delayed pathologic changes observed in the kidneys of mice of certain strains infected at birth with LCM virus (5). These observations suggest that glomeruli may be a promising source of antibodies in other chronic infectious diseases eliciting low antibody responses.

MICHAEL B. A. OLDSTONE
FRANK J. DIXON
Department of Experimental Pathology, Scripps Clinic and Research Foundation, La Jolla, California 92037

References and Notes

1. E. Traub, *Science* **81**, 298 (1935); *J. Exp. Med.* **63**, 847 (1936); *ibid.* **65**, 183 (1936); *ibid.* **68**, 229 (1938).
2. F. M. Burnet and F. Fenner, *The Production of Antibodies* (Macmillan, New York, ed. 2, 1949).
3. J. Hotchins, *Cold Spring Harbor Symp. Quant. Biol.* **27**, 479 (1962); M. Volkert, J. Larsen, *Progr. Med. Virol.* **7**, 160 (1965); C. A. Mims, *J. Pathol. Bacteriol.* **91**, 395 (1966).
4. Mouse brain passage strain was supplied by Dr. W. Rowe, National Institute of Allergy and Infectious Diseases, Bethesda, Maryland.
5. M. B. A. Oldstone and F. J. Dixon, in preparation.
6. H. Casey, "Standard Diagnostic Complement Fixation Method and Adaption to Microtests," *Public Health Monograph No. 74* (U.S. Dept. of Health, Education, and Welfare, Washington, D.C., 1965).
7. J. Marshall, W. Eveland, C. Smith, *Proc. Biol. Med.* **98**, 898 (1958); L. Felton and C. McMillian, *Anal. Biochem.* **2**, 178 (1961); B. Wood, S. Thompson, J. Goldstein, *J. Immunol.* **95**, 25 (1965).
8. E. Wasserman and L. Levine, *J. Immunol.* **87**, 290 (1961).
9. F. J. Dixon, T. S. Edgington, P. H. Lambert, *Fifth Int. Immunopathol. Symp.*, Punta Ala, Italy, 1967, in press.
10. F. J. Dixon, J. Feldman, J. Vazquez, *J. Exp. Med.* **113**, 899 (1961).
11. E. Lennette and N. Schmidt, *Diagnostic Procedure for Viral Rickettsial Diseases* (American Public Health Association, New York, ed. 3, 1964), pp. 731–732.
12. This is publication No. 243 from the Department of Experimental Pathology, Scripps Clinic and Research Foundation, La Jolla, California 92037, and was supported by USPHS grant AI 07007 and an AEC contract AT(04-3)-410. Dr. Oldstone was supported by USPHS training grant 5T1 GM 683.

5 September 1967; revised 6 October 1967

Habitat Selection by Chemically Differentiated Races of Lichens

Abstract. *The maritime European lichens of the aggregate species* Ramalina siliquosa *represent six chemical races. Where the races are sympatric they populate different habitats. Such intensive local ecological sorting of morphologically similar individuals accumulating different, highly specialized metabolic end products appears to be unknown in other plants.*

Some morphologically uniform lichens exhibit chemically different races that show distinct geographical distributions (*1*). Our study establishes that where the ranges of these races overlap, the races may select different ecological habitats. This differentiation into chemical races seems to be controlled genetically. Although a few instances of genetically controlled, quantitative differences with regard to physiological processes (especially photosynthesis and respiration) in ecotypes of flowering plants are known (*2*), no comparable examples in plants of habitat selection by qualitatively different races characterized by highly complex metabolic end products have been reported.

The unusual extracellular compounds that accumulate on lichen hyphae show taxonomic correlations of great magnitude. Generally, every individual of a morphological race produces the same substance or substances, but some morphologically uniform lichens exist in multiple chemical types that are interpreted as species by some authors and as "chemical strains" by others (*3*). The exact number of lichens showing chemical races is unknown, but a recent count (*1*) in 17 selected genera showed that 99 morphologic types exist together as 240 chemical variants. The biological interpretation of this variation has been impeded because few field observations on the behavior of chemical races have been made (the races usually do not occur together) and because laboratory experiments have been impractical (intact lichens are notoriously difficult to culture) (*4*). However, it has recently been shown (*5, 6*) that *Ramalina siliquosa* (Huds.) A. L. Sm.—in the broad taxonomic sense one of the most common maritime lichens of western Europe—is made up of six chemical races. The aggregate species ranges from Portugal to arctic Norway and eastward through the Baltic to the Soviet Union, and the component chemical races, while having much more restricted distributions, are all sympatric in western Britain. We have now found that where the races occur together they select different habitats.

