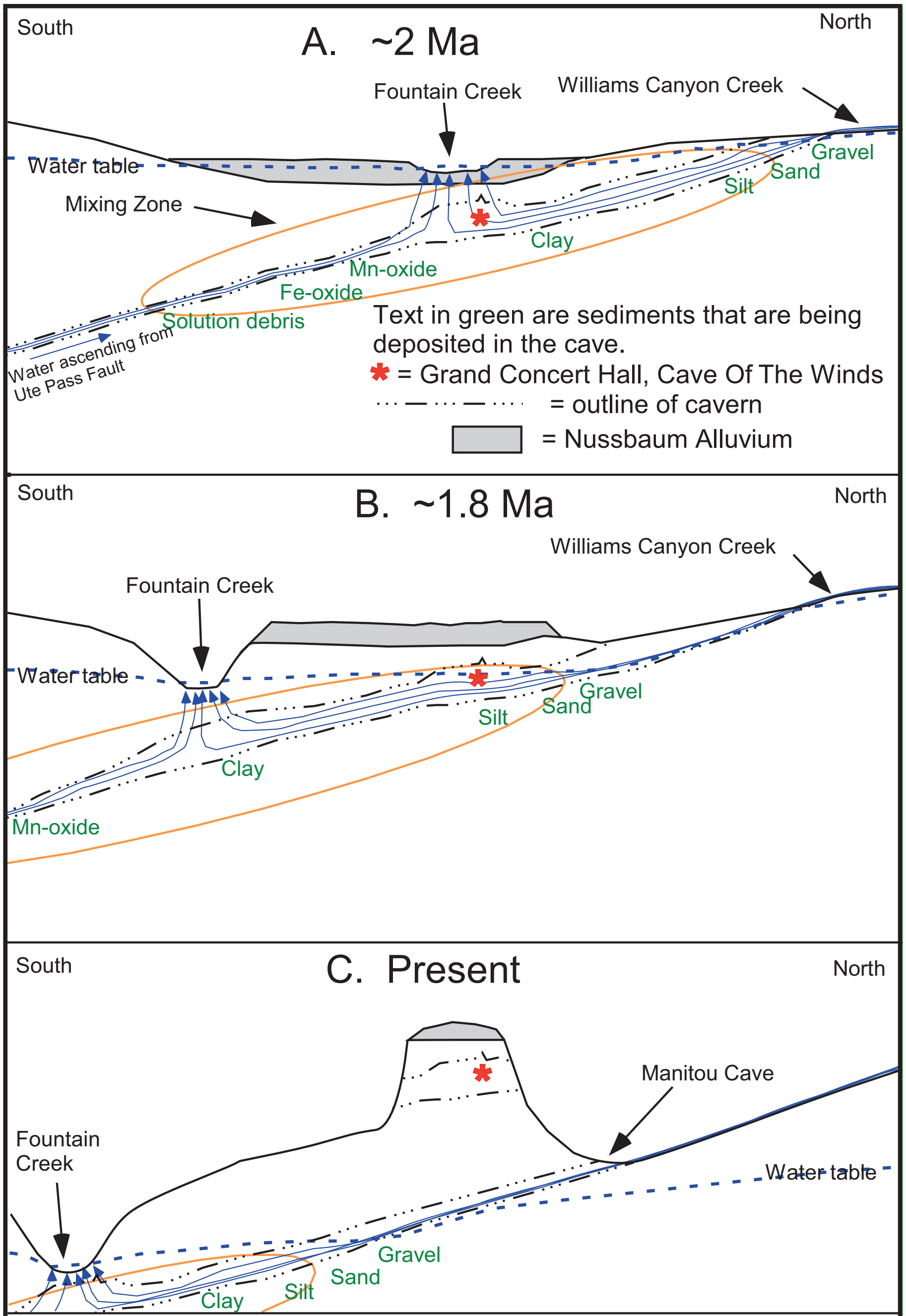


Figure 7. Schematic cross sections showing the sequence of changes in the water table, topographic setting, and depositional phases over the last ~2 Ma.

Nussbaum Alluvium was being deposited at the same time that clay was being deposited in the Grand Concert Hall the (Fig. 7A). As Fountain Creek downcut and moved to the south, the water table dropped (Fig. 7B). The drop in the water table coincided with drop in the water depth in rooms like the Grand Concert Hall. As the water depth dropped, the velocity of the water passing through the room increased. The increased stream energy changed the sedimentation regime from clay deposition to silt, sand, and gravel deposition (Fig. 7B). Fluvial sedimentation at Cave of the Winds stopped as Fountain Creek moved further to the south and downcut further (Fig. 7C). The relationship between the Nussbaum Alluvium and the sediments in the cave indicate that the silt-clay interface in the Grand Concert Hall took place after the Nussbaum was deposited. More specifically, the silt-clay interface should be the same age as the Nussbaum Alluvium minus the time it took for Fountain Creek to downcut and drop the water table to the level of the Grand Concert Hall (Fig. 7B).

The sediment floor of the Grand Concert Hall, where the paleomagnetic data was obtained, is about 20 m below the Nussbaum Alluvium. The age of the Nussbaum Alluvium (~1.9 Ma) and its height above modern streams (200 m) provides an estimate of the average down-cutting rate of 10.5 cm/1000 years. Accordingly, accumulation of coarse sediments in the cave 20 m below the Nussbaum Alluvium probably would have begun ~1.7 Ma.

The estimated 1.7 Ma age of the clay-coarse sediment interface correlates well with the onset of the Olduvai Subchron at 1.9 Ma (~2.2 m depth, Fig. 6). This is the most probable correlation. Alternatively, one could match the normal-polarity sequence (1.0 to 2.2 m depth, Fig. 6) with the Jaramillo Subchron (Harland *et al.,* 1982) or the Gauss Chron (Fig. 6). These correlations, however, would result in an age of ~1.0 Ma or ~ 2.6 Ma, respectively, for the clay-coarse-sediment interface, which is estimated to be 1.7 Ma, thereby making these alternate correlations unlikely.

The complete paleomagnetic correlation shown on Fig. 6 follows from correlation of the normal-polarity interval between 1.0 and 2.2 m in depth with the Olduvai Subchron. According to the correlation suggested here, the oldest cave sediment was deposited about 4.3 Ma, a date that agrees quite well with the previously discussed probable age of the major onset of cave formation (7 Ma to 4 Ma).

CONCLUSIONS

Cave of the Winds is a phreatic cave dissolved from the calcite-rich Manitou, Williams Canyon, and Leadville Formations. Dissolution occurred along joints associated with Laramide faulting and folding. Paleokarst features, such as sediment-filled fissures and caves, indicate that some of the passages at Cave of the Winds are related to cave-forming episodes that started soon after the deposition of the Ordovician Manitou Formation and continued to the beginning of the Cretaceous Laramide Orogeny. Most speleogenesis, however, occurred in the last ~5.0 Ma.

The Nussbaum Alluvium was assigned an age of ~1.9 Ma by means of aminostratigraphy. The age of the Nussbaum Alluvium and its relation to coarse grained sediments at Cave of the Winds were used to fix an age of ~1.7 Ma for the onset of coarse grained sedimentation in the cave. This enabled the identification of the Olduvai Polarity Subchron in the coarse grained sediments. Correlation of the magnetostratigraphy of cave sediments with the accepted polarity time scale indicates that the dissolution of cave passage started ~4.2 Ma and stopped ~1.5 Ma.

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HOW LONG DOES EVOLUTION OF THE TROGLOMORPHIC FORM TAKE? ESTIMATING DIVERGENCE TIMES IN ASTYANAX MEXICANUS

KAKO DOLGO TRAJA EVOLUCIJA TROGLOMORFNIH OBLIK? OCENJEVANJE DIVERGENČNIH ČASOV PRI ASTYANAX MEXICANUS

Megan L. PORTER[1], Katharina DITTMAR[2] & Marcos PÉREZ-LOSADA[3]

Abstract UDC 551.44:597
591.542

Megan L. Porter, Katharina Dittmar & Marcos Pérez-Losada: How long does evolution of the troglomorphic form take? Estimating divergence times in Astyanax mexicanus

Features including colonization routes (stream capture) and the existence of both epigean and cave-adapted hypogean populations make *Astyanax mexicanus* an attractive system for investigating the subterranean evolutionary time necessary for acquisition of the troglomorphic form. Using published sequences, we have estimated divergence times for A. mexicanus using: 1) two different population-level mitochondrial datasets (cytochrome b and NADH dehydrogenase 2) with both strict and relaxed molecular clock methods, and 2) broad phylogenetic approaches combining fossil calibrations and with four nuclear (recombination activating gene, seven in absentia, forkhead, and α-tropomyosin) and two mitochondrial (16S rDNA and cytochrome b) genes. Using these datasets, we have estimated divergence times for three events in the evolutionary history of troglomorphic *A. mexicanus* populations. First, divergence among cave haplotypes occurred in the Pleistocene, possibly correlating with fluctuating water levels allowing the colonization and subsequent isolation of new subterranean habitats. Second, in one lineage, *A. mexicanus* cave populations experienced introgressive hybridization events with recent surface populations (0.26-2.0 Ma), possibly also correlated with Pleistocene events. Finally, using divergence times from surface populations in the lineage without evidence of introgression as an estimate, the acquisition of the troglomorphic form in *A. mexicanus* is younger than 2.2 (fossil calibration estimates) – 5.2 (cytb estimate) Ma (Pliocene).

Key words: *Astyanax mexicanus,* divergence time, troglomorphy, subterranean, evolution.

Izvleček UDK 551.44:597
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Megan L. Porter, Katharina Dittmar & Marcos Pérez-Losada: Kako dolgo traja evolucija troglomorfnih oblik? Ocenjevanje divergenčnih časov pri Astyanax mexicanus

Značilnosti, ki vključujejo tudi kolonizacijske poti in obstoj tako epigejičnih kot hipogejičnih populacij vrste *Astyanax mexicanus,* ji omogočajo, da predstavlja zanimiv sistem za proučevanje evolucije in časa, potrebnega za razvoj podzemeljskih troglomorfnih oblik. Za *A. mexicanus* smo na podlagi že objavljenih sekvenc ocenili divergenčni čas ob uporabi: 1) dveh različnih populacijskih mitohondrialnih podatkovnih baz (citokrom b in NADH dehidrogenaze 2), obe z natančno in sproščeno metodo molekularne ure, in 2) razširjenega filogenetskega pristopa v kombinaciji s fosilno kalibracijo ter štirimi jedrnimi geni (rekombinacijski aktivacijski gen, »forkhead kontrolni gen« in α-tropomiozin) in dvema mitohondrialnima genoma (16S rDNA in citokrom b). Ob uporabi navedenih podatkovnih baz smo ocenili divergenčni čas za tri dogodke v zgodovini razvoja troglomorfnih populacij *A. mexicanus.* Prvič, razhajanje med podzemeljskimi haplotipi se je zgodilo v Pleistocenu, verjetno v odvisnosti od nihanja vode, ki je omogočilo kolonizacijo in posledično izolacijo v novih podzemeljskih habitatih. Drugič, verjetno je v povezavi s pleistocenskimi dogodki pri eni liniji podzemeljskih populacij *A. mexicanus* prišlo do introgresivne hibridizacije s takratnimi površinskimi populacijami (0.26-2.0 Ma). Z uporabo divergenčnega časa površinskih populacij tistih linij, ki ne kažejo introgresije ocenjujemo, da je troglomorfna oblika *A. mexicanus* mlajša od 2,2 (ocene fosilne kalibracije) do 5,2 milijona let (cytb ocena) (Pliocen).

Ključne besede: *Astyanax mexicanus,* divergenčni čas, troglomorfizem, podzemlje, speleobiologija, evolucija.

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Received/Prejeto: 06.12.2006

INTRODUCTION

Understanding the evolution of the cave form has fascinated biologists interested in subterranean faunas since Darwin. Termed 'troglomorphy', the suite of progressive and regressive characters associated with cavernicolous animals can be observed in the worldwide convergence of form found in the cave environment, exhibited in similar structural, functional, and behavioral changes across diverse taxonomic groups. Much of the debate over troglomorphy has centered on the evolutionary mechanisms responsible for character regression, generally argued to be either neutral mutation or natural selection. Several studies, *(Gammarus minus* - Culver *et al.*, 1995; *Astyanax mexicanus* – Jeffery, 2005) have shown eye degeneration is the result of selection, and, in the case of *A. mexicanus,* is caused by the pleiotropic effects of natural selection for constructive traits. Another, less studied, aspect of understanding troglomorphy is the evolutionary time required to gain the cave form. Because it is generally difficult to pinpoint the time of subterranean colonization and isolation from surface ancestors, few troglomorphic species offer the opportunity for quantitative estimates of the evolutionary time spent in the subterranean realm. Therefore, the time of cave adaptation is thought of in relative terms, where the degree of eye and pigment reduction indicates the period of cavernicolous evolution and therefore the relative phylogenetic age of each species (Aden, 2005).

In evolutionary studies of cave adaptation, *Astyanax mexicanus* has become a model system (Jeffery, 2001). The advantageous features of *A. mexicanus* as a model system include the existence of both surface and troglomorphic cavefish populations, with several cave fish populations having evolved constructive and regressive changes independently (Jeffery, 2001). Furthermore, since the discovery of the species in 1936 (Hubbs & Innes, 1936), there has been an extensive amount of research devoted to characterizing developmental, phylogenetic, taxonomic, and biogeographic aspects of the species (Jeffery, 2001; Mitchell *et al.*, 1977; Wiley & Mitchell, 1971;). In terms of being a model system for understanding the evolution of the troglomorphic form, *A. mexicanus* has at least one additional favorable attribute. The primary mode of *A. mexicanus* subterranean colonization is via stream capture, with most of the captured surface drainages no longer supporting epigean populations (Mitchell *et al.*, 1977). These captures provide discrete colonization events correlated with divergence time from surface populations and therefore with the time of subterranean evolution.

Molecular studies that have looked at *A. mexicanus* phylogeography indicate that at least two independent invasions of surface *Astyanax* have occurred (Dowling *et al.*, 2002a; Strecker *et al.*, 2003, 2004). These two distinct *A. mexicanus* genetic lineages consist of cave fish from La Cueva Chica, La Cueva de El Pachón, El Sótano de Yerbaniz, El Sótano de Molino, El Sótano de Pichijumo, and La Cueva del Río Subterráneo (lineage A) and from La Cueva de los Sabinos, El Sótano de la Tinaja, La Cueva de la Curva, and El Sótano de Las Piedras (Lineage B) with different evolutionary histories - Lineage A clusters with closely related epigean populations while lineage B has no closely related epigean counterparts. The close association of Lineage A to epigean populations (as estimated by mitochondrial markers) is thought to be the result of either recent subterranean colonization or reflect recent introgressive hybridization with surface populations, while lineage B is considered to be a more ancient colonization event from surface populations that are extinct in the region (Dowling *et al.*, 2002a; Strecker *et al.*, 2004). Although the evolutionary histories of different hypogean A. mexicanus populations are complex, the two lineages offer the unique opportunity to estimate the divergence time required for the evolution of the troglomorphic form based on discrete times of colonization and the previous molecular studies of their phylogeography. At least one other study has estimated lineage ages in *A. mexicanus* populations; however, this study was based on a single gene molecular clock estimate and did not specifically estimate the divergence times of the cave populations (Strecker *et al.*, 2003). Here we use three different sets of publicly available sequence data and known fossil calibrations and apply multiple phylogenetic approaches to estimate the age of cave colonization and stream capture events, and to provide an estimate of the time necessary to acquire the troglomorphic form in *A. mexicanus.*

METHODS

Sequence Data

Data were acquired from Genbank (http://www.ncbi.nlm.nih.gov/) from previously published studies of *A. mexicanus* and characiform fishes (Tab. 1). These studies provided three different datasets, consisting of: 1) population-level haplotype datasets for the mitochondrial cytochrome b (cytb; Strecker *et al.*, 2004) and NADH dehydrogenase 2 (ND2; Dowling *et al.*, 2002a) genes, and 2) a species-level dataset of four nuclear (recombination activating gene – RAG2; seven in absentia – sina; forkhead – fkh; and *α*-tropomyosin - trop) and two mitochondrial genes (16S rDNA and cyt*b*) from representatives within the Otophysi (Calcagnotto *et al.*, 2005). Divergence times from all three data sets were estimated and compared.

Species-level Phylogenetic Analyses

The species-level dataset included selected Otophysi, Characiformes, and Characidae sequences (see Tab. 1), and was analyzed using Anotophysi species as outgroups. Representative *A. mexicanus* cyt*b* haplotype sequences from the Strecker *et al.,* (2004) study were included in the dataset of characiform species to estimate divergence times based on fossil calibrations for comparison with population-based estimates utilizing substitution rates. Alignments of protein-coding regions were trivial and were accomplished using amino acid translations. Sequences of the trop gene spanned an intron, which was removed due to significant length variation (70-836 bp) leading to ambiguous alignments. The alignment of the 16s rDNA gene was generated using the E-INS-i accuracy-oriented strategy of MAFFT v.5 (Katoh *et al.,* 2005). All of the individually aligned genes were then concatenated to form a single dataset consisting 3770bp in length. The concatenated dataset was analyzed with PAUP* 4.0b10 (Swofford, 2000) using maximum parsimony and implementing the parsimony ratchet method (Nixon, 1999) using a batch file generated by PAUPRat with the default parameters for 5000 replicates (Sikes & Lewis, 2001).

Divergence time estimation

Population analysis. Dates of divergence were inferred for A. mexicanus lineage A and B cave fish populations using the cyt*b* and ND2 datasets with BEASTv1.4 (Drummond & Rambaut, 2003). Because the cytb and ND2 haplotype datasets were generated from different studies, they cannot be combined. Therefore, each dataset was used to independently estimate the divergence times of the *A. mexicanus* cave-adapted haplotype sequences. Each dataset was analyzed using both strict and relaxed clock models (Drummond *et al.,* 2006) tested under constant and skyline models of population growth. As part of BEAST divergence time estimation, either a calibration point (fossil or geologic) or a gene-specific substitution rate is required. Because there are no geologic dates corresponding to *A. mexicanus* populations invading subterranean systems, substitution rates were used. For each gene, the range of substitution rates calculated for other freshwater fish were used. For cyt*b*, mean substitution rates ranged from 0.005 to 0.017 substitutions/site/million year (my) (Bermingham *et al.*, 1997; Burridge *et al.*, 2006; Dowling *et al.,* 2002b; Perdices & Doadrio, 2001; Sivasundar *et al.,* 2001; Zardoya & Doadrio, 1999) and for ND2 mean substitution rates ranged from 0.011 to 0.026 substitutions/site/my (Near *et al.,* 2003; Mateos, 2005). These independent rates were used to calibrate the rate of evolution of our datasets by either fixing the rate to the lowest and highest value estimated for each gene or using strong prior distributions on the substitution rates. Two independent MCMC analyses $2x10^7$ steps long were performed sampling every 2,000th generation, with a burn-in of $2x10^6$ generations. All the Bayesian MCMC output generated by BEAST was analyzed in Tracer v1.3 (Drummond & Rambaut, 2003).

Likelihood-based AHRS method. We used the likelihood heuristic rate-smoothing algorithm of (Yang, 2004) as implemented in PAML3.14 (Yang, 2001). Sequence data were analyzed using the F84+Γ model. Branches at each locus were classified into four rate groups according to their estimated rates. The oldest known fossil representatives of major lineages within the Ostariophysi are well established in recent literature (see Briggs, 2005 and references therein), and have been used in recent studies estimating molecular-based divergence times of Otocephalan clades (Peng *et al.,* 2006). These fossil representatives were used as calibration points for the AHRS divergence time analysis (Fig. 1, Tab. 2,). Fossil calibrations were accommodated as fixed ages and mapped to the basal node of the clade of interest. Given that most fossils are dated to an age range, the minimum and maximum ages of each fossil were used for divergence time estimations under separate analyses. Fossil dates were determined using the 1999 GSA Geologic Time Scale.

Tab. 1: Taxonomy, gene data, and Genbank accession numbers for sequences used in Characiformes phylogeny reconstruction. Abbreviations of mitochondrial gene sequences: 16S = 16S rDNA, cytb = cytochrome b; abbreviations for nuclear gene sequences: fkh = forkhead, RAG2 = recombination activating gene, sina = seven in absentia, trop = α-tropomyosin.

	16S	**cytb**	**fkh**	**RAG2**	**sina**	**trop**
Anotophysi (outgroup)						
Chanidae						
Chanos chanos	NC004693	NC004693	---	---	---	---
Gonorynchidae						
Gonorynchus greyi	NC004702	NC004702	---	---	---	---
Kneriidae						
Cromeria nilotica	NC007881	NC007881	---	---	---	---
Parakneria cameronensis	NC007891	NC007891	---	---	---	---
Otophysi (ingroup)						
CHARACIFORMES						
Anostomidae						
Leporinus sp.	AY788044	AY791416	AY817370	AY804095	AY790102	AY817252
Chilodontidae						
Chilodus punctatus	AY787997	---	AY817325	---	AY790056	AY817215
Prochilodontidae						
Prochilodus nigricans	AY788075	AY791437	AY817400	AY804120	AY790133	AY817278
Hemiodontidae						
Hemiodus gracilis	AY788027	AY791405	AY817353	AY804084	AY790086	AY817240
Parodontidae						
Parodon sp.	AY788065	AY791427	AY817390	AY804110	AY790123	AY817269
Serrasalmidae						
Colossoma macropomum	AY788000	AY791386	AY817328	AY804061	AY790059	AY817218
Cynodontidae						
Hydrolycus pectoralis	AY788033	---	AY817359	AY804088	AY790091	AY817244
Characidae						
Acestrorhynchus sp.	AY787956	AY791353	AY817288	AY804026	AY790014	AY817181
Aphyocheirodon sp.	AY787966	AY791363	AY817298	AY804031	AY790025	---
Astyanacinus sp.1	AY787969	AY791365	AY817301	AY804033	AY790028	AY817190
Astyanacinus sp.2	AY787987	---	AY817317	AY804051	AY790046	AY817209
Astyanax bimaculatus	AY787955	---	AY817287	AY804025	AY790013	AY817180
Astyanax mexicanus (Brazil)	---	AY177206	---	---	---	---
Astyanax mexicanus (haplotype AB)	--	AY639041	--	--	--	--
Astyanax mexicanus (haplotype AL)	--	AY639051	--	--	--	--
Astyanax mexicanus (haplotype EA)	--	AY639075	--	--	--	--
Astyanax mexicanus (haplotype FA)	--	AY639084	--	--	--	--
Astyanax mexicanus (haplotype GA)	--	AY639089	--	--	--	--
Astyanax mexicanus (haplotype GB)	--	AY639090	--	--	--	--
Astyanax scabripinis	AY787967	---	AY817299	---	AY790026	AY817188
Brycon hilarii	AY787976	AY791370	AY817307	AY804040	AY790035	AY817198
Bryconamericus diaphanus	AY787984	AY791375	AY817314	AY804048	AY790043	AY817206
Bryconops sp.	AY787985	AY791376	AY817315	AY804049	AY790044	AY817207
Chalceus erythrurus	AY787990	AY791379	AY817320	AY804053	AY790049	AY817211
Chalceus macrolepidotus	AY787999	AY791385	AY817327	AY804060	AY790058	AY817217
Cheirodon sp.	AY787995	AY791382	AY817324	AY804057	AY790054	---
Cheirodontops sp.	AY787996	AY791383	---	AY804058	AY790055	---
Creagrutus sp.	AY788001	---	---	AY804062	AY790060	AY817219
Exodon paradoxus	AY788013	AY791397	AY817340	AY804072	AY790072	AY817227
Gephyrocharax sp.	AY788014	AY791398	AY817341	AY804073	AY790073	AY817228
Hemibrycon beni	AY788020	AY791402	AY817346	AY804079	AY790079	AY817234
Hemigrammus bleheri	AY788017	---	AY817343	AY804076	AY790076	AY817231

	16S	**cytb**	**fkh**	**RAG2**	**sina**	**trop**
Hemigrammus erythrozonus	AY788023	---	AY817349	AY804081	AY790082	AY817236
Hemigrammus rodwayi	AY788034	---	AY817360	AY804089	AY790092	AY817245
Hyphessobrycon eques	AY788022	---	AY817348	AY804080	AY790081	AY817235
Inpaichthys kerri	AY788039	---	AY817365	AY804093	AY790097	AY817248
Knodus sp.	AY788041	AY791414	AY817367	AY804094	AY790099	AY817249
Moenkhausia sanctaphilomenae	AY788054	---	---	AY804104	AY790112	AY817261
Mimagoniates lateralis	AY788051	AY791420	AY817377	AY804101	AY790109	AY817259
Prodontocharax sp.	AY788064	AY791426	AY817389	AY804109	AY790122	---
Roeboides sp.	AY787994	AY791381	AY817323	AY804056	AY790053	AY817214
Salminus maxillosus	AY788080	AY791438	AY817405	AY804124	AY790137	AY817282
Triportheus angulatus	AY788082	---	AY817407	AY804125	AY790139	AY817283
Ctenolucidae						
Ctenolucius hujeta	AY787998	AY791384	AY817326	AY804059	AY790057	AY817216
Lebiasinidae						
Nannostomus beckfordi	AY788059	---	AY817384	---	AY790117	AY817265
Crenuchidae						
Characidium fasciatum	AY787992	AY791380	AY817322	AY804055	AY790051	AY817213
Erythrinidae						
Hoplias sp.	AY788031	AY791409	AY817357	AY804087	AY790090	AY817242
Alestidae						
Arnoldichthys spilopterus	AY787968	AY791364	AY817300	AY804032	AY790027	AY817189
Brycinus nurse	AY787970	AY791366	AY817302	AY804034	AY790029	AY817191
Phenacogrammus aurantiacus	AY788066	AY791428	AY817391	AY804111	AY790124	AY817270
Hepsetidae						
Hepsetus odoe	AY788030	AY791408	AY817356	AY804086	AY790089	AY817241
Citharinidae						
Citharinus citharus	AY787989	AY791378	AY817319	---	AY790048	---
Distichodontidae						
Distichodus sexfasciatus	AY788012	AY791396	AY817339	AY804071	AY790071	AY817226
Neolebias trilineatus	AY788063	AY791425	AY817388	AY804108	AY790121	AY817268
CYPRINIFORMES						
Cobitidae						
Misgurnus sp.	AY788053	---	AY817379	AY804103	AY790111	---
Cyprinidae						
Danio rerio	AY788011	---	AY817338	AY804070	AY790070	AY817225
Labeo sorex	AY788043	AY791415	AY817369	---	AY790101	AY817251
Gyrinocheilidae						
Gyrinocheilus sp.	AY788015	AY791399	---	AY804074	AY790074	AY817229
SILURIFORMES						
Callichthyidae						
Corydoras rabauti	NC004698	NC004698	---	---	---	---
Loricariidae						
Ancistrus sp.	AY787958	AY791354	AY817290	---	AY790016	AY817183
Bagridae						
Chrysichthys sp.	AY787957	AY791355	---	---	AY790017	AY817193
Heptapteridae						
Pimelodella sp.	AY787953	AY791351	AY817285	---	AY790011	AY817178
Ictaluridae						
Ictalurus punctatus	AY788040	AY791413	AY817366	---	AY790098	---

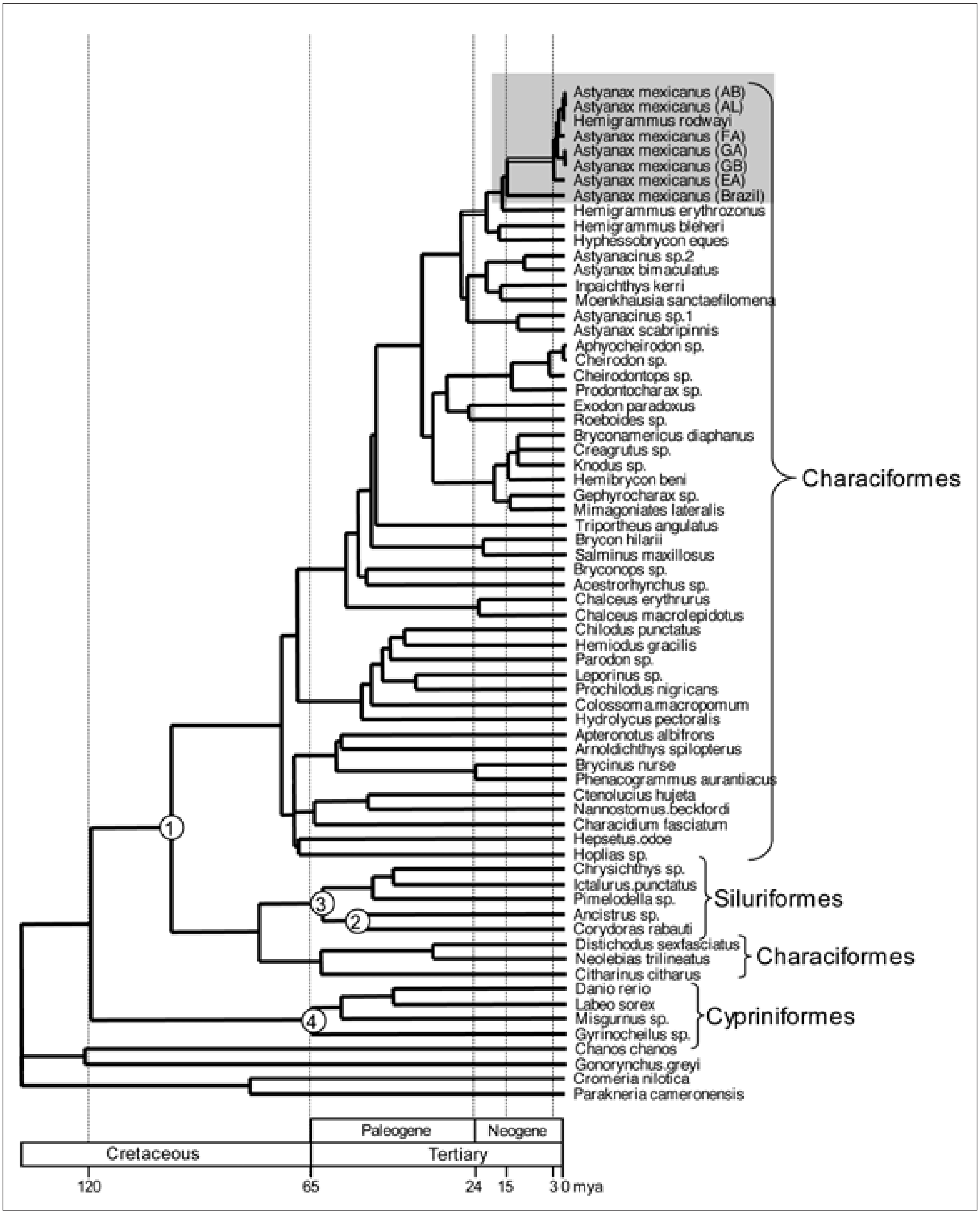

Fig. 1: Characiform divergence time chronogram estimated using a representative topology chosen from the set of 867 most parsimonious trees. White branches indicate branches where less than 75% of the most parsimonious trees were topologically congruent. The grey box indicates the clade of Astyanax mexicanus sequences. Fossil calibration nodes are numbered and correspond to Tab. 2. The major geologic periods are mapped onto the phylogeny.

