

PHENETIC RELATIONSHIPS AMONG POPULATIONS OF  
*PODARCIS SICULA* AND *P. MELISELLENSIS*  
(SAURIA: LACERTIDAE) FROM ISLANDS IN  
THE ADRIATIC SEA

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*Abstract*

Clover, R. C. (Department of Biology, California State University, Long Beach, California 90840) 1979. Phenetic relationships among populations of *Podarcis sicula* and *P. melisellensis* (Sauria: Lacertidae) from islands in the Adriatic Sea. *Syst. Zool.* 28:284-298.—Thirty-one island populations of *Podarcis sicula* and *P. melisellensis* from Yugoslavia were examined to determine phenetic similarities based on means of 15 characters. Both cluster analysis and multidimensional scaling (MDS) revealed the following patterns of variation: 1) the two species formed distinct groups; 2) within each species, OTUs from northern and southern islands grouped separately; 3) within *P. melisellensis*, OTUs from small islands tended to resemble other small island OTUs from geographically close islands. These patterns appear to contradict similarities implied by previous subspecific designations based largely on color and pattern differences. Genetic drift, gene flow, and selection are evaluated as explanations for observed phenetic patterns. Drift appears to be highly unlikely as a major force determining regional, large island, and small island similarities among OTUs. Channel depths and estimates of the rate of net increase in sea level suggest that the northern islands are younger than the southern islands, supporting the idea that gene flow has been restricted among the southern islands and between the two regions for a longer time than among the northern islands. Combined with differences in selection regimes, the recency of gene flow appears to have been important in determining north-south phenetic similarities. Populations on small islands are exposed to qualitatively different selection regimes than those on large islands. The closer similarity of northern, small island OTUs to large island OTUs suggests that the northern OTUs have not responded to small island selection regimes to the same extent that southern island OTUs have. [Phenetics; *Podarcis sicula*; *P. melisellensis*; Yugoslavia; Adriatic Sea, island populations.]

The taxonomic and ecological diversity of the lacertid lizards of the Mediterranean region make them favorable subjects for a variety of evolutionary studies. A number of studies have been reported, but the majority have concentrated on the taxonomy of geographic isolates. Of the 13 species of *Podarcis* (formerly in the genus *Lacerta*; Arnold, 1973) occurring in the region, more than 172 subspecies have been described, most of these being populations restricted to single islands (Mertens and Wermuth, 1960; Brelih, 1961; Lanza et al., 1971; Lanza and Capolongo, 1972). The extensive works on subspecific nomenclature have emphasized differences among populations showing geographic variation, but unfortunately may also have obscured patterns of similarity for which general explanations may exist (Wilson and Brown,

1953). Population biologists are especially interested in attempting to discover the underlying cause and effect networks responsible for widespread patterns of similarity since such patterns should be the result of the dynamic interactions of widespread ecological and evolutionary forces (Ehrlich and Holm, 1962).

The nature and extent of phenetic variation among local populations can generally be attributed to gene flow, genetic drift, and natural selection, yet it is difficult to distinguish the relative importance of these forces in determining patterns of geographic variation in natural populations (Gould and Johnston, 1972). This may be possible by examination of phenetic relationships among insular populations of lizards, however, since rates of gene flow are extremely low, environmental heterogeneity varies as a

function of island area, and numerous islands represent "replications" of populations subjected to similar environments. The purpose of this study is to describe phenetic relationships among insular populations of two polytypic species of *Podarcis* in order to identify patterns of similarity. Additionally, an attempt is made to estimate the relative importance of gene flow, genetic drift, and selection in determining these patterns.

#### MATERIALS AND METHODS

##### *Species Studied*

Two species of lacertid lizards which are widely distributed along the coast and the more than 1,200 islets, crags, emergent reefs, and islands of Yugoslavia were used in this study. The distributions of these species, *Podarcis sicula* and *P. melisellensis*, are of interest because they never seem to naturally cohabit small islands (<10 hectares) and appear to be spatially segregated on large islands and the mainland (Radovanović, 1965; Nevo et al., 1972). The insular distributions of these species are reticulate; in a group of small islands within 200 meters of one another, I found one island to be inhabited only by *P. sicula* and two others only by *P. melisellensis*. *Podarcis sicula* occurs on the northern coast of mainland Yugoslavia from the Istrian Peninsula to the mid-coast city of Split, and on the southern portion of the Balkan Peninsula, leaving a "sicula-free" zone between Split and Dubrovnik (Radovanović, 1959). This suggests the occurrence of two separate invasions of Yugoslavia from Italy, the apparent center of this species' range. The range of *P. melisellensis* is more restricted, being confined to the Dalmatian Coast of Yugoslavia and offshore islands.

Both species have undergone considerable evolution in size, color and pigmentation patterns. These characters have been emphasized in the description of numerous subspecies. Over the whole range of *P. sicula* 48 subspecies have been described (Mertens and Wermuth,

1960; Brelj, 1961; Lanza et al., 1971; Lanza and Capolongo, 1972); 40 of these occur only on islands. Of 18 described subspecies of *P. melisellensis*, 17 are found only on islands (Mertens and Wermuth, 1960).

##### *Localities and Specimens*

Specimens were collected from 31 locations (29 islands) in the central Yugoslav coastal region (Table 1). Seven of these locations are occupied by *P. sicula* and the remainder by *P. melisellensis*. Samples of both species were obtained from the single large island of Ciovo, and two samples of *P. melisellensis* came from separate locations on Lastovo (Fig. 1). The samples come from two geographically distinct areas in the central coast which are separated by a relatively large stretch of uninterrupted sea opposite the Vinisce peninsula (43°30'N, 16°00'E; Fig. 1). The northern islands belong for the most part to the Kornati archipelago, named after the largest island in this dense group of 147 islands (Filipi, 1972). Several nearby islands from which lizards were collected are not considered part of this archipelago, but are instead part of an adjacent archipelago, or are closely associated with the mainland. The islands in the southern region are not as densely packed in geographic space; however, several archipelagos exist (Fig. 1): the Lastovo archipelago (8, 9, 10, 11), the Vis archipelago (12, 13, 14), and the Svetac archipelago (15, 16, 17, 18). With the exception of Palagruza (1), Susac (3), Jabuka (18), Bisevo (13), and Kamik (17), the islands in both regions are surrounded by water less than 100 meters deep.

All specimens were collected in August 1971 at sites no larger than a square kilometer. Lizards were kept in captivity for periods of up to 3 weeks before being transferred to a -76 C laboratory freezer and stored for electrophoresis (see Gorman et al. [1975] for a discussion of genetic variation and relationships among many of these same individuals and populations). Localities, sample sizes, and

