THE NSS BULLETIN

VOLUME 40

NUMBER 4

Contents

Cover Photo: Thorough remelting of a ceiling surface results in drip pendant stalactites such as these in Catacombs Cave, Lava Beds National Monument, California. Field of view is about 10 in. wide. See page 20.

AN EVOLUTIONARY AND ECOLOGICAL ANALYSIS OF THE TERRESTRIAL ARTHROPODS OF CAVES IN THE CENTRAL PYRENEES

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Part One: Ecological Analysis with Special Reference to Collembola

ABSTRACT

Although caves present a wide variety of habitat types, the arthropods we studied suggest four basic categories: (1) cave depths (profondeurs), (2) entrances, (3) mixed caves (where there is no entrance/profondeur separation), and (4) underground rivers. Both sharing and partitioning of the environment occur in cave arthropods, usually involving closely related species. These processes generally appear to result from shared or differing ecological requirements.

Ecological factors associated with abundance and distribution of these species are extremely involved. The complex of critical factors varies greatly from one species to another, and there are no overall groupings of ecologically important features. In spite of the relatively simple nature of the cave profondeur environment, the governing factors appear to be generally more complex for troglobitic than for troglophilic species. Thus, diminishing the number of ecological variables does not, apparently, simplify the ecological web of relationships. It is probable, then, that the primary factor in determining the complexity of interaction is the stability and complexity of the habitat. Thus, the cave depths would harbor the most complex interactions and the entryways the least.

INTRODUCTION

I N 1967 AND 1968, we commenced an analysis of 58 caves in the departments of Haute-Garonne and Ariège, with the dual purpose of analysing the ecological relationships within these caves and of determining the factors which could best be used as indications of the ecological pressures upon certain species of Collembola. In the first part, we show how the animals utilized the caves, what sorts of subdivisions of the cave environment are important to the organisms, and to what degree the environment was partitioned or shared. The second portion was an attempt to use multiple regression techniques as an aid in determining what small group of factors represented the best predictors of the presence or absence of any given species and of its abundance; we sought to use this, along with other information, to make some approximations of the most important ecological factors affecting the abundance and distribution of certain species.

At the same time, we determined the evolutionary status of different populations of three of the species of cave Collembola involved in this study, using methods already developed (Christiansen and Culver, 1968 and 1969). Finally, we hoped to see whether there was any correlation between the evolutionary status of a population and the ecological pressure in its local habitat.

METHODS

The caves were visited from one to four times. During each visit, counts were made of animals observed or captured on a "random walk" pathway search. The searches lasted from 30 to 120 minutes, but usually exceeded 60 minutes in length. During the observation and collection period, one investigator dealt with mites, Collembola, and other small arthropods, while the second dealt with beetles, spiders, and other larger elements of the fauna. Densities of animals were recorded as numbers encountered per hundred minutes. Caves having distinct entry and profondeur regions were treated as two separate entities in all measurements. Altitude, temperature, and relative humidity near the floor were noted; however, only altitude is used in this analysis. Inasmuch as we had no way to determine variations in the climatic factors, their inclusion seemed unwarranted. A variety of other physical factors were estimated on a 6-point scale: 0 = none, 5 = maximum abundance observed in the region. The factors included: guano, wood, debris, wet speleothems, dry speleothems, corroded floor, breakdown, calcareous clay, non-

calcareous clay, sand and silt, gravel, organic soil, standing water, and running water.

Organic material was quantified as follows: Debris—tiny fragment = 1, one small good patch = 2, several moderate patches = 3, one large patch = 4, massive quantities = 5; guano—scattered small pieces = 1, one to three patches less than 2.5cm deep and 30cm square = 2, one patch more than 2m square or deeper than 2.5cm together with scattered other patches = 3, several such patches = 4, massive deposits = 5; wood—less than 2kg = 1, two to ten kilos = 2, ten to twenty-five kilos = 3, twenty-five to 100 kilos = 4, more than 100kg = 5.

Total passage length was recorded on a 4-point scale: one to ten meters = 1, 10 to 50m = 2, 50 to 100m = 3, and >100m = 4. A few caves were visited 2 or 3 times, and each of these visits was counted separately. This, in a sense, weighted these caves more heavily than single-visit caves; however, since both population and environment varied from one visit to another, it was thought acceptable to count repeated visits individually. Ecotypes in which more than 80% of the individuals in one species occurred are termed "prime habitats."

ANIMALS STUDIED

The study was limited to the mesofauna (*sensu* Rapoport, 1959) of the caves, and records were kept of all such elements; however, most of the analyses described below dealt only with Collembola, Apterygota, Coleoptera, Diplopoda, and Arachnida. Other forms represented were such minor elements of the fauna that their inclusion was not considered necessary for most analyses. Due to suspected inaccuracies in counting, the staphylinid beetles were also excluded. Table 1 shows the various forms observed, the number of observations, and the total number of individuals seen. Species identifications were made only in certain groups. Even within these groups, there were only a few cases (mostly Collembola) where sufficient numbers of one species were observed to permit separate analysis. In the faunal analyses, other forms were lumped together to a greater or lesser extent.

SUBDIVISION OF THE CAVE HABITAT

An attempt was made to discover how the organisms themselves divided the cave environment into discrete habitats. At the start, caves were divided into entry (E) (generally, the daylight or twilight zone) and profondeur (P) (cave depths) regions, where a clear separation existed. That is, where a cave included two or more clearly differentiated zones and one of these was near the entrance, the near-entrance zone was designated "E" habitat and the remainder of the cave was designated "P" habitat. In caves where it was not possible to make such a distinction and in which conditions were relatively uniform throughout, mixed (M) habitat was designated.

TABLE 1. Total number of caves where different animals were seen, and total number of individuals seen.

Group	Name entered in regression programs	Number of caves with this form	Total number of animals seen
Collembola			
Entomobryidae	entered separately		
Pseudosinella			
superduodecima TB		11	369
subduodecima TB		11	164
theodoridesi TB		14	345
decipiens TP		5	212
impediens TB		4	52
virei TB		10	91
Tomocerus			
problematicus TB		9	431
minor TP		23	808
	misc. entomobryids		
Pseudosinella			
sexoculata TP		3	6
alba TP		1	2
Heteromurus			
nitidus TP		8	199
Lepidocyrtus spp. TP		10	56
	other Tomocerines		
Tomocerus			
vulgaris TP		3	7
Tritomurus			
falcifer TB		2	5
	non-entomobryids		
Hypogastruridae			
Hypogastrura spp. TP		4	121
Mesachorutes sp. TP		1	60
Isotomidae (misc.) TP		6	20
Onychiuridae			
Onychiurus spp. TP		18	200
misc. non-entomobryids TP		5	18
Coleoptera (= Catopidae)			
Choleva			
angustata TP	bathyscines	2	72
Speonomus TB			
hydrophilus		8	175
infernus		7	64
diecki		2	38
stygius		7	72
abeillei		4	29
pyreneus		2	12
misc. species		4	12
Carabidae			
Bathysciola TP	Carabids		
meridionalis		1	1
ovata		5	113
Antrocharis			
querilhaci TB		1	4
Aphaenops TB			
crypticola		2	28
cerebrus		17	117
andeli		3	26
pluto		3	15
tiresias		3	24
hustacei		2	16
Geotrechus TP			
hydrophilus		1	12
sauleyi		1	3
orpheus		8	47
serrulatus		1	1
Hydraphaenops TB			
ehlersi		1	6
Sphodridae TP			
Centhosphodrus			
oblongus TP		6	22
Staphylinidae	Staphylinids		
Atheta			
subcavicola TP		2	130
Staphylinids (misc.) TP		9	224 (?)
Isopoda	Isopods		
Scotoniscus spp. TP		12	80
Trichoniscus spp. TP		2	17
misc. isopods		15	179
Pseudoscorpionida TP	pseudoscorpions	7	16
Opilionida	opilionids		
Ischropsalis spp. TB		8	95
Scotolemon			
lespesi TP		12	52
misc. opilionids TP		3	13
Acari (mites) TP	mites	26	896
Aranae	Spiders		
Leptoneta			
micropthalma TB		4	65
Meta			
menardi TP		27	305
Tegeneria spp. TP		10	45
misc. spiders TP		32	359
Diplopoda (Millipedes)	individually entered		
Polydesmids TP		14	302
Typhloblaniulus spp. TB		38	384
Chilopoda (centipedes) TP	centipedes	14	127
Pauropoda TP	pauropods	2	35
Thysanura			
Campodeidae TP	Campodeids	7	16
Trichoptera TP	misc. insects	4	217
Lepidoptera TP	misc. insects	13	129
Diptera	misc. insects	10	818
Mollusca TP	molluscs	14	41
Chiroptera (Bats)		23	217

TB = primarily trogloblitic, TP = troglophilic

The basic types of caves were designated: (Type 1) true caves with varied structure, (Type 2) true caves with uniform structure, (Type 3) artificial caves and mines, (Type 4) sinks (*i.e.*: vertical caves with no significant lateral extent), (Type 5) sinks combined with caves, and (Type 6) underground rivers. When this had been done, one could see clear faunal similarities and differences among the various cave types.

In general, underground rivers are unique in all respects. The sharpest distinctions among the remaining cave types are seen when caves are divided into three types: entry, profondeur, and mixed. With the exception of underground rivers, all habitats appear to be highly similar within categories and sharply distinct among categories. We tested this impression by ranking the order of abundance of the various organisms in each cave and then calculating Spearman's *Rho* for all pairs. Table 2 shows the clear separation of profondeurs from underground rivers and the somewhat less striking yet real identity of artificial caves and mines. With these removed from consideration, most correlations within the M and P groups are positive and either statistically significant or nearly so, while most inter-category correlations are negative or very low.

Another way to categorize caves is on the basis of the amount of organic material present. Preliminary analysis indicated that guano has an effect different from that of debris and wood, so the caves were divided on the basis of wood-plus-debris and on the basis of guano (alone). The guano in the study caves was entirely from bats; most of it was aged.

Caves were then broken into 5 categories, representing the kind and quantity of organic material in them. When the mean abundance of the various animal taxa was plotted, it could be seen that certain groups of organisms tend to prefer specific kinds of caves. Separations based on organic materials are not, however, as sharp or as consistent as are separations on the basis of cave type. Spearman correlation co-efficients made it clear that relatively little significant separation could be made on the basis of organic materials. Only caves rich in wood and debris and poor in guano possessed a separate identity, and even that was not statistically significant. Attempts to cluster caves on positive correlations showed no sensible groupings.

SUMMARY SUBDIVISION OF CAVE TYPES

The animals studied divided the caves into essentially four categories: (1) entrances, (2) profondeurs, (3) mixed caves, and (4) underground rivers/profondeurs. Within mixed and profondeur categories, cave type makes little difference. Within entrances, there does seem to be some differentiation of cave types. Very little overall difference in species composition or abundance can be ascribed primarily to differences in the quantity or quality of organic materials present.

ENVIRONMENTAL SHARING AND PARTITIONING

The simple product-moment correlations of the log-transformed data among the various taxonomic groups studied provided an indication of the way in which these animals share their environment. Log transformation of the data was used because, as will be discussed later, this normalized the distribution of most data. The negative biological correlations exist largely among collembolan species, with the exception of that between spiders and carabid beetles. As will be seen later, this can probably be explained by the fact that carabids have a depressing effect upon spider populations. This would indicate that, generally, the presence of one taxon does not tend to exclude any other taxon.

Sufficient collections of bathyscines, carabids, and entomobryids were made to permit further examination of the sharing and partitioning problem. Figure 1 summarizes niche partitioning and sharing among the major entomobryid Collembola in a comparative, quantitative manner.

The first noteworthy feature illustrated here is the very clear-cut environmental sharing and partitioning among the species of *Tomocerus* and *Pseudosinella*. The profondeurs are largely dominated by *P. theodoridesi* and *T. problematicus* and, in the great majority of cases, they occur together. It is of interest that *P. virei*, which in other areas is a major inhabitant of the profondeur, occurs in profondeurs only when *P. theodoridesi* and *T. problematicus* are absent. The two other species of *Pseudosinella*, *P. superduodecima* and *P. subduodecima*, have clearly

TABLE 2. Spearman's Rho for Rank Ordered relative abundance of different animal groups in different types of cave habitats (N = 17).

	1E	2E	5E	6E	1M	2M	3M	4M	5M	1P	2P	5P	6P
1E	1.000	.361	.520	.275	.039	-.039	.046	-.099	.130	.379	.228	.436	-.067
2E	—	1.000	.245	.801	.195	-.010	.098	.003	.114	.006	-.025	.224	-.010
5E	—	—	1.000	.131	.059	.239	.058	.192	.115	.252	.120	.507	.088
6E	—	—	—	1.000	.411	.216	.029	.143	.039	-.126	-.101	-.054	.364
1M	—	—	—	—	1.000	.819	.345	.591	.505	-.042	-.039	.001	.374
2M	—	—	—	—	—	1.000	.454	.832	.586	.163	.318	.088	.347
3M	—	—	—	—	—	—	1.000	.290	.310	.331	.469	.461	.120
4M	—	—	—	—	—	—	—	1.000	.574	.310	.264	.343	.162
5M	—	—	—	—	—	—	—	—	1.000	.228	.232	.343	-.115
1P	—	—	—	—	—	—	—	—	—	1.000	.825	.675	.168
2P	—	—	—	—	—	—	—	—	—	—	1.000	.580	.068
5P	—	—	—	—	—	—	—	—	—	—	—	1.000	-.184
6P	—	—	—	—	—	—	—	—	—	—	—	—	1.000

Key:
varied true caves	1	
uniform true caves	2	
artificial caves and mines	3	
sinks	4	
sinks with caves connected	5	
underground rivers	6	

entryway	E
profondeur	P
mixed cave	M

	E	M	P
E	.39	.09	.15
M	—	.53	.23
P	—	—	.69

$P < .05$ = -------------------------------
$P < .01$ = _____

Mean Correlation E, P and M habitats (exclusive of *6 P* types).