Tab. 2: Taxonomy and ages of fossils used as calibrations for divergence time estimation. Node # refers to Fig. 1.

Taxonomy	**Reference**	**Geologic age (MYA)**	**Node #**
Otophysi			
Characiformes	Gayet, 1982	Late Cretaceous (65-99)	1
Cypriniformes			
Catostomidae	Cavender, 1986	Paleocene (54.8-65)	4
Siluriformes	Gayet & Meunier, 2003	late Campanian-early Maastrichtian (68.2-77.4)	3
Corydoras	Cockerell, 1925	Late Palaeocene (61-65)	2

RESULTS

Population-level divergence time estimations. Estimates of the mean divergence times were not significantly different between strict and relaxed clock and population growth models and calibration methods of the substitution rate, but confidence intervals under the fixed substitution rate approach were narrower, as expected. Hence only the time estimates under the strict clock model, constant population size and minimum and maximum mean substitution rates for both genes are provided. Comparing the cytb and ND2 estimates of divergence times for the *A. mexicanus* A and B lineages show several features. First, the estimated ranges of divergence for cave haplotypes within each lineage were similar between genes (cyt*b* and ND2) and lineages (A and B), placing the divergence among hypogean populations between 0.141-0.885 Ma for lineage A, and 0.084-0.575 Ma for lineage B (Tab. 3). When comparing the estimates among genes within a lineage, however, the divergence times of hypogean and epigean haplotypes are different, with cytb estimates providing generally older estimates.

Species-level divergence time estimation. Using the maximum parsimony ratchet, the selected Characidae, Characiform, and Otophysi sequences generated 867 trees of score 11758. The 50% majority rule consensus of these trees was similar to the published research that generated the data (Calcagnotto *et al.*, 2005). Because a fully resolved tree with branch lengths is required for AHRS divergence time estimation and because very few branches in the consensus tree collapsed (e.g. were in conflict), a random tree from the set of 867 was used (Fig. 1). The *A. mexicanus* sequences included in the analysis clustered with other Characidae species, although were not monophyletic with other Astyanax species *(A. bimaculatus* and *A. scabripinnis).* The divergence time estimates for the representative *A. mexicanus* cave fish populations generated using this phylogeny with Otophysi fossil calibrations agreed well with the estimates of hypogean haplotype divergence from cyt*b* and ND2 using substitution rates (Tab. 3). However, the estimates of cave versus surface population divergence times based on fossil calibrations were in better agreement with ND2 than with cytb estimates. This is particularly interesting, as the only gene included in this dataset for *A. mexicanus* was cyt*b*.

Tab. 3: Comparison of divergence time estimates using substitution rates and molecular clock methods for cytochrome b (cytb) and NADH dehydrogenase 2 (ND2) mitochondrial genes, and for molecular methods incorporating fossil dates as calibrations.

	Substitution Rates		**Fossil Calibration**
	Cytb	ND2	
	Min – Max (Ma)	Min – Max (Ma)	Min – Max (Ma)
Lineage A			
cave	0.261 – 0.885	0.141 - 0.331	0.2-0.3
cave vs. surface	0.588 - 2.00	0.256 – 0.599	0.4-0.5
Lineage B			
cave	0.169 – 0.575	0.084 - 0.196	0.1-0.1
cave vs. surface	1.524 – 5.181	0.877 – 2.055	1.7-2.2
Lineage A vs. Lineage B	1.741 – 5.922	1.053 – 2.472	1.7-2.2

DISCUSSION

Previous molecular studies of *A. mexicanus* phylogeography indicate that at least two independent invasions of surface Astyanax have occurred (Dowling *et al.,* 2002a; Strecker *et al.,* 2003, 2004). Our estimates of divergence time from two different methods and three different datasets are in general agreement about the divergence times among the cave haplotypes in each lineage (Tab. 3). These estimates place cave haplotype divergence times in the Pleistocene, when it is suggested that climatic cooling of surface waters led to the extinction of *Astyanax* in North America (Strecker *et al.,* 2004). In particular, our data show an interesting pattern for lineage B haplotypes, which are proposed to be the older of the two lineages. The recent divergence times estimated for lineage B haplotypes (0.084-0.575 Ma) supports the hypothesis that after the initial colonization event, subterranean routes of colonization were associated with fluctuating groundwater levels in the Pleistocene (Strecker *et al.,* 2004). The fact that estimated times of within lineage divergence were similar also suggests that the divergence of subterranean haplotypes in both lineages were influenced by the same processes.

In order to determine the evolutionary age of the subterranean lineage, and therefore estimate the time required for evolution of the troglomorphic form, the divergence of the hypogean haplotypes from epigean populations is needed. However, the estimates from our three datasets did not agree, with cyt*b* molecular clock methods estimating older divergence times than either ND2 or fossil calibrated estimates. Some of the discrepancy is due to the fact that different sets of surface populations were sampled in each study (Dowling *et al.,* 2002a; Strecker *et al.,* 2004). For example, the most closely related surface population in the cyt*b* study were from Belize (Strecker *et al.,* 2004) while there were no closely related surface populations to lineage B haplotypes in the ND2 study (Dowling *et al.,* 2002a). However, this makes the older cytb estimates even more notable because lineage B haplotypes have no evidence of introgressive hybridization with surface populations. If we consider just lineage B hypogean divergence from surface ancestors as an estimate of subterranean evolution, the estimated time for acquisition of the troglomorphic form is 0.877-2.055 Ma (Quaternary – Tertiary boundary) based on ND2 and fossil calibrations, while it is 1.524-5.181 Ma (Pliocene) based on cyt*b*.

Although the estimates of divergence times among the three different datasets did not agree, comparison of estimates between the lineages show that lineage A diverged from surface ancestors more recently than lineage B (Tab. 3). This more recent divergence from epigean populations is congruent with previous hypotheses, that either lineage A populations represent a more recent subterranean invasion, or that they are an older invasion masked by more recent mitochondrial introgressive hybridization with surface forms (Dowling *et al.,* 2002a). In the few studies that have looked at other markers (allozymes, microsatellites, and RAPDs), it has been suggested that at least Chica and Pachón populations are the result of surface introgression (Avise & Selander, 1972; Espinasa & Borowsky, 2001; Strecker *et al.,* 2003). Furthermore, based on the degree of variability in troglomorphic features of each lineage A population, it has been suggested that different populations represent different degrees and patterns of surface introgression. In order to more accurately determine both the patterns of introgression in the lineage A populations, as well as the underlying relationships of the cave populations to each other in order to estimate subterranean evolutionary times, studies investigating more types of markers are needed.

Previous research of *A. mexicanus* populations throughout Mexico (including cavefish lineages A and B) estimated haplotype divergences to range from 1.8 – 4.5 Ma (Strecker e*t al.,* 2004). Our estimates suggest that divergence times among cave haplotypes and between lineage A cave and epigean haplotypes are much younger than this; however, hypogean divergences from surface ancestors in lineage B are concordant with these older dates.

The evolutionary history of cave adaptation in *A. mexicanus* is complex. Based on mitochondrial molecular clock estimates, our estimates of divergence times are congruent with previous hypotheses by showing lineage B to be a phylogenetically older subterranean lineage, with more recent divergence among subterranean systems. However, this study also provides quantitative dates for these events. Lineage A populations are estimated to be younger; however, these dates only represent mitochondrial lineages. Several of the populations in lineage A have been shown to be introgressed with surface forms (Chica, Pachón, and Subterraneo). To our knowledge, the hypothesis of surface introgression has not been investigated in the remaining lineage A populations (Molino, Pichijumo, and Yerbaniz). Understanding the patterns of introgression in all of the lineage A populations, and estimating the actual subterranean evolutionary time, requires investigating additional nuclear markers.

CONCLUSIONS

Features including colonization routes (stream capture) and the existence of both epigean and cave-adapted hypogean populations make *A. mexicanus* an attractive system for investigating the subterranean evolutionary time necessary for acquisition of the troglomorphic form. If it is possible to estimate the divergence time of closely related cave versus surface populations, we can estimate the age of subterranean occupancy. This same divergence time also has relevancy to geologic processes in the karst system by providing a rough estimate of the age of subterranean stream capture in particular regions. Based on published sequence data, we have estimated divergence times for three events in the evolutionary history of troglomorphic *A. mexicanus* populations. First, divergence times among cave haplotypes in both lineages occurred in the Pleistocene, possibly correlating with fluctuating water levels allowing the colonization, and subsequent isolation of, new subterranean habitats. Second, in lineage A, *A. mexicanus* cave populations experienced introgressive hybridization events with surface populations recently. Finally, using divergence times of lineage B from surface populations as an estimate, the acquisition of the troglomorphic form in *A. mexicanus* is younger than 2.2 (fossil calibration) – 5.2 (cytb) Ma (Pliocene). Given that there are at least 30 caves known to contain populations of *A. mexicanus* (Espinasa *et al.,* 2001; Mitchell *et al.,* 1977), the number of independent invasions and instances of introgressive hybridization may be even higher than currently understood. In order to fully understand the number of independent invasions, the history of introgression with surface populations, and the divergence times of cave and surface populations, a broader survey of cave fish populations and of both nuclear and mitochondrial markers is needed.

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AGE ESTIMATES FOR SOME SUBTERRANEAN TAXA AND LINEAGES IN THE DINARIC KARST

OCENE STAROSTI ZA NEKATERE PODZEMELJSKE TAKSONE IN ŽIVALSKE LINIJE NA DINARSKEM KRASU

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Abstract UDC 575.8:551.442(234.422.1)
591.542(234.422.1)

Peter Trontelj, Špela Gorički, Slavko Polak, Rudi Verovnik, Valerija Zakšek & Boris Sket: Age estimates for some subterranean taxa and lineages in the Dinaric Karst

Using a comparative phylogeographic approach and different independent molecular clocks we propose a timescale for the evolution of troglobionts in the Dinaric Karst that is relatively consistent over a wide taxonomic range. Keystone events seem to belong to two age classes. (1) Major splits within holodinaric taxa are from the mid-Miocene. They present the potential upper limit for the age of cave invasions. (2) Regional differentiation, including speciation, which can at least in part be associated with a subterranean phase, took place from early Pliocene to mid-Pleistocene. We suggest two to five million years as the time when most of the analyzed lineages started invading the Dinaric Karst underground.

Key words: subterranean, molecular clock, molecular phylogeny, phylogeography, Dinaric Karst.

Izvleček UDK 575.8:551.442(234.422.1)
591.542(234.422.1)

Peter Trontelj, Špela Gorički, Slavko Polak, Rudi Verovnik, Valerija Zakšek & Boris Sket: Ocene starosti za nekatere podzemeljske taksone in živalske linije na Dinarskem krasu

Z uporabo primerjalnega filogeografskega pristopa in neodvisnih molekularnih ur smo predlagali časovni potek evolucije troglobiontov Dinarskega krasa, ki velja za sorazmerno veliko število taksonov. Zdi se, da ključni dogodki pripadajo dvema obdobjema. (1) Glavne razdelitve znotraj holodinarskih taksonov so iz obdobje srednjega miocena. Predstavljajo zgornji potencialni časovni limit za naselitev jam. (2) Regionalna diferenciacija, vključno s speciacijo, ki je lahko vsaj deloma povezana s podzemeljsko fazo, naj bi se zgodila med zgodnjim in srednjim pleistocenom. Ocenjujemo, da se je začela invazija večine proučevanih živalskih linij v podzemlje Dinarskega krasa v obdobju med dvema in petimi milijoni let.

Ključne besede: podzemlje, molekularna ura, molekularna filogenija, filogeografija, Dinarski kras.

INTRODUCTION

The use of new molecular and systematic techniques using allozymes and DNA sequences has enabled us to see a new picture of the evolution and diversity of subterranean fauna (e.g. Avise & Selander 1972; Sbordoni *et al.,* 2000; Caccone & Sbordoni 2001; Leys *et al.,* 2003; Verovnik *et al.,* 2004; Gorički & Trontelj 2006; Lefébure *et al.,* 2006; Zakšek *et al.,* 2007). Molecular clock approaches should, at least in theory, enable us to date, to verify or to falsify previous hypotheses about the age of subterranean species. To be exact, it is usually not the age of a lineage or a taxon itself that is of special interest or under dispute, but the time since it has attained its subterranean nature, making it even more challenging. Hypotheses and models explaining cave invasions

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Received/Prejeto: 30.01.2007

and speciation in caves are well-elaborated (e.g. Rouch & Danielopol 1987; Holsinger 2000; Trajano 2005) and should thus offer good grounds for the timing of such events and for testing their correlation with geographical, geological and hydrographical counterparts. For example, Leys *et al.,* (2003) have shown that all evolutionary transitions to subterranean life in Australian dytiscids took place during the Late Miocene and Early Pliocene as a result of aridification. However, reliable data on the age of these events is surprisingly scarce. When such data are available, the accuracy is often below that of molecular clock rates. In fact, the use of molecular dating methods itself has introduced considerable uncertainty about how old subterranean species might be. While the youngest estimation, based on "classical" biological reasoning, is no more than 10,000 years (Sket 1997), the upper limit for the divergence of two subterranean sister species has been pushed to an incredible 110,000,000 years (Buhay & Crandall 2005).

Boutin and Coineau (2000) have argued that dating of cladogenetic events by a molecular clock is particularly useful in the case when the dates are corroborated by other methods. Since the obvious problem of the Dinaric Karst area is that reliable dating for clearly defined vicariant events or the age of available subterranean habitat is lacking, it has been impossible to corroborate molecular clock divergence by independent data. In this case a comparative phylogeographic approach might provide the means for an independent validation of age estimates. Comparative phylogeography seeks, as does historical biogeography, concordant geographical patterns of codistributed lineages (e.g. Arbogast & Kenagy 2001). The evolution of codistributed phylogeographic groups of different taxa is likely to have been driven by the same historical factors, like vicariant events or climatic shifts.

In this contribution we (1) identify common phylogeographic patterns among those troglobiotic taxa from the Dinaric Karst for which such data are available, and (2) estimate the timeframe of the corresponding cladogenetic events using a global molecular clock approach.

MATERIAL AND METHODS

The presented data were taken from several phylogeographic studies of subterranean animals in the Dinaric Karst, including the ubiquitous aquatic isopod *Asellus aquaticus* Linne (Verovnik *et al.,* 2004, 2005), the cave salamander P*roteus anguinus* Laurenti (Gorički 2006, Gorički & Trontelj 2006), and the cave shrimp *Troglocaris* s. lato (Zakšek *et al.,* 2007). Further, we included unpublished sequences from studies that are in progress, including leptodirine cave beetles and aquatic sphaeromatid isopods from the genus *Monolistra.* The age estimations for the last two groups should be regarded as preliminary because in-depth analyses of phylogenetic relationships and corroboration by further loci are still under way. We were only interested in a small number of well-supported splits and therefore used straightforward minimum evolution searches with bootstrapping as implemented in MEGA (Kumar *et al.,* 2004). Divergence time estimates are based on available clock-rate data for groups that are as closely related as possible (Caccone & Sbordoni [2001] for leptodirines, Ketmaier *et al.,* [2003] for *Asellus aquaticus,* and Sturmbauer *et al.,* [1996] and Schubart *et al.,* [1998] for *Monolistra).* To assure compatibility between molecular divergences we used the same models as were used in the original works describing the rates (Tamura-Nei distances with a gamma distributed rate variation among sites). Where more than one haplotype per population or lineage was analyzed we used net between group distances to correct for ancestral intraspecific diversity.

RESULTS

The split between major geographically defined lineages

The geographical distribution of troglobiotic (including stygobiotic) sister taxa can be used to infer independent cave invasions. For example, if the present-day ranges of two troglobionts are separated by large areas of non-karstic terrain without hypogean habitat, we can postulate an epigean last common ancestor. Examples of that kind can be found in the shrimp genus *Troglocaris,* with the *Hercegovinensis* lineage inhabiting Transcaucasian and SE parts of the Dinaric Karst where it is sympatric with the SE populations of the Anophthalmus lineage (Zakšek *et al.,* 2007). Their split estimated at 6–11

Myr ago is the oldest, although unlikely, possible time of cave invasion. The youngest split that could be reliably inferred from the phylogenetic tree and probably still occurred in surface waters, was the one between the Bosnian lineage and other *"Anophthalmus"* lineages. Because the karst area in Bosanska Krajina, to which the Bosnian clade is restricted, is so remote and isolated from the rest of the Dinaric populations, it is reasonable to assume that an underground connection between them could never have existed. The estimated time of this split, 3.7–5.3Myr ago, is hence the oldest possible age at which *Troglocaris anophthalmus* might have invaded the Dinaric Karst underground (Tab. 1).

For the cave salamander *Proteus anguinus,* exhibiting a distribution pattern similar to that of *Troglocaris,* the corresponding age of the Bosanska Krajina lineage was estimated at 4.4–5.4 Myr (Gorički 2006). However, older lineages exist that, theorethically, might have invaded caves even as early as 8.8–16 Myr ago (see also Fig. 1).

Another troglobiotic group restricted to the Dinaric Karst area and having a non-troglomorphic sister group is the Dinaric clade of *Asellus aquaticus* (see Verovnik *et al.,* 2005). The time of this split, and hence the maximum possible age of cave invasion is 3.8–4.8 Myr.

TIMING OF MORPHOLOGICAL CHANGES

Where possible, we tried to combine the biology (e.g. degree of troglomorphism, lack of gene flow) of taxa with corresponding data on paleogeography and paleohydrography to infer speculative scenarios on how and when lineages might have switched to subterranean life and evolved troglomorphic traits. For example, we have some indication about how long at most it takes a salamander population to become troglomorphic. Since the subspecies *P. a. parkelj* Sket et Arntzen has retained its ancestral, non-troglomorphic characteristics, it is reasonable to conclude that its sister lineage must have evolved troglomorphoses independently from other, less related troglomorphic lineages (Sket & Arntzen 1994; Gorički & Trontelj 2006; see Fig. 1). The split between the non-troglomorphic lineage and its last troglomorphic sister lineage was estimated at 0.5–0.6 Myr based on mitochondrial rDNA sequences, 1.1–2.4 Myr based on the mtDNA control region (Gorički 2006), and at 1.1–4.5 Myr by an allozyme clock (Sket & Arntzen 1994).

Asellus aquaticus has evolved several separate subterranean and troglomorphic populations. One of them, from the subterranean Reka River below the Kras/Carso Plateau, is genetically completely isolated from epigean populations at the Reka resurgence while there are no epigean populations in the Reka before the sink (Verovnik *et al.,* 2003, 2004, 2005; Fig. 2). Further, it has no mtDNA

Tab. 1. Estimated time (in million years) of some keystone events in the evolution of troglobionts in the Dinaric Karst.

Taxon	*Age of holodinaric group*	*Age of merodinaric group*	*Mid-Dinaric split*	*Northwest split*
Troglocaris (Dinaric and Caucasian lineages)[1]	7.9–15.1	n.a.	n.a.	n.a.
Troglocaris anophthalmus agg.[1]	n.a.	3.7–5.3	1.3–2.3	1.5–2.1
Troglocaris hercegovinensis agg.[1]	n.a.	3.8–4.8	n.a.	n.a.
Proteus anguinus[2]	8.8–16.0	n.a.	8.8–16.0	4.2–5.2
Asellus aquaticus (Dinaric clade)[3]	n.a.	3.8–4.8	n.a.	0.8–1.2
Microlistra[4]	n.a.	1.1–2.3	n.a.	n.a.
Pseudomonolistra hercegoviniensis[4]	n.a.	0.3–1.0	n.a.	n.a.
Monolistra caeca[4]	n.a.	1.8–3.7	n.a.	n.a.
Leptodirus hochenwartii hochenwartii et L. h. reticulatus[5]	n.a.	1.9–2.0	n.a.	n.a.

[1] *Using COI clock for shrimps (see Knowlton & Weigt 1998; Zakšek et al., 2007)*

[2] *Using 12S and 16S rDNA clock for Newts (see Cacconesee et al., 1997; Gorički 2006)*

[3] *Using COI clock for subterranean Asellota (see Ketmaier et al., 2003; Verovnik et al 2005)*

[4] *Using 16S r-RNA clock for fiddler crabs (Sturmbauer et al 1996) and land crabs (Schubart et all 1998)*

[5] *Using COI clock for subterranean leptodirine beetles (Caccone & Sbordoni 2001)*

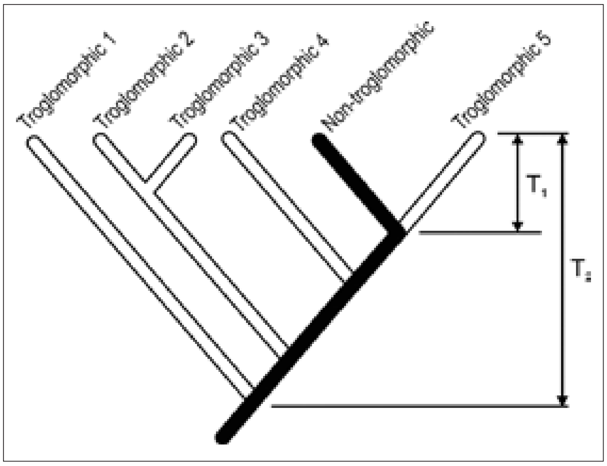

Fig. 1: A simplified view of the phylogenetic relationships obetween troglomorphic and non-troglomorphic Proteus anguinus populations (from Gorički and Trontelj 2006). Postulating a non-troglomorphic ancestor and unidirectional evolution toward troglomorphism, we can take the split between the black subspecies (non-troglomorphic) and its unpigmented sister lineage to estimate the maximal time (T1) needed for a salamander lineage to evolve the entire array of cave-related traits known in this taxon. If one accepts the notion of multiple independent cave invasions for Proteus, than T2 is the potentially oldest time since it has become subterranean.

and nuclear rDNA haplotypes in common with hypogean populations from the Ljubljanica River drainage with which the Reka drainage has been connected many times during the Pleistocene and occasionally even nowadays (Habič 1989). It is thus reasonable to assume that the ancestor of the subterranean Reka River population invaded hypogean waters and became cave-adapted before any secondary contact could occur. The estimated age of the Reka River lineage is 3.1–4.1 Myr (Verovnik *et al.,* 2004), making it a pre-Pleistocene troglobiotic relict (Verovnik *et al.,* 2004).

Monolistra, a troglobiotic group of freshawater sphaeromatid isopods, shows a high taxonomic and morphological diversity restricted to the Dinaric Karst and parts of the Southern Calcareous Alps. According to our preliminary results of a molecular phylogenetic analysis based on nuclear and mitochondrial DNA sequences, there are at least three well-supported monophyla. These are the subgenus *M. (Microlistra), M. (Monolistra)* caeca Gerstaecker, and the polytypic *M. (Pseudomonolistra) hercegoviniensis* Absolon. Several lines of evidence suggest that the common ancestors of each of these groups invaded cave waters polytopically (Sket 1986, 1994). While we remain ignorant about when and how often ancestral *Monolistra* lineages invaded subterranean waters, we can expect that the radiation of at least some of the three groups took place in the underground. Their ages

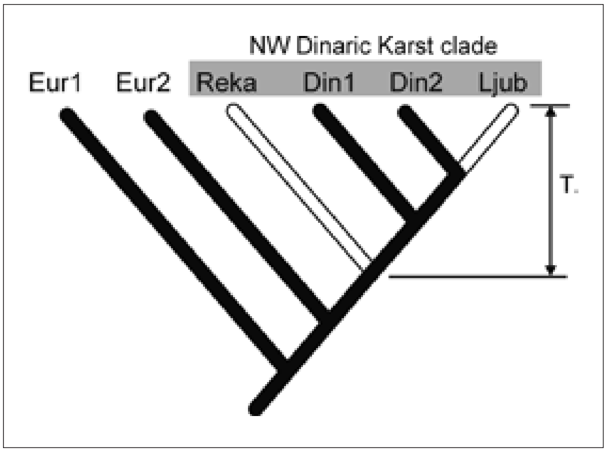

Fig. 2: The case of troglomorphic and non-troglomorphic lineages of Asellus aquaticus in the Dinaric Karst, highly simplified (from Verovnik et al 2004, 2005). The Reka and the Ljubljanica (Ljub) basin lineages have independently invaded subterranean waters and thus constitute separate taxa, although traditionally assigned to the same subspecies, A. a. cavernicolus. The subterranean Reka River population presents the oldest stygobiotic lineage of Asellus aquaticus. Because it is genetically completely distinct, it must have escaped interbreeding during various times of hydrological contact with surface populations. We therefore believe that it became a specialized stygobiont soon after the split at time T1. The Ljub lineage from the subterranean Ljubljanica River, although morphologically distinct, is still sharing mtDNA haplotypes with surface populations and thus represents a younger invasion. Eur and Din denote various epigean European and Dinaric lineages, respectively.

(maximally 0.4–3.7 Myr) give us an idea for how long some *Monolistra* lineages have been dwelling in the Dinaric Karst underground.

Leptodirus hochenwartii Schmidt, a highly troglomorphic leptodirine cave beetle, is the only terrestrial Dinaric troglobiont with available molecular dating. Using a leptodirine COI clock calibration by Caccone and Sbordoni (2001) we estimated the age of the *Leptodirus* lineage by dating the split with *Astagobius angustatus* Schmidt, its slightly less troglomorphic sister lineage. The estimated time of this split (8.7–9.8 Myr ago) is the oldest possible age at which the extremely specialized morphology of *Leptodirus* could have started evolving. Moreover, taking into account recent unpublished phylogenetic findings based on nuclear and mitochondrial gene sequences, the traditional subspecies of *Leptodirus* in fact represent distinct lineages with divergences well in the range of between species comparisons. These lineages all share the same constructive apomorphic troglomorphic characters, and it seems probable these troglomorphies have already existed at least at the time of their last common ancestor. The time of divergence between basal *Leptodirus* lineages hence represents the youngest possible age at which Leptodirus has evolved its full array of troglomorphic characters. Based on a yet incomplete taxonomic sample *(L. h. hochenwartii* Schmidt and *L. h. reticulatus* J. Müller) we tentatively dated it at 1.9–2.0 Mya.