TABLE 1. ISLANDS FROM WHICH SAMPLES WERE OBTAINED FOR THIS STUDY.<sup>1</sup>

| Island         | OTU | Sample Size | Subspecies                 | Island Area (ha) | Island Age | Region |
|----------------|-----|-------------|----------------------------|------------------|------------|--------|
| Palagruza      | 1   | 12          | <i>P. s. pelagosae</i>     | 30               | >17,000    | S      |
| Pod Kopiste    | 2   | 18          | <i>P. s. cazzae</i>        | 5                | 9,740      | S      |
| Susac          | 3   | 26          | <i>P. s. cazzae</i>        | 460              | >17,000    | S      |
| Kopiste        | 4   | 21          | <i>P. s. cazzae</i>        | 100              | 13,920     | S      |
| Ciovo          | 5   | 4           | <i>P. s. campestris</i>    | 2,880            | 1,000      | N      |
| Murter         | 6   | 13          | <i>P. s.</i> (undescribed) | 1,860            | 3,000      | N      |
| Sveta Katarina | 7   | 11          | <i>P. s. campestris</i>    | 5                | 7,210      | N      |
| Lastovo        | 8   | 12          | <i>P. m. lissana</i>       | 5,270            | 15,790     | S      |
| Lastovo        | 9   | 19          | <i>P. m. lissana</i>       | 5,270            | 15,790     | S      |
| Pod Mrcaru     | 10  | 15          | <i>P. m. lissana</i>       | 1.3              | 13,480     | S      |
| Tajan          | 11  | 12          | <i>P. m.</i> (undescribed) | 1.3              | 13,260     | S      |
| Vis            | 12  | 8           | <i>P. m. lissana</i>       | 9,003            | 15,790     | S      |
| Bisevo         | 13  | 14          | <i>P. m. lissana</i>       | 580              | 16,010     | S      |
| Greben         | 14  | 15          | <i>P. m. lissana</i>       | 6                | 9,520      | S      |
| Svetac         | 15  | 17          | <i>P. m.</i> (undescribed) | 460              | 15,350     | S      |
| Brusnik        | 16  | 20          | <i>P. m. melisellensis</i> | 5                | >17,000    | S      |
| Kamik          | 17  | 22          | <i>P. m. galvagnii</i>     | 1                | 15,350     | S      |
| Jabuka         | 18  | 8           | <i>P. m. pomoensis</i>     | 1                | >17,000    | S      |
| Ciovo          | 19  | 10          | <i>P. m. traguriana</i>    | 2,880            | 1,000      | N      |
| Zirje          | 20  | 10          | <i>P. m.</i> (undescribed) | 1,543            | 13,920     | N      |
| Mikavica       | 21  | 12          | <i>P. m. mikavicae</i>     | 0.6              | 11,170     | N      |
| Veli Puh       | 22  | 20          | <i>P. m. thetidis</i>      | 1.3              | 14,470     | N      |
| Vodeni Puh     | 23  | 12          | <i>P. m.</i> (undescribed) | 0.9              | 14,140     | N      |
| Purara         | 24  | 26          | <i>P. m. kornatica</i>     | 1.6              | 15,460     | N      |
| Mrtovenjak     | 25  | 38          | <i>P. m. kornatica</i>     | 9.0              | 14,800     | N      |
| Babina Guzica  | 26  | 26          | <i>P. m. kornatica</i>     | 1.17             | 13,150     | N      |
| Krpeljina      | 27  | 12          | <i>P. m.</i> (undescribed) | 1.26             | 9,190      | N      |
| Cavlin         | 28  | 29          | <i>P. m. kornatica</i>     | 14.1             | 9,960      | N      |
| Vrtlic         | 29  | 14          | <i>P. m. kornatica</i>     | 0.4              | 8,090      | N      |
| Mrvenjak       | 30  | 26          | <i>P. m.</i> (undescribed) | 64               | 9,190      | N      |
| Planac         | 31  | 14          | <i>P. m. var. imitans</i>  | 5                | 6,550      | N      |

<sup>1</sup> Samples sizes are for the males only. No subspecies have been described in several localities. Island areas were obtained from Gvozdenović (1975), Filipi (1972), and by planimeter measurements from nautical charts produced by Hidrografski institut Jugoslavenske ratne mornarice. Estimates of island ages are described in the text.

subspecific designations are given in Table 1.

### Characters

Because the primary purpose of the expedition was to obtain specimens for electrophoresis, only skins and heads were available for morphological studies. Snout-vent lengths and sex were recorded prior to skinning and removal of the heads. Fourteen additional characters were subsequently scored for each individual, including four morphometric and ten meristic characters. Morphometric characters were recorded to the nearest 0.1 mm using calipers or an ocular micrometer in a binocular dissecting scope. These measurements included width of

the occipital cap (HW), internasal width (NW), width of the occipital scale (OW), and head length (HL). The fifth morphometric character used was snout-vent length (SVL). The ten meristic characters (6 on the head, 4 on the skin of body and legs) were counted under a dissecting scope and included the total number for both sides of the following seven bilaterally symmetrical characters: Lower labials (LL), chin shields (CS), upper labials (UL), circumorbitals (CO), plaques on the second and third postnasals (SO2 and SO3, respectively), and femoral pores (F). The remaining three meristic characters consisted of the numbers of gular collar scales (G), transverse belly scute rows (BS), and dorsal scales in a

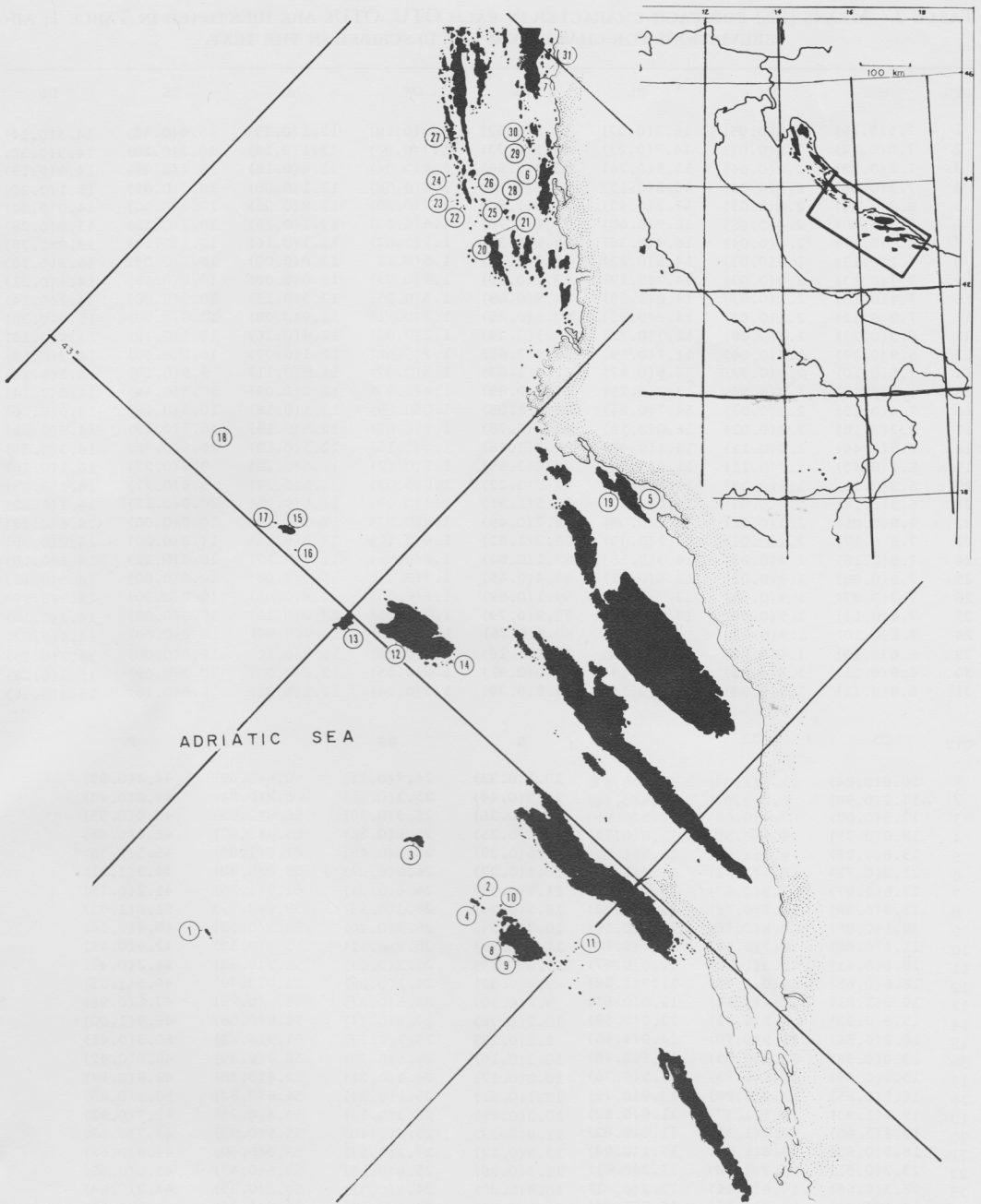


FIG. 1.—Map of central coastal region of Yugoslavia. The numbers near islands (black areas) correspond to the OTUs in Table 1. Insert shows location of the study area.

