AN ABSTRACT OF THE THESIS OF

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Abstract approved: Dr. Robert M. Storm

Dicamptodon is the single, extant genus of the ambystomatid subfamily Dicamptodontinae. Two species, *D. ensatus* (Eschscholtz) and *D. copei* Nussbaum are recognized. *D. ensatus* is found in the forested, mountain regions of northwestern California and western Oregon, in the Willapa Hills and Cascade Mountains of Washington, in extreme southwestern British Columbia, and in the northern and central Rocky Mountains of Idaho. *D. copei* is found in the Olympic Mountains, Willapa Hills and southwestern Cascades of Washington; and in the vicinity of the Columbia River Gorge in extreme northwestern Oregon. The two species are sympatric in the Columbia River Gorge, southern Willapa Hills, and southwestern Cascades of Washington.

The two species differ, among other characters, in blood serum proteins, sensitivity to thyroxine, mode of life history, body size, relative head size, limb length, tail height, tooth number, gill raker number, color, and degree of ossification of skeletal elements.

Geographic variation is prominent in D. ensatus. 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; and the northern subgroup can be further separated into a coastal subgroup and an interior highlands subgroup. These groups are all more-or-less verified by analysis of color of larvae and adults, and morphometric characters of adults.

These groups correspond geographically with major features of topography in the Pacific Northwest. The California 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, summer-dry mountains of northern California where the substrate is complex and of a different origin than the coastal substrate. Strong morphoclines occur across the Klamath-Siskiyou Region into southwestern Oregon. The Rocky Mountain Group is separated from the Cascade and Oregon Coast Range Group by the broad, arid Columbia Plateau.

Variation is slight over the relatively small range of D. copei, and what variation exists seems to be a function of geographic distance.

The dicamptodontines have 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 include: large heads, long limbs and tails, many teeth and gill rakers, propensity to transform, and perhaps the habit of vocalizing as a

terrestrial, defensive adaptation.

D. copei is viewed as a relatively recent derivitive 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 7-4,000 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 account for their current narrow zone of sympatry.

Subspecies of D. ensatus and D. copei are not recognized.

SYSTEMATICS OF THE SALAMANDER GENUS DICAMPTODON STRAUCH (AMPHIBIA : CAUDATA : AMBYSTOMATIDAE)

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My wife Margaret helped in the field and spent many hours typing this thesis.

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INTRODUCTION

Dicamptodon and its Relatives

While this is not the place to review the salamander family Ambystomatidae, brief comments on the taxonomic, zoogeographic, and ecological relationships within the family are needed to place *Dicamptodon* in perspective with its relatives. For details of ambystomatid classification see Tihen (1958), whose arrangement I follow with no modifications. Larsen (1963), Regal (1966), and Wake (1966) should be referred to for comments on the relationship of the family Ambystomatidae to other families of salamanders. Anderson (1969) provided a reasonably complete literature review of the genus *Dicamptodon*.

The family is composed of four, currently recognized, extant genera: *Ambystoma*, *Rhyacosiredon*, *Rhyacotriton*, and *Dicamptodon*. In addition, three fossil genera have been described. *Ambystomichnus* (Gilmore, 1928) is known only from footprints of Paleocene age (Fort Union Formation, western Montana, U.S.A.). Herre (1950, 1955) described *Wolterstorfiella* and *Barqmannia* as fossil ambystomatids

respectively from the Paleocene and Miocene of Europe. The relegation of Bargmannia to Ambystomatidae has not been questioned, but Auffenberg and Goin (1959) have suggested that Wolterstorfiella may be a hynobiid rather than an ambystomatid. Estes (1965) countered this suggestion, preferring Herre's original assignment to the Ambystomatidae. Estes (1965) has further suggested that a fourth fossil genus from the Paleocene of Europe, Geyeriella (Herre, 1950), is also an ambystomatid rather than a plethodontid as believed by Herre. With these conflicting opinions in mind, it appears that the fossil Bargmannia is the only definite record of the family Ambystomatidae outside North America.

Broadly speaking, the genus Ambystoma is centered in the eastern and southeastern United States (12 species) and in Mexico (13 species). There are only three endemic species of Ambystoma in western North America, two of which occur in the Pacific Northwest.

The genus Rhyacosiredon (4 species) is confined to Mexico. Rhyacosiredon, together with the genus Ambystoma, comprise the distinctive subfamily Ambystomatinae.

Rhyacotriton (1 species) is the sole genus of the subfamily Rhyacotritoninae. It is confined to the coastal

portions of northern California, Oregon, and Washington.

Dicamptodon (2 species) is the only extant genus of a third subfamily, Dicamptodontinae. The fossil genus Ambystomichnus from the Paleocene of western Montana has been assigned by Tihen (1958) to the Dicamptodontinae on the basis of its apparent bilobate palm of the manus and limb lengths relative to axilla-groin length (Peabody, 1954). Fossil trackways from Lower Pliocene deposits in the foothills of the central Sierra Nevada Range have been tentatively assigned to the genus Dicamptodon, but no formal description has been given (Peabody, 1959). Living and fossil Dicamptodontinae are known only from the northwestern, conterminous United States, and British Columbia, south of the Fraser River.

Dicamptodon and Rhyacotriton share several primitive features and have similar geographic distributions. Members of both genera have independent exoccipital and prootic bones, while these elements are fused into a single periotic in the Ambystomatinae. They have lacrimal bones which are lacking in the other living genera. The columnellae of Dicamptodon and Rhyacotriton are free elements, whereas fusion to the periotic is normal in Ambystoma and Rhyacosiredon. In addition, Dicamptodon

and Rhyacotriton both breed in the presumed ancestral, mountain brook habitat, while Ambystoma is primarily a pond breeder. Rhyacosiredon breeds in streams, but this may be a secondary adaptation. Correlated with stream breeding habits, Dicamptodon and Rhyacotriton have large pigmentless eggs, stream or brook type larvae, and prolonged incubation periods (Nussbaum; 1969a, 1969b).

These and other similarities led Regal (1966) to suggest that Dicamptodon and Rhyacotriton be placed together in the Dicamptodontinae, eliminating the category Rhyacotritoninae. It is important to note that most of the features common to Dicamptodon and Rhyacotriton are ancestral. I agree with Tihen (1958) and Wake and Ozetti (1969) that where possible phylogenies should be estimated through similarities in derived character states rather than ancestral character states, because ancestral traits may be independently retained in two or more groups which have been evolving along separate lines for long periods of geological time. When viewed from the standpoint of derived characters, Dicamptodon and Rhyacotriton show few similarities (Tihen, 1958). For this reason I believe Regal's (loc. cit.) proposed change in classification is undesireable, and that if followed would obscure important

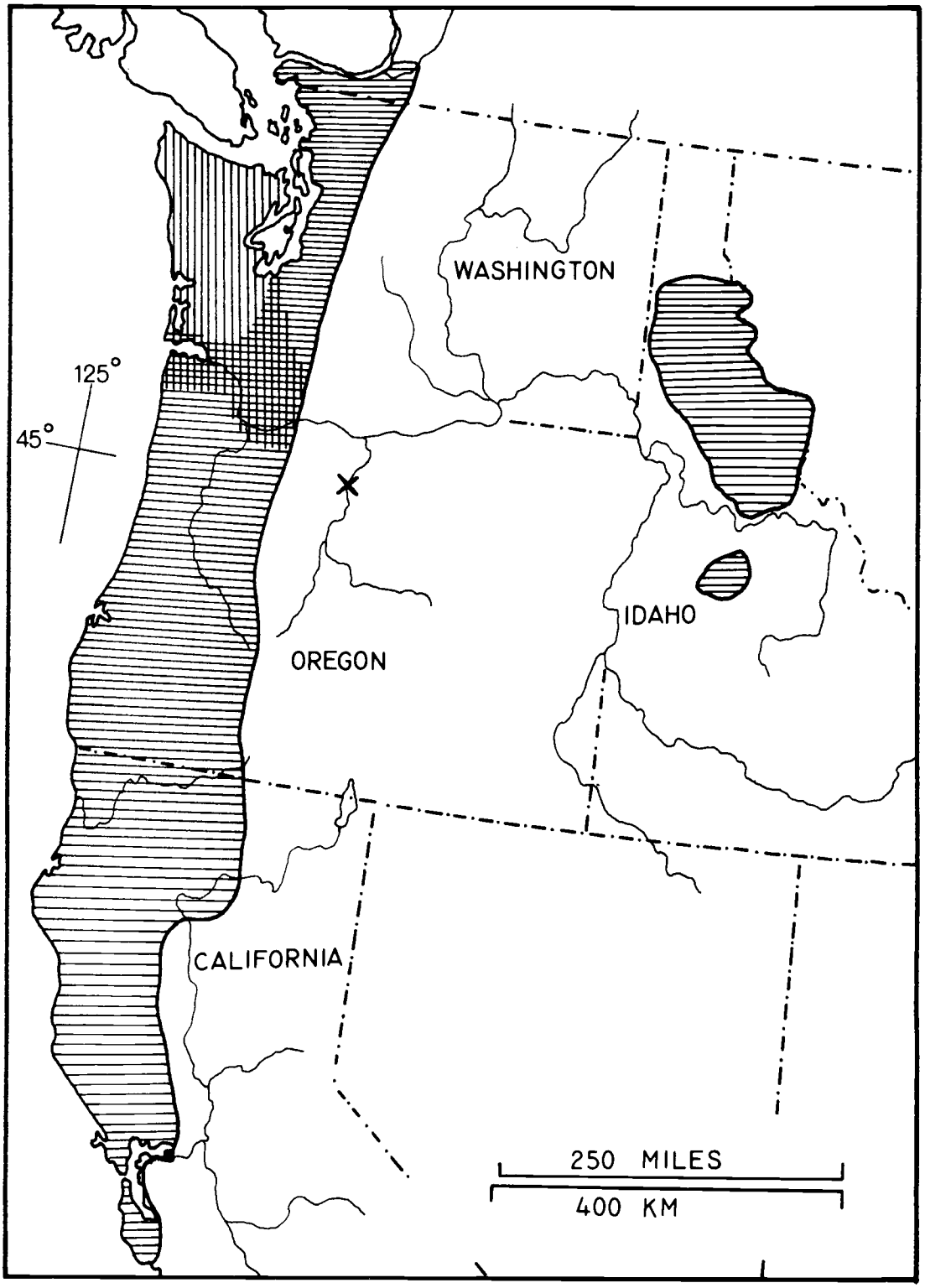


Figure 1. Range of D. ensatus (horitzontal hatching) and D. copei (vertical hatching). The X is an isolated population of D. ensatus at Oak Springs, Wasco Co., Oregon.

differences in the morphology and ecological positions of the two genera.

There are two known species of Dicamptodon. Dicamptodon ensatus (Eschscholtz) has been known under various names since 1833. Dicamptodon copei Nussbaum was described in 1970, when I realized that some populations of Dicamptodon in western Washington and northwestern Oregon were dimorphic. The ranges of the two species are shown in Figure 1.

Natural History of Dicamptodon

A general account of the life history and ecology of the two species is in preparation and will be published elsewhere. Briefly, the animals occur in the humid, forested regions of the Pacific Northwest and northwestern California. Both species breed in cold, clear streams, brooks, ponds, and lakes where gravel and boulders are abundant. Streams and lakes with sandy or muddy bottoms and with luxuriant, aquatic vegetation are generally avoided. Such habitats do not provide breeding sites.

The Pacific giant salamander, D. ensatus, may breed as sexually mature larvae or as fully transformed, terrestrial adults. If larvae are to metamorphose, they

do so only after their first year, and most often in their second year. Neotenic D. ensatus are at least three years old and usually older.

Cope's salamander, D. copei, is not known to metamorphose in nature. Larvae treated with thyroid substances in the laboratory reacted slowly, and after 18 months of continuous treatment had not attained the degree of transformation seen in fully metamorphosed D. ensatus. Larvae of the latter species completely transformed in less than three months under identical laboratory conditions and with identical thyroxine treatment (Nussbaum, 1970). Slow and apparently incomplete reaction to thyroxine, and attainment of sexual maturity in the larval stage at small size, relative to the size of neotenic D. ensatus, suggest that D. copei is a permanently aquatic species incapable of undergoing natural metamorphosis; but this is not yet certain.

Previous Observations on Geographic variation

Cope (1889) described two "varieties" of transformed Dicamptodon ensatus. His alpha form had a flat loreal region, a narrow muzzle, and marbling confined to the head with the rest of the body a 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 (= Dicamptodon ensatus). Cope (1889) listed USNM 5981 from "Chilowyuck Lake, Oregon" and an un-numbered 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 of, 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 can not be assumed that USNM 4053 was actually collected at the townsite of Astoria. The specimen from "Chilowyuck Lake, Oregon" (Territory ?) may have been collected at Chilliwack Lake, British Columbia.

Slater and Slipp (1940) made the following comparisons of specimens from Mannering Creek, Benewah Co., Idaho

(4 larvae and 1 adult; UPS 2689-92 and 2707) to specimens from Washington (numbers and localities not given): "...The larvae are darker with a bluish-brown color while Washington larvae are more of a tan brown, and they have shorter gills; in the adult the marbling is of a finer grain and darker, and the ventral surface is considerably darker; the vomerine and maxillary teeth are better developed; the rows of vomerine teeth have more curvature to them and there is a second row of small teeth posterior to the prominent rows which we do not find in Washington adults, and the prominent rows do not extend so far laterally in respect to the internal nares."

Nothing else of significance occurs in the literature on the subject of variation in Dicamptodon.

Purpose

The purposes of this investigation were: 1) to synthesize the available literature on the distribution of, the nomenclature of, and variation in the genus Dicamptodon; 2) to describe inter- and intraspecific variation, and to estimate relative similarities between populations; and 3) to attempt a zoogeographical analysis from data on distribution, geographic variation,

topography, climate, paleoecology, historical geology, and the natural histories of the two species.

A Note on Terminology

Throughout this paper, the term "larva" shall refer to any branchiate individual, whether sexually mature or not. "Neotene" specifies a sexually mature larva. The word "adult" will refer to any transformed, abranchiate, terrestrial individual, regardless of whether the animal is sexually mature or not. Some herpetologists will be opposed to the usage of "adult" in reference to both immature and mature metamorphosed individuals; but this approach eliminates a lot of adjectives, and should not lead to confusion in the context of the present paper.

NOMENCLATURAL HISTORY

The history of name usage for Dicamptodon is outlined in Figure 2, but additional comments are needed.