Areas of boldface numbers represent suggested cave groupings: Entrys, Mixed caves, and Profondeurs (see text).
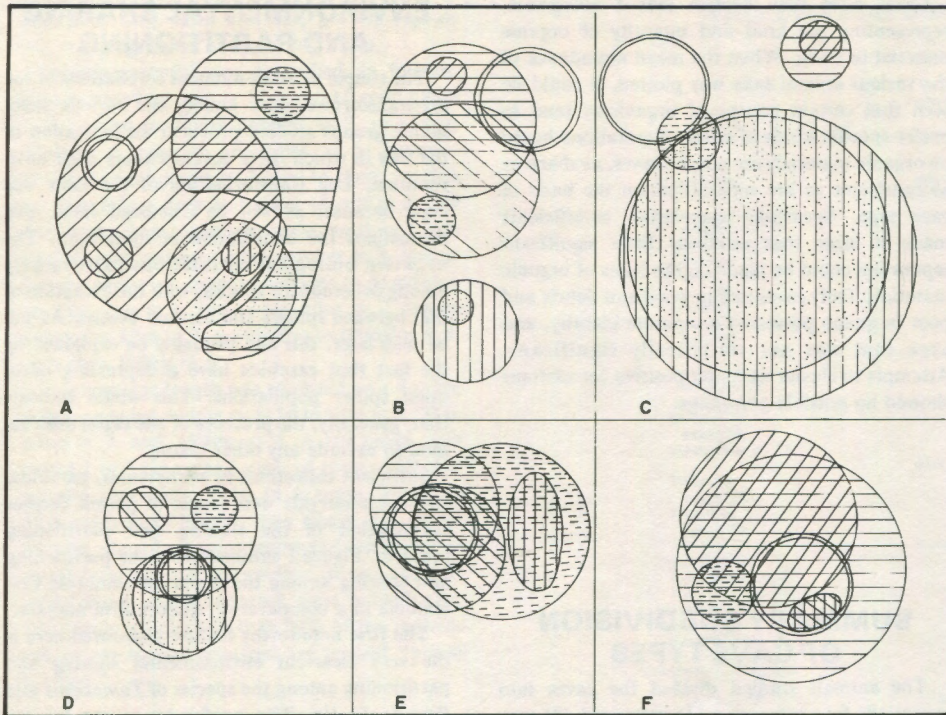
Subdivisions: A. true cave entrances, B. true mixed caves, C. true cave profondeurs, D. sink and underground river entrances, E. sinks, artificial caves and mines, and F. underground rivers (profondeur and mixed).

T. minor _____   T. problematicus _____
P. theodoridesi _____   P. subduodesima _____
P. superduodesima ___   H. nitidus _____
P. virei _____

Figure 1. Environmental sharing and partitioning in Entomobryid collembola. Areas of enclosures are proportional to total number of caves occupied. Overlapping regions represent co-occurrence.

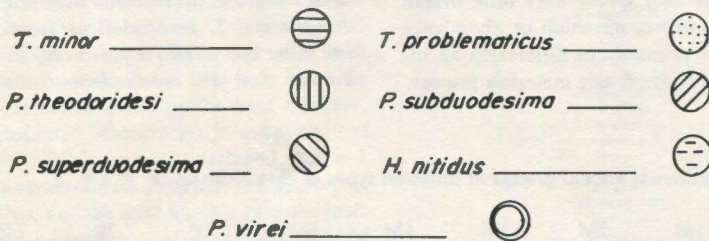partitioned the E and M environments, but each shares its primary niche with *T. minor* and *P. virei*, which partly occupy both. Only *Heteromurus nitidus* seems to cut across all lines, to be completely facultative and least exclusive in its habitats.

There is no clear evidence either of sharing or of partitioning among the Coleoptera, although some hint of preference can be seen. For example, *Speonomus infernus* probably favors the M environment. The large number of species found in relation to the number of observations makes resolution of these questions difficult on the basis of our samples.

If, however, we lump species together on a combination of taxonomic and ecological bases (see Table 3), it becomes possible to see evidence of partitioning. No statistically significant positive associations are revealed by the Cancela de Fonseca (1966) test. Highly significant negative associations occur between species of *Speonomus*,

however, and between this genus and *Anthrocaris*. Negative associations also occur between the three troglophilic carnivores and *Aphaenops* or *Hydraphaenops*.

We dealt only with those forms observed during our visits, and our contacts generally represented the major or commoner forms. In many of our study caves, additional species have been recorded at other times.

SUMMARY OF ENVIRONMENTAL SHARING AND PARTITIONING

In summary, then, both sharing and partitioning of the caves occurs among Collembola; partitioning occurs in Coleoptera. In the latter, partitioning involves larger taxonomic-ecological groups of species with many species being involved in one partitioning unit, while in the Collembola it is usually on an individual species basis.

TABLE 3. Frequency of occurrences of associations of different species of taxo-ecological groups of Coleoptera.

Associations	Number of Occurrences
A	14
B	6
C	8
D	3
AB	14
AC	34
AD	2
BC	10
BD	2
CD	0
ABC	1
ABD	1
ADC	0
BCD	0
ABCD	0
AA	3*
BB	3*
CC	13
AAB	1
AAC	1
ACC	4
BBC	1
AACC	1
ABCC	2

A = *Speonomus* and *Anthrocaris* (troglobitic omnivores)

B = *Choleva*, Sphodridae, and *Geotrechus* (troglophilic carnivores)

C = *Aphaenops* and *Hydraphaenops* (troglobitic carnivores)

D = *Bathysciola* (troglophilic omnivore)

* = Negative affinity P <.01

Double letters of same sort represent occurrence of two species of same group in same subdivision of same cave.

REGRESSION ANALYSIS PROCEDURE

In the course of this study, data of many sorts were derived for each of the caves studied (see *Methods*). It was hoped that the technique of multiple regression would allow us, first, to find some group of factors which represented the best predictors of the abundance of any given species within the cave and, second, to use these data to make some estimation of the major network of ecological factors affecting the cave organisms. To do this, we treated each species or group of species as a dependent variable and other ecological parameters as independent variables. Manual plots of most of the data showed that the distribution was better depicted as a log curve than as a linear curve, so both linear and log-transformed ratios were used. Both simple multiple regression programs and stepwise programs were used, allowing comparison of results and some insight into the relationships involved. In

addition, various factors were omitted from regression to see which correlations represented fused underlying variables and how relationships changed when these were removed. Where a taxon had clearly separable prime habitats (the cave type in which a particular species was most common), analyses were made using both prime habitats and all habitats combined. This enabled us to separate, to some degree, factors governing distribution and abundance (seen in combined programs) from those affecting abundance primarily (shown in prime habitat programs). Data were analyzed both in the prime habitat and elsewhere.

This work was done in 1969-70. Since that time, many new and better techniques have come to our attention; however, we feel that the techniques we used are still of some interest. The work was done on the University of Iowa computer using modified versions of "ANOVA", "REGAN", "NREAN1" and "2" programs, as well as other, subsidiary, statistical packages.

GENERAL DISCUSSION

The uses, limitations, and dangers of multiple regression analysis have been extensively discussed elsewhere (Watt, 1968). These dangers were kept in mind, and attempts to compensate for them were made. The problem of the assumed normal distribution of the data was particularly important with some of the biological variables, where the large concentration of O values produced skewed distributions at the lower ranges. This was compensated for in several manipulations by the fusion of variables (all troglophile Collembola or all troglobite Collembola). Manual plots indicated near normality for these fused variables, and use of the stepwise regression enabled us to see that this fusion did not strikingly affect the role of these variables.

Fortunately, our earlier competition, behavioral, and baiting studies (Christiansen, 1967, 1970a, 1970b) gave us some points of reference and checks, as did the general ecological knowledge we have developed. Thus, positive correlations among species of Collembola may represent a synergistic reaction. On the basis of the works mentioned above, we concluded that these positive correlations were really ecologically spurious, resulting from the fact that such biological factors are in turn correlated with other significant factors. In such cases, we re-examined the data with these spurious positive correlates removed with a view to exposing the underlying relationships.

In spite of all the serious limitations of this procedure, we feel that, by using all of the data available to us, we obtained final results approximating the goals which we set for the study. In most cases, however, we accounted for only a small quantity of the total variation within each species. More refined analysis will undoubtedly show great changes in the importance of individual parameters and will reveal new parameters of great importance.

We shall consider below the various factors associated with the abundance and distribution of the most common species and groups of organisms, then view the possible overall nature of these factors. We shall also consider the nature of the intercorrelations observed for each of the species or species groups studied. While we used many programs in the analysis of the data, the most fruitful of these was the stepwise regression, using the log-transformed data. Most of our discussion will concentrate on these programs.

CORRELATIONS WITH INDIVIDUAL SPECIES OF COLLEMBOLA

Tomocerus problematicus

An extremely high correlation between *T. problematicus* and *P. theodoridesi*, discussed

TABLE 4. Stepwise regression (dependent variable) of *T. problematicus*.

summary table, all locations.

Step number	Sign correlation	Variable entered	Multiple R^2	F value to enter or remove
1	-	*T. minor*	0.0956	10.0401
2	-	Misc. entomobryids	0.2015	12.4743
3	+	Standing water	0.2753	9.4589
4	+	Noncalcareous clay	0.3102	4.6583
5	-	Dry speleothems	0.3598	7.0464
6	-	Millipedes	0.3970	5.5637
7	+	Guano	0.4282	4.8569
8	+	Debris	0.4628	5.6653
9	-	*P. virei*	0.4938	5.3259
10	-	*P. impediens*	0.5132	3.4327

Final R^2 -0.58   No. steps—15

summary table, prime habitats

Step number	Sign correlation	Variable entered	Multiple R^2	F value to enter or remove
1	-	*T. minor*	0.1566	6.3134
2	-	Misc. Entomobryids	0.3560	10.2155
3	+	Noncalcareous clay	0.4763	7.3544
4	-	*P. impediens*	0.5608	5.9632
5	-	Millipedes	0.6051	3.3634
6	+	Calcareous clay	0.6396	2.7801
7	+	Campodeids	0.7110	6.9147
8	+	Altitude	0.7330	2.2205
9	+	Standing water	0.7586	2.7630
10	+	Wet speleothems	0.7735	1.6488

Figure 2. Ecological inter-correlations among variables affecting overall abundance and distribution of *T. problematicus*. Arrow width is proportional to significance of effect. Dotted arrows indicate doubtful relationships. Crosshatched arrows show (suspected) fused underlying variables. Names in parentheses represent features shown in stepwise procedure to be lumped under main effect arrow. Downward arrows represent negative correlates (depress population numbers) and upward arrows, positive correlates (elevate population numbers). Solid triangles represent fulcra showing net effect of the interacting correlates, *i.e.:* if the arrow be the main correlation, reinforcing variables press upward and counteracting variables press downward; the precise location of a fulcrum is arbitrary.
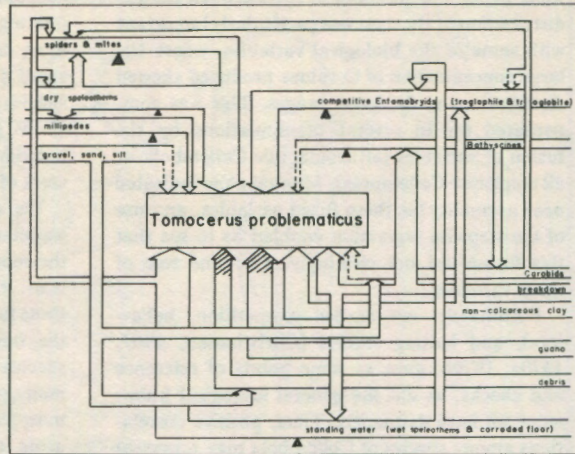

In addition to considering all habitats, as above, we ran programs with only the prime habitat for the species. When the overall program is contrasted with the prime habitat program (see Table 4), a much smaller number of significant correlates occurs. Eleven variables were eliminated from consideration either because their rarity prevents them from being a major factor or because they represented masking positive correlates (see *General Discussion*).

Examination of this program shows that two factors, the negative effect of competitive Collembola and the positive effect of clay, account for most (about 77%) of the correlations seen. This is in striking contrast to the overall program. In addition, the high R^2 achieved indicates a relatively minor role for the remaining climatic factors. All of these features are in basic agreement with earlier baiting studies (Christiansen, 1970b).

elsewhere, made it advisable not to consider these two together in stepwise regression. Examination of the results of the modified stepwise program, considering all habitats examined, indicated a negative effect of four collembolan groups as well as of Bathyscine beetles and spiders, and positive effects of miscellaneous tomocerines and carabids. When these last two positive correlations were examined in the simple multiple regression, we saw that both are greatly reduced in effect; thus, we can accept the logical explanation that they actually represent sums of other factors.

Removing these from the equation (see Table 4), statistically significant negative correlations appear with a number of species of Collembola, as well as with millipedes. Among the non-biological variables, only dry speleothems have a significant negative correlation. Guano, debris, breakdown, non-calcareous clay, and standing water are the most significant positive correlates. In addition, the stepwise program removal enables us to see where the effects of certain variables are actually fused. For example, when "dry speleothems" are placed in the equations, the negative effects of spiders and, to a lesser degree, of mites are greatly reduced, indicating a fusion of these three variables.