In western Europe all organisms inhabiting rocky shores are strikingly zoned (*7*). The fruticose *R. siliquosa* lichens form a conspicuous band just above a strip dominated by *Verrucaria maura*. The latter species is a black crustose lichen which brilliantly marks the top of the littoral zone, an ecological belt which, at least in sheltered localities, corresponds to the upper limit of the highest tides. Since the *R. siliquosa* zone in Britain consists of chemically different individuals, we tried to determine whether the distribution of the chemical types within it was correlated with any obvious environmental variables.

A small promontory with a well developed *Ramalina* vegetation was selected for study in Tre-Arddur Bay on Holy Island, North Wales. The headland presents cliff faces approaching three cardinal directions (south, west, and north), giving a total exposure of 225° (Fig. 1). The rock is quartz-chlorite-muscovite-schist of the Mona Complex (Precambrian). The ramalinas were sampled with six vertical line-transects, composed of strips of contiguous 1-foot-square (35 by 35 cm) blocks, passing through the entire *Ramalina* zone at each place sampled. The zone on the west face (Fig. 1, transect 5) is 25 feet (7.6 m) wide, the broadest of all, and some additional blocks at the bottom of it were therefore sampled to give a good representation of the plants occurring lowest down on the cliff. In every block the ten plants closest to the center were taken. The 980 individuals collected were assigned (by thin-layer chromatographic analysis) to the six known chemical types: five producing closely related depsidones elaborated in the medulla and one with no medullary lichen substances (*8*).

Even though the promontory is small (the northeast and south faces are only 45 m apart), the range of habitats presented by the faces bearing the ramalinas grossly exceeds the amplitude of tolerance of any of the component chemical races of the plants. Ninety-six percent of the plants produced either stictic acid (43 percent), hypoprotocetraric acid (30 percent), or norstictic acid (23 percent) (*9*), all with highly patterned distributions (Fig. 2). Plants that produce stictic acid were most abundant at the bottom of the west and south faces where they made up all of the ten-plant samples in most blocks (Fig. 2, right). The bottom of these transects, just above the *Verrucaria* zone and facing the sea, repre-

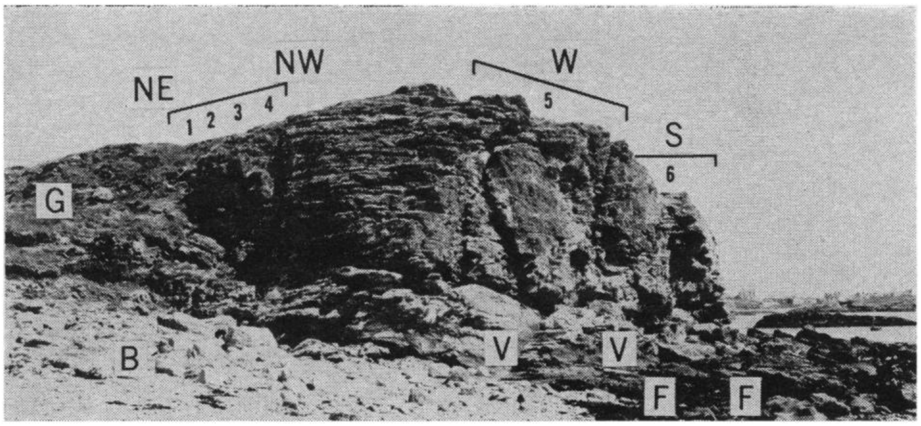


Fig. 1. The promontory in North Wales studied for the behavior of the chemical races of the *Ramalina siliquosa* lichens. All of the cliff faces support a *Ramalina* vegetation. To the south and west, the *Ramalina* zone faces the sea and is directly above a *Verrucaria maura* zone (*V*), which in turn is above the algae of the *Fucus-Ascophyllum* zone (*F*), here seen exposed at low tide. Toward progressively more sheltered conditions around the headland, the *Ramalina* zone on the northwest side faces a rocky beach (*B*); on the northeast, the most protected place of all, it faces a grassy slope (*G*). The location of the six line-transects, indicated by numbers, is approximate, and the distance between transects 1 and 2, 2 and 3, and 3 and 4 (actually 2.5, 3.4, and 4.1 m, respectively) is distorted by perspective.

