MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 149

Geographic Variation and Systematics of Salamanders of the Genus *Dicamptodon* Strauch (Ambystomatidae)

BY

RONALD A. NUSSBAUM

Ann Arbor
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INTRODUCTION

Dicamptodon is one of four extant genera of the strictly Nearctic salamander family Ambystomatidae. The family was most recently reviewed by Tihen (1958), and the relationships of the Ambystomatidae to other families of salamanders were discussed by Larsen (1963), Regal (1966), and Wake (1966). A literature review of the genus *Dicamptodon* was provided by Anderson (1969).

Dicamptodon differs from the more familiar ambystomatid genus *Ambystoma* by retention of a greater number of ancestral morphological character states (Tihen, 1958), and by virtue of a suite of adaptations related to a life cycle associated with breeding in mountain brooks and streams opposed to the pond and lake breeding adaptations of most *Ambystoma*. Like some species of *Ambystoma, Dicamptodon* has frequent populations which consist partially or entirely of neotenic individuals.

There are two known species of *Dicamptodon. D. ensatus* (Eschscholtz) has been known under various names since 1833, and *D. copei* Nussbaum was described in 1970. Both species occur in the mesic, forested regions of the Pacific Northwest and northwestern California (Fig. 1). The Pacific giant salamander, *D. ensatus*, may breed as sexually mature larvae or as fully-transformed, terrestrial adults. Cope's salamander, *D. copei*, consists largely of paedogenetic populations, although at least two cases of natural metamorphosis are known.

Previous reports on variation within the genus are few. Cope (1889) described two "varieties" of transformed *Dicamptodon*. His "alpha" form had a flat loreal region, a narrow muzzle, and a marbled color pattern confined to the head with the rest of the body uniform brown. The "beta" type had a swollen loreal region, broader muzzle, and marbling distributed over the entire upper body surfaces. Two specimens, USNM 4710 from "Oregon" and USNM 4053 from "Astoria, Oregon," were designated by Cope (1889) as alpha varieties. USNM 4710 is Baird and Girard's (1852) type of *Amblystoma tenebrosum* (=*D. ensatus*). Cope (1889) listed USNM 5981 from "Chilowyuck Lake, Oregon" and an unnumbered specimen from Body Bay, Latitude 38°18′ North on the California coast as beta varieties. The value of these observations is greatly reduced because of the problem of determining exact localities. "Oregon" could refer to either the State or the Territory of Oregon, and the latter encompassed the entire Pacific Northwest during the time in question. Many specimens shipped to eastern museums from the West Coast during the nineteenth century were labeled "Astoria" simply because Astoria was their point of departure. Therefore it cannot be assumed that USNM 4053 was actually collected at the townsite of Astoria. The specimen from "Chilowyuck Lake, Oregon" (Territory?)

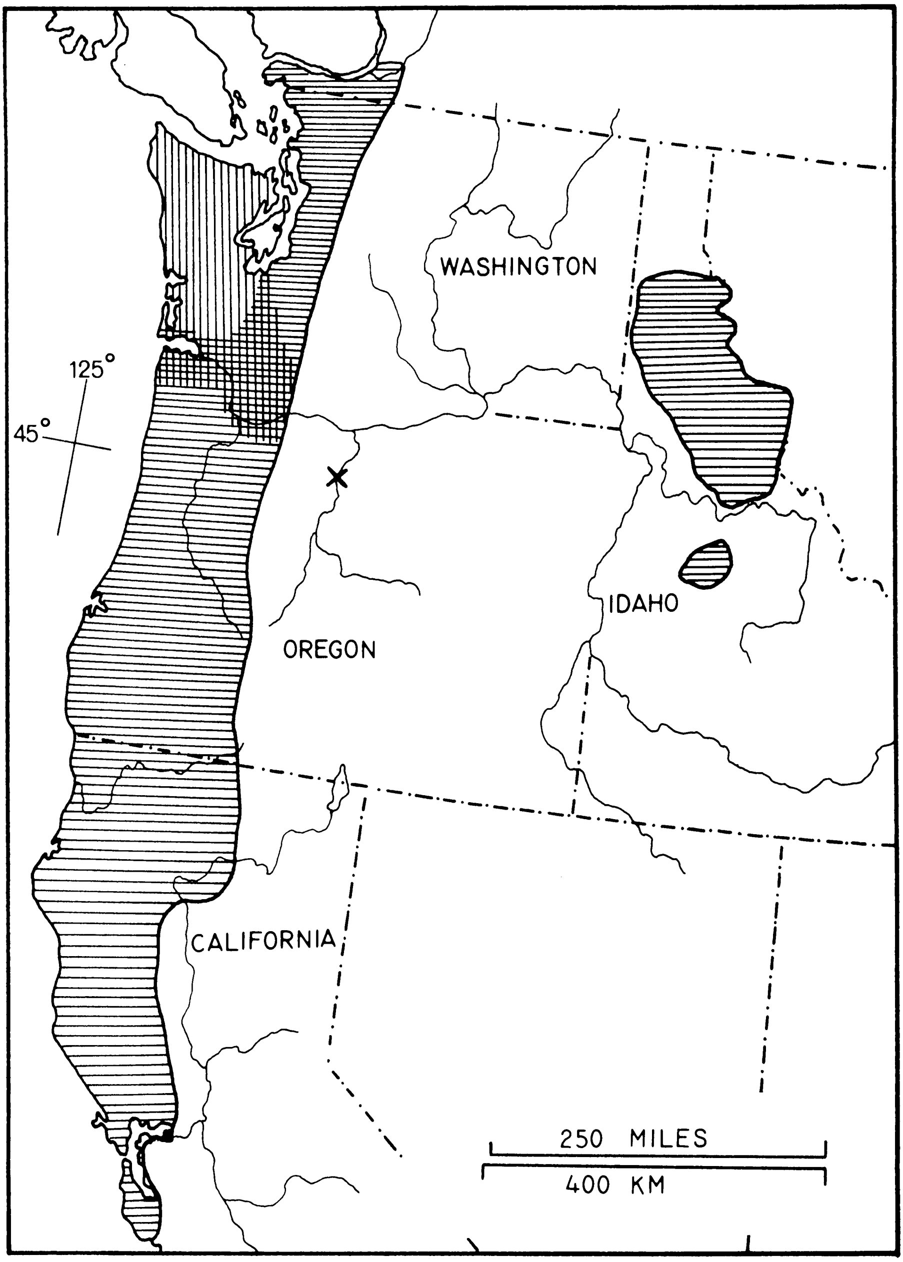

Fig. 1. Range map of *Dicamptodon ensatus* (horizontal hatching) and *D. copei* (vertical hatching). The X is an isolated population of *D. ensatus* at Oak Springs, Wasco Co., Oregon.

may have been collected at Chilliwack Lake, British Columbia. Slater and Slipp (1940) compared specimens of *Dicamptodon* from Mannering Creek, Benewah Co., Idaho (4 larvae and 1 transformed juvenile; UPS 2689-92 and 2707) with specimens from Washington (numbers and localities not given) and noted differences in color, gill length, and arrangement of vomerine and maxillary tooth rows. There are no other reports of variation in *Dicamptodon.*

The genus *Dicamptodon* has not been systematically reviewed, and as a result of the discovery of *D. copei* the taxonomic status of many populations is open to question. Data on life history and ecology are largely uninterpretable until the respective ranges and degree of sympatry of the two species are defined. Individuals from the disjunct populations in the Rocky Mountains of Idaho are known from casual observations to differ in appearance from coastal individuals, but the significance of these differences is unstudied, and a zoogeographic interpretation of the disjunction has not been attempted. These are the major problems to which this paper is addressed.

ACKNOWLEDGMENTS

I want especially to thank Dr. Robert M. Storm for advice, assistance and encouragement. I am indebted to Dr. Philip C. Dumas for the loan of electrophoretic equipment and for advice, and to Dr. Kenneth Gordon for information gained through informal discussions on biogeographical matters. Dr. Edmund D. Brodie, Jr. photographed specimens for me (Figs. 20 and 28), as did Dr. Jeffrey L. Briggs (Figs. 22 and 23) and Dr. Robert M. Storm (Fig. 21). Many of the Figures were drawn by Carol Clothier. Patricia J. Wynne prepared Figures 10, 24, 25, 26, 27, and 33. Drs. Brodie, Dumas and Storm reviewed and improved the manuscript, as did Drs. Ronald Altig, Nelson G. Hairston and Arnold G. Kluge.

Robert L. Peacock contributed specimens and accompanied me in the field on two eventful trips. Chris and Rita Maser donated specimens and provided useful field observations. Margaret, Kim, Ronna, and Archie Nussbaum helped immeasurably with the field work.

This study was supported in part by a Teaching Assistantship from the Zoology Department of Oregon State University; Computer Center grants from the Office of the Dean of Research, OSU; Grants-in-aid of Research from the Society of Sigma Xi; a grant from the Theodore Roosevelt Memorial Fund, administered by the American Museum of Natural History; and a National Science Foundation Summer Traineeship.

Thanks go to the following institutions and individuals for the loan of specimens: American Museum of Natural History (AMNH), R. G. Zweifel, G. W. Foley; Academy of Natural Sciences of Philadelphia (ANSP), J. E. Böhlke; British Columbia Provincial Museum (BCPM), G. C. Carl; California Academy of Sciences (CAS, CAS-SU), A. E. Leviton; Central Washington State College (CWSC), P. C. Dumas; D. E. Metter (DEM), uncatalogued specimens; Field Museum

of Natural History (FMNH), H. Marx; Los Angeles County Museum (LACM), J. D. Wright and R. Rivers; Museum of Comparative Zoology, Harvard University (MCZ), E. E. Williams; Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), R. C. Stebbins, D. B. Wake, R. B. Bury, S. B. Ruth; Oregon State University Museum of Natural History (OSUMNH), R. M. Storm; Pacific Lutheran University (PLU), J. W. Knudsen, W. R. Heyer; Southern Oregon College (SOC), S. P. Cross, J. O. Sullivan; Sacramento State College Museum of Natural History (SSCMNH), R. L. Livezey; University of British Columbia (UBC), I. McT. Cowan; University of Michigan Museum of Zoology (UMMZ), C. F. Walker; University of Puget Sound (UPS), G. Alcorn; United States National Museum, Smithsonian Institution (USNM), J. A. Peters, G. R. Zug; University of Washington (UW), R. C. Snyder; Washington State University, Conner Museum (WSU), G. E. Hudson.

NOMENCLATURAL HISTORY

The history of name usage for *Dicamptodon* is diagrammed in Figure 2. Eschscholtz (1833) described *Triton ensatus* from a transformed individual collected by him in 1824 on the northern coast of California, probably near Fort Ross, Sonoma County. In the same paper, H. Rathke described the internal anatomy from the dissected type specimen. No museum numbers were assigned to the type, and its dissected parts are almost certainly lost. However, the description

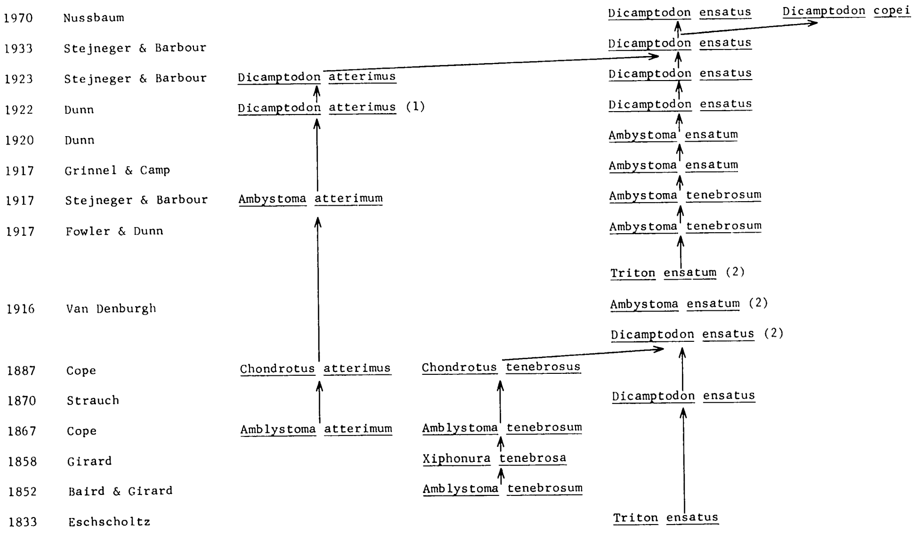

Fig. 2. Summary of the history of name usage in the genus *Dicamptodon*: (1) name not used, but inferred; (2) all three possibilities were listed and no decision was made.

is accurate, except that the tail is not continually curved upwards, even in life, as suggested by Rathke, and there is no doubt concerning the identity of *Triton ensatus* (=*Dicamptodon ensatus*).

I have examined the type of *Amblystoma tenebrosum*, and it is very similar in color, pattern, and general body form to transformed specimens taken in northern, coastal Oregon, but the exact locality must remain in doubt. The marbling is indistinct on the posterior, dorsal surfaces as noted by Cope (1889), but I have seen occasional individuals with faint or nonexistent marbling from all parts of the range of *D. ensatus*. There is no doubt that the type of *Amblystoma tenebrosum* is conspecific with *Dicamptodon ensatus*.

Cope (1867) described *Amblystoma atterimum* from a transformed specimen (USNM 5242) received from a surveying expedition commanded by Lieutenant John Mullen. The locality was given as "northern Rocky Mountains." I have examined USNM 5242, which is obviously an individual in a late stage of metamorphosis, hence the elongate, curved vomerine series and absence of marbling described by Cope. The dark dorsal and ventral color of the specimen is typical of larval and transformed *D. ensatus* from northern Idaho.

From 1867 until 1916, *Dicamptodon ensatus* masqueraded under three different names (Fig. 2), and Cope (1889) listed all three as valid species. Van Denburgh (1916) recognized that *Dicamptodon ensatus* and *Chondrotus tenebrosus* were synonymous, but he was vague as to his intentions. He discussed the synonymy under the heading "*Triton ensatum*," thus interjecting a new spelling into the nomenclature. Furthermore, he implied that either *Ambystoma ensatum* or *Dicamptodon ensatus* could be used, depending on the preference of the researcher. Since *tenebrosus* was the type species of *Chondrotus*, *Chondrotus* had become a junior synonym of *Dicamptodon* and hence no longer available. No mention was made of this or of the fate of the other species of *Chondrotus*, and therefore *Chondrotus atterimus* was left in limbo until Stejneger and Barbour (1917) listed it as *Ambystoma atterimum*. Dunn (1922) did not list *Dicamptodon atterimus*, but stated that there were two species of *Dicamptodon*. The second could only have been *D. atterimus*. Stejneger and Barbour (1933) gave no reason for synonymizing *D. atterimus* with *D. ensatus*.

Three minor points of confusion remain in the nomenclatural history of *Dicamptodon*. Firstly, Storer (1925) indicated in his list of synonymies that Fowler and Dunn (1917) had listed *Dicamptodon ensatus* under the name *Ambystoma tigrinum*. Storer apparently misread Fowler and Dunn, because the latter authors made no such mistake. Secondly, Grinnell and Camp (1917) stated that *Chondrotus lugubris* is a synonym of *Ambystoma ensatum*. I have been unable to determine the reason for this statement. Thirdly, Gray (1850) used the name *Ensatina eschscholtzii* to refer to specimens he had examined, but for some unknown reason he described *Dicamptodon* *ensatus* instead of *Ensatina*. Furthermore, he listed *Triton ensatus* as a synonym of *Ensatina eschscholtzii*. This double error led Cope (1867) to rename *Heredia oregonensis* Girard (= *E. eschscholtzii*) as *Plethodon ensatus*, since Cope recognized *Ensatina* as a plethodontid. Cope's friend and correspondent, St. George Mivart, informed him of the misusage of the specific name *ensatus*, and Cope (1869) corrected the error.

GEOGRAPHIC CONSIDERATIONS

The Pacific Northwest may be viewed, generally, as a series of north-south mountain ranges with intervening lowlands. The ranges are, from west to east, the Coast Range, the Cascade-Sierra Nevada Ranges, and the Rocky Mountains. The Coast, Cascade, and Sierra Nevada Ranges intermingle in southern Oregon and northern California in a region here referred to as the Klamath-Siskiyou Mountains. In Washington and northern Oregon the Willamette-Cowlitz-Puget Lowland separates the Coast and Cascade Ranges. South of the Klamath-Siskiyou Mountains, the Great Valley of California separates the Coast and Sierra Nevada Ranges. The broad Columbia and Great Basins form a major lowland barrier between the Cascade-Sierra Nevada chain and the Rocky Mountains. The Central Mountains (Blue Mountains) extend westward from the Rocky Mountains of Idaho across northeastern Oregon almost to meet the Oregon Cascades near Mount Jefferson, but the arid Deschutes River Valley intervenes. Only the relatively low and dry Okanogan Valley separates the Cascade and Rocky Mountain Ranges in north-central Washington and south-central British Columbia.

It is useful to think of the Pacific Northwest in terms of the physiographic provinces delineated by Allison (1962). The Pacific Border Province includes the Coast Ranges, the Klamath-Siskiyou Mountains, and the Willamette-Cowlitz-Puget Lowland. The proximity of the Pacific Ocean has a great ameliorating effect on the climate of this region. With the exception of the high Olympic Mountains of northwestern Washington, the average temperatures range from 14.5° to 16.5°C for July and 4.5° to 6.5°C for January. The average frost-free-season is from 160 to over 200 days. Average annual precipitation is from about 125 to 260 cm, less than 75 cm of which is from snowfall. The province is characterized by hemlock-spruce or Douglas Fir summerwet forests, and only the high Olympic Mountains exceed the forested Transition Lifezone.

In Oregon, the Cascade Mountains Province can be divided into eastern and western halves. The western slopes receive high amounts of precipitation, while the eastern slopes, lying in a rain shadow, receive much less precipitation. Average July temperatures are lower and average January temperatures are higher on the western slopes than on the eastern slopes. The western slopes are characterized by Douglas Fir summerwet forests and the eastern slopes by Ponderosa Pine summerdry forests. The high Cascades lie in the Canadian and Hudsonian Lifezones, with the higher peaks in the Arctic-Alpine Lifezones. In Washington, especially the northern part, the Cascade Mountains Province is not so easily divided into western and eastern halves, but the general aspect of the region is similar to the Oregon Cascades.

The Northern Rocky Mountains Province extends from northeastern Washington, east to northern Idaho and western Montana, and south in Idaho to the Snake River Plains. The climate of this region is much harsher, partially because of the absence of the ameliorating effect of the Pacific Ocean. Average annual precipitation is lower and more seasonal (much in the form of winter snow), and diel and seasonal temperature extremes are greater in this province than in either the Pacific Border or Cascade Mountains Provinces. Lifezones range from upper Sonoran to Arctic-alpine, and forests are highly varied and largely summerdry.

The Columbia Intermontane Province includes the Columbia Basin, Central Mountains (Blue Mountains), Harney High Lava Plains, Malheur-Owyhee Upland, and the Snake River Lava Plain. This province is mostly in the Upper Sonoran and Arid Transition lifezones characterized by Western Juniper (*Juniperus occidentalis*), and Sagebrush (*Artemisia* spp.). However, parts of the higher Central Mountains are in the Canadian and Hudsonian lifezones with pine and fir forests and cooler, wetter climates.

The Basin and Range Province of south-central Oregon and eastern California includes the Sierra-Nevada fault block range, other minor ranges, and intervening north-south trending basins. The province has an interior climate, with only the high Sierras receiving high amounts of precipitation.

The foregoing descriptions are necessarily brief and generalized. On a finer scale many complications enter the picture, notably in southwestern Oregon and northwestern California where several mountain ranges merge. This is an area of complex intermingling of vegetation types (Whittaker, 1961; Stebbins and Major, 1965; Franklin and Dyrness, 1969; Detling, 1968), and the meeting and mixing of distinctive faunas in this region is well documented (Remington, 1968). Diverse rock formations and a complicated geological history have led to a highly varied pattern of soil types and topography (Baldwin, 1964; Snavely and Wagner, 1963). Hybridization, speciation, and the formation of ecotypes and geographic variants (e.g. Gottlieb, 1968) are consequences of the complexity of the region.

DISTRIBUTION

RANGE OF *D. ENSATUS*

The Pacific giant salamander is most often found at altitudes ranging from sea level to about 960 m. The maximum altitude for a reliable sight record is 2160 m for a lake in Trinity Co., California; that for a documented record is 1880 m at White Creek Lake, Trinity Co., California (MVZ 71118). Other relatively high elevation records are: 1790 m, "Little Monster Lake," 2.4 km SE Pony Mountain, Trinity Co., California (MVZ 71123, 71126-7, 71129); 1790 m, Upper Bigelow Lake, Josephine Co., Oregon (WSU 56108); 1670 m, Bolan Lake, Josephine Co., Oregon (Ronald A. Nussbaum-RAN 4485-87, DEM un-numbered, LACM 40795). Possibly correlated with lowered lifezones in northern latitudes, there are no comparatively high elevation records for Washington, British Columbia or northern Idaho.

Over much of its range, *D. ensatus* is exceedingly common. Almost every permanent stream and seepage in the Coast and Klamath-Siskiyou mountains contains larvae of this species. The same is true for the lower, western slopes of the Cascade Range. For this reason nothing would be gained by listing or dot-mapping every known locality for these regions. However, some marginal areas in the eastern portion of the Cascade Range have been poorly collected and there are still relatively few known localities for Idaho and British Columbia.

In coastal regions, the Pacific Ocean forms a precise western boundary. I have often collected individuals within a few meters of the beach as have Reed (1949) and Ferguson (1956). One large neotene (OSUMNH 1) was taken from the stomach of a fish (unknown species) caught by commercial fishermen 4.8 km offshore. The animal was still alive when retrieved from the fish's stomach.

The southernmost limit of the range is documented by many specimens (MVZ, CAS) collected near Ben Lomond, Bonny Doon, Felton, and Empire Cave (just N Santa Cruz) Santa Cruz Co., California. However, Dr. Robert C. Stebbins has informed me of a sight record south of Monterey Bay in the Santa Lucia Range. If confirmed, this would extend the southernmost limit of the range by about 80 km.

The south bank of the Fraser River in extreme southwestern British Columbia marks the approximate northern limits of the range. Known localities in British Columbia are: Ascaphus Creek near Cultus Lake (PM 641), and Cultus Lake (PM 837-8).

In California, the easternmost record based on specimens examined by me is Hatchet Creek, 74 km NE Redding, Shasta Co. (MVZ 17158). CAS-SU 1656-58 are listed from "Mt. Lassen, Holmsworth Flat, near Shingletown, Lassen Co., California." This record is ambiguous, because both Shingletown and Mt. Lassen are in Shasta County. If the locality could be determined positively, it might represent the easternmost locality in California and a new county record.

Oak Springs, near Maupin, Wasco Co., is the easternmost locality in Oregon (OSUMNH 6046, 7224-26; RAN 4447). The site is 53 km east of the Cascade crest and is well within the Upper Sonoran Lifezone. Oregon Oak (*Q. garryana*) occurs at the spring site, but the surrounding vegetation is primarily Sagebrush (*Artemisia tridentata*), grasses, and desert annuals.

Populations at Lost Lake, Eagle Creek, and Starvation Creek, Hood River Co., Oregon are technically east of the Cascade crest, but these localities are also on the north-facing breaks of the Columbia River so that no real elevational barrier separates them from more westerly populations. No other populations are known east of the Cascade crest in Oregon. *D. ensatus* is not known from the high Cascades (Arctic-alpine Lifezone, above 2130 m) nor from the Hudsonian Lifezone of Oregon, but is expected in the latter. There are scattered records for the Canadian Lifezone on the western side, and *D. ensatus* is very common in the Transition Lifezone on the western slopes (below 1360 m).

D. ensatus can be found throughout the rest of western Oregon where local habitat is suitable, except for agricultural and urban centers in the Willamette Valley and in the dry basins of the Rogue and Umpqua rivers in southwestern Oregon. Occasional occurrence is expected in these latter regions.

Much the same relationships hold for *D. ensatus* in the Washington Cascades. Only two known localities are east of the crest. The easternmost record is Sears Creek, northwest of Wenatchee Lake, Chelan County (UPS 9437; WSU 59351-2; RAN 2197-98, 6360; DEM un-numbered). This locality is in the Canadian Lifezone, 21 km east of the crest. The other eastern locality is N side Kachess Lake, Kittitas County (UW un-numbered). The site is 13 km east of the crest, also in the Canadian Lifezone. There are two records on the crest, both in the Canadian Lifezone: Snoqualmie Pass, Kittitas County (RAN 1478-79, 4054-79); Stampede Pass, Kittitas County (LACM 40798).

D. ensatus is recorded from many localities on the western slopes of the Cascades in Washington, both in the Transition and Canadian lifezones. Hudsonian and Arctic-alpine Lifezones records are wanting. Parts of the Cowlitz-Puget Lowland are also uninhabited, but isolated occurrences are expected. *D. ensatus* occurs in the Willapa Hills (RAN 5139-40), where it is sympatric with *D. copei*. As yet, there are no definite records of *D. ensatus* on the Olympic Peninsula.

Known localities for *D. ensatus* in Idaho are: Valley Co.—South Fork Salmon River, 8.1 km N Knox (CAS-SU 10742-3); Dime Creek, 6.5 km N Knox (RAN 1173); Roaring Creek, 13.5 km N Knox (RAN 7539-62). Idaho Co.—Hamby Creek, 24 km S Selway River (RAN 7594-7609); Moose Creek (DEM un-numbered). Clearwater Co.—Silver Creek, 16 km NW Headquarters (un-numbered specimen, University of Idaho); Leuty Creek at junction of U.S.F.S. Trail 307, near Canyon Ranger Station (RAN 181); North Fork Fern Creek, 4.8 km NW Canyon Ranger Station (RAN 171). Shoshone Co.—Bear Creek, 11.3 km NW Canyon Ranger Station (RAN 172, 174-6, 178); Roundhouse Gulch, 0.8 km W Avery (RAN 4987-5030, 5754, 6687, 7689-7706, 7973-77, 8874-95); Bird Creek, 19.3 km E Avery (RAN 5183); Rock Run Creek, W Monumental Peak (UPS 2811-4). Latah Co.—Eldorado Gulch, White Pine Gulch, Mountain Gulch, all on the North Fork Palouse River (many specimens collected by Dr. Dean E. Metter and myself; some numbers are listed in Appendix I); S slope Baldy Mountain (University of Idaho, un-numbered). Benewah Co.—Mannering Creek, 19.4 km N Harvard (UPS 2689-92; RAN many specimens, see Appendix I).

Black (1970) and others indicated that *D. ensatus* occurs in western Montana. Apparently all such claims are based on the assumption that the type of *Amblystoma atterimum* (USNM 5242) was collected in western Montana. Actually, the only locality given was Cope's (1867) "northern Rocky Mountains," which could be anywhere in western Montana, northern Idaho, or in the Canadian Rockies. The alleged collector, Lieutenant Mullen, was in charge of a party surveying roads through western Montana and northern Idaho, especially in what is now Kootenai and Shoshone counties between Coeur d'Alene and Mullen (named for Lt. Mullen), a region where *D. ensatus* is known to occur. The type is very similar to other specimens I have collected in Shoshone County. Although it would not be surprising to find *D. ensatus* in Montana, I believe the type of *A. atterimum* was most likely collected in Shoshone Co., Idaho. In any case, there is no positive evidence for the occurrence of *D. ensatus* east of the Bitterroot Divide in Montana. Both E. K. Teberg (pers. comm.) and I have searched unsuccessfully for the species on the eastern slopes of the Bitterroots.

RANGE OF *D. COPEI*

Dicamptodon copei is found on both the Oregon and Washington sides of the Columbia River Gorge. In Oregon it is apparently confined to the immediate vicinity of the Gorge, with the southernmost locality in Oregon at Rhododendron, Clackamas County. The species is found throughout the Olympic Peninsula, in the Willapa Hills, and in the southeastern Cascades of Washington.

Known localities for *D. copei* in Oregon are: Clackamas Co.—near Rhododendron (MVZ 61637-38); Still Creek, 8 km up Still Creek Rd. from Hwy. 26 (RAN 7201). Multnomah Co.—Wahkeena Falls (RAN many specimens, see Appendix I; LACM 29429-34, 29436; PLU AO 838-41, AO 178, AO 168); Oneonta Gorge (RAN many specimens, see Appendix I). Clatsop Co.—NW side Saddle Mountain (RAN many specimens, see Appendix I); S Fk Quartz Creek, 9.2 km E Elsie (RAN 5371, 7427-33); Youngs River (CAS-SU 4968). Known Washington localities are: Wahkiakum Co.—Rock Creek, 14.6 km N Hwy. 407 (RAN 7514-36). Clark Co.—9.4 km E Vancouver (UPS 1985, 2736, 1395-99, 1402, 1059; AMNH 45941; FMNH 27114). Cowlitz Co.—type locality, Maratta Creek (holotype USNM 166784, paratypes USNM 166785-814; RAN 3755-65, 7489-500, 7505-12, 7888-92, 8555-64; DEM un-numbered); Elk Creek, 3.2 km W type locality (RAN 3693-97); Tributary of Cold Water Creek, 3.0 km E type locality (RAN 3698-99). Lewis Co.—6 km up Quartz Creek Rd. from Cispus River (RAN 9777-79). Skamania Co.—Upper Bean Creek, 4.8 km E Spirit Lake (AMNH 64841-42); Nine Foot Creek, 20 km NW Troutlake (RAN 4383-87, 4407-46, 4536, 4544-47, 4614-19, 4623-27, 4632, 4634-81, 5227, 5191-96, 7878-87, 8535-54, 8592-99, 8707-10, 8803; DEM un-numbered); 8 km W Mount Adams (UPS 5584); near Spirit Lake, T9N, R6E, NE 1/2 Sec. 1 (RAN 12802, 12866, 12996-13073). Mason Co.—1.9 km E Staircase Ranger Station (RAN 1489-91); Lake Cushman (PLU AO123, AO134, AO136-37; MVZ 41387-88; USNM 55276; FMNH 84809); Laundry Creek (MCZ 5885-87); Dry Creek (AMNH 20584); Elk Creek (AMNH 20571); Pebbleford Creek, Mt. Skokomish (AMNH 20576); Mt. Rose (AMNH 20582). Grays Harbor Co.—Merriman Creek, 7.5 km NE Quinault (RAN 2200, 4080-121, 4524, 5135-38, 6139-55, 6164-237, 6948-54, 8502; UPS 1839-40); July Cr., W side Quinault Lake (UPS 2736); Beaver Creek (RAN 6113-20). Jefferson Co.—3.2 km NE Grays Harbor Co. line up Quinault River (RAN 4692-707); Olympic Mountains (FMNH 84808); 24 km up Hoh River Rd. (UW un-numbered); 11.2 km W Graves Creek Ranger Station (OSUMNH 3423). Clallam Co.—4.8 km NNW Sappho (OSUMNH 9441-2); Deer Lake Trail (UW un-numbered); Canyon Creek (USNM 64322-24); Sol Duc Falls (UPS 1068-69, 1071, 1088); 1.6 km N Sol Duc Falls (UPS 1985); Cat Creek (USNM 64321).

D. ensatus and *D. copei* are sympatric at the following localities: Oregon—Oneonta Gorge and Wahkeena Falls, Multnomah County; Still Creek, Clackamas County; South Fork Quartz Creek and northwest side Saddle Mountain, Clatsop County. Washington—Rock Creek, Wahkiakum County; Quartz Creek, Lewis County; Maratta Creek (type locality of *D. copei*), Cowlitz County.

MATERIALS AND METHODS

SPECIMENS

I have examined most of the specimens of *Dicamptodon* available in the major museums of the United States and Canada (see Acknowledgments). Borrowed specimens were measured, but many were so poorly preserved that they could not be used as constituents of the OTUs (operational taxonomic units, *sensu* Sokal and Sneath, 1963). Those that were used are listed along with their respective OTUs in Appendix I. Most specimens used in this study were collected and uniformly preserved by me. These specimens are catalogued in the Museum of Zoology, University of Michigan. Only 209 transformed *D. ensatus* were available from museums; an additional 437 were collected during the course of this study. Larval *D. ensatus* from many localities were treated with thyroxine to force metamorphosis. These 425 "artificially" transformed individuals were used for analysis of color and pattern and for testing geographic variation and age-dependent variation in sensitivity to thyroxine. They were not used for morphometric comparisons because of possible undetected effects of the treatment on these characters. One hundred twenty *D. copei* were also treated with thyroxine.