Figure 2 summarizes the major influences among the factors studied affecting the overall distribution and abundance of this species and the significant inter-relationships among these factors. Because each of these probably represents an actual meshwork of features, the extreme complexity of the governing mechanisms is obvious. The relatively low values of R^2 achieved in this program probably indicate that additional, omitted, factors play a significant role in governing the overall distribution of the species. This is substantiated by the fact that the R^2, before removal of probable spurious correlates, is considerably greater. The low R^2 probably also indicates a major role for the unused climatic variables.
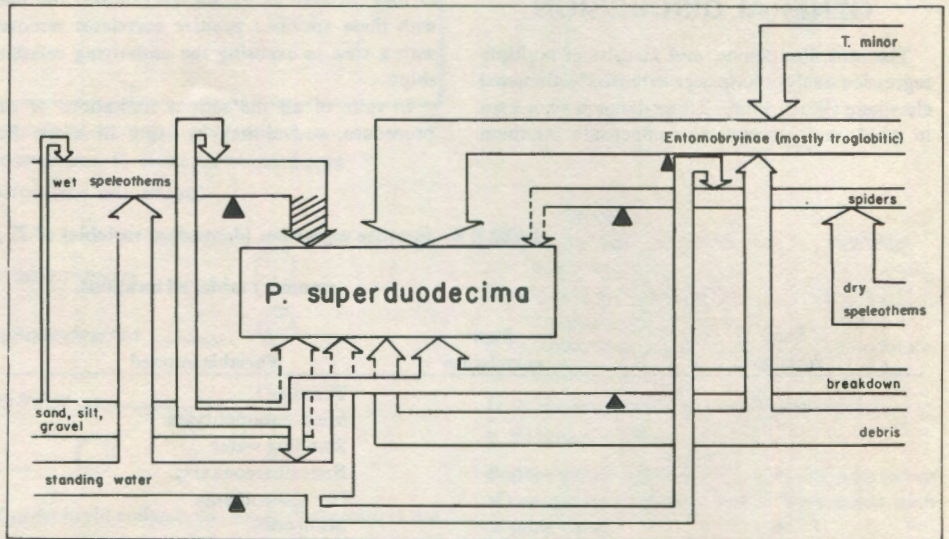
Figure 3. Overall ecological correlations affecting *P. superduodecima*. Symbolism as in Fig. 2.
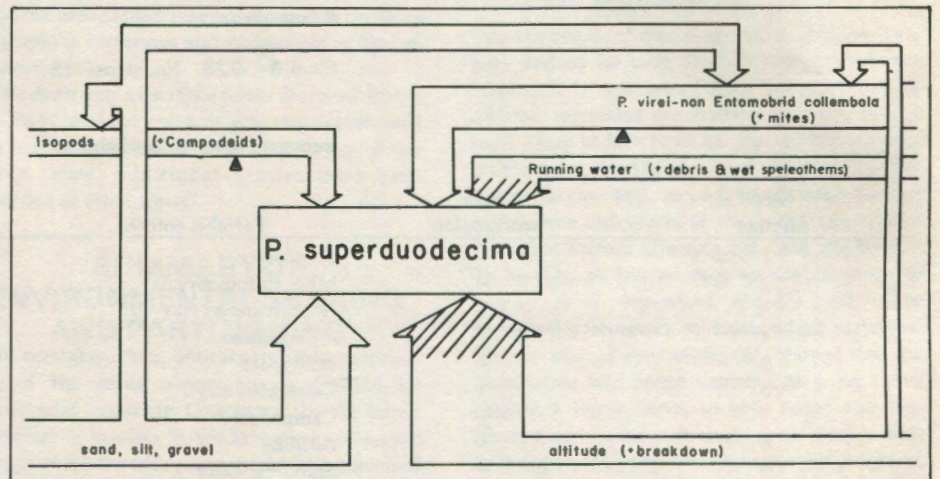
Figure 4. Prime habitat correlations affecting *P. superduodecima*. Symbolism as in Fig. 2.

TABLE 5. Summary table of stepwise regressions.

Dependent variable	Step number	Variable entered	Multiple R^2	Sign of correlation	Step number	Variable entered	Multiple R^2	Sign of correlation
		All locations				**Prime habitat**		
P. theodoridesi	1	Guano	0.1045	+	1	Misc. Entomobryids	0.1667	-
	2	Dry speleothems	0.1952	-	2	Debris	0.4202	+
	3	Debris	0.2551	+	3	Altitude	0.5223	+
	4	Misc. Entomobryids	0.3147	-	4	Campodeids	0.5776	+
	5	Total length	0.3578	+	5	Dry speleothems	0.6509	-
		Final R^2 0.52, No. steps: 11				Final R^2 0.79, No. steps: 10		
P. superduodecima	2	*P. subduodecima*	0.1302	-	1	Altitude	0.3181	+
	3	Breakdown	0.1889	+	3	Isopods	0.4820	-
	4	Sand silt	0.2198	+	4	*P. virei*	0.5138	-
	5	Isopods	0.2455	-	5	Sand/silt	0.5525	+
	7	*T. problematicus*	0.2943	-	6	Running water	0.5962	-
		Final R^2 0.44, No. steps: 19				Final R^2 0.66, No. steps: 10		
P. subduodecima	1	Breakdown	0.0801	+	1	Spiders	0.3118	-
	2	*P. superduodecima*	0.1574	-	2	Noncalcareous clay	0.4430	+
	3	Sand/silt	0.2328	+	3	Gravel	0.4999	-
	5	Noncalcareous clay	0.2770	+	4	Calcareous clay	0.5426	+
	6	Isopods	0.2887	-	5	Carabids	0.5963	+
		Final R^2 0.36, No. steps: 13				Final R^2 0.74, No. steps: 8		
T. Minor	1	Organic soil	0.2392	+				
	2	Guano	0.3375	-				
	3	Wood	0.3844	+				
	4	Altitude	0.4359	+				
	5	Bathyscines	0.4747	-				
		Final R^2 0.60, No. steps: 12						
Bathyscine beetles	1	Organic soil	0.1198	+				
	2	*P. virei*	0.2169	-				
	3	No. sp. carnivores	0.2940	+				
	4	Campodeids	0.3715	-				
	5	Altitude	0.4213	+				
		Final R^2 0.71, No. steps: 25						

Steps omitted represent variables originally entered and later removed.

Pseudosinella theodoridesi

Table 5 gives the summary results of the general and prime habitat stepwise regressions, after positive correlations (which were apparently spurious) have been removed. Examination shows many similarities between this and Table 4 (*T. problematicus*). Entomobryiform collembola and dry speleothems are major negative forces; however, in the case of the Collembola, only troglophile forms are involved. Again, guano and debris are positive correlates. Altitude is a new and significant positive correlate, and running water appears to substitute for gravel and sand as a negative pressure. The most striking changes are the loss of importance of non-calcareous clay and the reversal of correlation for breakdown.

When we examine the individual steps of the stepwise regression, it appears that the negative effects of breakdown and dry speleothems included secondary negative effects. It also appears that running water, campodeids, and total length represent fusions, but the component elements are less clear. In general, it appears that biological factors are less important to this species

than to *T. problematicus*, and that correlates are primarily with physical factors.

If we compare the figures of the prime habitat (again, with probable masking positive correlates and non-occurring variables removed—see Table 5) with the overall regressions, it is clear that the two sets of correlates are very similar. As with *T. problematicus*, there is a greater importance for a small number of variables. Competing Collembola, debris, and altitude account for about 65% of the total correlation observed. The high value of R^2 achieved would indicate a minor role within prime habitats for the unmeasured variables.

Pseudosinella superduodecima

Figure 3 summarizes some of the major overall correlates seen here. This species is of particular interest, because it shows both the weakness and the strength of the technique of stepwise regression. Organic soil showed a very strong positive correlation, initially (F 9.2), but this apparently represented a fusion of effects on a number of competitor species (mostly Collem-

bola). After these were entered, no significant residual correlation remained.

Furthermore, use of other programs enabled us to see that the actual effect of organic soil was largely mediated through a positive correlation with *Tomocerus minor* which, in turn, is negatively correlated with competing Collembola. For this reason, *T. minor* was removed in the consideration of interrelationships summarized in Table 5. It appears, therefore, that two species (*T. problematicus* and *P. subduodecima*) are the most important competitors, and this, along with the apparent strong correlation with breakdown, may largely account for the organisms' general limitation to mixed cave environments.

Examination of the prime environments, again eliminating variables of minor occurrence, shows a striking change in the major correlates (Table 5). These relationships are shown in Figure 4. Here, it can be seen that generally competitive Collembola and spiders lose their importance. The three most important correlates are sand-silt-gravel and altitude, both positively correlated, and running water, negatively correlated. Examination of the stepwise program indicates a fusion of features in both of the last two variables, as indicated in

Figure 4. The relatively low R² would seem to indicate that unmeasured factors play a major role in the local abundance of the species.

Pseudosinella subduodecima

The picture of this species (Table 5) is quite different from that of the previously discussed species. In the first place, the inter-relationships among variables is such that the stepwise program has a tendency to pick single variables representing sums of forces which are difficult to separate. In addition, clear-cut correlates, visible in all programs and not greatly affected by manipulation, are generally absent. The generally low R² values and poor delineation of features associated with the general distribution and abundance of this form lead to the conclusion that we have analyzed the factors governing the overall distribution of this species very poorly.

Even more striking is the change in relationships when we consider only prime habitats (Table 5). Most of the correlation with spiders appears to be negative. A positive correlation with cave clay is also important, while the few other correlated factors are insignificant. Unusual features are the failure of the removal of apparently spurious positive correlates (Carabids and non-entomobryids) to uncover any new significant variables and the great increase in total R² when consideration is limited to prime habitats.

Tomocerus minor

T. minor is the first opportunistic species to be discussed. The overwhelmingly positive role played by organic soil and wood in governing the abundance and distribution of the organism is unusual (Table 5). Together, these account for about 50% of the total correlation observed. The most powerful negative correlation is with total cave length; however, it seems likely that this is a summation of other effects. The only other significant negative correlation is with competitive Collembola.

The tremendous role of organic soil is most localities, where competition is most intense for these forms. Table 6 summarizes the relative presence or absence of the species, relative to the amount of organic soil. No other species shows such a clear correlation with a single parameter.

TABLE 6. *Tomocerus minor* **in association with organic soil.**

Proportion of organic soil (scale)	Localities with *T. minor*	Localities with *T. minor* absent
1	6	0
2	13	1
3	6	2
4	3	10
5	2	4

CORRELATIONS WITH SPECIES GROUPS

Most of the remaining species of Collembola were too rare to merit separate studies; however, a condensed program was run in which all troglophilic entomobryids and all troglobitic entomobryids were added together and treated as two variables. In addition, all guano, wood, and debris was summed as a single variable ("organic matter").

Generally, the troglobitic entomobryids were negatively correlated with troglophilic entomobryids and dry speleothems but positively correlated with standing water, breakdown, clay, and organic matter. In contrast, troglophilic entomobryids were negatively correlated with non-entomobryids and corroded floor, but positively correlated with organic soil, clay, and organic matter (in that order). It should be noted that the fusion of many species in each case resulted in a considerable loss of information in the form of significantly correlated variables.

SUMMARY OF SPECIES LEVEL INTERRELATIONSHIPS

The collembolan species studied in detail showed a great complexity of interacting factors governing their overall abundance and distribution. When abundance within prime habitats was compared to overall distribution and abundance, it was noticed that a smaller number of factors appeared to exert a controlling influence, although these differed strikingly from species to species. Furthermore, the R² was much higher for the prime habitat than for the overall habitat, indicating that unmeasured parameters (such as climatic conditions) probably play a much larger role in determining the locations in which organisms are found than they do in determining their abundance in prime habitats.

These results induce considerable doubt about our other results, since all of the non-collembolan analyses involved considerable lumping of species. In the case of the Bathyscine beetles, the overall similarities of the species concerned are suffi-

TABLE 7. Stepwise regression.

Dependent variable *T. problematicus* data from baiting study (Christiansen, 1970b).

Multiple R	0.6518
Std. error of est.	21.1252

Analysis of variance	DF	Sum of squares	Mean square	F ratio
Regression	3	13184.805	4394.934	9.848
Residual	40	17851.000	446.275	

Variables in Final Equation

Independent variables	Coefficient	Std. error	F to remove
(Constant	3.28782)		
Running water	3.56461	2.35194	2.2971
Carabids	24.50053	8.64099	8.0394
Corroded floor	5.44068	3.93305	1.9136

Variables not in Final Equation

	Partial corr.	Tolerance	F to enter
Bathyscines	0.07935	0.8886	0.2471
Gravel - sand	-0.16531	0.7328	1.0957
Dry speleothems	-0.02829	0.8292	0.0312
Millipedes	0.15737	0.9676	0.9904
Mites	-0.00087	0.6883	0.0000
Competitive ento-mobryids	-0.04561	0.6212	0.0813
Breakdown	0.12835	0.8437	0.6532
Calcareous clay	-0.10402	0.7829	0.4266

Summary Table

Step number	Variable entered	Multiple R²	F values to enter or remove
1	Carabids	0.2843	16.6831
2	Standing water	0.3973	7.6885
3	Corroded floor	0.4248	1.9136

ciently great to merit some examination. Table 5 shows that the primary negative correlates are with certain species of Collembola, campodeids, and isopods. Organic soil, breakdown, and running water furnish the main positive correlates. The negative biological correlations were generally lost when programs with lumped variables were used, indicating that the reactions to Collembola were very specific.

Similar analyses were run on carabid beetles, spiders, mites, and millipedes. The influences appear simpler, in all of these, than are those seen in the Collembola; however, this may be largely the result of a loss of information due to lumping of species.

Among Collembola, the factors correlated with troglobites are more complex than are those affecting troglophiles. A rather surprising feature is that in only one case (the prime habitat of *P. subduodecima*) are predators (spiders) a major negative correlate.

Each species or group of species has a unique combination of correlates. Generally competitive forms play a major negative role and a variety of non-biological features show the major positive correlations.

RELATIONSHIP BETWEEN CORRELATION AND ECOLOGICAL FORCES

The correlations we have examined may not actually depict the ecological factors affecting these organisms. Fortunately, it was possible to check, in a few cases, how well our results agreed with those of other studies.

In the case of *Tomocerus problematicus*, we have a good deal of supplementary information, including an extensive baiting study carried out in Moulis Cave (Christiansen, 1970a). In that study, food was concluded to be the primary positive governing force and troglophilic entomobryid competitors the primary negative force, while predators had a possibly minor negative role. This is in good agreement with our correlation studies, assuming that guano and debris represent food for this species. Furthermore, *T. problematicus* can survive on cave clay, only (Christiansen, 1970b), which could account for the positive correlation found with clay in this study, and with food in general.

This leaves, however, a large number of features which the regression analysis indicates to be of importance, but which Christiansen did not discover in his baiting study. Some cases, such as standing water, could have been simple oversight. To test this, we calculated the amount of each of the apparently correlated variables at each of the 45 main bait stations and weighted each factor according to its apparent importance. Then, we ran a stepwise multiple regression to see which were significant correlates (Table 7).

Since the baiting done in Moulis Cave furnished an excess of food at all locations, this factor became a constant and enabled us to consider only others. The agreement between this analysis and our overall program is excellent in the initial step of the regression. Only two factors show conflicting values—clay and bathyscine beetles. The negative correlation with clay in the Moulis

Cave baiting study is almost certainly due to its positive correlation with mites and with competitive Collembola. They are abundant here and include forms not commonly found elsewhere in the present study.