TABLE 2. MEANS (SE) FOR EACH CHARACTER IN EACH OTU. OTUs ARE IDENTIFIED IN TABLE 1; ABBREVIATIONS FOR CHARACTERS ARE DESCRIBED IN THE TEXT.

| OTU | HW        | NW        | HL         | SVL        | OW        | LL         | CS         | UL         |
|-----|-----------|-----------|------------|------------|-----------|------------|------------|------------|
| 1   | 7.5(0.19) | 2.1(0.05) | 16.2(0.37) | 64.5(1.52) | 2.0(0.10) | 12.1(0.23) | 10.0(0.00) | 14.3(0.14) |
| 2   | 7.0(0.12) | 1.9(0.03) | 14.7(0.23) | 58.1(0.73) | 1.7(0.07) | 12.1(0.19) | 10.3(0.20) | 14.9(0.30) |
| 3   | 7.2(0.13) | 2.0(0.04) | 15.5(0.26) | 63.4(0.96) | 1.8(0.06) | 12.6(0.18) | 10.2(0.09) | 14.9(0.15) |
| 4   | 7.9(0.08) | 2.1(0.02) | 16.5(0.15) | 67.5(0.70) | 1.8(0.08) | 12.1(0.08) | 10.0(0.05) | 15.1(0.20) |
| 5   | 8.0(0.20) | 2.4(0.03) | 17.2(0.43) | 70.4(1.60) | 1.7(0.28) | 12.8(0.25) | 10.0(0.00) | 14.0(0.00) |
| 6   | 8.3(0.30) | 2.4(0.08) | 16.9(0.60) | 71.6(2.70) | 1.6(0.10) | 12.1(0.16) | 10.2(0.12) | 13.9(0.28) |
| 7   | 8.2(0.17) | 2.4(0.04) | 16.4(0.36) | 69.0(1.34) | 1.7(0.07) | 12.1(0.16) | 10.2(0.12) | 13.9(0.28) |
| 8   | 7.1(0.13) | 1.9(0.03) | 14.6(0.22) | 60.3(1.14) | 1.6(0.11) | 12.0(0.00) | 10.1(0.08) | 14.3(0.18) |
| 9   | 7.3(0.13) | 2.0(0.03) | 14.7(0.19) | 63.1(0.99) | 1.5(0.05) | 12.0(0.00) | 10.0(0.00) | 14.4(0.21) |
| 10  | 7.4(0.15) | 2.1(0.03) | 14.8(0.28) | 60.8(0.89) | 1.5(0.05) | 12.3(0.15) | 10.0(0.00) | 14.2(0.14) |
| 11  | 7.9(0.12) | 2.1(0.03) | 14.9(0.20) | 63.5(0.85) | 1.3(0.11) | 11.9(0.08) | 10.0(0.00) | 15.3(0.36) |
| 12  | 6.3(0.32) | 1.7(0.08) | 12.7(0.72) | 53.1(3.29) | 1.2(0.06) | 12.4(0.26) | 10.1(0.13) | 13.9(0.13) |
| 13  | 5.9(0.27) | 1.7(0.08) | 11.7(0.59) | 48.9(2.61) | 1.2(0.08) | 12.1(0.07) | 10.0(0.00) | 14.3(0.13) |
| 14  | 7.5(0.10) | 2.0(0.03) | 14.6(0.17) | 62.3(1.03) | 1.5(0.07) | 11.8(0.11) | 9.9(0.18)  | 14.2(0.11) |
| 15  | 6.9(0.13) | 1.9(0.04) | 13.9(0.25) | 57.8(0.89) | 1.4(0.07) | 12.0(0.09) | 10.3(0.14) | 14.2(0.14) |
| 16  | 7.4(0.15) | 2.0(0.03) | 14.7(0.24) | 61.8(1.08) | 1.0(0.09) | 12.1(0.18) | 10.3(0.16) | 14.8(0.16) |
| 17  | 8.2(0.10) | 2.3(0.02) | 16.0(0.15) | 69.8(0.70) | 1.1(0.09) | 12.5(0.16) | 10.5(0.19) | 14.9(0.21) |
| 18  | 7.5(0.48) | 2.0(0.11) | 15.1(0.80) | 63.5(3.68) | 1.0(0.15) | 12.1(0.13) | 10.6(0.38) | 14.3(0.31) |
| 19  | 6.3(0.40) | 1.7(0.11) | 11.9(0.73) | 49.0(3.89) | 1.1(0.12) | 11.6(0.22) | 9.6(0.27)  | 14.1(0.18) |
| 20  | 5.3(0.31) | 1.4(0.08) | 10.0(0.62) | 41.0(3.22) | 1.0(0.07) | 11.6(0.22) | 9.6(0.27)  | 14.1(0.18) |
| 21  | 6.5(0.18) | 1.8(0.03) | 13.0(0.27) | 56.5(1.51) | 1.3(0.07) | 11.8(0.25) | 10.0(0.12) | 14.7(0.22) |
| 22  | 7.9(0.05) | 2.1(0.01) | 14.6(0.08) | 64.7(0.49) | 1.4(0.07) | 12.3(0.10) | 10.0(0.00) | 14.6(0.22) |
| 23  | 7.8(0.17) | 2.1(0.05) | 15.1(0.30) | 66.3(1.62) | 1.6(0.11) | 11.9(0.15) | 10.0(0.00) | 14.0(0.00) |
| 24  | 7.6(0.10) | 1.9(0.02) | 14.3(0.15) | 62.1(0.84) | 1.4(0.06) | 11.6(0.17) | 10.0(0.12) | 14.2(0.18) |
| 25  | 7.0(0.08) | 1.8(0.02) | 13.4(0.11) | 57.4(0.48) | 1.3(0.04) | 11.9(0.08) | 10.0(0.00) | 14.5(0.11) |
| 26  | 7.3(0.07) | 1.9(0.02) | 13.7(0.11) | 59.1(0.69) | 1.5(0.03) | 11.9(0.05) | 10.0(0.00) | 14.3(0.12) |
| 27  | 7.4(0.11) | 1.9(0.02) | 13.4(0.15) | 59.9(0.79) | 1.4(0.05) | 12.2(0.11) | 10.0(0.00) | 14.3(0.18) |
| 28  | 7.2(0.10) | 1.9(0.02) | 14.1(0.16) | 60.9(0.76) | 1.3(0.07) | 11.9(0.07) | 10.0(0.00) | 14.4(0.12) |
| 29  | 6.6(0.10) | 1.9(0.02) | 13.3(0.15) | 58.5(1.16) | 1.4(0.05) | 11.9(0.10) | 10.0(0.00) | 14.2(0.15) |
| 30  | 6.8(0.11) | 1.8(0.02) | 13.6(0.17) | 59.0(0.91) | 1.0(0.05) | 12.2(0.07) | 10.2(0.09) | 15.2(0.22) |
| 31  | 6.8(0.11) | 1.9(0.03) | 12.9(0.14) | 54.8(0.70) | 1.3(0.04) | 12.1(0.21) | 9.9(0.16)  | 15.0(0.36) |