CHARACTERS

Color and pattern of larval and transformed *Dicamptodon* vary greatly between populations. Because of the often subtle nature of the variation, all attempts to code and quantify these data failed. Therefore this information will be presented qualitatively, in terms of trends of variation in color and pattern throughout the ranges of the species.

The following measurements, estimated to the nearest 0.1 mm with Helios dial calipers, were taken from each specimen:

1. Snout-vent length (SVL)—from the tip of the snout to the anterior angle of the cloacal opening.
2. Body length (BL)—computed as SVL minus head length.
3. Axilla-groin length (AGL)—measured with fore- and hindlimbs perpendicular to the trunk.
4. Head width (HW)—at the angle of the jaws.
5. Head length (HL)—in larvae, the distance from the tip of the snout to the dorsalmost point of attachment of the gills to the occipital region (marks the dorsolateral junction of the head and neck). In transformed individuals this measurement was taken from the tip of the snout to the midpoint of a vertical groove on the side of the neck (marks the point of disappearance of the gills during transformation). These measurements have smaller coefficients of variation than the midline distance from the snout to the gular fold.

6. Forelimb length (FLL)--from the tip of the longest digit to the axilla when the limb is extended.

7. Hindlimb length (HLL)–from the tip of the longest toe to the groin when the limb is extended.

8. Tail length (TL)--from the anterior angle of the cloacal opening to the tip of the tail. This measurement was not used for larvae in the final analysis because many of the tail tips were in various stages of regeneration.

9. Maximum tail height (MTH)–self explanatory. Not taken from transformed individuals.

Larvae have six rows of gill rakers on each side. Counts were made for all six rows on the right side of every larva. Counts were made on the left side where obvious anomalies occurred on the right side.

Maxillary and premaxillary teeth were counted together in both larval and transformed individuals. Vomerine teeth were also counted in the two forms, with the right and left series summed to obtain a single value. *D. ensatus* larvae occasionally have a short, palatopterygoid series of teeth on one or both sides (Nussbaum, 1970). Although this series, when present, is in line with the vomerine series, the teeth were counted separately.

Costal grooves were counted on all larvae and on those transformed individuals with distinct grooves. The number of costal folds between adpressed limbs was estimated to the nearest 0.5 fold for all specimens.

The gonads of all specimens were examined to determine the state of maturity. Ova were counted and measured and notes were taken on the condition of the ovaries, oviducts, testes, vasa deferentia, and cloacal glands. Although most of these data will be presented elsewhere, some reference will be made to size in relation to sexual maturity in the present paper.

Osteological information was obtained from radiographs taken with a Type S-E Softex X-ray Apparatus. More detailed information was obtained from specimens cleared and stained, using the standard technique of maceration in 2 percent potassium hydroxide, staining in Alizarin red-S, and storing in 100 percent glycerine.

Blood serum proteins were analyzed by electrophoretic separation. Blood was drawn from the heart in capillary tubes, and the serum separated by centrifugation. Samples were run within one hour of the time the blood was drawn to avoid protein breakdown by bacteria. Samples of serum (0.25 μl) were placed on a biologically inert cellulose acetate membrane, and the proteins separated with a Beckman Microzone Cell, Model R-101. The proteins were allowed to migrate for 20 min. at 250 V, with a barbital buffer solution of pH 8.6 and ionic strength 0.075. Migration was stopped by placing the membrane in a fixative dye (0.2 percent Ponceau-S, 3.0 percent trichloroacetic acid, 3.0 percent sulfosalicylic acid) for 8 min. The excess dye was rinsed away with 5 percent acetic acid. The membrane was then dehydrated for 1 min. in 95 percent ethanol, transferred to a clearing solution of 25 percent glacial acetic acid and 75 percent ethanol (95 percent) for 1 min. and dried. The dried membrane was placed in a clear envelope and the pattern scanned with a Microzone Densitometer, Beckman Model R-110. The densitometer is equipped with an automatic integrator, and the relative amounts of the protein fractions can easily be determined through its use.

ANALYSIS OF CHARACTERS

The method of statistical analysis for some characters will be evident in the Results section. However, my treatment of body measurements and counts needs comment.

Means of body measurements cannot be directly compared because of differences in mean overall size (mean SVL). Differences in mean SVL could reflect true genetic divergence, but more often they merely reflect differences in population structure, sampling bias, or both. Taxonomists usually resort to the use of ratios or regression analysis to overcome this problem, and both techniques were used in this study. Individuals less than 65 mm SVL were not used in analyses involving body measurements in order to avoid some of the extreme variation caused by allometric growth.

Many authors have criticized the use of ratios in taxonomy (e.g., Marr, 1955; McIntosh, 1955; Simpson, Roe, and Lewontin, 1960; Sokal, 1965). Some objections, all interrelated, are:

1. Even if two variables are linearly related, the derived ratios will vary with size unless the corresponding regression line passes through the origin, a situation which seldom occurs. (However, the chances of arriving at false conclusions because of this phenomenon are minimized if the range of size is small and covers the same interval for all populations).
2. The errors of measurement of the two original variables may be compounded into a more serious error for the derived ratio.
3. If two variables differ in the same direction between populations, the ratios formed from the two variables may be nearly identical between populations; and hence important information is obscured unless a third, control variable (e.g., SVL) is examined in relation to the other two variables. (This may also be true in regression analysis).
4. Ratios, like percentages, are often not normally distributed, and therefore standard statistical tests are invalid.

Regression analysis also has drawbacks. Perhaps the most serious of these, at least in taxonomic studies, is that the theory of Model I regression requires the independent variables to be free from both error of measurement and normal, random variation. This of course is never the case except where the independent variable is mathematically or experimentally controlled. Model II regression allows for non-fixity of both variables, and Bartlett (1949) has provided a usable method. However, Bartlett's three-group method lacks the elegance of the least squares method of Model I regression, and most taxonomists have used the latter method despite the theoretical difficulties. McIntosh (1955) showed empirically that the use of Model I regression on Model II data, in a taxonomic study of the deer mouse (*Peromyscus*), did not greatly distort the analysis.

The problem of linearity versus curvilinearity is common to both regression and ratio analysis. In the present study, I tested for curvilinearity by inspection and through correlation analysis. All relationships were essentially linear over the range of size used, and no transformations were necessary.

Ratios are often distributed peculiarly, and special methods which take into account the variation in both "hidden" variables must be used to estimate the ratio variance (Hansen, Hurwitz, and Madow, 1953). The ratio estimate was determined by dividing the sum of the numerators by the sum of the denominators. Thus, for two variables x and y in a sample of n individuals,

$$\text{ratio estimate} = r = \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} x_i} = \frac{\bar{y}}{\bar{x}}$$

The variance of the ratio estimate is given by the formula:

$$S^2 = r^2\ (1-f)\ \left(\frac{V_x{}^2 + V_y{}^2 - 2pV_xV_y}{n}\right)$$

where V_x and V_y are coefficients of variation of the x_i and y_i respectively, and p is the Pearson product-moment correlation coefficient between the x_i and y_i. The sampling fraction, f, is the proportion of the total population sampled, and is equal to zero if, as in this case, the population is considered to be infinitely large. Populations of *Dicamptodon* are of course not infinitely large, but this approach results in wider confidence intervals about the ratio estimates, a conservative trait which I consider desirable.

The following 17 ratios were estimated for each population (L = larval character; A = transformed character, i.e., a character used to define OTUs composed of transformed individuals; see list of measurements for explanation of abbreviations):

1. HW/SVL (L,A)
2. FLL/SVL (L,A)
3. HLL/SVL (L,A)
4. MTH/SVL (L)
4. TL/SVL (A)
10. (FLL + HLL)/SVL (L,A)
11. AGL/SVL (L,A)
12. MTH/BL (L)
12. TL/BL (A)
13. HW/BL (L,A)

5. HL/BL (L,A)
6. (FLL + HLL)/AGL (L,A)
7. FLL/BL (L,A)
8. HLL/BL (L,A)
9. (FLL + HLL)/BL (L,A)
14. FLL/HW (L,A)
15. HLL/HW (L,A)
16. FLL/HLL (L,A)
17. HW/HL (L,A)

Model I regression was used to estimate regression coefficients (b) and intercepts (a). SVL was used as the independent variable (x), and BL, AGL, HW, HL, FLL, HLL, and MTH were set successively as dependent variables (y's) for analysis of larval characters. The analysis was the same for OTUs based on transformed individuals except that TL replaced MTH as a dependent variable.

In regression analysis, mean y's for each population can be predicted for any given x value. If the x value is the same for all populations then the corresponding $\bar{y}$'s can be compared, and methods are available for calculating confidence intervals for the $\bar{y}$'s. The magnitude of these confidence intervals depends on the difference between the arbitrarily chosen x value and the mean of x for the population. The confidence intervals reach minimum size at $x-\bar{x} = 0$; and therefore the greatest confidence in the predicted $\bar{y}$'s occurs when the $\bar{x}$'s are used as predictors. The mean SVL across OTUs was close to 88 mm for larvae and 110 mm for transformed individuals, and these two values were chosen to predict the $\bar{y}$'s.

The number of teeth, gill rakers, and trunk vertebrae vary discontinuously and theoretically should be treated as discrete variables. If these data are converted to frequencies or percentages, standard errors can be estimated with the method of normal approximation to the binomial, or confidence intervals can be looked up directly on statistical tables (e.g., Fisher and Yates, 1948). However, this approach is seldom used by systematists, and data of this type are usually reported as arithmetic means with confidence intervals calculated as if the data were normally distributed. Means are simpler to use than frequencies, and means are reported here for tooth and gill raker counts. However, I also checked for significant differences between populations using tests on frequencies. This latter, theoretically correct procedure proved to be much more conservative over the range of sample sizes used.

Tests were made for possible sexual dimorphism for all characters in all populations. Since none was found, data for the sexes were pooled for the final estimates. Significance levels are for $p < .05$ throughout this paper.

OPERATIONAL TAXONOMIC UNITS

Throughout this study emphasis was placed on comparison of larval rather than of transformed individuals. Necessity dictated this procedure. The number of usable museum specimens was disappointingly low, and I have not been able to collect adequate numbers or series of transformed *D. ensatus*. In the case of *D. copei*, comparisons are necessarily between groups of larvae.

I grouped larval OTUs into two categories referred to as primary and secondary OTUs. Primary larval OTUs are those composed of individuals collected by me at a specific locality (i.e., within one small portion of a single stream). These larvae were preserved in a uniform manner: killed in 0.2 percent chlorobutanol, positioned in a tray, covered and fixed with 10 percent buffered formalin for 24 h, washed in running water for 24 to 48 h, and stored in 50 percent isopropyl alcohol. Secondary larval OTUs are composed of larvae of varied origin, not necessarily uniformly preserved, and from a defined region rather than a specific locality.

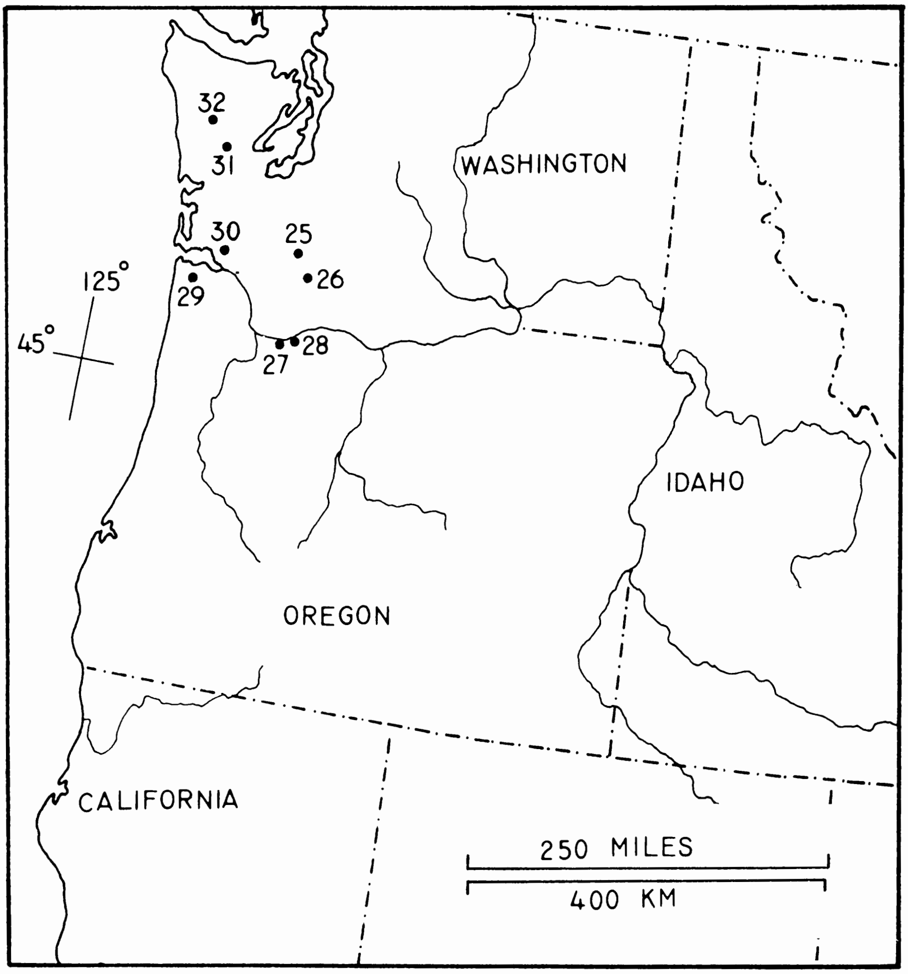

Fig. 3. Localities for populations of *Dicamptodon copei* by OTU number. See Appendix I for exact localities.

All OTUs of transformed *D. ensatus* are secondary OTUs, although many of the component specimens were collected and preserved uniformly by me.

OTUs will frequently be referred to by number. The 32 larval OTUs and the 12 formed from transformed *D. ensatus* are listed by number and defined in Appendix I, and the localities are mapped in Figures 3 and 14.

ESTIMATION OF SIMILARITIES BETWEEN OTUS

I used various multivariate techniques to estimate similarities between larval populations and subsequently to classify the populations. The data were arranged in an OTU by character matrix. Previous to all tests, the matrix was standardized by characters so that each character vector had a mean of zero and a variance of one. This eliminated the problem of different scales of measurement on the characters.

Estimates of similarity were based on either Pearson product-moment correlation coefficients (r) or on distances (d) in Euclidean hyperspace.

In the case of r, the OTUs may be viewed as variables (j) and the characters as cases (i). The symbol r_{jk}, will then denote the correlation between the j^{th} and k^{th} OTUs based on n characters. All possible r_{jk}'s were calculated with expected values ranging from -1.0 to +1.0. A highly positive r_{jk} suggests high similarity between the two OTUs in question. The d-scores represent average distances between OTUs when the OTUs are plotted in n-dimensional hyperspace, with characters representing the n-dimensions. The formula:

$$d_{jk} = \left[\sum_{i=1}^{n} \frac{(\overline{X}_{ij} - \overline{X}_{ik})^2}{n} \right]^{1/2}$$

was used to calculate the "taxonomic distance", d_{jk}, between the j^{th} and k^{th} OTUs. The symbols $\overline{X}_{ij}$ and $\overline{X}_{ik}$ are the mean character state values for the i^{th} character of OTUs j and k respectively. A low d_{jk} denotes high similarity as can logically be seen from the formula. For further explanation of these methods, see Sokal (1961) and Sokal and Sneath (1963).

CLASSIFICATION OF OTUS

The criterion for classification can be based on r_{jk}'s, d_{jk}'s, coefficients of association, error sums of squares, or any other appropriate measure of similarity or dissimilarity between OTUs. In this study, cluster analysis was initiated on either a r_{jk} matrix or a d_{jk} matrix. I used the weighted-pair-group-method (WPGM) and the unweighted-pair-group-method (UPGM) of Sokal and Michener (1958), the single-linkage-method of Sneath (1957), and a method described by Ward (1963). This latter technique is an agglomerativepolythetic method (here called HGroup) which calculates optimum groups by allowing only those two groups to cluster at each cycle which when clustered, would have the smallest possible within-group variance. In this manner, group heterogeneity is minimized. Before clustering begins, the matrix is viewed as containing maximum information. The cost of clustering, or the loss of information inherent in clustering is depicted in successive error matrices.

ORDINATION OF OTUS

A major weakness of cluster analysis is the inherent assumption that natural groups are present. If in fact populations vary in a continuous manner, then cluster analysis may result in highly artificial classifications. Ordination of OTUs on the first few principal axes is an independent method of determining the reality of groups indicated by cluster analysis.

The method of principal components has additional advantages in that it allows for "compression" of a large proportion of the total variance found in a multivariate system of correlated variables (characters in this case) into a few new, uncorrelated variables. These uncorrelated variables (principal components) are determined by orthogonal rotation of the original coordinate axes in such a manner as to minimize the covariance components of the sample variance-covariance matrix. Or, viewed in another way, the ordinates are sought whose direction cosines define lines such that the sums of squares of the projections of the OTUs onto the ordinates are maximized. The result is maximum variance among the OTUs, and hence maximum discrimination, along a few uncorrelated ordinates.

Assuming there is significant correlation among some of the original variables (characters), the first of the new, uncorrelated variables will "explain" the largest proportion of the variance in the original variance-covariance matrix. The exact proportion of the variance accounted for by the first principal component is the ratio of the first latent root of the sample variance-covariance matrix to the sum of the diagonal elements of that matrix. The second principal component will account for the next highest proportion of the cumulative variance and so on until all of the variance is accounted for. Details of principal component analysis can be found in any good textbook on multivariate statistics (e.g., Rao, 1952; Anderson, 1958).

In this study, principal components were used to examine similarities between OTUs based on projections of the OTUs onto the first three principal axes obtained from a matrix of correlations among characters (R-technique). I hoped that this method would provide a parsimonious summary of the relationships among the 32 OTUs and would either confirm or deny the results of cluster analysis.

FACTOR ANALYSIS

The mathematics of factor analysis is too complex to permit a detailed description of the method here. However, Harmon (1960), Cooley and Lohnes (1962), and Morrison (1967) are adequate references. Briefly, factor analysis may be viewed as a step beyond principal component analysis in that the uncorrelated principal axes are rotated to another set of coordinates which hopefully will demonstrate the relationships among the variables in their simplest form. The scores of the variables on the new simple structure axes (factors) are the "factor loadings," and these loadings represent correlations between variables and simple structure axes.

Factor analysis with OTUs as variables (Q-technique) has been used infrequently in taxonomy; this procedure, in certain forms, has been criticized by some statisticians (see Seal, 1966; Gower, 1966). However, Rohlf and Sokal (1962) obtained meaningful results (when compared to cluster analysis of the same data) with centroid factor analysis applied to three sets of species of bees. These authors viewed each of the rotated factors as a "type taxon," and the loading of an OTU on a rotated factor determined its affinity to that particular "type taxon." In this study factor analysis was done with a computer program (Oregon State University-BMDO3M) which employs a principal component solution with Varimax, orthogonal rotation. The correlation matrix was adjusted by placing the maximum absolute row values in the diagonal, and the number of factors preserved for rotation was equal to the number of positive eigenvalues. A second test was made by placing unities in the diagonals and preserving only those factors for rotation whose latent roots were equal to or greater than plus one.

RESULTS

LARVAL VARIATION

Body Proportions.—Ratio means and standard errors for larval populations are listed in Table 1. Many of these ratios varied significantly between populations, but because the ratios served as characters for multivariate comparisons there is no reason to discuss each ratio separately. However three ratios—(FLL + HLL)/AGL, HW/BL, and HL/BL—showed important trends and require further comment.

Figure 4 illustrates variation in the ratio (FLL + HLL)/AGL. The reciprocal of this ratio is called the "coupling value" and has previously been used in salamander taxonomy (Peabody, 1959; Brame and Murray, 1968). There is considerable significant variation among OTUs for this character, but beyond individual comparisons, two

TABLE 1

RATIO MEANS AND STANDARD ERRORS FOR LARVAL OTUS[1]

OTU	Ratio					
	1	2	3	4	5	6
1	.211 (.010)	.266 (.015)	.308 (.014)	.204 (.039)	.447 (.020)	1.163 (.019)
2	.214 (.005)	.259 (.010)	.306 (.006)	.204 (.019)	.463 (.012)	1.115 (.009)
3	.222 (.004)	.282 (.007)	.334 (.006)	.181 (.017)	.463 (.008)	1.185 (.007)
4	.219 (.004)	.258 (.005)	.305 (.005)	.177 (.014)	.469 (.006)	1.111 (.006)
5	.223 (.007)	.283 (.007)	.316 (.009)	.214 (.010)	.480 (.009)	1.183 (.012)
6	.221 (.008)	.257 (.009)	.300 (.007)	.222 (.014)	.497 (.007)	1.132 (.009)
7	.223 (.006)	.267 (.008)	.308 (.008)	.238 (.013)	.504 (.012)	1.158 (.010)
8	.216 (.005)	.250 (.007)	.294 (.009)	.228 (.013)	.501 (.010)	1.110 (.010)
9	.220 (.007)	.258 (.010)	.304 (.009)	.236 (.019)	.500 (.009)	1.155 (.009)
10	.222 (.005)	.268 (.008)	.304 (.005)	.237 (.020)	.497 (.006)	1.166 (.008)
11	.203 (.008)	.238 (.008)	.284 (.009)	.179 (.020)	.446 (.009)	1.052 (.011)
12	.234 (.013)	.247 (.013)	.289 (.009)	.232 (.018)	.535 (.010)	1.127 (.013)
13	.221 (.009)	.248 (.008)	.297 (.009)	.201 (.020)	.485 (.010)	1.116 (.013)
14	.224 (.008)	.269 (.008)	.316 (.008)	.215 (.019)	.514 (.009)	1.178 (.010)
15	.229 (.009)	.265 (.014)	.334 (.016)	.215 (.026)	.495 (.011)	1.240 (.028)
16	.228 (.023)	.267 (.013)	.339 (.016)	.214 (.053)	.467 (.028)	1.321 (.030)
17	.224 (.010)	.267 (.018)	.331 (.014)	.204 (.033)	.474 (.019)	1.257 (.020)
18	.211 (.007)	.278 (.007)	.332 (.009)	.226 (.019)	.478 (.008)	1.225 (.010)
19	.237 (.013)	.265 (.012)	.336 (.014)	.229 (.029)	.514 (.012)	1.274 (.015)
20	.235 (.009)	.263 (.010)	.333 (.015)	.222 (.032)	.505 (.015)	1.260 (.013)
21	.233 (.017)	.288 (.018)	.358 (.022)	.211 (.041)	.504 (.024)	1.426 (.026)
22	.240 (.012)	.268 (.021)	.344 (.019)	.235 (.026)	.546 (.014)	1.363 (.028)
23	.240 (.010)	.272 (.014)	.347 (.019)	.224 (.022)	.516 (.013)	1.343 (.013)
24	.234 (.015)	.273 (.020)	.399 (.004)	.205 (.049)	.514 (.025)	1.353 (.022)
25	.194 (.007)	.251 (.007)	.294 (.007)	.186 (.020)	.431 (.010)	1.032 (.011)
26	.177 (.006)	.249 (.007)	.292 (.006)	.154 (.027)	.385 (.012)	1.014 (.009)
27	.184 (.008)	.226 (.007)	.270 (.074)	.160 (.025)	.406 (.008)	0.954 (.008)
28	.175 (.011)	.232 (.007)	.277 (0.12)	.182 (.031)	.413 (.014)	0.954 (.011)
29	.180 (.005)	.242 (.006)	.278 (.008)	.176 (.012)	.429 (.007)	1.033 (.008)
30	.193 (.007)	.241 (.007)	.276 (.013)	.164 (.047)	.425 (.015)	1.009 (.012)
31	.167 (.007)	.233 (.018)	.277 (.017)	.144 (.026)	.415 (.012)	0.959 (.022)
32	.194 (.009)	.245 (.006)	.289 (.010)	.174 (.045)	.444 (.017)	1.028 (.013)

OTU	Ratio					
	7	8	9	10	11	12
1	.385 (.019)	.446 (.019)	.831 (.019)	.574 (.014)	.494 (.007)	.296 (.004)
2	.378 (.010)	.447 (.006)	.826 (.006)	.565 (.006)	.506 (.006)	.298 (.020)
3	.412 (.007)	.489 (.007)	.901 (.006)	.616 (.006)	.520 (.007)	.265 (.018)
4	.379 (.005)	.448 (.005)	.828 (.004)	.563 (.004)	.507 (.004)	.261 (.014)
5	.419 (.008)	.468 (.009)	.888 (.007)	.600 (.007)	.507 (.007)	.317 (.010)
6	.385 (.009)	.448 (.008)	.834 (.007)	.557 (.006)	.492 (.005)	.332 (.015)
7	.401 (.010)	.463 (.010)	.865 (.009)	.575 (.007)	.496 (.006)	.358 (.015)
8	.376 (.009)	.442 (.010)	.817 (.009)	.545 (.007)	.491 (.006)	.343 (.014)
9	.387 (.010)	.457 (.010)	.844 (.009)	.563 (.008)	.487 (.007)	.353 (.021)
10	.401 (.008)	.456 (.005)	.856 (.006)	.572 (.006)	.491 (.005)	.355 (.021)
11	.345 (.010)	.411 (.010)	.755 (.009)	.522 (.008)	.496 (.006)	.259 (.022)
12	.379 (.014)	.444 (.011)	.823 (.012)	.536 (.010)	.476 (.009)	.355 (.018)
13	.368 (.009)	.441 (.010)	.809 (.009)	.545 (.008)	.488 (.007)	.299 (.022)
14	.408 (.009)	.478 (.009)	.866 (.008)	.585 (.007)	.497 (.006)	.325 (.020)
15	.396 (.016)	.499 (.016)	.895 (.014)	.598 (.013)	.483 (.018)	.321 (.028)

TABLE 1-Cont'd

16	.391 (.015)	.498 (.020)	.889 (.016)	.606 (.012)	.459 (.019)	.314 (.061)
17	.393 (.019)	.487 (.015)	.881 (.015)	.598 (.013)	.475 (.014)	.301 (.036)
18	.411 (.007)	.491 (.009)	.920 (.008)	.610 (.008)	.498 (.004)	.334 (.021)
19	.401 (.012)	.509 (.015)	.910 (.012)	.601 (.012)	.472 (.008)	.346 (.030)
20	.395 (.009)	.501 (.013)	.896 (.009)	.595 (.012)	.472 (.007)	.334 (.036)
21	.433 (.017)	.538 (.019)	.970 (.017)	.645 (.019)	.453 (.012)	.318 (.048)
22	.414 (.022)	.532 (.020)	.947 (.021)	.612 (.019)	.449 (.010)	.363 (.022)
23	.412 (.017)	.527 (.019)	.939 (.016)	.619 (.015)	.461 (.006)	.339 (.024)
24	.414 (.026)	.513 (.060)	.927 (.014)	.612 (.007)	.452 (.022)	.310 (.056)
25	.359 (.008)	.420 (.009)	.780 (.008)	.545 (.006)	.528 (.006)	.265 (.022)
26	.345 (.009)	.405 (.008)	.750 (.008)	.541 (.006)	.534 (.005)	.213 (.029)
27	.318 (.007)	.380 (.007)	.698 (.006)	.496 (.006)	.520 (.005)	.224 (.026)
28	.328 (.009)	.391 (.015)	.719 (.012)	.509 (.009)	.534 (.005)	.257 (.034)
29	.346 (.007)	.397 (.008)	.743 (.006)	.520 (.005)	.504 (.005)	.252 (.013)
30	.344 (.010)	.393 (.016)	.737 (.013)	.517 (.010)	.513 (.005)	.233 (.050)
31	.330 (.021)	.391 (.019)	.721 (.019)	.510 (.016)	.531 (.010)	.204 (.028)
32	.354 (.009)	.417 (.013)	.771 (.011)	.534 (.080)	.520 (.006)	.251 (.050)

OTU	Ratio				
	13	14	15	16	17
1	.305 (.016)	1.261 (.011)	1.460 (.008)	.864 (.007)	.638 (.007)
2	.313 (.007)	1.208 (.011)	1.428 (.008)	.845 (.012)	.677 (.008)
3	.325 (.005)	1.269 (.009)	1.502 (.008)	.844 (.006)	.703 (.007)
4	.322 (.004)	1.176 (.005)	1.392 (.006)	.845 (.006)	.687 (.005)
5	.329 (.007)	1.273 (.008)	1.421 (.010)	.896 (.008)	.686 (.007)
6	.331 (.009)	1.164 (.008)	1.354 (.010)	.859 (.010)	.666 (.006)
7	.335 (.008)	1.198 (.007)	1.382 (.008)	.867 (.007)	.664 (.007)
8	.324 (.007)	1.157 (.007)	1.361 (.009)	.850 (.007)	.648 (.008)
9	.330 (.008)	1.174 (.009)	1.382 (.008)	.848 (.010)	.660 (.009)
10	.333 (.005)	1.203 (.008)	1.368 (.006)	.880 (.006)	.670 (.005)
11	.293 (.009)	1.176 (.008)	1.402 (.008)	.839 (.008)	.657 (.007)
12	.359 (.015)	1.058 (.016)	1.238 (.011)	.854 (.011)	.670 (.010)
13	.328 (.010)	1.125 (.012)	1.346 (.012)	.835 (.006)	.676 (.011)
14	.340 (.009)	1.200 (.010)	1.407 (.018)	.853 (.007)	.661 (.007)
15	.343 (.011)	1.154 (.013)	1.454 (.020)	.794 (.017)	.693 (.009)
16	.335 (.031)	1.169 (.027)	1.488 (.025)	.786 (.018)	.717 (.014)
17	.330 (.012)	1.191 (.021)	1.476 (.011)	.807 (.016)	.697 (.017)
18	.312 (.008)	1.318 (.007)	1.573 (.009)	.838 (.006)	.653 (.007)
19	.359 (.016)	1.117 (.019)	1.416 (.019)	.789 (.011)	.700 (.012)
20	.354 (.013)	1.116 (.014)	1.414 (.018)	.789 (.012)	.701 (.009)
21	.350 (.024)	1.235 (.031)	1.534 (.032)	.805 (.014)	.696 (.010)
22	.371 (.013)	1.116 (.017)	1.434 (.012)	.778 (.009)	.680 (.014)
23	.364 (.013)	1.134 (.014)	1.448 (.024)	.783 (.017)	.705 (.010)
24	.355 (.020)	1.167 (.019)	1.447 (.016)	.806 (.023)	.690 (.017)
25	.278 (.009)	1.292 (.008)	1.513 (.009)	.854 (.007)	.645 (.008)
26	.246 (.009)	1.402 (.008)	1.648 (.008)	.851 (.006)	.638 (.006)
27	.258 (.009)	1.232 (.007)	1.470 (.010)	.838 (.008)	.634 (.008)
28	.248 (.014)	1.325 (.012)	1.579 (.016)	.839 (.010)	.600 (.011)
29	.258 (.006)	1.342 (.008)	1.542 (.009)	.870 (.008)	.601 (.006)
30	.275 (.011)	1.252 (.009)	1.431 (.014)	.875 (.009)	.647 (.007)
31	.237 (.008)	1.392 (.018)	1.652 (.021)	.842 (.015)	.571 (.011)
32	.280 (.013)	1.265 (.008)	1.489 (.010)	.850 (.007)	.631 (.010)

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[1] Sample sizes and localities in Appendix I, localities mapped in Figures 3 and 14, OTUs 25-32 are *D. copei.*

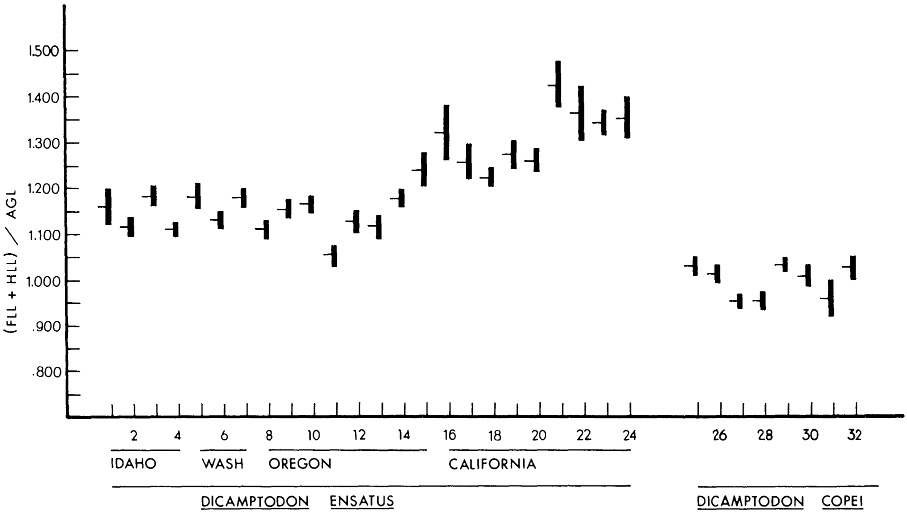

Fig. 4. Variation in the ratio (FLL + HLL)/AGL for larval *Dicamptodon*; means ± two standard errors; numbers on the abscissa refer to OTUs.