The significance of the negative mite and collembolan correlations is lost, however, when the standing water and corroded floor variables are entered. This is understandable, because mites and non-entomobryid Collembola are almost absent (Christiansen, 1970b) where there are standing water and corroded floors.

The reversal of the normal relationship between Bathyscines and *T. problematicus* is not explained; however, this is in any case a minor correlate of doubtful statistical significance. Thus, the earlier Moulis Cave analysis supports the conclusion that the correlations discussed here do, in fact, reflect underlying ecological pressures.

SPECIES VICARIANCE AND AFFINITY

A number of cases of co-occurrence (affinity) and of vicariance (ecological replacement) (Cassagnau, 1961) are visible in this study. The most striking case of affinity is seen in *T. problematicus* and *P. theodoridesi*. The range of the former is entirely within the range of the latter, and they are almost always found together (Figure 1), except that *T. problematicus* has a greater tendency to spill over into entrance habitats, where it competes with other forms.

This close ecological relationship between *P. theodoridesi* and *T. problematicus* poses peculiar problems. The very high degree of correlation between these two forced us to remove one as a variable from any stepwise correlation of factors affecting the other. Otherwise, the nature of the program would have caused this high correlation to mask the common factors underlying both distributions. It is possible that some direct synergistic effect exists between the two species, but evidence for this is weak. A stronger presumption is that their close correlation results from ecological similarity and the absence of exclusionary competition.

TABLE 8. Comparison of F levels for various environmental factors in simple and multiple regression analyses for *P. theodoridesi* and *T. problematicus*, with and without each other as independent variables. Intact numbers indicate F levels P < .10. Slashed numbers indicate F levels P > .10.

Dependent variable	*T. problematicus* theod. removed	*T. problematicus* theod. present	*P. theodoridesi* probl. removed	*P. theodoridesi* probl. present
P. superduodecima	- 4.58	- 2.93	.19	.61
P. decipiens	- 1.88	- 2.63	.78	.91
P. impediens	- .88	- 1.11	- .61	.91
P. virei	-10.38	-11.65	- .14	2.80
T. minor	- 7.89	- 3.53	- 4.88	- .91
Other Entomobryids	-32.04	- 6.30	-26.54	.91
Bathyscines	- 4.64	- 3.18	- .98	- .10
Spiders	- 2.42	.96	.91	.19
Opilionids	.88	3.03	.61	- .60
Millipedes	- 1.99	- 2.50	- .21	.28
Guano	2.32	5.35	1.73	.28
Debris	5.90	.19	12.08	6.82
Altitude	3.01	.28	4.92	2.49
Wet speleothems	- 3.41	- 1.81	.61	4.49
Dry speleothems	-12.59	- 6.50	-14.61	- .66
Corroded floor	.44	- .96	1.48	3.78
Breakdown	1.30	13.21	-10.84	-11.11
Non-calcareous clay	6.00	10.24	- .61	- 9.88
Sand and silt	- 1.51	.61	- .61	.02
Gravel	- .24	- 4.78	.61	4.15
Standing water	5.24	9.98	.28	- 1.74
Running water	.91	1.99	- 3.39	- 6.37
Total length of cave	.66	- .84	3.82	2.52

TABLE 9. Five largest positive and negative correlates, arranged in prime habitat stepwise regression, for three troglobitic collembola.

Rank	*T. problematicus*	*P. theodoridesi*	*P. virei*
NEGATIVE CORRELATES			
1	Other entomobryids	Other entomobryids	*P. superduodecima*
2	*T. minor*	Dry speleothems	Total length
3	Millipedes	*P. impediens*	Carabids
4	*P. impediens*	Bathyscines	*P. impediens*
5	*P. virei*	*T. minor*	Mites
POSITIVE CORRELATES			
1	Noncalcareous clay	Altitude	Guano
2	Campodeids	Debris	Breakdown
3	Calcareous clay	Campodeids	Debris
4	Altitude	Calcareous clay	Wet speleothems
5	Standing water	Opilionids	Sand Silt

Some idea of both the overall ecological similarities and the nature of the differences between the two species can be gained by comparing regression programs with and without the co-occurring species as an independent variable. In the latter case, underlying common ecological correlates should be exposed. In the former, these would be suppressed, and the factors included in the final equation would be primarily those which affect the two species differently. Table 8 summarizes the final F values for all factors showing statistically significant values.

This table shows that there are a group of variables which appear to have great common effect and which, generally, show only a reduction of this effect when the correlation associated with the alternative species is removed. Thus, *T. minor*, other Entomobryids, and dry speleothems appear to affect both species negatively, while guano, debris, and altitude affect both positively. The four other species of *Pseudosinella*, Bathyscines, and millipedes all seem to affect *T. problematicus*

but do not affect *P. theodoridesi*, while running water appears to affect only *P. theodoridesi* (negatively). Total cave length and corroded floor appear to affect *P. theodoridesi* positively, while breakdown, non-calcareous clay, standing water, and gravel have opposite effects on the two species —the first three favoring *T. problematicus* and the last favoring *P. theodoridesi*.

In summary, both of these species tend to have similar correlations with environmental parameters; however, by considering regression both with the species included and with it excluded from the equations, it is possible to see the degree of similarity and the nature of the separate effects. Thus, ability to share the same habitat probably stems from a variety of factors which affect each species differently. This would be especially true in regard to the presence of clay, which can be used as a supplementary food by *T. problematicus*.

P. virei furnishes a sharp contrast to the preceeding two species. It is quite similar to *P. theodoridesi* in morphology and habitat, but the two are rarely found in the same cave. Our

data for *P. virei* are inadequate for a thorough study. However, comparing the five most significant correlates of *P. virei* with those of the two preceeding species in their prime habitats (Table 9), it is seen that there is little other similarity between *P. virei* and either *T. problematicus* or *P. theodoridesi*.

SUMMARY OF INTERCORRELATION STUDIES

Table 10 summarizes the significant intercorrelations found in our various overall programs. No great uniformity of significant variables exists. Generally, Collembola, breakdown, wet speleothems, and organic soil are the most important variables. Other variables, such as standing water, clay, debris, and spiders, appear frequently to be major correlates of Collembola but not of other groups. There do not appear to be general groupings of organisms sharing common correlates but, rather, each form has a unique battery of parameters. Some similarities do appear among highly adapted troglobites and among troglophiles, but these are neither striking nor uniform.

GENERAL DISCUSSION

Caves represent an extremely varied environment, one that terrestrial arthropods divide naturally into four or five relatively distinct habitats. The factors which restrict or favor a given taxon in one of these habitats vary greatly. Thus, organisms occupying the same habitat generally do so for very different reasons, and the result is that the total distribution is unique for each species.

Cases of apparent competitive exclusion can also be explained on the basis of differing ecological requirements, as is demonstrated by the detailed analysis of *P. theodoridesi* or by *P. virei*. This high degree of niche individuality also permits a good deal of co-occurrence, most strikingly seen in the case of *P. theodoridesi* and *T. problematicus*.

The most surprising result of this study is the apparent complexity of factors correlated with the abundance and distribution of these cave species. Although microclimate was not considered in this study (and it is clear that this plays a major role in the distribution and variety of cave arthropods [Poulson and Culver, 1969; Juberthie, 1969; Christiansen, 1970b]), it is unlikely that this represents a simplifying variable. One bit of evidence supporting this is a comparison of *T. minor* living under varied microclimatic conditions with *T. problematicus* living under one microclimate in its prime habitat (profondeur). Because these experience very different conditions of microclimatic variability, the similar complexity of factors governing their abundance would be hard to explain were microclimate a simplifying variable. All the evidence suggests that the addition of microclimate would make the interactions more complex.

TABLE 10. Significant correlates from all programs using all localities.

	T. problematicus	P. theodoridesi	P. superduodecima	P. subduodecima	T. minor	Bathyscines	Mites	Typhloblaniulus	Carabids	Spiders
Troglobitic collembola	1 -	1 -	3 -	1 -	1 -	3 -	-1	—	2+	—
	(3+)*	(3+)	—	—	—	—	—	—	—	—
Troglophilic collembola	2 -	2 -	1+	1+	1+	—	2+	1+	1 -	2+
Bathyscines	1 -	1 -	—	—	1 -	—	1+	—	1+	—
Carabids	1+	1+	—	—	—	—	—	1 -	—	1 -
Spiders	1 -	1 -	1 -	1 -	—	—	—	—	1 -	x
Isopods	—	—	2 -	1 -	—	2 -	—	—	1+	—
Opilionids	—	—	—	—	—	—	—	—	—	1 -
Mites	1 -	1 -	—	—	1+	—	x	1 -	—	—
Campodeids	—	2+	—	—	—	2 -	1+	—	—	1 -
Typhloblaniulus	1 -	—	—	—	—	—	—	x	1 -	—
Wood	—	—	1+	—	1+	—	—	2+	—	—
Guano	2+	1+	1 -	—	1 -	—	—	—	—	—
Debris	2+	2+	2+	1+	—	—	—	1+	—	—
Altitude	—	2+	1+	—	2+	1+	—	2 -	—	—
Wet speleothems	1+	—	2 -	—	—	2+	2 -	2+	3+	—
Corroded floor	1+	—	—	1 -	1 -	2+	—	—	—	—
Calcareous clay	—	—	—	—	—	—	2+	—	—	—
Noncalcareous clay	2+	—	—	2+	2+	—	—	—	—	—
Sand silt	1 -	—	2+	1+	—	—	—	1 -	2+	—
Gravel	—	—	—	—	—	—	—	2 -	1 -	—
Organic soil	—	—	—	1 -	3+	2+	3+	—	3 -	—
Standing water	2+	—	2+	1 -	—	—	—	—	—	—
Length	—	3+	-2	-2	3 -	—	—	—	—	2 -
Breakdown	2+	2 -	2+	2+	1 -	1+	—	1 -	—	—
Dry speleothems	2 -	2 -	—	—	—	—	—	2 -	—	3+
Running water	—	2 -	-1	2+	—	2+	—	2 -	—	—

*Higher figure includes interaction between *T. problematicus* and
P. theodoridesi.
+ = positive, - = negative, 3 = primary, 2 = significant, 1 = minor

It can also be argued that all of our studies involved a considerable mixture of environments; however, our initial analysis showed that organisms tend to break the cave environment into four categories, and that, when consideration of a species is limited to the category of its prime habitat, the complexity of ecological interactions is still very great (see tables 4 and 5). Because caves are (physically) relatively simple environments, one might expect their significant ecological correlates to be relatively few. Our study indicates that the reverse is true.

The greatest complexity of interaction appears to occur in species from the profondeur (compare Figure 2 with Figure 3). The profondeur normally is the most stable region of the cave and has the narrowest range of physical variables. Stability favors predictability. Stability plus predictability may lower the extinction rate of small populations, thus bringing about greater biological complexity. In this way, profondeurs may furnish habitats similar to those of the tropics. Geologically, profondeurs are more stable than mines, artificial caves, and sinks, thus allowing greater lengths of time for evolution to operate.
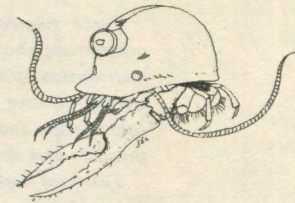
The discovery that these apparently simple cave ecosystems are, in reality, highly complex indicates that most published ecological analyses of them are too simplistic. Studies that purport to show correlations between population fluctuations or distribution limitations and a few environmental parameters are suspect, for reasons detailed in the present work: specifically, that the variable(s) chosen may be a spurious correlate representing the fusion of many underlying factors. One means of clarifying these situations, described in this paper, is to use stepwise regressions in combination with close familiarity with the fauna being studied.

ACKNOWLEDGEMENTS

LITERATURE CITED

Cancela da Fonseca, J. (1966)—L'Outil Statistique en Biologie du Sol, III: *Rev. Ecol. Biol. Sol* 3:381-408.

Cassgnau, P. (1961)—Ecologie du Sol dans les Pyrenees Centrales: *Actualities Sci. Indust.* 1283:1-235.

Christiansen, K. (1967)—Competition between Collembolan Species in Culture Jars: *Rev. Ecol., Biol. Sol* 4(3):429-462.

————(1970a)—Experimental Studies on Aggregation and Dispersion in Collembola: *Pedobiologia* 10:180-198.

————(1970b)—Invertebrate Populations in the Moulis Cave: *Ann. Spéléol.* 25:244-276.

———— and D. Culver (1968)—Geographical Variation and Evolution in *Pseudosinella hirsuta: Evolution* 22:237-255.

———— and ———— (1969)—Geographic Variation and Evolution in *Pseudosinella violenta: Evolution* 23:602-621.

Juberthie, C. (1969)—Relations entre le Climat, le Microclimat et les *Aphaenops cerebrus* dans la Grotte Sante-Catherine: *Ann. Spéléol.* 24:75-104.

Poulson, T. and D. Culver (1969)—Diversity in Terrestrial Cave Communities: *Ecology* 50(1):153-158.

Rapoport, E. (1959)—*Algunos Aspectos de la Biología de Suelos:* Bahía Blanca (Brazil), Univ. del Sur, Extension Cultural, 23pp.

Watt, K. (1968)—*Ecology and Resource Management:* NYC, McGraw-Hill, pp. 232-250.

Part Two: Evolutionary analysis of three species of Collembola

ABSTRACT

Three related species of cave Collembola, representing different levels of evolutionary cave adaptation, show little correlation between local ecological conditions affecting their abundance and distribution and the evolutionary status of the populations. The most highly evolved species shows a strong positive correlation between evolutionary status and both the probable date of initial colonization and the number of species in a cave. The two primitive species apparently are recent cave invaders and do not, as yet, show any clear evolutionary trends toward cave adaptation.

The most highly evolved cave species shows about twice as much intrapopulation variability as does either of the two primitive species. This, as well as life cycle and apparent selective forces, points to a major shift in evolution between the two primitive and the one advanced species.