TIMING OF PALEOHYDROGRAPHIC CHANGES

For some stygobiotic taxa with a broader Dinaric range, we identified two concordant geographic patterns possibly pointing to common underlying historical events, like changes in hydrographic connections. These vicariant patterns include (1) a split between a northwestern and southeastern Dinaric clade (mid-Dinaric split), and (2) a younger subdivision of the northwestern clade (or of a part thereof) into a western and eastern Slovenian lineage (Tab. 1).

It has been stated that some stygobiotic species inhabit areas that are hydrographically fragmented. The most parsimonious explanation of such distributions is that their ranges were hydrographically interconnected in the past. This may as well include the surface paleohydrography that was heavily fragmented by karstification. The (polytopic) immigration underground could thus have proceeded simultaneously with the separation of ancestral populations. We can illustrate this scenario by the case of some *Monolistra* lineages, namely of the subgenus *Microlistra* and of the species *M. (M.) caeca.* Some ten *Microlistra* spp. are perfectly allopatric in distribution, mainly bound to actual watersheds. Another group, *M. caeca,* inhabits at least three watersheds, in which four named subspecies have evolved. According to a 16S rDNA molecular clock (Sturmbauer *et al.,* 1996, Schubart *et al.,* 1998), the system began to fragment about three million years ago.

DISCUSSION

Before we reach any conclusions we would like to note that dating of keystone events in the evolution of subterranean life, as well as anywhere else in evolution (e.g. Graur & Martin 2004), remains a highly speculative enterprise. Of central concern should be the fact that we are relying on a more or less global clock within certain taxonomic boundaries. These clocks usually rely on single calibration points (e.g. the separation of the Sardinia-Corsica microplate from the Iberian Peninsula; Ketmaier *et al.,* 2003) and have mostly not been tested against independent geological events.

Further, all our timings assume linear accumulation of substitutions over time, i.e. the existence of a valid molecular clock. Although we can be quite sure that this assumption is violated to a certain extent, we can mitigate the problem by excluding those taxa from the analysis that violate the linearity assumption most. More sophisticated and realistically modeled approaches use a relaxed clock allowing for different local rates on different branches of the tree (e.g. Sanderson 2002). However, with single calibration points only, such approaches yield quite hopeless and certainly unrealistic intervals. For example, the age of the deepest split in the *Niphargus virei* (subterranean amphipod from France) complex was estimated at 14–19 Myr using a global *Stenasellus* clock, whereas the relaxed clock estimate was 22–71 Myr (Lefébure *et al.,* 2006).

Third, it should be noted that even with the aid of molecular phylogenetic tools the timing is still susceptible to incorrect estimations of relationships and incomplete taxonomic coverage. For example, the timing of the origin of the highly troglomorphic morphologies in *Leptodirus* depends on the most basal split in the taxon. By not having included all known subspecies, we are facing the risk that some other subspecies might have branched off earlier than the studied ones.

One potentially useful way to improve our informal confidence in the timing of evolutionary events in subterranean animals is to look for phylogeographic correspondence of timings derived from independent taxa with independent molecular clocks. At the present stage of most of our analyses such comparisons can only be preliminary. We can nevertheless notice that specific groups of events belong to different age classes, most markedly the gap between the age of holodinaric troglobionts and those with narrower distributions within the Dinaric Karst (Tab. 1). The recent lineages of *Proteus* and *Troglocaris* probably both originate from the Miocene Dinaride Lake System (Krstić *et al.,* 2003), and the age of both taxa reflects their differentiation long before they invaded the hypogean environment (Sket 1997; Gorički 2006; Zakšek *et al.,* 2007). Regional differentiation, including speciation, which can at least in part be associated with a subterranean phase, appears to be much younger, ranging from Pliocene to mid-Pleistocene. Based on these estimates plus the estimated age of the Reka River lineage of *Asellus aquaticus* (see above) we, tentatively, suggest two to five million years as the time when most of the analyzed lineages started invading the Dinaric Karst underground.

The mid-Dinaric split of Proteus and *Troglocaris anopthalmus* does not seem to originate from the same vicariant event as the latter was estimated to be younger by an order of magnitude. Another commonality of the phylogeographic pattern, the division between a western and an eastern clade in the Slovenian Dinaric Karst, might have a common hydrogeological cause in two stygobiotic crustaceans *(A. aquaticus* and *T. anophthalmus)* somewhere in the middle of the Pleistocene. In Proteus, however, the same split appears to be substantially older.

In the Dinaric Karst we were, so far, unable to find reliable time estimates for paleogeographic events to calibrate local molecular clocks in different lineages. Conversely, the timing of phylogenetic events can serve, inasmuch as we rely on global molecular clocks, to estimate the date of geographical, hydrographical, and geological changes (Sket 2002). The comparative phylogeographic approach and the use of different independent molecular clocks have enabled us for the first time to propose a timescale for the evolution of troglobionts that is relatively consistent over a wide taxonomic range. This timescale is a preliminary one, though. We expect it to change with the inclusion of further taxa, the study of more genes and the use of more accurate molecular dating approaches.

ACKNOWLEDGMENTS

We are indebted to many friends and colleagues who helped us with the acquisition of biological samples and accompanied us during field work. We thank Gregor Bračko and Jožica Murko-Bulič for their indispensable assistance in the lab. The presented work is the result of several research projects funded by the Slovenian Research Agency, and of the contract n° EVK2-CT-2001-00121- PASCALIS of the Fifth Research and Technological Development Framework Program supported by the European Community

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COBISS: 1.01

THE CHALLENGE OF ESTIMATING THE AGE OF SUBTERRANEAN LINEAGES: EXAMPLES FROM BRAZIL

IZZIV OCENJEVANJA STAROSTI PODZEMELJSKIH ŽIVALSKIH LINIJ: PRIMERI IZ BRAZILIJE

Eleonora TRAJANO[1]

Abstract UDC 551.44:597(81)
591.542(81)

Eleonora Trajano: The challenge of estimating the age of subterranean lineages: examples from Brazil

The applicability and effectiveness of different kinds of evidence used to estimate the age of lineages – morphological, molecular, phylogenetic, biogeographical, geological – are discussed. Examples from the Brazilian subterranean fauna are presented, using mainly fishes, one of the best studied groups, as a model. Only three taxa including troglobites are object of molecular studies, all in progress. Therefore, molecular clocks cannot be applied yet, and indirect evidence is used. Few phylogenies are available, *e.g.* for the catfish families Heptapteridae and Trichomycteridae. Theoretically, basal troglobitic clades are older than apical ones, but the possible existence of extinct epigean taxa belonging to such clades hampers the comparison. As well, the limitations of the use degrees of troglomorphism to estimate phylogenetic ages are analyzed with focus on the complexity of the mechanisms underlying morphological differentiation. Paleoclimatic reconstructions based on dating of speleothems from caves in northeastern and southeastern Brazil are available, but limited up to the last 200,000 years, thus useful for relatively recent lineages. Topographic isolation, probable for some fish groups from Central Brazil, is also within the time range of 10^5 years. Older dated events (in the order of 10^6 years or more) that may represent vicariant events affecting aquatic lineages with subterranean derivatives are related to the establishment of the modern South American main river basins. In view of the paucity of data useful for estimating the age of Brazilian troglobitic lineages, combined evidence, including morphology, systematics and biogeography, seems to be the best approach at the moment.

Key words: evolution of troglobites, degree of troglomorphism, Brazil, subterranean fishes, differentiation rates.

Izvleček UDK 551.44:597(81)
591.542(81)

Eleonora Trajano: Izziv ocenjevanja starosti podzemeljskih živalskih linij: primeri iz Brazilije

V prispevku je opisana uporabnost in učinkovitost različnih pristopov za ocenjevanje starosti živalskih linij s pomočjo morfologije, molekularne filogenije, biogeografije in geologije. Predstavljeni so primeri podzemeljske favne iz Brazilije, predvsem rib kot najbolj raziskane skupine. Molekularno-biološke raziskave, ki vključujejo tudi troglobionte, opravljamo na zgolj treh taksonih. Molekularne ure zaenkrat še ne moreme uporabiti, vendar zgolj posredne dokaze. Na voljo imamo le nekaj filogenetskih podatkov, npr. za morske zmaje iz družin Heptapteridae in Trichomycteridae. Teoretično so bazalni troglobitski kladi starejši od apikalnih, čeprav verjeten obstoj, sicer izumrlega epigejičnega taksona, ki pripada takim kladom, ovira primerjavo. Omejitve uporabe troglomorfizma za ocenjevanje filogenetske starosti smo analizirali s poudarkom na kompleksnosti mehanizmov, ki so osnova morfološkemu razločevanju. Razpoložljiva paleoklimatska rekonstrukcija, ki temelji na datiranju kapnikov iz jam severovzhodne in jugovzhodne Brazilije, je omejena na zadnjih 200.000 let in je kot taka uporabna le za relativno recentne linije. Topografska izolacija, ki verjetno velja za nekaj skupin rib iz osrednje Brazilije, spada v časovno obdobje 10^5 let. Starejši datirani dogodki (obdobje 10^6 let ali več), ki naj bi predstavljali vikariantske dogodke in ki so pomembni za vodne linije podzemeljskih sorodnikov, so povezane z razvojem današnjih glavnih južnoameriških porečij. Trenutno je, zaradi maloštevilnih podatkov, najboljša metoda za ocenjevanje starosti brazilskih troglobitskih linij kombinacija pristopov, ki vključujejo morfologijo, sistematiko in biogeografijo.

Ključne besede: evolucija troglobiontov, speleobiologija, stopnja troglomorfizma, Brazilija, podzemeljske ribe, razločevalno razmerje.

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Received/Prejeto: 06.12.2006

INTRODUCTION

The problem of estimating ages for subterranean or any other lineages starts with the very definition of age, whether the time since the isolation from the immediate sister-group (age of the cladogenetic event) or the beginning of differentiation, either the genetic or the morphological one (see Boutin & Coineau, 2000, for a discussion about the concept of phylogenetic ages). Different kinds of evidence have been used to establish ages of lineages, but their applicability depends on the aspect of age considered. Molecular studies may provide ages of genetic differentiation, independently of morphological change. Dating of potential geological isolation events, such as periods of climatic stress and large scale geological changes, may be used to infer the time in isolation. Inferences about relative times of isolation or differentiation also come out from comparative morphological studies within a phylogenetic and biogeographic framework. Ideally, all evidence should be combined to produce coherent hypotheses about the evolution of subterranean lineages in the temporal scale.

In Brazil, robust molecular studies encompassing exclusively subterranean (troglobitic) taxa started very recently and focus on a few fish groups with very specialized troglomorphic derivatives. Basically three groups are under study with focus on populations or species: the phreatobitic characiform *Stygicthys typhlops,* from a karst area in eastern Brazil (studied by F. P. L. Marques & C. R. Moreira); the Amazonian catfish genus *Phreatobius*, with phreatobic species collected in wells situated in alluvial plains (studied by J. Muriel Cunha); and the heptapterid subterranean catfish from Chapada Diamantina, northeastern Brazil, belonging to the genus *Rhamdiopsis* (F.A.Bockmann, pers. comm.), previously cited as a "new genus" (studied by R. Borowsky & M. E. Bichuette). Few phylogenetic studies with biogeographic analyses of larger groups including Brazilian troglobites are available.

Studies aiming to establish the ages of paleoclimatic fluctuations based on speleothem dating are also recent in Brazil, but are progressing quickly. Important climatic changes have been recorded in different karst areas, from the presently semiarid northeast to wet areas in the subtropical southeast. However, these studies are restricted to the late Quaternary, imposing limits to its application to the problem of establishing ages for subterranean lineages because many of these lineages probably have a more ancient origin. Older geological events, such as the Miocene – Plio-Pleistocene important changes that produced the modern Amazon River system, are useful to estimate the age of some Brazilian lineages.

Classically, the degree of troglomorphism, basically the reduction of eyes and pigmentation, has been used as a measure of the phylogenetic age for troglobitic animals (Poulson, 1963; Wilkens, 1973, 1982; Langecker, 2000). In spite of the many restrictions to its generalized application (see below), the degree of morphological specialization may, in certain cases, provide relative ages of isolation in the subterranean environment, being a supplement to molecular and geological evidence.

In the phylogenetic context, a lineage is a branch which departs from one node to another (hypothetical "ancestor"), from a node to a terminal, or an "ancestral" branch plus all the derived terminals, including extinct taxa (which remain unnoticed unless a fossil is known). The present discussion deals lineages including terminals. It must be noted that the ever present possibility of extinction of epigean terminals in a lineage leading to a troglobitic taxon is a source of bias that may produce overestimations of its time of isolation in the subterranean environment.

Among Brazilian subterranean taxa, fishes are by far the best studied group with focus on the currently discussed aspects. Thus, I took basically examples from these animals. For the sake of simplicity, I use herein the term "subterranean" as synonym of "troglobitic" (exclusively subterranean) species, to the exclusion of the equally subterranean, although not exclusively, troglophilic and trogloxenic populations.

DEGREE OF TROGLOMORPHISM AND PHYLOGENETIC AGE:

The use of the degree of troglomorphism to infer relative phylogenetic ages is based on the assumption that the rates of morphological differentiation are fairly constant among subterranean taxa, at least those regarding eyes and pigmentation, which tend to be lost along the isolation in subterranean habitats. To accept this notion, it is necessary to assume that the mechanisms of reduction are the same for each of these characters and that their reduction progress in parallel. However, there is strong evidence in contrary.

The occurrence of different mosaics of character states in closely related taxa suggests different mechanisms acting at different rates in each population. An illustrative example is provided by the armored catfishes, *Ancistrus cryptophthalmus,* from Central Brazil: in the large population found in Angélica Cave, pigmentation is more reduced but eyes are less reduced than in the much smaller population from Passa Três Caves (Reis et al., 2006). A study based on geometric morphometrics showed that the four known populations also differ in general body shape, with a mosaic in the deformation axes, indicating divergence probably due (at least partially) to topographic isolation (Reis *et al.,* op. cit.). Other mosaics are also observed among related heptapterids – among the Rhamdiini, *Pimelodella kronei* presents eyes more reduced than *Rhamdia enfurnada,* the opposite being observed for melanic pigmentation.

Such mosaics may encompass a larger number of characters, including behavioral and physiological ones. This is the case with the troglobitic amblyopsids, traditionally ranked in order of increasing degree of reduction of eyes and pigmentation as: *Typhlichthys subterraneus* < *Amblyopsis spelaea* < *A. rosae* (Poulson, 1963). Nevertheless, *A. spelaea* presents more specialized life history traits and feeding behavior, while *A. rosae* is more derived as regards to agonistic behavior and metabolic rates (both subject to reduction); the otherwise less derived *Typhlichthys subterraneus* is intermediate in relation to agonistic behavior and metabolic rates (Poulson, 1963; Bechler, 1983). Distinct selective pressures are likely to explain such mosaics. For this reason, attempts to rank species like these according to their degree of "adaptation" or specialization to the cave life are unconvincing.

In fact, the reduction of melanic pigmentation in subterranean fishes results from different, independent mechanisms, which may superpose. Morphological mechanisms affect the size and number of melanocytes, whereas physiological ones affect the ability to synthesize melanin. Apparently, this ability may be lost due to different mutations affecting at least distinct two steps in the synthesis of eumelanin, one upstream and the other downstream the synthesis of DOPA: the first corresponds to completely depigmented fish which respond to the administration of L-DOPA by synthesizing melanin, referred as DOPA(+) by Trajano & Pinna (1996) and tyrosinase-positive by Jeffery (2006); the second correspond to depigmented fish which to not respond to L-DOPA (DOPA(-) albinos; Trajano & Pinna, op. cit.). Among Brazilian completely depigmented subterranean fishes, *Stygichthys typhlops,* the new *Rhamdiopsis* from Chapada Diamantina and the armored catfish, *Ancistrus formoso* are DOPA(+), the heptapterid "*Taunayia*" sp. (actually a *Rhamdiopsis* – F.A. Bockmann, pers. comm.) is DOPA(-) (M.A. Visconti and V. Felice, pers. comm.), and one third of the population of the trichomycterid *Trichomycterus itacarambiensis* is DOPA(-), whereas the remaining two thirds have functional melanophores reduced in density.

The morphological mechanism is based on an additive polygenic system (Wilkens, 1988), resulting in a continuous variation in the first evolutionary steps and progressing towards complete depigmentation throughout the population at slower rates than that caused by the loss of the ability to synthesize melanin, which is based on monogenic systems (Wilkens, 1988). For instance, it has been demonstrated that albinism in different populations of Mexican Astyanax is caused by independent mutations in the same gene, *Oca2* (Protas *et al.,* 2005). Therefore, very pale but still pigmented fish species, with scattered micromelanophores (such as the *Trichomycterus* undescribed species respectively from Bodoquena and from Serra do Ramalho karst areas, and the *Ituglanis* spp. from São Domingos karst areas) may be younger than any of those DOPA(+) "albinos". Thus, the use of troglomorphic pigmentation as a measure of relative age should be restricted to related taxa retaining melanin (i.e., to the exclusion of DOPA albinos), where the degree of paleness is due to mutations in the additive polygenic system underlying the morphological, gradual mechanism.

Regression of eyes is also due to complex genetic systems. In the blind Mexican tetra characins, genus *Astyanax*, it has been shown that regression is caused by the inactivation of several genes that take part in the developmental control, and that growth factors acting at a lower level of this control appear to be involved in the degeneration of the eyes (Langecker, 2000). Clearly, studies on a much large sample of troglobitic species are needed before any inference about differentiation rates can be made.

Two other factors influence the rates of divergence: population sizes and life cycle strategies. Small populations tend to differentiate faster due to phenomena as genetic drift. Population sizes are highly influenced by ecological factors such as nutrient availability and the extent of habitats suitable for colonization. It is noteworthy that energy is higher in streams (higher carrying capacity), but phreatic habitats occupy larger areas and volumes. Because there is no taxonomic correlation with these factors, related species may differ in population sizes (for instance, populations respectively with 20,000 and 1,000 individuals were estimated for *A. cryptophthalmus* in Angélica and in Passa Três caves – Trajano, 2001a), thus in divergence rates. As well, nutrient availability may also be "perceived" differently even by taxonomically related species, depending on the efficiency of energy use. Such efficiency may be improved along the adaptation to the subterranean life, allowing for increase in population sizes, then in lowered differentiation rates.

K-selected life strategies imply lower differentiation rates due to delayed ages for first maturation and low reproductive rates (few individuals reproducing at given times), which work on opposite directions: delayed first maturation implies slow divergence rates (longer reproductive generations), whereas low reproductive rates result in lowered effective populations, which would accelerate divergence rates..

In conclusion, there is a complex balance between different genetic, ecological and biological factors, which may act in different directions to produce the actual divergence rates. Such rates may differ among related taxa, and even among different characters. Therefore, the degree of troglomorphism as a measure of age of subterranean lineages should be used with extreme caution.

GEOLOGICAL, PALEOCLIMATIC AND BIOGEOGRAPHICAL EVIDENCE:

Dating of paleoclimatic events based on growth phases of speleothems and similar deposits may be applied to subterranean lineages within the framework of the paleoclimatic model (Barr, 1968; Wilkens *et al.,* 2000). However, its cyclical nature imposes serious limitations because, without biological data (molecular, morphological, phylogenetic), it is not possible to establish in which phase the isolation first took place. As a matter of fact, isolation with differentiation may occur along several subsequent unfavorable phases intercalated with coalition phases, thus what really counts to produce genetic and/or morphological divergence is the sum of isolation periods (Trajano, 1995), and not simply the time since the first isolation event.

For instance, in northeastern Brazil there were nine dry phases (no speleothem growth) in the last 210,000 years, intercalated with short wet phases lasting from several hundreds to a few thousand years each. Overall, these periods of speleothem growth occupied only 8% of the studied period, i.e., around 20,000 years in contrast with 190,000 years with dry conditions, like the one prevalent nowadays in the region (Wang *et al.*, 2004). Hence, at least in the late Pleistocene, there was a much extended period of isolation for the hypogean fauna in northeastern Brazil – for lineages already established in subterranean habitats, from 190,000 to 210,000 years, depending on the occurrence or not of introgression with epigean relatives during the wet periods. As a matter of fact, several of the most highly specialized Brazilian troglobites have been found in this region (e.g., *Rhamdiopsis* catfishes, *Spelaeogammarus* amphipods, *Pongicarcinia xiphidophorum* isopods, *Coarazuphium* beetles), as well as the only Brazilian troglobitic scorpions, cockroaches and Ctenid spiders.

On the other hand, climatic changes were not as dominant in the subtropical southeast Brazil and dry phases were shorter, at least for the last 116,200 years (Cruz-Jr. *et al.,* 2005). Therefore, total time of isolation in subterranean habitats during the late Pleistocene was shorter in SE than in NE Brazil. Hypothetically, a population that became first isolated at a given time in the northeast would be much more differentiated, both genetically and morphologically, than another population first isolated at the same time in the southeast. If one considers "age" as the time of the first isolation, these two lineages have the same age; if "age" is the total time in isolation, then the first one is older. It is clear that, in a cyclical model, the degree of genetic differentiation do not provide a good evidence of age without a precise determination of the duration of each phase.

Geological and geographical events over larger temporal scales may provide more robust evidence. The genus *Phreatobius* is distributed around the Amazon basin, in tributary basins from both margins of the Amazon River. The first described species, *P. cisternarum,* lives underground in the alluvial fan around the Amazon delta, being collected in shallow hand-dug wells. Much latter, in the 1990´s, other species were found deeply buried in submerged litter banks in shallow "igarapés" (small tributaries) along the left margin of the Negro and Amazon rivers. More recently, a second phreatobic species was discovered in wells in the State of Rondônia, Rio Madeira basin, in the right margin of the Amazon drainage (J. Muriel-Cunha & J. Zuanon, pers. comm..; description in progress by J. Muriel-Cunha & M. de Pinna). This wide, peripheral distribution of the *Phreatobius* genus around the Amazon basin may be explained by an origin between the late Miocene and the late Pliocene (~2.5 Ma), when a gigantic lake, or a series of interconnected mega-lakes occasionally united to cover most or all of lowland Amazonia to a shallow depth (Campbell *et al.,* 2006). In fact, *Phreatobius* catfishes are adapted to shallow, hypoxic conditions, with dark pink to red skin indicating cutaneous breathing; since all known species exhibit this conspicuous trait, this is probably an ancestral condition for the genus. I suggest that the fragmentation of the lacustrine habitat during the late Pliocene, leading to the establishment of the modern Amazon River drainage system, may have been an isolation event for the ancestors of the extant species. Nevertheless, an older origin for cannot be ruled out.

On the other hand, *P. cisternarum* has been found not only north and south of the Amazon River mouth but also in the large Marajó Island in between, with no unequivocal morphological differentiation so far detected between these localities (Muriel-Cunha & Pinna, 2005). These populations were isolated during the formation of the Amazon delta, ~2.5 Ma ago, suggesting a high evolutionary stability, at least at the morphological level, possibly due to the environmental stability of the subterranean habitat.

The disjunct distribution also points to a very ancient origin for the Calabozoidea isopods. So far, this taxon is composed exclusively by three extant phreatobic species, one from the Orinoco basin, in Venezuela *(Calabozoa pellucida),* e two from Brazil, respectively from the São Francisco *(Pongycarcinia xiphidiourus)* and the Paraguay (undescribed species) river basins. The only connection between these regions is through the Amazon basin, and I speculate that the ancestors may have dispersed during or prior to the formation of the huge Lago Amazonas. Actually, the São Francisco lineage would be older, at least 5 Ma, which is the estimated age of separation of this basin based on studies of the biogeographical patterns in Brazilian freshwater fishes (Hubert & Renno, 2006). Messana *et al.,* (2002) argue for a close relationship between the Calabozoidea and the Oniscoidea isopods, thus both lineages have the same phylogenetic age, which goes back to the Jurassic-Cretaceous (gondwanic origin – L. A. Souza, pers. comm.). A phylogenetic study, that could add more light to this interesting problem, is waiting for the collection of additional specimens, what is proving to be very difficult in spite of the efforts of biologists and cave divers. Apparently these animals are very rare and/or live mainly in inaccessible, deep phreatic habitats.

Geomorphological events as alluvial erosion producing waterfalls that split populations (topographical isolation), once dated, also provide data useful to estimate the age of lineages such as the different populations of the armored catfish, *A. cryptophthalmus.*

PHYLOGENETIC AND MOLECULAR EVIDENCE:

In order to be minimally reliable and useful, molecular clocks must be based on well corroborated phylogenies with at least one node correlated to geographic or geological isolation events of known age. In cyclical models, such correlation is hampered when cycles are relatively short and repetitive, as is the case with the paleoclimatic fluctuations in the late Pleistocene in Brazil, adding a great deal of uncertainty to the molecular clock. Marine transgressions, which have been used to establish dates for vicariant events in epigean Brazilian taxa such as freshwater fishes, are of no use for subterranean lineages because almost all karst areas in Brazil are above the maximum sea levels. In any case, the conclusion of the molecular studies on *Phreatobius* spp., *S. typhlops* and *Rhamdiopsis* sp. from Chapada Diamantina will certainly open new interesting avenues in this field.

As already mentioned, few phylogenetic studies of groups including Brazilian troglobites are available, most at the genus level and incomplete in terms of taxa encompassed. Among fishes, the heptapterid catfishes were object of a phylogenetic study, but the cave species were not included (Bockmann, 1998). Phylogenetic and molecular studies on heptapterids are in progress, but the position of the *Phreatobius* genus and of the troglobitic *Rhamdiopsis* species within this genus are still unclear. Recently analyzed morphological data indicate that, within the genus *Rhamdiopsis,* "*Taunayia*" sp. is basal whereas the species from Chapada Diamantina have a more apical position in the phylogeny (F. A. Bockmann, pers. comm.). These two species independently adapted to the same kind of habitat, the upper phreatic zone connected to the surface through caves (Trajano, 2001b), having developed advanced characters states related to the hypogean life, including miniaturization. "*Taunayia*" sp., however, is even more specialized, presenting a hypertrophied lateral line system in the head, with behavioral evidence of enhanced mechano-sensory sensitivity. This, associated with its putative basal position in the *Rhamdiopsis* phylogeny, points to an older age for the lineage to which the troglobitic "*Taunyaia*" sp. belongs, much anterior to the late Pleistocene.

The phylogeny of the catfish family Trichomycteridae was also studied (Wosiack, 2002), but only one among 10+ troglobitic species presently known, *Trichomycterus itacarambiensis,* was included. It is an apical taxa in the phylogeny, indicating a relatively recent origin. A recent derivation of *T. itacarambiensis* from an epigean ancestor from the Upper São Francisco River basin is consistent with the morphological variation observed in eyes and pigmentation and also with the notion of a quick fixation of genes for albinism, since one third of the population is made of albinos. However, in the absence of a correlation between some node and dated geographic or geological isolation events, it is not possible to estimate an absolute age, even approximate, for this cave lineage.

COMBINED EVIDENCE:

For extremes in the inter-taxa variation, the troglomorphism degree may provide good evidence of relative ages. For instance, it is reasonable to suppose that fishes with slightly reduced eyes and pigmentation such as the heptapterids *Rhamdiopsis* sp. from Cordisburgo (eastern Brazil) and *Pimelodella spelaea,* from São Domingos (Central Brazil), are younger than the highly troglomorphic *Rhamdiopsis* sp. from Chapada Diamantina and "*Taunaya*" sp., from Campo Formoso. The two former species probably have been isolated topographically because they inhabit streams several meters above the base level, and an isolation period in the order of 10^5 years (estimated time for the erosional processes lead to the current landscape – A. Auler, pers. comm..) may be estimated. The two latter species inhabit presently semiarid karst areas in northeastern Brazil subject to extended periods of isolation at least during the last 210,000 years, but they probably became isolated well before. Thus, an estimate in the order of 10^5-10^6 years seems reasonable.

A molecular study focusing on the hypervariable Region I of MtDNA did not find any evidence of divergence between the cave populations of *Ancistrus cryptophthalmus* (Moller & Parzefall, 2001). However, geometric morphometric analyses showed a clear, statistically significant difference between these populations, but with some superposition with the epigean closest relatives (Reis *et al.,* 2006). Taken together, these data indicate a recent isolation of the cave populations from the epigean ones and also from each other, in the order of 10^4 -10^5 years.