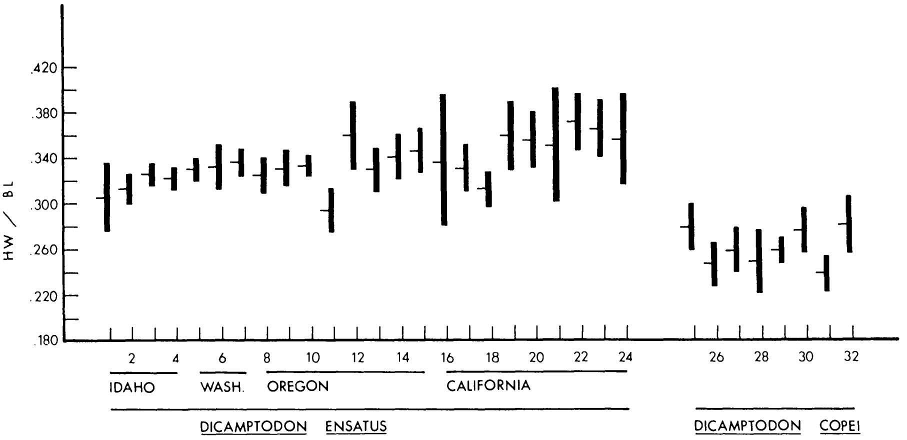

Fig. 5. Variation in the ratio HW/BL for larval *Dicamptodon*; means ± two standard errors; numbers on the abscissa refer to OTUs.

important trends are seen. Firstly, all populations of *D. copei* are significantly different from all populations of *D. ensatus* except for the Shoat Spring population (OTU 11) of *D. ensatus*. As will be seen, the Shoat Spring population is either intermediate between the two species or more similar to *D. copei* for many characters; justification for assigning the Shoat Spring population to *D. ensatus* will be deferred to the discussion. Secondly, southern Oregon and California populations of *D. ensatus* have higher values for this character than do more northern populations of *D. ensatus*.

Variation in the ratio HW/BL is summarized in Figure 5. There is a marked tendency for southern populations of *D. ensatus* to have higher values (wider heads) for this character than northerly populations. Variation appears to be clinal, with the exception of the Shoat Spring (OTU 11) and Nosoni Creek (OTU 18) populations which have lower values than might be expected. However, both of these populations are located on the easternmost periphery of the range of *D. ensatus* in southern Oregon and northern California, and the climate at both localities is relatively dry and hot. Peripheral isolation and suboptimum habitat may account for the peculiarities in many of the characters for these two populations.

All values of HW/BL for *D. copei* are lower than all values of *D. ensatus*, and most significantly so.

The ratio HL/BL shows a pattern of variation similar to that

TABLE 2

PREDICTED MEAN BODY MEASUREMENTS (MM) FOR LARVAL OTUS[1]

OTU	BL	AGL	HW	HL	FLL	HLL	TH
1	60.3	43.1	18.8	27.7	23.7	27.5	18.8
2	60.0	44.4	18.9	28.0	22.9	26.8	18.5
3	60.4	46.0	19.6	27.6	24.8	29.4	15.5
4	60.1	44.7	19.3	27.9	22.8	27.1	15.6
5	59.5	44.8	19.7	28.3	24.9	28.0	18.7
6	59.0	44.2	19.7	29.0	23.3	26.3	18.6
7	58.8	43.8	19.5	29.3	23.4	27.1	20.7
8	59.0	43.3	19.1	29.0	22.2	26.3	19.5
9	58.8	43.0	19.5	29.3	22.9	26.8	20.5
10	59.0	43.2	19.6	29.0	23.7	26.9	19.8
11	60.9	43.8	17.8	27.1	21.0	25.0	15.6
12	57.2	41.8	21.0	30.8	22.0	25.8	19.9
13	59.5	43.1	19.0	28.5	22.0	26.4	16.6
14	58.3	44.0	20.0	29.7	23.5	27.6	18.8
15	58.7	42.3	20.2	29.3	23.4	29.4	19.0
16	59.4	40.2	20.3	28.6	23.9	29.7	19.2
17	59.6	41.9	19.7	28.4	23.4	29.1	18.1
18	58.8	42.5	17.7	27.6	23.5	27.4	18.3
19	58.9	40.7	20.0	29.1	23.7	30.1	18.2
20	58.7	41.5	20.7	29.3	23.2	29.6	19.1
21	58.7	39.8	20.5	29.3	25.4	31.6	18.4
22	57.6	39.0	21.7	30.4	24.2	31.5	21.2
23	58.5	40.5	21.0	29.5	24.0	31.4	18.9
24	58.4	39.6	20.6	29.6	23.9	29.9	17.8
25	62.6	46.5	15.9	25.4	22.3	26.0	15.2
26	62.6	46.5	15.9	25.4	22.3	26.0	15.2
27	62.7	45.7	16.2	25.3	20.0	23.8	13.8
28	63.0	47.2	15.1	25.0	20.4	24.0	14.6
29	72.2	44.2	15.8	25.9	21.2	24.4	15.2
30	61.9	45.2	16.9	26.1	21.2	24.2	14.1
31	62.4	46.2	15.0	25.6	20.3	23.4	12.0
32	61.5	45.9	16.9	26.5	21.6	25.3	14.1

[1] Estimated from $\bar{y} = a + bx$ with a and b determined by least squares regression and x set at 88 mm SVL for all OTUs; see Appendix I for localities.

described above for HW/BL. These two ratios together merely reflect the fact that *D. copei* have smaller heads than *D. ensatus*, and that southern *D. ensatus* tend to have larger heads than northern *D. ensatus*.

Predicted mean body measurements ($\bar{y}$'s) for larval OTUs when SVL (as the predictor) is set at 88 mm are given in Table 2. Important trends discernible in the Table are as follows. In relation to SVL, *D. copei* generally has a longer body, greater axilla-groin distance, narrower and shorter head, shorter limbs, and lower tail fin than *D. ensatus*. Larval *D. ensatus* from the Klamath-Siskiyou Region and from other parts of California have larger heads and longer limbs than larvae of the same species from northern and inland (Idaho)

TABLE 3

COSTAL FOLDS BETWEEN ADPRESSED LIMBS FOR LARVAL OTUS

OTU	Frequency														$\bar{X}$
	+2.5	+2.0	+1.5	+1.0	+0.5	0.0	-0.5	-1.0	-1.5	-2.0	-2.5	-3.0	-3.5	-4.0	
1					2	2	10	1							-0.33
2					1	4	5								-0.02
3					4	17	8	1							-0.01
4				1	1	17	5	1							-0.01
5					1	6	6	7							-0.48
6				2	1	9	7	1							-0.01
7					1	8	7	4							-0.35
8					3	7	7	3							-0.03
9						7	8	4	1						-0.68
10							14	3							-0.59
11	1		3	12	2	5	2								+0.66
12				1	1	6	2								+0.05
13				2	3	4	6								+0.03
14						3	6	11	1						-0.73
15						1	2	2	1	1					-0.93
16							1	2	3	1					-1.29
17						1	1	4		2		1			-1.27
18							5	5	1						-0.82
19						1	1	6	3						-1.00
20						1	6	9	2						-0.78
21								1		2	2	1			-2.17
22								2	2					1	-1.80
23								4	3	2					-1.17
24								1	2	2	1				-1.75
25		3	6	11	8	2									+1.00
26		5	1	16	7	1									+1.04
27	1	11	7	4											+1.70
28		2	7	5	1										+1.33
29		1	2	12	4	1									+0.98
30		1	4	6	3										+1.11
31	1	2	1	1											+1.80
32			3	7	3	2									+0.87

populations. The Shoat Spring population (OTU 11) of *D. ensatus* is either intermediate between the two species or closer to *D. copei* for most of these ȳ's.

Costal Folds Between Adpressed Limbs.—Frequencies and means of costal folds between adpressed limbs are given in Table 3. For *D. ensatus*, limb overlap is greatest in southernmost populations. The Shoat Spring population (OTU 11) has the greatest mean non-overlap (+0.66) of any OTU assigned to *D. ensatus*.

Limbs of *D. copei* usually do not overlap, and the means of the 8 populations range from +0.87 to +1.80. Therefore the means for all populations of *D. copei* are higher than the means for all populations of *D. ensatus*. Over the size range used, there was no apparent ontogenetic variation for *D. ensatus*, but the number of folds between adpressed limbs increases with size in some populations of *D. copei* (Fig. 6).

Number of Trunk Vertebrae.—All specimens of both species had either 14 or 15 trunk vertebrae (Table 4). The modal number was 14 for all populations except Roaring Creek, Valley Co., Idaho (*D. ensatus*, OTU 1); Nine Foot Creek, Skamania Co., Washington (*D. copei*, OTU 26); and Merriman Creek, Grays Harbor Co., Washington (*D. copei*, OTU 32). These three populations are widely scattered geographically and apparently derived a mode of 15 trunk vertebrae independently. The fact that 2 of 8 populations of *D. copei* and only one rather isolated population of 24 populations of *D. ensatus* have a mode of 15 trunk vertebrae suggests that trunk elongation is more advantageous for *D. copei* than for *D. ensatus*. The narrow range of variation within populations (Table 4) and between populations reflects a conservative trend for this character which is common to most ambystomatids.

Number of Maxillary-Premaxillary Teeth.—Within-group correlation coefficients of number of maxillary-premaxillary teeth versus SVL are listed in Table 5. Although a few of the coefficients for *D.*

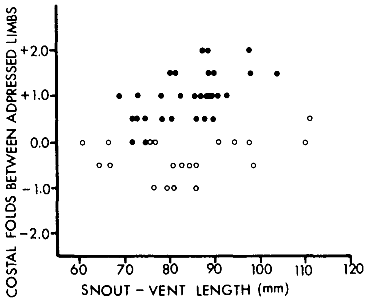

Fig. 6. Scatter diagram of number of costal folds between adpressed limbs in relation to SVL; solid circles are *D. copei* (OTU 25), open circles are *D. ensatus* (OTU 7).

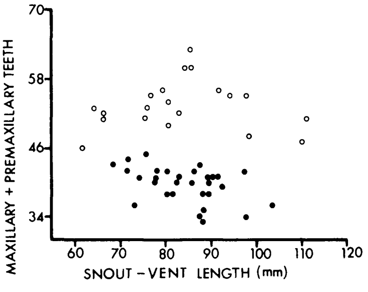

Fig. 7. Scatter diagram of number of maxillary-premaxillary teeth as a function of SVL; solid circles are *D. copei* (OTU 25), open circles are *D. ensatus* (OTU 7).

TABLE 4

NUMBER OF TRUNK VERTEBRAE AND PERCENT LARVAE WITH PALATOPTERYGOID TEETH[1]

			Palatopterygoid Teeth				
OTU	Trunk Vertebrae		Percent Specimens with Series			Mean Number of Teeth/Series	
	Frequency 14	15	Both Sides	Right Side	Left Side	Right	Left
1	3	21	0	0	0	0	0
2	15	0	0	0	0	0	0
3	34	0	0	0	0	0	0
4	32	2	0	0	0	0	0
5	19	1	25	45	25	5.6	5.0
6	22	2	30	30	45	4.8	5.1
7	22	0	30	30	70	6.0	6.2
8	30	0	20	25	30	7.0	7.2
9	28	2	36	43	64	7.7	8.3
10	29	1	53	59	71	6.3	8.1
11	28	0	0	0	0	0	0
12	24	0	70	80	70	8.9	8.9
13	28	2	0	0	0	0	0
14	29	1	48	57	57	8.3	8.6
15	NC	NC	57	57	72	7.3	8.2
16	NC	NC	43	43	57	10.0	7.0
17	18	2	56	67	56	6.5	7.2
18	17	2	1	27	36	6.3	5.5
19	NC	NC	36	45	45	3.8	4.6
20	NC	NC	94	100	94	6.3	7.8
21	NC	NC	0	0	0	0	0
22	NC	NC	0	0	0	0	0
23	12	0	0	0	0	0	0
24	12	0	0	0	0	0	0
25	9	0	0	0	0	0	0
26	8	28	0	0	0	0	0
27	25	2	0	0	0	0	0
28	27	1	0	0	0	0	0
29	29	3	0	0	0	0	0
30	22	2	0	0	0	0	0
31	NC	NC	0	0	0	0	0
32	7	20	0	0	0	0	0

[1] NC = no data for comparison.

ensatus are significant at $p < .05$, over half are not, which suggests that SVL contributes little to the variance of tooth number over the range of SVL studied. While most coefficients for *D. ensatus* are positive, all are negative for *D. copei*, and most significantly so. Therefore there is an inverse relationship between tooth number and size (age) in this species. Figure 7 shows these relationships in the form of a scatter diagram for the paratypes of *D. copei* (OTU 25) and sympatric *D. ensatus* (OTU 7).

TABLE 5

MAXILLARY-PREMAXILLARY AND VOMERINE TEETH FOR LARVAL OTUS[1]

OTU	Maxillary-Premaxillary Teeth				Vomerine Teeth			
	$\bar{X}$	SE	r-SVL	r-HW	$\bar{X}$	SE	r-SVL	r-HW
1	58.00	0.92	.440	.512	43.47	1.08	.470	.537
2	56.30	0.68	.109	.131	39.80	0.59	.683	.693
3	61.27	0.58	.176	.157	41.33	0.47	.336	.308
4	59.12	0.56	.241	.177	40.16	0.42	.039	.057
5	54.90	0.67	-.032	-.070	39.50	0.75	-.412	-.348
6	57.05	0.58	.049	.032	41.45	0.45	-.186	-.179
7	53.40	0.97	.025	.030	47.50	1.08	.495	.472
8	53.70	0.72	-.471	-.420	46.55	0.53	.096	.154
9	58.29	0.77	.418	.380	46.00	0.97	.169	.086
10	55.47	0.69	-.069	.016	42.35	0.61	.036	.134
11	47.16	0.66	.301	.396	37.12	0.50	.516	.553
12	56.30	1.00	.154	.286	43.50	1.19	-.340	-.240
13	53.75	0.53	.212	-.052	38.95	0.46	-.001	.148
14	57.05	0.63	.387	.375	45.71	0.95	.111	.152
15	59.14	0.91	-.023	-.066	47.43	2.52	-.004	-.155
16	56.86	3.65	.012	.208	44.71	3.68	-.268	-.136
17	56.11	1.31	.845	.779	42.00	1.31	.322	.252
18	52.09	1.06	.334	.405	42.00	0.66	-.331	-.215
19	57.18	1.30	.218	.450	47.64	1.18	-.204	-.199
20	57.06	0.55	.462	.469	48.22	0.84	.420	.399
21	62.50	2.69	.667	.631	50.67	2.22	.834	.757
22	58.40	2.61	.183	.263	48.60	2.30	.350	.447
23	62.44	1.40	.682	.689	46.89	1.73	.254	.303
24	67.50	1.69	-.049	-.060	53.17	2.73	.843	.884
25	39.53	0.54	-.442	-.371	34.40	0.75	-.240	-.203
26	48.90	0.77	-.114	-.106	36.33	0.63	.093	.087
27	37.74	0.82	-.329	-.481	35.43	0.53	-.399	-.434
28	39.80	0.96	-.510	-.553	36.73	0.56	-.130	-.043
29	46.48	0.62	-.562	-.573	34.19	0.51	.188	.272
30	47.79	1.29	-.582	-.604	42.36	0.98	-.630	-.620
31	47.20	0.49	-.346	-.473	43.80	1.46	.812	.799
32	47.80	0.98	-.477	-.373	42.86	0.67	.722	.700

[1] Within-group correlation coefficients of tooth number with SVL and with head width (HW) are listed; sample sizes in Appendix I.

Important information may be obscured by these statistics because a third possible correlate, sexual maturity, has not so far been considered. *D. copei* mature at a small size compared to *D. ensatus* (Nussbaum, 1970), and all specimens of *D. copei* used in this study were sexually mature. But *D. ensatus* larvae are not sexually mature, with noted exceptions, over the size range used. It is possible, then, that the inverse relationship between number of maxillary-premaxillary teeth and SVL in *D. copei* is related solely to the precocious sexual maturity of this species. One way to resolve this problem would be to examine tooth number in larger, paedogenetic *D. ensatus* to see if there is tooth loss in this species with the advent of sexual maturity. I am approaching this problem with tooth counts on individual bones, and the data will be presented elsewhere. One clue stems from the observation that the Shoat Spring population of *D. ensatus* (OTU 11) consists of relatively small, sexually mature specimens, but like most other populations of *D. ensatus*, the correlation coefficient for tooth number versus SVL is positive (.301). This fact argues against the hypothesis that factors associated with sexual maturity are responsible for tooth loss in *D. copei.*

The correlation coefficients in Table 5 are within-group coefficients and reflect ontogenetic relationships. Characters, or character means, may be correlated between populations, and between-group r's may indicate phylogenetic trends. The character which correlated most highly with mean number of maxillary-premaxillary teeth across the 32 larval OTUs was mean HW (r = .610). When the effect of size (mean SVL) is removed by partial correlation, the correlation between mean HW and mean number of maxillary-premaxillary teeth is even greater (.825). Hence, although the number of maxillary-premaxillary teeth is not necessarily positively correlated with HW within populations (ontogenetically), and indeed may be significantly negatively correlated, populations that have wider heads on the average also have higher numbers of maxillary-premaxillary teeth.

Since the range of SVL was about the same for all populations, no attempt was made to correct for size-dependent variation, and simple means and standard errors are reported for maxillary-premaxillary teeth (Table 5 and Figure 8). The Shoat Spring population of *D. ensatus* (OTU 11) has significantly fewer maxillary-

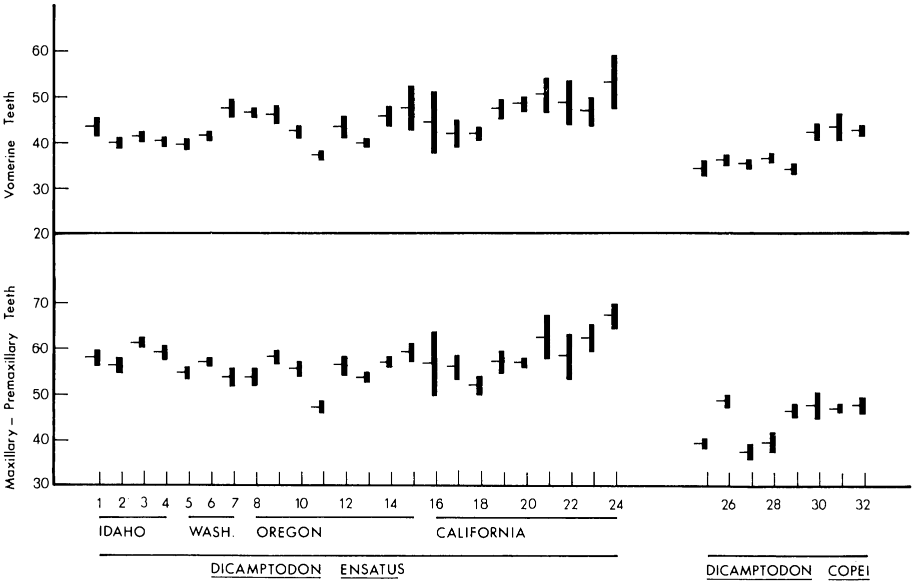

Fig. 8. Variation in mean number of maxillary-premaxillary and vomerine teeth for larval *Dicamptodon*; means ± two standard errors; numbers on the abscissa refer to OTUs (see Table 5).

premaxillary teeth than all other populations of *D. ensatus* and is not significantly different from five of the eight populations of *D. copei.* All OTUs of the latter species are significantly different from all OTUs of *D. ensatus* with the exception of the Shoat Spring population. Southern populations of *D. ensatus* have higher means than northern populations of the same species.

Number of Vomerine Teeth.—Scatter diagrams of vomerine teeth versus SVL (Fig. 9) show that there is little increase or decrease in tooth number with size. The within-group r's for number of vomerine teeth versus SVL and number of vomerine teeth versus HW are listed in Table 5. About two-thirds of the coefficients are not significant, and the significant coefficients show both positive and negative correlations. Since SVL did not, on the average, contribute significantly to the variance of vomerine tooth number, reporting these data as means seems justified.

Variation is summarized in Table 5, and Figure 8. The pattern of variation is similar to that for maxillary-premaxillary teeth, and indeed the between-group correlation of mean number of vomerine teeth versus mean number of maxillary-premaxillary teeth is significant and high (.753).

Palatopterygoid Teeth.—The presence of palatopterygoid teeth varies considerably within and between populations (Table 4). These teeth are entirely lacking in the four Idaho populations (OTUs 1-4), and none was present in many other specimens from Idaho. All populations of *D. ensatus* from Washington, Oregon, and California have individuals with palatopterygoid teeth with the following exceptions: Shoat Spring (OTU 11), Mary's Peak (OTU 13), Sonoma Co. (OTU 21), Napa Co. (OTU 22), Marin Co. (OTU 23), and south of San Francisco Bay (OTU 24). The fact that individuals from Sonoma Co., California southward lack palatopterygoid teeth is somewhat surprising since the population from Mendocino County (OTU 20) just to the north has the highest percentage of individuals with these teeth. In *D. ensatus,* the number of palatopterygoid teeth/series ranges from 1 to 15; the means range from 3.8/series to

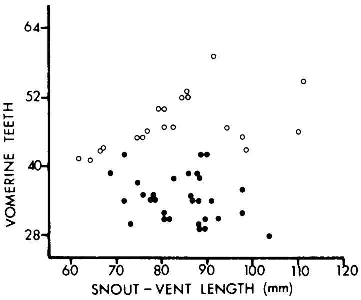

Fig. 9. Scatter diagram of number of vomerine teeth as a function of SVL; solid circles are *D. copei* (OTU 25), open circles are *D. ensatus* (OTU 7).

10.0/series, with no readily discernible pattern of variation. *D. copei* lack palatopterygoid teeth.

Palatopterygoid teeth, when present, are normally lost at metamorphosis. However, MVZ 51497, a recently transformed specimen, and MVZ 18327 and FMNH 84806, both older individuals, have short series of teeth on each side lateral to and aligned with the main vomerine series. Each lateral series is separated from the medial series by a distinct diastema, which results in a pattern similar to that seen in *Ambystoma gracile* and certain other species of *Ambystoma.* I believe these outer series result from an anomalous failure of the palatine portion of the palatopterygoid bone and the associated field for tooth development to be absorbed at metamorphosis. Rather, a portion of the palatine bone and associated teeth are incorporated into the reconstructed vomer. This anomalous condition may reflect a phylogenetically earlier, normal pattern of development identical with that seen in *Ambystoma gracile.*

Number of Gill Rakers.—Within-group correlation coefficients and scatter diagrams (not reproduced here) of number of gill rakers versus SVL indicate no ontogenetic change in number of gill rakers. However, between-group correlations show a significant relationship between head width and number of gill rakers for each of the six

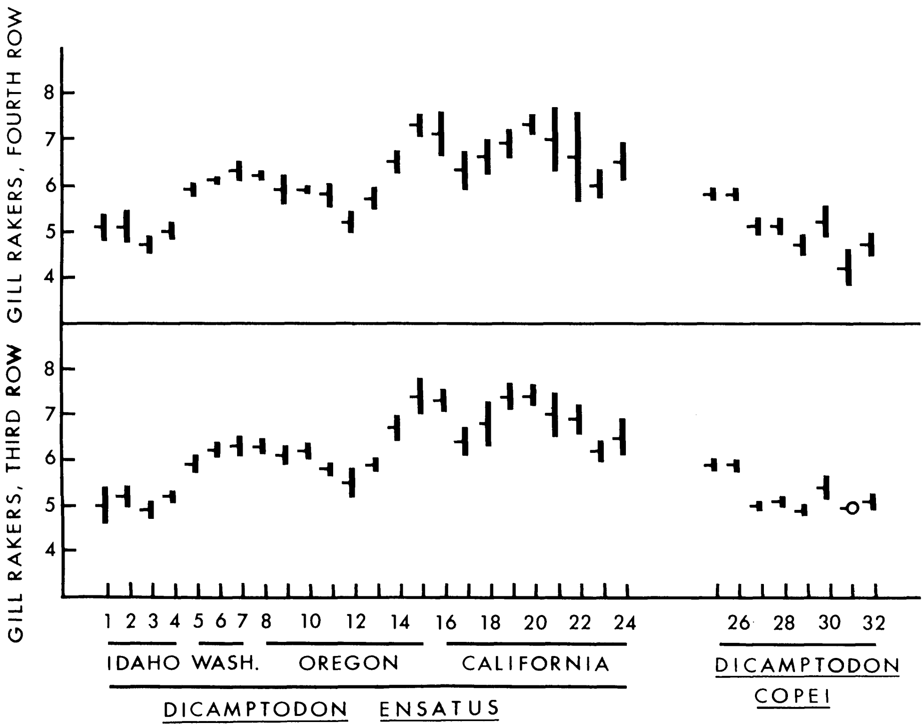

Fig. 10. Variation in the number of gill rakers on the third and fourth rows in *Dicamptodon*; means ± two standard errors; numbers of the abscissa refer to OTUs. OTU 31 had no variance on the third row.

TABLE 6

MEAN NUMBER OF GILL RAKERS PER ROW IN LARVAL *DICAMPTODON*[1]

OTU	1		2		3		4		5		6	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
1	5.20	0.17	5.07	0.12	5.00	0.20	5.13	0.17	4.33	0.19	3.40	0.13
2	6.00	0.21	5.30	0.15	5.20	0.13	5.10	0.18	4.30	0.15	3.20	0.20
3	5.23	0.09	5.00	0.05	4.93	0.10	4.70	0.11	4.38	0.10	3.63	0.10
4	5.36	0.14	5.16	0.07	5.04	0.07	5.00	0.10	4.20	0.15	3.40	0.12
5	6.00	0.15	5.90	0.16	5.90	0.10	5.85	0.08	4.95	0.09	4.00	0.00
6	6.70	0.16	6.35	0.15	6.15	0.11	6.05	0.05	5.20	0.17	4.60	0.13
7	6.90	0.07	6.80	0.09	6.30	0.13	6.25	0.10	5.70	0.13	4.70	0.11
8	6.75	0.12	6.85	0.08	6.25	0.10	6.15	0.08	5.50	0.15	4.85	0.11
9	6.57	0.17	6.29	0.16	6.07	0.13	5.93	0.16	4.86	0.14	4.29	0.13
10	6.77	0.14	6.53	0.12	6.18	0.10	5.94	0.06	5.29	0.11	4.29	0.11
11	6.24	0.14	5.92	0.17	5.76	0.09	5.80	0.14	5.12	0.12	3.96	0.09
12	6.00	0.15	6.10	0.18	5.50	0.17	5.20	0.13	4.40	0.16	3.40	0.22
13	6.15	0.17	5.65	0.13	5.85	0.08	5.70	0.13	4.60	0.13	4.10	0.10
14	6.81	0.16	6.86	0.17	6.67	0.14	6.48	0.15	5.67	0.16	5.05	0.15
15	7.29	0.29	7.71	0.29	7.43	0.20	7.29	0.18	6.43	0.20	5.43	0.20
16	7.43	0.30	7.00	0.22	7.29	0.18	7.14	0.26	5.86	0.14	5.00	0.22
17	6.67	0.17	6.78	0.22	6.44	0.18	6.33	0.24	5.33	0.17	4.56	0.29
18	7.18	0.23	6.82	0.18	6.82	0.26	6.64	0.20	5.64	0.15	5.27	0.30
19	7.64	0.15	7.55	0.16	7.36	0.15	6.91	0.16	6.00	0.00	5.18	0.12
20	7.67	0.14	7.50	0.15	7.44	0.12	7.33	0.11	6.39	0.16	5.67	0.14
21	7.83	0.17	7.00	0.00	7.00	0.26	7.00	0.37	5.83	0.17	5.00	0.26
22	7.20	0.45	7.00	0.00	6.80	0.45	6.60	0.55	5.40	0.55	5.20	0.45
23	7.56	0.38	6.78	0.22	6.22	0.15	6.00	0.17	6.11	0.11	5.33	0.24
24	6.83	0.31	6.67	0.21	6.50	0.22	6.50	0.22	5.17	0.17	4.67	0.21
25	6.27	0.08	6.03	0.08	5.93	0.08	5.80	0.07	5.03	0.06	4.00	0.05
26	5.90	0.10	5.83	0.08	5.93	0.08	5.83	0.08	4.23	0.10	3.43	0.11
27	4.78	0.09	5.13	0.07	4.96	0.08	5.13	0.10	4.13	0.13	3.13	0.13
28	5.13	0.17	5.40	0.16	5.07	0.07	5.13	0.09	4.27	0.12	3.20	0.14
29	4.62	0.11	5.10	0.10	4.91	0.07	4.67	0.13	3.67	0.11	2.91	0.14
30	5.07	0.07	5.14	0.10	5.36	0.13	5.21	0.19	4.43	0.14	3.43	0.14
31	3.80	0.20	4.40	0.24	5.00	0.00	4.20	0.20	3.80	0.20	3.00	0.00
32	4.67	0.13	4.73	0.18	5.13	0.09	4.67	0.13	3.60	0.13	2.53	0.13

[1] Anteriormost to posteriormost rows (1-6); sample sizes in Appendix I.

rows. The six r's range from .459 to .568. There is no between-group relationship between SVL and the number of gill rakers, as the six r's are not significantly different from zero.

Table 6 and Figure 10 show that southern Oregon and California populations of *D. ensatus* have higher mean gill raker counts for all six rows than northern populations and that *D. copei* generally have fewer gill rakers than *D. ensatus*, especially on the first, second, fifth, and sixth rows.

VARIATION IN TRANSFORMED *D. ENSATUS*

Body Proportions.—The 17 mean ratios and their standard errors for each of the 12 OTUs composed of transformed specimens are listed in Table 7. The ratios HW/SVL and HL/BL (ratios 1 and 5) increase in an imperfect cline from north to south. These trends indicate that southern transformed *D. ensatus* have larger heads than specimens from northern populations, a relationship which was shown above to be true for larval *D. ensatus* as well.

TL/SVL (ratio 4) shows that individuals from Idaho (OTU 1) have the shortest tails relative to SVL and that specimens from Washington and from Benton and Lincoln Counties, Oregon also have relatively short tails. Individuals from all populations from California, with the exception of those from Humboldt County (OTU 7), have relatively long tails. The longest tails are found in specimens from Lake County, California.

Figure 11 illustrates geographic variation in the ratio (FLL + HLL)/AGL (ratio 6). The first four OTUs (Idaho, Washington, and northern Oregon counties) have significantly lower values for this character than populations from southern Oregon and California, with the exception of the Humboldt County population.

The predicted y's for the 12 OTUs of transformed *D. ensatus* are given in Table 8. If OTU 7 (Humboldt County) is ignored, the following generalizations can be made. Individuals from the Klamath-Siskiyou Mountains and more southerly regions have shorter AGL's, wider and longer heads, longer limbs, and longer tails than specimens from Idaho, Washington and Oregon north of the Klamath-Siskiyou Mountains.

Costal Folds Between Adpressed Limbs.—Variation in the number of costal folds between adpressed limbs, estimated to the nearest 0.5 fold, is summarized in Table 9. Small sample sizes and unavoidable error associated with straightening the limbs and trunks of poorly preserved museum specimens reduce the value of these data. However, greater limb overlap is evident in populations south of the Klamath-Siskiyou Mountains (OTUs 5-12) than in populations north of this region (OTUs 1-4) with the exception of the Humboldt County population (OTU 7).

Number of Maxillary-Premaxillary Teeth.—For most of the 12 OTUs there is no significant correlation between SVL and number of maxillary-premaxillary teeth (Table 10), and there is no sexual dimorphism in tooth number. For these reasons, simple population means are reported.