INTRODUCTION

IN THE FIRST part of this project, we studied niche overlap and partitioning among cave organisms and determined which ecological factors in the cave are of primary importance in determining the abundance and distribution of the species of arthropods, *i.e.*: the important ecological pressures on each species. In this portion of the study, we determined the evolutionary status of different populations of three species of the collembolan genus *Pseudosinella*: *P. theodoridesi, P. subduodecima*, and *P. superduodecima* and attempted to analyze the evolutionary significance of their microgeographic variations. Then, we attempted to discover if there exists any relationship between the evolutionary status of a population and its ecological pressures (as determined in the first part of the project).

Figure 5. Map showing location and identification numbers of caves studied.
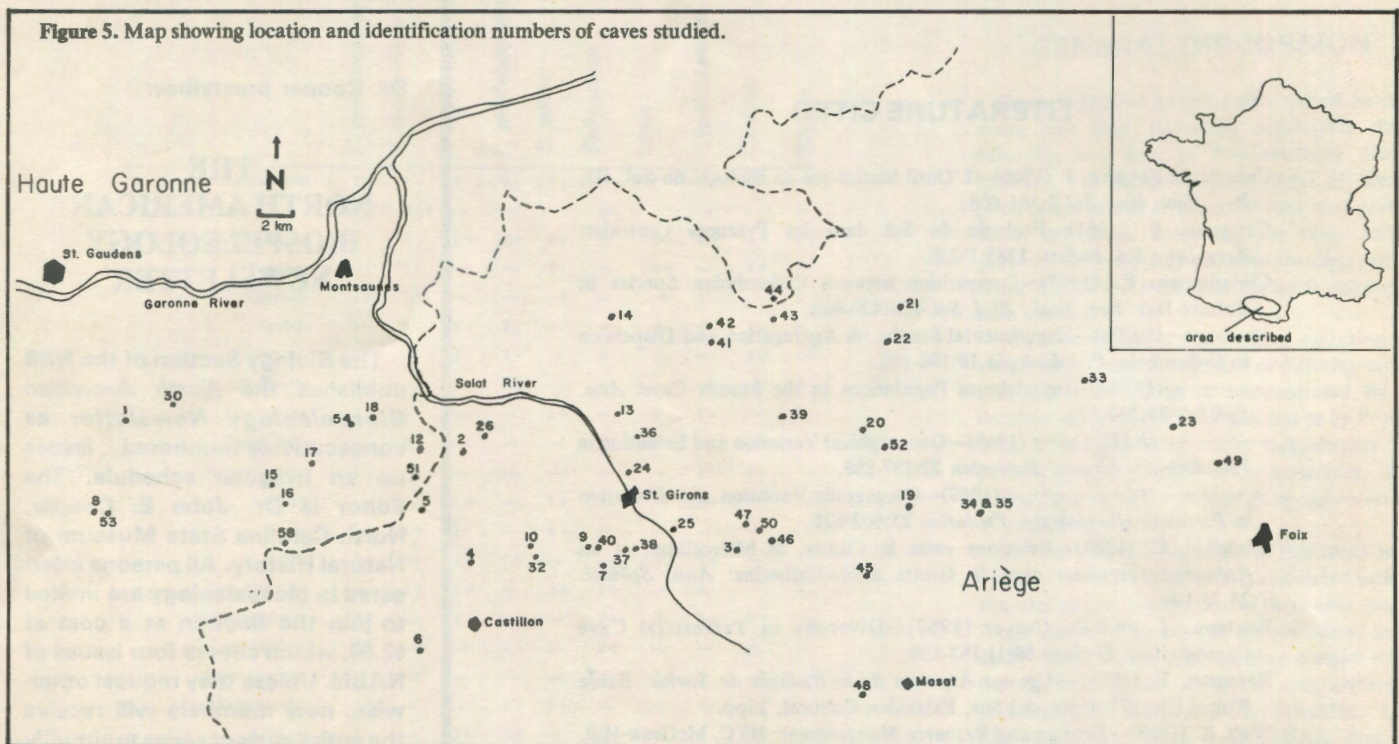
METHODS AND MATERIALS

The study area includes 627 sq km in the departements of Ariège and Haute-Garonne (France) (Figure 5). It encompasses the entire range of *P. theodoridesi* and some unknown (but major) portion of the ranges of the other two species. Fifty-eight caves were examined. Of these, 33 were found to contain one or more of the three species discussed.

The species differ in level of cave adaptation and morphology, but all are members of a single species group. *Pseudosinella theodoridesi* (Figure 6) is a highly evolved troglobite which is restricted largely to the profondeur of true caves. In comparison to the other two species, it is larger and has relatively longer antennae and furcula.

Pseudosinella superduodecima and *P. subduodecima* are very similar to each other, morphologically (Figure 6) and show few or no specializations for cave life. They are clearly separated, ecologically. The former is largely restricted to mixed cave habitats, while the latter occurs only in entrances and in simple sinks. The species, thus, show different degrees of morphological and ecological separation, in connection with cave adaptation.

The relative evolutionary status of each population of each species was defined, using techniques developed in earlier studies (Christiansen and Culver, 1968, 1969). The eyes are variable in number only in *P. theodoridesi*, while the foot

complex (Figure 7) and antennal base setae showed measurable variation in both *P. theodoridesi* and *P. superduodecima*. The overall evolutionary status of each cave population was determined by ranking each variable numerically on the basis of relative cave adaptation (1 through *n*) and summing ranks for all variables from each population.

OVERALL ECOLOGICAL AND EVOLUTIONARY CORRELATIONS

Each cave was ranked, according to its ecological condition, for the eight most significant variables uncovered in the prime habitats stepwise regression programs (see Part I). Each variable was weighted according to the increase it made in the R^2 and was given the sign of its regression co-efficient in this program. The quantities of each variable for each cave were summed after normalization (Christiansen and Culver, 1969). This final figure was then accepted as representing the overall ecological pressures associated with the presence and abundance of the given species in the given cave.*

If these local ecological conditions in the cave were a major factor in determining the evolutionary status of the animals, there should be a significant negative or positive correlation between the ecological pressures thus measured and the overall evolutionary status. If we consider the rank sum of all evolutionary features and of all ecological variables, a weak and statistically insignificant correlation is shown in all cases (Table 11A). However, on the basis of previous work, it appeared probable that the foot complex might be responding to different pressures than the remaining features (Christiansen and Culver, 1968). To test this, the evolutionary status (measured by all variables other than the foot complex) was measured against ecological pressures.

The results of this appear in Table 11B, which shows only a slightly better correlation than does Table 11A. On the basis of the earlier ecological work described in Part I, there was reason to believe that physical and biological parameters might operate differently for two of the species. The five most important physical factors and four or five most important biological factors, as shown in the stepwise progression, were tested against overall evolutionary status (tables 11C and 11D). It would appear from this that *P. superduodecima* shows more cave specialization (is more highly evolved) in generally more favorable environments, and that physical factors are more important than biological. *P. theodoridesi* is more highly evolved in favorable biological situations and possibly more highly evolved in less favorable physical localities, while the reverse is true in both cases for *P. subduodecima*.

The overall evolutionary factors lump together

* The results of this together with the rank ordering of these results may be obtained free on application to the NSS Library, Cave Avenue, Huntsville, Alabama 35810.
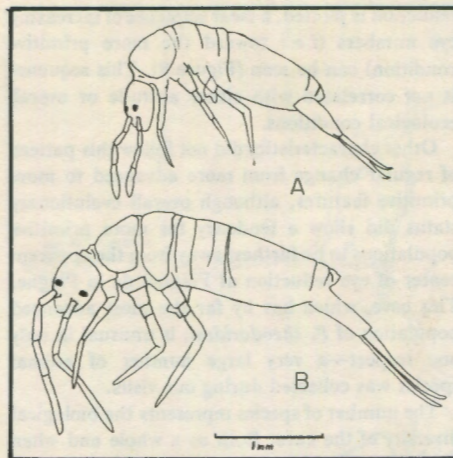

Figure 6. Habitus of A) adult *P. subduodecima* and *P. superduodecima* and B) adult *P. theodoridesi*, drawn to scale.
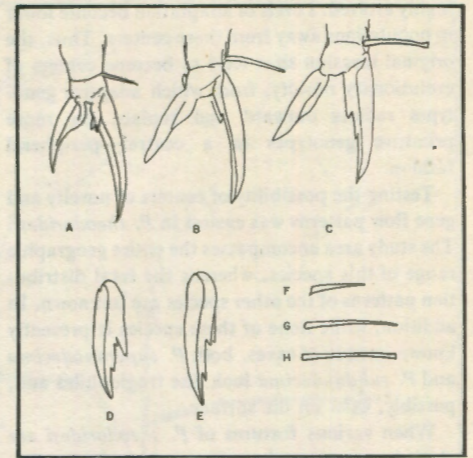

Figure 7. Differing conditions of foot structures. A-C—*P. theodoridesi*; evolutionary values (foot complex): A=3, B=2, C=1. D-H—*P. superduodecima*; evolutionary values (unguis) D=2, E=1; (tenent hair) G=2, H=1. The longest claw = 0.078mm and the shortest, 0.045.

TABLE 11.

A. Overall Spearman's Rho (D^2) between evolutionary status and ecological pressures.

Species	D2	N	P	Sign of better correlation
P. theodoridesi	327	14	.11	+
P. superduodecima	113	10	.19	+
P. subduodecima	332	13	.20	+

B. Same for evolutionary status exclusive of foot complex.

P. theodoridesi	295	14	.08	+
P. superduodecima	83	10	.07	+
P. subduodecima	337	13	.18	+

C. Overall evolutionary status compared to ecological pressure determined by five major physical factors.

P. theodoridesi	356	14	.14	-
P. superduodecima	83	10	.07	+
P. subduodecima	152	13	.02	+

D. Overall correlations with major biological factors.

P. theodoridesi	290	14	.08	+
P. superduodecima	135	10	.31	+
P. subduodecima	310	13	.40	-

many different kinds of features, and the individual correlations (Table 12) give considerably more information concerning the kinds of correlations which occur. It is noteworthy that body ratios show most of the significant correlations in the two troglophile species, while foot complex and head structure are more responsive in *P. theodoridesi*. It is also clear that correlations with overall evolutionary ranks do not entail significant correlations with even a majority of the component characteristics.

HISTORICAL FEATURES

It is obvious, that evolutionary status could be partly determined by the length of time the organisms have been living in caves and in centers of novelty gene outflow, as we found in *P. hirsuta* (Christiansen and Culver, 1968). The first factor

is impossible to attack directly, but, in mountainous regions such as ours, caves at higher elevations tend to be older. Assuming that surface ancestors first entered each cave as it was exposed to the surface, the altitude of a cave should be some measure of the antiquity of its population. Table 12D contains the correlations between altitude and evolutionary status of the three species studied. The correlation is strong and widespread in *P. theodoridesi*, but insignificant for the two other species.

According to the hypothesis developed in earlier works on *P. hirsuta* and *P. violenta* (Christiansen and Culver, 1968, 1969), centers of novelty develop in troglobitic forms at the sites of initial invasion. These areas represent both the longest periods of cave competition and adaptation and, also, the maximum gene input. The result is that these populations are the most

highly evolved. Levels of adaptation become lower in populations away from these centers. Thus, the original invasion sites tend to become centers of evolutionary novelty, from which adaptive genotypes radiate outward and replace the more primitive genotypes in a central—peripheral fashion.

Testing the possibility of centers of novelty and gene flow patterns was easiest in *P. theodoridesi*. The study area encompasses the entire geographic range of this species, whereas the total distribution patterns of the other species are unknown. In addition, while none of these species is presently known outside of caves, both *P. superduodecima* and *P. subduodecima* look like troglophiles and, possibly, exist on the surface.

When various features of *P. theodoridesi* are plotted on a map, they show only limited unity. One characteristic, eye number, appeared ideal for determining centers of novelty (as distinguished from ecological pressures). None of the ecological factors is suspected of being correlated with eye reduction; however, this reduction is clearly cave-dependent and should be spread readily from one population to another. When eye

reduction is plotted, a clear sequence of increasing eye numbers (*i.e.*: toward the more primitive condition) can be seen (Figure 8). This sequence is not correlated with either altitude or overall ecological conditions.

Other characteristics did not follow this pattern of regular change from more advanced to more primitive features, although overall evolutionary status did show a tendency for more primitive populations to be furthest away from the apparent center of eye reduction at Plagnol de la Plagne. This cave, which has by far the most advanced population of *P. theodoridesi*, is unusual in only one respect—a very large number of animal species was collected during our visits.

The number of species represents the biological diversity of the cave. Both as a whole and when divided into its component parts (see Part I), it shows little correlation with the overall abundance or presence of *P. theodoridesi*. However, Table 13 shows that number of other species co-occurring with *P. theodoridesi* is strongly correlated with the evolutionary status of the foot complex and antennal variables. No such correlation exists either in *P. superduodecima* or in *P. subduo-*

decima, although both of these species show some positive correlation between abundance and diversity of habitat. Diversity of habitat has been shown to be strongly correlated with available organic material (Poulson and Culver, 1969). This also proved true in our study. The product-moment correlations between species number and total organic material of all habitats in this study was 0.41 (P<0.001).

DISCUSSION AND CONCLUSIONS

It appears, on the basis of our study, that the immediate local ecological conditions associated with the presence or abundance of a given species are not generally correlated with the degree of cave adaptation of a given species. Physical factors are generally, if weakly, associated in a positive fashion with the evolutionary advancement of troglophile forms, but this probably reflects the fact that only under favorable conditions are the populations able to persist long enough to go through any significant adaptive change.

TABLE 12A. Near-significant and significant D^2 value of Spearman's Rho and associated probabilities between overall ecological pressures and the evolutionary status of individual characteristics.

Species	D^2 P. theodoridesi n = 14	P	D^2 P. superduodecima n = 10	P	D^2 P. subduodecima n = 13	P
Characteristic						
Hind tibiotarsus	+325	.10	///	///	///	///
4th abdominal segment	///	///	///	///	-247	.10
2nd thoracic segment	+300	.08	*	*	—	—
Tenant hair type	+303	.08	+50	.015	*	*

TABLE 12B. Significant correlation with ecological pressure determined by five major physical factors. ± = sign of the better correlation.