Preliminary molecular studies on *Ituglanis* species from São Domingos karst area are consistent with the observed morphological differences (Bichuette *et al.,* 2001) justifying the recognition of four species, each one in a separate microbasin that runs parallel westwards (Bichuette & Trajano, 2004). These catfishes are sympatric with the morphologically less specialized *A. cryptophthalmus, P. spelaea* and *Eigenmannia vicentespelaea* (Gymnotiformes), making São Domingos karst area a world hotspot of biodiversity for subterranean fishes. All the *Ituglanis* catfishes have eyes more reduced and are paler than the other species, presenting scattered melanophores, i.e., they are not DOPA albinos. Three among these Ituglanis species occupy a very specialized habitat, with adaptations to the phreatic environment that include miniaturization. Moreover, *I. epikarsticus,* and probably also *I. bambui* and *I. ramiroi* (Trajano & Bichuette, unpubl. data), live and disperse through the epikarst, whereas the other species are typical stream-dwellers, like their epigean relatives. In spite of intensive collecting efforts, no epigean *Ituglanis* catfish was found in São Domingos (the same is true for Pimelodella; Bichuette & Trajano, 2003). Taken together, these evidences indicate a longer time in isolation for the *Ituglanis* catfishes. In conclusion, the rich troglobitic ichthyofauna from São Domingos seems to be the result of anachronous isolation events, including both the extinction of epigean relatives due to unknown factors (for *Ituglanis* and *Pimelodella*) and topographic isolation (for *Ituglanis* spp. and also *A. cryptophthalmus).*

Anachronous isolation, possibly in association with different divergence rates, may also explain the disparity in troglomorphic degree observed for the subterranean fauna from the Upper Ribeira Valley karst area, SE Brazil. This fauna includes very specialized species, such as the pseudoscorpion *Spelaeobochica muchmorei* and the decapod *Aegla microphthalma,* to moderately troglomorphic species, such as the opilionid *Pachylospeleus strinatii,* the carabid beetle *Schizogenius ocellatus* and the catfish *Pimelodella kronei.* Within the framework of the paleoclimatic model, in view of the short isolation periods (= dry phases) during the late Pleistocene (see above) it is probable that all these species became first isolated in caves before this period.

ACKNOWLEDGEMENTS

I am grateful to Augusto Auler, Fernando P. L. Marques and Janice Muriel Cunha for the discussion of ideas and criticisms, and to Richard Borowsky for the critical reading and revision of the English style of an early version of the manuscript. Many data were gathered during studies sponsored by the Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP (grant n. 03/00794-5, among others). The author studies are also supported by the CNPq (fellowship and grant n. 302174/2004-4).

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COBISS: 1.01

PATTERN AND PROCESS: EVOLUTION OF TROGLOMORPHY IN THE CAVE-PLANTHOPPERS OF AUSTRALIA AND HAWAI'I – PRELIMINARY OBSERVATIONS (INSECTA: HEMIPTERA: FULGOROMORPHA: CIXIIDAE)

VZOREC IN PROCES: EVOLUCIJA TROGLOMORFNOSTI PRI JAMSKIH MREŽEKRILNIH ŠKRŽATKIH IZ AVSTRALIJE IN HAVAJEV – PRELIMINARNE UGOTOVITVE (INSECTA: HEMIPTERA: FULGOROMORPHA: CIXIIDAE)

Andreas WESSEL[1], Petra ERBE[1,2] & Hannelore HOCH[1]

Abstract UDC 591.542(94+739,9)

Andreas Wessel, Petra Erbe & Hannelore Hoch: Pattern and process: Evolution of troglomorphy in the cave-planthoppers of Australia and Hawai'i – Preliminary observations (Insecta: Hemiptera: Fulgoromorpha: Cixiidae)

The evolution of troglobites comprises three distinct problems: cave colonization by an epigean ancestor, the evolution of troglomorphies, and intra-cave speciation. The study of cave-dwelling planthoppers has contributed much to our understanding of troglobite evolution and provides useful model systems to test various aspects of the theoretic framework developed in recent years. Most promising in this respect are taxa with several closely related but independently evolved troglobiontic lineages, such as on the Canary Islands, in Queensland/Australia and on the Hawaiian Archipelago. Closely related species often occur in caves with comparable ecological parameters yet differ in their age. Here we use comparative age estimates for Australian and Hawaiian cave cixiids to assess the dynamics of reductive evolutionary trends (evolution of troglomorphy) in these taxa and cave planthoppers in general. We show that the degree of troglomorphy is not correlated with the age of cave lineages. Morphological alteration may not be used to draw conclusions about the phylogenetic age of cave organisms, and hypotheses based on such assumptions should be tested in light of these findings.

Key words: adaptive shift, cave adaptation, climatic relict, founder effect, reductive evolutionary trends, troglobites, troglomorphies.

Izvleček UDK 591.542(94+739,9)

Andreas Wessel, Petra Erbe & Hannelore Hoch: Vzorec in proces: Evolucija troglomorfnosti pri jamskih mrežekrilnih škržatkih iz Avstralije in Havajev Preliminarne ugotovitve (Insecta: Hemiptera: Fulgoromorpha: Cixiidae)

Evolucija troglobiontov zajema tri značilne korake: kolonizacija jame s površinskim prednikom, razvoj troglomorfnosti ter podzemeljska speciacija. Študija podzemeljskih mrežekrilnih škržatkov je prispevala veliko k našemu razumevanju evolucije troglobiontov in hkrati predstavlja uporaben modelni sistem za testiranje različnih teoretičnih pristopov, ki so bili razviti v zadnjih letih. V tem pogledu so najobetavnejši tisti taksoni, ki so si sicer sorodni, toda pripadajo evolucijsko neodvisnim troglobiontskimi linijami, kot so npr. tisti na Kanarskih otokih, v državi Queensland (Avstralija) in na havajskem arhipelagu. Bližje sorodne vrste se v jamah pogosto pojavijo v primerljivih ekoloških pogojih, vendar se razlikujejo v starosti. Za ugotavljanje dinamike trendov redukcijske evolucije (evolucija troglomorfizmov) teh taksonov in jamskih škržatkov na splošno, smo v prispevku uporabili ocene primerjalnih starosti za avstralske in havajske jamske škržatke. Ugotavljamo, da stopnja troglomorfnosti ni v korelaciji s starostjo jamskih linij. Zgolj morfološke spremembe pri organizmih se ne bi smele uporabljati za prikazovanje filogenetske starosti jamskih organizmov. Hipoteze, ki temeljijo na takšnih predpostavkah, bi morale biti preverjene v luči pričujočih ugotovitev.

Ključne besede: prilagoditveni premik, prilagoditve na podzemlje, klimatski relikt, učinek osnovatelja, redukcijski evolucijski trendi, troglobiti, troglomorfizmi.

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Received/Prejeto: 30.01.2007

INTRODUCTION

The origin of troglobites has fascinated evolutionary biologists since Darwin remarked on their curious and strong modification (1859: 177-178). He did not provide a 'Darwinistic' explanation for their evolution[1], however, this was subsequently supplied by August Weismann (1886)[2].

Troglobite evolution, i.e. the process leading to different, sometimes closely related species, which are highly adapted to life in subterranean spaces, comprises three somewhat independent phenomena and problems: (i) initial cladogenesis of a cave species, or the origin of a cave-dwelling bio-species from an epigean ancestor, which is basically the problem of isolation or rather (spatial) separation of a cave population from its epigean relatives; (ii) subsequent anagenetic transformation, which comprises the dynamics and driving forces of cave adaptation, the often so-called regressive evolution or reductive evolutionary trend, and, in some cases, (iii) subterranean (intra-cave) radiation.

RELICTS OR EXPLORERS?

A widely accepted concept aiming to explain the speciation event giving rise to a cave-dwelling and reproductively isolated bio-species, was developed by Thomas Barr in the 1960s, commonly known as the Climatic Relict Hypothesis (CRH):

"Troglobites have evolved from colonies of troglophiles which became isolated in caves through extinction of surface populations of the troglophiles" (Barr 1968: 96).

According to Barr, the evolution of troglobites is a two-step process: at first, it involves a preliminary, troglophilic stage without apparent troglomorphies or a disruption of geneflow between cave-dwelling and epigean populations. Following this initial cave colonization, the cave-dwellers become geographically separated, and thus genetically isolated, due to the extinction of parental epigean populations (supposedly caused by climatic change), at least in the region of the cave. Over time, reproductive isolation will inevitably follow as a side effect of genetic change by drift and natural selection (Barr 1968). Support and evidence for this concept was gained from the observed relict distribution of most troglobites known at that time, which were almost exclusively confined to temperate regions. Glaciation during the ice ages was suggested as the most important factor for the change of surface conditions (Barr 1968, Sbordoni 1982, Barr & Holsinger 1985).

This hypothesis remained without alternatives until the early 1970s, when Francis G. Howarth discovered the Hawaiian cave ecosystems (Howarth 1972). The lava tubes host, among other taxa, highly troglomorphic planthoppers that are parapatrically distributed with respect to their close epigean relatives, which are still extant, i.e. they are non-relictual troglobites. Consequently, Howarth (1981, 1986, 1987) formulated the Adaptive Shift Hypothesis (ASH):

"[...] potential food resource provides the driving force for the [...] evolution of cave species. Troglomorphic populations [...] evolve from pre-adapted habitual accidentals which [...] establish temporary populations in marginal underground habitats. Once an adaptive shift occurs, allowing a reproducing population to establish itself underground, then it is both the effects of strong new selection pressures and the release from previously strong selection pressures that bring about [...] troglomorphy" (Howarth 1986: 155).

While the exploitation of a large new habitat with new food resources may be the driving force in the evolution of troglobites according to the ASH, a major challenge for survival underground is probably the ability to locate mates and reproduce in the dark. A change in mating behaviour might thus have been the most important adaptive shift necessary for a successful colonization of caves, and would almost inevitably lead to reproductive isolation of the incipient cavernicolous species. The Hawaiian cave planthoppers provide a striking example for

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[1] "As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute their loss wholly to disuse." (Darwin 1859: 177)

[2] „As soon as such a cave immigrant has developed the ability to obtain food without the help of eyes a reduction of the eyes must commence, since as soon as the same are no longer neces-sary for the animals' existence, they are not influenced anymore by natural selection, because now it does not matter whether the eyes are a little worse or a little better. Now, no more selec-tion will take place between individuals with better and those with worse eyes, but both will have an equal chance to be preserved and reproduce. Individuals with better and those with worse eyes will cross from now on, and the result can only be a general degradation of the eyes. Pos-sibly this is helped by the circumstance that smaller and stunted eyes can even present an ad-vantage, since this allows other organs such as sensory and olfactory organs, which are more important for the animal now, to develop more strongly. Even without such effect, though, the lack of natural selection maintaining the eye's high level of organization will necessarily lead to its degradation, slowly or even very slowly, especially at the beginning of this process, but in-exorably." (Translated from the German; Weismann 1886: 16-17)

this process, and consequently played a pivotal role in the formation of the Adaptive Shift Hypothesis (Howarth 1986, Howarth & Hoch 2005).

A principal acceptance of the ASH does not necessarily invalidate the CRH, especially not in cases where the preconditions for the CRH are met, i.e. cave taxa displaying a relict distribution. However, a relict distribution observed today is not sufficient evidence to unconditionally accept the CRH, given the alternative present in the ASH [3]. The predictions arising from both hypotheses must be tested for every single system. For the CRH, we expect the closest epigean relatives at least to be allopatrically distributed compared to the cave species, while the ASH predicts a parapatric distribution of cave and epigean species, which are necessarily sistergroups (adelphotaxa). Conclusive evidence for a decision between both hypotheses may be gained from a well-founded phylogeny in conjunction with a sound knowledge of the geographic distribution of both cave and epigean taxa. The last requirement is often problematic, though, as the sampling of epigean relatives for some cave species is frequently insufficient. For some groups no epigean relatives are known at all, and it is only through intensive, directed search efforts that this obstacle may be overcome (see e.g. Stone 2004).

REDUCTIVE EVOLUTIONARY TRENDS

Once a population has shifted towards a permanently cavernicolous mode of living, the second problem of troglobite evolution – subsequent anagenetic transformation – arises. A basic assumption since Weismann (1886) has been a correlation between the degree of troglomorphy of a taxon and its residence time in caves. Cave adaptation is accordingly described as an orthogenetic, time-dependent process, which is an overall slow, gradual adaptation towards a stage of 'absolute troglomorphy'; see e.g. Wilkens (1986), for review see Barr (1968) and Howarth (1987). Traditional explanations for the mechanisms of this process includes (i) the accumulation of neutral mutations, (ii) pleiotropic effects, and (iii) natural selection for energy economy (Sket 1986, Culver 1982). Both the CRH (Barr 1968) and ASH (Howarth 1986), however, contain some notion of a founder effect: Barr with an explicit quotation of Mayr's genetic revolution (Mayr 1954) and Howarth with reference to the Carson model of founder effects (Carson 1968, 1975).

The process of cave adaptation is influenced by several parameters – such as availability of food, population density, microclimate of the caves and other biotic and abiotic factors of the cave ecosystem – , which make comparisons even between closely-related species exceedingly difficult, and generalisations even more so. An excellent opportunity to test the assumption of gradual and increased troglomorphy over time may nevertheless be found in radiations of cave-dwelling planthoppers inhabiting caves of different age.

CAVE-ADAPTATION IN PLANTHOPPERS

Studies during the last three decades have revealed numerous cases of evolution of cave-adapted planthoppers in tropical and subtropical caves. Among the Fulgoromorpha, 53 cave-dwelling species have been described from many parts of the world, four-fifth of them cixiids including the Australian taxa *Solonaima* and *Undarana* and the Hawai'ian *Oliarus* species (Hoch 1994, Hoch & Wessel 2006).

The adaptation to similar environments in cave planthoppers has led to the evolution of a very similar external morphology in different parts of the world and represents a striking example of parallel evolution. The morphological modifications of cave planthoppers are characterized by reductive evolutionary trends, as in most obligately cavernicolous animals. The degree of adaptation to a subterranean life varies greatly, primarily depending on their habitat in the cave or soil (Fig. 1). Most conspicuous are the reduction and loss of compound eyes and ocelli, tegmina, wings and bodily pigment. It has also been suggested that apparently non-troglomorphic characters have an increased adaptive value in the underground environment, such as e.g. the specialized spine configurations of hind tibiae and tarsi, which may possibly enhance walking on wet or rocky surfaces (Hoch & Howarth 1989a, 1989b, Hoch 2002).

The closest epigean relatives of cavernicolous Fulgoromorpha species all have immature stages living close to the soil, e.g. under the dead bark of rotting logs, in leaf litter or moss, or even within the soil, feeding on roots or perhaps on fungi (Remane & Hoch 1988). This mode of life has been considered an ecological pre-adaptation

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[3] "The evidence suggests that troglobites evolve from pre-adapted habitual visitors or accidentals in the cave rather than from well-adapted troglophiles. The former group requires an adaptive shift in order to fully exploit the cave resources. This adaptive shift may lead to the evolution of a troglobitic lifestyle. Well-adapted troglophiles on the other hand tend to remain opportunistic exploiters of the cave environment. Some temperate troglobites may fit the scenario of isolation by changing climates (Barr, 1968). However, many species including those in the tropics probably do not. I postulate that adaptive shifts led to the colonization of caves and evolution of troglobites, including most of those in temperate caves, but that the complex geological history of the continents including glaciations has obscured the early history and obfuscated the earlier distribution and the evolution of troglobites there." (Howarth 1981: 540)

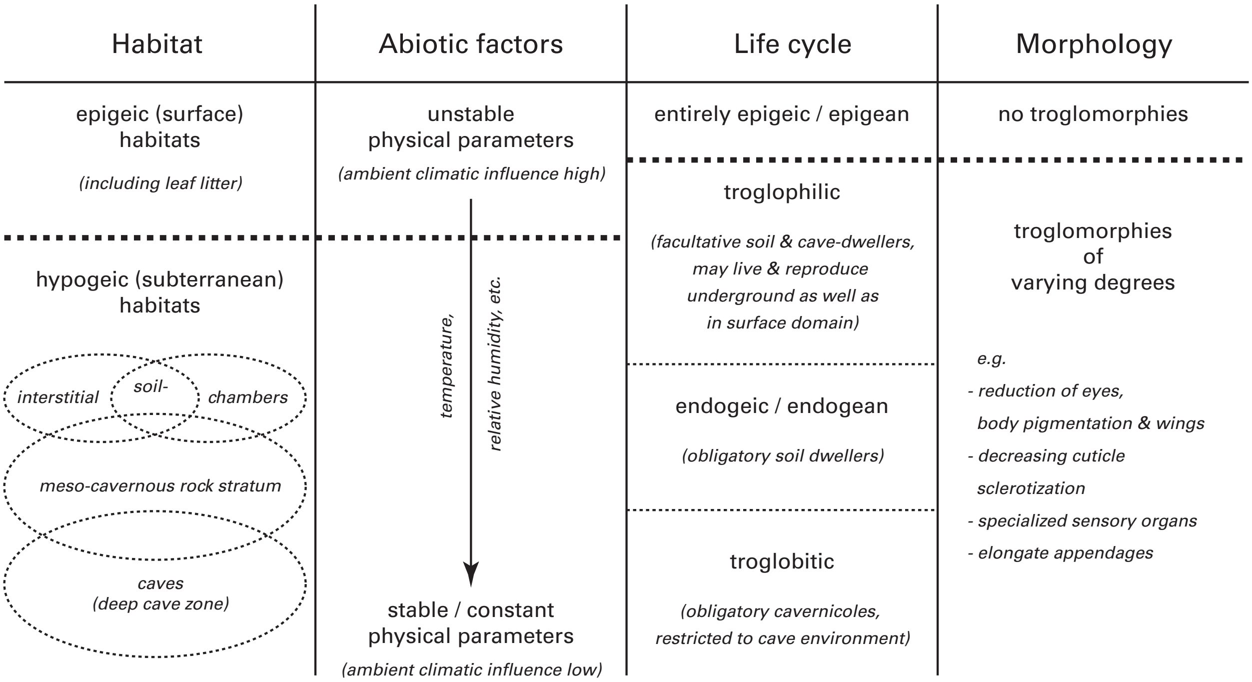

Fig. 1: Terminology of interdependence between physical parameters of the habitat and organismic adaptations (From Hoch et al. 2006).

to a later switch to a permanent (adult) life underground (Hoch 2002, Howarth & Hoch 2005).

CAVE-PLANTHOPPERS OF AUSTRALIA AND HAWAI'I

In Australia, closely related *Solonaima* and *Undarana* species have colonized old karst caves as well as younger lava tube systems. The four epigean *Undarana* species occur in the (rain)forest at the south of Queensland's east coast, while the two cave-dwelling species (*U. rosella,* Bayliss & Pinwills cave, Undara lava tube; *U. collina,* Collins cave) inhabit the lava caves of the McBride Formation in the dry grasslands westward of the Great Dividing Range (Hoch & Howarth 1989a). The epigean *Solonaima* species can be found all along the east coast (rain)forest, while the cave species inhabit lava tubes within the McBride Formation, too *(S. baylissa,* sympatric with *U. rosella),* as well as karst caves of the Chillagoe Karst Towers *(S. pholetor, S. stonei, S. halos, S. irvini)* and Mount Mulgrave *(S. sullivani)* (Hoch & Howarth 1989b). Thus, epigean and cavernicolous species of both Australian genera show an allopatric distribution.

On the Hawaiian islands the cave-dwelling species of the endemic, monophyletic *Oliarus* clade represent independent cave colonizations on islands of different age. With about 80 described epigean taxa (species and subspecies), *Oliarus* is the most speciose planthopper genus on the Hawaiian islands (Zimmerman 1948, Asche 1997). Based on morphological data, this diversity has been hypothesized to stem from a single colonization event (Asche 1997, Hoch & Howarth 1993). The first cave-dwelling species of the genus, *Oliarus polyphemus* Fennah, 1973 and *Oliarus priola* Fennah, 1973 (Fennah 1973) were discovered by Howarth (1972) on Hawai'i Island and Maui where they are endemic. Later, five more troglobitic taxa were discovered on the archipelago (Hoch & Howarth 1999). The seven cave-dwelling species owe their origin to several independent colonization events on three islands; on Molokai, one adaptive shift *(O. kalaupapae);* on Maui, three adaptive shifts *(O. priola, O. gagnei, O. waikau);* on Hawai'i Island, at least three adaptive shifts *(O. polyphemus, O. lorettae, O. makaiki)* (Hoch & Howarth 1999). The closely related epigean species of all cavernicolous *Oliarus* taxa occur parapatrically at the surface.

Both the Australian and the Hawaiian cave species complexes exhibit different degrees of troglomorphy. Figure 2 shows the heads of six Australian *Solonaima*, one epigean (1), three facultative cavernicolous (2-4), and two obligate cavernicolous species (5,6). Figure 3 depicts the habitus of six Hawai'ian Oliarus species, one epigean relative on the left (note the different scale), and five troglobitic species. The varying degree of eye reduction is clearly visible; two of the Hawaiian species even show a complete loss of eyes. The same pattern is seen in wing reduction.

The time factor is crucial for assessing the dynamics of troglobite evolution. Unfortunately, though, it is

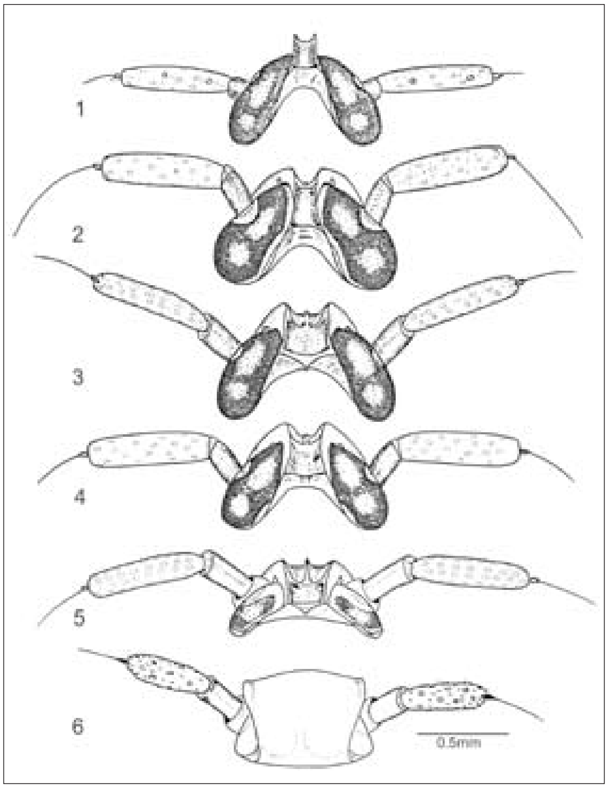

Fig. 2: Australian Solonaima species, heads, dorsal view. 1, S. solonaima (epigean); 2. S. sullivani; 3, S. pholetor; 4, S. stonei; 5, S. irvini; 6, S. baylissa. (From Hoch & Howarth 1989b).

rarely possible to obtain direct estimates of the age of the cave lineages. Rather, the maximum age of the habitat is usually employed - at least if an active colonization of caves *sensu* Howarth is assumed - , or even just the maximum age of the underlying geological structure. By these measures, the maximum age for the troglobitic *Oliarus* lineages on Hawai'i is the age of the islands: 1.8 myr for Molokai, 1.3 myr for Maui, and less than 400,000 y for Hawai'i Island.

In the case of the Australian troglobitic cave planthoppers, the situation is even more complex. At first sight their distribution fits the Climatic Relict Model sensu Barr very well assuming a late Miocene desertification, i.e. replacement of the rain forest by dry savannah or grassland east of the Great Dividing Range (see Kemp 1978, Truswell 1990). While not *per se* refuting the relict hypothesis, we do not exclude the possibility of adaptive shifts for the Australian cave planthoppers as well. In that case, Australian cave taxa may be much older than hitherto assumed. Also, the late Miocene climatic change is not necessarily be regarded as the sole reference point for the calculation of the maximum age of the Australian cave planthoppers. What could matter instead is the availability of the caves as a suitable novel habitat.

The limestone of the Chillagoe Tower Karst and Mitchell-Palmer Karst are presumably of Silurian origin, and the current main caves were formed by phreatic solution during the last 5-10 million years (Ford 1978, Jennings 1982, Pearson 1982). Remnant older passages and solution breccias near the tops of many towers indicate the existence of caves since the area was uplifted and the limestone was exposed in the mid-Tertiary about 20-25 million years ago (Howarth 1988).

The much younger Undara lava flow (190,000 years old) covers portions of older flows within the McBride Formation (Atkinson *et al.,* 1976), some of which may date back from the Pliocene, i.e. more than 2.5 million years ago (Best 1983). The cave animals could have migrated through the mesocavernous systeme into young basalt and colonized new caves in each flow in succession.

"The troglobitic species could be, and probably are, older than the age of their caves" (Howarth 1988).

PHYLOGENETIC AGE AND TROGLOMORPHY

Against this background we here attempt to assess the problem of the dynamics of reductive evolutionary

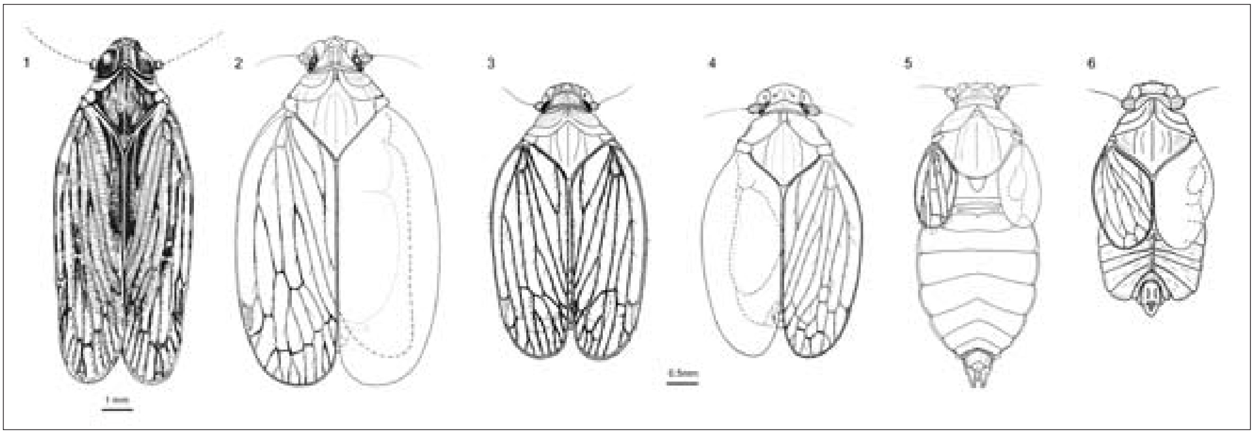

Fig. 3: Hawai'ian Oliarus species, habitus, dorsal view. 1, epigean Oliarus species (O. tamehameha); 2, O. kalaupapae; 3, O. lorettae; 4, O. gagnei; 5, O. waikau; 6. O. polyphemus. (1, from Zimmermann 1948; 2-5, from Hoch & Howarth 1999; 6, Hoch, Original).

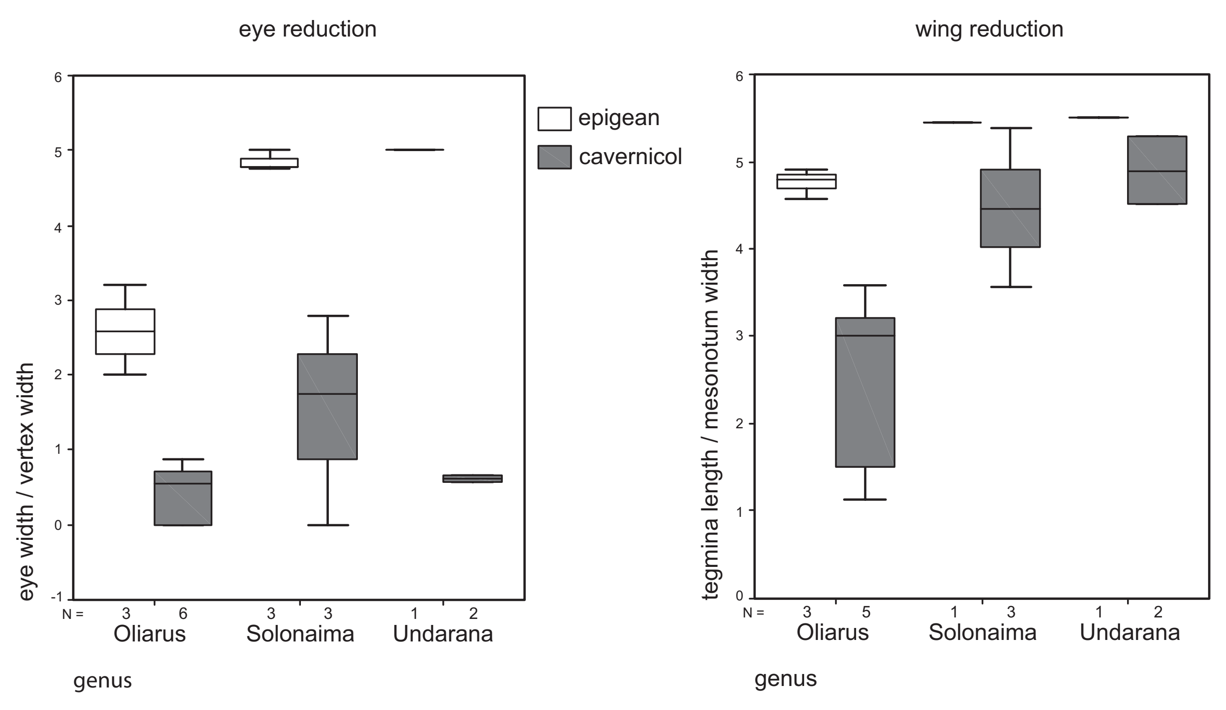

Fig. 4: Variability of relative eye width and relative tegmina length in epigean and cave-dwelling species (O. polyphemus, O. lorettae, O. makaiki (no wing measurements), O. gagnei, O. waikau, O. kalaupapae; S. pholetor (stonei), S. irvini (halos), S. baylissa; U. collina, U. rosella).