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

Baird and Girard (1852) designated USNM 4710 from "Oregon" as the type of Amblystoma tenebrosum. I have examined the type, 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 nonexistant marbling from all parts of the range of D. ensatus. There

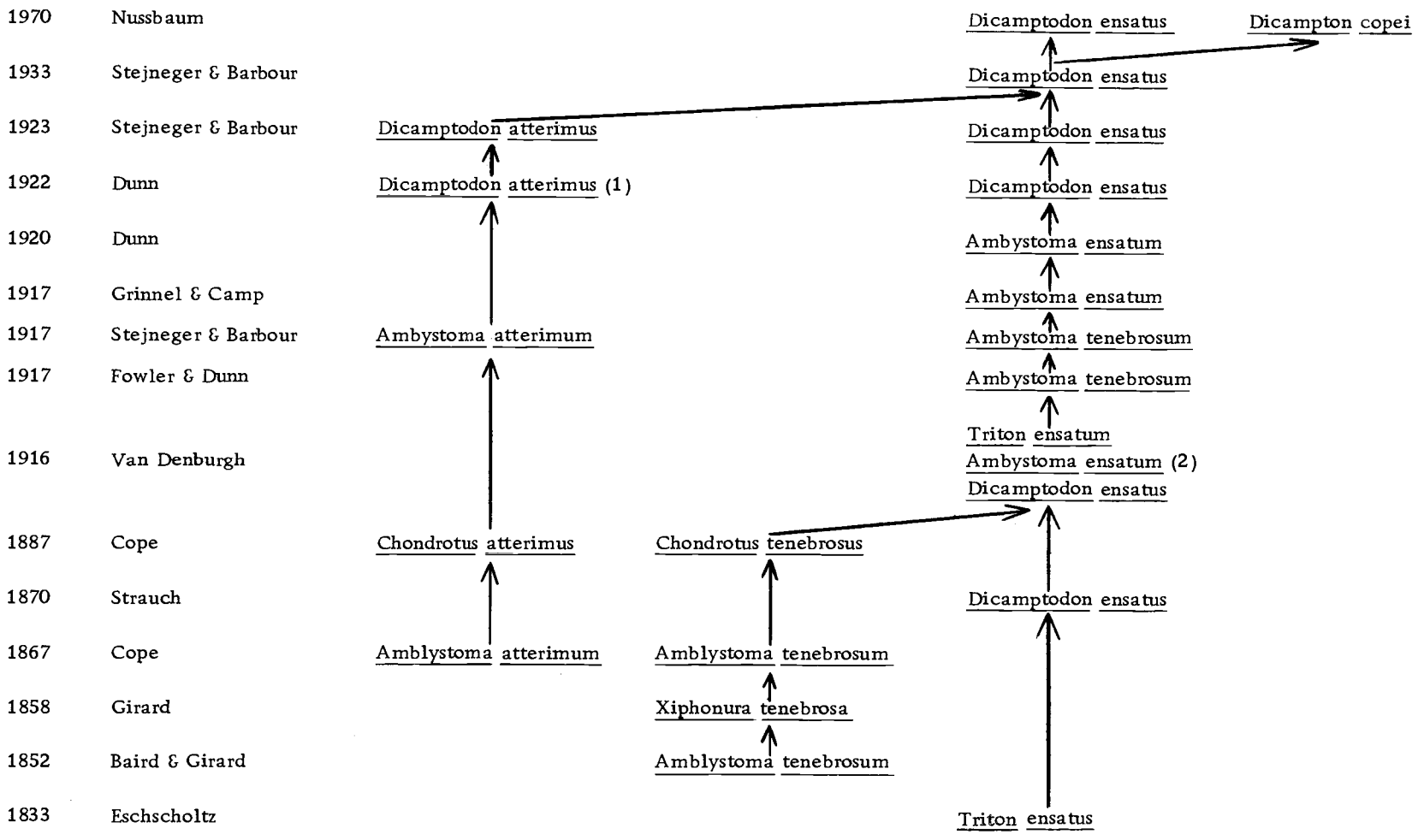


Figure 2. Summary of the history of name usage in Dicamptodon; (1) name not used, but inferred; (2) all three possibilities were listed and no decision was made.

is no doubt that Amblystoma tenebrosum is synonymous with Dicamptodon ensatus and is not an earlier name for Dicamptodon copei.

Cope (1867) described Amblystoma atterimum from a transformed specimen (USNM 5242) received from a surveying expedition commanded by Lieutenant John Mullen. The location was given as "northern Rocky Mountains." I have examined USNM 5242, and it 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 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. First, Storer (1925) intimated 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. Second, Grinnel and Camp (1917) state that Chondrotus lugubris is a synonym of Ambystoma ensatum. I have been unable to determine the reason for this statement. Perhaps the authors meant to state that C. tenebrosus or less likely, that C. atterimus was a synonym, rather than C. lugubris. Third, 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

Because this study is primarily concerned with geographic variation, it is necessary to provide a background on the topography and climate of the area under consideration, namely the Pacific Northwest and northwestern California.

The region may be viewed, generally, as a series of north to south trending 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 to almost meet the Oregon Cascades near Mount Jefferson,

but the low, arid Deschutes River Valley intervenes. Only the relatively low and dry Okanogan Valley separates the Cascade and Rocky Mountain Ranges in north-central Wasington 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 Section, 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 due to snowfall. The province is characterized by hemlock-spruce, or Douglas fir, summer-wet forests, and only the high Olympic Mountains exceed the Forested Transition Life-zone.

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, summer-wet forests and the eastern slopes by ponderosa pine, summer-dry forests. The high Cascades lie in the Canadian and Hudsonian Life-zones, with the higher peaks in the Arctic-Alpine Life-zones. 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 due to 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. Life-zones range from upper Sonoran to Arctic-alpine, and forests are highly varied and for the large part summer-dry.

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 for the most part in the Upper Sonoran and Arid Transition Life-zones, characterized by western juniper (Juniperus occidentalis), and sagebrush (Artemisia, spp.). However, parts of the higher Central Mountains are in the Canadian and Hudsonian Life-zones, 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 to south trending basins. The province has an interior climate, with only the high Sierras receiving significant 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 comingling of distinctive faunas in this region is well documented (Remington, 1968). Diverse rock formations and a complicated geological history has 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 not a creature of high places. It is most often found at altitudes ranging from sea level to about 950 m. The maximum, reliable sight record is 2160 m for a lake in Trinity Co., California. One specimen (MVZ 71118) examined by me was collected at 1880 m, White Creek Lake, Trinity Co., California. This appears to be the maximum, documented record. Other relatively high elevation records are: 1790 m, "Little Monster Lake", 2.4 km SE Pony Mountain, Trinity Co., California (MVZ 71123, 71126, 71127, 71129); 1790 m, Upper Bigelow Lake, Josephine Co., Oregon (WSU 56108); 1670 m, Bolan Lake, Josephine Co., Oregon (RAN 4485-87, Dean E. Metter un-numbered, LACM 40795). Possibly correlated with lowered life-zones in northerly latitudes, there are no comparatively high elevational records for Washington, B.C., and 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 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, and Reed (1949) and Ferguson (1956) have reported similar observations. 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 stomach of the fish.

The southern most 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 possible 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 SW British Columbia marks the approximate northern limits of

the range. Known localities in British Columbia are: Ascaphus Creek near Cultus Lake (PM 641), Cultus Lake (PM 837-8) and Chilliwack Lake (USNM 5981).

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 somewhat ambiguous, because both Shingletown and Mt. Lassen are in Shasta Co. 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 due east of the Cascade Crest, and is well within the Upper Sonoran Life-zone. Oregon oaks (Q. garryana) occur at the spring site, but the surrounding vegetation is primarily sagebrush (Artemisia tridentata), grasses, and desert annuals. The population is isolated here, along with a population of Taricha granulosa, and both populations owe their existence to the cold, permanent nature of the spring. Storm (1966a) has urged protection for these populations

and I agree with him. The animals are not abundant at Oak Springs and indiscriminant collecting should be avoided.

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 evelational 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 Life-zone, above 2130 m), nor from the Hudsonian Life-zone of Oregon, but is expected in the latter. There are scattered records for the Canadian Life-zone on the western side, and D. ensatus is very common in the Transition Life-zone 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 Co. (UPS 9437; WSU 59351-2; RAN 2197-98, 6360; Dean E. Metter, Univ. Missouri, un-numbered). This locality is in the Canadian Life-zone, 21 km east of the Crest. The other eastern locality is N side Kachess Lake, Kittitas Co. (UW un-numbered). The site is 13 km east of the Crest, also in the Canadian Life-zone. There are two records on the Crest, both in the Canadian Life-zone: Snoqualmie Pass, Kittitas Co. (RAN 1478-79, 4054-79); Stampede Pass, Kittitas Co.(LACM 40798).

D. ensatus is recorded from many localities on the western slopes of the Cascades in Washington, both in the Transition and Canadian Life-zones. Hudsonian and Arctic-alpine Life-zone records are wanting. Parts of the Cowlitz-Puget Trough 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, I have no definite records of D. ensatus on the Olympic Peninsula.

Known localities for D. ensatus in Idaho are:: Valley Co.: S. Fk. 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 (uncataloged, Dean E. Metter); Surveyor Creek, 7.6 km NW Falls Creek on the Clearwater River (E.K. Teberg, uncatalogued): 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); N. Fk. 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 N. Fk. Palouse River (many specimens collected by Dr. Dean E. Metter and myself; some numbers are listed in Appendix A); S slope Baldy Mountain (University of Idaho, un-numbered): Benewah Co.: Mannering Creek, 19.4 km N Harvard (UPS 2689-2692; RAN many specimens, see Appendix A).

Black (1970) and others indicate 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 "northern Rocky Mountains" (Cope, 1867), 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. The party spent considerable time surveying in 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 Co. 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 (personal communication) and myself 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.

Know 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); Multnamah Co.: Wahkeena Falls (RAN many specimens, see Appendix A; LACM 29429-34, 29436; PLU AO 838-41, AO 178, AO 168); Oneonta Gorge (RAN many specimens, see Appendix A): Clatsop Co.: NW side Saddle Mountain (RAN many specimens, see Appendix A); 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 USMN 166784, paratypes USNM 166785-814; RAN 3755-65, 7489-500, 7507-12, 7888-92, 8555-64; Dean E.

Metter, un-numbered); Elk Creek, 3.2 km W type locality (RAN 3696-97); 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; Dean E. Metter, un-numbered); 8 km W Mount Adams (UPS 5584): Mason Co.: 1.9 km E Staircase Ranger Station (RAN 1489-91); Lake Cushman (PLU A0123, A0134, A0136-37; MVZ 41387-88; USNM 55276; FMNH 84809); Laundry Creek (MCZ 5885-87); Dry Creek (AMNH 20584); Elk Creek (AMNH 20523); Staircase Camp (AMNH 20526, 20542); McTaggart 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 in Oregon: Oneonta Gorge and Wahkeena Falls, Multnomah Co.; Still Creek, Clackamas Co.; S. Fk. Quartz Creek and NW side Saddle Mountain, Clatsop Co.: and at these localities in Washington: Rock Creek, Wahkiakum Co.; Quartz Creek, Lewis Co.; Maratta Creek (type locality of D. copei), Cowlitz Co.

MATERIALS AND METHODS

Specimens

I have examined most of the specimens of Dicamptodon available in the major museums of the United States and Canada, and the names of these institutions are listed in the acknowledgements. Most borrowed specimens were measured and recorded, but many were so poorly preserved that they could not be used as constituents of the OTU's (operational taxonomic units, sensu Sokol and Sneath, 1963). Those that were used are listed along with their respective OTU's in Appendix A.

Over the past eight years I have collected Dicamptodon extensively throughout its range. Most of the specimens used in this study were obtained during this time; and the familiarity with Dicamptodon gained by this field work has enabled me to interpret data on variation with greater confidence.

I have seen nearly 14,000 specimens of Dicamptodon. Of these, 523 were D. copei, 746 were adult D. ensatus, and the remaining 12,500± were larval D. ensatus. Many of the larval D. ensatus were examined and released in the field. Only 309 adult D. ensatus were available in

museums; the remaining 437 were collected during the course of this study. An additional 425 adult D. ensatus were examined, but these were collected as larvae and treated with thyroxine to force metamorphosis. These "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 and twenty D. copei were also treated with thyroxine.

Characters

Color and pattern of larval and adult Dicamptodon vary greatly between populations. Because of the often subtle nature of the variation, all attempts to code and quantify these data failed to serve a purpose. 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 for 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. 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 differentia, 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.

Extensive data gathered on developmental osteology and comparative blood serum proteins will only be partially developed here.

Osteological information was obtained from radiographs taken with a Softex X-ray Apparatus, Type S-E. More detailed information was obtained from specimens cleared and stained using the standard technique of

maceration in two percent potassium hydroxide, staining in alizerin 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 minutes at 250 volts, 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 eight minutes. The excess dye was rinsed away with five percent acetic acid. The membrane was then dehydrated for one minute in 95 percent ethanol, transferred to a clearing solution of 25 percent glacial acetic acid and 75 percent ethanol (95 percent) for one minute, 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 methods of statistical analysis for some characters will be self-evident in the results section. However, my treatment of body measurements and counts needs comment.

Means of body measurements can not 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. In this study, individuals less than 65 mm SVL were not used in analyses involving body measurements.

Many authors have critisized 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 attains. (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 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 useable 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.

I used both ratios and Model I regression to compare body proportions between populations.

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:

$$\text{ratio estimate} = r = \frac{\sum_{i=1}^{n} Y_i}{\sum_{i=1}^{n} X_i} = \frac{\bar{Y}}{\bar{X}}$$

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 the 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 desireable.

The following 17 ratios were estimated for each population (L = larval character; A = transformed character, i.e., a character used to define OTU's composed by transformed individuals; see list of measurements on page 33 for explanation of abbreviations):

1.	HW/SVL	(L,A)	10.	FLL+HLL/SVL	(L,A)
2.	FLL/SVL	(L,A)	11.	AGL/SVL	(L,A)
3.	HLL/SVL	(L,A)	12.	MTH/BL	(L)
4.	MTH/SVL	(L)	12.	TL/BL	(A)
4.	TL/SVL	(A)	13.	HW/BL	(L,A)
5.	HL/BL	(L,A)	14.	FLL/HW	(L,A)
6.	FLL+HLL/AGL	(L,A)	15.	HLL/HW	(L,A)
7.	FLL/BL	(L,A)	16.	FLL/HLL	(L,A)
8.	HLL/BL	(L,A)	17.	HW/HL	(L,A)
9.	FLL+HLL/BL	(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 OTU's 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 $\overline{Y}$'s can be compared, and methods are available for calculating confidence intervals for the $\overline{Y}$'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 $X-\overline{X} = 0$; and therefore the greatest confidence in the predicted $\overline{Y}$'s occurs when the $\overline{X}$'s are used as predictors.

The mean SVL across OTU's was close to 88 mm for larvae and 110 mm for transformed individuals, and these two values were chosen to predict the $\overline{Y}$'s.

The number of teeth, gill rakers, and trunk vertebrae vary discontinuously and thoeretically 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., tables in Fisher and Yates, 1948). However, this approach is seldom used by herpetologists, and data of this type are usually reported as arithmetic means with confidence intervals calculated as if the data were normally distributed. There is a certain facility in using means rather than frequencies, and this approach was used here for tooth and gill raker counts. However, I also checked for significant differences between populations using tests on frequencies. This latter, thoeretically 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.

