

information and assistance during my stay there. Invaluable assistance in the field was given by my wife, Isabelle, and by Dr. Ralph Philbrick of the Santa Barbara Botanic Garden.

LITERATURE CITED

- Critchfield, W. B. 1966. Crossability and relationships of the California big-cone pines. U.S. Forest Service Res. Paper NC-6N.
- Forde, M. 1964. Variation in natural populations of *Pinus radiata* in California. New Zealand J. Bot., 2(4):459-501.
- Haller, J. R. 1962. Variation and hybridization in ponderosa and Jeffrey pines. Univ. Calif. Pub. Bot., 34:123-166.
- Haller, J. R. 1965. The role of 2-needle fascicles in the adaptation and evolution of ponderosa pine. Brittonia, 17:354-382.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. New York. 312 pp.
- Weidman, R. H. 1939. Evidences of racial influence in a 25-year test of ponderosa pine. J. Agr. Res., 59:855-887.

DISCUSSION OF RELICTUAL AND DIVERGENT EVOLUTION

Dr. F. Harlan Lewis: As a basis for discussion, I would like to pose a question which is of particular interest to some of us. What changes have occurred in the island flora since it has been separated from the mainland — other than the fact that the goats have eaten a good deal of it? Dr. Haller has suggested, for example, that some of the characters that differentiate island and mainland populations of Torrey pine represent divergence on the island. This is what we have come to expect; when a population is separated on an island it ought to change. But I question this generalization.

Consider the differences between northern and southern populations of *Pinus muricata* on the mainland. If these populations can differ without one of them being on an island, I see no reason to assume that divergence on an island is the explanation for differences such as those between the Torrey pine populations. The island distribution may be irrelevant to the fact that they are different; perhaps the difference is older than the island. Do we have evidence that there has been divergence of the plants on the islands since they became separated from the mainland?

Dr. J. R. Haller: Divergence had to occur sometime.

Dr. Lewis: Of course, but if the divergence is not associated with the island, there is unlimited time for the occurrence of this divergence. It could be associated with any difference in environment during the Tertiary; and if you need to, you can go back even further. One of the reasons for studying islands, presumably, is to determine what happens to populations on an island that would not happen otherwise. Divergence apparently is not necessarily an island phenomenon.

Dr. Robert F. Thorne: Dr. Carlquist has recently written a book, *Island Life*, which we will all know about shortly, and also has two papers, I believe, in press now. One is on loss of dispersibility among island plants and animals and the other on loss of in-breeding (i.e., obligate cross-pollination from an increase in dioecism). I think he has some very pertinent things to say about divergence of island populations from their mainland relatives.

Dr. Lewis: I was not thinking of the floras of oceanic islands that have considerable age. I have no doubt that divergence has occurred in the Hawaiian Islands.

Dr. Thorne: Dr. Carlquist makes reference to a good many things on our own California Islands, such things as the development of woodiness and gigantism on the islands — even something about our island *Lyonothamnus*. You might get the author, who is here, to say something about that. But this development of gigantism, loss of dispersibility, increase in cross-pollination —

Dr. Lewis: I doubt that an argument for the evolution of gigantism on our islands will stand critical examination since there are mainland fossil records of shrubs such as *Rhamnus* and *Prunus* which, in the absence of fossils, might be thought to represent the development of gigantism on the islands. In these instances, gigantism certainly did not develop on the islands; and in other cases in which fossils are lacking, island races may be relictual rather than the products of divergence on the islands.

Dr. Sherwin Carlquist: We think that divergence has taken place in plants on the California Islands; it has probably taken place in rapidly evolving herbaceous groups. I have looked for it particularly in composites. I think the island tarweeds are examples where some divergence has taken place. Among the best examples that one expects to find are those on Guadalupe, which is generally conceded to be oceanic; the tarweeds are there, also *Senecio palmeri* and *Perityle incana*. We do not know for sure that they never occurred on the mainland, but the parallelisms (and they are quite numerous) suggest that these plants may have done at least some of their evolving on Guadalupe.

Dr. Peter H. Raven: The amount of endemism on most of the islands, which is relatively low as I have pointed out, now suggests that there has been enough divergence to produce things to which we give normal taxonomic recognition by virtue of their having been on the islands. In other words, per island, the number of endemics is about the same as comparable areas on the mainland. But with respect to San Clemente, and particularly with respect to Guadalupe, one suspects that the much higher levels of endemism might reflect divergence. This is particularly true, for instance, for the 32 peculiar endemics out of 160 species on Guadalupe Island. Also the lack of any evidence of connection to the mainland seems to make it rather likely that at least some of those endemics are not relicts, but did develop on Guadalupe Island. Possibly the same is true on San Clemente Island, but for the others I would say, in general, there is no evidence for divergence on the islands.

Dr. Thomas R. Howell: There are a number of endemic subspecies, and in some cases species, of birds that occupy or have

occupied these islands. If the Santa Cruz Island jay, which is a much larger and deeper blue form than the scrub jay that occupies the mainland, is a relict, it is hard to see where it is relict from. The "continental" form is found right up to the coast. The insular subspecies are found only on Santa Cruz and not on Santa Rosa or on any of the other islands where there are suitable habitats for these jays. So in this case, it seems hard to explain in any other way but that the bird has simply been isolated on that island and has diverged. If it is a relict, you would expect it at least on some of the other islands where there are suitable habitats today, or presumably were in the past; or you would expect it to occupy some adjacent area on the mainland. I think the same could be said in a number of other examples.

Dr. Raven: I would like to comment on the example of the Santa Cruz Island jay. It does not really seem convincing to me as an example of divergence on the island. Without a fossil record, one would conclude on the same bases that *Lyonothamnus* had originated *in situ* on the islands; yet it is known from all over the western United States in the Tertiary fossil record. Similarly *Salvia brandegei* was thought until recently to be an endemic of Santa Rosa Island, and one would surely have thought that it originated there; but recently a shrub was found along the roadside at Santo Tomas in Baja California. On the other hand, I do not think that, just because we have got these things on the mainland, it necessarily tells us where they have diverged.