Between-group correlation coefficients for mean number of maxillary-premaxillary teeth versus mean SVL and versus mean HW are .058 and .256 respectively. The variable that correlated highest

TABLE 7

RATIO MEANS FOR TRANSFORMED *DICAMPTODON ENSATUS*[1]

OTU	Ratio					
	1	2	3	4	5	6
1	.215 (.02)	.266 (.01)	.329 (.02)	.738 (.01)	.376 (.01)	1.215 (.01)
2	.215 (.01)	.264 (.02)	.326 (.02)	.764 (.02)	.400 (.02)	1.231 (.03)
3	.208 (.01)	.265 (.01)	.327 (.01)	.757 (.01)	.399 (.01)	1.243 (.02)
4	.211 (.01)	.256 (.03)	.327 (.02)	.764 (.02)	.391 (.02)	1.233 (.04)
5	.221 (.01)	.270 (.02)	.347 (.03)	.755 (.02)	.404 (.01)	1.327 (.03)
6	.221 (.02)	.278 (.02)	.347 (.02)	.780 (.02)	.425 (.02)	1.363 (.02)
7	.213 (.01)	.261 (.01)	.328 (.01)	.741 (.02)	.404 (.01)	1.233 (.02)
8	.222 (.02)	.279 (.02)	.352 (.01)	.798 (.02)	.426 (.02)	1.348 (.02)
9	.234 (.02)	.270 (.03)	.344 (.02)	.829 (.03)	.424 (.01)	1.319 (.03)
10	.231 (.01)	.275 (.02)	.362 (.02)	.770 (.04)	.435 (.02)	1.405 (.03)
11	.229 (.01)	.268 (.01)	.342 (.01)	.764 (.01)	.428 (.01)	1.293 (.02)
12	.220 (.01)	.272 (.01)	.350 (.01)	.789 (.01)	.414 (.01)	1.336 (.02)

OTU	Ratio					
	7	8	9	10	11	12
1	.366 (.01)	.453 (.02)	.819 (.02)	.595 (.02)	.490 (.01)	1.016 (.01)
2	.370 (.03)	.456 (.02)	.826 (.02)	.590 (.02)	.479 (.02)	1.069 (.02)
3	.370 (.02)	.457 (.01)	.827 (.01)	.591 (.01)	.476 (.01)	1.059 (.01)
4	.356 (.03)	.455 (.03)	.812 (.03)	.583 (.02)	.473 (.02)	1.063 (.02)
5	.379 (.02)	.488 (.03)	.866 (.02)	.617 (.02)	.465 (.01)	1.089 (.02)
6	.395 (.03)	.495 (.02)	.890 (.03)	.625 (.02)	.458 (.02)	1.111 (.03)
7	.367 (.01)	.460 (.02)	.827 (.01)	.589 (.01)	.478 (.01)	1.040 (.02)
8	.398 (.02)	.502 (.02)	.900 (.02)	.631 (.01)	.468 (.01)	1.138 (.02)
9	.385 (.03)	.490 (.02)	.875 (.02)	.615 (.02)	.466 (.02)	1.181 (.02)
10	.395 (.02)	.520 (.02)	.915 (.02)	.638 (.02)	.454 (.02)	1.105 (.04)
11	.382 (.01)	.489 (.01)	.871 (.01)	.610 (.01)	.472 (.01)	1.091 (.01)
12	.384 (.01)	.495 (.01)	.879 (.01)	.622 (.01)	.465 (.01)	1.115 (.01)

OTU	Ratio				
	13	14	15	16	17
1	.294 (.02)	1.238 (.03)	1.536 (.03)	.806 (.01)	.784 (.02)
2	.301 (.02)	1.227 (.02)	1.514 (.01)	.810 (.01)	.754 (.01)
3	.291 (.01)	1.273 (.01)	1.570 (.01)	.811 (.01)	.730 (.01)
4	.294 (.01)	1.212 (.03)	1.549 (.03)	.783 (.01)	.751 (.02)
5	.311 (.01)	1.218 (.02)	1.569 (.03)	.776 (.02)	.770 (.01)
6	.314 (.02)	1.258 (.01)	1.574 (.01)	.799 (.01)	.740 (.02)
7	.299 (.02)	1.228 (.02)	1.540 (.02)	.797 (.01)	.739 (.01)
8	.317 (.02)	1.256 (.03)	1.582 (.02)	.794 (.01)	.744 (.01)
9	.333 (.02)	1.157 (.04)	1.474 (.03)	.786 (.02)	.784 (.02)
10	.332 (.02)	1.190 (.01)	1.567 (.02)	.760 (.01)	.762 (.01)
11	.328 (.01)	1.167 (.01)	1.491 (.01)	.783 (.01)	.766 (.01)
12	.312 (.01)	1.233 (.01)	1.587 (.01)	.777 (.01)	.753 (.01)

[1] Standard errors in parentheses; see Appendix I for sample sizes.

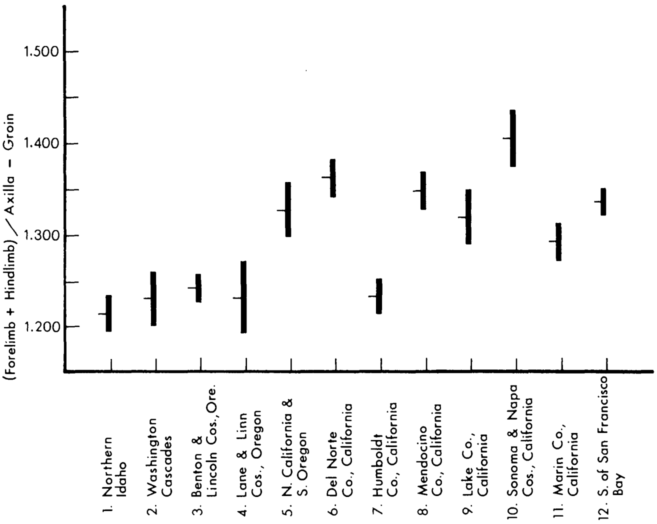

Fig. 11. Variation in the ratio (FLL + HLL)/AGL for transformed *D. ensatus*; means ± two standard errors.

TABLE 8

PREDICTED MEAN BODY MEASUREMENTS (MM) FOR TRANSFORMED *D. ENSATUS*[1]

OTU	BL	AGL	HW	HL	FLL	HLL	TL
1	79.9	53.9	23.5	30.1	29.3	36.3	81.3
2	78.5	52.7	23.7	31.5	29.2	36.0	83.9
3	78.7	52.3	22.9	31.6	29.1	35.9	83.3
4	78.3	50.0	23.2	31.7	30.0	37.2	84.3
5	78.4	51.2	24.4	31.7	29.7	38.3	85.4
6	77.4	50.8	24.4	32.6	30.6	38.4	85.9
7	78.2	52.3	23.5	31.8	28.9	36.4	81.5
8	77.5	51.7	24.2	32.5	30.8	38.6	87.9
9	76.9	51.4	25.6	33.1	31.3	39.4	87.6
10	76.8	50.0	25.2	33.2	30.0	39.6	86.1
11	76.9	51.6	25.4	33.1	29.9	38.0	83.9
12	77.7	51.0	24.3	32.3	30.0	38.6	86.5

[1] Estimated from $\bar{y} = a + bx$ with a and b determined by least squares regression and x set at 110 mm SVL for all OTUs; localities in Appendix I.

with the mean number of maxillary-premaxillary teeth on a between-group basis was mean number of vomerine teeth (r = .854).

Variation among means shows that individuals from the extreme southern portion of the range (south of San Francisco Bay, OTU 12) have the highest number of maxillary-premaxillary teeth (Fig. 12). Specimens from Marin, Napa, Sonoma, Lake, and Mendocino counties, California also have high numbers of maxillary-premaxillary teeth in comparison with northern specimens.

TABLE 9

COSTAL FOLDS BETWEEN ADPRESSED LIMBS FOR TRANSFORMED *DICAMPTODON ENSATUS*[1]

OTU	Number of Costal Folds													
	-4.5	-4.0	-3.5	-3.0	-2.5	-2.0	-1.5	-1.0	-0.5	0.0	+0.5	+1.0	+1.5	$\overline{X}$
1							3	7		2				- .96
2				1	2	4	3		1	1			1	-1.57
3					2	7	9	6	3	3				-1.33
4					1		2	2			1	1		- .86
5				1	2	3	1							-2.21
6				2		6	1	1						-2.05
7				1	1	3	4	6	2	2		1		-1.18
8	1			3		1	3	1						-2.33
9				1	1	1	1	2						-1.83
10	1		1	2	4		2	1						-2.55
11			1	6	3	8	5	7	3	1				-1.79
12		1	4	8	3	8	4	2	1		1			-2.29

[1] Frequencies and means listed; sample sizes in Appendix I.

TABLE 10

MAXILLARY-PREMAXILLARY AND VOMERINE TEETH FOR TRANSFORMED *DICAMPTODON ENSATUS*[1]

OTU	Maxillary-Premaxillary Teeth				Vomerine Teeth			
	$\overline{X}$	SE	r-SVL	r-HW	$\overline{X}$	SE	r-SVL	r-HW
1	88.75	1.18	.071	.006	40.50	1.10	-.302	-.368
2	80.77	2.00	.416	.420	33.54	1.23	.176	-.270
3	80.53	1.18	.213	.213	32.27	0.81	-.164	-.155
4	88.86	2.06	.687	.680	38.57	0.92	.291	.289
5	81.29	6.00	.727	.687	39.14	2.34	.768	.734
6	84.40	2.20	-.663	-.548	36.20	1.33	-.047	-.062
7	84.25	2.49	.232	.218	37.25	0.73	.070	-.041
8	91.88	3.40	-.190	-.213	41.25	2.85	-.012	-.037
9	91.50	3.71	-.275	-.485	40.00	1.21	.807	.752
10	96.91	3.98	-.077	-.126	39.91	1.72	.143	.128
11	95.76	1.58	-.045	-.055	42.00	0.81	.056	.033
12	103.44	2.41	-.110	-.087	44.31	0.93	.149	.172

[1] Within-group correlation coefficients for tooth number versus SVL and HW are listed; sample sizes in Appendix I.

Number of Vomerine Teeth.—As indicated by the relatively high between-group correlation between mean number of maxillary-premaxillary teeth and mean number of vomerine teeth ($r = .854$), the two vary in the same direction, and hence what has been written

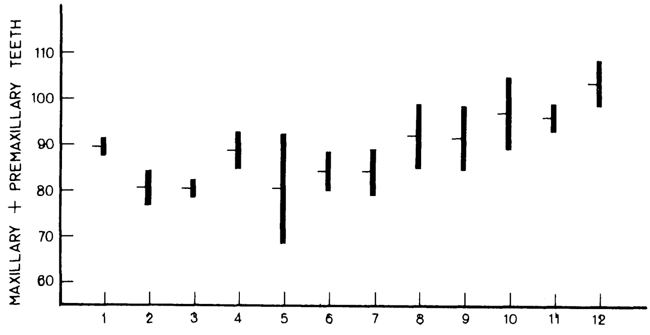

Fig. 12. Variation in number of maxillary-premaxillary teeth in transformed *D. ensatus*; means ± two standard errors; numbers on abscissa refer to OTUs, see Fig. 11.

above on geographic variation in the number of maxillary-premaxillary teeth also largely applies to variation in the number of vomerine teeth (Table 10).

MULTIVARIATE COMPARISONS OF OTUS

Comparison of Larval Populations.—Figure 13 is a phenogram which shows the results of HGroup cluster analysis on the d_{jk} matrix based on 25 characters. The characters are the means of the 17 ratios, mean number of maxillary-premaxillary teeth, mean number of vomerine teeth, and mean number of gill rakers on each of the six rows. At $d_{jk} = 2.0$, there are four groups designated A, B, C, and D. Group A is composed of populations of *D. ensatus* from California and extreme southern Oregon. Group A can be divided into a southern subgroup (OTUs 21, 22, 23, and 24) and a northern subgroup (OTUs 15, 16, 17, 18, 19 and 20) which are geographically divided somewhere in southern Mendocino County.

Group B may be described as a Cascade and Oregon Coast Range group of *D. ensatus*. Two northern Coast Range populations (OTUs 12 and 13) form a subgroup within Group B. OTU 14 is a southern Oregon coastal population, but it links with the Cascade subgroup of Group B, and this fact may reflect the mingling of the Coast and Cascade Ranges in southwestern Oregon.

Group C is primarily a Rocky Mountain group of *D. ensatus*; however, OTU 5, which is the northernmost Cascade population in Washington, also joins with this group. It is evident that Group B and Group C are more similar to each other than to the other groups.

Group D is widely separated phenetically from the first three groups and, with one exception, contains populations which I recognize as *D. copei*. The exception is OTU 11, Shoat Spring, which for reasons discussed below I assign to *D. ensatus*.

An unweighted-pair-group (UPGM) cluster analysis (Sokal and

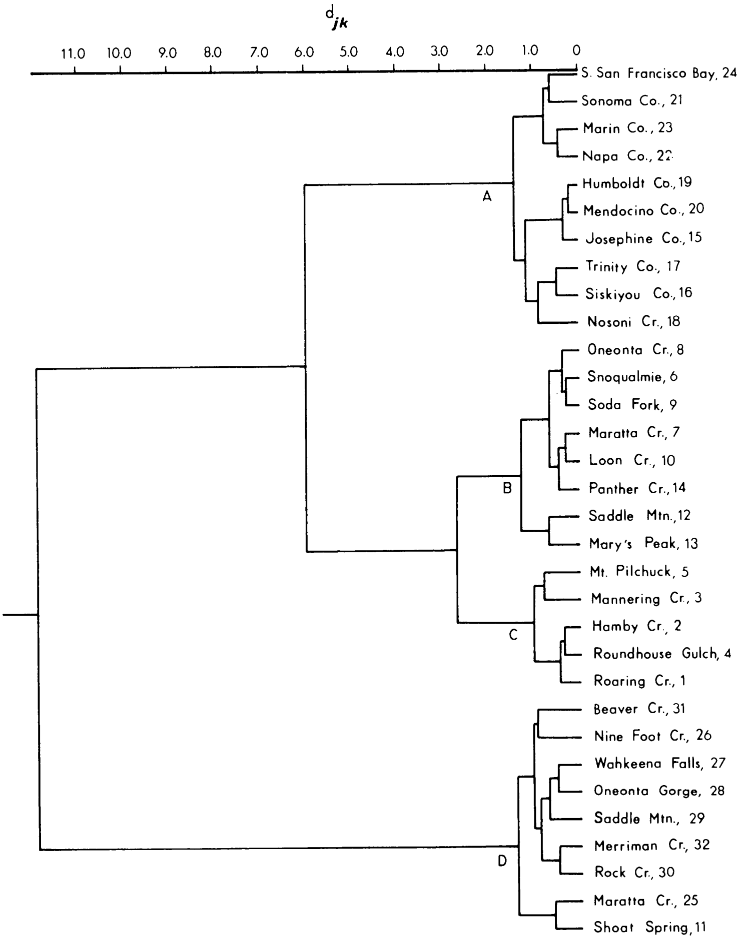

Fig. 13. Phenogram of larval OTUs based on HGroup cluster analyses of the d_{jk} matrix.

Michener, 1958) was performed on the between-group correlation matrix based on the same 25 characters listed above for HGroup analysis. The correlation coefficients were transformed to Fisher's z statistic before clustering. The results were similar to HGroup analysis, with minor differences in linkage at the lower levels. The results have been used here only to illustrate similarities between populations of larval *D. ensatus* in relation to geography (Figures 14 and 15).

Principal components were calculated from a standardized character by OTU (25 by 32) matrix. The 25 characters were the same as listed for HGroup analysis; R-technique was used with projection of the larval OTUs onto the component axes. For a description of the matrix algebra involved in determining the position of individuals (OTUs) on component axes see Cooley and Lohnes (1971). The first three principal components accounted for 92 percent of the total

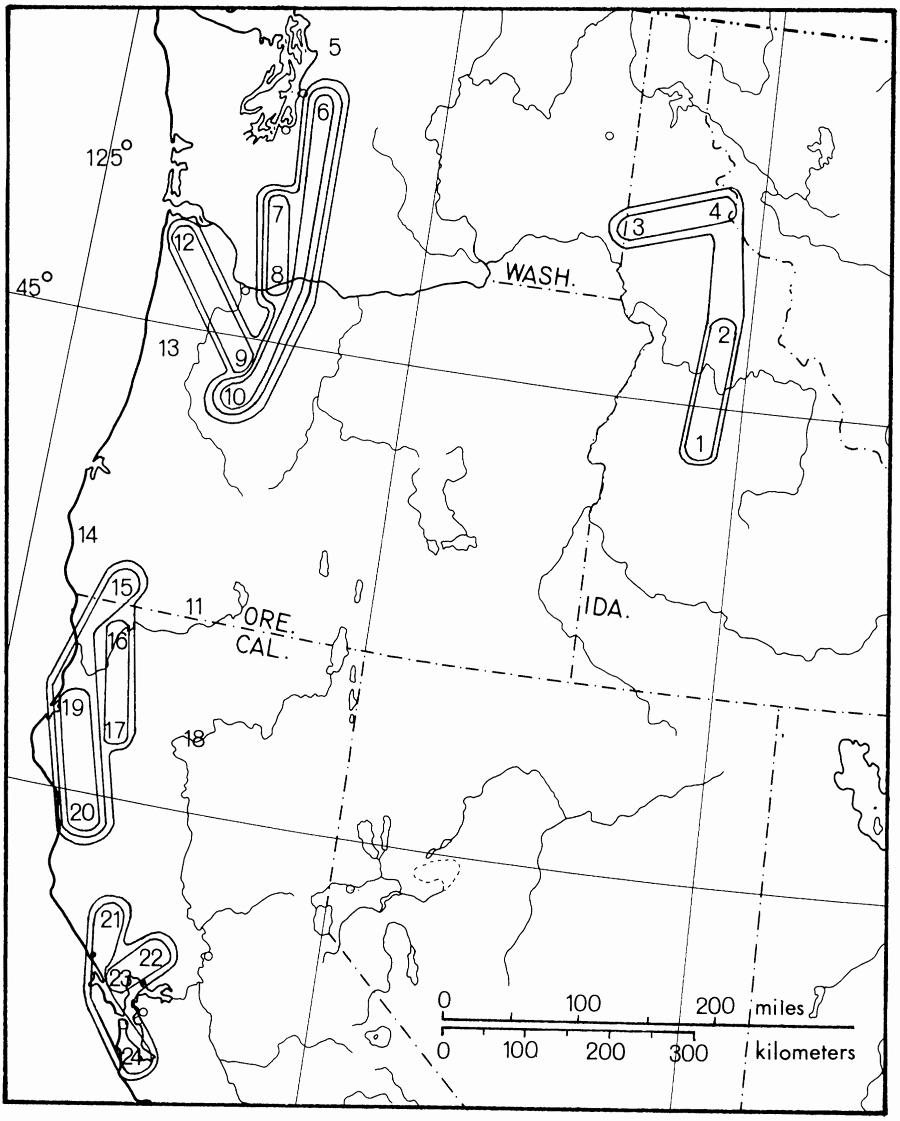

Fig. 14. Clusters of OTUs of larval *D. ensatus* shown in relation to geography. UWPG clustering of the r_{jk} matrix. Successive rings indicate more inclusive groupings. Results of first 15 cycles shown.

variance in the multivariate system, and only the first three components were used in subsequent analysis.

Ordination of the larval OTUs on the first two and three principal axes is illustrated in Figures 16 and 17 respectively. In Figure 16, lines have been drawn around the OTUs which formed the four major groups in HGroup and UPGM cluster analysis; it is apparent that the first two principal components, which account for 84 percent of the total variance, discriminate the four groups reasonably well. Furthermore, the linear distances between the four

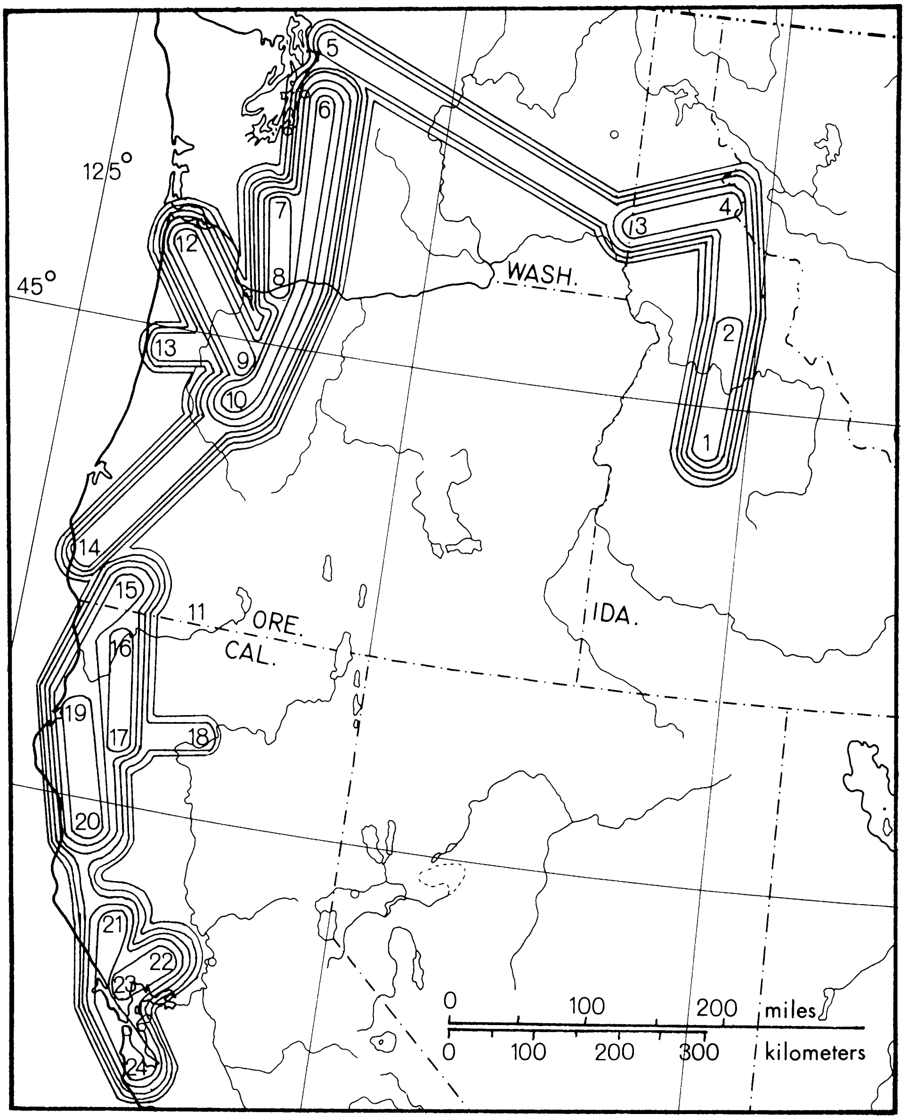

Fig. 15. Complete clustering of OTUs of larval *D. ensatus*. See Figure 14 for explanation. OTU 11 is shown not clustered because it clustered with *D. copei*.

groups, based on these two uncorrelated variables, correlate well with the relative degree of isolation of the four groups indicated by the linkage pattern of HGroup analysis (Fig. 13). Therefore, the results of cluster analysis are largely confirmed by component analysis.

Figure 17 shows the plane of the axes of the first two components "tilted" so that the third principal axis can be illustrated. The most interesting feature revealed by the third axis is the low values for OTUs 1, 2, 3, 4, and 5, which together form the Rocky Mountain Group. OTU 5 is shown in Figure 16 to be closer to other Cascade OTUs than to Rocky Mountain OTUs, but its value for

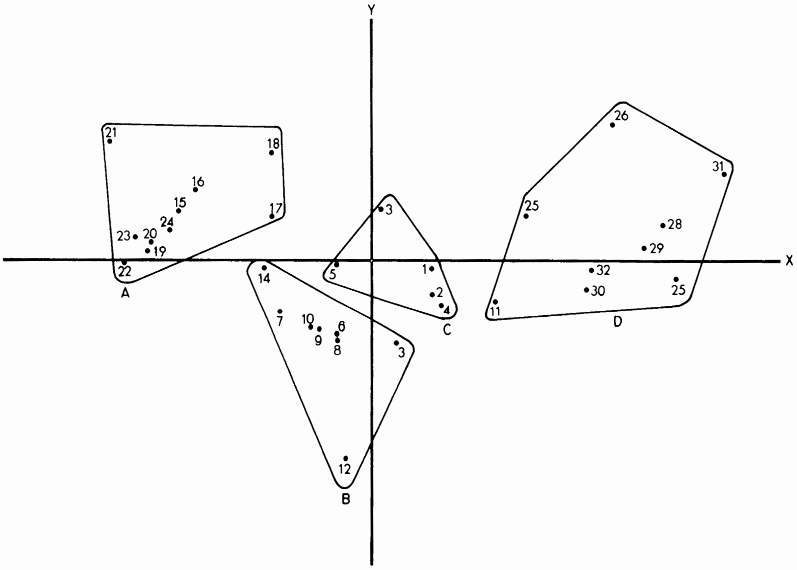

Fig. 16. Ordination of larval OTUs on first two principal components. The first component (X) accounted for 52 percent of the total variance and the second component (Y) accounted for an additional 32 percent (84 percent of total). Lines have been drawn around the OTUs which correspond to the 4 major stems of HGroup cluster analysis (A, B, C, and D of Fig. 13).

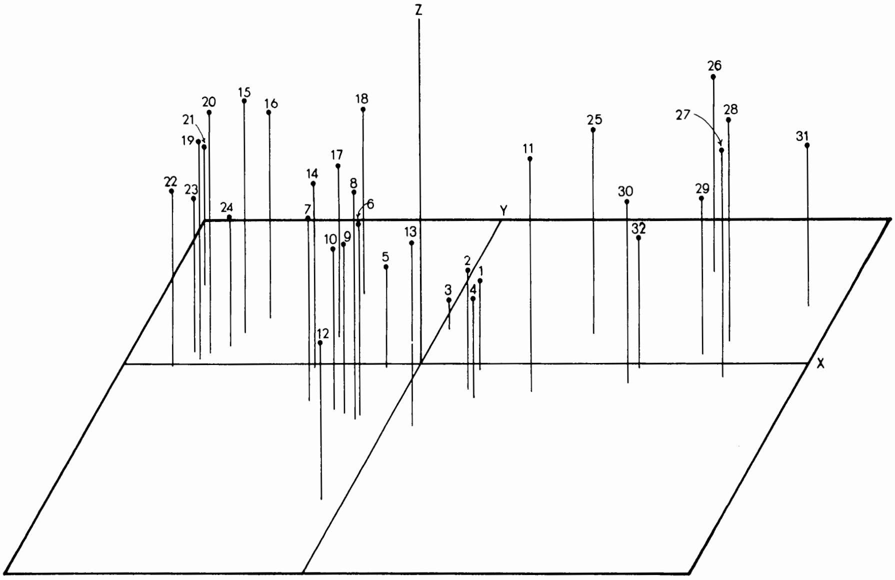

Fig. 17. Ordination of larval OTUs on the first three principal components. The third component (Z) accounts for 8 percent of the total variance. The three components together account for 92 percent of the variance.

the third component places it in an intermediate position between Groups B and C.

OTU 11, Shoat Spring, which clusters with *D. copei* in HGroup and WPGM analysis is shown by component analysis to be intermediate between the *D. copei* and *D. ensatus* OTUs.

Factor analysis of larval OTUs (Q-technique, 25 by 32 matrix) was done with two different sets of criteria for rotation. In the first case maximum absolute row values were placed in the diagonal, and the number of factors rotated was equal to the number of positive eigenvalues. In the second case unities were placed in the diagonal, and the number of factors preserved for rotation was equal to the number of eigenvalues equal to or greater than +1. The results are given in Tables 11 and 12. The letters in the "Stem" columns of the two tables correspond to the letters which define the stems in the phenogram of HGroup cluster analysis (Fig. 13). For the most part only the highest score for each OTU is listed in the Tables, but a few of the second highest scores are given in parentheses where discussion is needed.

Under the first set of conditions (Table 11) the five OTUs of Stem C all load high on Factor III; thus Factor III defines a Rocky Mountain Group of *D. ensatus*. The eight OTUs of Stem B all load high on Factor II, which is then a Cascade-Oregon Coast Range Factor. OTU 5C has its second highest loading on Factor II, and this fact may indicate its intermediacy, both taxonomically and geographically, between members of Stems B and C. OTU 11 (Shoat Spring), although a southern Cascade population, does not load high with other Cascade populations on Factor II. Rather, OTU 11 loads highest on Factor V. The only other OTU which correlates relatively high with Factor V is OTU 25, a *D. copei* OTU; and it may be significant that OTUs 11 and 25 form a subcluster within Group D in HGroup analysis. The fact that no other OTU has its highest loading on Factor V reveals the isolated nature of OTU 11 and lends support to my decision to assign OTU 11 to *D. ensatus* (see below).

The eight OTUs of Stem (Group) D all load highest on Factor I, which defines the *D. copei* taxon.

Members of Stem A, the California-Southwest Oregon Group of *D. ensatus*, do not correlate particularly high on any factor, and their highest loadings are scattered over Factors II, IV, VI, VII, and X. OTU 18 from Shasta Co., California has the highest loading of this group, and it loads on Factor IV. OTU 18 is geographically the most isolated member of Group A, and other characters which were not used in factor analysis, such as color, show it to be one of the most distinctive OTUs morphologically. Notice, however, that OTUs 16 and 17, Siskiyou and Trinity counties, also have their highest loadings on Factor IV. Siskiyou, Trinity, and Shasta counties are geographically close, and hence this relationship might be expected. These three OTUs also form a separate substem of Group A in

TABLE 11

ROTATED FACTOR SCORES FOR LARVAL OTUS[1]

OTU	Stem	Factor Preserved for Rotation									
		I	II	III	IV	VII	VI	VII	VIII	IX	X
1	C			.768							
2	C			.796							
3	C			.816							
4	C			.730							
5	C		(.223)	.803							
6	B		.893								
7	B		.917								
8	B		.795								
9	B		.856								
10	B		.939								
11	D	(.283)				.757					
12	B		.777								
13	B		.555								
14	B		.624								
15	A						.207				
16	A				.093						
17	A				.104						
18	A				.847						
19	A		.181								
20	A		.134								
21	A				.224						
22	A							.233			
23	A										.207
24	A						.086				
25	D	.703				(.533)					
26	D	.615									
27	D	.729									
28	D	.808									
29	D	.839									
30	D	.834									
31	D	.831									
32	D	.841									

[1] Based on 25 characters; the number of factors rotated was equal to the number of positive eigenvalues; maximum absolute row values in diagonal; the highest score for each OTU is listed, as is the second highest score in parentheses for some OTUs; letters correspond to stems in Figure 13.

HGroup analysis. The failure of factor analysis to discriminate a clear-cut Group A may reflect the heterogeneity of Group A, the dominance of the most aberrant member (OTU 18), an artifact of the criteria for rotation, or a combination of these possibilities.

A different picture emerges with the second set of rotation criteria (Table 12). Factor III still defines the Rocky Mountain Group of *D. ensatus*, but in this case Stem B is ill defined by any factor, and *D. copei* is not well delineated. However, Stem A, which was poorly defined under the first set of conditions is now well defined

TABLE 12

ROTATED FACTOR SCORES FOR LARVAL OTUS[1]

OTU	Stem	Factor Preserved for Rotation				
		I	II	III	IV	V
1	C			.827		(.298)
2	C			.839		(.011)
3	C		(.431)	.847		
4	C		(.142)	.771		
5	C			.857	(.249)	
6	B	.072				
7	B				.081	
8	B					.030
9	B					.310
10	B			.226		
11	D		-.020		(-.178)	
12	B	.217				
13	B	.241				
14	B	.346				
15	A	.702				
16	A	.823				
17	A	.892				
18	A				.933	
19	A	.832				
20	A	.755				
21	A	.863				
22	A	.881				
23	A	.936				(.113)
24	A	.829				(.453)
25	D		(.250)		.381	
26	D		.600		(.250)	
27	D		.328		(-.041)	
28	D		.308		(.219)	
29	D		(.241)	.266	(.248)	
30	D		.171	(.070)		
31	D		.477		(.102)	
32	D		(.310)	.357		

[1] Based on 25 characters; the number of factors rotated was equal to the number of eigenvalues equal to or greater than +1; unities in diagonal; the highest score for each OTU is listed, as is the second highest score in parentheses for some OTUs; letters correspond to stems in Figure 13.

by Factor I. The fact that OTU 18A still loads highest on Factor IV demonstrates its relative isolation within Group A. OTU 11D (Shoat Spring) is shown to be isolated from all other OTUs by the fact that it is the only one with a negative highest loading. Its two highest loadings are, however, on Factors II and IV, the two factors over which the *D. copei* OTUs (D's) have their highest loadings. Examination of the distribution of the second highest loadings of Stem C OTUs suggests the Rocky Mountain Group of *D. ensatus* may be broken into three subgroups. The first would be a Central Rocky

Mountain subgroup (OTUs 1 and 2), the second a Northern Rocky Mountain subgroup (OTUs 3 and 4), and the third an extreme Northern Cascade-Rocky Mountain subgroup (OTU 5).