| OTU | CO         | S02        | S03        | G          | BS         | DS         | FP         |
|-----|------------|------------|------------|------------|------------|------------|------------|
| 1   | 20.8(0.84) | 11.5(1.33) | 11.6(0.53) | 10.7(0.33) | 24.7(0.31) | 66.6(1.49) | 44.4(0.93) |
| 2   | 17.2(0.98) | 5.2(0.59)  | 9.9(0.56)  | 10.5(0.44) | 25.2(0.25) | 66.9(0.81) | 43.8(0.48) |
| 3   | 17.3(0.67) | 7.4(0.66)  | 10.5(0.65) | 10.8(0.36) | 25.3(0.30) | 66.8(2.05) | 45.0(0.55) |
| 4   | 18.0(0.73) | 8.4(0.51)  | 11.0(0.74) | 13.1(0.25) | 25.6(0.24) | 65.4(1.02) | 46.8(0.49) |
| 5   | 19.8(0.95) | 8.5(1.04)  | 11.8(1.93) | 9.5(0.29)  | 24.3(0.48) | 61.5(1.85) | 45.5(1.55) |
| 6   | 21.2(0.71) | 8.1(0.93)  | 11.2(1.19) | 10.5(0.27) | 24.8(0.27) | 63.0(0.82) | 44.3(1.21) |
| 7   | 27.6(2.87) | 7.5(0.67)  | 14.9(0.91) | 11.5(0.45) | 24.6(0.24) | 61.9(1.15) | 41.2(0.75) |
| 8   | 15.9(0.58) | 11.3(0.78) | 11.9(0.72) | 10.5(0.34) | 25.3(0.39) | 59.6(0.97) | 51.0(1.01) |
| 9   | 14.1(0.67) | 12.6(0.76) | 12.8(0.51) | 10.7(0.24) | 25.8(0.26) | 55.5(0.53) | 48.4(0.54) |
| 10  | 11.1(0.88) | 8.7(0.64)  | 10.7(0.55) | 11.4(0.39) | 25.8(0.31) | 55.5(0.59) | 42.9(0.42) |
| 11  | 15.0(0.41) | 12.3(1.36) | 12.0(0.87) | 9.6(0.19)  | 26.3(0.33) | 51.8(0.53) | 44.3(0.48) |
| 12  | 16.6(0.65) | 11.0(1.70) | 11.3(1.28) | 9.4(0.32)  | 24.1(0.23) | 54.0(0.78) | 46.5(1.05) |
| 13  | 19.2(1.21) | 13.4(1.14) | 12.0(0.83) | 9.4(0.20)  | 24.5(0.27) | 55.3(0.79) | 47.6(0.96) |
| 14  | 15.9(0.93) | 9.5(0.72)  | 12.0(0.59) | 10.2(0.26) | 24.2(0.24) | 54.9(0.68) | 48.9(1.00) |
| 15  | 16.2(0.54) | 15.9(0.70) | 14.9(0.96) | 9.1(0.22)  | 25.2(0.27) | 51.9(0.62) | 50.5(0.41) |
| 16  | 13.4(0.34) | 13.7(0.73) | 11.5(0.48) | 10.3(0.16) | 24.5(0.20) | 56.8(0.39) | 48.8(0.42) |
| 17  | 15.1(0.45) | 11.1(0.85) | 11.5(0.76) | 10.0(0.17) | 24.9(0.21) | 52.6(0.38) | 49.8(0.54) |
| 18  | 14.5(0.85) | 13.9(0.99) | 10.9(0.79) | 10.3(0.31) | 25.1(0.23) | 54.8(0.82) | 50.5(0.85) |
| 19  | 19.2(1.90) | 18.1(1.37) | 11.6(0.82) | 10.3(0.29) | 25.3(0.29) | 53.4(0.75) | 41.7(0.92) |
| 20  | 19.2(1.90) | 18.1(1.37) | 11.6(0.82) | 11.0(0.39) | 25.4(0.40) | 53.9(0.92) | 43.7(0.63) |
| 21  | 18.5(0.62) | 16.8(1.02) | 13.1(0.84) | 13.0(0.12) | 27.2(0.17) | 53.8(0.60) | 44.8(0.62) |
| 22  | 23.2(0.91) | 13.3(0.68) | 12.2(0.81) | 11.3(0.30) | 25.6(0.15) | 53.6(0.47) | 43.0(0.49) |
| 23  | 16.3(0.66) | 14.4(1.16) | 12.2(0.81) | 10.9(0.38) | 24.9(0.31) | 50.3(0.39) | 43.2(0.64) |
| 24  | 15.6(0.44) | 13.9(0.96) | 12.5(0.74) | 11.3(0.25) | 26.6(0.22) | 50.7(0.35) | 41.8(0.28) |
| 25  | 15.3(0.33) | 13.7(0.71) | 14.1(0.55) | 12.5(0.28) | 26.4(0.14) | 53.9(0.36) | 41.6(0.31) |
| 26  | 15.3(0.57) | 15.9(0.64) | 11.5(0.52) | 11.2(0.26) | 26.2(0.16) | 52.0(0.42) | 45.6(0.38) |
| 27  | 19.5(0.98) | 14.8(1.53) | 12.2(0.46) | 12.3(0.37) | 25.8(0.35) | 53.1(0.60) | 44.1(0.53) |
| 28  | 17.5(0.41) | 17.9(0.65) | 12.2(0.46) | 11.8(0.14) | 28.1(0.17) | 53.4(0.41) | 44.0(0.31) |
| 29  | 16.4(0.64) | 16.6(0.87) | 12.1(0.83) | 11.6(0.31) | 25.3(0.16) | 47.1(0.46) | 43.2(0.46) |
| 30  | 18.6(0.51) | 13.9(0.83) | 13.7(0.61) | 10.1(0.20) | 25.6(0.18) | 53.8(0.34) | 42.5(0.52) |
| 31  | 25.4(1.24) | 19.7(1.43) | 15.8(1.04) | 11.6(0.29) | 26.0(0.10) | 53.0(0.77) | 43.1(0.62) |

series at midbody (DS). Because sexual dimorphism was apparent in many of these characters, and because males were collected more frequently than females, data only from males were used for the analyses. Color and pattern variations were not considered in this study due to the difficulty of objectively quantifying variations in these characteristics.

#### *Clustering and Ordination Procedures*

Estimation of phenetic relationships by clustering places OTUs in discrete classes while ordination represents OTUs in a multidimensional space where overlap on some axes may occur. Neither approach is necessarily superior for infraspecific levels of analysis (Sneath and Sokal, 1973:367-368; Soulé, 1967), so both approaches have been used here.

Since some of the characters have leptokurtotic distributions, a "nonparametric" multidimensional scaling (MDS) technique of ordination was used which requires no more than ordinal relations in the original similarity matrix (Shepherd, 1962). The chief advantage of MDS over parametric multivariate procedures is that nonlinear metric data, and even ordinal data, are acceptable. The intent of the method is simply to depict the inherent patterns of a similarity matrix in a geometric picture with a minimum number of dimensions while maintaining a close agreement with the initial matrix of similarity data.

Of all the clustering techniques available, those most frequently used in biological applications employ algorithms for sequential, agglomerative, hierarchical, and non-overlapping (SAHN) clustering (Rohlf, 1970). Various criteria for linking OTUs are used in different SAHN methods (e.g., single linkage, complete linkage, etc.); a full discussion of these is found in Sneath and Sokal (1973). A technique developed by Ward (1963) iteratively searches for the two OTUs which, when clustered, results in a minimization in the reduction of the sum of squares of distances between clusters at each cycle,

thus giving rise to sharply defined clusters (Everitt, 1974). This method, like MDS, results in a minimization of an objective function (sum of squares between sets), although dense clusters may be divided into unacceptable partitions (Wishart, 1969). Because the goal of this study was to describe the general patterns of similarity among populations which may not exhibit a hierarchical system of relationships, but rather, a reticulate pattern (Soulé, 1967), Ward's method was chosen because of its tendency to give sharply defined groups.

Due to the large number of populations sampled, and the heterogeneity of sample sizes among the 513 adult male lizards, the means for each of the 15 characters in each of the 31 samples (Table 2) were the population characters used for analyses. Analyses of variance for each character showed that significant geographic variation exists for all characters at the 0.005 level of significance. The means were standardized and a matrix of taxonomic distances ( $D_{ij}$ ) was computed from these standardized values. Clustering and ordination procedures were applied to this matrix of  $D_{ij}$  values.

## RESULTS

### *Phenetic Similarity versus Taxonomic Relationships*

Although the matrix of  $D_{ij}$  values (Table 3) is complex, comparisons between species and among subspecies can be made. The taxonomic distances tend to corroborate taxonomic relationships previously derived from consideration of coloration, size, and scalation at the species level (Radovanović, 1959). Some overlap in  $D_{ij}$  values occurs between species, but the mean  $D_{ij}$  for interspecific comparison is significantly larger than the  $D_{ij}$  within either species, and the smallest  $D_{ij}$  between species is larger than a number of  $D_{ij}$  within each species (Table 4).