Species	+D^2 P. theodoridesi	P	+D^2 P. superduodecima	P	+D^2 P. subduodecima	P
Characteristic						
Hind tibiotarsus	///	///	+228	.08	///	///
Dens	///	///	+245	.10	///	///
Mucro	///	///	+ 78	.008	*	*
4th abdominal segment	///	///	///	///	+ 62	.03
Cephalic diagonal	- 200	.08	+246	.10	///	///
2nd thoracic segment	+288	.07	///	///	*	*
4th antennal segment	- 308	.08	///	///	+///	///
Unguis, total length	- 289	.07	///	///	- 140	.34
Unguis, length over basal tooth apex	- 236	.04	+101	.02	///	///
Unguis type	- 274	.06	*	*	*	*
Number of eyes	- 304	.08	*	*	*	*
Total length	+223	.03	///	///	///	///

TABLE 12C. Significant correlation with ecological pressure, determined by four of five biological factors. *four variables, †five variables.

Species	±D^2 P. theodoridesi*	P	±D^2 P. superduodecima†	P	±D^2 P. subduodecima†	P
Characteristic						
4th abdominal segment	///	///	26	.002	///	///
Cephalic diagonal	///	///	///	///	+208	.06
2nd thoracic segment	+261	.06	*	*	—	—
4th antennal segment	+222	.04	///	///	///	///
Unguis, total length	///	///	///	///	- 196	.05
Unguis, length over basal tooth apex	+301	.08	///	///	///	///
Empodium type	+259	.06	*	*	*	*

TABLE 12D. Significant correlations with altitude.

Species	D^2 P. theodoridesi	P	D^2 P. superduodecima	P	D^2 P. subduodecima	P
Characteristic						
Hind tibiotarsus	298	.08	///	///	///	///
Dens	198	.02	///	///	///	///
Mucro	///	///	*	*	209	.06
4th abdominal segment	228	.04	64	.03	///	///
Cephalic diagonal	254	.05	///	///	///	///
2nd thoracic segment	278	.07	*	*	///	///
Unguis, total length	279	.07	///	///	///	///
Unguis, length over basal tooth apex	286	.07	///	///	///	///
Unguis type	329	.10	*	*	*	*

The one clearly cave-modified species (*P. theodoridesi*) showed a distinct correlation between altitude of cave (probably associated with the age of the initial colonization) and evolutionary status. This was reflected in most of the body measurement characteristics, while the foot complex and antennal lengths were better correlated with the biological diversity of the caves. Eye number showed a radiation pattern from an advanced center to primitive peripheral populations, as was seen earlier in *P. hirsuta*, but this was only slightly paralleled in other characteristics.

It would appear that, in *P. theodoridesi*, evolutionary advance is determined largely by the length of time the animals have been in a given cave and how diverse is the biological environment which they face. These factors do not, however, influence the same characteristics of the organism, nor do they operate in the same fashion. Favorable or unfavorable local conditions for population abundance have only a minor effect on the evolutionary status.

This last statement, apparently, also holds true for the non-cave-modified species studied. The evolutionary status of such forms is correlated neither with the biological diversity nor the ages of the caves. Thus, it appears that a major change in the nature of the selective process has occurred between the two primitive species and the highly evolved cave form. This difference is reflected in the variability within populations of each of these species. Individual character variances seen in *P. theodoridesi* are about twice as large as are those of either *P. subduodecima* or *P. superduodecima*. This would suggest that the former species has reconstructed the epigenotype, while the last two are recent cave isolates (Barr, 1968). The morphological evidence, combined with the absence of surface records for any of these forms, supports this idea.

The fact that *P. subduodecima* and *P. superduodecima* are recent cave invaders is further substantiated by the fact that their life spans and reproductive cycles are very similar to those of surface forms, unlike most troglobites (Poulson and White, 1969). Our failure to discover any factors clearly associated with evolutionary advancement in these forms is probably related to this recent colonization and the concomitant lack of large-scale evolutionary change. In effect, these species are still in the "period of preparation" (Vandel. 1964).
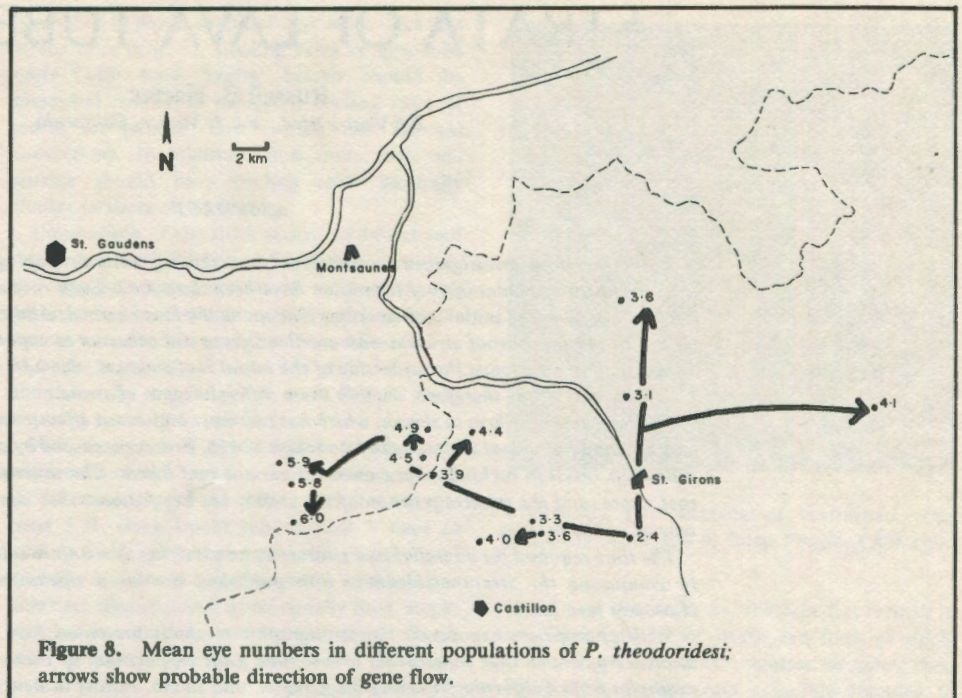

Figure 8. Mean eye numbers in different populations of *P. theodoridesi;* arrows show probable direction of gene flow.

TABLE 13. Correlation between evolutionary status and number of species seen in cave in *P. theodoridesi*.

Characteristic	D^2	P
Hind tibiotarsus	>400	>.10
Dens	>400	>.10
Mucro	>400	>.10
4th abdominal segment	>400	>.10
Cephalic diagonal	>400	>.10
2nd thoracic segment	404	>.10
4th antennal segment	245	.05
Unguis, total length	259	.06
Unguis, length over basal tooth apex	131	<.01
Empodium type	164	.01
Unguis type	147	<.01
Tenant hair type	270	.07
Number of eyes	212.5	.03
Total length	>400	>.10

LITERATURE CITED

Barr, T.C., Jr. (1968)—Cave Ecology and the Evolution of Troglobites: *Evolutionary Biol.* 2:35-102.

Christiansen, Kenneth and David Culver (1968)—Geographical Variation and Evolution in *Pseudosinella hirsuta: Evolution* 22:237-255.

———, ——— (1969)—Geographical Variation and Evolution in *Pseudosinella violenta: Evolution* 23:602-621.

Poulson, Thomas and David Culver (1969)—Diversity in Terrestrial Cave Communities: *Ecology* 50:153-158.

——— and W.B. White (1969)—The Cave Environment: *Science,* ns 165:971-980.

Vandel, Albert (1964)—*Biospéléologie:* Paris, Gauthier-Villars, 607 pp.

STRATA OF LAVA TUBE ROOFS

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ABSTRACT

Several previous investigators have observed hot, flowing, lava developing roofed channels, and at least five distinct modes of roof formation have been described. Each roofing mechanism results in a first layer of lava (the initial roof stratum*) that spans the lava channel. Additional strata may be added on top of the initial roof stratum—as overflows from the tube, or as separate flows of lava. Ceiling linings, deposited against the underside of the initial roof stratum, also add to the total roof thickness. Lava cave roofs can, therefore, include three different types of strata.*

Cooling causes the lava to shrink, which has two most important effects: strata tend to part from one another, and individual strata break into rough blocks. Fractures caused by cooling stresses within lava tube roofs result in rockfalls that expose the various roof layers. Characteristic textures on surfaces of roof strata, and the relative position of the strata, are key features that can be used to determine the type of strata present.

The time required for an initial roof stratum or an overlying flow unit to solidify can be approximated by comparing the stratum thickness with published measured thicknesses of solidified crust on Hawaiian lava lakes.

With appropriate exposures, the stratigraphic methods presented here can be used to find the sequence of events that constructed a lava tube roof. Application of these techniques, illustrated by examples from California, Washington, Oregon, and Idaho, results in new information regarding the formation history of lava tubes.

INTRODUCTION

LAVA TUBES are distinguished from open lava channels by the presence of a roof. The following discussion introduces stratigraphic methods that are useful for discovering the developmental history of lava tube roofs. *Strata*, in this study, are small flow units or other layers of lava that were deposited separately and successively. The most prominent partings within tube-forming lava flows (excluding cooling cracks) are those between strata. Roof strata of lava tube caves may be observed in section at breakdown entrances and at areas of roof breakdown within caves.

TYPES OF ROOF STRATA

Formation of the Initial Roof

Open channels containing hot flowing lava have been observed as they roof and become lava tubes. The process of roofing has been described at least five different ways:

1. "In one process, the crust attached to the bank grew slowly across the stream and ultimately met the crust growing from the opposite side." (Peterson and Swanson, 1974, p. 211)

2. "Splashing, spattering, and overflow along the channel result in accretion of lava as levees... The levees may continue to build until they arch over the channel and fuse to form an agglutinated roof." (Greeley, 1971, pp. 222-223)

3. "The crust is at first thin and unstable, repeatedly breaking up and floating downstream. Eventually, however, floating crusts form a jam across the river, more crusts pile against the jam, and a permanent roof is established that is gradually extended upstream." (Wentworth and MacDonald, 1953, p. 45)

4. "...the chilling of a skin around protruded pahoehoe toes..." (Wentworth and MacDonald, 1953, p. 43)

5. "At the advancing front the lava seems to come out of its tunnel and flow in an open red river of fire as much as several hundred feet long. This then appears to clog up and cool on top, and the lava pushes out in great and small lobes, piling one over the other and eventually forming a new tunnel underneath for the molten lava. The latter will then again break out and go through the same process as before." (Baldwin, 1953, p. 3)

Additional roofing processes may be described in the future (one more is described in the examples below), but the net result is that a mass of solidified lava spans the channel and roofs it. This mass, or single layer of lava, is here named the *initial roof stratum*. In types one and four above, the initial roof stratum is a simple, single layer of crust. Type two is a single layer, composed of small clots of lava that have fused together. Type three is a jumbled mass of plates that have fused underneath to become a continuous lava layer. Type five is a mass of lobes having a continuous lava layer below.

If a lava layer is attached to the channel walls with no other stationary, solidified layer above or below it, it is (at least locally) the initial roof stratum. The initial roof stratum covering a hole in an earlier roof may overlie, extend, or underlie the stratum that the hole is in.

Overlying Lava Layers

Once the initial roof has formed, thickening of the roof by overflows from the tube, or by lava derived from other sources, often occurs. If the overlying lava contains tubes, the tubes in the overlying lava will have their own roof strata. The emplacement of overlying lava has been described as follows:

"It is to be remarked that at Matavanu the lava-stream is highest in the centre over the line of the tunnel, and tends to become more so owing to frequent small flows of lava which, whenever the flow beneath is obstructed from any cause, rise to the surface and then spread out and solidify there." (Anderson, 1910, p. 630)

"Several thin flow units commonly are visible in the roof of the tube also, and are formed by repeated small overflows from the openings in the tube roof." (Wentworth and MacDonald, 1953, p. 45)

"Burial of covered tubes by surface flows of pahoehoe occurred quickly in many cases on Mauna Ulu,... because of repeated eruptions of thin layers of fluid lava." (Cruikshank and Wood, 1972, p. 427)

Ceiling Linings

Lava within a tube can subside after the roof has formed and continue to flow at a lower level within the tube. This has been observed (through skylights of active tubes) and photographically illustrated by Peterson and Swanson (1974, their plates LIIA, LIIB, LIII, and LIVB).

A surge of lava can refill the tube, perhaps overflow through holes in the roof, and bury the tube as described above. As this happens, a ceiling lining is emplaced inside the tube. Conceptually, any time that the lava level drops (allowing the upper walls and roof to cool), rises again to fill the tube, and then drains away, a ceiling lining is deposited.

Jaggar (1919, p. 137) described the rising of lava in an open channel:

> "The mechanism of rising, at the times when the deep rumble was heard, appears to be extended the whole length of the visible stream. The lava started to rise in the channel and in a few minutes it was brimming level with the banks, as though the whole mass inflated at once. There was no wall of added liquid advancing from above, nor was there any obvious damming and pooling to make the fluid back up from below. It simply rose with a rumble and it was an even chance as to whether it would overflow somewhere or not."

Jaggar's observation is important here, because it indicates that the lava stream is inflated, rather than overridden, by the fresher incoming lava. If the channel were completely drained or thoroughly cooled before the influx of fresh lava, the remnants of the old lava stream would be overridden.

When overriding occurrs, the upper surface of a lining may be the hot fluid top of the fresh lava rather than inflated older lava that is covered with crusts or a cool top surface. A lining formed from this cooler, more rigid, material can be expected to make a poor fit with the ceiling; but a lining that is soft and pliable will readily conform to the shape of the ceiling.

A result of poorly fitted ceiling linings is that small lenticular cavities are often left between the lining and the lava above. Within such cavities, the lining top will not normally be remelted, but may be lightly glazed. If the floor and ceiling of such a cavity are thoroughly remelted, this indicates that both cooled together and may be considered as one stratum.

If a lining does not stick to the lava above, it either will stand alone, or will fall when support from below is taken away. That is, the lining will behave essentially in the same manner as an initial roof stratum. If a ceiling lining sticks to the ceiling above it, the lining may be supported by the lava above. The degree to which a lining sticks to the ceiling should depend upon the fluidity of the ceiling surface, and the fluidity of the lava surface pressed against it. A ceiling covered with hot remelt ought to bond with any lining emplaced against it. A fluid upper surface of a lining will adhere readily to the ceiling.