All calculations were done by computer with programs especially prepared for this study.

Operational Taxonomic Units

Throughout this study emphasis has been placed on comparison of larval rather than transformed individuals. Necessity dictated this procedure. The number of useable museum specimens was disappointingly low, and I have not

been able to collect adequate numbers or series of adult D. ensatus. In the case of D. copei, comparisons are necessarily between groups of larvae.

I have grouped larval OTU's into two categories referred to as primary and secondary OTU's. Primary, larval OTU's 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 hours, washed in running water for 24 to 48 hours, and stored in a final solution of 50 percent isopropyl alcohol. Secondary, larval OTU's are composed of larvae of varied origin, not necessarily uniformly preserved, and from a defined region rather than a specific locality.

All OTU's of adult D. ensatus are secondary OTU's, although many of the component specimens were collected and preserved uniformly by me.

OTU's will frequently be referred to by number. The 32 larval OTU's and the 12 OTU's formed from transformed D. ensatus are listed by number and defined in Appendix A, and the localities are mapped in Figure 30

and Appendix B.

Estimation of Similarities Between OTU's

I used various multivariate techniques to estimate similarities between larval populations and to subsequently 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 distances (d) in Euclidean hyperspace.

In the case of r, the OTU's 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} OTU's based 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 OTU's in question. D-scores represent average distances between OTU's when the OTU's are plotted in n-dimensional hyperspace, with characters representing

the n-dimensions. The formula:

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

was used to calculated the "taxonomic distance", d_{jk}, between the j^{th} and k^{th} OTU's. The symbols $\bar{X}_{ij}$ and $\bar{X}_{ik}$ are the mean character state values for the i^{th} characters of OTU's 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 OTU's

Numerous methods of cluster analysis are available which can be used to calculate hierarchical arrangements of OTU's. 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 OTU's.

In this study, cluster analysis was initiated on either a r_{jk} matrix or a d_{jk} matrix. I experimented with the weighted-pair-group-method (WPGM) and the unweighted-pair-group-method (UPGM) of Sokal and Michner

(1958), the single-linkage-method of Sneath (1957), and a method described by Ward (1963). This latter technique is an agglomerative-polythetic 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 OTU's

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 OTU's on the first few principal axes is a satisfactory method for 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 OTU's onto the ordinates are maximized. The result is maximum variance among the OTU's, 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 OTU's based on projections of the OTU's onto the first three principal axes obtained from a matrix of correlations among characters (R-technique). I hoped this method would provide a parsimonious summary of the relationships among the 32 OTU's, and either confirm or deny the results of cluster analysis.

Factor Analysis

The mathematics of factor analysis is sufficiently complex to disallow a detailed description of the method here. Harmon (1960), Cooley and Lohnes (1962), and Morrison (1967) are adequate references.

To the uninitiated, 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 called "factor loadings", and the loadings represent correlations between variables and simple structure axes.

Factor analysis with OTU's as variables (Q-technique) has been used infrequently in taxonomy; and this procedure, in certain forms, has been critisized by some statiticians (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".

The results of Q-type factor analysis will be developed here only in part, and the results of R-type factor analysis will be presented in a separate paper.

Data Processing

Measurements on individuals were initially reduced to means, variances, standard errors, and coefficients of variation of populations with computer programs especially prepared for this study.

Another special program was prepared to calculate correlation coefficients and taxonomic distances between OTU's. Input is an OTU by character matrix. The program standardizes the matrix by character, prints out character means and standard deviations, population means and standard deviations, a matrix of correlations among characters, a matrix of correlations among OTU's, and a matrix of distances between OTU's.

HGroup cluster analysis was performed with a program provided by Veldman (1967) and adapted to the OSU computer system. Program HGroup is linked to the previous program so that clustering and similarities are outputed on one run.

Principal component analysis was done with BMD01M, a standard program in the OSU computer library. The program computes principal components of standardized data and ranks each case by the size of each principal component.

Factor analysis was carried out with OSU-BMD03M. The program employs a principal component solution with Varimax, orthogonal rotation. In this study, 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. These ratios served as characters for multivariate comparisons, and there is no reason to discuss variation for each separate ratio. However, two ratios show important trends of variation and will be singled out for comparison.

Figure 3 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 OTU's for this character, but beyond individual comparisons, two important trends are seen. First, 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

Table 1. Mean ratios and their standard errors (parentheses) for larval OTU's. Samples sizes and localities given in Appendix A, and localities mapped in Appendix B and Figure 30. Ratios defined in text. OTU's 25-32 are D. copei.

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 (.012)	.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)

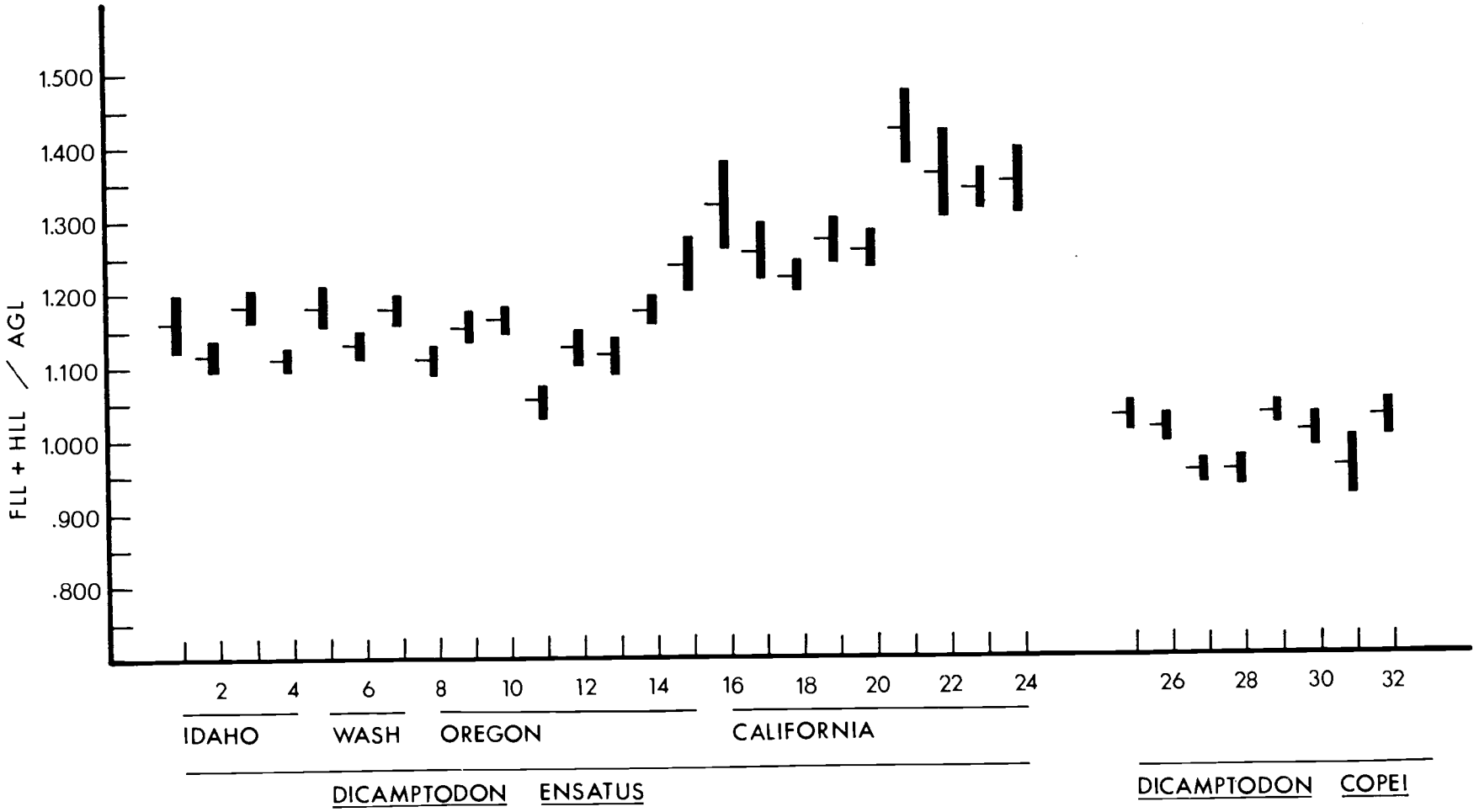
Table 1. (continued)

OTU	Ratio					
	7	8	9	10	11	12
1	.385 (.019)	.446 (.019)	.831 (.019)	.574 (.014)	.494 (.007)	.296 (.044)
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)
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)

Table 1. (continued)

OTU	Ratio				
	13	14	15	16	17
1	.305 (.016)	1.261 (.011)	1.460 (.008)	.864 (.007)	.683 (.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)

Figure 3. Variation in the ratio FLL + HLL/AGL for larval Dicamptodon; means ±2 standard errors.


FLL + HLL / AGL
1.500
1.400
1.300
1.200
1.100
1.000
.900
.800
2
4
6
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IDAHO
WASH
OREGON
CALIFORNIA
DICAMPTODON ENSATUS
DICAMPTODON COPEI

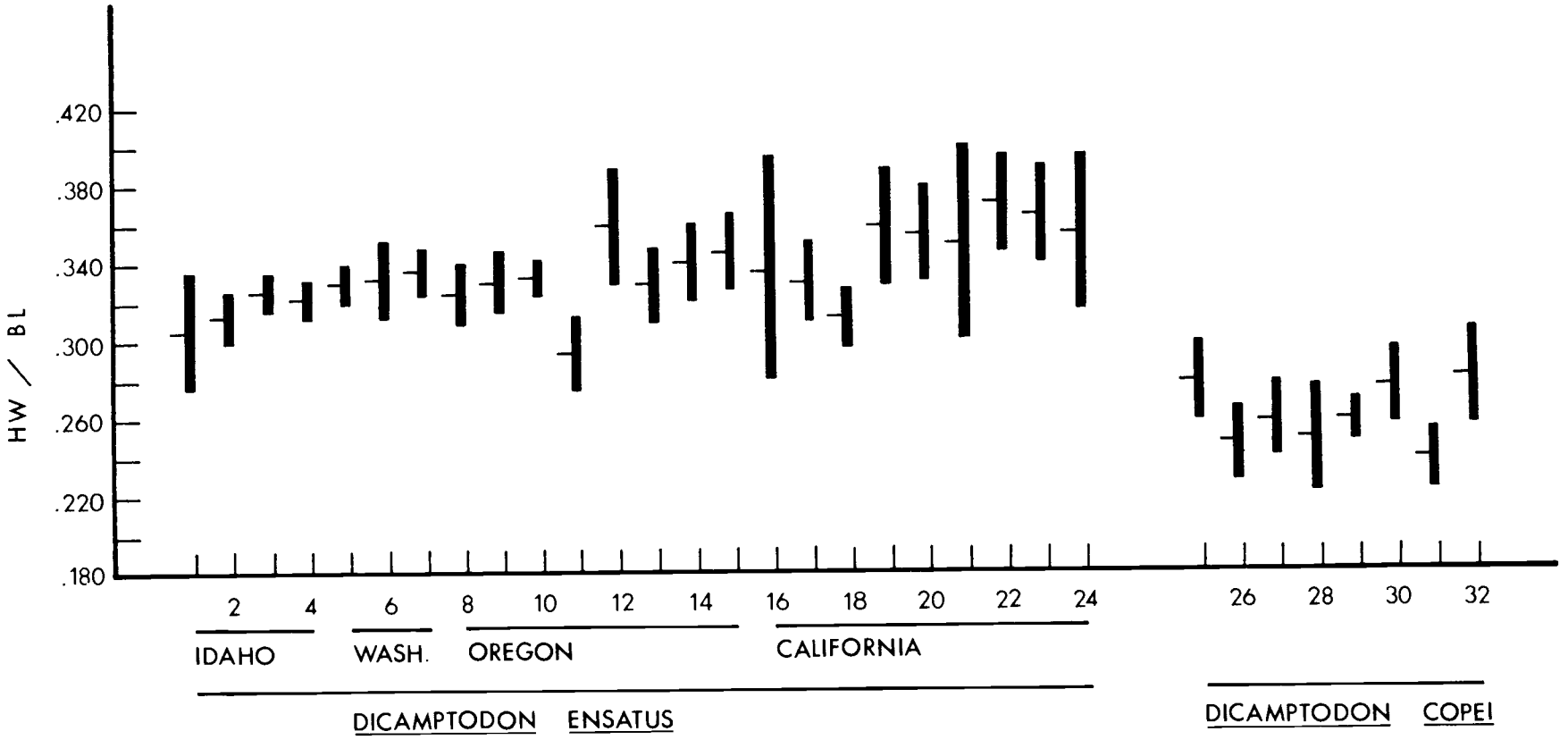


Figure 4. Variation in the ratio HW/BL for larval Dicamptodon; means ±2 standard errors.

population to D. ensatus will be deferred to the discussion section. Second, southern Oregon and California populations of D. ensatus have higher values for this character than more northern populations of D. ensatus.

Variation in the ratio HW/BL is summarized in Figure 4. 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 probably 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 described above for HW/BL. These two ratios together merely reflect that D. copei have smaller heads

than D. ensatus, and that southern D. ensatus tend to have larger heads than northern D. ensatus.

Predicated mean body measurements ($\bar{Y}$'s) for larval OTU's when SVL (as the predictor) is set at 88 mm are given in Table 2. Important trends discernable 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) 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 $\bar{Y}$'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.

Table 2. Predicted mean body measurements (mm) of population of larval Dicamptodon; estimated from $\bar{Y} = a + bX$ where a and b are determined through least squares regression and X is set at 88 mm SVL for all populations. See Appendix A for localities.

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

Table 3. Costal folds between adpressed limbs of larval Dicamptodon. OTU's 25 to 32 are D. copei. See Appendix A for sample sizes.

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						1	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

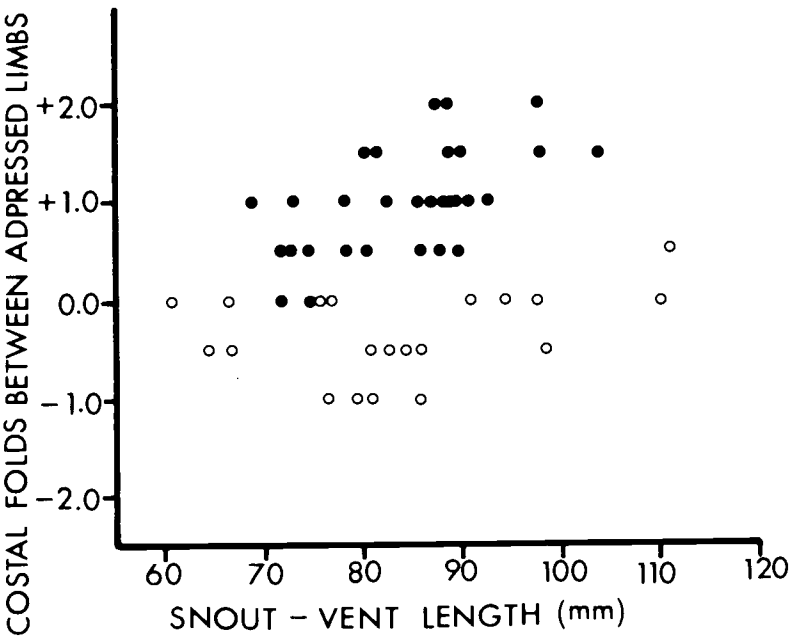


Figure 5. Scatter diagram of number of costal folds between adpressed limbs as a function of SVL; solid circles = D. copei (OTU 25), open circles = D. ensatus (OTU 7).