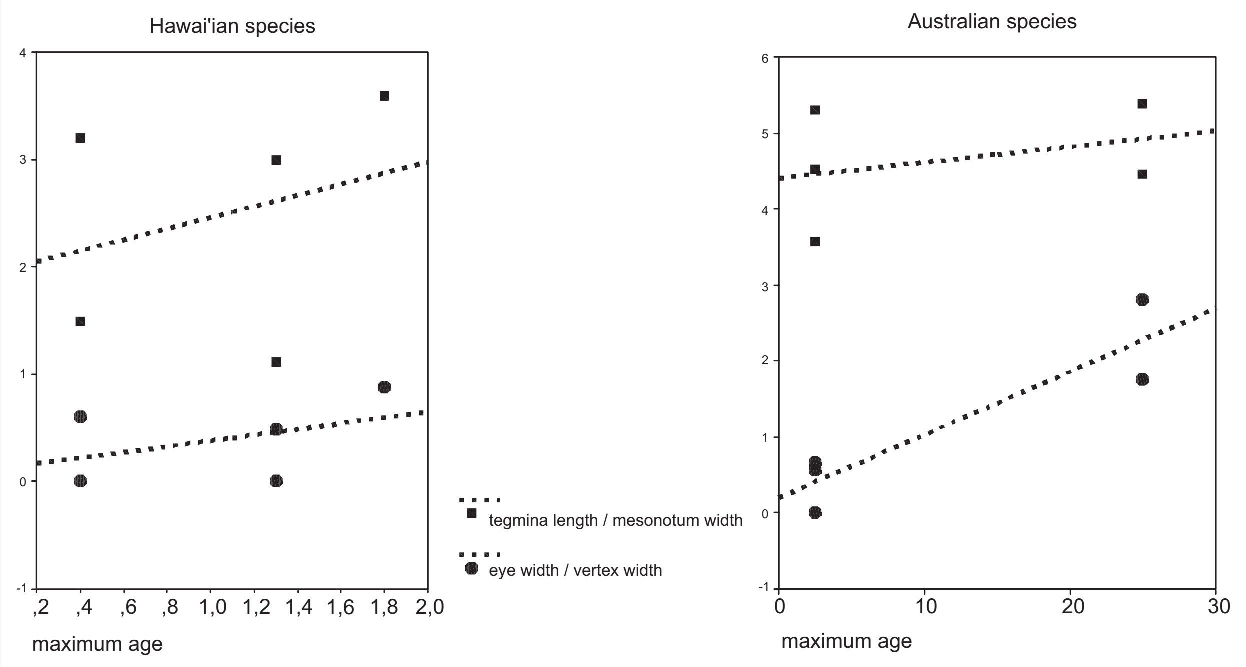

Fig. 5: Correlation of indices for troglomorphic characters with the maximum age of inhabited cave formations (O. polyphemus, O. lorettae, O. gagnei, O. waikau, O. kalaupapae; S. pholetor (stonei), S. irvini (halos), S. baylissa; U. collina, U.

trends (troglomorphies) or regressive evolution. A major obstacle in this context is the poor comparability of characters across different taxonomic groups. A strict approach should aim at analyzing character evolution in monophyletic groups where similar (morphological) pre-conditions or pre-adaptations for parallel evolution may safely be assumed. While we are aware of these problems, we nevertheless found it useful to employ a quantification of troglomorphic characters in order to achieve at least a preliminary idea of the possible correlation between troglomorphy and lineage age. We computed two 'troglomorphy indices' for all Hawaiian and Australian taxa from which data were available by using two characteristic troglomorphic characters in cavernicolous planthoppers: the reduction of eyes and the reduction of the tegmina. Eye reduction is apparently coupled with an obvious broadening of the vertex (see Fig. 2), so the index eye diameter: vertex width gives a clear statistical signal, ranging from 2-5 in epigean species with fully developed eyes to 0 in eyeless species. For the second index relative tegmina length we computed the absolute tegmina length: mesonotum width. Values ranges from 4.6-5.5 in epigean and from 1.1 to 5.3 in facultative and obligatory cavernicolous species.

The conspicuous differences between epigean and cave-dwelling species are clearly reflected in both indices (Fig. 4). If the data are plotted against the maximum age of the cave species, the *a priori* expectation is a clear negative correlation, at least for the Hawaiian taxa: the oldest cave lineages should exhibit the highest degree of troglomorphy. In contrast, we surprisingly found a weak (not significant) positive trend (Fig. 5). The same unexpected trends are seen in the Australian planthopper species.

Our results presented here, although preliminary, do not provide any evidence for cave-adaptation as a gradual orthogenetic process. Instead, we rather postulate that founder effects indeed play an important role in the origin of cave species. A correlation of the observed trends with particular ecological parameters of the cave environment cannot be excluded based on our data, but clearly this hypothesis needs further testing, especially in respect to selection pressures exerted by the conditions in high stress environments (such as caves) (Hoch & Howarth 1989b, Howarth 1993). We can conclude with some certainty, however, that even in closely related species the degree of troglomorphy cannot be employed to infer the phylogenetic age of the cave lineages.

ACKNOWLEDGEMENTS

We thank Dr. Thomas von Rintelen, Museum für Naturkunde der Humboldt-Universität zu Berlin, for helpful discussions and many useful suggestions.

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RULES OF CLIMATE, SOIL AND VEGETATION ON DEVELOPMENT OF THE KARSTSYSTEM

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In the evaluation of environmentally sensitive karst regions for nature conservation value the most useful information is supplied by the changes in the ecological conditions of the climate-soil-vegetation system. The changes in the system determine matter and energy cycles. A change in any of the three factors involves changes in the other two and eventually in the future functioning of the whole karst system. Climate influences the physical, chemical and biological processes of the karst system. Air temperature, humidity, precipitation and evaporation influence the water and matter cycles. Temperature regulates life processes of the biota. Matter transport is a function of soil, vegetation, relief and climatic parameters. The karst regions of various nature are characterised by different processes. In landscape planning and management this mechanism of interactions has to be taken into consideration in every case in the future.

TIME AND KARST PROCESSES: SOME CONSIDERATIONS

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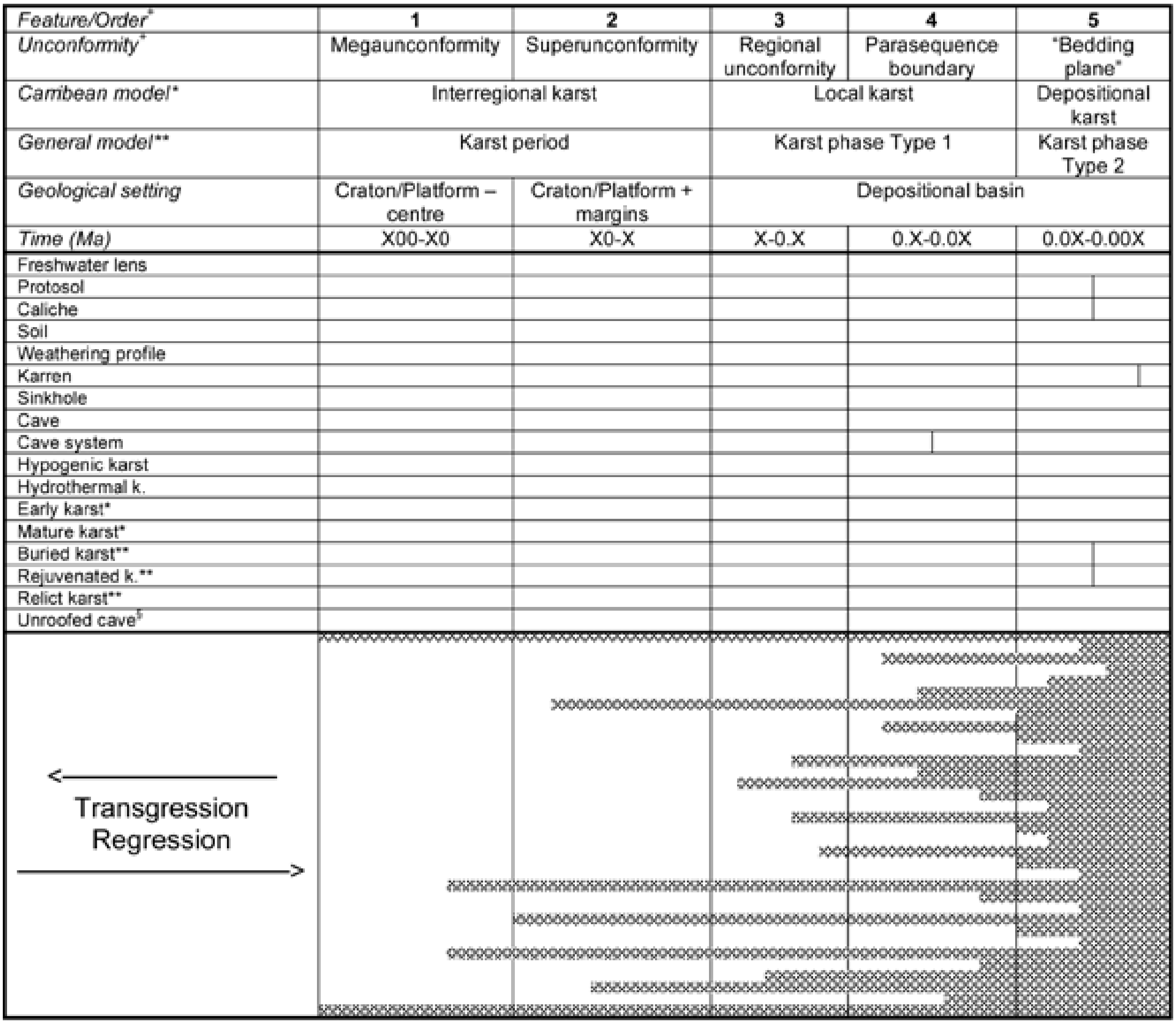
Karst evolution is particularly dependent upon the time available for process evolution and on the geographical and geological conditions of the exposure of the rock. The time scale for the development of karst features cannot be longer than that of the rocks on which they form. The longer the time, the higher the hydraulic gradient and the larger the amount of solvent water entering the karst system, the more evolved is the karst (Tab. 1). In general, stratigraphic discontinuities, i.e. intervals of nondeposition (disconformities and unconformities), directly influence the intensity and extent of karstification. The higher the order of discontinuity under study, the greater will be the problems of dating processes and events. The order of unconformities influences the stratigraphy of the karst through the amount of time available for subaerial processes to operate. Results of paleokarst evolution are best preserved directly beneath a cover of marine or continental sediments, i.e. under sediments, which terminated karstification periods or phases. The longer the stratigraphic gap the more problematic is precise dating of the age of the paleokarst, if it cannot be chronostratigraphically proven. Therefore, ages of paleokarsts has been associated chiefly with periods just or shortly before the termination of the stratigraphic gap. The characteristic time scale for the development of a karst surface landform or a conduit is 10 to 100 ka.

Determining the beginning and the end of the life of a karst system is a substantial problem. In contrast to most of living systems development of a karst system can be „frozen“ and then rejuvenated several times (polycyclic and polygenetic nature). The principal problems may include precise definition of the beginning of karstification (e.g. inception in speleogenesis) and the manner of preservation of the products of karstification. Therefore, karst and cave fills are relatively special kinds of geologic materials.

The end of karstification can also be viewed from various perspectives. The final end occurs at the moment when the host rock together with its karst phenomena is completely eroded/denuded (tze end of the karst cycle) or sunken into the subduction zone. In such cases, nothing remains to be dated. Karst forms of individual evolution stages (cycles) can also be destroyed by erosion, denudation and abrasion, complete filling of epikarst and covering of karst surface by impermeable sediments, without the necessity of the destruction of the whole sequence of karst rocks. Temporary and/or final interruption of the karstification process can be caused by the fossilisation of karst due to loss of its hydrological function. Such fossilisation can be caused by metamorphism, mineralisation, marine transgressions, burial by continental deposits or volcanic products, tectonic movements, climatic change

Tab. 1: Evolution of selected karst features in time on the background of transgression-regression set within one hypothetical karst period related to unconformity order



Feature/Order+	1	2	3	4	5
Unconformity+	Megaunconformity	Superunconformity	Regional unconfornity	Parasequence boundary	"Bedding plane"
*Carribean model**	Interregional karst		Local karst		Depositional karst
*General model***	Karst period		Karst phase Type 1		Karst phase Type 2
Geological setting	Craton/Platform – centre	Craton/Platform + margins	Depositional basin		
Time (Ma)	X00-X0	X0-X	X-0.X	0.X-0.0X	0.0X-0.00X
Freshwater lens					
Protosol					
Caliche					
Soil					
Weathering profile					
Karren					
Sinkhole					
Cave					
Cave system					
Hypogenic karst					
Hydrothermal k.					
Early karst*					
Mature karst*					
Buried karst**					
Rejuvenated k.**					
Relict karst**					
Unroofed cave§					

+ sensu Esteban (1991); * sensu Choquette & James (1988); ** sensu Bosák *et al.,* (1989); § sensu Mihevc (1996); Weathering profile = more evolved weathering cover (like laterite, bauxite, kaoline, etc.); Hypogenic karst = deep-seated karst, interstratal karst, intrastratal karst, subjacent karst, subrosion. a

etc. Nevertheless, in contrast to living organisms, the development of the karst system can be „frozen" and rejuvenated even for a multiplicity of times (polycyclic and polygenetic nature of karst). Further, the dynamic nature of karst can cause redeposition and reworking of classical stratigraphic order, making the karst record unreadable and problematic for interpretation.

Known karst records for the 1st and 2nd orders of stratigraphic discontinuity cover only from 5 to 60 % of geological time (time not recorded in any correlated sediments in old platforms usually represents 40 to 90 % of time). The shorter the time available for karstification, the greater is the likelihood that karst phenomena will be preserved in the stratigraphic record. While products of short-lived karstification on shallow carbonate platforms can be preserved by deposition during the immediately succeeding sea-level rise, products of more pronounced karstification can be destroyed by a number of different geomorphic processes. The longer the duration of subaerial exposure, the more complex are those geomorphic agents.

The dating of cave initiation and evolution, i.e. the origin of the void within the bedrock is more problematic. The age of the erosional cave falls between the age of the host rock and that of the oldest dated fill. With the inception theory, the true start of speleogenesis can hardly be estimated. Many caves contain only very young fills, older ones having been excavated during repeating cave exhumations/rejuvenations caused by changes in hydraulic conditions, spring position, climate, etc. The minimum age for the cave initiation phase is estimated to be a minimum of 10 ka and cave enlargement up to accessible diameters usually takes about 10-100 ka under favourable conditions.

URANIUM-THORIUM AGES OF STALAGMITES FROM KATERLOCH CAVE (STYRIA, AUSTRIA)

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Speleothems recently experienced growing importance in the light of paleoenvironmental research. Absolute age determination using Uranium-series methods allow for precise age constraints of environmental information preserved in speleothems, particularly in stalagmites and flowstones.

Katerloch Cave, situated within the Styrian Karst Province near Graz was chosen as an object of extensive paleoenvironmental studies. Abundantly decorated cave chambers show a clear dominance of stalagmites over stalactites, many of them being several meters in length. The majority of stalagmites are of the candle-stick type, a morphology suggesting fast growth.

Five inactive stalagmites were recovered and dated using the U-Th method. In addition, drill cores were obtained from the base of in-situ growing stalagmites. The dating of calcite sub-samples of these cores give an age of growth inception of the respective stalagmites. Age measurements were carried out using Multi Collector-ICP-Mass Spectrometry at the Institute of Geology at Bern, Switzerland. Our dating campaign allowed detecting several speleothem generations: stalagmites from the current Interglacial, the Marine Isotope Stage 3 and the Last Interglacial (MIS 5.5), indicating major speleothem growth during relatively warm (and wet?) climate conditions. The ages of two stalagmites are beyond the range of the U-Th method, i.e. they are older than ~ 450 kyr.

Two Holocene stalagmites, 73 and 139 cm in length, yielded ages between 10.32 ± 0.13 and 7.02 ± 0.14 kyr and between 9.80 ± 0.24 and 7.88 ± 0.09 kyr, respectively. Age models derived from dating of multiple subsamples along the stalagmite growth-axis suggest growth rates of 0.2 to 0.7 mm/yr. These rates are very high compared to caves in the alpine region. Two stalagmites from the preceding Interglacial (MIS 5.5) suggest similar growth rates than those of the Holocene stalagmites. Furthermore, fast growth of speleothems in Katerloch Cave is corroborated by stalagmite petrography, displaying a lamination of alternating white-porous and compact-translucent layers.

COPEPOD CRUSTACEAN DIVERSITY IN SOUTH FLORIDA KARST, U.S.A.

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Southern Florida is mostly occupied by the Everglades, an extensive subtropical wetland ecosystem that formed during the past 5,000 years when peat and marl were deposited within a pre-existing limestone depression in the southern peninsula. The high porosity of the limestone of the aquifer allows for considerable flux between surface water and ground water. Hydrologically, karst systems in South Florida are very open, and numerous epigean invertebrates often penetrate the aquifer by means of sinkholes, some of them establishing permanent populations in the aquifer.

The inventory of free-living freshwater copepods recorded from peninsular Florida includes a total of 65 taxa: 9 calanoids, 41 cyclopoids, and 15 harpacticoids.

Two-thirds (44) of these are known from Everglades National Park and adjacent areas, partly as a result of more intensive sampling in this area; 10 have so far been found only in the Everglades. Of the species collected in central and northern Florida, 2 calanoids and 1 cyclopoid have been found only in the state, whereas all the others are widespread in North America and beyond. South of the Everglades, in the Florida Keys, recent collections from small permanent or ephemeral surface waterbodies, some of them brackish, yielded 2 species of calanoids, 27 cyclopoids, and 11 harpacticoids, adding 1 calanoid, 2 cyclopoids and 9 harpacticoids to the list for Florida. Ten species of cyclopoids and 1 harpacticoid collected in the Florida Keys were already known from the Everglades.

In peninsular Florida, the Nearctic fauna is predominant, but a small Neotropical component is present (1 calanoid, 6 cyclopoids, and 5 harpacticoids); 1 cyclopoid species is considered to be introduced. In the Florida Keys, the assemblage consisted mainly of cosmopolitan or Neotropical continental cyclopoids (1 introduced), and Neotropical, coastal harpacticoids, with only 2, Neotropical continental calanoids.

Because the Florida peninsula is relatively young geologically, we did not expect that a diverse endemic groundwater fauna would be present. However, several taxa that are usually known elsewhere from surface water, were collected in subterranean water in the Florida Everglades during the dry season, likely an adaptation to survive the drought. This happened for the 2 species of calanoids, 16 of the 27 cyclopoids, and 4 of the 13 harpacticoids; among them, stygophile taxa were represented by 6 cyclopoids and 3 harpacticoids. The species occurring in groundwater in the Everglades are either widely distributed elsewhere in North America or in the neotropics, members of speciose genera with both epigean and hypogean species, or members of predominantly marine groups with some brackish- or freshwater representatives. The low diversity of harpacticoids in groundwater habitats in the Everglades is surprising, because harpacticoids include the largest number of stygobitic forms within the copepods. The closest area in which true stygobitic copepods have been found is northern Florida, which has an older geological history. The relatively young age of the Everglades may not have allowed some taxa enough time to disperse here, or may not have allowed sufficient time for groundwater colonizers to evolve adaptations to life in subterranean habitats.

Besides the young geological age, historical and environmental conditions may also account for the Everglades' relatively depauperate groundwater copepod fauna. Both the higher-elevation marshes and the deeper central sloughs undergo periodic droughts of varying severity, which affect the composition of the copepod fauna. The hydrological regime is irregular because of variations in rainfall and water-management activities, and groundwater communities are dominated by surface copepods that colonize groundwater mainly during the dry season. The abundance and species richness decrease with depth, and sharply below the 3-m depth, due to high permeability of the limestone above 3 m and to the presence of a semipermeable layer at lower depths. Groundwater copepod communities are more similar on a local scale: when local surface-water populations enter the shallow aquifer by following the receding water table, they do not generally disperse widely through the groundwater system. The dissimilarity in communities over larger distances may reflect differences in surface habitats, as well as limitations on dispersal by different local porosities of the limestone.

BLACK SEA LEVEL FLUCTUATIONS BASED ON THE STUDY OF SUBMERGED SPELEOTHEMES FROM DOBROGEA (ROMANIA)

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Several speleothem samples from Piatra Cave (Dobrogea, South-East Romania) were dated by means of alpha and mass spectrometry, in order to obtain absolute datings of the episodes during which speleotheme formation occured here. Piatra Cave is a submerged cave located a few kilometers far from the Black Sea shore at an absolute altitude of 1-2 m, thus being suitable for recording the sea level oscillations that took place in the past. Nine dates were performed by alpha spectrometry and one by mass spectrometry. In spite of a low Uranium content (0.04 – 0.1 ppm), all subsamples showed good chemical extraction yields, thus providing analytical reliable dates. One of the stalagmites appears to have been grown very fast during the Eemian (OI 5e), betwen 112 ± 10 ka and 122

± 13.5 ka (1σ). Another sample, dated by TIMS method yielded a date of 597 +108/-53 ka. Although these dates are not sufficient for a detailed analysis of the Black Sea oscillations, they reveal two periods of time during which environmental conditions here were favourable for speleotheme deposition as the cave was emerged. Most interesting are the samples dated from the warm OI substage 5e during which, the Black Sea level is supposed to have been 10 m higher than the present one. The area, during the Quaternary, being virtually stable from the tectonic point of view (except for a narrow coastal area), leads us to three possible situations that allowed speleotheme formation: either there was a slight subsidence in the area (around 15 m), or the sea-level was more than 15 meters lower than previously believed. The third possibility could be that during the main transgression that rose the level 10 meters above the present one, there has been a short period of low-stand.

HIGH-RESOLUTION SPELEOTHEM RECORDS FROM SOQOTRA ISLAND (YEMEN), AS RECORDERS OF INDIAN OCEAN MONSOON VARIABILITY

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The arid tropical island Soqotra is situated in the Indian Ocean between the Horn of Africa and the Arabian Peninsula. Here a bi-annual rainy season is active, due to the passing of the inter-tropical convergence zone (ITCZ) twice each year, known as the Indian Ocean Monsoon system. Only recently more than 35 km of underground cave passages in around 50 caves were discovered and explored, revealing an important karst potential for paleoclimate and paleoenvironmental research.

By evaluating the first available meteorological data (rainfall and temperature) from the last 5 years, we calculated that approximately 85% of the rainfall is related to the NE Monsoon period, while only 15% is related to the SW Monsoon period with an important irregular geographical distribution over the island. Differences in the oxygen isotope composition of meteoric water versus groundwater are used to estimate amount and timing of karst aquifer recharge, because seasonal fluctuations of rainwater oxygen isotopic composition are related to the amount of rainfall. Karst aquifer recharge at the NE limestone plateau takes only place during the NE Monsoon rainy period when a rainfall threshold of 80-90mm is exceeded, explaining the more negative cave drip waters and groundwater in general. Because the controls on the isotopic composition of nowadays forming speleothem calcite could be monitored in this region, two caves in this area were chosen as research location.

A sampled speleothem from Hoq Cave (S STM1) and one from Casecas Cave (S-STM5) have formed over the last 6 ka BP and the last 1 ka BP (U/Th dating) respectively. Carbon and oxygen isotopic measurements were performed at a resolution up to 50 m, corresponding to a time resolution of up to one month. The two sampling locations, distant of 6km, display similar isotopic changes in both speleothems over the last 1 ka. The speleothems also clearly registered seasonal variations, coinciding with the alternation of dark compact and white porous layers, representing annual banding in both stalagmites. These observations suggest that the speleothems reliably registered Monsoon climate variability.

EVOLUTIONARY CHANGE IN CAVE ADAPTED ORGANISMS

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Change of selective constraint on a gene may be expected following changes in the environment or life history. This is especially true for switches to the cave environment. The purpose of this work is to explore selective pressures and functional change on a variety of protein coding genes across cave- and non cave related taxa to assess general patterns of evolutionary changes in different lineages, and whether (and to what extend) they depend on environmental conditions. Protein coding sequences that appear to be undergoing adaptive evolution or changes of function along specific branches of the tree will be analyzed in detail as to determine the specificity and functionality of those changes. Results of this work will be incorporated into the publicly accessible TAED database (http://www.sbc.su.se/~liberles/TAED2002/) and will help pinpoint target genes for future studies on cave organisms and their environment (e.g., karst).

TEMPO OF CHANGES IN KARST BIOLOGICAL VERSUS PHYSICAL PROCESSES

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Time is an essential parameter for understanding any ecosystem. Lansdcape, habitats, community composition, genetic pools and species distribution change with time, in a more or less connected way. Yet, integrative approaches linking physical and biological karst processes in a time perspective are scarce in the literature. One of the intriguing property of subterranean karst systems is that time required for biological or physical processes may differ considerably from that required for similar processes in surface karst or non-karst systems. Essential aspects of this peculiar tempo of changes in karst are presented here. Their interest for understanding paleogeography and organism evolution are discussed.

KARST AS A MODEL SYSTEM TO EXAMINE TERRESTRIAL MICROBIAL BIOGEOGRAPHY PATTERNS THROUGH TIME: AN EXAMPLE FROM THE EPSILONPROTEOBACTERIA

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The evolutionary mechanisms that govern the distribution of microbes on Earth are poorly understood. The concept that geographic isolation among microorganisms can lead to endemism is controversial. Because microbes are small in size, are metabolically tenacious, and are overwhelmingly abundant on Earth, microbes may be distributed everywhere and therefore may not be affected by geography. However, some studies reveal that various taxa have restricted distribution patterns. Many microbial biogeography studies have been conducted to test for microbial species endemism, but these studies have been conducted in habitats with high dispersion (e.g., aquatic, and specifically oceanic, habitats). Consequently, there have been few studies of microbial biogeography in terrestrial habitats. Karst, in particular, is a discontinuous habitat typified by different hydrostratigraphic units in distinct geologic provinces formed over time. While the karst habitat may be similar in its physicochemical and geological conditions from one locale to another, microbial groups colonizing karst may reflect biogeography because of genetic exchange limitations. In the separated karst habitats, speciation events could be high. Considering the ubiquity of karst worldwide, understanding the types of microbial communities in cave and karst systems, as well as determining what geologic and geochemical processes may control microbial species distribution and diversity, are critical aspects to preserving the integrity of the karst ecosystem and to predicting ecosystem changes that may occur following disturbances.

The *Epsilonproteobacteria* taxonomic class is an ideal microbial group to investigate endemism, biogeographic diversity, and possible mechanisms controlling bacterial evolution in karst. Members of this class are found in many different sulfur-rich environments, including marine and terrestrial aquatic settings. Although investigated less, *ε-Proteobacteria* from terrestrial settings are potentially

widely distributed. Our previous investigations diagnosed novel evolutionary lineages within the ε-Proteobacteria from one terrestrial subsurface environment, Lower Kane Cave (LKC) in Wyoming (USA). Two lineages dominated the subterranean communities and were related to organisms identified from other sulfur-rich terrestrial habitats (contaminated groundwater and caves), but not to microbes from marine habitats, including deep-sea hydrothermal vent sites and marine sediments.