CRUST SOLIDIFICATION RATE

Peck, Moore, and Kojima (1966) experimentally measured the crustal solidification rate of ponded Hawaiian basaltic lava. Although future refinement of the relationship between crust thickness and time is probable, a first approximation can be derived from their published data. It is possible to plot a graph of lava crust thickness versus time (Fig. 1). Cooling rates of lava tube roofs (with lava flowing below) should be somewhat similar to measured cooling rates of crusts on ponded lava (which has internal convection). In addition, flow units that cool outside should have cooling rates generally similar to those of lava lakes.

Comparison of the thickness of an initial roof stratum or overlying flow unit with Figure 1 gives the approximate amount of time that was required for the stratum to solidify. For example, a crust 6 in. thick required on the order of 12 to 33 hours to solidify. A crust 2 ft thick required about 5 days to solidify. A crust 6½ ft thick required a month to solidify.

Note that each of 3 crusts 1 ft thick would require about 2⅓ days to solidify, making a total solidification time of not quite 7 days, but a single crust 3 ft thick would take almost 9 days to solidify. This means that a cave roof consisting of several strata would actually solidify in much less time than that required by an equally thick single stratum. In addition, complex initial roof strata (such as those consisting of spatter, lobes, or plates) solidify much more quickly than simple crusts do. Since linings are not exposed to the outside atmosphere, they probably cool more slowly than do either initial roof strata or overlying flow units.
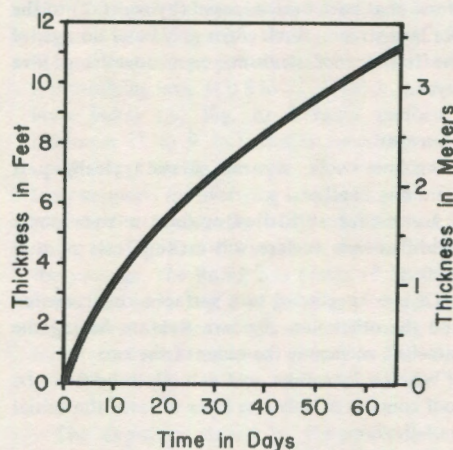

Figure 1. Graph of lava crust thickness versus time. The curve represents the approximate mean values of the extremes of the experimental data. Data from Peck, Moore, and Kojima, 1966.

METHODS AND MODIFICATIONS

Identification of Surfaces

Two general types of top surface are common on basaltic lava flows: aa and pahoehoe. Aa is clinkery, jagged, and spiny. Pahoehoe is smooth, rounded, or ropy (Fig. 2). Lava tubes are common in pahoehoe, but rarely occur in aa.

The upper surface of an initial roof stratum is a diagnostic feature. For example, if the top of an

Figure 2. Top surface of festooned ropy pahoehoe. Scale is 1 ft long. Pisgah, California.

initial roof stratum is aa, the tube has formed in aa. Since initial roof strata can form of single crusts, fragmental crusts, spatter, or lobes, their top surfaces range from smoothly rounded to rough and jagged. It is sometimes possible to determine the mode of roofing by examining the top surface of the initial roof stratum.

Overlying lava may have a top surface that is characteristic of aa, but, since pahoehoe is generally associated with lava tubes, pahoehoe is more common. The top of a ceiling lining is usually like the upper surface of any other lava, except that its general shape conforms to the ceiling above.

The underside of a pahoehoe flow unit molds an impression of the surface it flows over. For instance, a cast of ropy pahoehoe is unmistakable (Fig. 3). Other, less obvious but more ubiquitous, features of pahoehoe casts are stringy bits of spatter (essentially coarse Pele's hair) and chips of older lava embedded in the cast surface (Fig. 4). The chips attest to an imperfect parting of the two
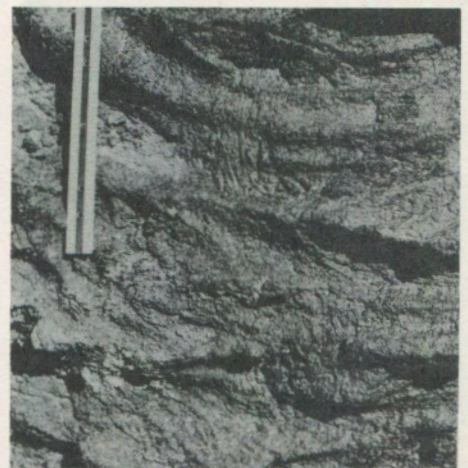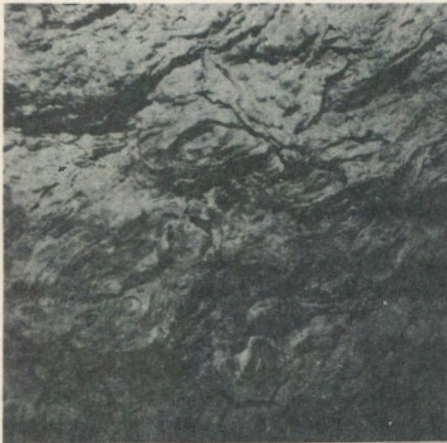

Figure 3. Cast of ropy pahoehoe. Scale is 1 ft long. Pisgah, California.

Figure 4. Closeup of pahoehoe lava cast. Diagnostic features of such casts are chips and 'strings' of lava embedded in the cast surface. Field of view is about 10 in. wide.

layers. Pahoehoe lava that overlies a lava tube can often be identified by its cast underside.

The underside of an initial roof stratum or ceiling lining is commonly covered either with lava drips remaining from the separation of the liquid lava below, or with lava drips caused by remelt of the ceiling. The two types of lava drips look similar, and, although they can be differentiated, it is not necessary to do so here. Exfoliated and cleanly fractured surfaces also occur, but these surfaces do not provide stratigraphic information.

Breakdown and Remelt

While lava still flows through hot tubes, partial or complete collapse of roofs may occur (Peterson and Swanson, 1974, p. 218). Thus, a layer of lava once deposited does not always remain. It may fall into the lava stream, where the loose fragments can be removed by the flowing lava.
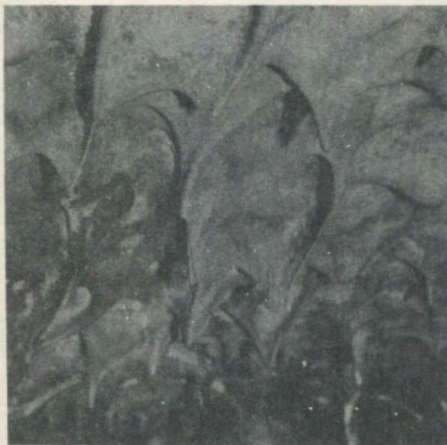
Figure 5. Thorough remelting of a ceiling surface results in drip pendant stalactites such as these in Catacombs Cave, Lava Beds National Monument, California. Field of view is about 10 in. wide.

Rockfall in lava tubes occurs primarily because of cooling, which causes the lava to shrink and crack. If the cracked blocks of the roof do not happen to key together to form an arch, they will fall. All or part of a lava tube roof may collapse while hot lava still flows through the tube. Where this happens, fracture surfaces and sometimes cast surfaces are exposed to intensely hot gases and radiant heat.

The effect of intense radiant heat inside a lava tube is described by MacDonald and Eaton (1964, p. 76):

"Small stalactites formed as the tube roof dripped slightly from refusion by heat radiated from the surface of the liquid stream beneath. No detectable gas was being given off through the hole in the tube."

The exposed lava may remelt surficially, resulting in a lightly glazed appearance. Deeper remelting allows the surface to run and drip, making drip pendant stalactites (Fig. 5). Since later remelting of any exposed surface can occur, a remelted ceiling alone does not indicate that it is a particular type of roof stratum.

The shape of a remelted lava tube ceiling may be smooth, irregular, or stepped. A smooth curve across the whole width of the tube is typical of an initial roof stratum or a lining. A lumpy or irregular surface is usually the remelted underside of overlying lava. If the ceiling makes inverted steps, the steps are probably the remelted edges of strata that have been exposed (by rockfall) to the hot lava stream. Such edges may be of linings, of the initial roof stratum, or of overlying lava layers.

Concepts

As lava cools, separate strata typically part from one another.

Lava that solidifies against a previously solidified lava surface will make a cast of that surface.

Of two interfacing lava surfaces, one remelted and the other not, the lava stratum having the remelted surface is the older of the two.

When a lava tube initially solidifies, the roof consists of only one layer of lava; the initial roof stratum.

The initial roof stratum may be buried by overflows of lava from the same tube, or by lava from another source, thickening the whole roof over the tube.

Linings of lava deposited against the ceiling of a lava tube also add to the total roof thickness.

The initial roof stratum is the oldest possible stratum of any in the roof. Each successive overlying flow unit is younger, going upward. Each successive ceiling lining is younger, going downward (away from the initial roof stratum).

Only one initial roof stratum can be present, but multiple linings and overlying strata may occur.

If no overlying strata are present, the highest stratum in the roof is the initial roof stratum.

If the under surface of a stratum is a cast, that stratum and all strata above it are overlying lava.

If the whole under surface of a stratum is remelted, all roof strata lying below the remelt are linings.

Gravity can remove lower strata as breakdown, while higher strata remain.

A lining may be deposited against the underside of overlying lava (if the initial roof stratum has fallen away), but overlying lava cannot be deposited directly on top of a lining.

In moderately straight passages, linings tend toward uniformity in thickness at a given tube cross section. Initial roof strata are generally uniform in thickness, although they are not so uniform as are linings. Overlying flow units are often thicker, but have less uniform thickness, than initial roof strata.

Correlation of the relative ages of ceiling linings and overlying lava layers is not generally possible. If a lining lies against the underside of overlying lava, or if the lining is continuous with the overlying flow unit, their relative ages are apparent.

APPLICATION TO COOLED LAVA TUBES

Example 1

Wind Cave is located near Bend, Oregon. Breakdown covers most of the cave floor, so the questions arise: what does the cave roof consist of? and, is it the remnant of a thick initial crust over the tube?

Near the Black Hole entrance to Wind Cave, is a cast of festooned ropy pahoehoe in the cave ceiling (Fig. 6). The cast demonstrates that, at least in the vicinity of this exposure, the cave roof consists entirely of overlying lava. The initial roof stratum and any ceiling linings that may have been present are now missing from the cave roof.

Example 2

Just inside the entrance of CD Twelve Cave, Pisgah, California, is the exposure shown in Fig. 7. The highest part of the ceiling is an unmodified cast surface, so that layer is overlying lava. Below

Figure 6. View looking up at ceiling in Wind Cave, Oregon, showing the negative impression of festooned ropy pahoehoe. The festooned portion is several feet wide.

Figure 7. (left) Two roof strata in CD Twelve Cave, Pisgah, California. The pencil (5¼ in.) is placed near the top of the initial roof stratum, which is 13 in. thick here. Above the pencil is the cast underside of overlying lava. At the bottom of the photograph is the underside of the initial roof stratum, covered with common lava stalactites.

Figure 8. (right) Roof strata exposed in Station Eight Cave, Pisgah, California. A is the initial roof stratum, with remelted underside. B is a lining, with remelted underside. C is the cast underside of overlying lava. Field of view is about 2 ft wide.

the cast surface is a smoothly arched, single-crust layer 13 to 17 in. thick that is remelted on the underside and is continuous with the topmost layer of the wall. Because of its uniform thickness, it is not another overlying flow unit. Since it lies atop the wall of the lava channel, it cannot be a lining. Therefore, the layer is the initial roof stratum and, because of its thickness, it required about three days to solidify.

The overlying lava is about 2½ ft. thick and is a complex stratum composed of small flow lobes and rubble. It apparently was fed by a small overflow 20 ft away. If it had been one stratum, it could have taken a week to solidify but, because it is composed of a number of thinner strata, it should have taken much less.

Example 3

At the main entrance to Spj Cave, Pisgah, California, two roof strata are present. Both strata are thoroughly remelted on the underside, so the lower one is a lining. The lining continues down the walls 1 to 4 ft below the uneven ceiling and ends at a nearly horizontal level, showing that the tube did not empty completely before the lining was emplaced. The lining is 6 to 8 in. thick.

The upper layer in the roof, 2 to 3 ft thick, blends in a smooth curve with the unlined wall. The lack of any step from the wall to the ceiling, and the lack of overlying strata at the entrance exposure, suggest that the upper roof layer is an initial roof stratum. The lower several inches of this layer is continuous crust with an irregular top. The upper portion of the layer is a mass of bulbous lobes, each about 10 in. in diameter. Some of the lobes are visibly connected with the lower phase of the stratum, showing that the lobes and underlying crust are stratigraphically synchronous. The upper part of the probable initial roof stratum, then, consists of lobes that are continuous with a thinner crust below.

This appears to be a smaller scale version of the sort of roof described by Baldwin (type 5, above). Because this initial roof stratum is not one simple

layer of crust, it should have cooled faster than an equivalent thickness of single crust. This initial roof stratum could have solidified in as little as half a day, but did not take more than 8 days.

Example 4

Station Eight Cave at Pisgah, California, has especially good inside and outside exposures of its roof strata. Figure 8 shows the layers of the roof 30 ft from the upstream cave entrance. A few feet from the site of Figure 8, the highest layer (C, Fig. 8) has a cast of ropy pahoehoe on its underside, so it is overlying lava. It is 8 to 12 in. thick. The next layer below (A, Fig. 8) is fairly uniform in thickness (7 to 9 in.) and is remelted on the underside. Outside the cave, it is seen that this layer supports the overlying lava, so it is the initial roof stratum. Below the initial roof stratum is a lining (B, Fig. 8) 6 to 8 in. thick. In the center of the passage, the lining has plates of lava crust embedded in its top. The floating pieces of crust here prevented the lining from conforming to the initial roof stratum, but elsewhere the lining conforms closely to the underside of the lava above.

The exposure shown in Figure 9 lies just downstream from Figure 8. Here, the initial roof stratum and lining B have partially fallen out. A second lining (D, Fig. 9) has been emplaced against the 3 older roof strata.

The set of roof strata can be traced continuously upstream to the cave entrance, where B (there, 10 in. thick) is the only layer present. At the entrance, then, stratum B is the initial roof stratum. A small portion of stratum A is present at the side of the entrance, but it made only a thin spatter levee, and did not roof the channel that far upstream. Thus, in this case, a single stratum (B) is both a lining and an initial roof stratum, depending on where the terms are applied. Stratum C directly overlies both A and B.