Limbs of D. copei usually do not overlap, and the means of the eight 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 this character (Figure 5).

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, and they obviously arrived at a mode of 15 trunk vertebrae independently. The fact that two populations of D. copei and only one rather isolated population 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 (see Table 4) and between populations reflects a conservative trend for this character which is common to most ambystomatids.

Table 4. Number of trunk vertebrae, based on radiography and cleared specimens of both larvae and adults; and percentage of larvae per OTU with palatopterygoid teeth. NC = No data for comparison.

OTU	Trunk Vertebrae Number		Palatopterygoid Teeth				
			Percent Specimens with Series			Mean Number of Teeth/Series	
	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

Number of Maxillary + Premaxillary Teeth

Within-group correlation coefficients for number of max-premax teeth versus SVL are listed in Table 5. Although a few of the coefficients for D. 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 6 shows these relationships in the form of a scatter diagram for the paratypes of D. copei (OTU 25) and sympatric D. ensatus (OTU 7).

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 small size (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 max-premax teeth and SVL in D. copei is related solely to the precocious, sexual maturity of this species. One way

Table 5. Means and standard errors of max-premax and vomerine teeth for larval Dicamptodon. Within-group correlation coefficients of tooth number with SVL and with HW are also given. OTU's 25 to 32 are D. copei. See Appendix A for sample sizes and localities (also Appendix B and Figure 30 for localities).

OTU	Max-Premax Teeth				Vomerine Teeth			
	$\bar{X}$	s.e.	r-SVL	r-HW	$\bar{X}$	s.e.	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

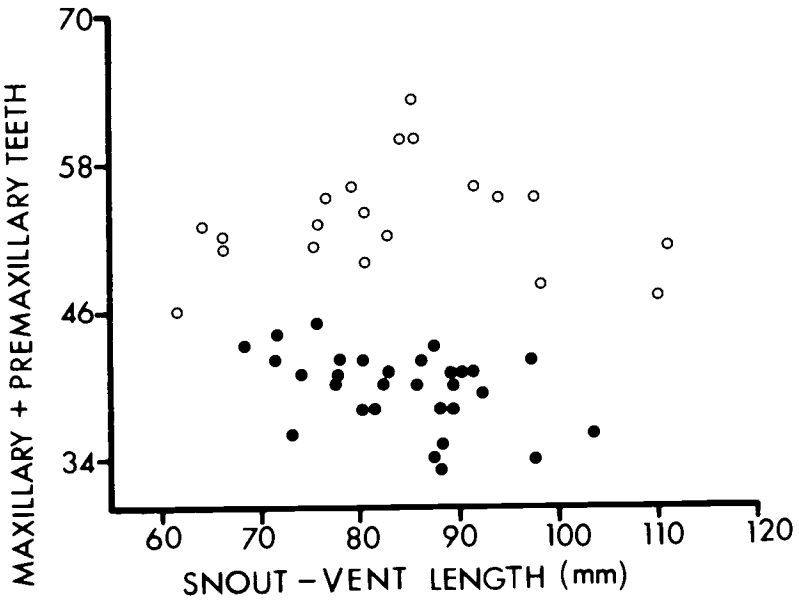


Figure 6. Scatter diagram of number of max-premax teeth as a function of SVL; solid circles = D. copei (OTU 25), open circles = D. ensatus (OTU 7).

to resolve this problem would be to examine tooth number in larger, neotenic 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 sexual maturity alone is responsible for tooth loss in D. copei.

The r's for SVL versus HW in Table 5 are within-group coefficients and reflect ontogenetic relationships. Between-group correlation coefficients of characters, based on mean values for populations (R-technique), suggest phylogenetic trends. The character which correlated highest with mean number of max-premax teeth across the 32 larval OTU's was mean HW ($r = .610$). The between-group r for mean number of max-premax teeth and mean SVL was -.179, and that for mean SVL with mean HW was .514. Using these latter r's, a partial correlation coefficient can be calculated

between mean number of max-premax teeth and mean HW, which shows the relationship when the variance contributed by SVL (size) has been accounted for. This partial r is .825, as opposed to .610 before the effect of SVL has been removed. Within-group r's (in Table 5) can be averaged by transforming them to Fisher z scores and re-transforming the mean z to a mean within-group r. With this method, the mean within-group r of HW versus max-premax teeth was .080. This figure compared to the corresponding partial, between-group r (.825) shows that while there is no (on the average) significant, ontogenetic relationship between HW and number of max-premax teeth, there is a significant and high "phylogenetic" correlation between these two characters.

Since the mean within-group r for SVL versus max-premax teeth was not significantly different from zero, and 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 (Table 5 and Figure 7). The Shoat Spring population of D. ensatus (OTU 11) has significantly fewer max-premax teeth than all other populations of D. ensatus, and is not significantly different from five

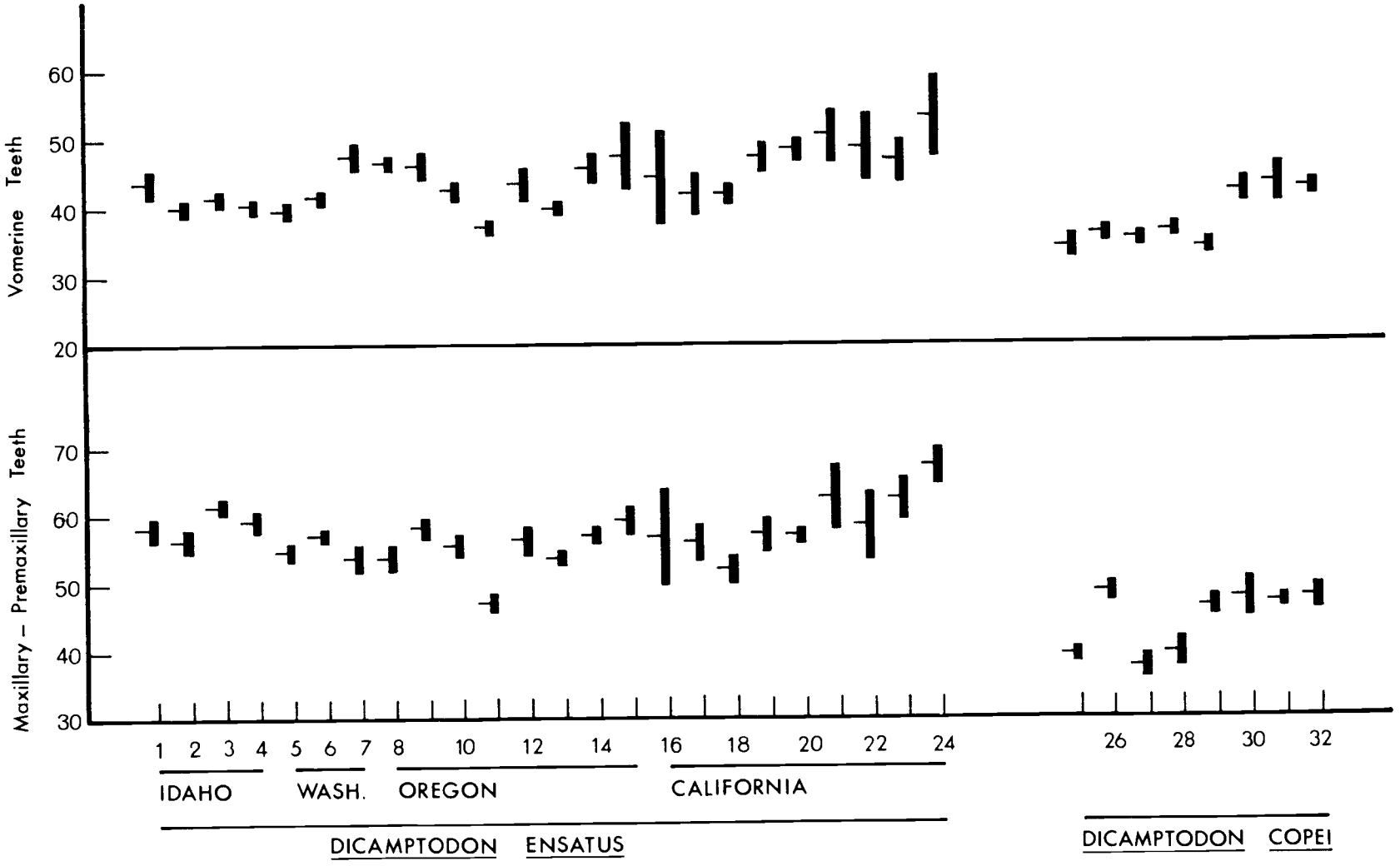


Figure 7. Variation in mean number of max-premax and vomerine teeth for larval Dicamptodon; means ±2 standard errors.

of the eight populations of D. copei. All OTU's of the latter species are significantly different from all OTU's 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 (Figure 8) show there is little increase or decrease in tooth number with size. The within-group r's for vomerine teeth versus SVL and versus HW are listed in Table 5. About two thirds of the coefficients are not significant, and the remaining, 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 simple means seems justified.

Variation is summarized in Table 5 and Figure 7. The pattern of variation is similar to that for max-premax teeth, and indeed the between-group correlation of mean number of vomerine teeth versus mean number of max-premax teeth is significant and high (.753).

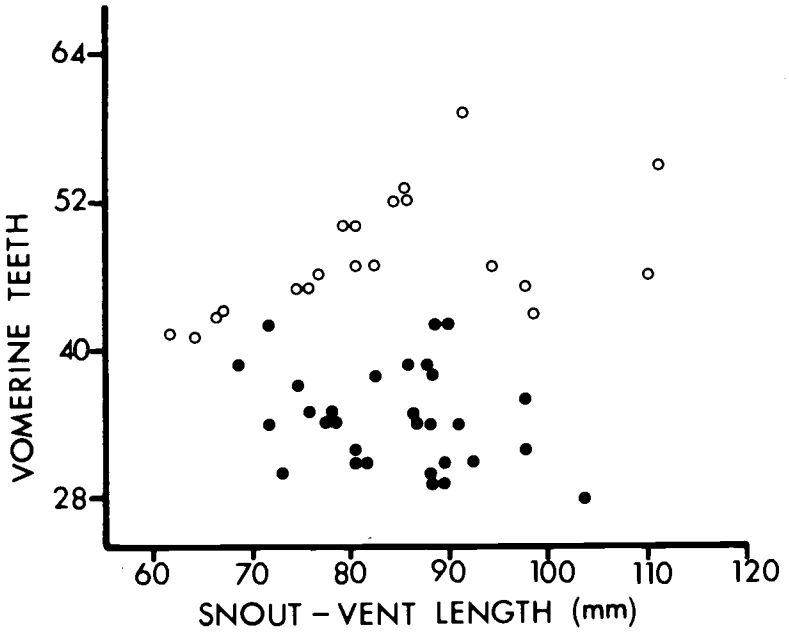


Figure 8. Scatter diagram of number of vomerine teeth as a function of SVL; solid circles = D. copei (OTU 25), open circles = D. ensatus (OTU 7).

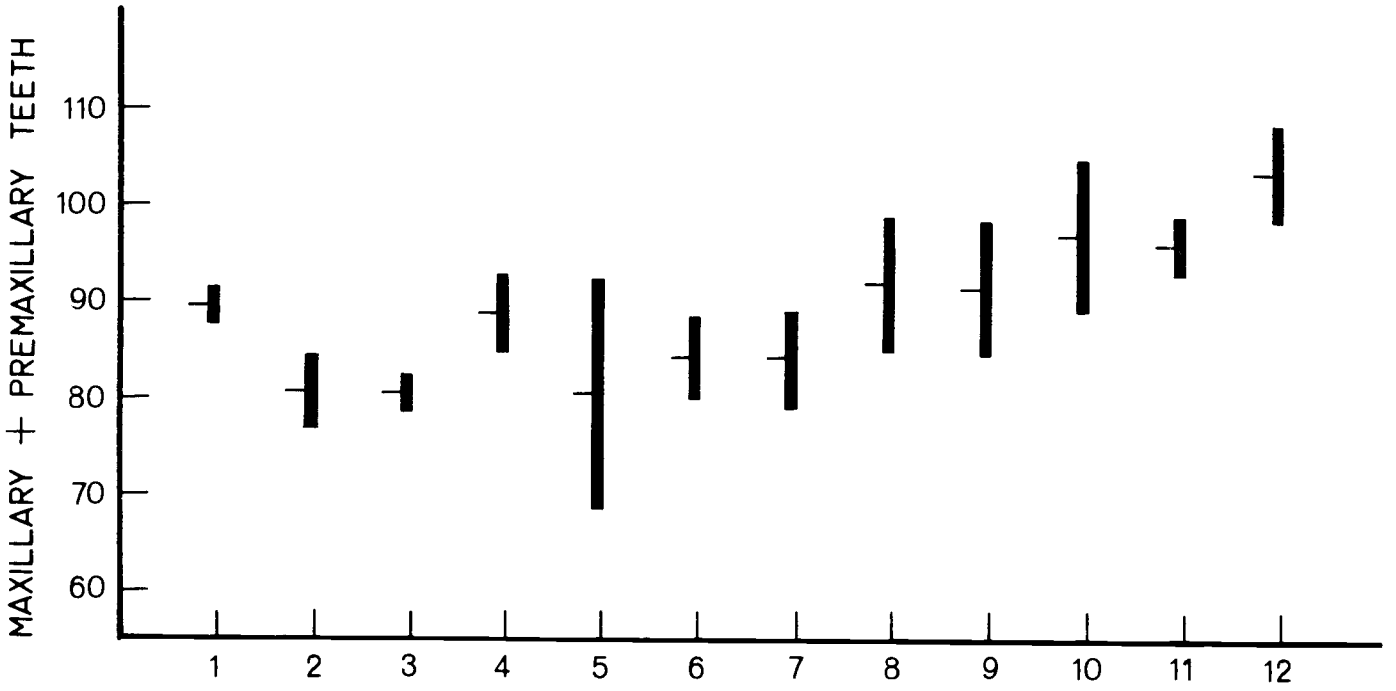


Figure 9. Variation in mean number of max-premax teeth in adult D. ensatus; means ±2 standard errors.