Comparison of Populations of Transformed *D. ensatus*.—Four different cluster analyses were run on transformed *D. ensatus* using d_{jk} matrices, calculated from standardized data in all cases. Two analyses were based on Sokal and Michener's (1958) weighted-pair-group method (WPGM). Nine characters, including the 7 predicted y's (Table 8) and the mean numbers of maxillary-premaxillary teeth and mean numbers of vomerine teeth (Table 10), were used in one case; 19 characters, including the 17 mean ratios of Table 7 and the 2 means of tooth numbers (Table 10), were used in the second case. HGroup analysis was also run on these two sets of characters.

The results of the two analyses based on WPGM are summarized in Figure 18. The phenograms are similar in that both have two major stems. Stem Y represents a Southern Group in both phenograms, and Stem Z represents a Northern Group in both phenograms. One inconsistency occurs from the standpoint of geography. OTU 7, Humboldt Co., California, clusters with the Northern Group in both

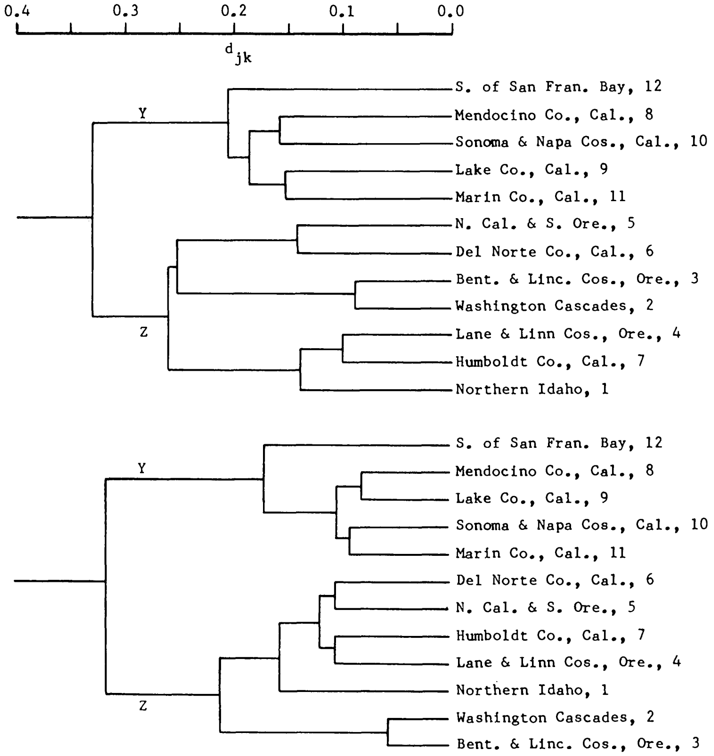

Fig. 18. Phenograms of OTUs of transformed *D. ensatus* based on WPGM clustering of the d_{jk} matrix. Upper phenogram based on 19 characters and the lower on 9 characters, as described in the text.

phenograms. However, other less easily quantified characters such as color and general body conformation indicate that specimens from Humboldt County are not more closely related to northern populations than to adjacent populations in California. The fact that the Humboldt County population clusters with northern populations is an artifact of the variation in the particular characters used in cluster analysis. If a larger number of characters were used, I believe the Humboldt County population would cluster with the Southern Group, although it would remain a somewhat distinctive OTU.

The results of the two HGroup analyses are shown in Figure 19. Again, a Southern Group (Y) and a Northern Group (Z) are evident. It is of interest that in the upper phenogram of Figure 19 the subgroup composed of OTUs 5 and 6 clusters with Z, and in the lower phenogram it clusters with Y. This observation may reflect the intermediate position, both geographically and taxonomically, of these two OTUs.

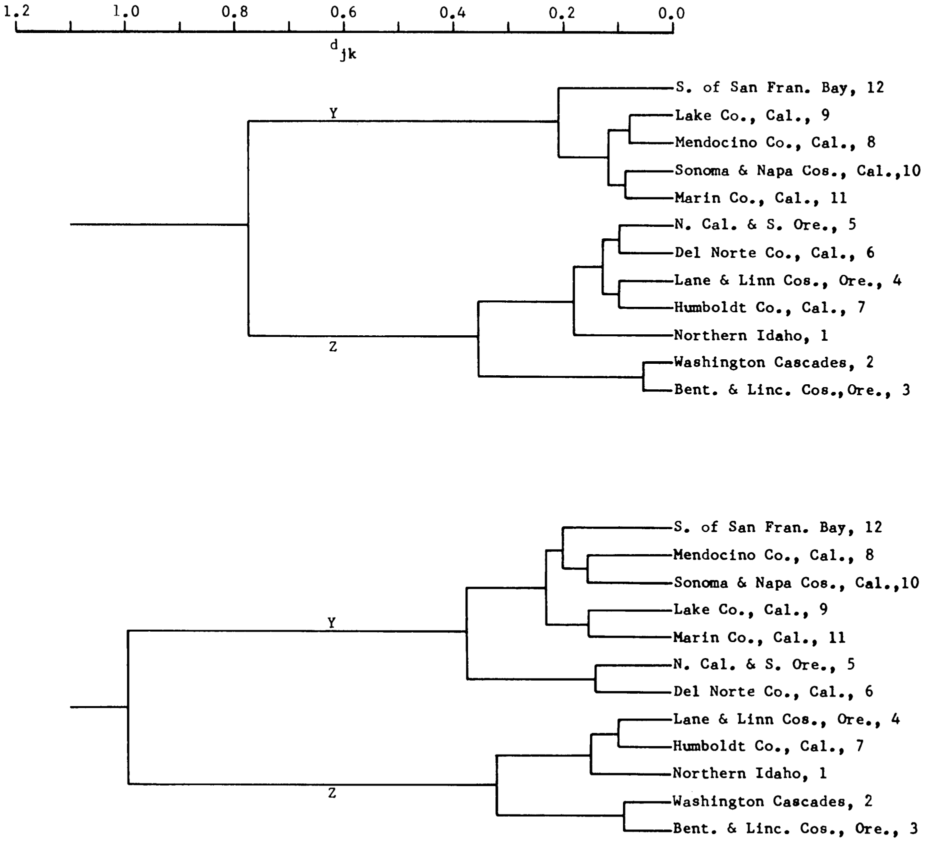

Fig. 19. Phenogram of OTUs of transformed *D. ensatus* based on HGroup clustering of the d_{jk} matrix. Upper phenogram based on 9 characters, lower phenogram on 19 characters as explained in the text.

VARIATION IN COLOR AND PATTERN

Color and Pattern of Larval *D. ensatus*.—Color and pattern of larval *D. ensatus* vary considerably between populations. However, if the subtleties of microgeographic variation are overlooked, it is possible to determine broad patterns of color variation, and these will be described. My terminology for chromatophores follows that of Bagnara (1966). In *Dicamptodon*, light yellow chromatophores can only be referred to as xanthophores, but the coppery gold chromatophores may be referred to as either xanthophores or erythrophores because they are intermediate in color between the two types.

Young larvae, less than 55 mm SVL, are bicolored, with light brown to dark brown upper parts and immaculate, white venters. Closer examination of the dorsum shows that while brown melanophores dominate, some black melanophores are present. Concentrations of black melanophores form irregular dark mottling over the dorsa of larvae from some populations. The upper portion of the caudal fin is often heavily mottled with black, light-edged blotches; and almost every small larva has a prominent, black tail-tip. A few, light yellow xanthophores and scattered, tiny aggregations of coppery gold erythrophores are present on the lateral and dorsal surfaces. Small, white, longitudinal streaks occur along the sides of many individuals, but these streaks are usually filled in with brown as the

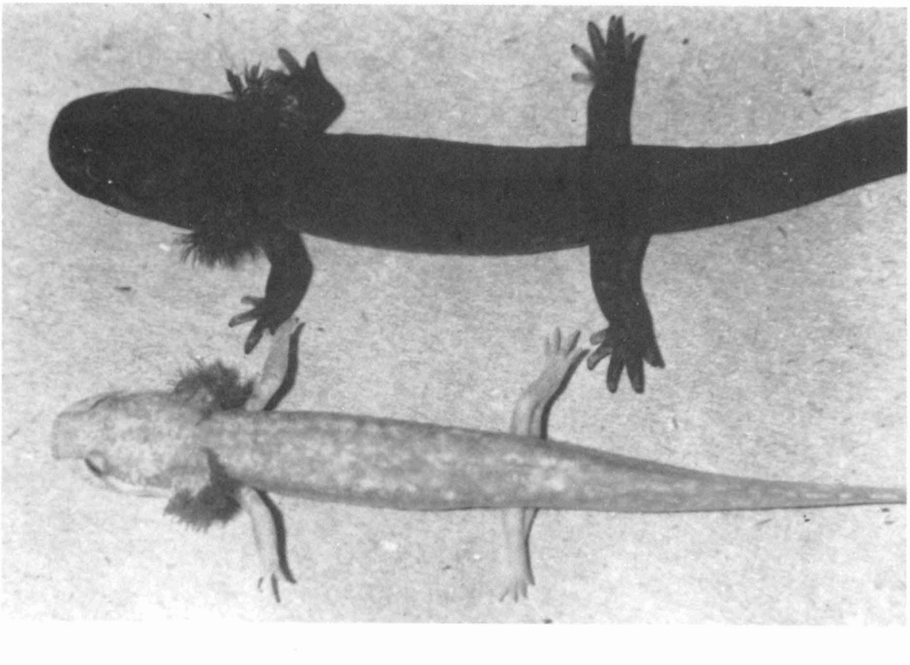

Fig. 20. Two larval *D. ensatus* from Greasy Creek, Benton Co., Oregon. Partial albino (RAN 4021; 55 mm SVL) and normally colored individual. Note the light stripes behind the eyes of both individuals.

larvae grow older. Often the lateral line organs of larvae of all ages are accentuated by dark brown melanophores which create rows of small brown spots along the sides, over the head, and on the ventral portion of the pectoral girdle. On the pectoral girdle, a semicircle of lateral line organs is found on each side. A short yellow stripe is usually present behind each eye. The stripe extends posteriorly from the eye to a point just above the angle of the jaw, or occasionally beyond to the gill region (Fig. 20). The gills are dark purple with scattered black melanophores and sparse yellow xanthophores on the fimbriae. The tips of the digits are usually cornified and black (Fig. 21).

Larger individuals may have dark ventral surfaces. Melanophores encroach ontogenetically from the sides onto the venter so that young larvae from all populations have white venters, and older larvae may or may not have dark venters depending on local variation in the ontogenetic process. The dorsal coppery gold erythrophores increase with age, and they are especially numerous on the heads of larger larvae. Usually the first indication of metamorphosis is a sudden

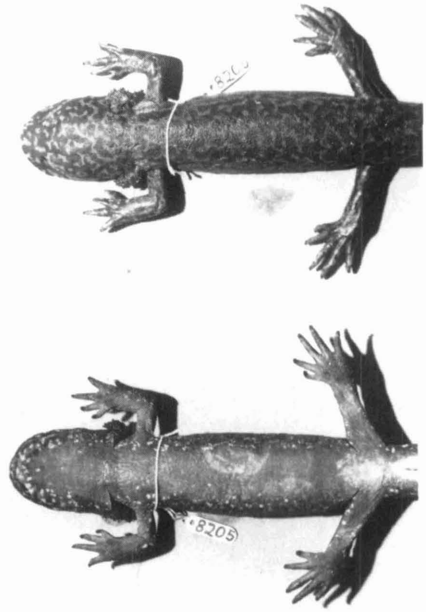

Fig. 21. Dorsal and ventral view of neotenic *D. ensatus* (male, 129 mm SVL) from the East Fork of the North Fork of the Trinity River, Trinity Co., California. Larvae from the Siskiyou-Trinity Region are highly mottled, and some have a pattern superficially resembling the marbling of transformed individuals, as does this specimen (RAN 8205). Note the black, cornified toe tips. The semicircular scars on the venter result from bites inflicted by other sexually mature individuals.

increase in the number of coppery gold flecks beyond the concentration attained in normally ageing larvae. Erythrophores are so numerous in some older larvae that the dorsum appears to be coated with a golden sheen overlying the reticulum of brown melanophores. Upon transformation the erythrophores arrange themselves into the characteristic marbled pattern of the terrestrial salamander. The golden marbling appears first on the head, where the larval erythrophores are most numerous, and spreads posteriorly on the dorsal surfaces.

The dark blotches on the tail and the black tail-tip of young larvae fade with age. The dorsal and lateral surfaces of large neotenic *D. ensatus* are usually solid dark brown with no hint of the earlier mottling.

Larvae from all parts of Idaho are sufficiently similar to be described together. Young larvae are darker than similarly aged individuals from coastal regions, and they have little dorsal mottling. They have faint stripes behind the eyes, and the tip of the tail is only slightly darker than the rest of the dorsum. The venter is white. Larvae longer than 60 mm SVL have dark, purple-brown dorsal surfaces, and dorsal marking of any kind is rare. The dark tail-tip is no longer evident. The ventral surface is dark blue-gray because of the invasion of melanophores. A faint yellow stripe can be seen behind the eyes of some older individuals.

Larvae from Washington and Oregon north of Jackson, Josephine, and Curry Counties share certain similarities in color and pattern. By comparison to larvae from Idaho, the dorsal surfaces are lighter brown, dorsal mottling is more prominent, and the yellow stripes behind the eyes are generally more distinct. The tail fin is more vividly marked with light-edged black blotches, and the tail-tip is conspicuously black in young larvae and usually does not completely fade in older larvae. The venter of young larvae is white as in young larvae from Idaho, and in many populations in this region, e.g., near Mount Rainier, the venter remains white in older individuals. Usually, however, the venter of older larvae changes to a light gray or yellow-brown color. In extremely old larvae the venter may become quite dark. Intermediate-sized larvae from the MacKenzie River drainage, Lane Co., Oregon have dark gray venters, superficially resembling the pattern seen in similar-sized larvae from Idaho.

Larvae from Trinity and western Siskiyou Counties, California are boldly marked and are thus strikingly different in appearance from all other larval *D. ensatus* (Fig. 22). Young larvae from this region are not greatly different in color from similarly aged larvae from adjacent areas, but the dorsal surfaces of older larvae are highly variegated with white to yellow spots, blotches, streaks, and bars. Some have a pattern which superficially resembles the marbled condition of transformed individuals (Fig. 21). The lighter mottling

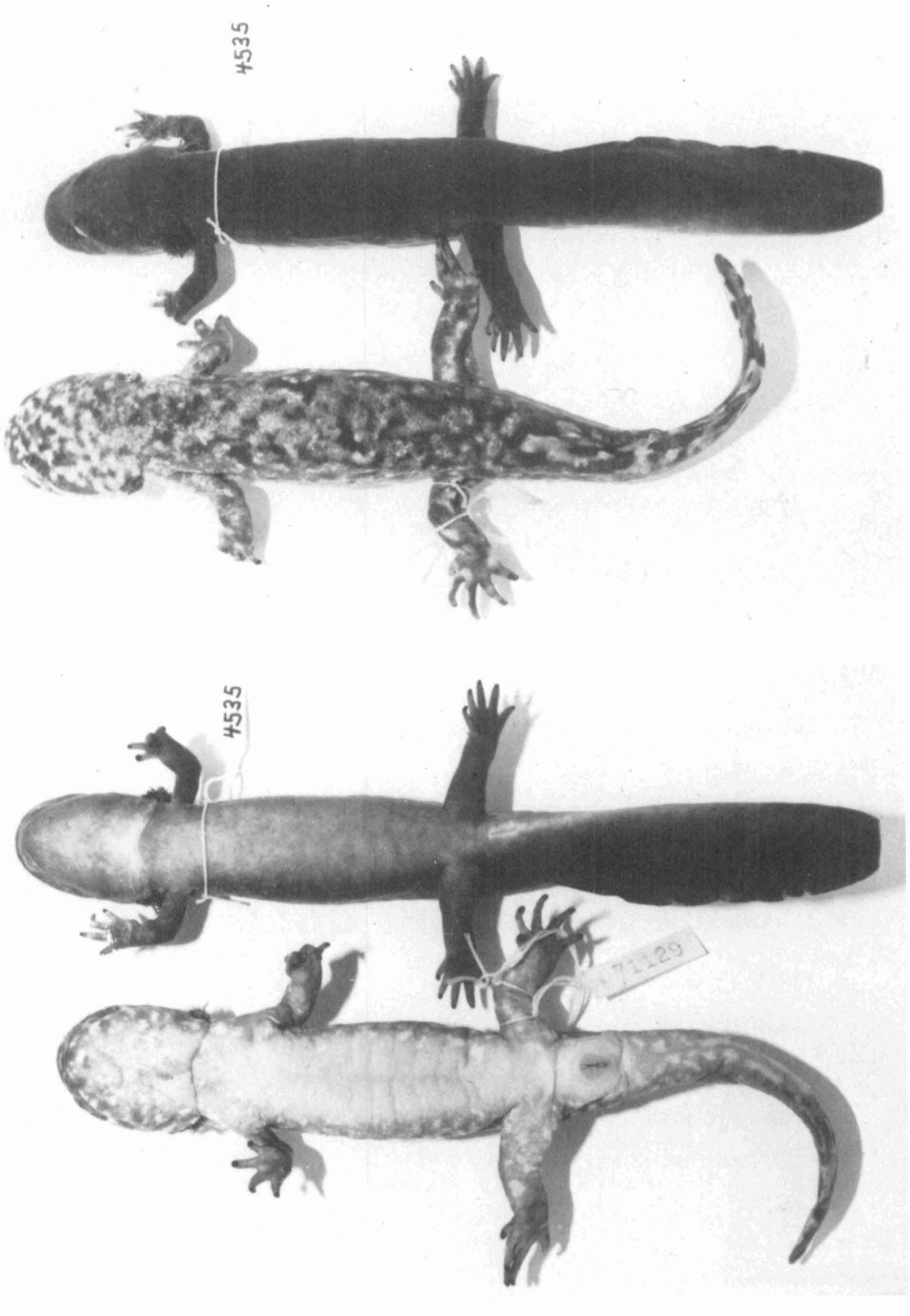

Fig. 22. Mottled larval *D. ensatus* (MVZ 71129; 105 mm SVL) from "Little Monster Lake," Trinity Mtns., Trinity Co., California; and plain, dark larval *D. ensatus* from Oneonta Gorge, Multnomah Co., Oregon. The photo illustrates geographic variation in size at sexual maturity. The swollen vent of the "Monster Lake" specimen identifies it as a sexually mature male; the other larva is immature.

of larvae from this area extends onto the ventrolateral surfaces, and the midventers range in color from light gray to smoky yellow.

The parent rock found over much of the Trinity-Siskiyou region is usually lighter in color than rocks from surrounding regions, and the coarse-grained texture of the predominantly granitic rocks which litter the stream bottoms provide a background against which the highly mottled endemic larvae are well camouflaged (Fig. 23). There can be little doubt that the distinct color and pattern of larvae in the Trinity-Siskiyou region is a result of selection for background color-matching (eucrypsis).

Larvae from the lower coastal counties of northern California (Del Norte, Humboldt, Mendocino) and from adjacent Oregon (the southern portions of Curry, Josephine, and Jackson Counties) are not as vividly marked as larvae from the Trinity-Siskiyou region, but most have some degree of spotting, streaking, or blotching. They often have especially prominent yellow stripes behind the eyes. Larvae from these counties often appear intermediate in color between larvae from the Trinity-Siskiyou region and larvae from the northern Coast Range and Cascade Range of Oregon.

Individuals from Nosoni Creek (OTU 18) and nearby areas on the northeast and east sides of Shasta Lake, Shasta Co., California are uniform, dark brown dorsally with dark venters. Therefore, although

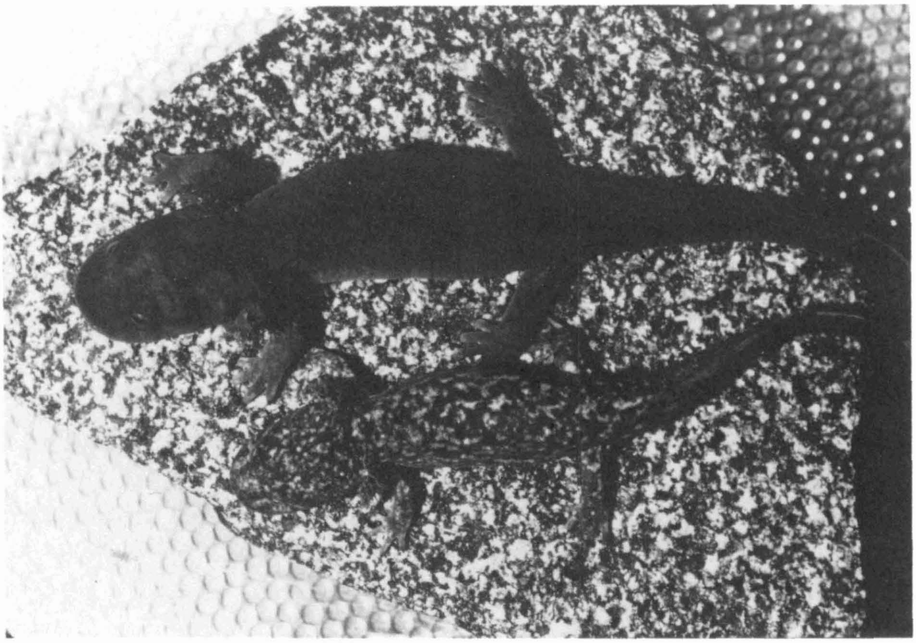

Fig. 23. Larval *D. ensatus*. Mottled specimen (RAN 5226; 80 mm SVL) from James Creek, Trinity Co., California. The background is a rock from the streambed of James Creek. Dark larva is from Mary's Peak, Benton Co., Oregon. The photo illustrates background color matching in larval *D. ensatus*. The color of larvae in most populations matches the color of the substrate to some degree.

larvae from this area are similar in other respects to larvae from the Trinity-Siskiyou region, larvae from the two areas are strikingly different in color and pattern. This fact probably reflects selection for uniform larval color in the Shasta region because of the plain color of the local substrate.

In the region south of San Francisco Bay and in Marin, Sonoma, Napa, Lake, and Glenn Counties, California, larvae are plain light brown on the dorsal surfaces with white or yellowish white venters. Some dark mottling may appear on the tail fin of larvae from this region, but dorsal patterns of any kind usually do not occur. Larvae of some populations in this area are reddish brown dorsally, with white venters in young larvae and light, yellowish white venters in older larvae. Larvae intermediate in color between this plain pattern and the highly mottled pattern of larvae from the Trinity-Siskiyou region can be found in southern and southeastern Mendocino County. Larvae of intermediate color are expected in northwestern Glenn County, southwestern Tehama County, and northern Lake County.

Two color anomalies of larvae are noteworthy. The first is the occurrence of partial albinos in Greasy Creek, Benton County, Oregon (Fig. 20). Three of these individuals (RAN 4021-2, 6900) were taken within a 3-m section of the stream. These larvae have pigmented eyes and faint dorsal patterns which disqualifies them as true albinos.

The second color anomaly is a highly mottled young larva (RAN 8888) collected in Roundhouse Gulch (OTU 4), Shoshone Co., Idaho. As noted above, larvae from Idaho are normally plain dark brown on the dorsal surfaces. This specimen is the only one of several hundred larvae seen from Roundhouse Gulch, and the only one observed from Idaho, with a mottled pattern. The pattern is not unlike that of larvae from the Trinity-Siskiyou region of California, and perhaps such a mutant form would be selected for given the speckled substrate that prevails in the Trinity-Siskiyou region.

Color and Pattern of Larval *D. copei*.—Nussbaum (1970) gave a brief comparison of the color of *D. copei* with sympatric larval *D. ensatus* (OTUs 7 and 25 of the present study). At 50 mm SVL, *D. copei* have white venters, but at 90 mm SVL, melanophores have completely encircled the body, and *D. copei* usually have darker venters than similar-sized, sympatric *D. ensatus*. The lips of the cloaca may remain white in older individuals of *D. copei*. The tail of *D. copei* has less mottling at all sizes than sympatric *D. ensatus*, and *D. copei* lack the prominent black tail-tip of larval *D. ensatus*. In general, the tail of *D. copei* is colored like the trunk region, whereas the tail of *D. ensatus* is often more boldly marked than the trunk. The dorsum and sides of young and old *D. copei* have patches of yellowish tan and clumps of white, punctiform granular glands which are especially noticeable at the base of the tail fin. These glands are much less conspicuous in larval *D. ensatus*. As in larval *D. ensatus*, the toes are capped with black cornified skin. The gills of *D. copei* are purple-black with fewer light yellow xanthophores on the fimbriae than in *D. ensatus*. *D. copei* also have coppery gold erythrophores on the dorsal surfaces, but these are fewer than in *D. ensatus* at all sizes, and the failure of these pigment cells to increase rapidly in number with age may partly explain why *D. copei* usually fail to develop a complete marbled pattern when forced to metamorphose (see below).

Within its relatively restricted range, *D. copei* shows little noteworthy variation in color and pattern. However, specimens from Wahkeena Falls, Multnomah Co., Oregon and Nine Foot Creek, Skamania Co., Washington (OTUs 26 and 27) are darker both

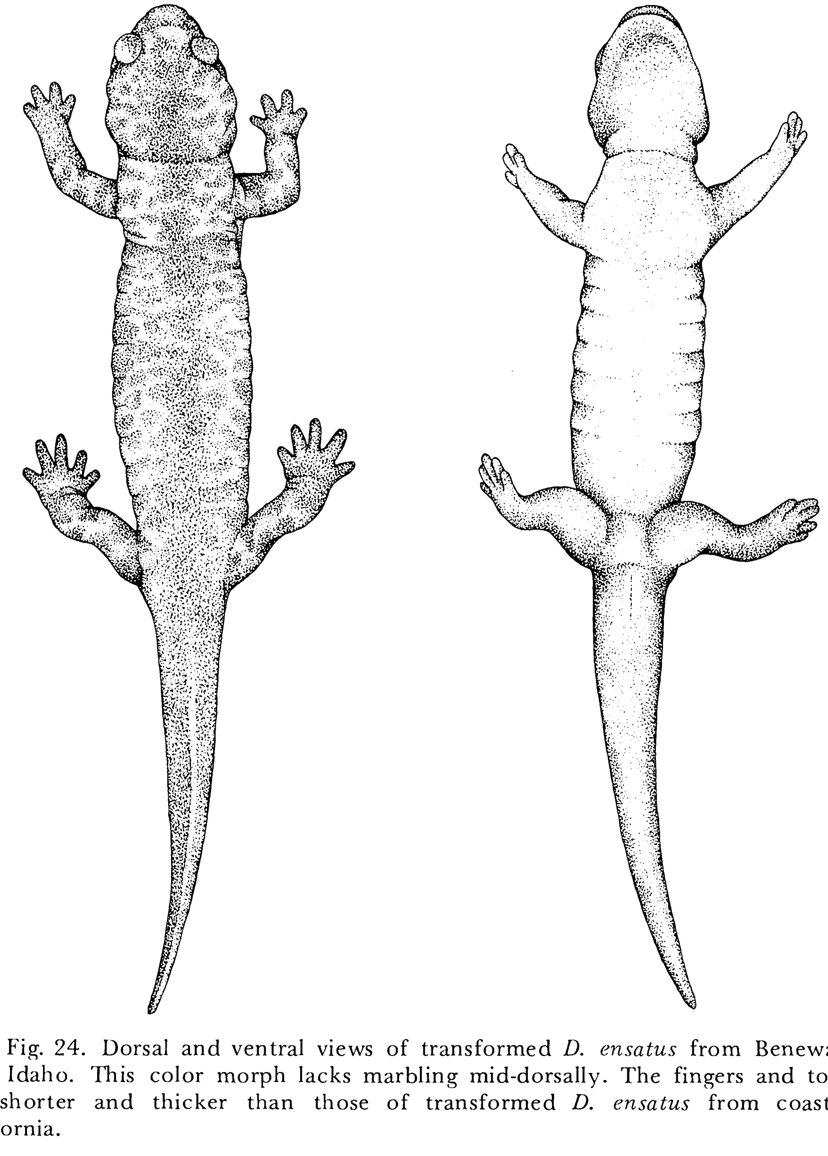

Fig. 24. Dorsal and ventral views of transformed *D. ensatus* from Benewah Co., Idaho. This color morph lacks marbling mid-dorsally. The fingers and toes are shorter and thicker than those of transformed *D. ensatus* from coastal California.

dorsally and ventrally than *D. copei* from other areas. Correlated with the darker pigment, the light-colored aggregations of granular glands are not as conspicuous in larvae from these two populations.

Color Pattern Variation in Transformed ***D. ensatus*****.**—Color and pattern of transformed *D. ensatus* have been described by Bishop (1943), Stebbins (1951), and others. It is generally written that the dorsum has a light ground color with darker marbling. The description given above of the ontogeny of color through metamorphosis shows that the reverse is true. The ground color is dark (derived from the larval condition), while the marbling effect is caused by the increase in number and the aggregation of coppery gold erythrophores into an irregular golden reticulum.

The dorsal pattern is highly variable within populations, and the dorsal color may change with age. Young individuals often have bright, distinct, golden marbling, but the density of erythrophores may decrease with age so that the underlying layer of melanophores dulls the golden color of the marbling. Old individuals may become quite patternless except on the head where faint golden marbling remains. One color morph from Idaho does not have a marbled dorsal pattern, even at early age, but incomplete marbling is usually evident along the sides (Fig. 24).

Specimens from Idaho are darker, both dorsally and ventrally, than specimens from the Pacific Border portion of the range, and this dark color is related ontogenetically to the darker ground color of larvae from Idaho. Marbling is finer grained in Idaho specimens and does not extend onto the margin of the lower jaw as is usually the case with coastal individuals (Fig. 25). North of the Salmon River in Idaho, two basic types of dorsal marbling are found. The first type is normal, fine-grained marbling as in Figure 26; the second type has a plain, dark, middorsal region, with some indication of marbling along the sides as shown in Figure 24. South of the Salmon River, only the marbled morph has been found, but the plain-backed morph is expected. The marbling of specimens from south of the Salmon River is even finer than in specimens from north of the Salmon River (Fig. 26).

In Washington and in the Cascades of Oregon, the venters are white to light gray with the exception of dark gray venters found in individuals from the MacKenzie River drainage of Lane Co., Oregon. Specimens from the Cascades have coarser marbling (Fig. 27) than those from Idaho (Fig. 26).

Transformed *D. ensatus* from the northern Coast Range of Oregon are also relatively light colored, but the marbling is more variable in that both coarse- and relatively fine-grained specimens are found.

Individuals from southwestern Oregon and northern, coastal California are somewhat intermediate in color and pattern between specimens from northern Oregon and specimens from the extreme

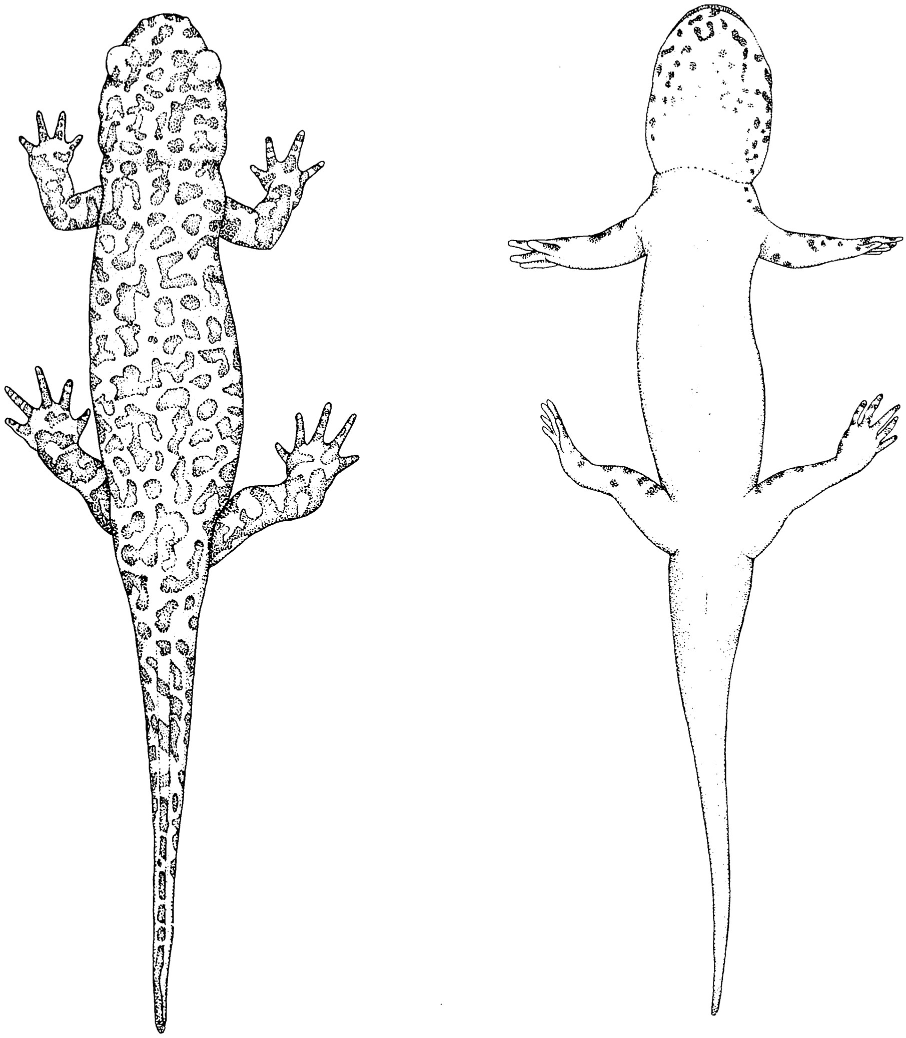

Fig. 25. Dorsal and ventral views of transformed *D. ensatus* from Santa Cruz Co., California.

southern portion of the range in California. They usually have light gray venters, very coarse marbling, and the ground color is lighter brown than in northern specimens. The marbling of some specimens from this area is often so coarse as almost to obscure the darker ground color.