The sequence of events that resulted in the present cave roof included these: 1. Stratum A grew inward from the edges and roofed the

channel, taking about 1½ days to solidify. 2. Stratum B, with some thin plates of crust floating on top, lined A and extended upstream beyond the edge of stratum A as a roof crust, taking almost two days to solidify. 3. Stratum C flowed over A and B, thickened the roof, and solidified in 1½ to 2½ days. 4. The tube cooled, strata A and B stoped out, and the breakdown was removed by the lava stream. 5. The tube refilled, causing lining D to cool against strata A, B, and C. 6. The tube drained, cooled, and breakdown fell, giving the present exposures.

Example 5

Golden Dome Cave, Lava Beds National Monument, California, has a good exposure of two roof strata about 175 ft upstream from the entrance. Most of the ceiling surface is remelted, but rockfall has sectioned some portions of it. The upper layer has a cast surface on its underside.
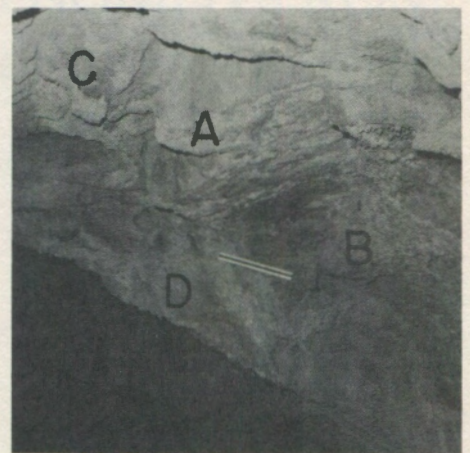
Figure 9. Roof strata exposed a few feet downstream from Figure 8. Strata A, B, and C are the same as in Figure 8. A second lining (D) covered the broken edges of A and B and the cast underside of C. The scale is 12 in. long.

Figure 10. Roof strata exposed in Dynamited Cave, Washington. The passage width is about 15 ft.

Figure 11. Linings fill an eruptive fissure near the King's Bowl in the Great Rift National Landmark, Idaho. The linings are each several inches thick.

Below this is an extremely vesicular layer one to 1½ in. thick. Except for the freshly broken areas, the undersides of both layers are heavily remelted. Remelt also covers pockets where fragments of the lower layer fell out during the active life of the tube. The lower walls are coated with a thin wall lining.

The tube is too wide (more than 10 ft) for the thin lower layer to stand by itself, so that layer cannot be the initial roof stratum. It is not overlying lava, because it is too thin and uniform. The lower stratum is certain to be a lining.

Although a more complex sequence is possible, at a minimum the following events occurred: 1. A roof crust (initial roof stratum) solidified over the lava stream. 2. One or more lava flow units buried the initial roof stratum. 3. The tube cooled, and the initial roof stratum completely fell out in this area. 4. A surge of hot, frothy, lava carried the

breakdown away and filled the tube to the ceiling, emplacing a thin lining against the overlying lava. 5. The tube cooled once more, and pieces of the lining fell out. 6. An additional flow of very hot lava (which only partly filled the tube) caused remelting of the upper walls and ceiling. 7. The lava tube cooled a final time and a small amount of breakdown fell.

The roof strata here indicate that the developmental history of this lava tube is more than ordinarily complex. Whereas one cooling period with its attendant physical stresses is expected, this tube has had at least three.

Example 6

The roof strata exposed in portions of Dynamited Cave, Washington, are vertical rather than horizontal (Fig. 10). Their vertical position does not fit any of the previously described modes of roof formation. Thickness of the layers is very uniform. Flowmarks and remelt are present on the sides of the vertical layers that face the passage center.

The roofing mechanism is apparent once it is understood that the vertical layers are wall linings. The open lava channel repeatedly filled to overflowing, subsided, and filled again. Each time the lava level rose it left linings on the upper walls of the channel. The linings gradually grew in from the sides until they joined at the middle, making a complete roof over the lava channel. The 'initial roof stratum' in this case includes all of the linings as a set.

Eruptive fissures can line shut in the same manner, shown by an exposure near King's Bowl, Idaho (Fig. 11). Here, two eruptions left thin linings in the narrow fissure and closed it. Note that if magma fills a fissure and cools there, it then constitutes the common intrusive feature known as a dike.

CONCLUSIONS

Lava channels can form roofs in at least six ways:
1. Wholesale crusting of the lava stream.
2. Agglutination of lava splash and spatter in arched levees.
3. Jamming and fusion of floating crustal plates.
4. Crusting of whole lava toes.
5. Underriding of cooled lobes by the lava stream.
6. Lining shut of the upper walls of a deep lava channel.

Three general types of strata occur in lava tube roofs: initial roof strata, overlying lava, and linings. The various strata can be identified in cooled lava tubes by their surfaces and geometric interrelationships. The mechanism of roofing (formation of initial roof stratum) can be established for cooled lava tubes if sufficient exposures are present. Indications of the mode of initial roof stratum formation include: single crusts with no internal complexities, lumpy or clotted outer surfaces, plates with sutures at distinct boundaries, lobes connected to a continuous lava layer below, or roof consisting of vertical linings. The presence either of overlying lava or of ceiling linings in a cave roof is evidence that the initial lava tube roof has been modified.

The approximate amount of time needed for an initial roof stratum or overlying lava stratum to solidify can be determined by comparing the stratum thickness with known thicknesses of crust on Hawaiian lava lakes.

Detailed sequences in the formation of lava tube roofs, including the amount of time required for them to solidify, can be determined through examination of roof strata in cooled lava tube caves.

REFERENCES

Anderson, Tempest (1910)—The Volcano of Matavanu in Savaii: *Geol. Soc. London, Quart. Jour.* **66**:621-630.

Baldwin, E.D. (1953)—Notes on the 1880-81 Lava Flow from Mauna Loa: *Volcano Letter #520*: 1-3.

Cruikshank, D.P. and C.A. Wood (1972)—Lunar Rilles and Hawaiian Volcanic Features: Possible Analogues: *The Moon* **3**:412-447.

Greeley, Ronald (1971)—Observations of Actively Forming Lava Tubes and Associated Structures, Hawaii: *Modern Geol.* **2**:207-223.

Jaggar, T.A. (1919)—Activity of Mauna Loa Volcano: *Hawaii Volcano Observatory, Bull.* **7**:136-142.

MacDonald, G.A. and J.P. Eaton (1964)—Hawaiian Volcanoes During 1955: *U.S. Geol. Survey, Bull.* **1171**, 170 pp.

Peck, D.L.; J.G. Moore; and G. Kojima (1966)—Temperatures in the Crust and Melt of Alae Lava Lake, Hawaii, after the August 1963 Eruption of Kilauea Volcano—a Preliminary Report: *U.S. Geol. Survey, Prof. Paper 501D*:1-7.

Peterson, D.W. and D.W. Swanson (1974)—Observed Formation of Lava Tubes During 1970-71 at Kilauea Volcano, Hawaii: *Stud. Speleol.* **2**:209-222.

Wentworth, C.K. and G.A. MacDonald (1953)—Structures and Forms of Basaltic Rocks in Hawaii: *U.S. Geol. Survey, Bull.* **994**, 98 pp.

PRELIMINARY RESULTS ON GROWTH RATE AND PALEOCLIMATE STUDIES OF A STALAGMITE FROM OGLE CAVE, NEW MEXICO: DISCUSSION

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Harmon and Curl (1978) base their entire paper upon two radiometric dates, obtained from the top and from the bottom of a stalagmitic slab from Ogle Cave, New Mexico: $126,000 \pm 26,000$ and $207,000 \, ^{+64,000}_{-40,000}$ years, respectively. The 80,000-year difference is attributed to slow-growth during a pluvial period, which correlates neatly with the well-documented northern-hemisphere penultimate glaciation.

The results are, in fact, subject to severe statistical limitations and, actually, should be read as: "there is a 68% chance that the true top age lies between 100,000 and 152,000 years, and that the bottom age lies between 167,000 and 271,000 years." *Only a 68% chance!* To increase one's precision to the 95% level would mean accepting age ranges of 74,000 to 178,000 for the top and 127,000 to 335,000 for the bottom, at which point the calculation of drip rates and paleoclimatic correlations would become meaningless. (One might also question why, if typical ranges of water hardness and P_{CO_2} are considered in the drip rate calculations, should not the more obvious range in standard deviation errors of the ages be considered?)

It is my feeling that all articles of a "preliminary results" nature should contain sufficient data to present a reasonably precise picture of the true state of things; only the fine detail would be filled in by subsequent analyses. If this cannot be done by the preliminary results, then they should not be published, because they will inevitably be regarded as "gospel truth" by other workers and the non-scientist. Worse still, the "findings" of this type of paper will propagate into future papers as concrete evidence for supporting accepted doctrine or new hypotheses, by people who should know better. Radiometric dating results are particularly prone to over-use and should, at least, be replicated or determined in greater number before being published.

REFERENCE

Harmon, R.S. and R.L. Curl (1978)—Preliminary Results on Growth Rate and Paleoclimate Studies of a Stalagmite from Ogle Cave, New Mexico. *NSS Bulletin* **40**:25-26.

PRELIMINARY RESULTS ON GROWTH RATE AND PALEOCLIMATE STUDIES OF A STALAGMITE FROM OGLE CAVE, NEW MEXICO: REPLY

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We would like to thank Mr. Gascoyne for his comment on our recent paper which presents some $^{230}Th/^{234}U$ chronologic data for a stalagmite from Ogle Cave, New Mexico (Harmon and Curl, 1978). He has raised two important points and we welcome the opportunity to discuss these issues.

In reporting our data we have followed the conventional procedure of other workers in the field by defining the uncertainty limits of both measured isotope ratios and ages calculated from these ratios in terms of $\pm 1\sigma$ confidence level of the counting statistics. For readers who may be unfamiliar with the significance of such uncertainty limits, Mr. Gascoyne correctly points out the large increase in age range resulting from consideration of the $\pm 2\sigma$ confidence limits.

However, the results of the Uranium Series Intercomparison Program (Harmon and Ku, 1976; Harmon, *et al.*, in press) have shown that the commonly reported $\pm 1\sigma$ limits for both $^{234}U/^{238}U$ and $^{230}Th/^{234}U$ isotope ratio measurement very closely approximate the true measurement precision provided there are no problems with spike calibration and tail corrections.

It should also be pointed out that the Ogle Cave stalagmite shows no signs of post-depositional diagenetic alteration or U migration; $^{230}Th/^{232}Th$ ratios are high indicating that the sample was free of detrital Th contamination, and the $^{230}Th/^{234}U$ ratios are in correct stratigraphic order. Because of this we have more confidence in the resulting ages than would be the case for two stratigraphically unrelated samples having the same analytical

uncertainties.

The mean of the two reported ages is 167 x 10^3 years, with a standard deviation of about $\pm$ 30 x 10^3 years. The two measurements do, of course, constitute a replicate, permitting variance reduction, and the result supports the hypothesis that this stalagmite fragment grew primarily during the penultimate glaciation.

The estimated time span of growth, involving a difference of error-subject age determinations, is relatively less accurate. However, using a "classical" statistical interpretation is a poor choice for two reasons: ages must be positive and the age of the basal layer of the stalagmite (a_2) must be greater than that of the top layers (a_1). Both of these facts have been taken into consideration in a statistical analysis that goes, briefly, as follows:

Measured and real ages were presumed log-normally distributed (negative ages therefore impossible) and a Bayesian estimation of the expected real ages was performed using the noninformative but constrained joint prior p (ln a_1, ln a_2)$\propto K$ for $a_2 > a_1 > 0$, and zero otherwise. The resulting expectation and confidence interval estimators for the period of growth, using the data reported in Table 1 of Harmon and Curl (1978), are

Expected period of growth	88,000 years
70% confidence level	36,700 to 141,000 years
90% confidence level	17,200 to 175,000 years

These confidence intervals are admittedly too broad for us to indulge in overly strong claims for precise temporal matching of the growth of this piece of a stalagmite with the penultimate glaciation, but it was not improper to use the expected growth period in estimating drip rates. The estimated variance of possible water hardness gave a six-fold variability in estimated drip rate, which is of the same order of magnitude as the growth-period confidence intervals; the variance in the latter therefore contributes relatively little to the overall variance. That is, considering either alone would give the drip rate range quoted; including them both would expand that range to about 350 to 4000 seconds between drops.

Of more concern to us is the philosophical question raised by Mr. Gascoyne concerning the publication of "preliminary" results. His statement arguing that "preliminary" results should contain sufficient data to present a reasonably precise picture with the fine details to be filled in by subsequent publication is short-sighted in its reasoning. If a work is sufficiently complete to present a precise account of a problem or project, then there is likely to be insufficient need for a subsequent publication. This is especially true as regards geochronologic work of the kind under discussion here. Such work is often undertaken to provide base-line data for a larger, more comprehensive project, *e.g.* a paleoclimate or geomorphological study. But yet the geochronologic data from a few carefully selected samples can themselves be valuable and worthy of publication in the short term.

It is our feeling that papers which present "preliminary" results can be an important vehicle in the transfer of information in cases where there may be a lengthy delay between the time the first analytical data are obtained and the final project report is published. However, in such cases it is the responsibility of the author of "preliminary" reports to ensure the quality of the data, to call attention to the "preliminary" nature of such data, and to refrain from placing elaborate interpretations in such data. Past that point responsibility for the use or abuse of "preliminary" data lies with the subsequent user.

REFERENCES

Harmon, R.S. and R.L. Curl (1978)—Preliminary Results on Growth Rate and Paleoclimate Studies of a Stalagmite from Ogle Cave, New Mexico: *NSS Bulletin*, 40:25-26.

Harmon, R.S. and T.-L. Ku (1976)—The Absolute Limits of the ^{230}TH/^{234}U Dating Method: Preliminary Results from the Geochronological Interlaboratory Comparison Project (*abs.*): *Geol. Soc. America Abs. for* 1976: 903-904.

Harmon, R.S., T.-L. Ku, and R.K. Matthews (1978)—The Limits of U-series Analysis: Phase I Results of the Uranium-series Intercomparison Project: *Geology*, in press.