Microbial mat samples from six cave and nine karst spring locations were collected, including the Frasassi Caves (Italy) and Movile Cave (Romania). 16S rRNA gene sequences were amplified, cloned, and sequenced from total community DNA extractions using general and ε-proteobacterial lineage-specific primers. From a total of 336 sequences used for phylogenetic analyses, 71 ε-proteobacterial species-level lineages (operational taxonomic units, OTUs) were identified from cave and spring habitats. We recognize the fact that biogeographic interpretations based on the presence or absence of 16S rRNA genes should be made cautiously. However, five OTUs, consisting of sequences from up to nine locations, came from different continents and from karst systems with varying speleogenetic histories. Analyses of single copy genes (rpoB and aclB) from selected karst locations are currently underway to test distribution and occurrence pattern differences between the multiple copy genes (e.g., 16S rRNA gene) and single-copy genes. We expect the number of OTUs will be more than that observed with the 16S rRNA gene.

Our initial 16S rRNA gene sequence investigations do not reveal a correlation between the relative speleogenetic age of the cave, the age of the carbonate host rocks, and the microbial group (or OTU). Although most of the systems have formed within the past 500 ka (thousand years) in carbonate rocks ranging up to 400 Ma (millions of years old), all of the cave and spring locations are currently inundated by modern sulfidic waters that are the consequence of distinct regional hydrostratigraphic conditions. These data suggest that extremely ancient, large-scale geological processes and events (e.g., depositional basin sedimentology and geochemistry, plate tectonics, regional karstification events) must have influenced the ancestral distribution of these groups, which were likely marine in origin.

Once ε-Proteobacteria colonized these terrestrial habitats, limited dispersal capabilities (i.e. no cyst or spore formation) and hydrostratigraphic barriers to genomic exchange led to site-specific lineage evolution. In our analyses, this is indicated by more than 89% of the OTUs consisting of sequence groups from single sampling locations. Furthermore, three OTUs (comprised of sequences from more than one location) were retrieved from the same geographic region, illustrating the potential importance of biogeography in terrestrial ε-Proteobacteria distribution patterns. The large percentage of site- and region-specific OTUs detected in our study indicates potentially high site-specific endemism effects for some terrestrial ε-proteobacterial lineages and possibly some recent (on an evolutionary/geologic time scale) exchange on a regional scale.

RADIATION SCENARIOS FOR AUSTRALIAN CAVE-ADAPTED PLANTHOPPERS

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Cave-adaptation, the shift to a life underground, can provide critical information to understand evolutionary change in general, but the process of cave-adaptation is still not well understood and controversially discussed.

Planthoppers, especially of the family Cixiidae (Insecta: Homoptera: Fulgoromorpha) inhabited caves in many parts of the Tropics and Subtropics independently. These evolutionary lineages are ideally suited models to study the concepts of genetic differentiation and speciation dynamics. One of those planthopper taxa is the Australian genus Solonaima. This genus is endemic to Queensland and New South Wales and contains epigean as well as cavernicolous species. The epigean species occur in the rainforest habitats along the east coast, while the cave-dwelling species are restricted to more arid areas western to the Great Dividing Range (Chillagoe & Mitchell Palmer Karst and Undara Lava Tubes). This relictous pattern seems to be due to the extinction of epigean species in the Outback according to the retreat of habitat starting with the desertification of inner Australia in Miocene, Pliocene.

The observed species display different degrees of troglomorphy, which are incongruent with the age of the caves, as the highest derived species occur in young lava tubes, while less cave-adapted species occur in older

Tower Karsts, which also leads to the assumption of several cave invasion events.

According to the cladogram only two cave-invasions are requisited, one for S. sullivani and one for the other cavernicolous species, although the problem of homoplasis in cave-adaptation has to be considered. If more than one ancestral epigean Solonaima species inhabited once the Outback, from which all cavernicolous species (except S. sullivani) descended, all hints for this are vanished with these hypothetic ancestral species and/or veiled by cave inhabiting conditioned homoplasis.

Hence, morphometrical statistics and variation studies concerning aedeagal characters were conducted additionally, allowing to reconstruct scenarios for the invasion history of the extant populations:

1. Multiple cave-invasion scenario
2. Single initial cave-invasion scenario

To accommodate these results a hypothesis merging the relict hypothesis (Barr 1968) and the adaptive-shift hypothesis (Howarth 1986) had to be formulated.

CAVE-DWELLING PLANTHOPPERS OF THE GENUS SOLONAIMA (INSECTA: HEMIPTERA: CIXIIDAE) IN AUSTRALIA: RELICTS OR EXPLORERS?

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The evolution of obligately cavernicolous terrestrial organisms is still controversially discussed. Traditionally, cave colonization has been interpreted as a response to adverse (climatic/ecological) conditions on the surface leading to the extinction of epigean populations, "trapping" troglophilic populations inside underground environments. These populations subsequently acquired morphological (troglomorphies) and behavioral alterations. The patterns commonly observed in temperate regions seem to support this assumption. The discovery of terrestrial obligate cavernicolous invertebrates (mainly arthropods) in the tropics, however, with close epigean relatives still extant, challenged this view. Here, cave colonization and -adaptation could also be the result of an active process, driven by the exploitation of novel food resources, such as roots.

Here we present a model system which allows us to test these hypotheses.

The Australian planthopper genus *Solonaima*, endemic with ca. 15 species in Queensland and New South Wales, contains epigean as well as facultative and obligatory cavernicolous species. The cave-dwelling species display varying degrees of troglomorphy pertaining to eye- and wing reduction. Epigean *Solonaima* species occur in rainforest habitats along the East Coast while the cave-dwelling species are restricted to more arid areas west of the Great Dividing Range.

To test the existing hypotheses on our model system, the following criteria should be applied, while these hypotheses are not necessarily considered to be oppositional:

Relict hypothesis	*Adaptive shift hypothesis*
- deterioration of climatic conditions on the surface	- stable climatic conditions on the surface
- close epigean relatives not extant	- close epigean relatives extant
- cavernicolous taxa are of the same phylogenetic age	- cavernicolous taxa are of different phylogenetic age

The current distribution pattern seems to support the relict hypothesis in the case of the cavernicolous Solonaima species: Epigean and cavernicolous species occur allopatrically. It is conceivable that in the course of the gradual desertification of central Australia during Miocene/Pliocene, when rainforests retreated eastwards, being replaced by a more xerophilic flora, *Solonaima* species survived in (the still moist) cave refugia and subsequently acquired troglomorphies.

The observation, however, of varying degrees of troglomorphies in cavernicolous Solonaima species may account for different phylogenetic age of these taxa and thus, be an indication for an adaptive shift. Hence it cannot be excluded that cave colonization and -adaptation in *Solonaima* occurred before the period of desertification, making an initial adaptive shift prior to the development of the extant relictual pattern assumable.

STYGOFAUNA FROM A KARSTIC ECOSYSTEM IN THE PONOR MOUNTAINS, WESTERN BULGARIA: PRESENT KNOWLEDGE AND RESEARCH CHALLENGES

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The Ponor Mountains (Western Bulgaria) are part of the Balkan Ridge, with altitude 400 - 1473 m a.s.l. and more than 120 caves and chasms. The massif is formed mainly by Mesozoic rocks. Two basic rock complexes can be distinguished regarding to the karstification: Triassic karstic complex, formed by lime and dolomites with maximum depth 600m; and upper Jurassic complex with depth 100-150m. The two aquifers are hydrologically isolated. Basic collector of underground waters is the Triassic complex with annual outflow 2900 dm^3/s from which 80% is leaving the system through the Iskretski izvori spring. This is the biggest spring in Bulgaria (maximum discharge 35000 dm^3/s). The Jurassic complex (average outflow 120 dm^3/s) is lacking superficial outflow which determines its precipitation alimentation.

The stygofauna is very heterogeneously distributed and its composition varies greatly from one station to another. From the aquifer with rocks with Triassic age are found 21 species while from the Jurassic one are found only 7. The common species for the two aquifers are 5 amongst which with higher frequency of occurrence are *Niphargus bureschi, Speocyclops lindbergi* and *Stygoelaphoidella elegans.* At present 25 stygobionts are known from the Ponor Mountains: from Mollusca (2), Hirudinea (1), Acari (1), Copepoda (16), Syncarida (1), Isopoda (1), Amphipoda (3) groups. Crustacean assemblages are natural indicators of the typological characteristics of the system (hydrogeological division of karst, potential subsurface water connections, hydrological regime, contaminants transformation and bioaccumulation). Some of the main challenges to be faced in future concern understanding regional and fundamental functioning and structure of subterranean aquatic ecosystems. The issues to be solved with the help of invertebrate communities are: origin and circulation pattern of groundwater flow in a fractured karstic aquifer; relationships between groundwater hydrodynamics and contamination; connections among the underground areas and understanding differences that may make individual areas unique in terms of fauna; assessment of the contemporary condition and extent of human perturbation on the Ponor Mountains ecosystem; measures for protection and management.

A CONTEXT FOR EARLY FARMING IN THE CENTRAL DALMATIAN POLJE: EVIDENCE FROM SEDIMENTS AND SOILS

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The formation of and sedimentation processes in poljes (large, elongate, flat-bottomed karstic valleys) are uncertain and may be unique to each polje – dependent on climate, bedrock chemistry, and groundwater. One aim of our work on the Early Farming in Dalmatia Project at the Danilo Bitinj and Pokrovnik archaeological sites is to elucidate polje sedimentary history. Analysis of his sediment record will inform the conditions of Neolithic settlement and earliest agriculture. To this end we are examining granulometric and ground-penetrating radar data from these valleys, and reconciling this GPR data with ground-truthing from soil profiles to create a three-dimensional subsurface map. We will use both the texture and 3-D form of the deposits to reconstruct the geomorphic setting prior to and during Neolithic occupation. We hope that ground-truthing the GPR data, along with textural and soils analyses will enable further interpretations concerning the presence and extent of debris fans, the presence of erosive surfaces in the bedrock and sediments, and evidence for high-energy sedimentation events. Large limestone clasts (5-50 cm) present in valley soils (on- and off-site) may be the product of *in situ* bedrock weathering or the result of high-energy or high-viscosity events. X-ray fluorescence analysis of bedrock and of valley clasts may also help resolve this question.

MORPHOLOGICAL EVIDENCE OF MULTIPLE CAVE LEVEL DEVELOPMENT IN THE UPPER BASIN OF SOMESUL CALD RIVER, BIHOR MTS., ROMANIA

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The karst on the upper basin of Somesul Cald River is situated in the Apuseni Mts., Romania, on the NE border of Padis karst plateau. It covers a relative small surface, superimposed on the drainage basins of Ponor, Alunu Mic, Alunu Mare and Firii valleys, all right hand affluents of Somesul Cald River.

Two main types of karst are found in the area: slope karst and plateau karst. The slope karst includes numerous caves situated at different elevations on the slopes of the above-mentioned valleys, vertical cliffs and partly denudated caves. The plateau karst is less extended, being present mainly on the northern sector of the area, at the springs of the Firii and Ponor valleys. Numerous dolines punctuate the surface, and some shafts gave access to deep and long cave systems, among them being the Avenul din Poienita-Humpleu karst system, the second longest in Romania.

Down cutting of Somesul Cald river and subsequent lowering of the base level triggered the genesis of a multi-stage, well-defined karst system, developed along the rivers that cross this area.

Here we report the results of a long-term cave survey project, aiming to correlate cave levels from the upper basin of Somesul Cald river, and construct a chronology of the karstification processes in the area. By combining morphologic observations (both in caves and at the surface) with detailed mapping of the caves we were able to link the Quaternary evolution of the Somesul Cald River and its tributaries with the cave systems presents on the slopes of the rivers, and also establish a relative chronology of the karstification processes that affected the area. Moreover, morphological observations in the caves show that the early stages of cave development took place mainly under phreatic conditions, while later ones were in vadose conditions, as the entire area was uplifted.

HYDROSTRATIGRAPHY OF THE KARST AQUIFERS OF FLORIDA

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In the United States, two highly-productive carbonate aquifers occur within peninsular Florida: 1) the Floridan aquifer, primarily composed of Eocene to Oligocene carbonates generally unconfined in the northwestern part of the peninsula and confined in the remainder; and 2) the Biscayne aquifer of southeastern Florida, predominately unconfined and mostly Pleistocene in age. Combined, these two aquifers provide potable water for about 17 million Florida residents.

Much of the unconfined Floridan and Biscayne aquifers are in low-lying, coastal, and subtropical environments. Both are composed of karstified eogenetic carbonates that have not been deeply buried and therefore retain substantial primary porosity. Permeability within eogenetic aquifers is highly heterogeneous, with the matrix as much as 107 times as permeable as the matrix of telogenetic carbonates.

The karst features manifest within the unconfined Floridan and Biscayne aquifers offer contrasting examples of cavernous-scale (>2-cm diameter) porosity found within eogenetic karst. Both aquifers, however, differ considerably from epigenic karst in telogenetic limestones, where water flows from sinkholes to springs through fractures and discrete conduits. Groundwater in eogenetic karst similarly can travel through large conduits and fractures, but in contrast, also through mazes of stratibound touching-vugs and rock matrix.

Detailed petrophysical and geophysical studies demonstrate an organization to the hydrostratigraphy of both aquifers. For example, cavernous porosity is com-

monly layered. The origins of the cavernous porosity are primarily associated with fluctuations in sea level. In the unconfined Floridan aquifer, stratiform cavities at 5 m, 12-15 m, 21 m, and 30 m above modern sea level occur at elevations similar to geomorphic terraces in Florida, suggesting cavity formation during higher paleo-altitudes of sea level and water table. Likewise, cavities at depths of 15 m, 40 m, 70 m, and 90-120 m below the modern water table generally agree with depths of marine terraces submerged in the Gulf of Mexico, which formed at previously lower altitudes of sea level and water table. Distinctly different from the unconfined Floridan aquifer, cavernous porosity in the Biscayne aquifer commonly occurs as horizons of cm-scale, touching-vug porosity within the upper and lower boundaries of depositional cycles.

A LOCAL DEVELOPMENT OPPORTUNITY FOR A KARST AREA – THE MUNICIPALITY OF ALVAIÁZERE

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Located in the Leiria district (Portugal centre), the municipality of Alvaiázere it has an area of 160 km2 and it dominates the karst landscape with many characteristic karstic features.

It is an area that presently is facing many problems concerning local development, a decreasing and ageing population are causing a dramatic scenario for its future as a municipality, which implies a big challenge for it's own future, concerning economy, social and environmental policies. Other threats like infrastructures are a problem for the cultural, historic and geomorphologic heritage in this area.

Despite this scenario, this area has many characteristics and features that can be a good opportunity for the development of a sustainable development strategy, based in its own values. Its an area in which culture, geomorphology and landscape are closely linked and also an excellent opportunity to develop research at the interface between geomorphology and human sciences.

Many values can also if not identified be lost forever, not only geomorphologic values but also cultural, historic, among many others.

A recent research has showed that this territory has a good potential for the development of a local strategy, similar to a geopark, based in this known and unknown values, but only after being identified this values.

The mountains of Alvaiázere and Ariques are probably the most important area in this municipality concerning to the existence of some of this important values. Karst features like lapiés, caves, doline, a karst valley are present here among many others. Also a rich biodiversity exists here, that´s why this area is included in the place Natura 2000 – Sicó/Alvaiázere.

Other value with great importance is the late Bronze Age walled settlement of the mountain of Alvaiázere, one of the largest known habitats from this age in the west of the Iberian Península. Dinosaur footprints are also present in this area, not only in the mountains but also in the surrounding area.

The municipality of Alvaiázere from these values can create and stimulate a global strategy for sustainable territorial development along with geoconservation in this beautiful karst area and a door for the future.

GEOCHEMICAL AND PHYSICAL PROPERTIES OF STALAGMITES AS A MARKER OF PALEOENVIRONMENTAL CHANGES

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Stalagmites are archives of palaeoclimatic information and many geochemical and physical properties can be used to interpret former environmental conditions that may have occurred during their growth. When calibrated against the present conditions in the cave system, the composition and growth rate of stalagmites can be interpreted in terms of former surface climate.

An extensive 2-year monitoring of the modern cave system shows that isotopic $\delta^{18}O$ of the cave drips is equal to the mean annual $\delta^{18}O$ of the local precipitation (- 7.2‰); the $\delta^{13}C$ a product of soil organic matter, whereas Mg and Sr concentration is determined primarily by the dolomitic bedrock. The complex karst hydrology modifies the final drip composition through differential transport, storage and mixing, whilst cave air temperature is seasonally variable due to links with the external atmosphere provided through the cave stream and multiple entrances, although mean temperature is equal to that above the cave (7.2°C). Cave air pCO_2 is similarly variable.

A newly sampled stalagmite is analysed together with SU967 a sample previously documented within the literature. The lamina thickness chronology duplicates that of SU967. High-resolution records of $\delta^{13}C$ and $\delta^{18}O$ are shown together with high and low-resolution Mg and Sr acquired using a variety of new and well-established techniques. Inter and intra-stalagmite variation in $\delta^{18}O$, Sr and Mg is good with excellent replication demonstrated. The $\delta^{13}C$ is more variable between samples. Statistically significant co-variations are found between these stalagmite records, instrumental records and climate reconstructions. Finally T/P and summer temperature are reconstructed producing a multi-proxy record of climate for NW Scotland.

HISTORICAL BIOGEOGRAPHY OF THE GENUS MESONISCUS CARL, 1906

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The genus Mesoniscus is a morphologically well-defined group, clearly apart from the other groups of the Oniscidea, with only two species - *Mesoniscus alpicola* (Heller, 1858) and *Mesoniscus graniger* (Frivaldsky, 1865) - and a distribution strictly limited to the Alpino-Carpathic Chain and, as such, particularly interesting from a biogeographical point of view.

The spreading of the genus Mesoniscus allows us to notice that the two species are clearly spatially separated: *Mesoniscus alpicola* is found exclusively in the Alps; *Mesoniscus graniger* is spread in the whole Carpathic Chain, from the Northern and the Romanian Carpathians, South-Danube Carpathians, the Dinarids and the Julian Alps.

There are two hypotheses regarding the origin of the species *Mesoniscus graniger:* a Northern Carpathian origin / a Bohemian one (implying a southward spreading along the Carpathic Chain to the Dinarids and the Julian Alps) or, of contrary, an Illyric origin, followed by a northward migration from the Dinarids and the South-Danube Carpathians, through the Romanian Carpathians, up to the Northern Carpathians.

The Northern Carpathian origin hypothesis of the species *Mesoniscus graniger* is argued by an earlier and longer connection between the Alps and the Carpathians and also by a later connection between the Dinarids and the Carpathians.

But recurring land bridges between the Alps and the Dinarian-Pelagonian-Anatolian landmass, anterior to the connection Alps-Bohemian Massif-Carpathians, suggest and argue for an Illyric origin, also sustained by the subsequent isolation of the Dinarids from the Alps and the Carpathians.

IMPACTS OF ACIDIC PEAT BOG DRAINAGE ON HOLOCENE KARST DEVELOPMENT IN SOUTHEAST ALASKA, USA

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The Tongass National Forest of Southeast Alaska, USA covers nearly 6.9 million hectares of mountainous offshore archipelago with extensive mature temperate rain forests. Because of the accretionary terrane geologic setting, the geology there is extremely complex and heterogeneous, and includes numerous blocks of limestone that have been intensively karstified. These extensive areas of carbonate bedrock are focused mainly on the northern portion of Prince of Wales Island. The last glacial activity in the area occurred with the Wisconsinan (Marine Isotope Stage 2) glacial advance during the Pleistocene epoch. This approach strongly influenced the karst landscape. The development of muskeg peatlands has occurred in poor drainage areas where compacted glacial sediments and silts have been deposited over the bedrock below. The decomposition of the Sphagnum mosses leads to highly acidic waters with pH as low as 2.4. The measurement of continuous water chemistry at a muskeg input location and the down gradient karst resurgence found that the carbonate karst system acts as a buffer for the highly acidic muskeg waters. Over the gradient of the system, the pH increases from 3.89 to 7.22 and the predicted and measured dissolution rates drop from the insurgence to the resurgence of the system. These organic acids from the muskeg waters at the insurgence contribute to the highest recorded dissolution rates for natural karst systems. Depending upon the model used to calculate dissolution, rates ranged from 0.09 cm/yr to 2.5 cm/yr of wall retreat. The karst resurgence does not differ significantly from other karst springs that do not have highly acidic inputs. As such, the acidic muskeg waters are rapidly depleted upon entering the karst system and do not propagate very far down gradient. This is supported by the presence of pits located where the muskeg waters run onto the carbonate areas. These pits have formed since the last glaciation which is backed up by both the dissolution rates and by the geomorphology in the area.

TIME IN KARST: A BIOSTRATIGRAPHIC PERSPECTIVE

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Almost 150 years ago Louis Aggassiz demonstrated that there are only three essential methods by which the natural sciences can operate: comparative, ontogenetic and palaeontologic. Major differences between them are in the way in which the time component of phenomena is considered. The aspect of time is excluded from the scope of the comparative method: an act of comparison as well as its results are the mathematic structures open to further comparisons and testing. They are instant sources of formally objective nomological-deductive hypotheses largerly invariant to contextual changes. The *ontogenetic* method operates with the phenomena whose temporality can be eywitnessed by our personal presence and immediately expressed in terms of a smooth continuous time scale, corresponding to exposure of time in common life. The outputs of the ontogenetic method are the historical-narrative hypotheses whose reliability is entirely determined by the reliability of particular observer and the observation techniques. The *paleontological* method is the way to treat the phenomena for which a temporality is an essential trait of them but stays far beyond the scope of the ontogenetic method. Almost all the phenomena within the scope of this symposium fall in the domain of the palaeontological method and our comprehension of them is thus potentially biased by essential inconsistency of palaeontological method.

These phenomena can be well mutually compared but their temporality can only be derived of the assumption that the difference revealed by an act of comparison is an instant function of time. Of course, the fossil record, including that relevant for study of karst phenomena, is almost never continuous. On contrary, it is fragmentary in more respects and its density exponentially decreases with time distance. Moreover, as pointed out by Eldredge

and Gould (1972), in large time scales, the fossil record exhibits the punctuated equilibria pattern: alternation of sudden large-scale rearrangements with long periods of stasis. In other words, the time scale generated by fossil record is in no way smoth and continuous but discrete and non-linear. Exactly the same is apparently valid for dynamics of karst development and the record that is available for its study.

The major problem of the paleontologic method and dating karst phenomena lies in absence of a direct feedback control over reliability of the empirical ordinance relations between outputs of comparative analysis and time. Of course, these relations can be biased in many ways and the proposed time datum is never exact but a mere estimate which confidence limits should be specifically discussed in every single case. The methodological syllogism often applied in order to prevent possible dating bias is „count from top stratigraphy“: choosing the upper confidence limit , least distant from now, as a real datum. Traditional application of that technique in „safe“ dating is seemingly the more pertinent the less complete the record is and less robust its dating power is. This may lead to extensive underestimation of the real time span of the phenomena being studied. In dating of karst phenomena the respective bias is even more serious because what is available for study is not the true karstification events and/or the processes producing them but in most instances merely the epiphenomena of their past incidence (infillings of underground cavities, speleothemes etc.). Any data obtained from karst infillings and/or any other karst phenomenon is thus necessarily „a possible minimum age“ , i.e. the upper most confidence limit of karstification stage.

Regardless of various instrumental techniques, biostratigraphy remains to be the most significant source of dating particularly for time slices of distant past. Of course, just from them, the fragmentarity of fossil record is greatly pronounced, in general, and any effort of biostratigraphic dating must hence be performed in full respect to this fact.

The procedure of biostratigraphic dating includes the following steps: (i) a careful comparative analysis undertaken both with the morphometric characteristics of all items composing the respective record and with taxonomic and structural composition of the sample. The reliability of the result clearly depends not only on extent of the data obtained from the record under study but even more importantly on the quality and extent of the data taken in comparison (both recent and fossil), (ii) transcription of the specificities of the record revealed by step (i) into terms of its time distance from well dated records. As the rules of the respective transcriptions are essentially quite specific for each particular taxon and even each trait under study, the procedure (ii) actually results in a large set of different data with greatly variegated confidence limits. The next step should hence include (iii) a comparison of them and application of the techniques discriminating their actal meaning and producing the consensus date. An instant summary of previous comparisons is provided in form of a biostratigraphic system: a set of ordinance rules regarding the phenomena repeatedly revealed in multiple previous analyses. With a formal biostratigraphic system, a practical performance of the step (iii) is essentially simplified namely in that it reduces amount of the comparative effort to be performed onto answering few questions put by definitions of particular units of the respective stratigraphical system. Such an approach works quite well and effectivelly if the fossil record in study is rich and reliable in respect to representation of particular index fossils and, at the same time, of course, if the biostratigraphic system applied is actually responding to the purpose. This means that its units must be sufficiently well defined and balanced with respect to local and temporal variations in the criteria discriminating them. The finer the time scale on which the biostratigraphic system operates the lesser is its reliability beyond the geographic limits of its type area. Simply said, the absolute reliability is not granted for any biostratigraphic system and its dating power is the smaller the less representative is the actual fossil record. Unfortunately, this is the typical case in the study paleokarst phenomena. Often we obtain only few poor fragments belonging to the taxa not representing real index fossils. Such cases requires application careful case-specific analyses by a well trained palaeontologist, including ad hoc reconsiderations of confidence limits for any possible date that would come in account. It rests upon the karst scientists, of course, to claim such a challenging approach from the palaeontologists cooperating in the study and to expect from them a detailed accounts of the possible confidence limits for the final date they propose. With respecting the above rules, the biostratigraphic approach will undoubtedly continue to play its essential role among the tools by which the information on time in karst is gained.

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BIOGEOGRAPHY OF STYGOBIOTIC CYCLOPOIDS (CRUSTACEA: COPEPODA) FROM BALKAN PENINSULA FOCUSED ON ACANTHOCYCLOPS KIEFERI LINEAGE

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Evolution of subterranean fauna in Balkan Peninsula has mainly been governed by the geographical patterns of region and its geological history. The Balkan region boasts high level of endemism, particularly in caves, which are well known as Pleistocene glacial refugia. We studied the biogeography of subterranean Cyclopida (Crustacea: Copepoda) of the Balkans on a regional scale. By far the richest sub-region is the Dinaric Mountains, which form the western part of the peninsula (defined by the political borders of the states from former Yugoslavia), followed by the eastern (Bulgaria and S-SE Romania) and the southern Balkans (Greece and Aegean Islands). For the stygobiotic cyclopoids, the average observed number of species per country is 12.7 and the total diversity is 69. Thus, α-diversity accounts for 18.4% of the regional diversity and β-diversity contributed for 81.6% to regional diversity. The Cyclopinae fauna is comprised of Nearctic-derived epigean forms (i.e. *Acanthocyclops, Diacyclops* and *Speocyclops)* of which the most diversified genus is *Diacyclops* with 27 taxa known. The faunistic connection between western and central Europe is supported by the species widespread in Mediterranean region (e.g. Spain and southern France) as well as cosmopolitan stygobionts found throughout Europe. Bray-Curtis similarity coefficients indicate that the Transylvanian Plateau (NW Romania) is closely related to western Balkans (similarity level 41.38%) than to that of northern part of Bulgaria (30.3%).

The *Acanthocyclops kieferi* lineage was analyzed in detail. Thirteen of 17 species in the lineage are endemic to the Balkans. We hypothesize that these 13 species have a common ancestor and arose as a result of vicariant events in the Miocene. These resulted in their isolation in subterranean waters.

AGE CONSTRAINTS FOR KARST FORMS AND PROCESSES IN APULIA (SOUTHERN ITALY)

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Apulia region, in the south-eastern part of Italy, has three main karst reliefs, named Gargano, Murge and Salento; they show in outcrop a wide part of the apulian foreland (Ricchetti *et al.,* 1992). Their morphological history started in the upper Cretaceous (Luperto Sinni *et al.,* 1991), followed on in the Tertiary age, and developed its major karst forms during the Quaternary (Neboit, 1975; Grassi *et al.,* 1982).

Recently, different kind of researches have been collecting data in Gargano (Sauro, 2000; Caldara & Palmentola, 1993) as in Murge plateau (Sauro, 1991; Bruno *et al.,* 1995; Castiglioni & Sauro, 2000; Palmentola & Iurilli, 2002) and in Salento peninsula (Mastronuzzi & Sansò, 1991; 2001). These recent works, with the help of studies still in progress, are giving further contributions for reconstructing the evolution of karst. For instance, in hypogean geomorphology and speleological research, karst *morphosequences* (Dramis & Bisci, 1998) are used, relating cave forms with deposits, some of which could be dated (Iurilli *et al.,* 2005).