In the interior Trinity-Siskiyou region and in Shasta Co., California, transformed individuals are also coarsely marbled, but the dorsal ground color and the ventral surfaces are darker than in specimens from the northern coastal region of California. Those from the Trinity-Siskiyou region have white spots or streaks along the sides, which are apparently carried over from the highly mottled larval condition.

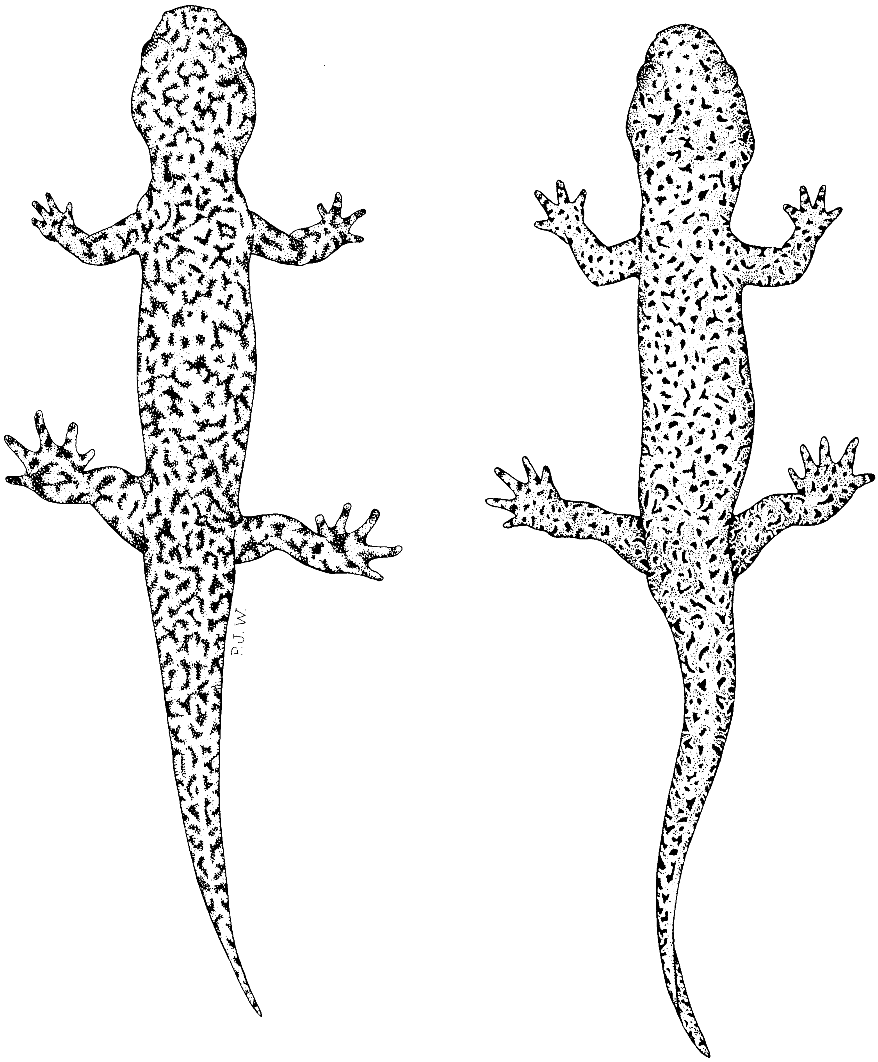

Fig. 26. Two transformed *D. ensatus* from Idaho illustrating two degrees of fine-grained marbling. The one on the left is typical of specimens from north of the Salmon River; the finer-grained pattern (right) is characteristic of individuals from south of the Salmon River.

Specimens from south of San Francisco Bay and from Marin, Napa, Sonoma, southern Mendocino, southern Glenn, and southern Lake Counties, California are white ventered, coarsely marbled and have light, often reddish brown, dorsal ground color. The light ground color combined with the coppery marbling causes animals from this region to have an overall reddish tan appearance as opposed to the darker dorsal hues characteristic of northern specimens. While most specimens from Washington, Oregon, and California have marbling or blotching of erythrophores on the margin of the mandible,

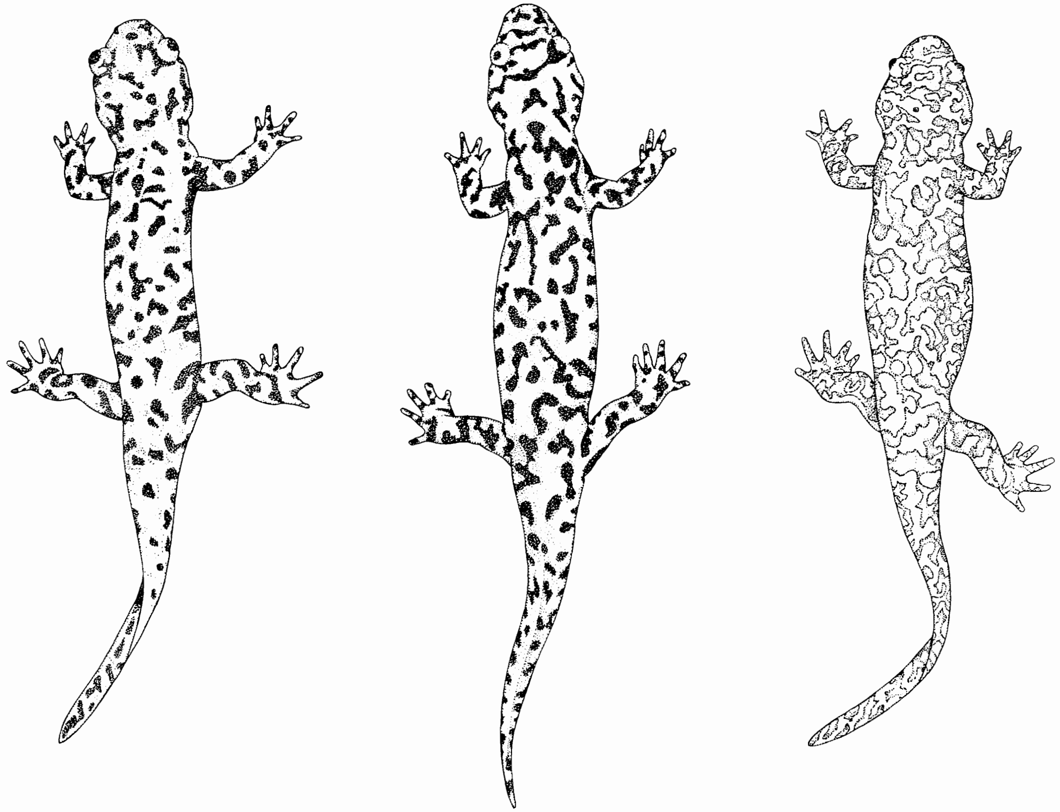

Fig. 27. Dorsal pattern of transformed *D. ensatus* from the southern Cascade Mountains of Washington (left and middle) and from Marin Co., California (right). The two Washington specimens show dark background color and two varieties of snout shape often encountered in metamorphosed individuals. The California specimen has a lighter (reddish-brown) ground color.

specimens from this region often show the extreme of this condition, with marbling extending onto the chin, throat, and underside of the forelimbs and pectoral girdle. This pattern is especially prominent in specimens from south of San Francisco Bay.

Individuals from the coastal portions of Mendocino and Humboldt counties are somewhat similar in color and pattern, dorsally and ventrally, to specimens from the San Francisco Bay area, but they do not have extensive marbling on the chin.

SIZE AND SEXUAL MATURITY

In some populations of *D. ensatus*, larvae always metamorphose before becoming mature. The size at maturity varies among those populations with neotenic larvae. In general, larval *D. ensatus* do not mature until they are 115 mm SVL or longer, but there are important exceptions. At Nosoni Creek, Shasta Co., California (OTU 18) larvae mature at 95 mm SVL; at 100 mm SVL in parts of Siskiyou, Trinity and Humboldt counties, California; at 88 mm SVL in Bolan Lake, Josephine Co., Oregon; at 85 mm SVL in Shoat Spring, Jackson Co., Oregon (OTU 11); and at 107 mm SVL in Eldorado Gulch, Latah Co., Idaho. These data do not reflect a regular geographic pattern of variation. It appears that highly local environmental factors determine the size at which larval *D. ensatus* mature. The extent to which the size and age at maturity is genetically controlled is unknown.

D. copei mature at smaller sizes than larval *D. ensatus*. Where the two species are sympatric there is no overlap, i.e., within one locality, the largest *D. copei* is always smaller than the smallest paedogenetic *D. ensatus*. There is some interpopulational variation in size at sexual maturity for *D. copei*. At Oneonta Gorge (OTU 28) and Wahkeena Falls (OTU 27), Multnomah Co., Oregon, *D. copei* mature at 65 mm SVL; 77 mm SVL at Saddle Mountain (OTU 29), Clatsop Co., Oregon; 77 mm SVL at Rock Creek (OTU 30), Wahkiakum Co., Washington; 75 mm SVL at Beaver Creek (OTU 31) and Merriman Creek (OTU 32), Grays Harbor Co., Washington; 67 mm SVL at Maratta Creek (OTU 25), Cowlitz Co., Washington; and 81 mm SVL at Nine Foot Creek (OTU 26), Skamania Co., Washington.

The average and maximum size of larval *D. ensatus* varies between populations and is related to the occurrence or nonoccurrence of paedogenesis. The largest paedogenes are found in the Cascade Mountains of Washington and Oregon and in the Coast Range of Oregon. No exceptionally large paedogenes are known from Idaho and California.

Apparently the largest documented paedogene reported previous to my studies was 286 mm total length, collected at Oak Grove, Clackamas Co., Oregon (Bishop, 1943). In fact, many specimens greatly exceed this size. The largest I am aware of is a female (RAN 13469) from the Columbia River Gorge, Multnomah Co., Oregon. At the time the specimen was collected, the measurements were 205 mm SVL and 351 mm total length. This individual is the largest non-fossil ambystomatid so far reported (Nussbaum and Clothier, 1973).

Transformed *D. ensatus* cannot definitely be said to vary in size geographically because too few specimens are known. However, only relatively small specimens have so far been collected in Idaho. The largest known is RAN 782, a male from Mannering Creek, Benewah Co. which measures 134.9 mm SVL and 228.3 mm total length. Some relatively large individuals have been collected in the San Francisco Bay area, e.g., CAS 43579 is a female from Marin County which measures 169.9 mm SVL and 303.8 mm total length, and CAS 41712 is a female from San Mateo County which is 166.0 mm SVL and 301.6 mm total length. The largest transformed *D. ensatus* are found in Oregon and Washington. The record is an unnumbered specimen in the collections at the University of Washington. The animal was collected in Renton, King Co., Washington, and measured 333 mm total length after five years in alcohol. In life, this salamander probably exceeded 345 mm total length.

Transformed *D. ensatus*, of a given population, normally mature at about the same sizes as do paedogenes of the same population, that is, usually at sizes greater than 115 mm SVL.

Maximum size (SVL) records for *D. copei* by locality are: Oneonta Gorge, RAN 4284, male, 96.1 mm; Wahkeena Falls, RAN 7723, male, 93.9 mm; Saddle Mountain, RAN 7467, female, 90.2 mm; Rock Creek, RAN 7529, male, 100.1 mm; Beaver Creek, RAN 6119, male, 86.9 mm; Merriman Creek, RAN 4112, male, 99.2 mm; Maratta Creek, USNM 166805, male, 103.8 mm; and Nine Foot Creek, RAN 4657, female, 113.5 mm.

SENSITIVITY OF LARVAE TO THYROXINE

Nussbaum (1970) reported that larval *D. ensatus* and larval *D. copei* react differently to thyroxine. When similar-sized larvae of the two species were placed together in water with powdered beef thyroid gland, *D. ensatus* transformed completely in three months, but individuals of *D. copei* did not fully transform even after 11 months. Gills, labial folds, and tail fins had completely atrophied, eyelids were formed, and eye protrusion was well advanced. Gold erythrophores had segregated on the snout to form a marbled pattern, but there was no gold pigment posterior to the angle of the jaws. Treatment of *D. copei* was continued beyond the 11 months reported in 1970, and after 2 years and 10 months there was little additional change except that gold pigment had spread posteriorly to a point just behind the eyes.

The thermal histories, collection dates, collection sites, photoperiods and dosages per unit time were the same for all larvae used in the experiment, and the temperature was held constant at 10°C during the test period. The experiment was done in duplicate with identical results. *D. copei* were sexually mature and *D. ensatus* sexually immature over the range of sizes used (70-100 mm SVL), and it might be argued that this fact invalidates the experiment. However, other experiments showed that smaller, immature *D. copei* were also relatively insensitive to thyroxine, and that larger, mature *D. ensatus* were only slightly less sensitive than immature *D. ensatus*. Therefore the observed differences in sensitivity cannot be attributed to the effects of sexual maturity.

Further observations showed that many larval *D. ensatus* would initiate and complete metamorphosis under a variety of laboratory conditions without the use of metamorphogens. *D. copei* of all sizes from many localities were held in the laboratory for up to three years, and none transformed without the administration of thyroxine.

The experiments described above were done on animals collected at Maratta Creek, Cowlitz Co., Washington, the type locality of *D. copei*. Larval *D. ensatus* from many other localities throughout the range have been studied. Apparently transformation in first-year larvae from all localities is abnormal. When first-year larvae are treated with thyroxine, they may show signs of transformation such as initial gill reduction, initial labial fold reduction, and color changes on the snout. However, these changes are usually out of sequence when compared with normal transformation, and none of the changes goes to completion. Pathological restlessness and tissue degeneration occur, and the final outcome is always death.

Larvae of *D. ensatus* in their second and third years respond readily to thyroid treatment, and many will transform spontaneously. This observation holds for larvae from all populations studied so far, and these include populations from throughout the range. Although some differences in the speed of transformation and the sequence of metamorphic events has been noted between populations, these differences are minor and cannot be considered of taxonomic importance.

As noted above, sexual maturity does not inhibit metamorphosis in *D. ensatus*, but old age can. In the earlier experiments (Nussbaum, 1970) it was found that paedogenes from Maratta Creek showed only a slightly delayed reaction to thyroxine, but only relatively small (young) paedogenes were used in those experiments. Recent tests showed that larger (older) paedogenes from Maratta Creek transformed slowly, and that the rate was inversely proportional to size. Apparently the tissues become increasingly insensitive to thyroxine with age. But even the largest paedogenes will transform safely in seven to nine months at 10°C if proper precautions are taken to avoid fouling of the water and if the concentration of thyroxine in the bath is not too high. As in the Maratta Creek population, age-dependency of reaction time is evident for paedogenetic *D. ensatus* from Loon Creek, Lane Co., Oregon; Greasy Creek, Benton Co., Oregon; Oneonta Gorge, Multnomah Co., Oregon; Quartz Creek, Clatsop Co., Oregon; and Nosoni Creek, Shasta Co., California.

Individuals representative of all the OTUs of *D. copei* listed in Appendix I, except for OTUs 30 and 31, have been tested for sensitivity to thyroxine. With the exception of individuals from Nine Foot Creek, Skamania Co., Washington (OTU 26) and Merriman Creek, Grays Harbor Co., Washington (OTU 32), all test animals reacted much the same as did *D. copei* from Maratta Creek. *D. copei* from Nine Foot Creek were even less sensitive than those from Maratta Creek. After 12 months, gills and labial folds were gone, but no gold pigment appeared on any of the 30 test animals. Unlike *D. copei* from Maratta Creek, those from Nine Foot Creek never completely regained a normal feeding response, and after 12 months most were badly emaciated. *D. copei* from Merriman Creek, on the Olympic Peninsula, also transformed slowly by comparison to *D. ensatus*, but at a faster rate than *D. copei* from Maratta Creek. At the end of 12 months they were feeding regularly and had developed a complete pattern of gold marbling on the dorsum (Fig. 28). However, they retained the small-headed, attenuate, short-limbed appearance of artificially transformed *D. copei* from the other localities.

There are two records which indicate that *D. copei* occasionally metamorphose in nature. The first is a specimen (USNM 64320) collected 21 August 1921 along the Hoh River on the Olympic Peninsula, Jefferson Co., Washington. It is the only known, naturally transformed *Dicamptodon* from the Olympic Peninsula. The specimen is sexually mature at small size (87.6 mm SVL) as is characteristic of *D. copei*, and it has the attenuate appearance of artificially transformed *D. copei*. The specimen has a color pattern remarkably similar

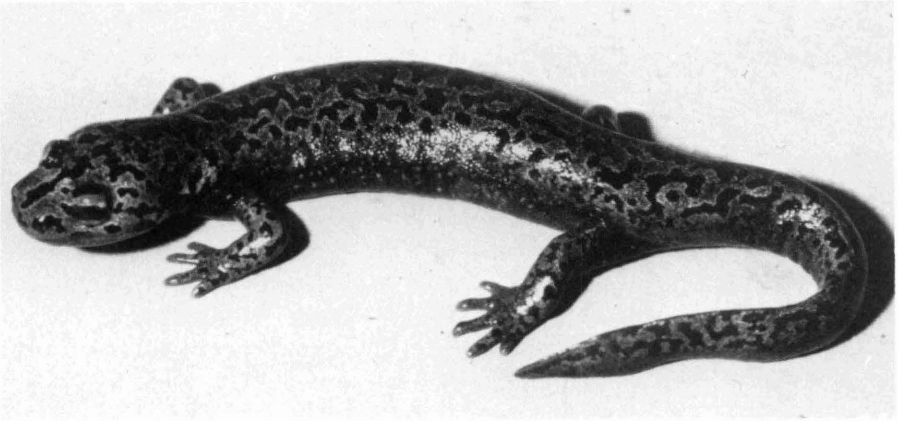

Fig. 28. *Dicamptodon copei* from the Olympic Peninsula, Grays Harbor Co., Washington after 12 months of continuous thyroxine treatment.

to that of *D. copei* from the Olympic Peninsula which have been forced through metamorphosis (Fig. 28).

The second record of transformed *D. copei* in nature is a specimen (MVZ 116631) recently collected by Dr. Robert C. Stebbins near Spirit Lake, Skamania Co., Washington. The specimen (81.1 mm SVL) is immature and recently metamorphosed as indicated by the curved vomerine tooth rows. The dorsum is patternless as in artificially metamorphosed *D. copei* from this portion of the Cascade Mountains.

BLOOD SERUM PROTEINS

Electrophoretic patterns of blood serum proteins were obtained for larvae and transformed individuals from several localities in Idaho and Washington. Some of these data are summarized in Tables 13 and 14 and in Figures 29 and 30.

The serum protein fractions have been assigned arbitrary numbers to facilitate discussion. Fraction 1 has a relative mobility comparable to human albumin, 2 and 3 are comparable to alpha-globulins, 3 and perhaps 4 to beta-globulins, and 5 and 6 to gamma-globulins. However, the chemical structures of the serum proteins of salamanders are not known, so that direct comparison to human proteins is not possible; nor is it possible to assume that the numbers I have assigned to the fractions represent homologous proteins across populations. The bands actually represent classes of proteins, and it would be possible with more refined techniques, such as disc electrophoresis, to resolve the fractions into subfractions. It is likely that bands of similar mobility represent proteins which serve similar functions in all vertebrates, despite the fact that slight differences in chemical structure may exist. Evidence for this hypothesis comes from the observation that some species of salamanders are polymorphic for particular bands (Coates, 1967; Newcomer, 1968; Highton and Henry, 1970). If slight variation in a protein seriously altered a vital function, then polymorphism could not occur.

Coates (1967) found no sexual dimorphism in the serum proteins of three species of newts (*Taricha*), and he found that animals kept for long periods in the laboratory had patterns indistinguishable from freshly caught animals. Newcomer (1968) reported identical results for many species of ambystomatids, and my conclusions are the same for both species of *Dicamptodon*. Furthermore, transformed specimens of *D. ensatus*, within one population, have identical patterns whether transformation was induced or natural. Only induced specimens of transformed *D. copei* were available, and only those that had received at least 18 months of thyroid treatment were used.

TABLE 13

RELATIVE DENSITY OF SERUM PROTEIN FRACTIONS[1]

Species	Stage	Locality	Relative Density of Fractions							
			1	2	3	$3'$	4	5	Total	N
D. copei	larval	Nine Foot Cr., Wash.	24.8 (1.7)	15.3 (1.1)	25.9 (1.8)		18.7 (0.7)	15.7 (0.8)	100.9 (4.9)	12
D. copei	transformed	Maratta Cr., Wash.	41.3 (3.0)	41.0 (3.9)	24.6 (1.9)		19.9 (0.7)	17.6 (0.8)	144.3 (6.6)	7
D. ensatus	larval	Maratta Cr., Wash.	28.1 (2.2)	19.3 (1.9)	25.1 (1.9)		38.8 (1.8)	22.2 (1.4)	133.6 (5.7)	9
D. ensatus	transformed	Maratta Cr., Wash.	40.0 (2.8)	21.3 (2.2)	18.1 (2.2)		45.1 (3.6)	25.8 (2.5)	150.3 (10.4)	8
D. ensatus	larval	Mannering Cr., Ida.	24.6 (1.9)	17.4 (0.2)	20.6 (3.9)	16.8 (0.7)	16.8 (2.3)	20.0 (2.5)	116.2 (5.7)	5
D. ensatus	intermediate	Mannering Cr., Ida.	36.5	20.0	15.0	18.5	13.5	22.5	126.0	5
D. ensatus	transformed	Mannering Cr., Ida.	49.0 (3.0)	28.8 (1.7)	15.8 (1.3)	15.4 (1.2)	16.8 (3.8)	28.2 (4.3)	152.0 (8.9)	5
D. ensatus	transformed	Valley Co., Ida.	56.0	25.0	8.0	20.0	16.0	28.0	153.0	1
D. ensatus	larval	Mt. Pilchuck, Wash.	26.7 (1.5)	21.3 (1.6)	32.8 (4.3)		41.2 (2.8)	19.8 (2.1)	142.5 (6.7)	6

[1] Means and standard errors in parentheses are listed.

TABLE 14

ALBUMIN TO GLOBULIN RATIOS AND RELATIVE MIGRATION OF SERUM PROTEINS[1]

Species	Stage	Locality	A/G	A + 2/G−2	Rf of Fractions						
					1	2	3	3′	4	5	N
D. copei	larval	Nine Foot Cr., Wash.	.33 (.02)	.67 (.04)	.96 (.01)	.84 (.01)	.36 (.01)		.23 (.01)	.08 (.01)	12
D. copei	transformed	Maratta Cr., Wash.	.40 (.02)	1.35 (.14)	.91 (.02)	.80 (.02)	.36 (.01)		.26 (.01)	.08 (.01)	7
D. ensatus	larval	Maratta Cr., Wash.	.26 (.01)	.55 (.04)	1.06 (.01)	.81 (.01)	.61 (.01)		.27 (.01)	.08 (.01)	9
D. ensatus	transformed	Maratta Cr., Wash.	.37 (.01)	.70 (.03)	.94 (.01)	.75 (.01)	.58 (.01)		.23 (.01)	.08 (.01)	8
D. ensatus	larval	Mannering Cr., Ida.	.27 (.03)	.58 (.05)	.99 (.01)	.78 (.02)	.59 (.02)	.39 (.01)	.23 (.01)	.11 (.01)	5
D. ensatus	intermediate	Mannering Cr., Ida.	.39	.80	.97	.76	.54	.37	.21	.11	2
D. ensatus	transformed	Mannering Cr., Ida.	.46 (.02)	1.01 (.04)	.97 (.02)	.80 (.01)	.55 (.01)	.39 (.01)	.20 (.01)	.12 (.01)	5
D. ensatus	transformed	Valley Co., Ida.			1.04	.84	.57	.35	.17	.12	1
D. ensatus	larval	Mt. Pilchuck Wash.	.23 (.01)	.52 (.04)	1.06 (.01)	.82 (.01)	.63 (.01)		.21 (.01)	.07 (.01)	6

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[1] A/G = albumin/globulin; A + 2/G − 2 = first two fractions/remainder; relative migration (Rf) compared to human albumin; means and standard errors in parentheses are listed.

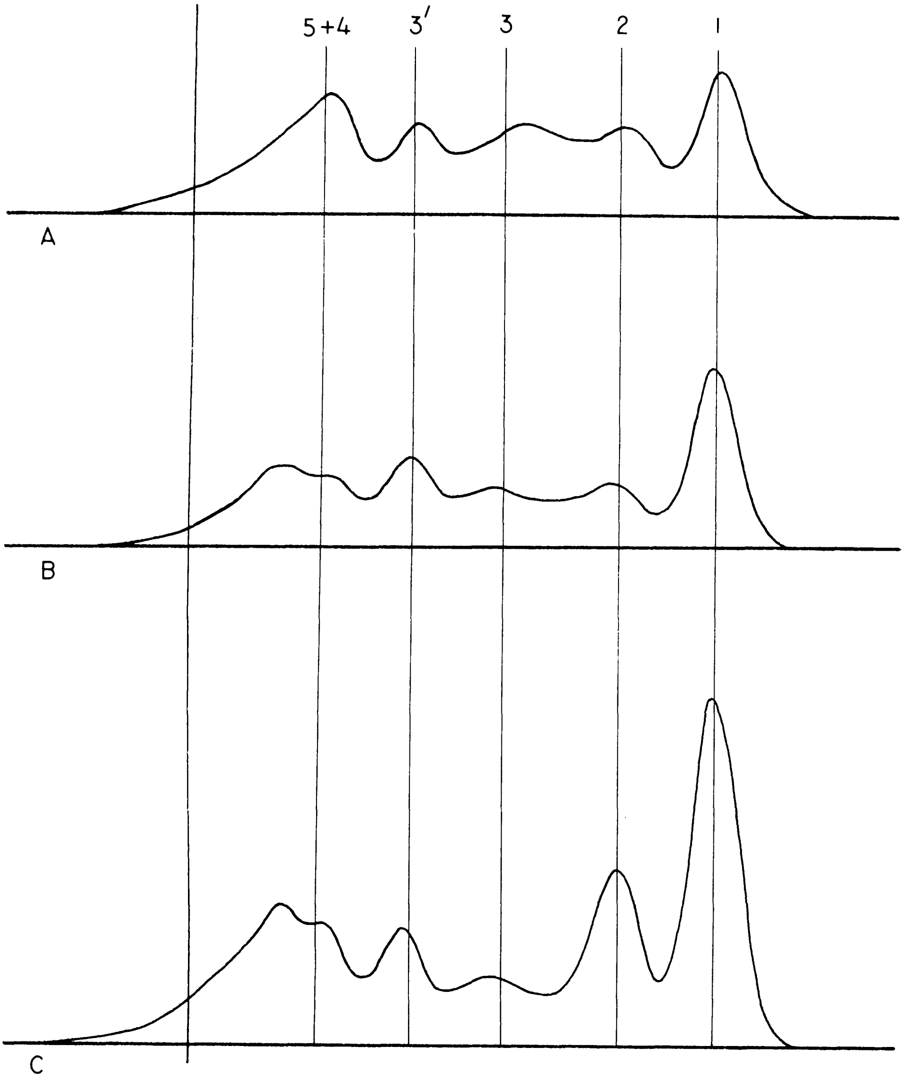

Fig. 29. Ontogenetic changes in blood serum proteins in *D. ensatus* from Benewah Co., Idaho. A is the larval pattern, B is from a specimen in the process of metamorphosing, and C is from a completely metamorphosed individual. See text and Table 11.

A comparison of the electrophorograms of larval and transformed *Dicamptodon* from a given locality shows that there is an increase in the total amount of blood serum protein associated with metamorphosis (Figs. 29 and 30), and that the increase is largely because of increases in fractions 1 and 2. Assuming for the present that fraction 1 is an albumin, the ratio of albumin to total globulin (A/G) can be defined, and A/G is shown in Table 14 to be significantly higher after transformation for both *D. copei* and *D. ensatus*.

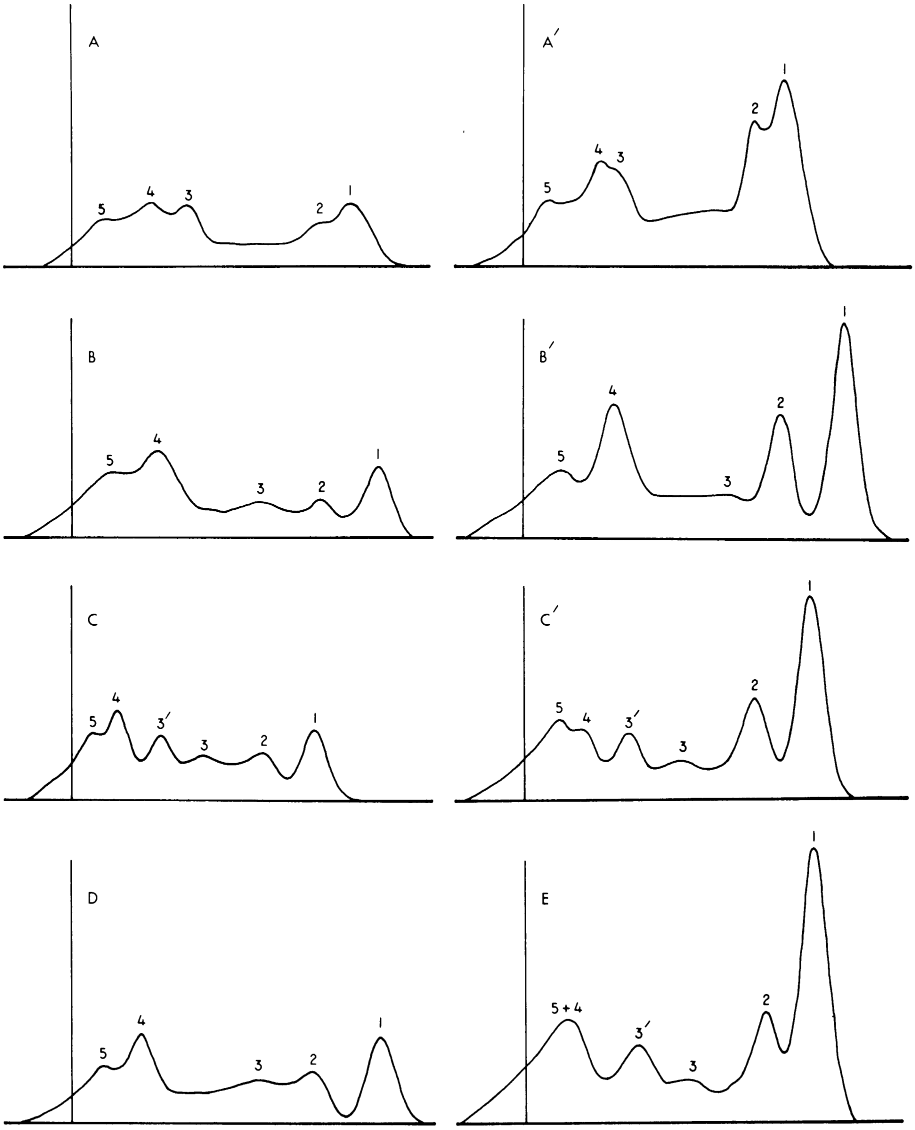

Fig. 30. Ontogenetic and phylogenetic variation in blood serum proteins of *Dicamptodon*. A and A′ are the patterns for larval and transformed (2 years thyroxine treatment) *D. copei* from Maratta Creek, Cowlitz Co., Wash.; B and B′ for larval and transformed *D. ensatus* from Maratta Creek; C and C′ for *D. ensatus* from Mannering Creek, Latah Co., Idaho; D is the larval pattern for *D. ensatus* from Mt. Pilchuck, Snohomish Co., Wash., and E is the pattern for transformed *D. ensatus* from Valley Co., Idaho.