Comparisons of  $D_{ij}$  values within and between subspecies reveal both similarities to, and departures from, the relation-

TABLE 3. TAXONOMIC DISTANCES ( $D_{ij}$ ) AMONG 31 OTUs BASED ON 15 CHARACTERS.

| OTU | 1     | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    |
|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1   | 0.000 |       |       |       |       |       |       |       |       |       |
| 2   | 1.003 | 0.000 |       |       |       |       |       |       |       |       |
| 3   | 0.877 | 0.714 | 0.000 |       |       |       |       |       |       |       |
| 4   | 0.968 | 1.089 | 0.889 | 0.000 |       |       |       |       |       |       |
| 5   | 0.969 | 1.499 | 1.105 | 1.453 | 0.000 |       |       |       |       |       |
| 6   | 0.995 | 1.307 | 1.122 | 1.301 | 0.766 | 0.000 |       |       |       |       |
| 7   | 1.113 | 1.684 | 1.606 | 1.527 | 1.266 | 1.055 | 0.000 |       |       |       |
| 8   | 0.985 | 1.083 | 1.098 | 1.218 | 1.379 | 1.419 | 1.674 | 0.000 |       |       |
| 9   | 1.062 | 1.218 | 1.170 | 1.188 | 1.415 | 1.462 | 1.638 | 0.478 | 0.000 |       |
| 10  | 1.674 | 1.489 | 1.517 | 1.642 | 1.708 | 1.680 | 1.987 | 1.367 | 1.204 | 0.000 |
| 11  | 1.340 | 1.308 | 1.343 | 1.344 | 1.619 | 1.599 | 1.817 | 1.170 | 0.868 | 1.322 |
| 12  | 1.523 | 1.387 | 1.459 | 1.935 | 1.638 | 1.783 | 2.017 | 1.039 | 1.182 | 1.353 |
| 13  | 1.586 | 1.467 | 1.622 | 1.974 | 1.932 | 2.053 | 2.116 | 1.060 | 1.196 | 1.589 |
| 14  | 1.036 | 1.232 | 1.325 | 1.355 | 1.349 | 1.452 | 1.581 | 0.581 | 0.649 | 1.322 |
| 15  | 1.519 | 1.634 | 1.669 | 1.873 | 1.745 | 1.781 | 1.886 | 0.883 | 0.864 | 1.682 |
| 16  | 1.316 | 1.186 | 1.268 | 1.389 | 1.534 | 1.455 | 1.861 | 0.788 | 0.785 | 1.098 |
| 17  | 1.520 | 1.486 | 1.356 | 1.475 | 1.319 | 1.121 | 1.798 | 1.274 | 1.230 | 1.450 |
| 18  | 1.512 | 1.385 | 1.461 | 1.612 | 1.600 | 1.361 | 1.917 | 0.965 | 1.044 | 1.299 |
| 19  | 1.609 | 1.468 | 1.660 | 1.956 | 1.984 | 2.026 | 2.064 | 1.236 | 1.181 | 1.255 |
| 20  | 2.234 | 2.175 | 2.386 | 2.524 | 2.767 | 2.864 | 2.707 | 1.842 | 1.837 | 2.033 |
| 21  | 1.628 | 1.650 | 1.734 | 1.553 | 2.202 | 2.086 | 1.958 | 1.299 | 1.076 | 1.515 |
| 22  | 1.029 | 1.444 | 1.426 | 1.396 | 1.308 | 1.315 | 1.369 | 1.009 | 0.774 | 1.280 |
| 23  | 1.071 | 1.464 | 1.303 | 1.280 | 1.326 | 1.309 | 1.077 | 1.206 | 0.979 | 1.480 |
| 24  | 1.378 | 1.511 | 1.638 | 1.525 | 1.849 | 1.761 | 1.687 | 1.167 | 0.842 | 1.248 |
| 25  | 1.469 | 1.484 | 1.532 | 1.473 | 1.941 | 1.876 | 1.739 | 1.220 | 0.915 | 1.233 |
| 26  | 1.232 | 1.331 | 1.368 | 1.370 | 1.680 | 1.659 | 1.787 | 0.813 | 0.558 | 1.196 |
| 27  | 1.194 | 1.291 | 1.262 | 1.278 | 1.607 | 1.549 | 1.702 | 1.051 | 0.969 | 1.236 |
| 28  | 1.538 | 1.638 | 1.622 | 1.532 | 1.996 | 1.895 | 1.922 | 1.268 | 0.976 | 1.415 |
| 29  | 1.443 | 1.557 | 1.644 | 1.661 | 1.869 | 1.866 | 1.833 | 1.113 | 0.902 | 1.325 |
| 30  | 1.480 | 1.327 | 1.383 | 1.592 | 1.813 | 1.786 | 1.817 | 1.240 | 1.042 | 1.351 |
| 31  | 1.679 | 1.912 | 1.849 | 1.849 | 2.110 | 2.125 | 1.794 | 1.597 | 1.407 | 1.918 |
|     | 11    | 12    | 13    | 14    | 15    | 16    | 17    | 18    | 19    | 20    |
| 11  | 0.000 |       |       |       |       |       |       |       |       |       |
| 12  | 1.588 | 0.000 |       |       |       |       |       |       |       |       |
| 13  | 1.543 | 0.609 | 0.000 |       |       |       |       |       |       |       |
| 14  | 1.112 | 1.080 | 1.145 | 0.000 |       |       |       |       |       |       |
| 15  | 1.313 | 1.106 | 1.041 | 1.030 | 0.000 |       |       |       |       |       |
| 16  | 0.998 | 1.109 | 1.204 | 0.853 | 0.989 | 0.000 |       |       |       |       |
| 17  | 1.218 | 1.630 | 1.857 | 1.326 | 1.404 | 0.889 | 0.000 |       |       |       |
| 18  | 1.343 | 1.249 | 1.454 | 1.140 | 1.068 | 0.615 | 0.794 | 0.000 |       |       |
| 19  | 1.455 | 0.787 | 0.730 | 1.243 | 1.268 | 1.273 | 1.927 | 1.505 | 0.000 |       |
| 20  | 2.110 | 1.540 | 1.130 | 1.867 | 1.859 | 1.998 | 2.748 | 2.278 | 1.032 | 0.000 |
| 21  | 1.330 | 1.646 | 1.414 | 1.470 | 1.429 | 1.420 | 1.934 | 1.627 | 1.196 | 1.446 |
| 22  | 1.051 | 1.325 | 1.451 | 0.798 | 1.202 | 1.085 | 1.358 | 1.248 | 1.231 | 1.962 |
| 23  | 1.060 | 1.507 | 1.500 | 1.181 | 1.288 | 1.289 | 1.409 | 1.492 | 1.427 | 2.055 |
| 24  | 1.010 | 1.499 | 1.462 | 1.091 | 1.315 | 1.267 | 1.710 | 1.459 | 1.079 | 1.672 |
| 25  | 1.185 | 1.436 | 1.355 | 1.285 | 1.319 | 1.281 | 1.781 | 1.549 | 0.994 | 1.549 |
| 26  | 0.933 | 1.180 | 1.135 | 0.912 | 1.061 | 0.959 | 1.469 | 1.167 | 0.913 | 1.536 |
| 27  | 1.250 | 1.220 | 1.267 | 1.128 | 1.470 | 1.182 | 1.562 | 1.321 | 1.044 | 1.636 |
| 28  | 1.150 | 1.657 | 1.550 | 1.465 | 1.414 | 1.400 | 1.774 | 1.517 | 1.263 | 1.713 |
| 29  | 1.217 | 1.149 | 1.084 | 1.065 | 1.146 | 1.158 | 1.703 | 1.376 | 0.784 | 1.349 |
| 30  | 0.922 | 1.240 | 1.110 | 1.297 | 1.129 | 1.025 | 1.477 | 1.379 | 1.073 | 1.695 |
| 31  | 1.483 | 1.707 | 1.420 | 1.685 | 1.411 | 1.647 | 2.026 | 1.912 | 1.427 | 1.648 |
|     | 21    | 22    | 23    | 24    | 25    | 26    | 27    | 28    | 29    | 30    |
| 21  | 0.000 |       |       |       |       |       |       |       |       |       |
| 22  | 1.302 | 0.000 |       |       |       |       |       |       |       |       |
| 23  | 1.195 | 0.888 | 0.000 |       |       |       |       |       |       |       |
| 24  | 0.866 | 0.742 | 1.042 | 0.000 |       |       |       |       |       |       |
| 25  | 0.612 | 1.055 | 0.984 | 0.670 | 0.000 |       |       |       |       |       |
| 26  | 0.794 | 0.730 | 1.013 | 0.583 | 0.733 | 0.000 |       |       |       |       |
| 27  | 1.004 | 0.903 | 1.040 | 0.935 | 0.976 | 0.621 | 0.000 |       |       |       |
| 28  | 0.616 | 1.161 | 1.120 | 0.715 | 0.765 | 0.663 | 0.925 | 0.000 |       |       |
| 29  | 0.846 | 0.781 | 1.103 | 0.704 | 0.736 | 0.541 | 0.774 | 0.949 | 0.000 |       |
| 30  | 1.111 | 1.264 | 0.968 | 1.143 | 0.914 | 1.010 | 1.210 | 1.161 | 1.032 | 0.000 |
| 31  | 1.016 | 1.501 | 0.948 | 1.367 | 1.059 | 1.271 | 1.383 | 1.206 | 1.194 | 0.962 |