Palatopterygoid Teeth

The presence or absence of palatopterygoid teeth varies considerably within and between populations (Table 4). These teeth are entirely lacking in the four populations from Idaho (OTU's 1-4), and none was seen in any of many additional specimens from various parts of Idaho.

All populations of D. ensatus from Washington, Oregon, and California have individuals with palatopterygoid teeth with the following exceptions. Individuals from 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) lack palatopterygoid teeth. The fact that individuals from Sonoma Co., California and from localities south of Sonoma Co. lack palatopterygoid teeth is somewhat surprising since the population from Mendocino Co. (OTU 20) has the highest percentage of individuals with these teeth of any of the OTU's. Perhaps larger samples would show these teeth occasionally occur in individuals south of Mendocino Co.

None of the D. copei from any of the eight populations has a palatopterygoid series on either side.

The number of palatopterygoid teeth/series ranges from 1 to 15. The means range from 3.8/series to 10.0/series, with no readily discernable pattern of variation.

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 as an anomolous, 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 remodeled vomer. It is tempting to speculate that these anomalies are atavistic traits and reflect a phylogenetically earlier, normal pattern of development identical with that seen in Ambystoma gracile.

Table 6. Means and standard errors of gill rakers per row in larval Dicamptodon, anteriormost to posteriormost (1-6) rows. See Appendix A for sample sizes and localities. OTU's 25 to 32 are D. copei.

OTU	1		2		3		4		5		6	
	$\bar{X}$	s.e.	$\bar{X}$	s.e.	$\bar{X}$	s.e.	$\bar{X}$	s.e.	$\bar{X}$	s.e.	$\bar{X}$	s.e.
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

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 shows a significant phylogenetic relationship between head width and number of gill rakers for all six rows. The six r's range from .459 to .568. There is no phylogenetic relationship between SVL and the number of gill rakers, as the six r's are not significantly different from zero.

Table 6 shows that southern Oregon and California populations of D. ensatus have higher means of 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.

Color and Pattern of Larval D. ensatus

Color and pattern of larval D. ensatus varies considerably between populations, and ontogenetic variation greatly complicates the subject. However, if the subtleties of microgeographic variation are overlooked, it is possible to determine broad patterns of color variation,

and these patterns will be briefly described. The reader should recognize that this topic is only touched on here, and a more thorough analysis awaits field work in critical areas.

Young larvae, less than 55 mm SVL, are bicolor, 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. (My terminology of chromatophores follows that of Bagnara (1966). The light-yellow chromatophores can only be called xanthophores, and the coppery-gold chromatophores may just as well be called xanthophores as erythrophores because they are intermediate in color between the two types.) Small, white, longitudinal streaks occur along the sides of many

individuals, but these streaks are usually filled in with brown as the larvae grow older. Often the lateral line organs of larvae of all ages are accentuated by dark-brown melanophores, creating 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 neat semicircle of lateral line organs is found on each side, with the open sides facing laterally. 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 (Figure 10). 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 (Figure 11).

Larger individuals may have dark ventral surfaces. Melanophores encroach from the sides onto the venter ontogenetically, 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 sign of

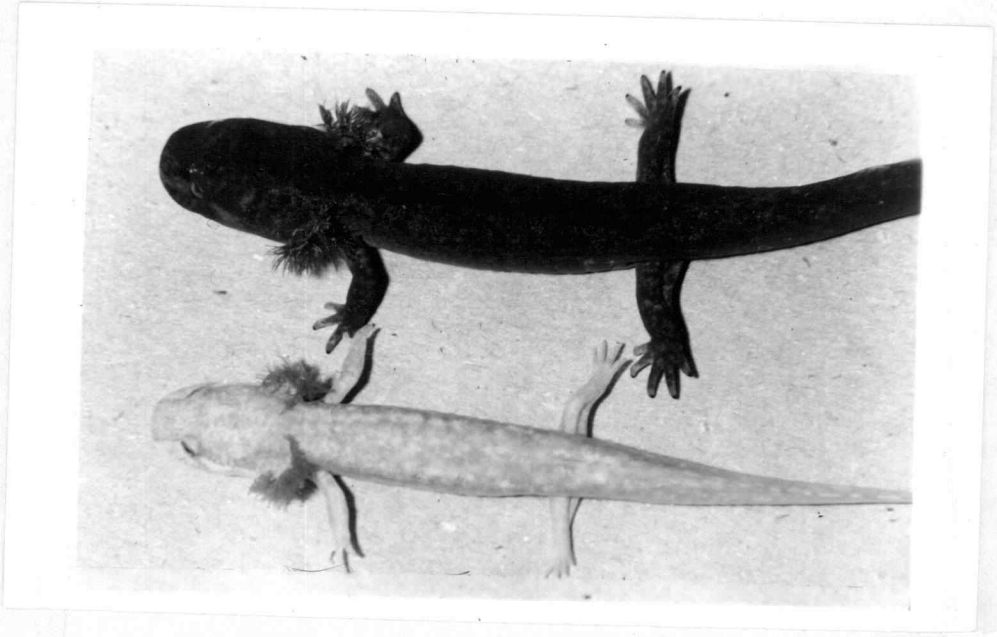


Figure 10. Two larval D. ensatus from Greasy Creek, Benton Co., Oregon. Partial albino (RAN 4021; SVL = 55 mm) and normal coloration. Note light stripes behind eyes, and regenerating left hind limb of albino.

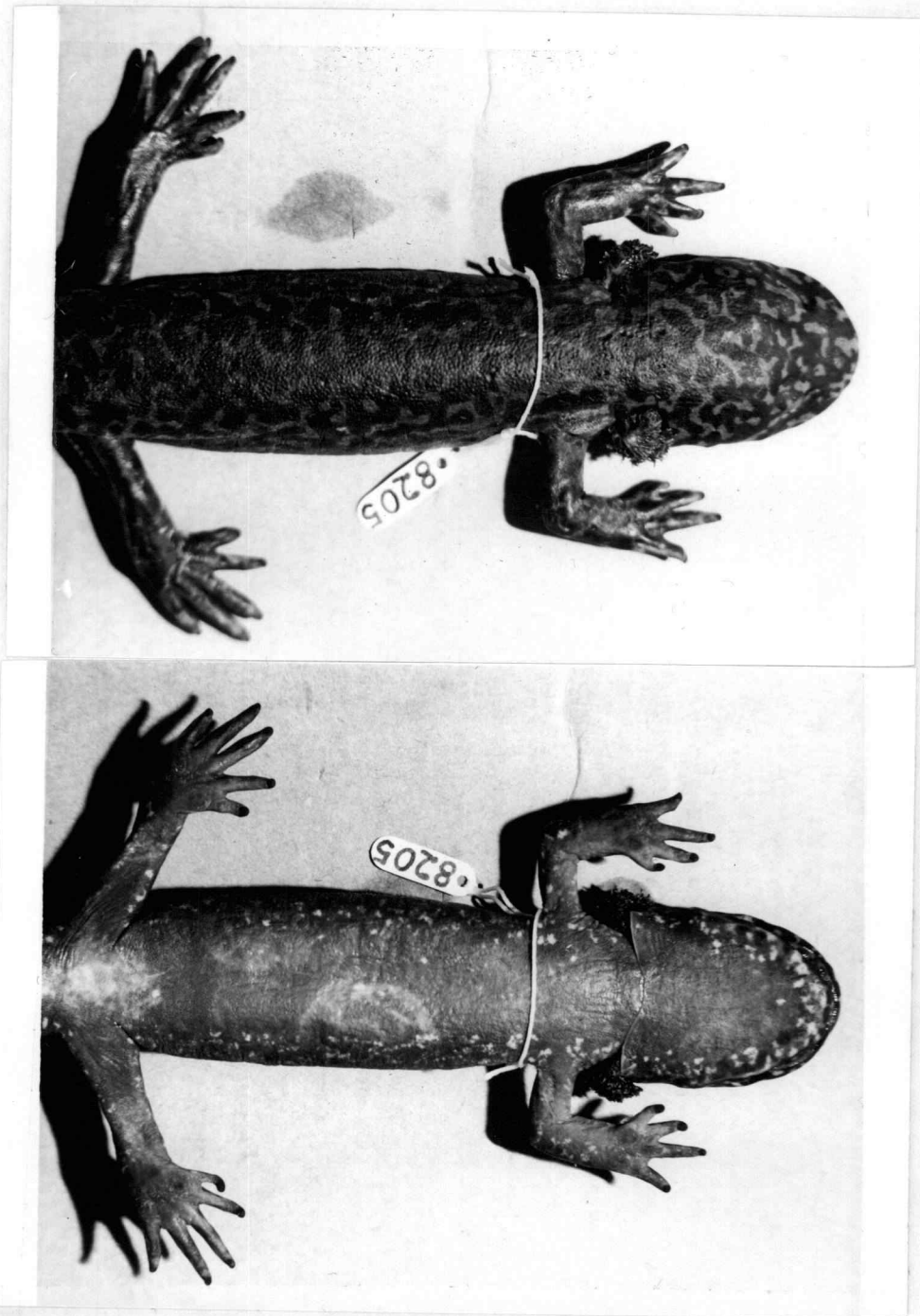


Figure 11. Dorsal and ventral view of neotenic D. ensatus (male, SVL = 129 mm) from the E. Fk. of the N. Fk. of the Trinity River, Trinity Co., California. Larvae from the Siskiyou-Trinity Region are highly mottled and some have a pattern superficially resembling the marbling of adults, as does this specimen. Note the black, cornified toe tips. The semicircular scars on the venter result from territorial fighting in sexually mature specimens.

metamorphosis is a sudden increase in the number of coppery-gold flecks beyond the concentration attained in normally aging 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. Larger 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 due to 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 apparent. 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 turns 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 County, 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 (Figure 12). 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 (Figure 11). The lighter mottling of larvae from this area extends onto the ventrolateral surfaces, and the mid-venters 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 predominently granitic rocks which litter the stream bottoms provide a background against which the highly mottled, endemic larvae are well camouflaged (Figure 13). There can be little doubt that the distinct color and pattern of larvae in the Trinity-Siskiyou Region is a result of strong selection for background, color matching.

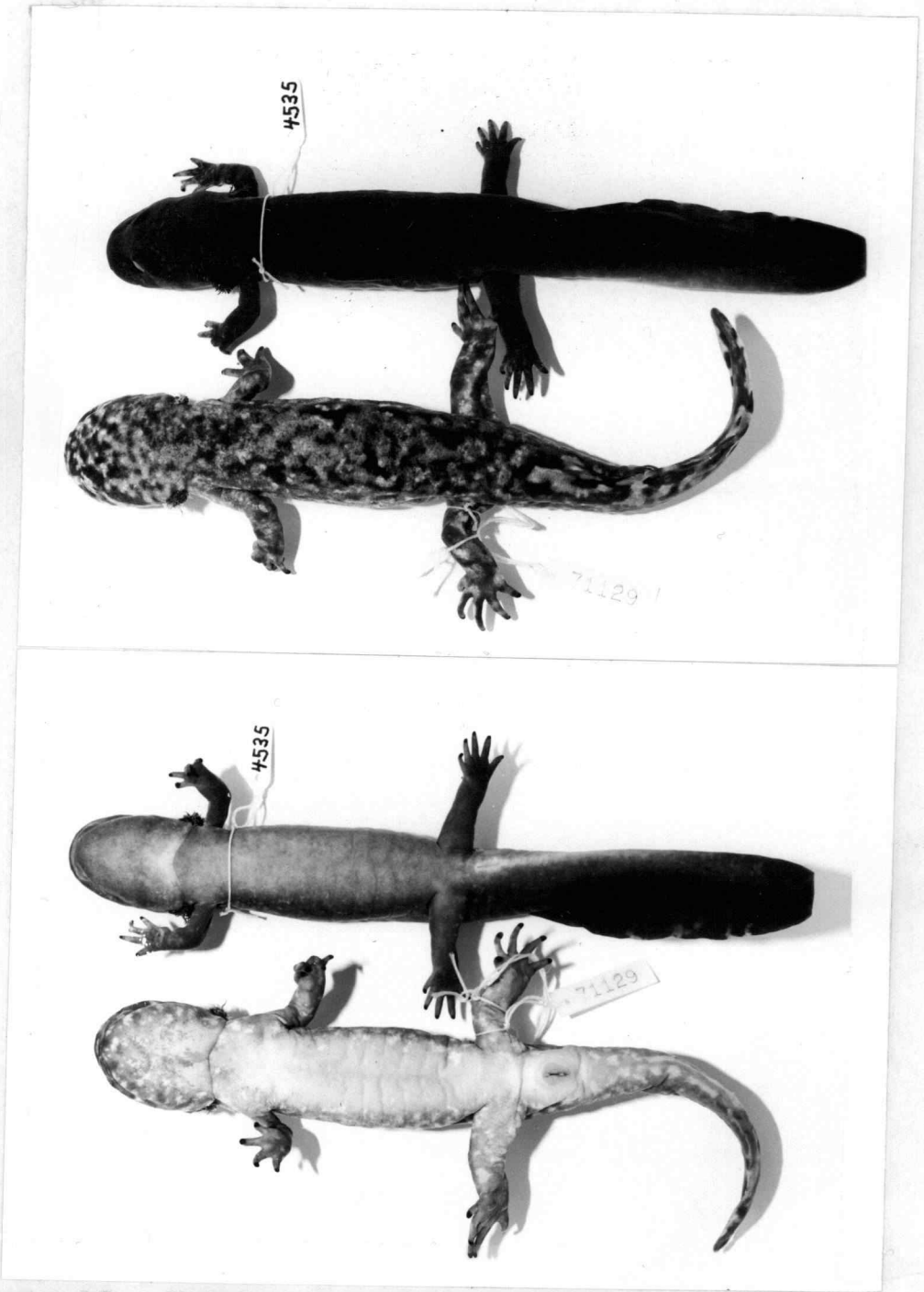


Figure 12. Mottled larval D. ensatus (MVZ 71129; SVL = 105 mm) from "Little Monster Lake", Trinity Mtns., Trinity Co., California, and plain dark larval D. ensatus from Oneonta Gorge, Multnomah Co., Oregon. The photo illustrates geographic variation in size at sexual maturity. The swollen vent of the "Monster Lake" specimen identifies it as a sexually mature male, the other larva is immature.