Frieden, Herner, Fish, and Lewis (1957) first demonstrated that albumin fractions are denser in frogs than in tadpoles. This phenomenon seems to have general validity for frog metamorphosis (Frieden, 1961), but it has not been studied closely in urodeles. Hahn (1962) showed that it occurs in *Ambystoma tigrinum*, and the occurrence in the two species of *Dicamptodon* suggests that it may be generally true of salamanders. Wald (1960, 1961) summarized evidence to show that in vertebrates there is a correlation between the occurrence of albumin and terrestriality. Apparently the ontogenetic and phylogenetic appearance of serum albumin is related to the need to conserve water in peripheral tissues and to improve the transport capacity of blood in terrestrial animals (Whipple, 1956).

The ratio of the sum of fractions 1 and 2 to the sum of the remaining fractions (A + 2/G - 2) increases even more drastically at transformation in the two species than does the ratio A/G (Table 14). This reflects the fact that fraction 2 also shows a relatively greater increase at metamorphosis than the slower fractions. Such an increase was not noted by Frieden (1961) for frogs nor by Hahn (1962) for *Ambystoma tigrinum*. Because fraction 2 is also a fast protein, it may share some of the physiological duties of fraction 1, and this would perhaps explain its increased concentration at metamorphosis.

Comparison of the patterns for *D. copei* with those for *D. ensatus* shows that there are important differences between the two species (Fig. 30). Fractions 1 and 2 are closely associated in *D. copei* and less so in *D. ensatus*. *D. copei* lacks a recognizable band between Rf .36 and .80, but *D. ensatus* has a band in this region. *D. copei* has three slow fractions, whereas sympatric *D. ensatus* has only two slow fractions (Fig. 30A, A′, B, B′).

Geographic variation is evident for *D. ensatus*. Whereas the patterns for Mt. Pilchuck (D) and Maratta Creek (B and B′), both Washington Cascade populations, are identical, they differ from the patterns for northern Idaho (C and C′) and central Idaho (E). The patterns for the two Idaho populations are the same, and this is significant because the two populations may be disjunct or at least have reduced gene flow between them.

The major difference between the patterns for Idaho and Washington *D. ensatus* is the occurrence of a sixth band, 3′, at about Rf .37 in both Idaho samples. The single band in the gamma-globulin region of the pattern for central Idaho (E) actually represents two bands. In the particular electrophorogram illustrated, bands 4 and 5 had not fractionated sufficiently for the densitometer to distinguish them. This also occurred with occasional samples from northern Idaho (Fig. 29).

Other populations of *D. ensatus* from Washington and Idaho were sampled. Patterns for animals from Snoqualmie Pass, Kittitas Co., Washington; Mount Rainier, Pierce Co., Washington; Eldorado Gulch, Latah Co., Idaho; and Roundhouse Gulch, Shoshone Co., Idaho demonstrated relationships identical to those outlined above.

Newcomer (1968) examined the plasma proteins of six transformed *D. ensatus* (three from near San Francisco and three from Benton and Lane Counties, Oregon) by starch gel electrophoresis. Because Newcomer used a different technique and because he analyzed plasma rather than serum proteins his results are not directly comparable to mine. Newcomer showed that California and Oregon specimens differed in that the fastest band for the California specimens had a Rf of .98 (by comparison with human albumin) and those from Oregon specimens had a Rf of .89 for the fastest band. Also, Oregon specimens had a band at Rf .64 which was absent in California specimens, and California specimens had a band at Rf .38, apparently absent in Oregon specimens. Newcomer noted no intrapopulation variation.

No geographic variation has been detected in the blood serum proteins of *D. copei*, but so far only specimens from Maratta Creek, Cowlitz Co., and Nine Foot Creek, Skamania Co., Washington have been tested.

COMPARATIVE LARVAL OSTEOLOGY

A detailed account of the comparative developmental osteology of the two species of *Dicamptodon* is deferred to a separate paper. Only the major and obvious points of difference and similarity between the larval forms of the two species are offered here.

Hilton (1946, 1948) stated that the carpals and tarsals are cartilaginous in larval *D. ensatus* of all sizes, including large paedogenes, but are ossified in transformed *D. ensatus*. Hilton implied that ossification of the mesopodial elements was associated with metamorphosis. From my material it is evident that ossification of these cartilages is a result of ageing rather than of metamorphosis (although the two processes are not entirely separable). Young transformed *D. ensatus* may retain cartilaginous ankles and wrists, but invariably ossification occurs as the animals age; contrary to Hilton's results, many large, paedogenetic *D. ensatus* have bony carpals and tarsals. However, larval *D. ensatus* less than about 140 mm SVL seldom have these elements ossified. The mesopodial elements of *D. copei* are, by contrast, often ossified at sizes as small as 70 mm SVL (Figs. 31 and 32).

Fig. 31. Radiographs, taken at two different exposures, of a larval *D. ensatus* (upper in both radiographs, RAN 9861, 99 mm SVL, immature male) and a larval *D. copei* (lower, RAN 9845, 97 mm SVL, mature male). Both from Maratta Creek, Cowlitz Co., Washington. Note the ossified mesopodial elements and greater ossification of the long bones in the limbs of *D. copei*. In the lower

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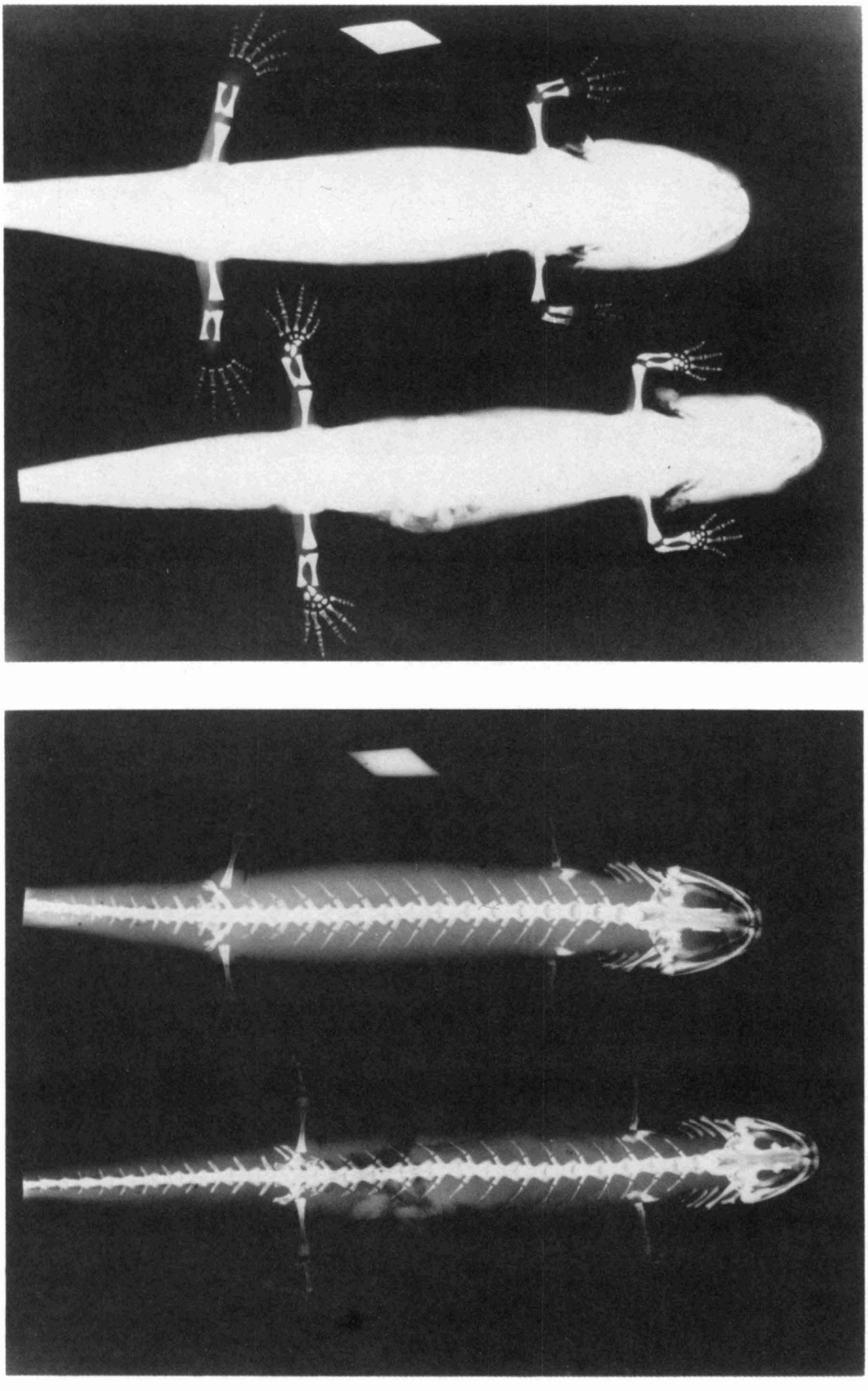

radiograph, note the ossification centers in the pubic plate of *D. copei*, and the greater ossification of the coracoid elements in *D. copei*. Ossification centers are also seen in the hyobranchial apparatus (projecting on either side of the orbitosphenoids) of *D. copei*, which are absent in *D. ensatus*.

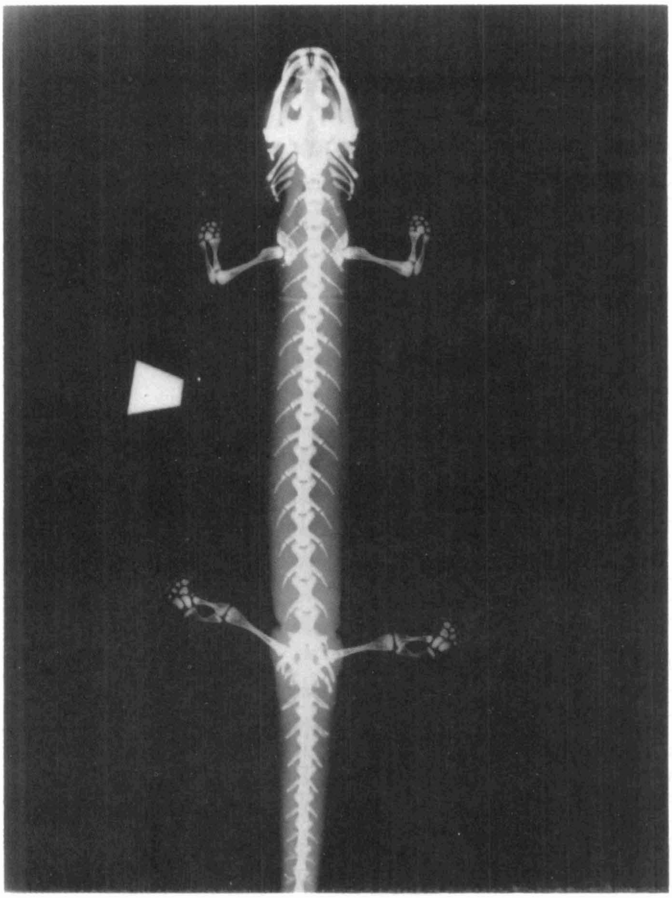

Fig. 32. Radiograph of larval *D. copei* from Nine Foot Creek, Skamania Co., Washington (RAN 8710, 105 mm SVL, mature male). The degree of ossification is even greater in this specimen than in the smaller *D. copei* of Figure 31. Especially note the coracoids, long bones, mesopodials and angularity of the skull. Two small tuberosities for increased muscle attachment project laterally from each squamosal.

The pubic portion of the pelvic girdle is cartilaginous in larval *D. ensatus* smaller than 140 mm SVL, whereas two separate centers of ossification are usually present in *D. copei* larger than 75 mm SVL. In the larger specimens of *D. copei*, mineralization has spread, rod-like, anterolaterally along each pubic half (Figs. 31 and 32).

In smaller larvae of *D. ensatus* (less than 140 mm SVL), the second basibranchial, the posterior half of the ceratohyal, and the epibranchials are the only ossified elements of the hyobranchial apparatus. In *D. copei* larger than 75 mm SVL, additional centers of ossification are seen in the anterior half of the ceratohyals (Figs. 31 and 32), and the first ceratobranchials are also ossified over much of their length. These latter elements are ossified in some extremely large paedogenetic *D. ensatus*.

Other parts of the skeleton of *D. copei* seem to be in advanced stages of ossification compared to larval *D. ensatus* of similar size. For instance, the scapulae are the only parts of the pectoral girdle which are ossified in *D. ensatus*, while in addition large portions of the coracoid cartilages in the regions around the glenoid fossae are mineralized in *D. copei* (Figs. 31 and 32). Inspection of Figure 31 shows that the ends of the humeri, femora, ulnae, radii, fibulae, and tibiae are ossified to a greater extent in *D. copei* than in *D. ensatus*. The squamosal, especially the dorsal portion, of *D. copei* is sculptured with tuberosities and ridges for increased muscle attachment, and this sculpturing lends an overall angularity to the appearance of the skull (Fig. 32). This region of the skull remains rounded and smooth in similar-sized *D. ensatus*, but the angular condition of the squamosal is attained in old, large, paedogenetic *D. ensatus*.

DISCUSSION AND CONCLUSIONS

SPECIES OF *DICAMPTODON*

Analysis of variation of populations of *Dicamptodon* from throughout its range reveals only one major discontinuity, which leads to the conclusion that the genus contains only two species, *D. ensatus* and *D. copei*. The diagnostic characteristics of these species were given by Nussbaum (1970). The possibility that the two species are really only subspecies is eliminated by the fact of microsympatry at several localities with no evidence for intergradation or hybridization.

The possibility that the two species of *Dicamptodon* are morphs of a single polymorphic species is a more difficult problem to resolve, especially so because polymorphism is known to occur in larval forms of other species of Ambystomatidae. Powers (1907) described a remarkable case of polymorphism in larval *Ambystoma tigrinum* in which slender-bodied, small-headed forms and compact-bodied, large-headed forms occurred within single populations. Although a parallel between *D. copei* and larval *D. ensatus* is obvious, I will show that the situation described by Powers for *A. tigrinum* is unique and entirely different from that which obtains in *Dicamptodon*.

Powers ascribed the variation in larval *A. tigrinum* to differences in feeding habits, growth rates, and swimming activity during development, and he wrote that the final form of a particular larva depends on its exposure to various combinations and "dosages" of these factors. Therefore an array of possible body forms exists. Such continuous variation does not occur in *Dicamptodon*. There are no intermediate forms between *D. copei* and larval *D. ensatus* where they occur together, and the type of variation described by Powers is not found in either species of *Dicamptodon* where one species occurs outside the range of the other.

More recently, Rose and Armentrout (1970) and Smith and Reese (1971) reported a type of polymorphism in larval *A. tigrinum* which is apparently genetically controlled and discontinuous, i.e., with no intermediate forms. This type of variation is more comparable to the situation found in *Dicamptodon*, and Smith and Reese (1971) suggested that cryptic speciation rather than polymorphism may be involved in these particular populations of *A. tigrinum.*

Another line of evidence indicates that the variation found in *Dicamptodon* is not attributable to polymorphism. Eleven broods of *D. ensatus* and 19 broods of *D. copei* were reared from eggs to various ages in the laboratory. In all cases eggs from female *D. copei* developed into *D. copei*, and eggs from female *D. ensatus* always developed into *D. ensatus*. Species characteristics were observable even in the hatchlings, and there was no divergence of body form within a brood as noted by Powers (1907) for *A. tigrinum.*

From 1933 until the description of *D. copei* in 1970, the genus *Dicamptodon* was considered monotypic. Specimens of *D. copei* were available, but because *D. copei* and larval *D. ensatus* are not readily distinguishable by cursory examination, *D. copei* went unnoticed. As is so often the case with cryptic species, life history and physiological attributes rather than morphological characteristics were the keys to the recognition of two species of *Dicamptodon*. These attributes include differences in size at sexual maturity and sensitivity to thyroxine. Subsequent to the discovery of life history and physiological differences, the meaning of previously noted morphological variation rapidly came into focus.

GEOGRAPHIC VARIATION

Major Patterns of Variation.—As expected, most populations of *D. ensatus* have evolved minor distinguishing features, especially when fine details of color and pattern are considered. However, microgeographic variation aside, broader patterns of variation are evident which seem to reflect major geographic features of western North America.

D. ensatus from Marin, Napa, Sonoma, southern Lake, and Glenn Counties and from counties south of San Francisco Bay are distinct from *D. ensatus* from the northern counties of California. Larvae and transformed individuals from these southern counties have the largest heads and highest numbers of maxillary-premaxillary and vomerine teeth of all larval and transformed *Dicamptodon*, and larvae lack palatopterygoid teeth. Larval OTUs from this area have (FLL + HLL)/AGL values which are significantly higher than for all other OTUs, except possibly for larvae from Siskiyou County, California (OTU 16). The larvae have white venters and are not so mottled dorsally as larvae from northern California, especially when compared to larvae from the interior highlands of northern California. Transformed *D. ensatus* from the southern counties have white venters derived from the larval form and a light, reddish-brown dorsal ground color with coppery tan marbling. Marbling on the chin is most prominent in specimens from this area.

The distinctness of *D. ensatus* in these southern populations may partly reflect the unique local habitat. The coastal redwood forest which covers much of this region is the oldest, most stable forest ecosystem in western North America. Perhaps more important is the effect of local topography and drainage patterns. Most of northwestern California is drained by rivers that flow generally in a northwesterly direction. A few major rivers such as the Klamath and Hayfork Rivers flow southwest at their upper ends, but swing around to the northwest on their lower ends. The major rivers which drain this section of California are from south to north: Garcia, Navarro, Big, Ten Mile, Mattole, Eel, Van Duzen, Mad, Redwood Creek, Trinity, Klamath, and Smith. At the headwaters of these drainages, a major ridge or divide occurs, which for convenience I will refer to as the "North Coast Divide." To the east and south of it, waters flow to the interior (Sacramento River Drainage) or to the coast in the vicinity of San Francisco Bay. The North Coast Divide begins on the coast near Gualala, Mendocino County and runs eastward south of the Garcia River Drainage, turns northward around the headwaters of the Navarro River, parallels the Russian River to the west of it, and turns southwest to separate the headwaters of the southward flowing Russian River and northwesterly flowing Eel River. The Divide then runs northward to form the crest of the Coast Range.

The North Coast Divide corresponds with the break in variation between southern and northern populations of *D. ensatus* in California, and such a geographic feature is expected to have a strong influence on gene flow and dispersal in a salamander with stream-dwelling larvae like *D. ensatus*.

The North Coast Divide may also have an influence on distribution and variation in other northwestern amphibians. Of particular interest is its apparent limiting effect on the range of the Olympic salamander, *Rhyacotriton olympicus*, and the tailed frog, *Ascaphus truei*, both of which are stream adapted species and closely associated with the same habitats as *D. ensatus* in northern regions. The southern limit of *R. olympicus* is near the mouth of the Garcia River, and the southern limit of *A. truei* is near the mouth of the Navarro River. These two rivers are the southernmost major drainage which are still north of the North Coast Divide. The ranges of other amphibians which are characteristic of the Northwestern Herpetofauna may also be influenced by the North Coast Divide. For example, the northwestern salamander, *Ambystoma gracile*, is found only as far south as the mouth of the Gualala River in the immediate vicinity of the North Coast Divide. The California newt, *Taricha torosa*, is largely limited to the south and east of the Divide, and the stream-breeding red-bellied newt, *Taricha rivularis*, is largely confined to the north and west of the Divide. The clouded salamander, *Aneides ferreus*, is not found south of the Divide, and the Divide corresponds very roughly with the zone of intergradation between the Oregon salamander, *Ensatina eschscholtzi oregonensis* and the yellow-eyed salamander, *E. e. xanthoptica.*

San Francisco Bay has not been a major barrier to gene flow in *D. ensatus*, at least in the near past. There are, however, a few minor differences between populations on either side of the Bay. Transformed specimens from the south side have the most extensive chin and throat marbling of all *D. ensatus* and both larvae and transformed specimens from the south side have higher numbers of maxillary-premaxillary and vomerine teeth.

Populations of *D. ensatus* in the more northern counties of California and in extreme southern Curry, Josephine, and Jackson Counties, Oregon form a natural group based on measured characteristics. On a finer scale, color and pattern, especially of larvae, vary considerably within this area. Populations in the humid coastal region of northern California form a subgroup within this northern group, and populations in the drier interior highlands form a second subgroup (Fig. 13). In color, larvae and transformed *D. ensatus* from the humid coastal subgroup are intermediate between those from the interior highlands subgroup and those from south of the North Coast Divide. The humid forests of the Bay Area extend northward along the California coast in slightly altered form, and the North Coast Divide is least prominent near the coast. More or less continuous gene flow, perhaps slightly interrupted by the low North Coast Divide, would be expected in this humid corridor, and selection pressures along the corridor should not differ greatly because of similarities in climate and substrate. In the interior highlands, a different and unique phenotype, especially in larval coloration, is maintained by selective pressures created by harsh interior climates and the distinctive and complex nature of the substrate. Predominantly downstream dispersal from these highlands to the north California coast causes a mixing of phenotypes in the north coast region of California, and hence the intermediacy in color of specimens from this area.

On a broader level, all populations of *D. ensatus* south of southern Curry, Josephine, and Jackson Counties, Oregon are bound together by certain basic similarities, including both morphometric and colorimetric features (Group A, Fig. 13). To the north, the Klamath-Siskiyou Mountains mark the area of most rapid change in overall appearance of both larval and transformed *D. ensatus*. Populations in northern Curry, central Josephine, and southwestern Jackson Counties, Oregon are in an area of most rapid change (note the positions of larval OTUs 14 and 15, Fig. 4).

The Klamath-Siskiyou Mountains have had an important influence on distribution and variation in many other northwestern amphibians and reptiles. The western red-backed salamander, *Plethodon vehiculum*, and Dunn's salamander, *Plethodon dunni*, are largely limited to the north of the region, and the California slender salamander, *Batrachoseps attenuatus*, and the black salamander, *Aneides flavipunctatus*, are largely limited to the south of it. Some species which occur on both sides of the Klamath-Siskiyou Mountains exhibit strong morphoclines across the region. For example, two subspecies of the northern alligator lizard, *Gerrhonotus coeruleus*, are found on either side of the region. And in a sense the region has its own distinctive herpetofauna. The painted salamander, *Ensatina eschscholtzi picta*, is confined to the region, as is the Siskiyou Mountain salamander, *Plethodon stormi*. Many other plants and animals are similarly affected by the distinctive geographic position and complex ecology of the Klamath-Siskiyou Mountains (Stebbins and Major, 1965; Remington, 1968; Whittaker, 1961).

With minor local deviations, populations of *D. ensatus* in the Cascade Mountains of both Oregon and Washington are remarkably uniform in body form and color. Populations in the northern Coast Range of Oregon have distinctive features, but animals from this region are more similar to animals from Cascade populations, especially those directly east, than to any other *D. ensatus*. The northern end of the Willamette Valley forms only a slight barrier to gene flow between populations in the bordering mountain ranges. Several large streams head in the Cascades and flow out onto the Willamette Valley, and, together with western tributaries of the Willamette River, could have provided dispersal routes between the Cascade and Coast Ranges of northern Oregon. The relatively humid Columbia River Gorge may also be an important dispersal route between the two mountain ranges.

The Willamette Valley is only a weak barrier for most species of amphibians and reptiles. No form of raciation or major variation is associated with the Willamette Valley. Only the Oregon slender salamander, *Batrachoseps wrighti*, and the Cascades frog, *Rana cascadae*, are limited to one side of the Willamette Valley (the Cascade side), and the Cascades frog is a high elevation form which probably would not find suitable habitat in the Coast Range.

Populations in the southern Coast Range of Oregon show greater affinities to populations in the Cascades than to populations in the northern Coast Range of Oregon. This relationship also holds true for *Plethodon vehiculum* (Brodie, 1970), and probably results from the complex intermingling of the Coast, Siskiyou, and Cascade Mountains in southwestern Oregon. Two major rivers, the Rogue and Umpqua, which head in the Cascades and cross into the Coast Range, provide likely avenues of dispersal and gene flow between the two areas.

The Columbia River, which is as much as 4.8 km wide near its mouth, and its Gorge break the continuity of the Cascade Range between Oregon and Washington. To *D. ensatus*, this major topographic feature is hardly a barrier at all, because populations on either side of the Gorge are nearly identical for most characteristics. Storm (1966) summarized evidence which shows that the Columbia River Gorge has had little effect on the distribution or variation of other northwestern aquatic amphibians. However, strictly terrestrial species of salamanders are affected by the presence of the Gorge. *Aneides ferreus* and *Batrachoseps wrighti* are restricted south of the Gorge and *Plethodon dunni* barely occurs north of the Gorge. *Plethodon vandykei* is restricted north of the Gorge. Though occurring on both sides, *Plethodon larselli* shows distinct morphological differences on either side (Brodie, 1970).

Populations of *D. ensatus* in the Rocky Mountains form a natural group. The most characteristic features of these populations are the dark dorsal and ventral hues of both larvae and transformed specimens and the fine-grained marbling of the latter. Individuals from these populations also show close relationship in various measurements and counts as indicated by the larval phenogram (Fig. 13). Furthermore, the electrophoretic pattern of blood serum proteins is distinct for Rocky Mountain *D. ensatus* when compared to populations in the Cascade Mountains of Washington.

Variation between populations in the Rocky Mountains is slight, but the dorsal color pattern of transformed *D. ensatus* from the Central Rocky Mountains in Valley Co., Idaho is even finer grained than the pattern found in specimens from the Northern Rocky Mountains. This relationship may indicate that the relatively dry Salmon River Valley is an effective barrier to gene flow between the two areas; or it could suggest a cline from fine-grained patterns in the north to extremely fine-grained patterns in the south. Unfortunately it is not yet known whether these populations are truly disjunct. Two sight records near the old mining camp of Dixie, Valley County, indicate that the populations may not be as widely separated as the present range map indicates (Fig. 1).

In body form, *D. ensatus* from the Rocky Mountains are most similar to *D. ensatus* from the northern Cascade Mountains, as suggested by the results of cluster analysis of larval OTUs (Figs. 14 and 15). Transformed specimens and larvae from the two areas have darker dorsal and ventral hues than animals from southern regions, but the Rocky Mountain forms are the darkest. Transformed *D. ensatus* from the northern Cascades have coarser marbling than those from Idaho, but, in general, not as coarse as the marbling of specimens from south of the Klamath-Siskiyou Mountains.

D. copei shows little variation within its relatively small range. It may be of some significance that the three populations which occur in Oregon (OTUs 27, 28, 29) cluster with each other (Fig. 13) before clustering with populations from north of the Columbia River in

Washington, but, in general, variation between OTUs is slight and appears to be simply a function of geographic distance. For instance, the two most similar populations are OTUs 27 and 28, and they are less than 6 km apart.

The Effects of Isolation.—A population of *D. ensatus* is isolated at Oak Springs, Wasco Co., Oregon (Fig. 1). The site is in the Upper Sonoran Lifezone with the typical aspect of northern, cold deserts. The temperature of the spring is constant at 12.5°C and the volume of flow does not fluctuate. The surrounding habitat seems unfavorable for terrestrial *Dicamptodon*. In general body form, larvae from Oak Springs are identical to specimens of *D. ensatus* from the nearby Cascades and Columbia Gorge of northern Oregon. However, their color is quite distinctive. Hatchlings are dark brown with scattered light dots over the dorsum. Older larvae are light tan-brown dorsally and have peculiar yellow dots (0.5-1.5 mm diameter) scattered at irregular intervals on the dorsal and lateral surfaces. No other population of *D. ensatus* has individuals colored like this. Larvae show signs of sexual maturity at about 90 mm SVL. But larvae at least occasionally metamorphose naturally at Oak Springs, and the dorsal marbled pattern of transformed individuals is similar to the pattern found in adults from the northern Cascade Range. It appears that only the distinctive color of the larvae and sexual maturity at a relatively small size reflect effects of isolation.

Another isolated population of *Dicamptodon* occurs in Shoat Spring (OTU 11) in a relatively dry section of the southern Cascades in Oregon. The spring is large, cold (9°C), and permanent with no seasonal fluctuations in volume or temperature. The site is in a forest of scattered Ponderosa Pine (*Pinus ponderosa*) and Incense Cedar (*Libocedrus decurrens*) with a sparse shrub understory. The climate is too dry to support a rich herb layer, and reddish, porous, volcanic soil exposed over wide areas contributes to the xeric aspect of the region. The terrestrial habitat is unfavorable for *Dicamptodon*, and only the stable nature of the spring and the presence of large numbers of aquatic snails, which the larvae feed on almost exclusively, allow the population to exist.

As noted earlier, larvae from Shoat Spring are similar to *D. copei* for some characteristics. However, I am convinced that OTU 11 properly belongs in *D. ensatus* and that its similarity to *D. copei* is superficial and is a result of convergent evolution. Limb length and head size constitute the most striking similarities between larvae of OTU 11 and *D. copei*, although for these characters Shoat Spring larvae are intermediate between *D. copei* and *D. ensatus* (Figs. 4 and 5). OTU 11 has fewer maxillary-premaxillary and vomerine teeth than *D. ensatus*, and it falls in the range of *D. copei* for these characters. But earlier I showed there is a strong between-population correlation between head size and tooth number so that the relatively small heads of OTU 11 would account for fewer teeth.

Paedogenesis at a small size is another point of similarity between OTU 11 and *D. copei.* Transformed individuals have not been collected at Shoat Spring, and the apparent abandonment of the terrestrial stage of the life cycle might be expected in an isolated population with a highly stable, aquatic environment and a hostile terrestrial environment. However, contrary to the situation in *D. copei*, larvae from Shoat Spring readily metamorphose when treated with metamorphogens, and fully transformed individuals are obtained in three months at 10 C. Therefore although both *D. copei* and OTU 11 consist largely, if not entirely, of larval forms, the physiological causes of paedogenesis are different between the two.

Short, weak limbs relative to body length and small heads are characteristic of many aquatic salamanders, as is paedogenesis in its various forms. These common features of *D. copei* and OTU 11 have likely evolved independently as convergent aquatic adaptations. OTU 11 has evolved one aquatic adaptation not found in any *D. copei.* The toes of larvae from Shoat Spring are wide-based resulting in a triangular, webbed shape.

That OTU 11 belongs with *D. ensatus* is shown by many similarities, some of which are not easily quantified and which were not used in cluster analysis. The subtleties of head shape are lost in simple measurements of length and width, and although relatively small, the heads of larvae from Shoat Spring are shaped more like the heads of larval *D. ensatus* than *D. copei.* Their heads lack the angularity of the heads of *D. copei*, and the radiographs show that the skull is smooth and rounded as in larval *D. ensatus.* The skeletons of Shoat Spring larvae are relatively unossified as in similar-sized larval *D. ensatus.* The overall conformation of the body of larvae from Shoat Spring is robust compared to *D. copei*, and is hence more like *D. ensatus.* Their color is distinctive (light tan-brown dorsally with some mottling and smoky-brown venters) but more like larval *D. ensatus* than *D. copei*; and they lack the conspicuous granular glands of *D. copei.* Transformed specimens obtained by treating larvae from Shoat Spring with thyroxine have coarse marbling, similar in pattern and hue to transformed *D. ensatus* from the Siskiyou-Trinity-Shasta regions.

Shoat Spring is 360 km south of known populations of *D. copei.* Populations to the north, south and west are *D. ensatus.* This geographical relationship plus the many similarities to *D. ensatus* lead me to conclude that OTU 11 is a distinct population of *D. ensatus* which has evolved characteristics superficially similar to *D. copei.* Isolation on the extreme periphery of the range of *D. ensatus* in marginal habitat has allowed evolution to proceed unaffected by gene flow from other populations, and the extreme environmental conditions have produced strong selection pressures which led to the paedogenetic mode of reproduction and aquatic morphological adaptations.