TABLE 4. MEAN  $D_{ij}$  BETWEEN AND WITHIN *P. sicula* AND *P. melisellensis* (DIAGONAL) WITH RANGES (LOWER NUMBERS). ABOVE DIAGONAL ARE STUDENT'S *t* SCORES FOR COMPARISONS BETWEEN MEAN  $D_{ij}$ . DEGREES OF FREEDOM ARE IN PARENTHESES.

|                         | Between Species     | <i>P. sicula</i>          | <i>P. melisellensis</i>   |
|-------------------------|---------------------|---------------------------|---------------------------|
| Between Species         | 1.607<br>.985–2.864 | <i>t</i> = 11.3*<br>(187) | <i>t</i> = 11.5*<br>(442) |
| <i>P. sicula</i>        |                     | 1.158<br>.714–1.684       | <i>t</i> = .929<br>(295)  |
| <i>P. melisellensis</i> |                     |                           | 1.229<br>.478–2.748       |

\*  $P < .0001$ .

ships implied by subspecific designations of traditional taxonomy. In *P. sicula*, the range of  $D_{ij}$  within *P. s. cazzae* is greater than the range of  $D_{ij}$  between *P. s. cazzae* and the single island endemic subspecies, *P. s. pelagosae*. Within *P. s. campestris*, the range of  $D_{ij}$  is generally larger than the range between this subspecies and the other two subspecies sampled in this study (Table 3). In *P. melisellensis*, the range of  $D_{ij}$  within *P. m. lissana* is greater than the range of  $D_{ij}$  between the three insular endemics *P. m. melisellensis* (16), *P. m. galvagnii* (17), and *P. m. pomoensis* (18). The lizards from Ciovo (19—*P. m. traguriana*) appear to be more closely related to those from Bisevo and Vis (*P. m. lissana*) than are other OTUs from within the latter subspecies (Table 3). However, within *P. m. kornatica*, taxonomic distances are quite low (mean = 0.69) and homogeneous (Table 3).

#### Cluster Analysis

The results of Ward's hierarchical clustering method are shown in Fig. 2. At about the level of 3.0, four main groupings are apparent. Cluster A (Fig. 2) contains all seven *P. sicula* OTUs, while B, C, and D contain only *P. melisellensis* OTUs. Cluster B includes only *P. melisellensis* OTUs from the southern region, and Cluster D contains only *P. melisellensis* OTUs from the northern region, with the single exception of OTU 11. Cluster C contains four OTUs from large islands in both regions. Within each of

these groups some remarkable linkages occur.

Cluster A (*P. sicula*) has two main subclusters, one including OTUs 1–4 from southern islands, the other containing northern island OTUs. OTUs 5 and 6 from large northern islands, grouped closely while OTU 7, also in the northern group, is from a small island.

The southern island *P. melisellensis* (Cluster B) also has two subgroups. One contains OTUs 8, 9, and 15 from relatively large islands, and OTU 14, from an island very near the southern large island, Vis. The second subcluster contains OTUs 16, 17, and 18 from the small islands in the Svetac archipelago and OTU 10 from a small island in the Lastovo archipelago.

Cluster C contains four *P. melisellensis* OTUs from large islands, two of which are located in the southern region (12 and 13) and two (19 and 20) in the northern region.

Three groupings exist within the northern *P. melisellensis* OTUs (Cluster D, Fig. 2). One group contains OTUs from small, geographically close islands near the southern end of the Kornati archipelago (21, 25, 28). None of these islands is considered to be part of the Kornati archipelago, as strictly defined by Yugoslav geographers (Filipi, 1972). The second group in this cluster comes from four small islands in the Kornati islands (22, 24, 26, 27) and a small island nearer the mainland (29). The third group in Cluster D contains four OTUs from widely sep-



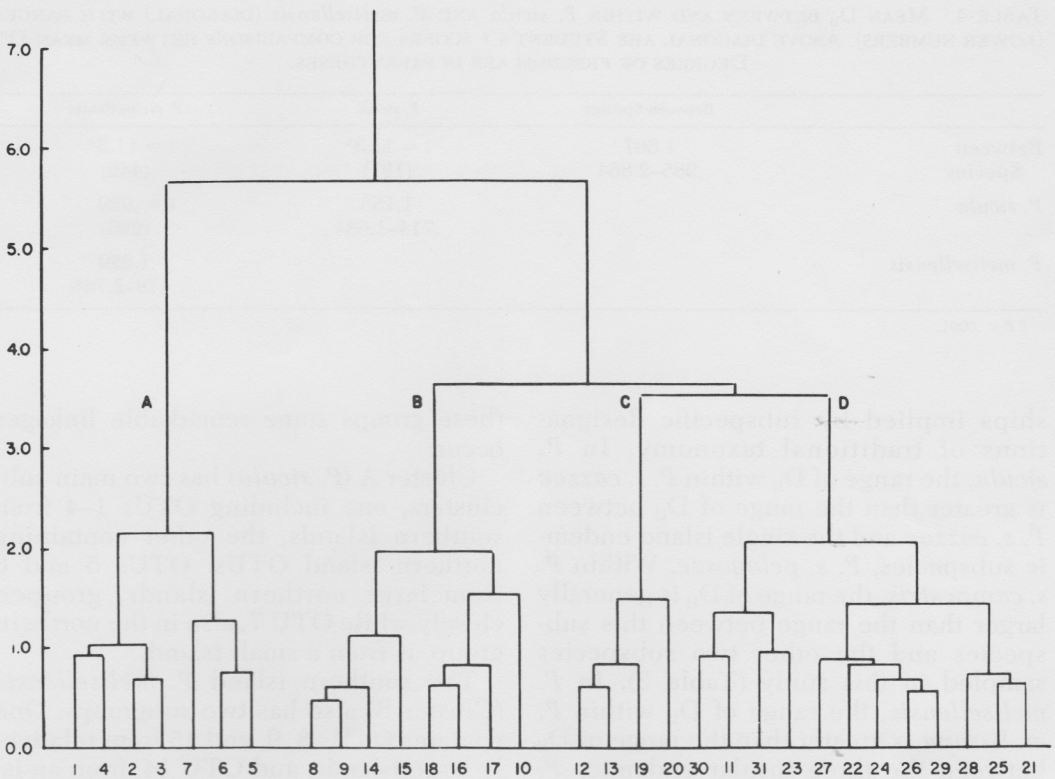


FIG. 2.—Phenogram of 31 samples of *Podarcis* based on Ward's cluster analysis of taxonomic distances derived from 15 character means.

arated geographic areas. OTU 11 from the small southern island of Tajan is linked with OTU 30 from a moderately sized island near the southern tip of the Kornati archipelago. Lizards from Vodeni Puh (23), a small island on the seaward side of the Kornati archipelago, linked with OTU 31 from the small northernmost island in the study area (Fig. 2).

In summary, clustering procedures revealed the following general patterns: the two species clustered separately, and within each species the northern and southern island OTUs formed distinct subgroups. A less obvious but persistent pattern which emerged was that the OTUs from small islands within each region tended to cluster, while large island OTUs formed distinct clusters or subclusters. The same distance matrix was subsequently subjected to UPGMA, com-

plete linkage, and centroid clustering algorithms. Although these gave differing results in sequence and group composition, the same general patterns emerged. Cophenetic correlations between the matrix of taxonomic distances and the phenograms derived from the various clustering schemes were not high, but quite similar, ranging from 0.58 to 0.67. Additionally, a similar distance matrix based on the same characters was computed for the female means. The same general patterns were clearly evident, although three *P. melisellensis* OTUs formed a separate subcluster of the group containing all the *P. sicula* OTUs.