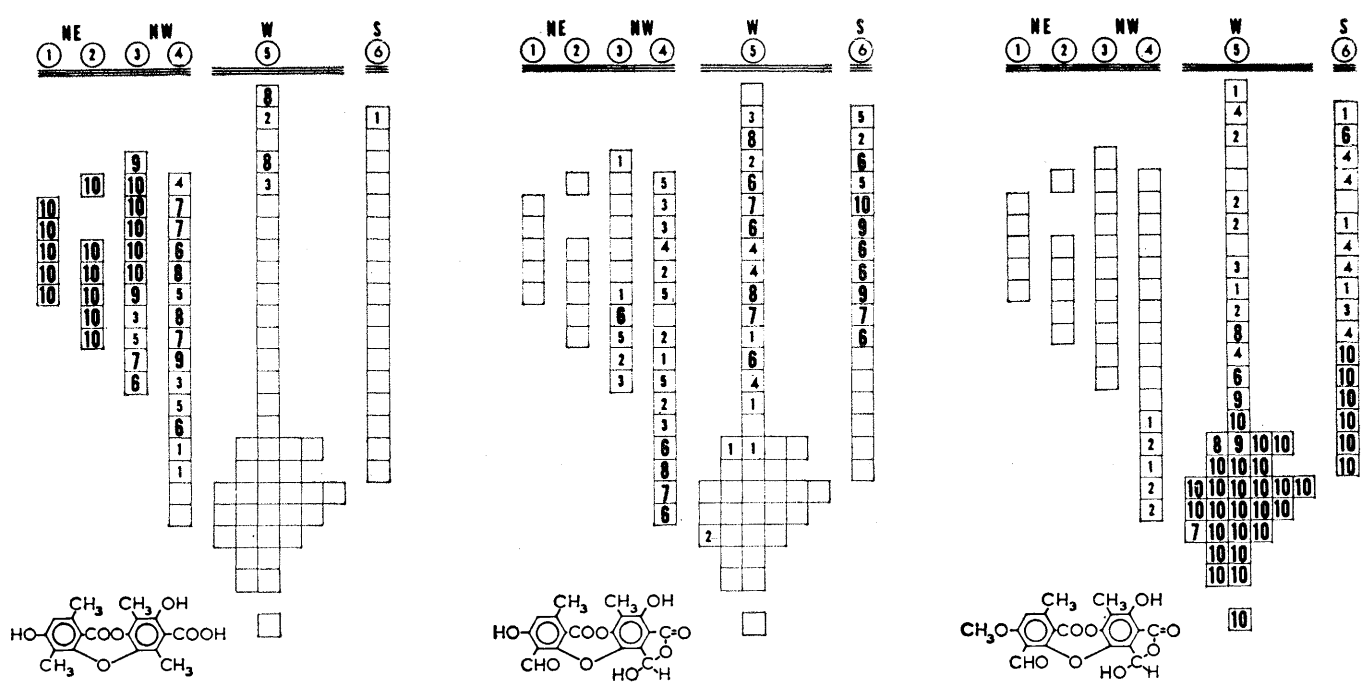
sents the part of the *Ramalina* zone subject to the harshest environmental conditions.

Plants that produce hypoprotocetraric acid, the ecological antithesis of those that produce stictic acid, totally dominate the most sheltered habitat (Fig. 2, left), the northeast exposure facing the land and fronted by a grassy slope. Westward, around the cliff toward progressively harsher conditions, the zone of hypoprotocetraric acid-producing plants moves up until only a few plants of this type are found at the very top of the cliff facing the sea.

Between the conditions of extreme exposure and extreme shelter, an intermediate zone is populated primarily by plants producing norstictic acid (Fig. 2, center). Although they do not seem to form the extensive pure stands that the other two types do, their total nonrepresentation in the two extreme habitats seems to indicate a sensitive adaptation to the intermediate conditions.