Subspeciation.—Arguments could be made for subspecific recognition of some populations of *D. ensatus*. The Rocky Mountain Group is distinctive, but there is north-south variation within this Group. Populations south of the Klamath-Siskiyou Mountains form a recognizable subset, but on a finer scale these populations exhibit considerable heterogeneity. Microgeographic variation, especially in color and pattern of larvae, is apparent for most populations. For these reasons little would be gained and much would be obscured by naming subspecies of *D. ensatus*. Variation in *D. copei* is slight and is a function of geographic distance; therefore no subspecies are recognized.

HISTORICAL SPECULATION

The subfamily Dicamptodontinae has probably been confined to western North America throughout its evolutionary history; at least the present ecological relationships, distribution, and meager fossil record would suggest this.

The ancestors of modern *Dicamptodon* probably originated from a hynobiid-like stock sometime during the Cretaceous Period in the circumpolar forest of arctic North America. This temperate forest has been named the Arcto-Cretaceo-Tertiary Geoflora, or simply the Arcto-Tertiary Geoflora (Chaney, 1959), and its distributional history and paleoecological implications have been well studied (e.g., Axelrod, 1948, 1960; Chaney, Condit, and Axelrod, 1944; Dorf, 1960; Detling, 1968; MacGinitie, 1958).

During the Cretaceous, the Arcto-Tertiary Geoflora was confined north of what is now about Latitude 52°N. At this time the Pacific Northwest was covered with tropical forests (Neotropical-Tertiary Geoflora), and the climate was probably not suited to the *Dicamptodon* mode of living.

There is some evidence that climates were cooler in the Pacific Northwest during the Paleocene Epoch. Royce (1965) described the Paleocene Pipestone flora of north-central Washington as a warm temperature phase of the Arcto-Tertiary Geoflora, and fossil redwoods are known from the Paleocene Chuckanut flora near Bellingham, Washington. Chaney (1951) stated that the Paleocene Fort Union flora of western Montana indicated a well-forested region in which fossil redwoods (*Metasequoia*) were common. The fossil dicamptodontine, *Ambystomichnus montanensis*, was associated with the Fort Union flora (Peabody, 1954), and hence the earliest record of a *Dicamptodon*-like salamander is with a redwood-type forest. This southern incursion of Arcto-Tertiary elements during the Paleocene seems to be correlated with the culmination of the Laramide Orogeny (Mackin, 1937).

The Eocene Epoch was an erosional phase of geological history, and the low, rolling plains of western North America were covered largely with tropical forests. Apparently the temperate-tropical ecotone was near Latitude 50°N (Kay and Colbert, 1965), and, therefore, during the Eocene dicamptodontines were confined entirely north of their present area of distribution.

The rate of orogenic activity increased sometime in the Oligocene Epoch, and the changing land-sea relationships resulted in cooler climates which brought the Arcto-Tertiary Geoflora southward again into the Pacific Northwest. This cooling trend has continued from the Oligocene to the present, and Arcto-Tertiary elements have characterized the Pacific Northwest since the Oligocene.

From Oligocene to Upper Miocene time, most of the Pacific Northwest was covered by a homogeneous, temperate, summerwet forest dominated by redwoods. Many fossil floras of the period are known from the Pacific Northwest, but the wide-ranging Bridge Creek flora of the Upper Oligocene is the best known. Chaney (1925) studied the flora where it is exposed in the John Day Basin of north-central Oregon, and he found that the flora consists of fossil redwoods and other plants whose living counterparts make up a large percentage of the modern redwood forest of northern California and southwestern Oregon. Of 18 modern species which are highly characteristic of the modern forest, 12 are represented by close relatives in the Bridge Creek flora.

It can only be inferred that from Oligocene to Upper Miocene time ancestral *Dicamptodon* was found throughout much of the Pacific Northwest since there were no major elevational barriers and hence no dry, interior basins (Snavely and Wagner, 1963). The fossil newt, *Paleotaricha oligocenica*, was associated with this type of forest in Oregon, and its presence suggests that the northwestern urodele fauna was already established by Upper Oligocene time.

During Upper Miocene-Lower Pliocene time, the relatively low, uniform relief of the Pacific Northwest was broken by volcanism which along with complex arching (Hodge, 1938) created the Cascade Range. At about the same time, the Columbia Plateau was epeirogenically uplifted (Kummel, 1961) and the high elevations, in addition to the rain shadow imposed by the new Cascade Range, created a hostile, interior climate over most of eastern Oregon and Washington. The effects of these climatic changes are well documented in series of fossil floras in Oregon (Chaney, 1944, 1959) and in Washington (Smiley, 1963). The floras show the gradual replacement of redwood forests by xeric vegetation, and, by Lower Pliocene time, redwoods were confined to the western side of the Cascade Range.

It can be assumed that the potential range of *Dicamptodon* and other humid forest species was greatly reduced in size and restricted to coastal regions, and perhaps to somewhat less favorable habitat in the interior Rocky Mountains, by these drastic environmental changes. It is known that a *Dicamptodon*, along with *Taricha* sp. and

Batrachoseps sp., lived in the central Sierra Nevada region of California in Lower Pliocene times (Peabody, 1959). These fossil salamanders lived in association with the Table Mountain flora described by Condit (1944). *Sequoia* is apparently absent from the flora, but other components of the redwood forest are present which perhaps suggests a relatively dry facies of the old redwood forest.

Orogeny continued through Pliocene time into the Pleistocene, accentuating the basin and range topography of the Northwest and further restricting the range of montane species. Extremes of elevation and climate created lifezones which, with northward migration of elements from the Madro-Tertiary Geoflora (Axelrod, 1958), produced the characteristic vegetation zones seen today in the Pacific Northwest. By Pleistocene time, the old northern redwood forest was reduced to a mere remnant in northwestern coastal California and southwestern Oregon, where it occurs today.

Over the past 100,000 years or more, the Pacific Northwest has been subjected to a complex series of at least five glaciations (if Neoglaciation is counted) with minor stades and interglacial periods (Richmond, 1965). In general, pollen analyses of peat bogs indicate that lifezones were lowered and boreal species pushed southward during glacial maxima and that these trends reversed during interglacial periods (Hansen, 1947; Heusser, 1960, 1965).

Following the last glacial maximum a period of maximum warmth and dryness occurred in the Northwest; called the Hypsithermal or Altithermal Interval by some authors, it lasted from about 7,000-4,000 years B.P. During this period, lifezones were located farther north and higher up the slopes than they are today.

Considering the information at hand, I believe the most parsimonious explanation of the evolution of *Dicamptodon* is as follows. The old, northern, summerwet Arcto-Tertiary Geoflora has always been the center of evolution for the Dicamptodontinae. In Cretaceous and early Paleogene times, dicamptodontines ranged over wide areas of what is now western Canada and Alaska. In the later Paleogene ages they spread into the Pacific Northwest with the Arcto-Tertiary Geoflora. Mild speciation and extinction may have occurred in peripheral areas, but the line has always been conservative, having found a successful life pattern in a stable environment relatively free from competitors. When the old northern forest became restricted in the Neogene, so did the distributional area of the Dicamptodontinae. By Pleistocene time, the primitive habitat of *Dicamptodon* was limited to a restricted area in the northern coastal fog belt of California and southwestern Oregon.

There is evidence that individuals of *D. ensatus* living today in the redwood forests are more similar to ancestral *Dicamptodon* than are individuals from northerly regions. Peabody (1954, 1959) showed that the Paleocene *Ambystomichnus* and the Lower Pliocene *Dicamptodon* sp. had longer legs than modern *D. ensatus*, and he suggested that they had longer tails. I have shown that the longest-legged living *D. ensatus* are found in the modern redwood forests, and it appears that the longest-tailed specimens are also found there. Other presumably ancestral features of these southern populations are large heads, high numbers of maxillary-premaxillary and vomerine teeth, and high gill raker counts. Individuals with the extreme expression of these primitive characters are found in the San Francisco Bay Area south of the North Coast Divide, and it is here where the lowest percentage of paedogenes is found. The ancestral generalized *Dicamptodon* would not be expected to be paedogenetic; nor would such a specialization be desirable in a stable forest ecosystem, with humid, equable climates where the terrestrial habitat is highly productive and predictable.

Another hypothetically ancestral feature of populations from the San Francisco Bay Area is the propensity for transformed individuals to vocalize as a means of defense or threat (Maslin, 1950; Bogert, 1960). Maslin (1950) reported "true vocal cords" in specimens from California, and individuals have been heard vocalizing in the field in California on many occasions by myself and others. California specimens can easily be induced to vocalize in captivity, but I have never heard vocalization in transformed individuals from Oregon, Washington, and Idaho despite many attempts to induce it in many individuals; nor are there any verified reports of vocalization in individuals from these northern regions.

Vocalization is clearly a terrestrial adaptation and, along with long limbs, compact bodies, many teeth, and proclivity for transformation, indicates a primitive, terrestrial, adaptive complex characteristic of *D. ensatus* in its presumed ancestral habitat.

Populations north of the Klamath-Siskiyou Region are more specialized, and their history has been tied with pluvial and glacial activity in unstable environments. During glacial maxima, continental ice and mountain glaciers greatly restricted the range of *Dicamptodon* to relatively southern latitudes and low elevations. At the borders of the glaciers, paedogenesis was selected for because of the hostile terrestrial environment and the permanency and predictability of abundant waterways from meltwater and high precipitation. Of interest here is the observation of Tihen (1955) that populations of fossil *Ambystoma tigrinum* associated with glacial maxima were paedogenetic, while those found in deposits of interglacial origin were types that normally transformed.

From 25,000 to about 10,000 years ago, Pinedale Glaciation dominated the Rocky Mountains, and at times the Cordilleran ice sheet pushed out onto the Columbia Plateau in north-central Washington (Richmond et al., 1965). At the same time, mountain glaciers capped the Cascade Range, the Olympic Range, and the Blue Mountains of northeastern Oregon (Crandell, 1965).

Early during this last episode of glaciation, perhaps a segment of ancestral *D. copei* became isolated in western Washington. More or less surrounded by continental ice to the north and mountain glaciers to the east in the Cascades, western Washington must have acted as a refugium for montane species, and Dumas (1966) has suggested that *Rana cascadae* evolved from ancestral *Rana pretiosa* in this hypothetical refugium. Given a relatively small gene pool, no inward gene flow, abundant moisture, and a tendency toward the paedogenetic habit, evolution toward fixation of paedogenesis and the associated attenuate body form proceeded rapidly.

Palynological evidence (Heusser, 1965) indicates that about 12,000 years ago during the last glacial maximum a Lodgepole Pine parkland existed just south of the Cordilleran ice sheet in north-central Washington. Given maximum pluvial activity, such a belt would have been suitable for *D. ensatus*, and the range of the species was probably continuous along the lower, eastern slopes of the Washington Cascades, across central Washington, and on the lower, western slopes of the Rocky Mountains (Fig. 33). The low Columbia River Gorge may have served as a connecting link between populations of *D. ensatus* on the eastern slopes of the Cascade Range and populations to the west of the Cascades in Oregon. Mountain glaciers in the Klamath-Siskiyou Region interrupted gene flow between California and Oregon populations, but low coastal connections may have maintained some continuity. In the ancestral habitat of coastal California, populations were largely unaffected by glaciation.

After the ice retreated, parkland forests spread into the areas left barren by the ice. But soon a drying trend set in which lasted until about 4,000 years ago. Palynological studies (Hansen, 1947) indicate that grasses, chenopods, and composites replaced the pine forests of north-central Washington and spread far up the Okanogan Valley into British Columbia. It was during this period that the inland population of *D. ensatus* became separated from the coastal populations. The range of *D. ensatus* shifted in accordance with northward and upward-moving lifezones. The dry eastern slopes of the Cascades were abandoned, and perhaps relict populations were left at sites such as Oak Springs and Shoat Spring on the eastern periphery of the range. Perhaps also at this time the Central Rocky Mountain population was isolated from northern Idaho populations as xeric vegetation spread up the low Salmon River Valley. The relatively small area where *D. ensatus* occurs south of the Salmon River is today a small "island" which receives about 78 cm precipitation per year. Surrounding areas receive much less, and 80 cm per year seems to be near the minimum for *D. ensatus* except at spring sites. With the ice barriers gone, adjustments in the ranges of the western Washington population (now *D. copei*) and *D. ensatus* caused them to overlap, and there has been no resultant introgression.

If this hypothetical history is correct, then *D. copei* would be more closely related to northern populations of *D. ensatus* than to

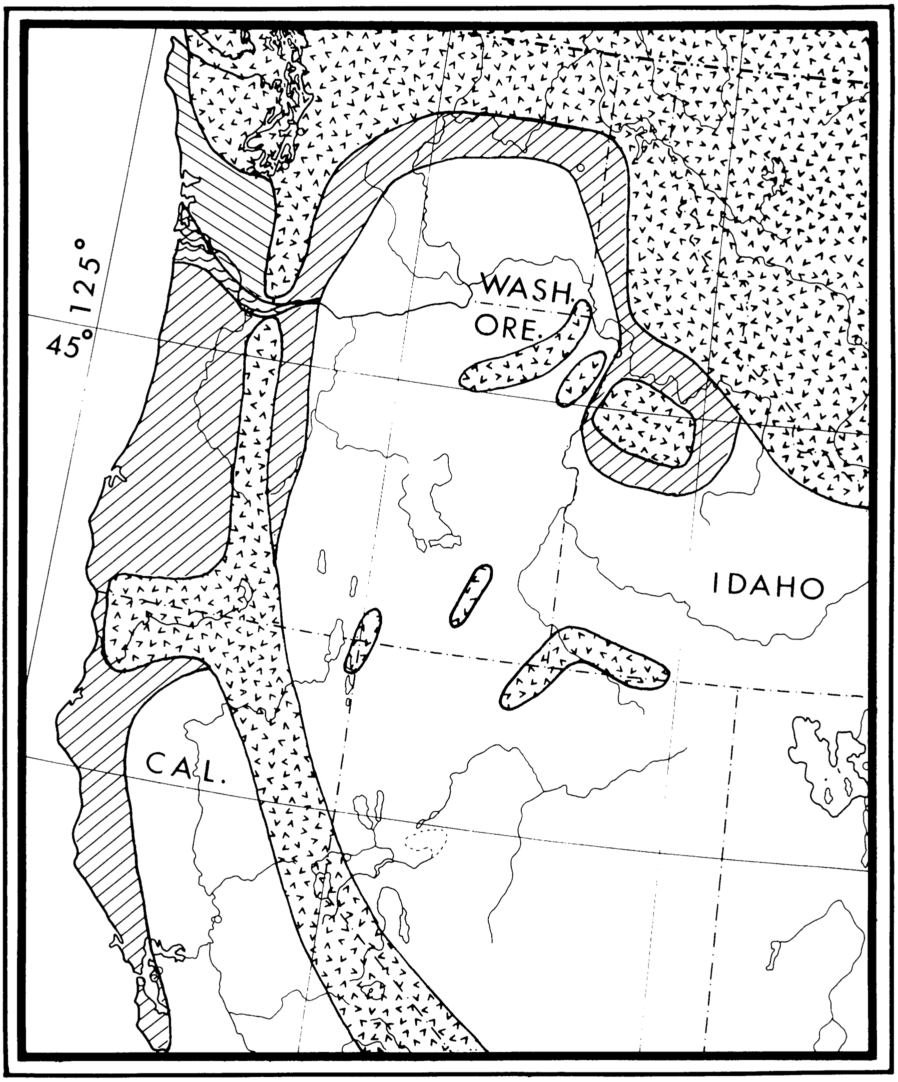

Fig. 33. Hypothetical range map of the genus *Dicamptodon* during the last glacial maximum (about 12,000 years ago). The hatching which slopes up to the right represents the hypothetical range of *D. ensatus*; the hatching which slopes up to the left indicates the range of ancestral *D. copei*. "v" symbols indicate the maximum extent of permanent ice and snow fields.

southern populations, and this seems to be the case, as indicated by similarities in morphology and life history. The theory also requires that inland *D. ensatus* show affinity to northern Cascade *D. ensatus* and this has been shown.

SUMMARY

Previous to 1970 the genus *Dicamptodon* was thought to consist of a single, broad-ranging species, *D. ensatus*. The discovery of a second species, *D. copei* (Nussbaum, 1970), caused the taxonomic status of many populations to be open to question. Since the genus had not been systematically reviewed, a thorough analysis of variation within the genus was necessary.

All available museum specimens were examined, and new material from throughout the range of the genus was collected. Specimens were arranged into 32 larval OTUs and 12 OTUs of transformed specimens. Emphasis was placed on larval OTUs because larvae were more readily available and because one species, *D. copei*, consists almost entirely of larval populations. Variation in morphometric characters, color, blood serum proteins, larval osteology, sensitivity of larvae to thyroxine, and size at maturity was analyzed. Multivariate techniques were applied to the morphometric data in order to objectively estimate similarities between OTUs.

A single, major discontinuity was identified, and hence only two species, *D. ensatus* and *D. copei*, are recognized. Although the ranges of the two species are largely allopatric, a narrow zone of sympatry occurs. Microsympatry was observed at eight localities, and there was no evidence of intergradation or hybridization at these sites. The possibility that the two species are in reality morphotypes of a single polymorphic species was entertained and rejected, mainly because it was found that the two forms breed true to type.

D. ensatus is a highly vagile species ranging from San Francisco Bay northward through northwestern California, western Oregon, western Washington exclusive of the Olympic Peninsula, and extreme southwestern British Columbia where it has yet to be reported north of the Fraser River. *D. ensatus* occurs as a geographic isolate in the Rocky Mountains of northern Idaho. It has also been reported in Montana, but no voucher specimens exist. *D. ensatus* breeds in seepages, streams, and mountain lakes. Some populations are entirely neotenic, others have mixtures of neotenic and terrestrial adults, and yet others have only terrestrial adults. Facultative neoteny allows *D. ensatus* to fully exploit local conditions, and may be largely responsible for its success across a broad range of latitude, elevation, and habitat types.

D. copei has a restricted range in extreme northwestern Oregon and western Washington, where climates are relatively mild and precipitation uniformly high. The species is almost entirely neotenic, with only two known instances of natural metamorphosis. Obligate neoteny restricts the range of *D. copei* to areas of predictably high precipitation and to stream and lake systems which are not subject to drying over long intervals of time.

Geographic variation is prominent in *D. ensatus*, as is expected for species occupying a wide range of habitat types. Multivariate analysis of morphometric characters of larval populations discriminates three groups: a Rocky Mountain Group, a Cascade and Oregon Coast Range Group, and a Californian Group. The first two groups seem to be more similar to each other than either is to the Californian Group. The Californian Group can be divided into a southern subgroup and a northern subgroup; the northern subgroup can be further separated into a coastal subgroup and an interior highlands subgroup. This arrangement of groups is confirmed by analysis of color variation of larvae and transformed individuals, and morphometric variation in transformed individuals.

The geographic distribution of these groups corresponds with major features of topography in the Pacific Northwest. The Californian Group is confined south of the geologically old and complex Klamath-Siskiyou Mountains. The southern Californian subgroup is found south of the "North Coast Divide," and the northern subgroup is found north of this Divide in an area of northwestern drainage. The interior highlands subgroup of the northern Californian subgroup is found in the higher summerdry mountains of northern California where the substrate is largely plutonic in origin, opposed to the extrusive and sedimentary origin of the coastal substrate. Strong morphoclines occur across the Klamath-Siskiyou Mountains into southwestern Oregon. The Cascade and Oregon Coast Range Group occupies a rather homogeneous region characterized by relatively mild climates, mixtures of volcanic and sedimentary substrates, and Douglas Fir-Western Hemlock forests. The Rocky Mountain Group is separated from the Cascade and Oregon Coast Range Group by the broad, arid Columbia Plateau. Because the interior Rocky Mountain populations are geographically isolated from the coastal populations the criterion of reproductive isolation cannot be used to determine the taxonomic status of the Rocky Mountain Group. This group is considered to be conspecific with *D. ensatus* for the following reasons. Firstly, individuals from the Rocky Mountains are more similar to coastal *D. ensatus* than to *D. copei*, both in morphology and mode of life history. Secondly, although there are distinct morphological differences between coastal *D. ensatus* and Rocky Mountains populations, the differences are not as great as those between coastal *D. ensatus* and *D. copei*; therefore it would not be justifiable to erect yet a third species to contain the populations in the Rocky Mountains. Although distinct groups of *D. ensatus* are recognized, the presence of subgroups and microgeographic variation within subgroups argues against naming subspecies, and none is recognized.

Variation is slight over the relatively small range of *D. copei*, and what variation exists seems to be a function of geographic distance; no subspecies are recognized.

The dicamptodontines have apparently been an evolutionarily conservative group confined to the humid, temperate Arcto-Tertiary environments of western North America throughout their Cretaceous and Tertiary history. A remnant of the once wide-spread ancestral habitat occurs today in the humid fog belt of northwestern California and southwestern Oregon. *D. ensatus* living in this area today exhibit the most primitive features of all living *Dicamptodon.* These features include: large heads, long limbs and tails, many teeth and gill rakers, tendency to transform, and perhaps the habit of vocalizing as a terrestrial, defensive adaptation.

D. copei is viewed as a relatively recent derivative of an *ensatus*-like ancestor. This ancestor is believed to have had a propensity for neoteny and body attenuation associated with life in the extreme climatic, physical, and biotic environments imposed by Pleistocene glaciation. Isolation in western Washington during a glacial maximum allowed these tendencies, along with small body size, to be selected for unhampered by gene flow from outside populations. It is thought that the *ensatus*-like ancestor of *D. copei* was more similar to recent northern populations of *D. ensatus* than to recent Californian populations of *D. ensatus*. Californian populations were relatively unaffected by Pleistocene climatic extremes, as they passed this period in the milder ancestral environment of southern coastal latitudes.

During the last glacial maximum the Rocky Mountain populations were probably continuous with populations on the lower eastern slopes of the Washington Cascades, via a connecting wet, forested parkland which existed south of the Cordilleran ice sheet in north-central Washington. This parkland was broken up after the ice retreated during the Altithermal interval, about 7,000-4,000 years ago, and it was at this time that the Rocky Mountain Group became isolated.

Postglacial readjustments in the ranges of *D. copei* and *D. ensatus* may account for their current narrow zone of sympatry.

APPENDIX I

Larval OTUs (*D. ensatus*)

1. Roaring Creek, Valley Co., Idaho; Western Larch, Englemann Spruce, Lodgepole Pine, Ponderosa Pine, Grand Fir, summer dry; precip. 78 cm/yr.; frost free season (FFS) 80 days; primary; RAN 7537, 7542, 7544-51, 7557-9, 7561-2, n = 15.

2. Hamby Creek, Idaho Co., Idaho; Douglas Fir, Grand Fir, Ponderosa Pine, summerdry; precip. 102; FFS 90; primary; RAN 7599, 7601-9; n = 10.

3. Mannering Creek, Benewah Co., Idaho; Western White Pine, Western Red Cedar, Western Hemlock, Grand Fir, summerdry; precip. 127; FFS 160; primary; RAN 696-70, 986, 1013, 1016, 3999, 4001-5, 4007, 4010-1, 4014, 4016-7, 4300, 4311, 4315-6, 4325, 4327-30, 4336-7, 4345, 4349; n = 30.

4. Roundhouse Gulch, Shoshone Co., Idaho; burned over, Western Hemlock (?), summerdry; precip. 100; FFS 100; primary; RAN 4987-5001, 5003, 5005-6, 5008, 5010, 5018, 5020, 5028, 5030, 5183; n = 25.

5. Mount Pilchuck, Snohomish Co., Washington; second growth Douglas Fir, Western Hemlock, summerwet; precip. 230; FFS 300; primary; RAN 3558, 3572, 3590-2, 3594-600, 3603-4, 3607-10, 3614, 3619; n = 20.

6. Snoqualmie Pass, Kittitas Co., Washington; Douglas Fir, summerdry; precip. 205; FFS 130; primary; RAN 4057-61, 4063-7, 4070-3, 4978, 4683-5, 4689, 4691; n = 20.

7. Maratta Creek, Cowlitz Co., Washington; Douglas Fir, summerdry; precip. 210; FFS 120; primary; RAN 3223, 3243, 3260, 3292-3, 3304, 3309, 3311, 3322, 3395, 3397, 3402, 3405, 3409, 3410, 3439, 3442, 3448, 3458, 3465; n = 20.

8. Oneonta Gorge, Multnomah Co., Oregon; Douglas Fir, summerdry; precip. 210; FFS 170; primary; RAN 4215, 4219-21, 4224-5, 4228, 4234, 4237, 4243-9, 4252, 4255, 4258, 4260; n = 20.

9. Soda Fork, Linn Co., Oregon; Douglas Fir, summerdry; precip. 180; FFS 115; primary; RAN 4535, 5189, 6947, 6979-82, 6987-8, 6990, 7979, 7981, 7999, 8000; n = 14.

10. Loon Creek, Lane Co., Oregon; Douglas Fir, summerdry; precip. 190; FFS 110; primary; RAN 7254, 7256, 7260, 7262, 7269-70, 7272-4, 7278-80, 7282-3, 7286-7, 7289; n = 17.

11. Shoat Spring, Jackson Co., Oregon; Ponderosa Pine, Incense Cedar, summerdry; precip. 60; FFS 120; primary; RAN 8082-3, 8089-91, 8127-9, 8134-6, 8134-6, 8138-9, 8142-3, 8145-8, 8150-2, 8154-6; n = 25.

12. Saddle Mountain, Clatsop Co., Oregon; Douglas Fir, Western Hemlock, summerwet; precip. 230; FFS 290; primary; RAN 4461, 4470-2, 5367-70, 5433, 5435; n = 10.

13. Mary's Peak, Benton Co., Oregon; Douglas Fir, Noble Fir, summerdry; precip. 140; FFS 200; primary; RAN 1570, 1657, 2068-70, 2835, 3132-3, 3137, 3712, 4123, 6369, 6597, 6742, 6751, 6887-8, 7324, 7334, 7338; n = 20.

14. Panther Creek, Curry Co., Oregon; Douglas Fir, brief summerdry periods; precip. 200; FFS 230; primary; RAN 3822-4, 3828, 3832-3, 3835, 3841, 3844, 3846, 3848-50, 3854, 3857, 4485-7, 4500-2; n = 21.

15. Josephine Co., Oregon; southern part of county; generally summerdry; secondary; RAN 4485-7, CAS-SU 7408, WSU 56108, LACM 40795-6; n = 7.

16. Siskiyou Co., California; western half of county; generally summerdry; secondary; MVZ 18335, 18339, SSCMNH 20, CAS 85424, CAS-SU 2074-5, 2081; n = 7.

17. Trinity Co., California; Ponderosa and Digger Pine, summerdry; secondary; MVZ 84443, 38726, 51505-6, 71129, 71126, SSCMNH 634, 611 (2 specimens); n = 9.

18. Nosoni Creek, Shasta Co., California; Digger Pine, Canyon Live Oak, summerdry; precip. 90; FFS 120; primary; RAN 8097-8, 8102, 8105-6, 8111, 8117-21; n = 11.

19. Humboldt Co., California; coastal portion of county; Redwood, Douglas Fir, summerwet; secondary; MVZ 38741, LACM 10674-8, 29418, 29422, CAS-SU 7386-7, 1600; n = 11.

20. Mendocino Co., California; Redwood, summerwet; secondary; MVZ 73723, 73720, MCZ 23556, CAS-SU 2701, 2704-8, 4615, 5778-9, 22983, FMNH 84810, 84814-5, 84817-8; n = 18.

21. Sonoma Co., California; Redwood, summerwet; secondary; MVZ 76723, 76726, LACM 10683, CAS-SU 17946, 17949, 18096; n = 6.

22. Napa Co., California; Redwood, summerwet, secondary; MVZ 36212-3, CAS-SU 7356-8; n = 5.

23. Marin Co., California; Redwood, summerwet, secondary; CAS 44143-4, 63722-7, 93736; n = 9.

24. South of San Francisco Bay, California; Redwood, summerwet; secondary; CAS 4064, CAS-SU 10854, MVZ 69448, 71095, RAN 7851, 7856; n = 6.

Larval OTUs (*D. copei*)

25. Same as *D. ensatus*, OTU 7; USNM 166785-814; n = 30.

26. Nine Foot Creek, Skamania Co., Washington; Douglas Fir, short summerdry periods; precip. 210; FFS 110; primary; RAN 4544-7, 4623-6, 4632, 4636-8, 4640-2, 4650-4, 4656-7, 4661-4, 4672, 4678-9, 4681; n = 30.

27. Wahkeena Falls, Multnomah Co., Oregon; Douglas Fir, short summer-dry period; precip. 210; FFS 170; primary; RAN 1665, 1667-9, 4518-9, 6721-6, 7714-6, 7718, 7720-4, 7727-8; n = 23.

28. Same as *D. ensatus*, OTU 8; RAN 4046, 4549-50, 4278-80, 4282, 4284, 4286-90, 7667, 7669; n = 15.

29. Same as *D. ensatus*, OTU 12; RAN 7427, 7429, 7438-9, 7442, 7445, 7447, 7449, 7451-2, 7455, 7458-61, 7463-8; n = 21.

30. Rock Creek, Wahkiakum Co., Washington; Douglas Fir, short summer-dry periods; precip. 200; FFS 200; primary; RAN 7514, 7516-7, 7519, 7523-4, 7529-36; n = 14.

31. Beaver Creek, Grays Harbor Co., Washington; Douglas Fir, short summerdry periods; precip. 240; FFS 220; primary; RAN 6114-5, 6117-9; n = 5.

32. Merriman Creek, Grays Harbor Co., Washington; Douglas Fir, Western Hemlock, summerwet; precip. 280; FFS 300; primary; RAN 4082, 4084, 4098, 4101, 4103-4, 4111-4, 4116, 4118-21; n = 15.

OTUs (*D. ensatus*) of Metamorphosed Individuals

1. Idaho; RAN 782, 1147, 1480, 5754, 7893, 7975-6, 8997-8, 9002-4; n = 11.

2. Washington; FMNH 84806, 84807, LACM 29440, UMMZ 135140, RAN 1156, UPS 5012, 7230, 5981, 5982, 9010, USNM 5981, 62503, WSU 59335; n = 13.

3. Benton and Lincoln Counties, Oregon; OSUMNH 1441, 3704, 3706-7, 3710-4, 3678-9, 4316, 4730, 5250, 6462, 8477, RAN 2034-5, 2600, 2855-6, 2914, 2961, 4622, 8991-3, 8994; n = 30.

4. Lane and Linn Counties, Oregon; OSUMNH 19, 4315, 4625, 4653, 9402, RAN 8995-6; n = 7.

5. Northern California and Southern Oregon; includes parts of western Siskiyou and Trinity Counties, Cal. and parts of southern Josephine and Jackson Counties, Ore.; MVZ 18327, 52275, OSUMNH 1560, SSCMNH 634, USNM 46170, 57001, 85466; n = 7.

6. Del Norte Co., California; AMNH 68102, CAS 29105-6, FMNH 31813, LACM 74-5, MCZ 23052, MVZ 29508-9, 42696; n = 10.

7. Humboldt Co., California; CAS 44903-5, 51492, 80086, 80164, LACM 29415-7, 29428, MVZ 16089, 18973, 41234, 42463, 44365-7; n = 20.

8. Mendocino Co., California; CAS 80989, 81590, 81845, CAS-SU 2203, 4370, FMNH 84820, MCZ 23558, MVZ 40971; n = 8.

9. Lake Co., California; CAS 45125, CAS-SU 1850, MVZ 18188, 68142, 72207, 74502; n = 6.

10. Sonoma and Napa Counties, California; AMNH 14454, CAS 27142, 33384, CAS-SU 5192, MVZ 45844, 58253-4, 63768, 66485-6, SSCMNH 432; n = 11.

11. Marin Co., California; CAS 17804, 27332, 43579, 44142, 50172, 63089, 63803, 66367, 81601, 93526, 93528, 93531, 93541, 101808, MCZ 4364, MVZ 2405, 4841, 6345, 8573, 12596, 40665-6, 45590, 51356-7, 59854, 63770, 69669, SSCMNH 424, USNM 48675, 50337, 53597-8, WSU 46329; n = 34.

12. South of San Francisco Bay; ANSP 16053-4, 16998, CAS 41712, 47992, 54018, 71978, CAS-SU 891, 900, 2202, 2236, 3471, 3921, 4468, 20189-90, 20195, MVZ 8238, 12453, 35481, 35483-5, 58382, 60907, 69449, 72663-7, 85129; n = 32.

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This paper is based in part on a doctoral dissertation presented to the faculty of the Department of Zoology, Oregon State University, June, 1972.

Accepted for publication, December 15, 1975.