#### Ordination

The ordinations of the OTUs on the first three dimensions are shown in Fig. 3. The coefficient of alienation decreased

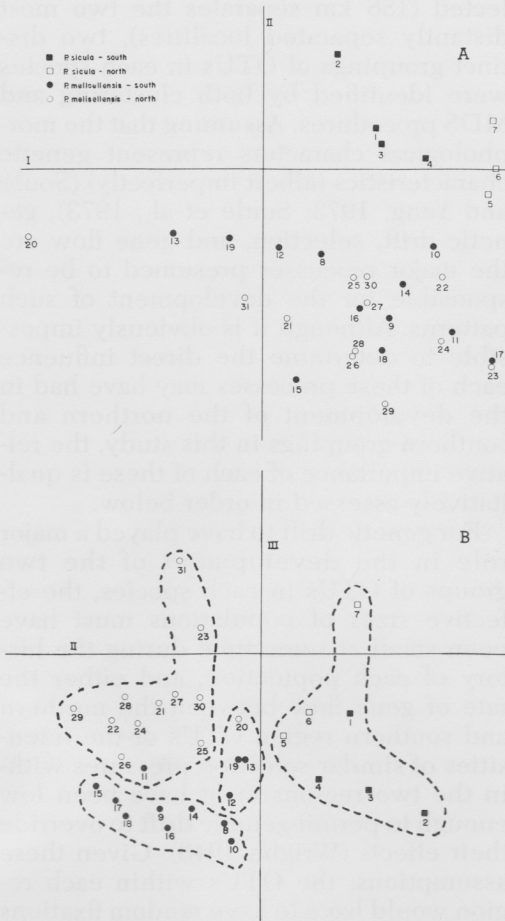


FIG. 3.—Ordination of 31 samples of *Podarcis* by multidimensional scaling. A. Plot of first two coordinate axes. B. Plot of axes II and III, with the results of cluster analysis superimposed on the ordination (dotted line).

abruptly from 0.309 with one dimension to 0.049 with three dimensions; the decrease in this coefficient was negligible after five dimensions had been computed. Thus, the patterns of the relationships inherent in the  $D_{ij}$  matrix were summarized in the first five dimensions of MDS. The first coordinate axis distributed the OTUs roughly according to island size and distance from the mainland (Fig. 3A). The *P. melisellensis* from large islands near the mainland (e.g., OTUs 19 and 20) have low loadings on this axis while *P. sicula* from large islands near the main-

land (e.g., OTUs 5 and 6) have high loadings. This axis also separates species, except for overlap of OTUs of the two species from small islands. The second axis clearly distinguishes the OTUs of the two species, and the third axis separates the OTUs of the northern and southern islands within each species (Fig. 3B). The remaining axes did not reveal any obvious overall patterns of similarity, although many of the discrepancies between specific relationships identified in the clustering procedure and those identified by MDS were resolved at these higher dimensions. For example, the two OTUs from Lastovo (8 and 9) have the smallest taxonomic distance of all pairs and were the first to combine in the clustering, but they were further apart on the first and second axes of MDS than many pairs of OTUs which had larger  $D_{ij}$  values and clustered quite separately from one another (e.g., OTUs 17 and 22). The fourth and fifth axes tend to bring the Lastovo OTUs together and separate OTUs 17 and 22.

The marked similarity of MDS and the clustering procedure are shown in Fig. 3B where the results of the clustering are superimposed on the MDS ordination. The same major groups are clearly defined. Thus, in spite of some minor discrepancies, the results of the MDS ordination procedure were remarkably similar to those of the clustering procedure.

## DISCUSSION

### *Subspecies and Phenetic Similarity*

The relative degree of variation of  $D_{ij}$  values within *P. melisellensis* appears to corroborate the *distinctiveness* of insular isolates of this species implied by the large number of described subspecies. The much smaller variation in  $D_{ij}$  values for *P. sicula* may be simply due to the smaller number of populations sampled, or may reflect less actual differentiation of isolated populations of this species. However, in both species there is little agreement between *relationships* implied by subspecific categories and those

implied by taxonomic distances. A possible exception may be the lizard populations from islands in the Kornati archipelago. Among the five island populations belonging to *P. m. kornatica*,  $D_{ij}$  values are small, although so are those between OTUs belonging to this subspecies and OTU 22 from Veli Puh, described as a separate subspecies (*P. m. thetidis*) by Radovanović (1959).

The lack of agreement between the relationships implied by subspecific nomenclature versus those implied by taxonomic distances, cluster analysis, and MDS, may be attributable to the choice, number, and weighting of different characters. Radovanović (1959) employed some of the same characters considered here (HW, SVL, DS, BS, FP, GS), but, in addition, included observations on coloration and dorsal pattern. Although coloration and dorsal pattern vary considerably between species as well as among populations within each species, considerable variation in color and pattern also occurs within populations (Gorman et al., 1975; personal observation). It is clear that Radovanović (1959) weighted these characters heavily in his qualitative analysis of intraspecific variation of both species, and in some cases described new subspecies on the basis of very small sample sizes not likely to include all color variants that occur in local populations. Hence, small  $D_{ij}$  values between OTUs designated as different subspecies may be due to general, overall genetic-phenetic similarities detected by examination of a number of characters whose variations are in turn determined by a much larger number of genetic loci, despite differences in color and pattern. Likewise, large  $D_{ij}$  values between OTUs within the same subspecies suggests greater overall genetic and phenetic variation despite similarities of color and pattern.

*Northern and Southern Regions:  
Drift, Selection, or Gene Flow?*

Despite the relatively small geographic area from which the samples were col-

lected (188 km separates the two most distantly separated localities), two distinct groupings of OTUs in each species were identified by both clustering and MDS procedures. Assuming that the morphological characters represent genetic characteristics (albeit imperfectly) (Soulé and Yang, 1973; Soulé et al., 1973), genetic drift, selection, and gene flow are the major processes presumed to be responsible for the development of such patterns. Although it is obviously impossible to determine the direct influence each of these processes may have had in the development of the northern and southern groupings in this study, the relative importance of each of these is qualitatively assessed in order below.

For genetic drift to have played a major role in the development of the two groups of OTUs in each species, the effective sizes of populations must have been small at some time during the history of each population, and either the rate of gene flow between the northern and southern region OTUs or the intensities of similar selection pressures within the two regions must have been low enough to permit genetic drift to override their effects (Wright, 1948). Given these assumptions, the OTUs within each region would have to have random fixations of genes with similar phenotypic expressions, and different sets of similar genes would have to be fixed in the two different regions in order to attribute similarities within, and differences between the two regional groups in each species to genetic drift. Even if the probability of random fixation of alleles for a given phenome were quite high (e.g., 0.5), the probability that the same phenome would result in the eleven OTUs of southern *P. melisellensis* is vanishingly small ( $P = 0.5^{11}$ ). However, genetic drift may be responsible for much of the variation that exists among OTUs within each region and within each species (Gorman et al., 1975).

Genetic drift coincident with the colonization of these islands by a very small number of propagules (i.e., "founder ef-

fects," Mayr, 1963) from two different source populations could possibly account for the northern and southern phenetic groupings of these two species. However, except for a few islands in this study area, it is unlikely that many of these insular populations were founded by overwater dispersal of a few propagules. Rapidly accumulating geological data from this area show that the Adriatic Sea is a basin on a continental shelf, divided into northern and southern portions by a shallow transverse ridge which runs from Gargano, Italy (the "spur" on the "boot" of Italy), through Palagruza (1) and the Svetac archipelago to near Split, Yugoslavia (Lort, 1977; Celet, 1977). The present coastlines of these basins are the net result of rapid local subsidence (Celet, 1977; Filipi, 1972) and eustatic increases in sea levels due to melting of Pleistocene glaciers (Fairbridge, 1960; Emery and Garrison, 1967; Milliman and Emery, 1968; Vail et al., 1978). Since most of the islands in the two regions of the study area are surrounded by water less than 100 meters deep, they were probably connected to one another and the mainland during the last glacial lowstand when sea levels were about 130 meters lower than at present (Fairbridge, 1960; Emery and Garrison, 1967; Milliman and Emery, 1968; Vail et al., 1978). The last eustatic rise in sea levels, and the continuing subsidence of the area possibly due to rebound movements of the nearby deglaciated alpine areas (Walcott, 1972) have resulted in a slow strangulation of mountain ranges and peninsulas, isolating the lizard populations inhabiting them. Thus, there is not much evidence to support overwater colonization and founder effects arising from small numbers of propagules from two different source areas as a genetic drift mechanism responsible for the northern and southern groupings observed in the data.