The chemical type with no lichen substances (3 percent) seems to reach its maximum abundance at the center of the zone occupied by the norstictic acid-producing plants. Although only nine plants were found that produce salazinic acid and two that produce protocetraric acid, these chemical types may be more abundant at other localities nearby (*6*). The local omission of individual biotic zones is a well-documented phenomenon in the ecology of these shores (*7*).

One explanation for the chemical variation reported here would be to interpret environment as determining medullary chemistry. However, the sharp zonation of the most abundant chemical races (Fig. 2) and the fact



hypoprotocetraric acid   norstictic acid   stictic acid

Fig. 2. A graphic summary of the results, showing the distribution of the three most common chemical races: the hypoprotocetraric acid type (left), the norstictic acid type (center), and the stictic acid type (right). The numbers 1 to 6 in circles refer to the six vertical transects, the position of which on the cliff is indicated by corresponding numbers in Fig. 1. The 1-foot-square (35 by 35 cm) blocks of the transects are shown in their topographic position with respect to each other from transect to transect. Ten plants were taken from each of the 98 blocks, the numbers indicating how many plants per block were of each type. Some corresponding blocks have values totaling less than ten because data for 42 individuals of three additional but rare chemical types are not given here. Where blocks are missing altogether, there were no *Ramalina* lichens.

that where the races occur together the chemical types retain their identity are best explained by an environmental sorting by habitat of physiological races determined by genetic factors. The sample blocks were very small and the chemically different plants in blocks made up of mixtures (about half of the 98 blocks) were necessarily capable of growing within a few centimeters of each other. Two types of plants were found in 24 percent of the blocks, three types in 22 percent, and four types in 4 percent. The accumulating phenolic substances in these lichens seem to be a phenotypic expression of the genetically determined physiological races that is equivalent to morphologic traits in other organisms—for example, the highly zoned species of plants (other lichens and benthic algae) and animals (barnacles, limpets, and mussels) in the littoral communities below the *Ramalina* belt. Seen in this light, the selection of habitat by these morphologically similar but chemically different races of lichens results from the same phenomenon that produces zonation in species of strikingly different morphology, namely, the physiological differences that underlie and delimit the amplitude of ecologic tolerance (*10*). Although we might expect that genetically defined physiological races revealed phenotypically by complex chemical constituents (rather than by morphological traits) and associated with distinct habitats would be a common product of evolution in plants, no examples other than the one described here seem to be known.

WILLIAM LOUIS CULBERSON
CHICITA F. CULBERSON
Department of Botany,
Duke University,
Durham, North Carolina 27706

References and Notes

1. M. E. Hale, Jr., *The Biology of Lichens* (Edward Arnold, London, 1967), pp. 138-144.
2. O. Björkman, *Brittonia* **18**, 214 (1966).
3. W. L. Culberson, in *McGraw-Hill Yearbook of Science and Technology* (McGraw-Hill, New York, 1964), pp. 262–263.
4. W. L. Culberson, *Science* **139**, 40 (1963).
5. C. F. Culberson, *Phytochemistry* **4**, 951 (1965).
6. W. L. Culberson, *Brittonia* **19**, 333 (1967).
7. J. R. Lewis, *The Ecology of Rocky Shores* (English University Press, Ltd., London, 1964), pp. 192–236.
8. Part of each sample was extracted with acetone at 50°C. Chromatograms were run to 10 cm on Merck precoated, analytical-layer SiO_2-F_{254} plates in a solvent system of benzene, dioxane, and acetic acid (95 : 25 : 4, by volume); they were viewed in shortwave ultraviolet light, sprayed with 10 percent H_2SO_4, and heated in an oven at 100°C. The following substances were identified: hypoprotocetraric acid (dark gray, 0.18); norstictic acid (yellow, 0.30), usually accompanied by an unknown substance (orange, 0.08); stictic acid (orange, 0.22), often with norstictic acid and always with two unknown substances (orange, 0.15; brown, 0.01); protocetraric acid (dark gray, 0.02); and salazinic acid (yellow-brown, 0.09). Samples showing no spots for medullary substances on the chromatogram were retested by treating the residue with a solution of 20 percent K_2CO_3 and 10 percent KOH (1 : 1, by volume). Crystals of the red complex salt of norstictic acid were observed in a few preparations, and these samples were counted as the norstictic acid type. But some samples, which showed no positive crystal test and a second negative chromatogram, were scored as the acid-free type. These samples always gave notably small, sometimes nearly invisible, residues from the acetone extract.
9. Norstictic acid is probably the precursor of stictic acid, to which it would be converted by O-methylation. Although plants with stictic acid often contain some norstictic acid, there is a definite upper level to the concentration of norstictic acid with respect to stictic acid, and norstictic acid is invariably the minor constituent in plants also producing stictic acid. Plants producing norstictic acid without stictic acid are considered distinct. They also contain an unknown substance, not found in the stictic acid plants, that probably results when the mechanism for the conversion of norstictic acid to stictic acid is blocked.
10. At least some chemical races of morphologically uniform lichens show no differences in habitat ecology. In the only other case studied [M. E. Hale, Jr., *Brittonia* **15**, 126 (1963)], differences in the local distribution of chemical races of *Cetraria ciliaris* were not associated with any apparent environmental factors, and the differences in the overall geographic ranges of the races appeared to be the consequence of macroclimatic and historical factors.
11. Supported by NSF grants GB-1239 and GB-4494, NIH grant GM-08345, and Duke University Research Council. We thank Professor G. F. Asprey for laboratory facilities at University College, Cardiff; Professor J. G. C. Anderson of that institution for the identification of the substrate rock; and Professor W. D. Billings for criticism of the manuscript.