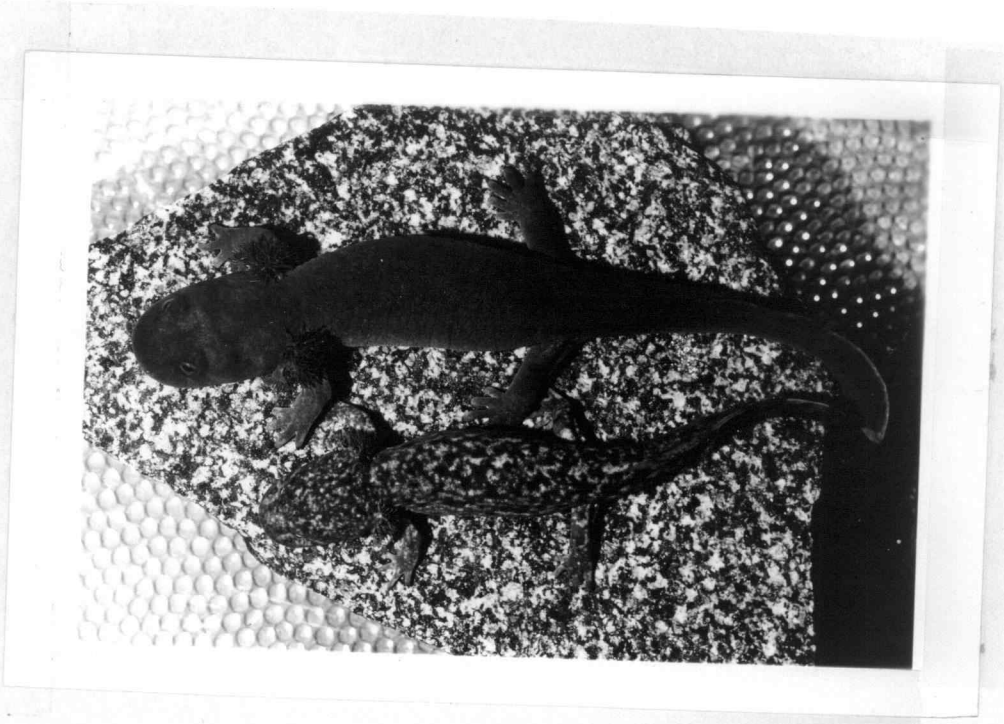


Figure 13. Larval D. ensatus. Mottled specimen (RAN 5226; SVL = 80 mm) from James Creek, Trinity Co., California, against a rock from the streambed of James Creek. Dark larva is from Mary's Peak, Benton Co., Oregon. The photo illustrates background color matching in larval D. ensatus. The color of larvae in most populations matches the color of the substrate to some degree.

Larvae from 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 area, 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 County, California are plain, dark-brown dorsally, with dark venters. Therefore, although 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 a breakdown in selection for dorsal mottling in the Shasta Region, because of the drab 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 patterning of any kind usually does not occur. Some populations of larvae from 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 (Figure 10). Three of these individuals (RAN 4021-2, 6900) were taken within a three meter section of the stream. Since the three larvae were nearly identical in size and were found close together, it is assumed they are part of a brood which consisted solely of partial albinos. Two of the larvae were discovered when parts of their tails were seen projecting from beneath rocks. If their tails had been

the normal, darkly mottled color of typical larvae from this region, the two larvae surely would not have been detected. The 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 County, 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 to sympatric larval D. ensatus (OTU's 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, puntiform 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 County, Oregon and Nine Foot Creek, Skamania County, Washington (OTU's 26 and 27) are darker both 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.

Variation in Transformed D. ensatus

Body Proportions

The 17 mean ratios and their standard errors for each of the 12 OTU's composed of transformed specimens are listed in Table 7.

The ratios HW/SVL and HL/BL (ratios 1 and 5) increase in a roughly clinal manner 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 also.

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. The

Table 7. Mean ratios and their standard errors (parentheses) for OTU's of transformed D. ensatus. See Appendix A for sample sizes and localities, and page 41 for definition of ratios.

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)

longest tails are found in specimens from Lake County, California; and individuals from all populations from California with the exception of those from Humboldt County (OTU 7) have relatively long tails.

Figure 14 illustrates geographic variation in the ratio FLL + HLL/AGL (ratio 6). The first four OTU's (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 mean $\overline{Y}$'s for the 12 OTU's 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 Region 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 Region.

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 unavoid-

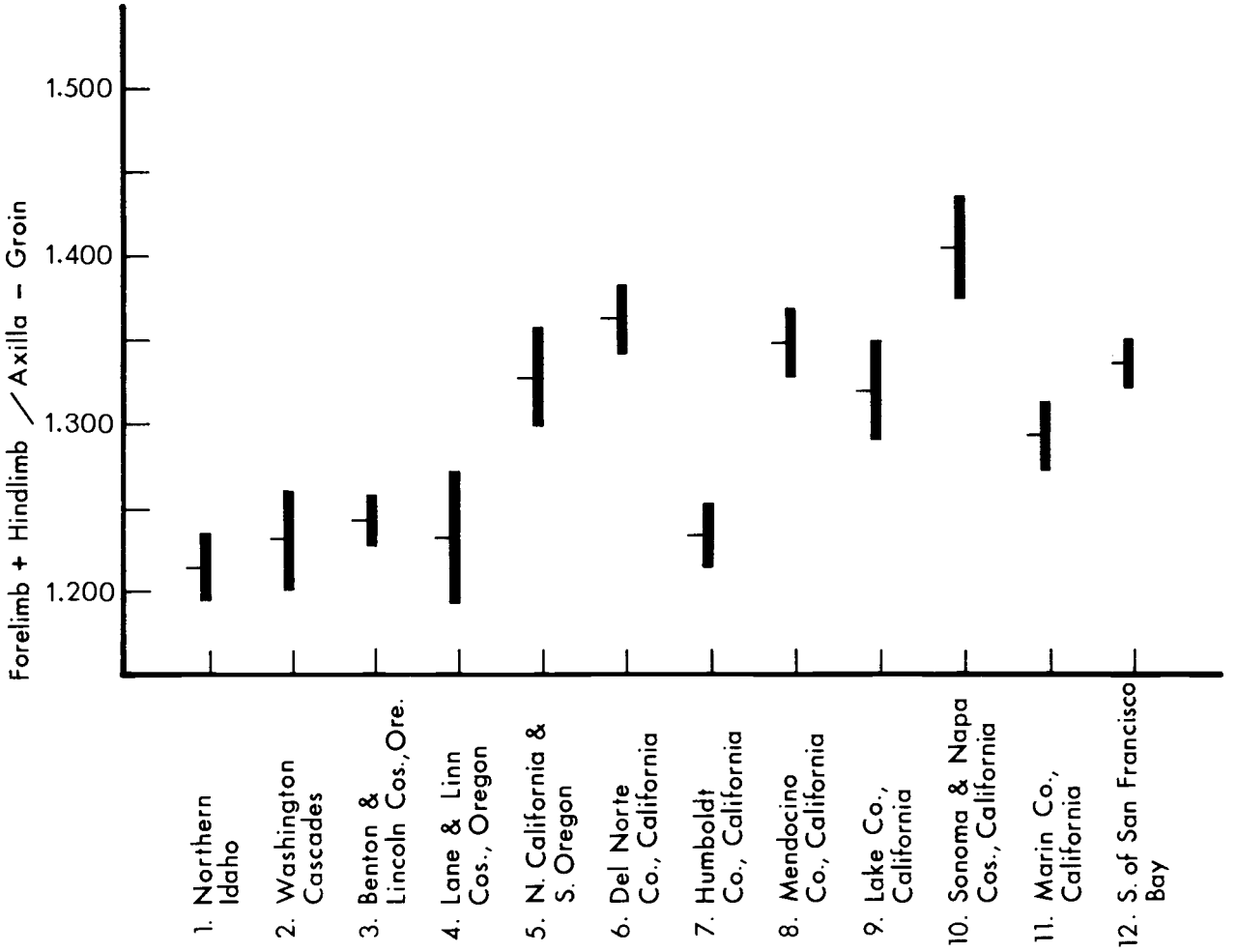


Figure 14. Variation in the ratio FLL + HLL/AGL for transformed D. ensatus. Means ±2 standard errors.

Table 8. Predicted mean body measurements (mm) of populations of adult D. ensatus; estimated from $\bar{Y} = a + bX$ where a and b are determined through least squares regression and X is set at 110 mm SVL for all populations. See Appendix A for localities of OTU's.

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

Table 9. Costal folds between adpressed limbs for populations of transformed D. ensatus. Frequencies and means are given. See Appendix A for sample sizes and localities.

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	$\bar{X}$
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

able 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 Region (OTU's 5-12) than in populations north of this region (OTU's 1-4), with the exception of the Humboldt County population (OTU 7).

Number of Maxillary + Premaxillary Teeth

For most of the 12 OTU's there is no significant correlation between SVL and number of max-premax 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 number of max-premax teeth versus SVL and versus HW are .058 and .256 respectively. Therefore, there is no phylogenetic relationship between size and tooth number, and there is only a weak relationship between tooth number and head width. The variable that correlated highest with the number of max-premax teeth on a between-group basis was number of vomerine teeth ($r = .854$).

Table 10. Number of max-premax and vomerine teeth of transformed D. ensatus. Within-group correlation coefficients of tooth number with SVL and with HW are also given. See Appendix A for sample sizes and localities.

OTU	Max-Premax Teeth				Vomerine Teeth			
	$\bar{X}$	s.e.	r-SVL	r-HW	$\bar{X}$	s.e.	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

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 max-premax teeth. Specimens from Marin, Napa, Sonoma, Lake, and Mendocino Counties, California also have high numbers of max-premax teeth by comparison to northern specimens.

Number of Vomerine Teeth

As indicated by the relatively high, between-group correlation between number of max-premax teeth and number of vomerine teeth ($r = .854$), the two vary in the same direction, and hence what has been written above on geographic variation in the number of max-premax teeth also largely applies to variation in the number of vomerine teeth (Table 10).

Color and 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 (Figure 15).

Specimens from Idaho are darker, both dorsally and ventrally, than specimens from the Pacific Border portion of the range (Figures 15, 16 and 17), 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

Figure 15. Dorsal view of two adult D. ensatus. Dark animal (SVL = 127 mm) is from Benewah Co., Idaho, light, marbled animal is from Mendocino Co., California. Not all adults from Idaho are plain-backed, but most have dark dorsal and ventral hues.

Figure 16. Dorsal view of two adult D. ensatus. Dark specimen (SVL = 106 mm) with fine-grained marbling is from Benewah Co., Idaho. Lighter specimen is from Mt. Pilchuck, Snohomish Co., Washington.

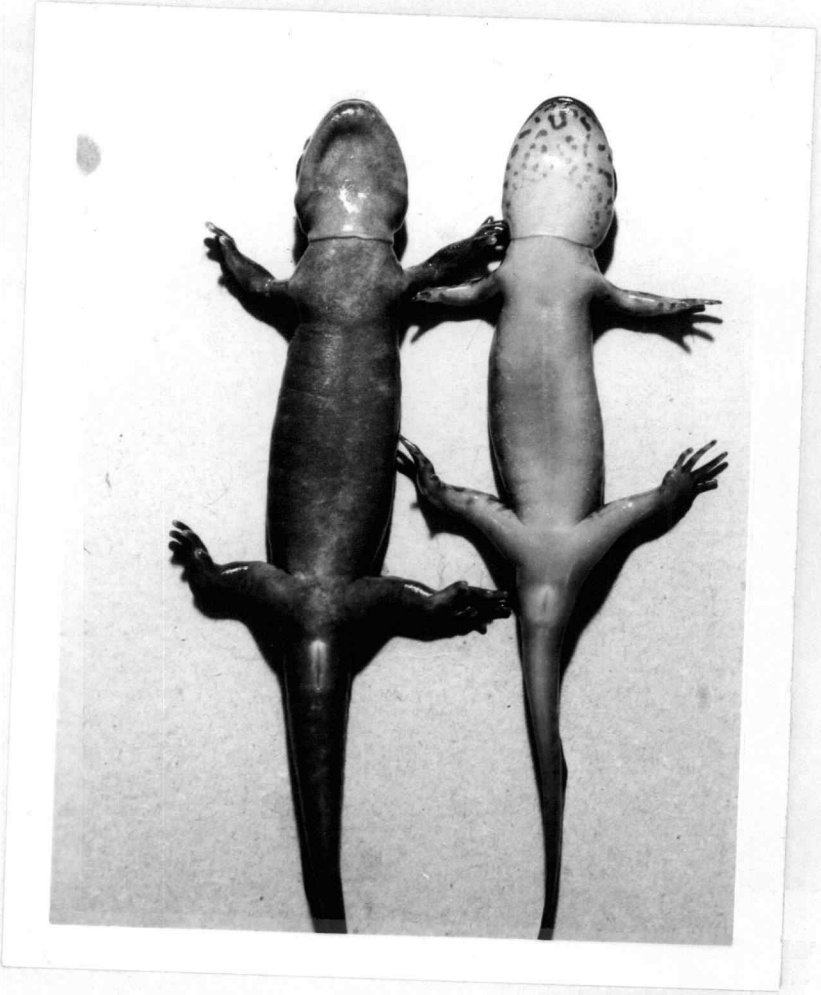


Figure 17. Ventral view of adult D. ensatus from Latah Co., Idaho (dark specimen, SVL = 96 mm) and from Santa Cruz Co., California.

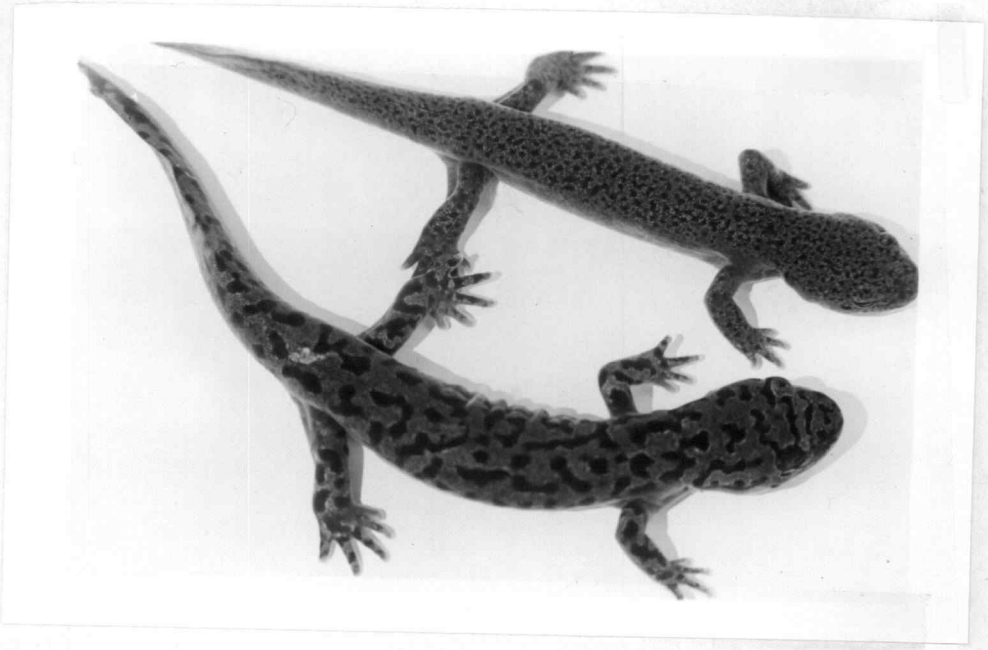


Figure 18. Adult D. ensatus from Roaring Creek, Valley Co., Idaho (dark, fine-grained specimen, SVL = 88 mm) and from Maratta Creek, Cowlitz Co., Washington.