For selection to be considered a major cause of the regionality, general differences between, but similarities within the two regions must be established for

selection regimes. Although differences undoubtedly exist between islands, only a modicum of evidence exists which supports the idea of different *regional* selection regimes. Climatic data, for example, show that average annual rainfall is 789 mm both at Sestrice, in the Kornati archipelago, and at Hvar, roughly near the center of the southern portion of the study area (Gvozdenović, 1975). Likewise, mean January and July temperatures are respectively, 7.1 C and 23.5 C at Sestrice, and 8.4 C and 24.8 C at Hvar. Annual precipitation is higher and the range of temperatures is greater on islands near the mountainous coast than those more distant, but this should affect islands at different locations within regions and not lead to great inter-regional differences (since samples came from both distant and near islands in each region). Likewise, geological formations, through their indirect influence on plant and animal life, may play a substantial role in determining different selection regimes between islands, but with the exception of a few southern islands which have igneous soils and bedrock, nearly all of the islands in both regions have limestone substrates.

Although climatic and geological data appear similar for the two regions, there are some real differences in biotic parameters which may contribute to different regional selection regimes. Plant species diversity and biomass are greater in the southern region than in the northern region of the study area. The islands of the Kornati archipelago (147 islands = 69 km<sup>2</sup>) are inhabited by 150 plant species while the large southern islands of Hvar and Korcula (579 km<sup>2</sup>) are reported to have 460 species of plants (Filipi, 1972). Much of the difference between these figures can be attributed to area-diversity relationships (MacArthur and Wilson, 1967), yet even the small southern islands appear to have a greater biomass and species diversity than small northern islands (Gvozdenović, 1975; pers. obs.). In addition to vegetational differences, several of the southern islands (large and

small) are occupied by *Lacerta oxycephala*, a species which appears to be restricted to the rocky edges of islands where it co-occurs with *P. sicula* or *P. melisellensis*. It is clear that biotic differences exist between the two regions, but extensive fieldwork will be necessary to provide strong inference that these differences represent different selection regimes.

Despite the fact that the OTUs are all separated by expanses of water which are probably large relative to the overwater dispersal abilities of these lizards, gene flow may have played a significant role in the evolution of the northern and southern phenetic groupings. If for any reason gene dispersal were restricted between regions but not within regions, then any neutral or selectively advantageous genetic characteristic acquired by a population in one region would be expected to become widespread in that region by gene flow, and contribute to phenetic differentiation between regions due to a lack of gene flow. The two-step formation of the Adriatic Basin suggests the opportunity for such a series of events. As the last Pleistocene glaciation ended, the southern portion of the basin was already below present day sea levels, so the rising sea level began to cut off land masses from the mainland and from each other by flooding connecting lowlands. Until this time, gene flow among populations on these upland areas was possible, at least in principle. The northern portion of the basin is believed to have subsided below present sea levels only quite recently. In fact, historical records indicate the continuing rate of subsidence of this area to be about one meter per millennium; the present day islands of Kornat, Katina, and Dugi Otok (Kornati archipelago) were a single land mass about 2,000 years ago (Filipi, 1972). The channel separating these islands is now 2.2 meters deep, and partially submerged ruins of Roman architecture reaching across the channel attest to the recency of the subsidence. It seems likely that gene flow among present insular populations in the

northern region was overland until quite recently. The crude estimates of island ages (Table 1) are based on channel depths and the assumption of a linear rate of eustatic increase in sea levels due to glacial melting (110 years/meter) until about 6,000 years ago when present sea levels were attained (Fairbridge, 1960; Emery and Garrison, 1967). Subsequently, subsidence and a slower eustatic rise in sea level were assumed to have occurred at a linear rate of 1,000 years/meter (Redfield, 1967; Filipi, 1972). It is clear even from these crude estimates of island ages that the lizards of the northern islands were capable of exchanging genes much more recently than those of the southern islands, and that while the opportunity for gene flow existed within the northern region, gene dispersal between regions could only occur overwater and at much lower rates.

#### *Large Island Populations*

Within each species the phenetic similarities among OTUs from large islands suggest that evolutionary forces act differently on large islands than on small islands. Since both species are found in a wide variety of habitats, populations on large islands are also undoubtedly quite large; consequently, genetic drift is probably ineffective as an evolutionary force promoting similarity of large island OTUs. Gene flow among large islands does not seem a likely explanation either, particularly since the large island cluster of *P. melisellensis* (Fig. 2) contains islands from both the northern and southern regions. Furthermore, overwater dispersal of lizards among islands should be more affected by distance than by island size (MacArthur and Wilson, 1967). Thus, it is doubtful that gene flow among large islands has been a significant force leading to their phenetic similarity. Selection regimes on large islands may be qualitatively quite similar, however. Large islands in the Adriatic resemble mainland areas in terms of habitat diversity, presence of humans, predators, and competitors, while small islands generally lack

these features. Due to these similarities of large islands' biotic features, selection regimes on large islands are believed to be largely stabilizing, and large island OTUs should most closely resemble mainland populations.

#### *Phenetic Relationships within the Southern and Northern Regions*

Within each species and within each region, the major evolutionary forces may vary. Thus, for example, among the southern *P. melisellensis* OTUs there exists an overall similarity which distinguishes them from northern OTUs, but differences among OTUs within this region may be attributable to differences between selection regimes, or to the different likelihood of genetic drift on large and small islands within the region. Likewise, close similarity among several OTUs within a region may be due to recent elimination of gene flow among them by a small net increase in sea level. Some evidence exists to support all of these modes of evolution, but because of their complex interactions, they will be treated in detail elsewhere.

#### *The Time-Divergence Theory of Insular Evolution*

The phenetic relationships discussed in this paper may be compared to the genetic relationships described for some of these OTUs by Gorman et al. (1975). Although they only examined lizards from the southern islands (and some mainland *P. sicula*), they found that OTUs from small islands fringing larger islands in an archipelago closely resembled the OTUs from the larger island of the group, suggesting that gene flow prior to isolation was at least partially responsible for genetic similarities. However, examination of particular loci led these authors to conclude that a major portion of the geographic variation in gene frequencies was the result of selection, and only for three loci was genetic drift likely to have been a significant force. Their results were interpreted as supporting the

"time-divergence theory of variation" (Soulé and Yang, 1973) which states that evolutionary rates in island lizard populations are inversely proportional to island size, the unique environments of small islands resulting in strong directional selection pressures and a corresponding erosion of genetic variation. On small islands, lacking predators, competitors, and habitat diversity, lizard populations reach extremely high densities and experience conditions quite unlike those experienced by lizards on larger islands and the mainland. Strong directional selection is likely to be a dominant force determining genetic and phenetic characteristics on small islands.

The theory predicts that populations on large islands, young small islands, and old small islands should be increasingly dissimilar to the mainland populations. Although samples of both species from mainland areas are needed to "test" this prediction, the data from island populations are consistent with the theory. OTUs from the young, (northern) small islands are more homogeneous and tend to be less dissimilar to the large island OTUs (12, 13, 19, 20) than the older (southern) OTUs from small islands. This suggests that the populations on small northern islands have not yet responded to small island selection regimes to the same extent as the southern small island populations have. However, additional evidence from other island systems and species is needed to rigorously test this hypothesis.

#### ACKNOWLEDGMENTS

I thank George C. Gorman for inviting me to accompany his field expedition to Yugoslavia and encouraging me to examine morphological variation in the lizards we collected. Gorman, M. Soulé, E. Nevo, D. Goldsmith, T. Papenfuss, A. Keller, and V. Jovanović aided in collecting specimens. I am very grateful to Larry Leamy for critically reviewing earlier drafts of the manuscript and providing encouragement unendingly. Robert Howard and Richard Grogan aided in preparing the figures. This study was supported in part by a grant from the Foreign Currency Program, Office of International Activities, the Smithsonian Institution, to George C. Gorman, and by California State University, Long Beach Foundation.

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Manuscript received September 1978

Revised April 1979