On the other hand, surface geomorphology can relate karst forms with the local geological setting giving further constraints to apulian karst history (Marsico & Selleri, 2005).

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“AGE OF KARST IN GLACIATED TERRAIN”, WITH EXAMPLES FROM NORWAY AND SVALBARD

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Karstification of the Caledonian metacarbonates in Scandinavia and Svalbard developed in pace with a landscape that was heavily eroded during the Quaternary glaciations. On the Norwegian mainland, nappe tectonics led to the formation of stripe karst, and regional metamorphosis effectively destroyed most primary stratigraphic and fabric structures which normally guide cave inception processes. Instead, we are left with coarsely crystalline marbles that are almost as impermeable as granites. Karstification and speleogenesis is therefore dictated by late tectonic fracturing in the brittle regime and by chemical contrasts at lithological contacts. Karstification occurred both during ice cover *(subglacial speleogenesis)* and in ice-free periods. During stadials, water supply was dictated by the thermal conditions within the ice-sheets. Due to the chemistry and immense water supply in the ice-contact environment, enlargement of pre-existing caves *(speleogenesis sensu lato)* was very efficient, whilst the formation of a proto-cave from a fracture *(speleogenesis sensu stricto)* is slower than in a non-glacial situation. The present-day conditions on Svalbard may serve as a model for how caves developed on the Norwegian mainland during the Quaternary. Most relict caves in the present landscape may be explained by both interglacial and subglacial evolution phases, but a small number of very large passages may have survived since the Tertiary.

THREE-DIMENSIONAL ARCHITECTURE AND ASSOCIATED STRUCTURES WITHIN A LOWER ORDOVICIAN ELLENBURGER COALESCED, COLLAPSED PALEOCAVE SYSTEM

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The three-dimensional, interwell-scale architecture of a Lower Ordovician Ellenburger coalesced, collapsed-paleocave system was constructed by integrating ground-penetrating radar (GPR), shallow core, and outcrop data. The data were collected near Marble Falls in central Texas over an ~800- × ~1,000-m area. Integration of rock facies from core descriptions with GPR-reflection response identified several paleocave facies that can be deciphered and mapped using GPR data alone: (1) continuous reflections image undisturbed strata; (2) relatively continuous reflections (tens of meters or more), characterized by faults and folds, image disturbed strata; and (3) chaotic reflections having little to no perceptible continuity image heterogeneous, collapsed, cave-related facies that cannot be individually resolved using GPR data. These latter facies include highly disturbed strata, coarse-clast chaotic breccia, fine-clast chaotic breccia, and sediment fill.

The three-dimensional architecture of the coalesced, collapsed-paleocave system, according to core and GPR data, indicates that trends of brecciated bodies are as much as 350 m wide, 1,000+ m long, and tens of meters high. These brecciated bodies are coalesced, collapsed paleocaverns. Between the brecciated bodies are areas of disturbed and undisturbed host rock that are jointly as much as 200 m wide. As a cave system is buried, many structural features form by mechanical compaction, such as folds, sags, and faults. The folds and sags measure from a few meters to several hundreds of meters in width. Collapse-related faults are numerous and can have several meters of throw. Most are normal faults, but some reverse faults also occur.

RESERVOIR-MODEL ANALOGS AND PORE-NETWORK SUMMARY FOR ELLENBURGER COALESCED, COLLAPSED-PALEOCAVE SYSTEMS

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Paleocave systems are not easy to describe, and no simple description can be applied to these reservoir types. Edges of the productive karsted reservoirs are generally structurally controlled, extent and magnitude of porosity are difficult to define, and pore networks evolve with depth.

Collapsed-paleocave reservoirs commonly display an internal rectilinear pattern in which trends of porous breccias (chaotic and crackle breccias) are separated by tighter rock. The pattern probably reflects penecontemporaneous-karst regional fracture patterns. The breccias may be several thousands of meters across, kilometers long, and 100+ meters thick. These scales are larger than individual caves, indicating the collapse and coalescing of cave systems that formed at composite unconformities.

A detailed description of a paleocave system in central Texas can be used as an analog for understanding breccia (reservoir) distribution and reservoir heterogeneity. The three main facies are undisturbed host rock, disturbed host rock (crackle brecciated), and collapsed cave passages (chaotic breccias). The brecciated reservoir zones are separated by tighter, nonbrecciated zones.

A complication in understanding paleocave reservoirs is that the pore network evolves from a megapore system near the surface to a crackle-breccia-dominated pore system with deep burial. Delineation of reservoir burial history, therefore, helps us comprehend the pore network present. The reservoir may be fairly well connected because of the large amount of fracturing, and strong heterogeneity of reservoir quality should be expected. Fortunately, many Ellenburger reservoirs are dolomitized, and the dolomite promotes preservation of pores into the very deep subsurface (>7,000 m).

BIODIVERSITY OF BELGIAN GROUNDWATERS AND CHARACTERIZATION OF THEIR STYGOBIOTIC FAUNA FROM A HISTORICAL AND ECOLOGICAL PERSPECTIVE

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In spite of its supposedly protection from major climatic changes, the subterranean domain in northern Europe seems to have been badly affected by the Quaternary glacial activity during the Pleistocene, resulting in a impoverished fauna.

In Belgium, two complementary processes ("dispersal" and "refugial"), of unknown relative explanatory value, have probably played a role in shaping the composition of post-glacial groundwater fauna. Faunal and ecological characterizations of the Belgian groundwater biodiversity were carried out in order to assess in what extent the present-day stygobiotic fauna can be attributed to one of these processes.

A total of 202 sampling sites were selected in four hydrogeographic basins within the catchment basin of the Meuse River. Sites were equally divided among the saturated and unsaturated zones of fractured aquifers (karst) and within the hyporheic and the phreatic zones of porous aquifers. Selected environmental parameters were gathered in parallel (17 variables).

More than 140 species were recorded inhabiting Belgian groundwater environment, with representatives of the Amphipoda, Cladocera, Copepoda, Hydrachnidia, Isopoda, Oligochaeta, Ostracoda, Mollusca, Syncarida and Nematoda. Thirty stygobiont species were identified. To date, the total number of stygobiotic species recorded in Belgium is 41, of which 10 species were new to the Belgian fauna.

The number of occurrences for stygobiotic species was always low; and 40% of sampled sites had no stygobi-

onts. A few species were exclusive to one zone although no statistically significant differences were observable in species richness between the different stratification levels considered (basin, aquifer-type, and hydrological zone).

It appeared justified to consider the stygobiotic fauna of Belgium as species-poor and mostly constituted of widely distributed species, with broad ecological tolerance. This corresponds to the view of a post-glacial colonisation of the Walloon karst by eurytopic species dispersed from refugia south of the ice and permafrost (Dispersal hypothesis). The nearly absence of endemic species suggests that the scenario of an ancient fauna having survived in local refugia (Refugial hypothesis) remains marginal.

MTDNA ANALYSIS IN THE GROUNDWATER AMPHIPOD NIPHARGUS FROM THE MEUSE VALLEY (BELGIUM)

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Niphargus is a widespread stygobiont amphipod genus, of which six species are known to occur in Belgium. These species are: *N. schellenbergi, N. fontanus, N. kochianus dimorphopus, N. virei, N. aquilex* and *N. pachypus.* (The animals can be caught in wells, caves, sources and resurgences.) Belgian Niphargus populations live close to the north or north-western border of the species' distributions. Peripheral populations often show a decrease in genetic diversity relative to central populations, from which they may also be more or less isolated. In addition, they may be subject to different selection pressures, possibly reinforcing genetic differentiation and in some cases even speciation. Therefore, we want to investigate to what extent the Belgian Niphargidae are genetically comparable and/or differentiated from populations elsewhere in Europe. This information is required to assess the conservation value of the Belgian populations and to uncover eventual cryptic diversity.

We started this research with a mtDNA analysis of Belgian *N. schellenbergi, N. fontanus* and *N. kochianus dimorphopus.* Individual DNA was extracted with the QIAamp DNA Mini kit (Qiagen), using the legs from one side of a specimen, so that the remainder of the body could still be used for morphological study. Several sets of primers were tested for the mitochondrial gene fragments cytochrome oxidase c subunit I (COI), cytochrome B (cytB), 12S and 16S. The COI primers (LCO 1490: 5'-GGTCAACAAATCATAAAGATATT GG-3', HCO 2198: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3') yielded successful amplifications in the three species. The standard primers for cytB (UCytB 151F: 5'-TGT GGRGCNACYGTWATYACTAA -3' and UCytB 270R: 5-AGGAARTAYCAYTCNGG YTG-3') only worked for *N. schellenbergi* and *N. kochianus dimorphopus,* and the 12S primer pair (kindly provided by P. Trontelj) only yielded good amplification products in *N. schellenbergi.* Hence more primers will have to be tested.

Amplified DNA fragments were purified using a GFX DNA and Gel Band Purification Kit (Amersham Biosiences) or the Wizard SV Gel and PCR Clean-up System (Promega), according to the manufacturers' protocols. Sequencing was performed using an automated DNA sequencer (Applied Biosystems 3130 Genetic Analyzer). In this way we screened (up till now) 150 individuals for COI (approximately 650 bp long), 60 individuals for cytB (app. 350 bp long) and 140 individuals for 12S (app. 510 bp long).

For COI, we found 12 haplotypes within *N. schellenbergi* (18 populations, sequence divergence (p-distance) within the species 0,14%), 2 haplotypes within *N. kochianus dimorphopus* (one population, sequence divergence 6,3 %) and one haplotype within *N. fontanus* (one population). The divergence found in the *N. kochianus dimorphopus* population (sequence divergence 6,3 %) is high compared to the other species studied and to some other subterranean amphipods, especially since we only analysed one population. Finston *et al.,* (Mol. Ecol. 16 (2007): 355-365) found sequence divergences for COI of less than 1,8 % between subterranean amphipod populations (genus *Pilbarus*) caught within a tributary. The three taxa that we studied were well-differentiated by sequence divergences of 31,1 % between *N. schellenbergi* and *N. fontanus,* 37,5 % between *N. schellenbergi* and *N. kochianus dimorphopus,* and 22,9 % between *N. fontanus* and *N. kochianus dimorphopus.*

For 12S, we found 9 haplotypes within *N. schellenbergi* (18 populations) with an overall mean sequence divergence of 1,2 %. So the sequence divergence for 12S is tenfold higher than the sequence divergence for COI, within the same populations.

While amplifying cytB, we often obtained a pattern that looked like a 'double' sequence within a single individual. Sometimes one of both was readable and so it turned out that there were indeed two kinds of sequences, with a sequence divergence between the two groups of 15,1 % (sequence divergence within the groups are 1,1 % and 0,6 %). Whether these two kinds of sequences represent a case of heteroplasmy or involve nuclear cytB copies (numts) remains to be investigated.

QUANTIFYING PALEOCAVE COLLAPSE FROM 3D SEISMIC DATA: EXAMPLES FROM THE PALEOZOIC SECTION IN THE NORTHERN FORT WORTH BASIN, TEXAS

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The Lower Ordovician Ellenburger Group of western and central Texas displays excellent paleokarst, both in outcrop and subcrop (e.g., cores), reflecting multiple exposure events. In the northern Fort Worth Basin, circular collapse structures representing suprastratal deformation above these collapsed-paleocave systems are well-known drilling hazards for tight-shale gas wells (Lower Carboniferous Barnett Formation). It is, consequently, important to understand their geometries in detail; the collapse features are therefore imaged using 3D seismic data. This study provides quantitative analysis of the timing of collapse and geometrical characteristics of these largely concentric structures. Concentric faults extend vertically 760 to 1,060 m from the Lower Ordovician Ellenburger Group. The largest structures remained active longer, influencing deposition of a younger, Upper Carboniferous fluvial system. A defining parameter of these features is the upward-narrowing trough of the sag zone. A rectilinear paleokarst system is identified, with coalesced passage and cavern systems aligning along NW-SE and NE-SW trends. This orthogonal trend reflects the rectilinear fracture and joint system within the Ellenburger Group that was preferentially exploited by karst weathering processes. Collapse appears to have been incremental, with significant collapse occurring after about 300 m of overburden had been deposited. A set of criteria are outlined for quantifying the geometries of collapse-generated sag structures identified on seismic data (as opposed to sags generated by other processes—e.g. pull-apart basins). This template provides valuable information for defining seismically resolvable karst-collapse features worldwide.

STYGOBIOTIC ISOPODA: A TOOL TO ASSESS WORLD CHANGES

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The fauna of the subterranean aquatic realm is rich, widely distributed and certainly underestimated, in number and, moreover, in the potential to provide a good insights into the evolution of each taxon, of the environment they colonize and of the paleogeographic events that shaped them. Within this fauna the Isopoda constitute an important portion. They are present in all the subterranean environments so far explored. Several different taxa of various families do colonize different areas with several species whose number is mostly related to the research effort. The populations are composed mostly by endemic species, a common aspect of the subterranean habitats, due in general to the long time since each of them have colonised these ecosystems. Some of these taxa are ancient relicts, while others are more recent colonisers. We will concentrate on few of these.

Relict taxa:

1. Calabozoidea, South American, restricted to few localities in Venezuela, and Brazil.

2. Phreatoicoidea, colonizing Australia, in a great variety of freshwater habitats, wells and caves in India, and caves and riverbeds in South Africa.
3. Stenasellidae widely distributed, they colonize different subterranean ecosystems from the Far East to America, accounting for an old conquest of the subterranean aquatic habitats.

Ancient and recent colonisers:

the Mediterranean genera of the Cirolanidae with strict relationships to genera of other regions. The family has different levels of endemic areas, is widely distributed with several stenoendemic genera.

THE RECONSTRUCTION OF THE PLIOCENE PALEOENVIRONMENT OF THE UNROOFED CAVES WITH FOSSIL REMAINS OF MARIFUGIA CAVATICA FROM THE ČRNOTIČE QUARRY, PODGORSKI KRAS, W SLOVENIA

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From the morphology of the caves, cave sediments and remnants of fossil cave animals and other fossils reconstructions of the paleoenvironments in which they were formed can be made. However it is difficult not to mix the evidences from different environmental settings which followed during the whole speleogenesis of a cave.

Here we present the reconstruction of the early Pliocene paleogeography of the Podgora karst and caves with fossil remains of cave animal *Marifugia cavatica.*

The unroofed caves and other caves discovered in Črnotiče quarry on the edge of the Podgora karst show a very complex speleogenesis and proved to be very important for the understanding of the evolution of SE part of the Kras plateau. Fill in the largest of fossil horizontal unroofed caves was roughly dated back to 4.2–5.2 Ma (Bosak *et.al.,* 1999). Later work in the quarry reveal a new part, a side passage of the same cave in which the cave animal serpulid *Marifugia cavatica* tubes attached to the walls were preserved (Mihevc 2000, Mihevc *et. al.,* 2001, 2002). Sediments were dated by paleomagnetic methods to 2.5–3.6 Ma (Bosak *et. al.,* 2004).

Most important part of the cave is phreatic or epiphreatic, more than 17 m high and 4-8 m wide water passage. There are large scallops on the walls of the passage with attached *Marifugia cavatica* tubes indicating rather slow flow and stable environment. It was located in low position with small gradient and was already a result of a long speleogenesis. Water with discharge several hundred litres per second flowing trough the cave system was coming from a sinking river, ponors of the river were close to the preserved part of the cave. At least part of catchment area of the sinking river was on Eocene flysch marls. There were fish living in a river and floods were washing in drowned small mammals.

Filling of the passage which preserved the sessile tubes of *Marifugia followed* was probably a result of a fast change, maybe collapse in other part of the cave. Later gradient both outside and in karst enlarge, the fine sediments in the upper part of the profile were eroded and replaced by coarser sediments. In that part of the cave wall no serpulid tubes were found. Water left the cave and in a dry passage more than 7 m thick flowstone layer was deposited.

Today the surface is at 420 m a.s.l. and is cutting the flowstone fill of the passage exposing it on the surface as a typical unroofed cave. Nearest water table caves where Marifugia cavatica still lives are karst springs about 2 km away in elevation about 50 m a.s.l.

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FORMATION AND EVOLUTION OF THE PERI-MEDITERRANEAN KARST DURING THE MESSINIAN SALINITY CRISIS AND THE PLIOCENE: EVIDENCE FROM THE ARDÈCHE VALLEY, SOUTHERN FRANCE

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During the Messinian–Pliocene eustatic cycle, the Mediterranean Sea was characterized by a short lived (5.95–5.32 Ma) sealevel fall, which attained −1500 m in some areas. The study of benchmark levels permits the chronology and dynamics of this event to be established. In the Rhône's middle valley, our investigations allow a new interpretation for the genesis of the Ardèche endokarst. A fall in base-level was responsible for both the incision of the so-called Messinian canyons as well as a deep karst development. Karst systems were formed in association with the Messinian canyons of the Ardèche and Rhône Rivers. During the flooding of the Mediterranean Basin (5.32 Ma), these karst systems were filled by water and plugged by sedimentary infilling of the rias. This mechanism pushed groundwater backward through the karst system, which in turn formed diagnostic "chimney-shafts".

These pathways were geometrically connected to the position of the Pliocene benchmark levels. Consequently, the Messinian Salinity Crisis was responsible for two karst responses. The first was concomitant with the crisis itself and corresponds to the formation of a karst system. The second followed the Messinian Salinity Crisis and corresponds to the *per ascensum* adaptation of this karst system in Vauclusian karsts by the formation of "chimneyshafts".

THE CARBONATE HYDROGEOCHEMISTRY OF THE KRKA RIVER, CROATIA

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The Krka River is incised into a broad plateau underlain by folded carbonate rocks along the Dalmatian coast of Croatia. The Krka River drains a surface watershed of ~2,610 km^2, and receives flow contributions from a network of interconnected subsurface watersheds of unknown configuration. At eight separate locations, tufa structures have developed across the river perpendicular to flow, and have grown to a size that interferes with that flow.

The purpose of this investigation is to characterize the hydrogeochemical condition of the Krka River to define the geometry of subsurface components of the watershed, the chemistry of the water delivered by those individual components, and the effect of subsurface contributions on the process and location of tufa precipitation.

To determine the mechanisms responsible for tufa precipitation, we investigated the carbonate chemistry, temperature, pH, and topography of the Krka. We determined the carbonate content by in situ titration every ~2.0 km along the 72-km length of the Krka. Values of pH ranged from 7.4 to 8.4; the concentration of total carbonate ranged from 300 to 500 ppm. We collected 32 samples of modern tufa from sites close to the titration stations, and analyzed those samples by X-Ray Diffraction. Within limits of analytical precision, all samples were identical in mineralogy, with calcite the predominant mineral. Aragonite, magnesium calcite, magnesite, stenonite, and quartz were identified at much smaller percentages.

In tufa-precipitating river systems with well characterized hydrologic inputs, such as Havasu Creek, AZ, pH and carbonate content follow a systematic trend of rising pH and decreasing carbonate content with distance from the source. In the Krka system, that simple pattern is not realized; sequential subsurface inputs apparently alter the hydrochemistry and, ultimately, the process of tufa precipitation. Within the Krka system, we identified three short segments of the river through which systematic rise of pH and decline in total carbonate content document distance downstream from a discrete subsurface source. Those segments are separated by reaches in which variation of those chemical parameters follows no clear pattern, suggesting that subsurface inputs to the Krka vary both in space and time.

DJARA CAVE (WESTERN DESERT OF EGYPT) AS A PALEOENVIRONMENTAL, AND PALEOCLIMATIC INDICATOR

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Djara Cave is one of the few caves in the Western Desert of Egypt containing speleothems. It is located close to the Farafra–oasis in western Egypt and was first visited by the German GERHARD ROHLFS on 24th December 1873, who found an extensive speleothem (stalactites, stalagmites and flowstones) development in this cave, part of them are covered by sand The cave was then visited and studied by many research groups (geological, geomorphological and archeological) due to its importance as a paleoclimatic indicator for the desert. The cave is located on an Eocene plateau to the west of the Nile valley, which consists of highly fractured carbonates of the Naqb Formation. Today, the Western Desert of Egypt, where the cave is located, is part of the hyperarid Eastern Sahara and belongs to the subtropical desert climate zone. High temperatures, low humidity and strong winds cause high potential evaporation rates in excess of 5000mm per year. In contrast, the interpolated annual precipitation sum is less than 5mm with sparse rain on only 1–5 days per year on average. The cave temperature is 23°C year- round and appears to stay very close to the external mean temperature.

U/Th datings of speleothems by α–spectrometry yielded ages ranging from 140 ± 15.9 kyr to 283 ± 56 kyr (Brook *et al.,* 2002). One TIMS date yielded 201.05 ±2.1 kyr. A number of samples was beyond the U/Th dating limit (~ 500 kyr for TIMS dating, ~ 350 kyr for α–spectrometry) (Holzkämper, 2004). Isotopically depleted values, which were also measured within earlier investigations, suggest that enhanced African summer monsoon and westerly circulation during the winter months advected precipitation to the Western Desert enabling speleothems to form in the recently hyper–arid region. A number of covered hearths in the close vicinity of the cave have been found by previous expeditions, some of which were dated with the radiocarbon method. These and additional datings of ostrich egg shells yielded ages between 9.7 kyr to 5.5 kyr, indicating that wetter conditions prevailed in the area during this time interval. So Djara Cave is a great source of information for the paleoclimate of the Sahara, showing the change from wet, dry to hyperarid conditions through time.

MORPHOMETRIC ANALYSIS OF THE LEPTODIRINAE BEETLES WITH RESPECT TO THEIR HYPOTHETIC SUCCESSIVE HISTORICAL COLONISATION OF SUBTERRANEAN HABITATS IN SLOVENIA

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The animal morphology is, besides recent molecular investigations, still an unavoidable classical approach in the analysis of taxonomic groups in space and time. The understanding of the adaptatiogenesis for living in hypogean habitats can contribute to the research of the karst evolution. In Slovenia, within the subfamily Leptodirinae (Cholevidae = Leiodidae), three morphological groups have been established representing unique lineages with respect to their adaptations to preferred habitats. Three species of the epigean lineage live in moos and litter, while two troglobitic lineages have been recognized among 34 species and 38 subspecies. Most of them belong to the bathyscioid type sensu Jeannel with an ovoid body and relatively robust short appendages resembling adaptations in edaphic beetles. The second troglobitic leptodirine lineage represents the ultra evolved leptodiroid type sensu Jeannel with specially transformed, mostly enlarged body and gracile, long thin appendages. The species of the first troglobitic group live more or less in all karstic regions of Slovenia till Karavanke/Karawanken Mts., known to be the border of the continuous distribution of troglobites in the Central Europe. The species of the second group are limited to the Dinaric Karst. In this study, the morphometric comparisons between selected species of the three groups as well as the outgroup of Cholevinae were carried out to find statistical differences between them. The authors suggest that the detailed analysis of the two evolutionary successive troglobitic lineages can support the discussion about the karst evolution.

THE TIME WHEN NEANDERTHALS VISITED ROMANIAN CAVES

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ABSTRACT

Humanoid footprints in the fossil record are rare. A survey of the literature reveals only two well documented, dated cases. The one, from ~325 ka in Italy (Mietto *et al.*, 2003), represents a very early, pre-Neanderthal human. The other, from ~117 ka in Africa (Gore, 1997), is likely a *Homo sapiens sapiens* print. Here we report the first clearly *Homo sapiens neanderthalensis* footprint. It was found in Vârtop Cave, Romania. The person stepped into calcareous mud that later hardened. The 22 cm long print suggests a body height of ~1.46 m; a gap of 1.6 cm marks the separation of big toe and second toe. The date of the footprint is constrained by the date of the deposition of the mud (~97 ka, dated by U-Th isochron method) and the date on the base of a nearby stalagmite on top of the mud (~64 ka). Thus the Vârtop Cave person lived in Romania sometime between 97 and 64 ka, long before the earliest known *Homo sapiens sapiens* remains in Europe (~35-30 ka) (Carciumaru & Anghelinu, 2000; Trinkaus *et al.*, 2003). To our knowledge, this is the first discovered and dated *Homo sapiens neanderthalensis* footprint.

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ISOTOPIC INVESTIGATIONS OF CAVE DRIP WATERS AND PRECIPITATION: APPLICATIONS TO HYDROGEOLOGICAL AND PALEOCLIMATE STUDIES IN FLORIDA, USA

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Precipitation and in-cave drip waters from speleothems at three caves that transect the Gulf coast of the Florida peninsula from North to South have been collected to satisfy three research goals. 1) Quantify the variability of the isotopic signal of precipitation and drip waters at each cave and isolate the primary factors that control that isotopic variability both at the site and regional scale. 2) Determine the fraction of meteoric waters that originate in the Atlantic Ocean and Gulf of Mexico at each site. 3) Calculate the recharge rates through the vadose zone of the aquifer matrix at each site. In addition to weekly water samples, instrumentation inside and outside each cave monitors hourly data on temperature and relative humidity; acoustic loggers acquire data on drip rates beneath active speleothems attached to unfractured blocks of the aquifer matrix. The relationship between the isotopic composition ($\delta^{18}O$ and $\delta^{2}H$) of cave waters and meteoric sources is critical for reconstructing paleoclimates using speleothem data. This study will serve as a first of its kind in the southeastern US where the impacts of confounding variables such as temperature, vapor source, storm frequency and intensity, distance from shore, and soil/water/rock interactions are poorly understood.

Determining precipitation sources will shed light on how the climate of the Florida Peninsula is affected by regional weather patterns such as the Atlantic Multi-decadal Oscillation, El Niño, and the Intertropical Convergence Zone. For example, rainfall from tropical systems in the summer show a depleted $\delta^{18}O$ signal when compared to frontal precipitation events during the winter.

Calculating recharge rates will help us better understand the transport of meteoric waters through the epikarst and into the underlying Floridan Aquifer. All three caves formed in the eogenetic Ocala limestone where matrix permeabilities are high, 10^{-11} m^2 to $10^{-13.8}$ m^2. The lag times between precipitation events and changes in drip rate from the aquifer matrix are short at all three caves, on the order of days to weeks, compared to caves in the telogenetic, low-permeability limestones of the midcontinent.

SPELEO-FAUNA OF THE MONTI SIMBRUINI REGIONAL NATURAL PARK

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In the region of Lazio there live 50% of total Italian species due to its environmental variety.

A sampling and a study about speleo-fauna has been done for two years (starting in 2002) in 30 different caves (24 of then biospaeleologically unknown) in the Central Appennino in the Monti Simbruini Natural Park.

During this research probably new species belong of Orders of Araneae and Coleoptera are to be found. The Coleoptera is a Curculionidae *Otiorhynchus (Lixorhynchus)* similar in morphological characters to *O. gianquintoi* (F. Solari, 1936) (det. G. Osella); the Spider is a Centromerus considered, from Dr. P. Pantini, similar to *C. puddui* (known only in a Sardegna's cave). This sample needs a comparison with samples of *C. cinctus* (known in Corsica and Algeria).

Specialization level of cave fauna of Monti Simbruini and Volsci, in particular Monti Lepini (the better biospeleologically known mountains complex in central Italy). The Specialization Index (Sbordoni *et al.* 1977) has been calculeted. This Index uses the report between the number of troglobiontes and the total of eutrglobious species (the total of troglobiontes and trglophilus). This index appears independent both of cave morphology and development.

From preliminary observations it is seen that troglobiontes of Monti Simbruini are fewer than the troglobiontes of Lepini. Moreover in Monti Lepini endemic species are more and with areas of endemicity larger than the Simbruini's species. The specialization Index is higher for Monti Lepini fauna than for Monti Simbruini.

The different kinds of cave fauna in the two mountains complex could be due to two different reasons, probably together:

1) The geological kinematics of the zone: The mountain chain of Volsci emerged 1.5 million years before than Monti Simbruini, and so cave fauna of Monti Simbruini could be in a more in arrears evolutive level than Volsci one.

The different climatic conditions: In Volsci is usual to find uncovered karst with mediterranean clima. This condition simplify the separation between fauna of humid environment, typical of caves, and external fauna; so allopatric division is favoured and speciation too.

GENESIS AND AGE OF ICE ACCUMULATIONS IN CAVES

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Perennial ice exists in a significant number of caves in Europe and elsewhere in the world. Ice in caves accumulates through complex freezing and melting processes, which eventually lead to the development of laminated deposits, with clear ice layers alternating with impurity-rich ones. This deposition style offers good perspectives for the use of ice accumulations in caves as paleoclimatic archives, as they contain a large number of climatic proxies: O, H and C stable isotopes, pollen, beetle remains etc. However, in order to be able to make best use of these proxies, a good age model is needed for the hosting ice.