18 September 1967

Gekkonid Lizards Adapt Fat Storage to Desert Environments

Abstract. Coleonyx v. variegatus *is adapted to feed voraciously after deprivation of food and to withstand long periods without food. In 4 days specimens converted enough food into reserves to increase their weight by about 50 percent. Total deprivation of food resulted in very gradual loss of weight, which, if maintained, would result in 4 days of feeding being sufficient to sustain the animal for periods of 6 to 9 months.*

Fat tails of many geckos, certain skinks, and other lizards have long been considered to serve as areas for deposition of fat to be drawn upon when food is scarce (*1*). Experimental studies of the adaptable value of these reserves, especially under natural or simulated natural conditions, are lacking. Cogger (*2*) kept alive without food specimens of the Australian geckos *Oedura marmorata, O. monilis,* and *O. lesueurii* at ambient temperatures (Sydney) for between 9 and 12 months; this time was reduced by approximately 75 percent in the absence of water. It has generally been assumed that fat reserves have been evolved for use during hibernation, but I suggest that they are drawn on most extensively by species living in areas where, for seasonal reasons such as drought, food often may be unavailable for long periods during hot weather. Under such conditions the animal has a high metabolic rate, and large reserves may be necessary to ensure its survival. In a study of the *O. marmorata* complex (*3*), I showed that the greatest tail enlargement took place in the northern half of Australia where there is no hibernation but where prolonged shortage of food probably occurs during hot, dry weather.

Ground geckos of the genus *Coleonyx* inhabit North and Central America, ranging from the arid desert regions of the southwestern United States to the jungles of Panama. Klauber (*4*) has shown that *C. v. variegatus* is a desert form inhabiting southwestern Utah, Arizona, extreme southern Nevada, southern California, and northwestern Mexico. Several authors (*4–6*) have noted that these geckos are numerous in spring but rare later in the year; it has been suggested that they descend into holes as the ground dries and the weather becomes hotter (*5*). They hibernate between October and March, and their optimum temperature is between 27° and 29°C (*7*). It is recorded that *C. v. variegatus* eats its shed skin (*8*), a habit that may be an important source of protein under fasting conditions (*9*). In referring to their voracious appetite. Smith (*10*) notes that food (chiefly beetles and spiders) consists of items of all sizes, some so large that they must be forced down by serpentine movements of the jaws.

Colonies of *C. v. variegatus* were maintained in captivity in Scotland and Australia for many months and bred successfully. The vivarium temperature rose to 29° to 30°C during the day (heat supplied for 12 hours daily) and fell to 16° to 18°C at night. The geckos had continuous access to water and were fed mainly on *Tenebrio* larvae.

While the food requirements of active, adult males and nongravid females