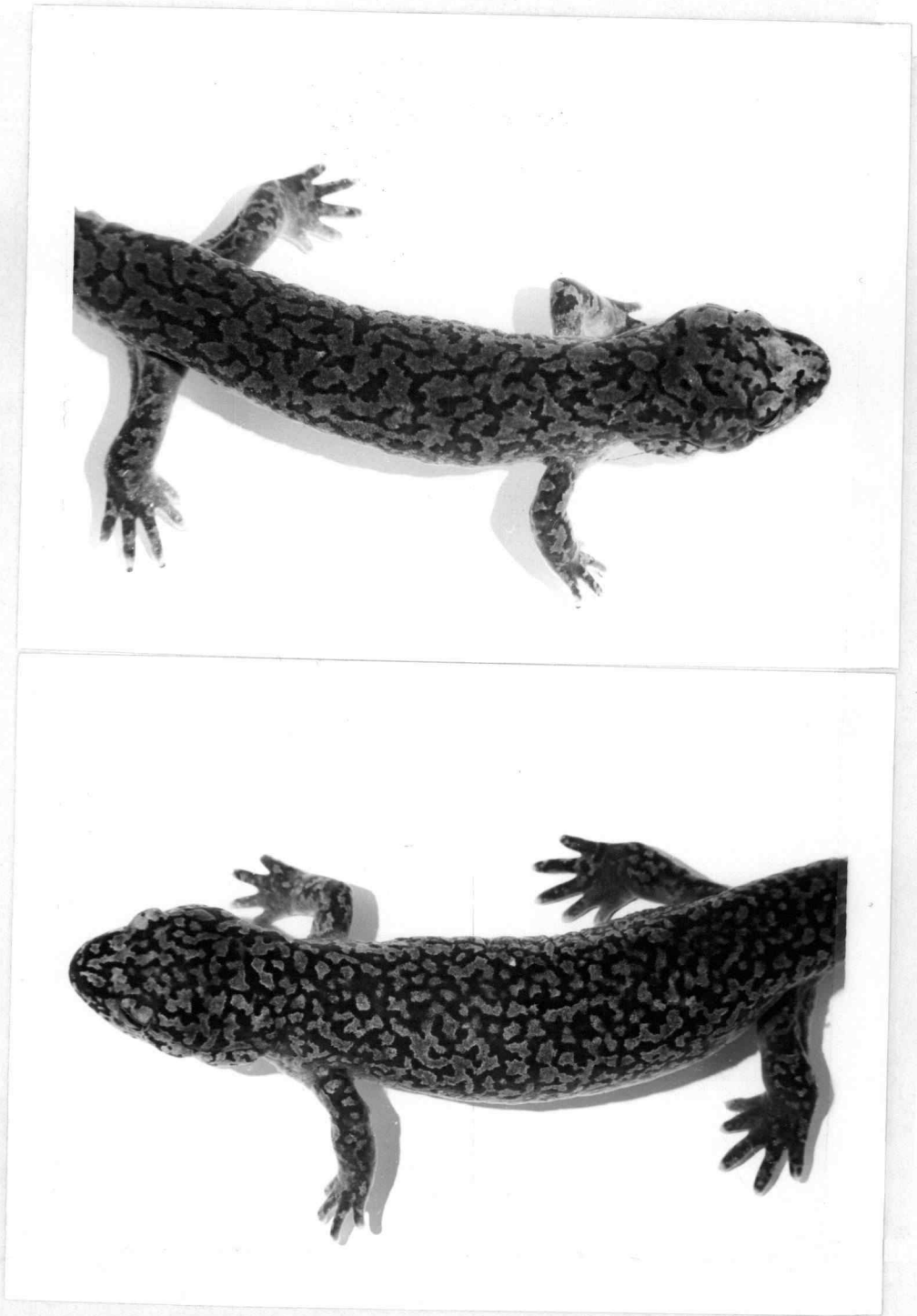


Figure 19. Adult D. ensatus from Mary's Peak, Benton Co., Oregon (SVL upper specimen = 113 mm).

Figure 20. Adult D. ensatus from coastal, Humboldt Co., California. Note extremely coarse marbling in lower animal (MVZ 44365; SVL = 118 mm). Upper specimens: MVZ 44366, SVL = 111 mm; MVZ 44367, SVL = 126 mm.

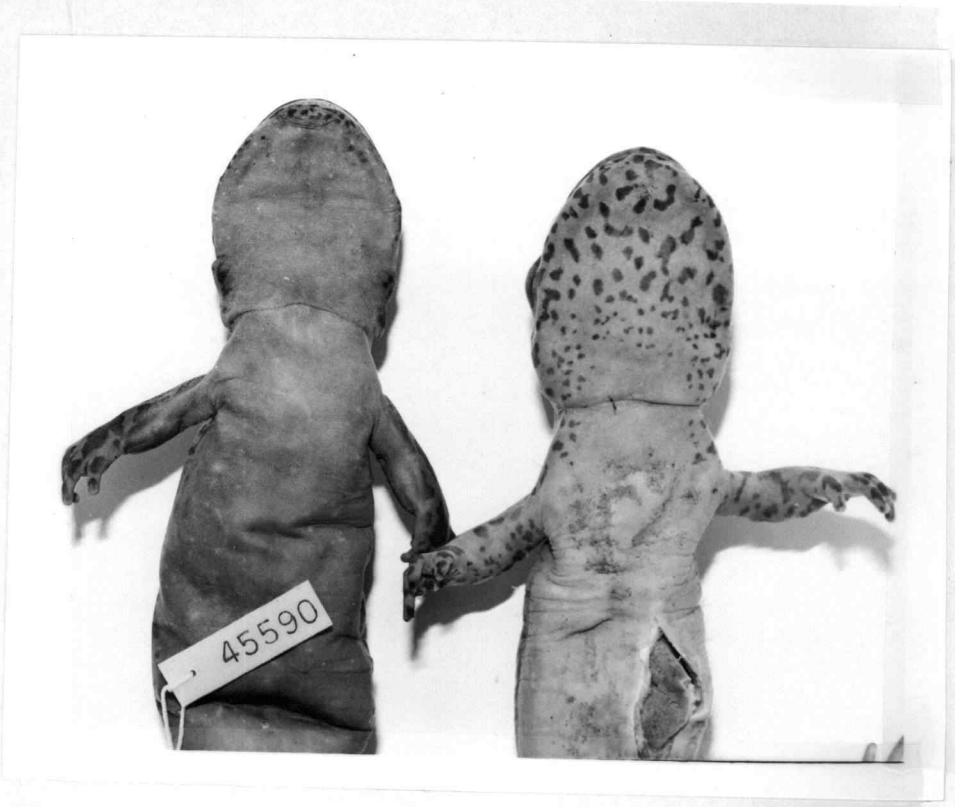


Figure 21. Ventral view of chin and throat of two adult D. ensatus from near San Francisco Bay. Extreme throat marbling on specimen from south of San Francisco Bay (MVZ 69449; SVL = 134 mm). Marbling confined to margin of jaw on specimen from north of Bay (MVZ 45590; SVL = 121 mm).

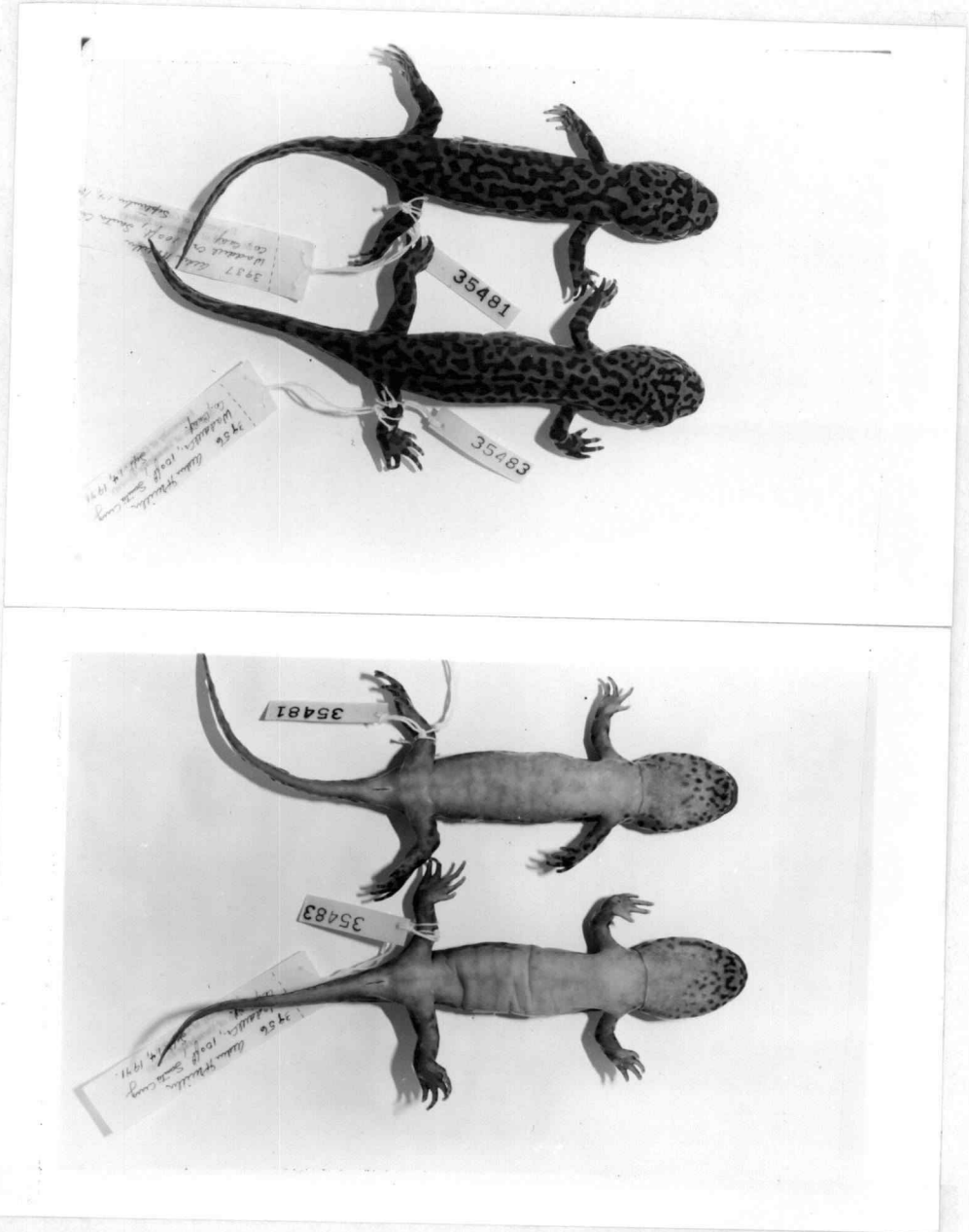


Figure 22. Ventral and dorsal views of two specimens from south of San Francisco Bay (MVZ 35481, SVL = 81 mm; MVZ 35483, SVL = 86 mm). Photo shows light-colored venters, light-colored dorsa with coarse marbling and extreme throat marbling of animals from south of the Bay.

(Figure 17). 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 16; the second type has a plain, dark, mid-dorsal region, with some indication of marbling along the sides as shown in Figure 15. South of the Salmon River, only the marbled morph has been found, but the plain-back 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 (Figure 18).

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 County, Oregon. Figure 18 shows the dorsal pattern of a typical Cascade specimen compared to an inland specimen from south of Salmon River. The coarser marbling of the Cascade specimen is obvious.

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 fined-grained specimens are found (Figure 19).

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 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 to almost obscure the darker ground color (Figure 20).

In the interior Trinity-Siskiyou Region and in Shasta County, 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.

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 gives animals from this region 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, 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 (Figures 17, 21, and 22). 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 Bay area, but they do not have extensive marbling on the chin.

Size and Sexual Maturity

The size at which larval *D. ensatus* become sexually mature varies geographically, and larvae from some populations always transform before maturity is reached. This subject is complicated by the fact that age and size are not necessarily correlated between populations, and the relationship between age and size may be determined by genetic factors, ecological factors, or both. Further complications arise because there is no basic information on the effects of age as compared to the effects of size

on sexual maturity, and it is difficult to sort out these factors as age and size are highly correlated within populations.

In general, larvae of D. ensatus are not sexually mature until they reach sizes greater than 115 mm SVL, but there are important exceptions. Larvae may become neotenic at Nosoni Creek, Shasta County, California (OTU 18) at 95 mm SVL; as low as 100 mm in parts of Siskiyou, Trinity, and Humboldt Counties, California; 88 mm at Bolan Lake, Josephine County, Oregon; 85 mm at Shoat Spring, Jackson County, Oregon (OTU 11): and 107 mm at Eldorado Gulch, Latah County, Idaho.

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 neotenic D. ensatus. There is some geographic variation in size at sexual maturity for D. copei. At Oneonta Gorge (OTU 28) and Wahkeena Falls (OTU 27), Multnomah County, Oregon, D. copei show signs of sexual maturity at 65 mm SVL; 77 mm at Saddle Mountain (OTU 29), Clatsop County, Oregon; 77 mm at Rock Creek (OTU 30), Wahkiakum County, Washington; 75 mm at Beaver Creek (OTU 31) and Merriman Creek (OTU 32),

Grays Harbor County, Washington; 67 mm at Maratta Creek (OTU 25), Cowlitz County, Washington; and 81 mm at Nine Foot Creek (OTU 26), Skamania County, Washington.

The average and maximum size of larval D. ensatus varies geographically and is related to the occurrence or non-occurrence of neoteny. The largest neotenes are found in the Cascade Mountains of Washington and Oregon and in the Coast Range of Oregon. No exceptionally large neotenes are known from Idaho and California.

Apparently the largest, documented neotene reported to date is 286 mm total length, collected at Oak Grove, Clackamas County, Oregon (Bishop, 1943). Many specimens greatly exceed this size. The largest I am aware of is a female collected by me in the Columbia Gorge, Multnomah County, Oregon. At the time the specimen was collected, the measurements were 205 mm SVL and 351 mm total length. The specimen is still alive in the laboratory so no museum number can be cited. This animal is incidentally, the largest non-fossil ambystomatid so far reported.