Using present-day ice formation as a model, we propose a genetic and evolutionary model for the formation of ice deposits in selected caves from Apuseni Mountains, Romania.

In order to achieve our goal, we firstly developed a model for the present-day accumulation of ice, using glaciological, meteorological and geochemical (tritium dating) analyses. We found that the ice has a well structured response to external climatic forcing, its melting or building-up being controlled mainly by variations in precipitation (i.e., availability of dripping water), while temperature is acting as a second order controller (e.g., dripping water can determine the accumulation of ice, if air temperature is bellow O°C, or can lead to ice melting, if air temperature is above 0°C). Air temperature itself has a limited influence on the dynamics of ice, due to peculiar morphology of caves, witch do not allow warm air penetration inside the caves during summer (cold air traps). Winter air is entering the cave at a high rate, but in the absence of dripping water has a reduced influence on the dynamics of ice. This model, combined with detailed stratigraphic measurements of the existing ice bodies enabled us to reconstruct the past dynamics of the ice. By plotting the data obtained against ^{14}C values, we were able to build a good age-depth scale for the last 1000 years, as basis for further paleoclimatic reconstructions, using ice in caves as sources of information

PALEOCLIMATIC SIGNIFICANCE OF THE MAMMAL CAVE FOSSILS

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The importance of the fossils from caves sediments is obviously from the paleoclimatic interpretations point of view.

The paleontological studies above the mammals from the Upper Pleistocene from Romania reveal a distinct particularity in comparison with other mammals associations from the rest of the Europe.

We will reconstruct the paleoenvironment from the last glacial cycle (Wurm) on the basis of the mammal cave fossils discovered in few cave from Romania. The research made in carstic deposits from the last glacial cycle, is based on systematic survey in few of the most important paleontological sites.

The remains accumulated here have different origins: bones abandoned here by the primitive hunters, scavengers and from natural causes (death) when the cave was used like shelter (Ursus spelaeus and Crocuta spelaea). For the small mammals the main remains sources was the existence, next to the entrance of the caves, of the carnivorous bird's nests. The remains was accumulated in chronological positions and represent a mirror for the mammalian associations from the outside, especially for the small mammals.

OPTICALLY STIMULATED LUMINESCENCE ANALYSIS OF THE SPELEOTHEMS IN CROATIA

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The luminescence dating covers a range of analytical methods that can be applied over different time periods in different minerals and in different environmental conditions. The optical stimulation allows very small luminescence signals to be detected. In most cases the minerals analyzed with this method were quartz and feldspars, because they are able to store energy in a crystal structure. This energy is deposited mainly by ionising radiation from environment and by cosmic radiation. The analysis of this energy is the base of the luminescence dating method. In our work we have analyzed the speleothems mainly consist of calcite or aragonite. The sources for the optical stimulated luminescence were the laser coherent light and the non coherent light emitting diodes (LED) sources.

KARST AS A MODEL SYSTEM TO EXAMINE TERRESTRIAL MICROBIAL BIOGEOGRAPHY PATTERNS THROUGH TIME

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The evolutionary mechanisms that govern the distribution of microbes on Earth are poorly understood. Continental plate motion and geologic processes have changed the distribution of terrestrial and marine life throughout Earth's history. Confinement to certain locations has resulted in speciation events and even endemism. For microscopic life, however, the concept that geographic isolation plays a role in microbial species diversity is controversial. Because microbes are small in size, are metabolically tenacious, and are overwhelmingly abundant on Earth, microbes may be distributed everywhere and therefore may not be affected by geography. Many microbial biogeography studies have been conducted to test for microbial species endemism, but these studies have been conducted in habitats with high dispersion (e.g., aquatic, and specifically oceanic, habitats). There have been relatively few studies to characterize microbes living in terrestrial habitats where it is assumed that there has been limited dispersal due to the geographic and hydrostratigraphic barriers. Hypothetically, similar to what has been observed for organisms living on islands, microbial communities in the terrestrial subsurface, and specifically in caves and karst settings, would have had less opportunity to exchange genetic information because of barriers to gene flow and exchange; therefore, speciation events would be higher. Considering the ubiquity of karst worldwide, understanding the types of microbial communities in cave and karst systems, as well as determining what geologic processes may control microbial species distribution and diversity, are critical aspects to preserving the integrity of karst ecosystem and to predicting changes in ecosystem that may occur following disturbances.

SPELEOGENESIS IN 15 DAYS

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Although corrosion is very important from the speleogenetical point of view field measurements of corrosion are still very scarce. While the number of long-lasting speleogenetical interpretations and evolution modeling of karst aquifers still grows, actual values of corrosion are not yet well established. One should ask, if these interpretations of cave development fit into the field acquired data. On the basis of this question we started to measure the intensity of corrosion at several different underground streams, which flow in the epiphreatic zone. Measurements were done with limestone tablets as their preparation is easy and accuracy of the method (up to 0.0001 mm) is precise enough to detect measurable changes in one year.

Due to significant improvement of the methodology, which allows to measure corrosion in streams with velocities over 3 m/s, in the period from 2005 to 2006 corrosion at 68 different sites was measured. The average measured intensity was –0.02 mm/a. Gathered values are in accordance with measurements accomplished by dr. A. Mihevc, who measured corrosion on cave walls with micro-erosion meter. Measurements gave us insight into the activity of caves from the view of corrosion – some cave systems were recognized as corrosively active, while others have fossil cave rocky relief. On 29 locations the intensity of corrosion is greater than 0.005 mm/a. This means that at such places corrosion can be measured in 15-day intervals. This is so short period of time, that we can recognize the influence of individual hydrological event, *i.e.* at low, medium or high water conditions. If the intensity of corrosion was almost the same through the year, in 6 separate cave systems we could measure it daily.

On the basis of annual measurements we decided to place 78 limestone tablets in the following caves: Križna jama, Nova Križna jama, Lekinka, Pivka jama, Tkalca jama and Jelovička jama. In these caves we are measuring spatial and temporal differences of corrosion in 15-, 30- and 50-day intervals. Although the caves have quite different recent speleogenesis our results show that in the period of low water levels corrosion does not occur at any experimental sites. Unexpectedly, at some places important flowstone deposition was observed. It seems that the

majority of corrosion is done during medium high water levels, which are relatively frequent. The highest corrosion efficacy is certainly characteristic for high waters, but such hydrological events are quite rare. In the ponor cave Lekinka at medium high water level influence of the distance from the cave entrance was very well observed, namely the corrosion intensity in 65 m water course fell from 0.003 mm in 15 days to 0.002 mm in the same period.

A MAMMAL-DATED MID-EOCENE CAVE COLLAPSE IN THE QUERCY PALEOKARST, SW FRANCE

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The largest part of the Quercy regional area, SW France, is made of a thick Jurassic limestone platform, which contains a dense net of karstic voids. These voids are filled with clay deposits, within which phosphatic crusts developed. Intense mining of this ore, in the last 19th century quarter, revealed the fossiliferous richness of the fillings, mostly with terrestrial vertebrate remains. Their study, renewed for the last forty years, produced a corpus of fossil data and their bearing into various fields: knowledge of groups from amphibians to mammals, evolution of lineages, biochronology, paleoecology, paleoenvironments, and so forth. The fossil documented period in the Quercy phosphatic area now extends through 30 million years, from the early Eocene up the early Miocene. Studied mammal lineages allowed numerical dating (Escarguel *et al.,* 1997).

The Laprade net (Tarn-et-Garonne dept.) is mostly an unroofed cave, this resulting from the strong plioquaternary erosion of the platform. Since mining, infilling red clay still occur in restricted parts. At the N-W end, this clay yielded a vertebrate fauna, the age of which is Mid-Eocene, MP 14 of the European mammal scale (Sudre *et al.,* 1990). Its numerical dating is – 41.35 M.a. ± 0.426. In the NW underground gallery, the E wall at entrance consists of chaotic superposition of large limestone blocks, some of metric size. This results from a vault and/or wall local collapse. The infilling red clay between the blocks simply extends the bearing-fauna one outside. Its age postdates the collapse, without significant time between collapse and filling. Similar collapses often occur in active karst systems, most of time without clear cause. However, the Laprade filling dating sent back us to another paleokarstic place in Quercy, the Prajoux one (Lot dept.). There, few mammal remains predate a fault movement, at ca – 41.5 M.a. (Astruc *et al.,* 2000). The closeness of the two datings is best understood as relating to the same intense tectogenic and seismic period of the pyrenean orogen, effects of which being distally preserved. The Laprade collapse together with the Prajoux fault support such interpretation. Here, the dating method relies on evolutionary data of mammal lineages. While other, chemical dating methods, will soon be settled and allow checking.

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VARIATIONS IN SPELEOTHEM TRACE ELEMENTS AND Δ13C IN CENTRAL FLORIDA: POTENTIAL FOR PALEOCLIMATE RECONSTRUCTION

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A stalagmite collected from Briar Cave in central Florida, provided the first Late Holocene Paleoclimatic record for Florida using speleothems. The stalagmite was analyzed for trace elements Sr and Mg and for carbon isotopes. Thermal ionization mass spectrometry of uranium-thorium isotopes indicate the speleothem was precipitated during the last 4200 years. When Sr/Ca and Mg/Ca time series data is combined with Uranium series dating techniques, the age of paleoclimate variations may be deduced. Using Sr/Ca and Mg/Ca ratios to learn past climatic data is under debate. Many academics believe temperature, effective rainfall, recharge rates, and vegetation patterns can be found from trace elements in speleothems, others argue that only the speleothem growth rate may be obtained from trace elements. Results showed that Sr concentrations are negatively correlated with $\delta^{13}C$, a relationship we inferred to record changes in soil productivity. Magnesium concentrations were not found to be significantly correlated with hemispheric temperature, however results suggest the residence time of percolation waters maybe the controlling factor. Coeval changes in the Sr content and $\delta^{13}C$ signals, as induced by soil productivity, can only be explained by changing precipitation above the cave. Both proxies record a 170-180 year solar cycle that has also been found in the Gulf of Mexico marine records. Consequently, this result provides evidence of an extra-terrestrially driven modulator of precipitation in central Florida.

DETERMINATION OF PAST FLOW REGIMES FROM SCALLOPS OF BEYYAYLA CAVE (BILECIK – TURKEY) BY USING BOOTSTRAP HYPOTHESIS TESTING METHOD

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Caves provide natural archives of records of the palaeohydrologic conditions. Scallops are among the corrosion – morphologies that may provide such records. In this paper scallops at the walls of the passage of the Beyyayla Cave in Turkey were measured and statistically analysed to infer about the past hydrologic conditions. The cave is located within a dissected – relict karst, and it exhibits poly phase passage morphology. Relicts of scallops on the passage walls vary in shape and size. Data collected in the cave were analyzed by the bootstrap hypothesis test to determine the number of modes in the multimodal histogram, which is obtained over the collected data set. The results of analyses revealed that the cave had been affected by at least two flow regimes.

URANIUM-SERIES DATING OF SPELEOTHEMS: ESTABLISHING TIME AND FORCING OF CARBONATE DEPOSITION IN KARST SYSTEMS

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Over the last few years cave science has seen an strong increase in interest from other academic disciplines as well as from the general public. This development is largely due to the growing awareness of the importance of karst

systems as groundwater resources in many regions of the world as well as the recognition that within these subsurface environments information about past climate and hydrology is reliably recorded in carbonate deposits. Paleoclimate scientists currently are very keen to study speleothems and some regard them even as valuable as ice cores from Polar regions.

Although most speleothem studies are currently targeted toward providing high-quality records of climate and environmental change outside cave networks, these results are also undoubtedly of great significance for a better understanding of long-term dynamics within karst systems. Examples include the frequency of cave flooding recorded as detrital-rich layers in stalagmites, drought periods as indicated by narrowly spaced speleothem laminae and/or microhiatus, overgrowths of marine organisms on speleothems in near-coastal caves during sea-level highstands, and the occurrence of intermittent speleothem deposition in cold-climate caves prone to freezing. These studies therefore provide critical data for assessing the role of climate forcing of karst hydrological processes on timescales ranging from annual to millennial. Given the inherently complex nature of karst systems and the fact that these systems evolve over time, results obtained from individual speleothem samples, however, will require thorough validation to arrive at robust interpretations.

KARST DEVELOPMENT AT THE RACISZYN AREA (KRAKÓW – WIELUŃ UPLAND, S POLAND) – PRELIMINARY RESULTS.

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In September 2005 in a quarry near Raciszyn (Kraków-Wieluń Upland, S Poland) we discovered a new small cave. The entrance was placed on the bottom of the lowest exploitation level. Both geographical and geological position of the cave allows us to expect new data on evolution and development of karst in this part of Poland. The cave is a part of larger geological structure i.e. a large slit that runs along the whole quarry. During the exploration about 20 samples of speleothems from the cave and other parts of quarry have been collected to the further Th/U analysis. We have found at least three generations of speleothems separated by erosion surfaces and clastic sediments (mostly clays). This indicates complicated history of the cave and radical changes of hydrogelogical conditions during Pleistocene in this area. The oldest discovered speleothems are older than 350 ka, and probably older then 1.2 Ma, and exceeds the method's range. Next generation of speleothems developed between 233 and 118 ka. The youngest speleothems were Holocene age.

A COMPARATIVE REVIEW OF FOREST MANAGEMENT HISTORY IN SOME HUNGARIAN KARST AREAS

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Vegetation is one of the karstecological factors. As such it directly affects microclimate and soil and thus indirectly the whole system. Due to their geographical position, the potential vegetation of Hungarian karsts is mixed-stand deciduous forest so forest management methods in the past and present are a key issue in today's karst surface development. On the other hand karst is a special environment with characteristic surface features and special water balance, which needs special considerations in management. This study aims to reveal the similarities and differences of past forest management in the different karst regions of Hungary.

THE KARSTIC REJUVENATION PROCESSES ON THE ALADAG MOUNTAIN (EASTERN OF CENTRAL TAURUS MOUNTAINS, TURKEY) SINCE THE LAST GLACIAL MAXIMUM

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The karstic processes had been ruled in Aladağ region with the continental conditions for the beginning of the Paleocene-Eocene era in the area. The trace of this term and the later karstification as Later Miocene can be seen on the paleokarstic ore deposits at Aladag region. The morphologic development surfaces can be seen since the Upper Miocene on the area. The Aladag Karst Plateau that bounded with Zamanti River and Ecemiş strike slipped fault zone is also an uplift area on the border of the Central and Eastern Taurus Belts. The plateau consists of two main different parts which are as high altitude karst area and lower fluviokarstic area. The high altitude karst area has been intensively affected from the Quaternary glacial processes. The most of glacial were as valley type but also traces of ice cap glacial have been found on the mountain. The resignation of the last glacial was continued till the 7000 year BP. The landforms of epikarst were scraped and plugged through the last glacial period while the glacial were using the mature karstic basin. This processes affected the karst hydrological system and morphological structure as hanged karst springs, unwalled shafts, unroofed caves and polycyclic dolines on the area. The rapid uplift of the plateau according to close region and the glacial flow also caused to deep incision of the Aladag Mountain.

KARST IN THE CORDISBURGO REGION, MINAS GERAIS STATE, BRAZIL

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The Karst in Cordisburgo is considered to be one of the most significant karst regions in Minas Gerais State, Brazil. It is distinguished for both the magnificent potential of its endokarst and the important archaeological, paleontological, historical and tourist sites it offers. Minas Gerais, the third most important industrial area in Brazil, has intensive farming and mining activities as well. According to the Instituto Brasileiro de Geografia e Estatística (2001), about 35.83% of the economically active population is employed in farming, cattle raising, planting and fishing; 40.70% in the general services; 15.07% in the industrial sector and 8,40% in small commerce sectors, which is basically primary needs-oriented. Although there are some exceptions, this scenario leads to problems with natural resources management, especially in karst areas. Cordisburgo is located at about 110 km north of Belo Horizonte, the Minas Gerais State capital city, on the Late Proterozoic metasedimentary carbonate rocks of Grupo Bambuí (600-500 Ma B.P.). The predominant climate is typical of tropical regions: two well defined seasons, a characteristic of the Cerrado. The annual temperature average is 22° C and the annual rainfall average is 1230 mm. This particular karst area is characterized by elongated massive limestone reliefs in the E-W direction (maximum height of 1055 m), intercalated by *poljés* (minimum height of 715 m) with temporary lagoons. The endokarst is developed in four main caves with horizontal development equal or superior to 1000 m (Gruta da Morena - 4620 m; Lapa Nova do Maquiné - 1312 m; Gruta do Salitre - 1098 m; Gruta do Toboga - 1000 m). There are also 10 other caves that are developed in limestone. The city of Cordisburgo was first discovered by the 17th century explorers called *Bandeirantes*, and later became a settlement which was officially

established by a priest in 1883. The toponym reinforces the sacred meaning of the place: *Cordis* = heart; *Burgo* = city, an allusion to the Sacred Heart of Jesus. In the 19th century, this area was studied by Peter Wilhelm Lund, who found important paleontological sites there, such as the Lapa Nova do Maquiné cave (1834). It is important to notice that Lund discovered important evidences of the pre-historic South American fauna from the Pleistocene in this cave. This cave is also known as the first Brazilian touristic cave. In the 20th century (1956) the area was described in famous novels by an important Brazilian writer (Guimaraes Rosa), when he wrote about the relationship between farmers and the *sertanejos*, the 'cerrado cowboys' and the landscape. Traditionally the population used the karst waters as their primary resource for agriculture, farming and domestic usage. According to COPASA, the company that provides for water distribution and sewage treatment in the county, the supply comes from a 20.0 l/s outflow well. As a result of the intensive agricultural and farming activities, the drinking water supply of the municipality may be significantly exploited and contaminated. Nowadays, the municipality is investing much more in tourism. Besides all this, there is another important element that points out to the importance of that area conservation: the quarry expansion towards it, which is about to become a reality. Due to these threats, the conservation of this speleological and natural patrimony is urgent. Now the region is being studied by Travassos & Kohler, who are developing a map of the karst phenomena, intended to be the basis for the geoenvironmental compartmentation of that region, offering important subsides for the sustainable management of that environmental scenario, especially for the susceptibility of the karst aquifer to contamination. Processes that are similar to those mentioned by Kovačič and Ravbar (2005) take place at Cordisburgo. The presence of a thin soil cover leads to rapid water percolation in plantations and pastures, accelerating the contamination of the aquifer. Other distant areas of non-carbonated rocks may act as allogenic recharge areas that concentrate pollutants from different human activities as well. There are no sanitary landfills to protect groundwater from the leachates in that area. The only solid waste disposal process is an inappropriate site. So, it is important to establish systematic studies in the area and, according to Kranjc (2000, p.123), also invest in the education of all inhabitants, from politicians and experts to pupils who may be of influence to the threat and the protection of karst areas and the water supply. As a starting move *"the most important task is to fill the gap between the karst specialists with their knowledge and "non-karst" specialists, also highly educated, with sometimes striking ignorance of karst and karst water."* (KRANJC, 2000, p.123).

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COMPARATIVE ANALYSIS OF CAVE-PLANTHOPPER RADIATIONS IN AUSTRALIA AND HAWAI'I — PRELIMINARY RESULTS (HEMIPTERA: FULGOROMORPHA: CIXIIDAE)

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Ongoing studies have revealed numerous cases of parallel evolution of cavernicolous planthoppers all over the world in tropical and subtropical caves. Given that concepts of genetic change and speciation dynamics are subject to review by natural model systems, the comparative study of these independent evolutionary lineages and radiations can provide critical information.

We survey species complexes from Australian and Hawai'ian caves exhibiting different degrees of troglomorphy. In Australia (Qld), *Solonaima* and *Undarana* species have colonized old karst caves as well as young lava tubes. On the Hawai'ian Islands, the cave-dwelling *Oliarus* species represent at least seven independent cave colonizations on three islands of different age, including the *Oliarus polyphemus* species complex from various, partly still active volcanic systems on Hawai'i Island .

The diversity of external factors (e.g., ressource availability and stability, migration possibilities, macro- and microclimatic changes, predators) as well as internal factors (e.g., genetic variability, population structure and density) allows us to incorporate these into concepts of time and mode of evolutionary change in cave organisms.

THE EARLIEST TIME OF KARST CAVE FORMATION

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Karst cave development in carbonate rock is predicated by the existence of such rock, so the earliest a cave can form is synchronous with carbonate deposition. A hierarchy of cave development conditions can be established based on the postdepositional evolution of carbonate porosity into three time-porosity stages that conform to the rock cycle as stated by Choquette and Pray (1970, p. 215): "the time of early burial as eogenetic, the time of deeper burial as mesogenetic, and the late stage associated with erosion of long-buried carbonates as telogenetic". In diagenetic order, from immature to mature host rock, a progression can be established:

A) Eogenetic Caves - The carbonate rock is in its environment of deposition; cave development can be presented as three progressive stages:

1) Constructional - Caves formed by deposition of a soluble rock at the instant the rock is deposited. Example: Tufa caves; the rock is the end product of earlier carbonate dissolution but the void itself not produced by dissolution.

2) Syndepositional – Caves formed by dissolution while rock deposition is occurring. Examples: Caves formed in lagoonal carbonate sands when beach sands prograde over them, or eolian calcarenites deposited across existing surface stream channels.

3) Syngenetic – Caves formed subsequent to deposition by dissolution while rock lithification is occurring. Examples: Eolian calcarenites invaded by a fresh-water lens and mixing zone, or subtidal carbonates exposed to meteoric water by uplift associated with tectonics and/or glacioeustasy.

B) Mesogenetic Caves – The carbonate rock is buried, isolated from surficial processes, and undergoing diagenetic maturation. By definition, all karst caves developed in mesogenetic rocks are hypogenic.

C) Telogenetic Caves – The carbonate rock is diagenetically mature and exposed to the surficial weathering environment.

A fourth category, *metamorphic*, could address caves formed in carbonates that have been metamorphosed into marbles. The hierarchy does not require a fixed chronology. Geologic processes operate at different rates in different areas. For example, some New Zealand Oligocene carbonates are telogenetic as a result of the vigorous tectonic burial and uplift, while rocks of similar age in Florida are still eogenetic. The age of the rock can be misleading, what is important is the diagenetic character of the rock at the time of cave genesis.

THE DINARIC KARST EVOLUTION – THE CAVE SHRIMPS' MOLECULAR AND GEOLOGICAL POINT OF VIEW

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The cave dwelling shrimps of the genus *Troglocaris* show a disjunct distribution in European karstic groundwaters: in the Dinaric Karst on the Balkan Peninsula, on the West Caucasus and in South France. The phylogenetic relationships within the genus based on the sequences of two mitochondrial and one nuclear gene showed a monophylum with two main lineages constituted of the Dinaric and Caucasian taxa. Both lineages have geographically largely separate ranges: one is extending from Italy to Bosnia and Herzegovina and the other from Bosnia and Herzegovina and Montenegro over Caucasus. Absolute dating of phylogenetic events is possible by using calibration points from the fossil record or vicariant events. In the atyid shrimps, or even more ideally in the *Troglocaris* group, points like that are not available. Therefore the molecular clock approach has been used to estimate the divergence dates among the clades. The divergence dates were estimated using substitution rate divergences previously defined in other decapods. The split between *T. inermis* from France and the surface-living *Dugastella valentina* from Spain is about 10 Myr old, but they had common predecessor with Dinaric and Caucasian *Troglocaris* taxa in the middle Miocene, about 15 Myr ago. The most unexpected is a relatively young split between Caucasian and Dinaric Troglocaris populations that was estimated at 6-11 Myr. The Dinarides represent a complex land formed during the Terciary and Quaternary. The tectonics strongly controlled the formation of many small Neogene basins within the Dinarides which were geological characterized by fresh-water sedimentation. The analysis of faunal characteristics which occurred in sediments in the Neogene fresh-water basins within the Dinarides showed many similarities between North Croatian Basin and Northern Bosnia region. The higher number of deep splits within the cave shrimps in the southern Dinaric Karst might be a result of the Miocene Dinaride lake system geographically comprising parts of Croatia, Bosnia-Herzegovina and Montenegro, where *Troglocaris* lineages are taxonomically more diverse than in the NW part of Dinaric Karst. Younger lineages within *Troglocaris* are congruent with hydrographically isolated areas in the Dinaric Karst. All age estimates are rough, calibration point within the Dinaric Karst would enable us to develop a more precise dating of a cladogentic events for *Troglocaris* and other cave taxa in the area.

CHANGE DETECTION AND TIME-SERIES FROM AERIAL-, AND SATELLITE IMAGES ON THE BUKK-PLATEU (BÜKK-FENNSÍK), HUNGARY

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The most common form of land use in Hungarian karsts is woodland. An integrated forest management taking into account considerations of environmental protection as well could insure the conservation of karsts in a near-natural state. Before World War II, the forests of the Bükk Mountains were owned by the state. While earlier the forests were mainly cut down to increase the area suitable for grazing, after the war deforestation followed due to a highly increased claim for wood production. The exploitation of forests also had an impact on their age composition. The foundation of the Bükk National Park in 1977 meant a turning point in the history of the area's forests, introducing the concept of sustainable management.

In this study we compared time-series of aerial images in order to follow changes in the investigation area. These images were taken by the military cartography in the years 1956, 1965, 1975, 1987, 1988, 2004, related to the revision of earlier maps. We define the horizontal and vertical changes of the area such as increase the net of the

forestry roads which is close-textured that even before, and the height of forest based on digital surface models which contain the height of the trees above the digital elevation model. The species composition of the stands was defined by the supervised classification of Landsat satellite imagery.

TIME RECORDED IN CAVE DEPOSITS – 10 YEARS OF PALEOMAGNETIC RESEARCH IN SLOVENIAN CAVES

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The palaeomagnetic and magnetostratigraphic research of karst deposits has been carried out since October 1997 in 17 caves and 2 surface sites located in different geological units and geographical settings of Slovenia. Totally 33 sedimentary profiles and more than 2,000 samples have been sampled and processed by the standard palaeomagnetic analyses (thermal and alternating field demagnetisation, magnetic susceptibility measurements, etc.).

After the last massive marine transgression during Eocene, when thick pile of flysch siliciclastics deposited, in the most of the area studied, there is no evidence of younger marine sediments, even if they have been expected by some authors (e.g., Rögl 1998). The area was thus exposed to denudation. Correlate sediments preserved in isolated basins in vicinity, belonging to Miocene Paratethys deposits, are about 6-10 Ma old (e.g., Márton *et al.,* 2002).

Cave karst deposits (both clastic and chemogenic) offer the record of processes, which evidences have not been preserved on the surface of most of karst regions of Slovenia and can help to decipher the younger geological and tectonic history.

The start of our paleomagnetic and magnetostratigraphic research was framed by chronostratigraphic models of cave infilling compiled by Rado Gospodarič (e.g., 1981, 1985, 1988) from different sources and applied methods. He dated cave deposits to period up to 350 ka and only some deposits were expected to be older (ca 600-900 ka; e.g. Gospodarič 1985). But later data of Th/U dating of speleothems from different Slovenian caves (Zupan 1991, Mihevc 2001) indicate that a lot of speleothems are older than explained by Gospodarič. Even much greater age of caves and karst surfaces suggest the studies of unroofed caves. With assumption that the caves were developed deep below surface and considering recent denudation rate these caves and sediments in them can be 1 – 5 Ma years old (Mihevc 1996, 2001).

Performed paleomagnetic and magnetostratigraphy studies, combined by numerical dating methods, mineralogical, petrological, geochemical, paleontological and geomorphological analyses, offered surprisingly new time frame for cave depositional processes – they proved that most of analyzed sediments can be up to several millions of years old, including sites studied by Rado Gospodarič. The oldest paleontologically correlated ages have been found in the Račiška pečina Cave in the Classical Karst – about 3.5 Ma.

The obtained data of correlated- and numerical-ages of cave/karst deposits supported the new trends and ideas concerning the evolution of karst surfaces especially in the region of the Classical Karst, indicated that cave deposits occurring now in different altitudes can be of the same age, and proved that deposits in caves, now unroofed, are very ancient.

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Acta carsologica
36, 1 (2007)

Izdala in založila
Slovenska akademija znanosti in umetnosti
in
Znanstvenoraziskovalni center SAZU
v Ljubljani

Grafična priprava in tisk
Tiskarna Lotos Postojna

Naklada 800 izvodov

ACTA CARSOLOGICA

ISSN 0583-6050 · LETNIK/ VOLUME 36 · ŠTEVILKA/NUMBER 1 · LJUBLJANA 2007

ISSN 0583-6050

9 770583 605015

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ZNANOSTI IN UMETNOSTI

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