Transformed D. ensatus can not 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 County 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 un-numbered specimen in the collections at the University of Washington. The animal was collected in Renton, King County, 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 neotenes 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,

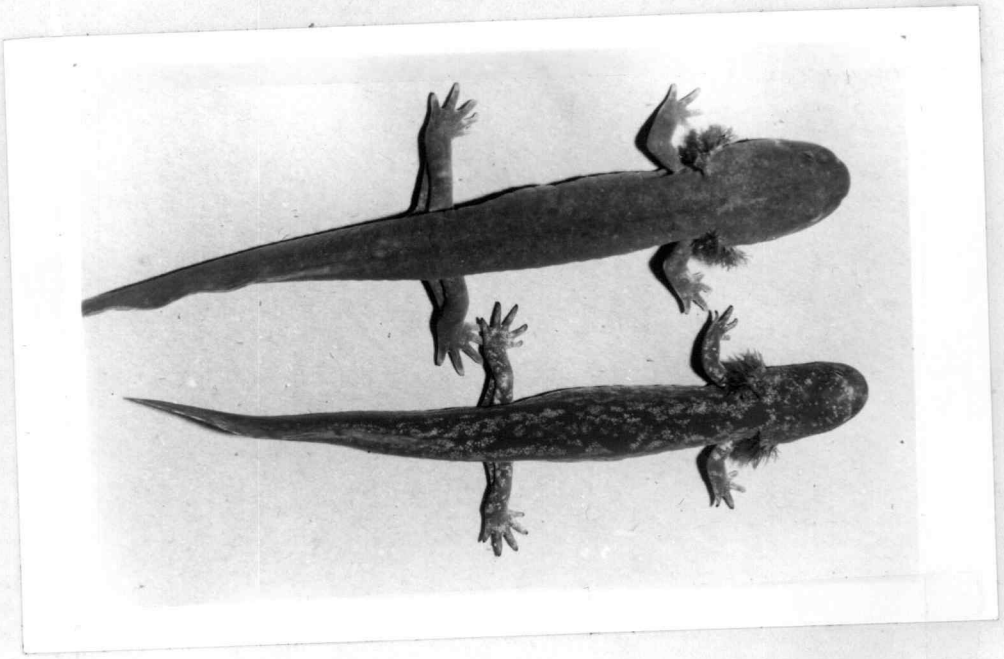
103.8 mm; and Nine Foot Creek, RAN 4657, female, 113.5 mm.

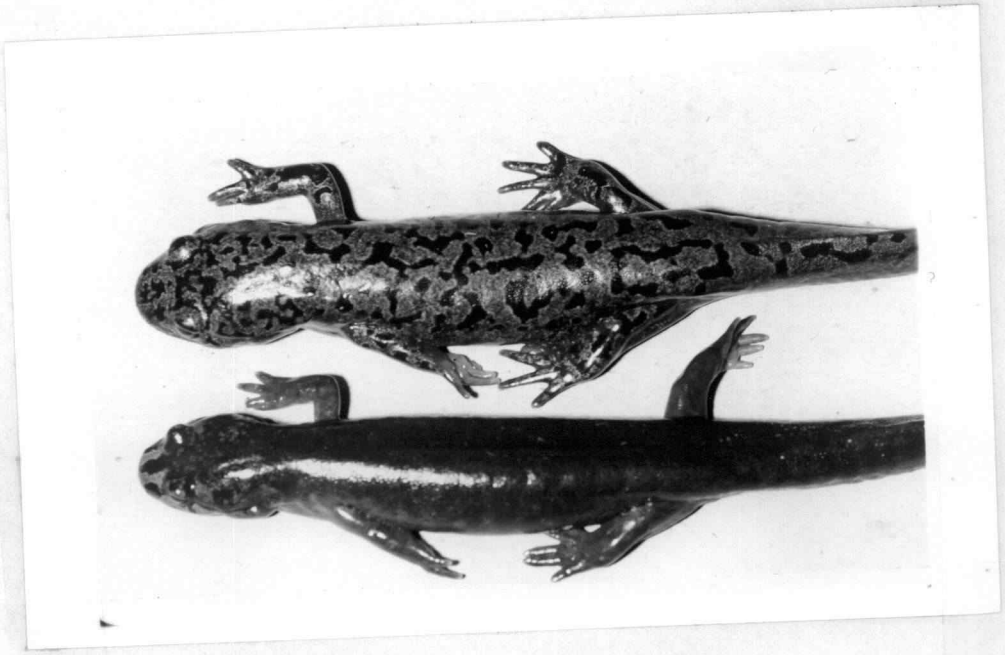
Sensitivity of Larvae to Thyroxine

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 eyes (Figure 23). Treatment of D. copei was continued beyond the 11 months reported in 1970, and after two years and ten months there was little additional change, except that gold pigment had spread posteriorly to a point just beyond 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

Figure 23. Upper photo: Dorsal view of the holotype of D. copei (upper specimen, USNM 166784, SVL = 92 mm) compared to a larval D. ensatus of similar size collected at the same locality (Maratta Creek). Lower photo: Dorsal view of transformed D. ensatus (upper) and D. copei (lower). Both were collected as larvae at Maratta Creek and received identical thyroxine treatment. Photo after 11 months of continuous treatment. Note the longer limbs, robust body, and complete marbling in D. ensatus. Both are about 94 mm SVL.





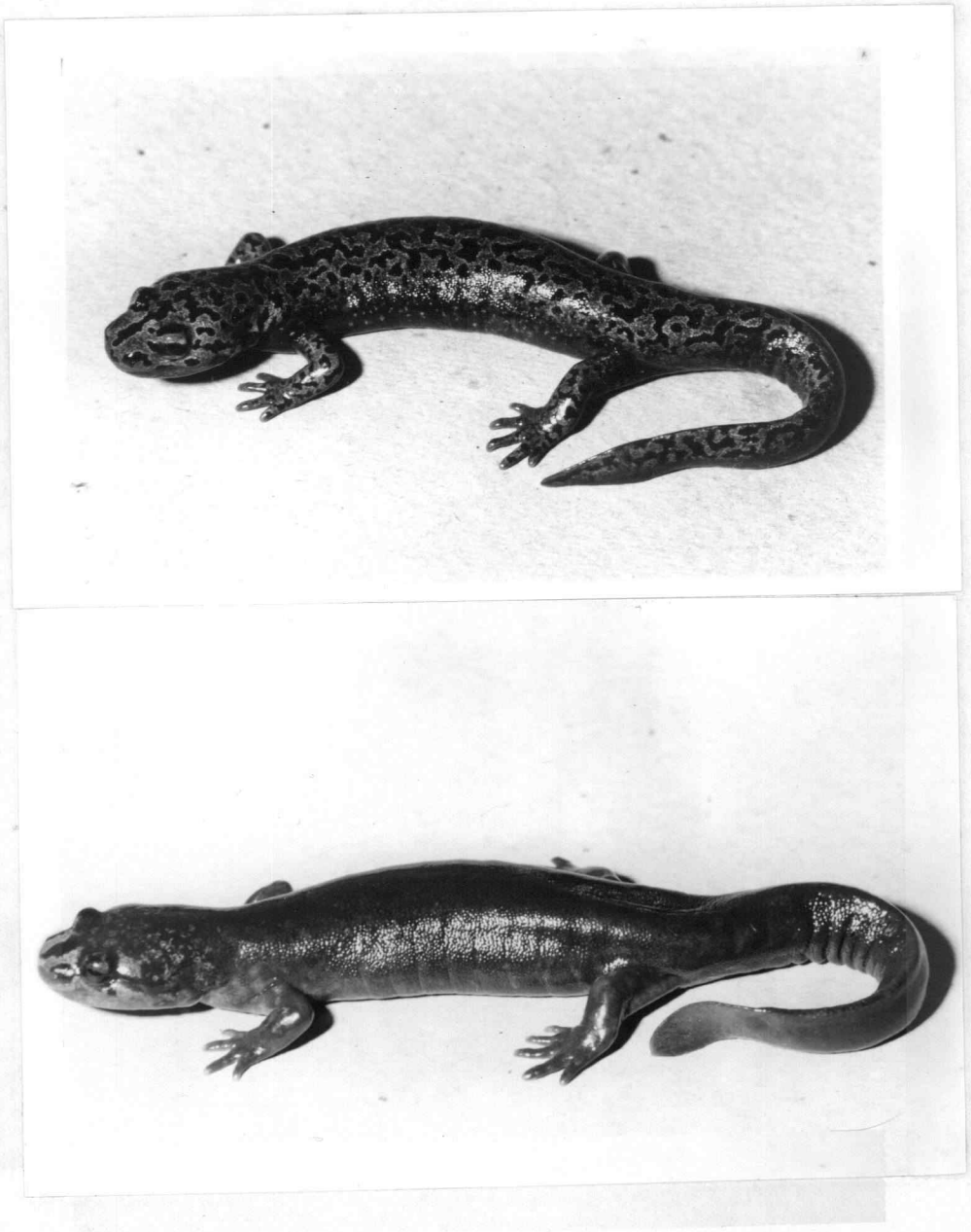


Figure 24. Transformed D. copei. Upper animal from Merriman Creek in the Olympic Mountains, Grays Harbor Co., Washington, after 12 months of continuous thyroxine treatment (SVL = 91 mm). Lower animal from Maratta Creek, Cascade Mountains, Cowlitz Co., Washington, after 11 months treatment (SVL = 87 mm). Note the attenuate bodies and short limbs.

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 can not 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 have been held in the laboratory for up to three years; and none has transformed without the administration of thyroxine.

The experiments described above were done on animals collected at Maratta Creek, Cowlitz County, Washington, the type locality of D. copei, so that nothing was learned of geographic variation in sensitivity to thyroxine. Studies of variation are still in progress, and only partial results will be described here.

Larval D. ensatus from many 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 to 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 largely minor, and at present can not 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

neotenes from Maratta Creek showed only a slightly delayed reaction to thyroxine, but only relatively small (young) neotenes were used in these experiments. Recent tests show that larger, old and scarred neotenes from Maratta Creek transform slowly, and the rate is directly proportional to size. Apparently the tissues become increasingly insensitive to thyroxine with age. But, even the largest neotenes 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. Age-dependency of reaction time is evident for neotenic D. ensatus from Loon Creek, Lane County, Oregon; Greasy Creek, Benton County, Oregon; Oneonta Gorge, Multnomah County, Oregon; Quartz Creek, Clatsop County, Oregon; and Nosoni Creek, Shasta County, California; as well as from the Maratta Creek population.

Individuals representative of all the OTU's of D. copei listed in Appendix A, except for OTU's 30 and 31, have been tested for sensitivity to thyroxine. With the exception of individuals from Nine Foot Creek, Skamania County, Washington (OTU 26) and from Merriman Creek, Grays Harbor County, Washington (OTU 32), all test animals reacted much the same as did those 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, dorsal marbling (Figure 24). However, they retained the small-headed, attenuate, short-limbed appearance of artifically-transformed D. copei from the other localities.

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 Table 11 and Figures 25 and 26.

The serum protein fractions have been assigned arbitrary numbers to facilitate discussion. Fraction 1 has

Table 11. Summary of relative density and relative migration (compared to human albumin) of serum proteins of Dicamptodon. Means, and standard errors in parentheses are given.

Species	Stage	Locality	Relative Density of Fractions						
			1	2	3	3'	4	5	Total
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)
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)
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)
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)
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)
D. ensatus	intermediate	Mannering Cr., Ida.	36.5	20.0	15.0	18.5	13.5	22.5	126.0
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)
D. ensatus	transformed	Valley Co., Ida.	56.0	25.0	8.0	20.0	16.0	28.0	153.0
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)

Table 11. (continued)

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

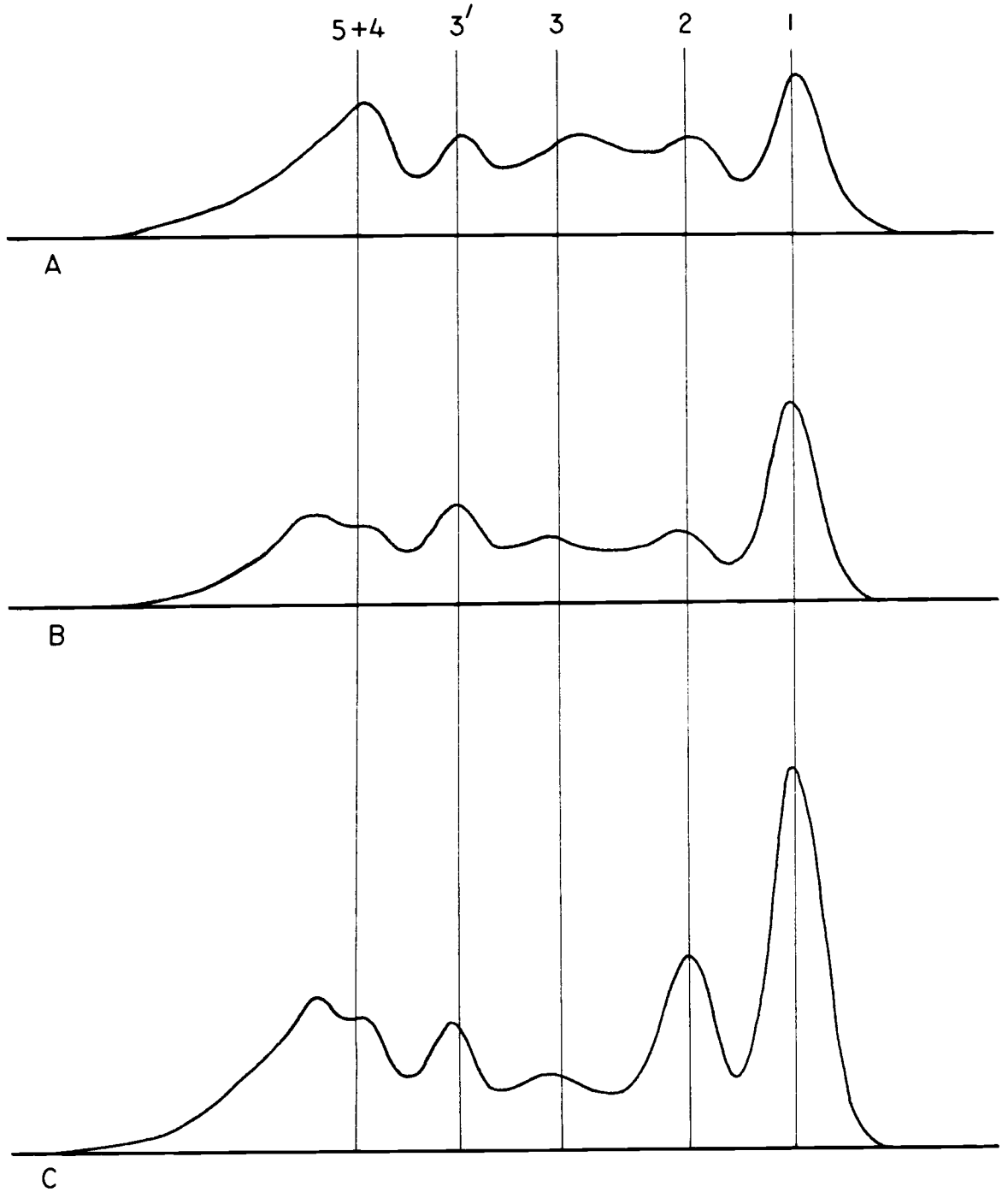
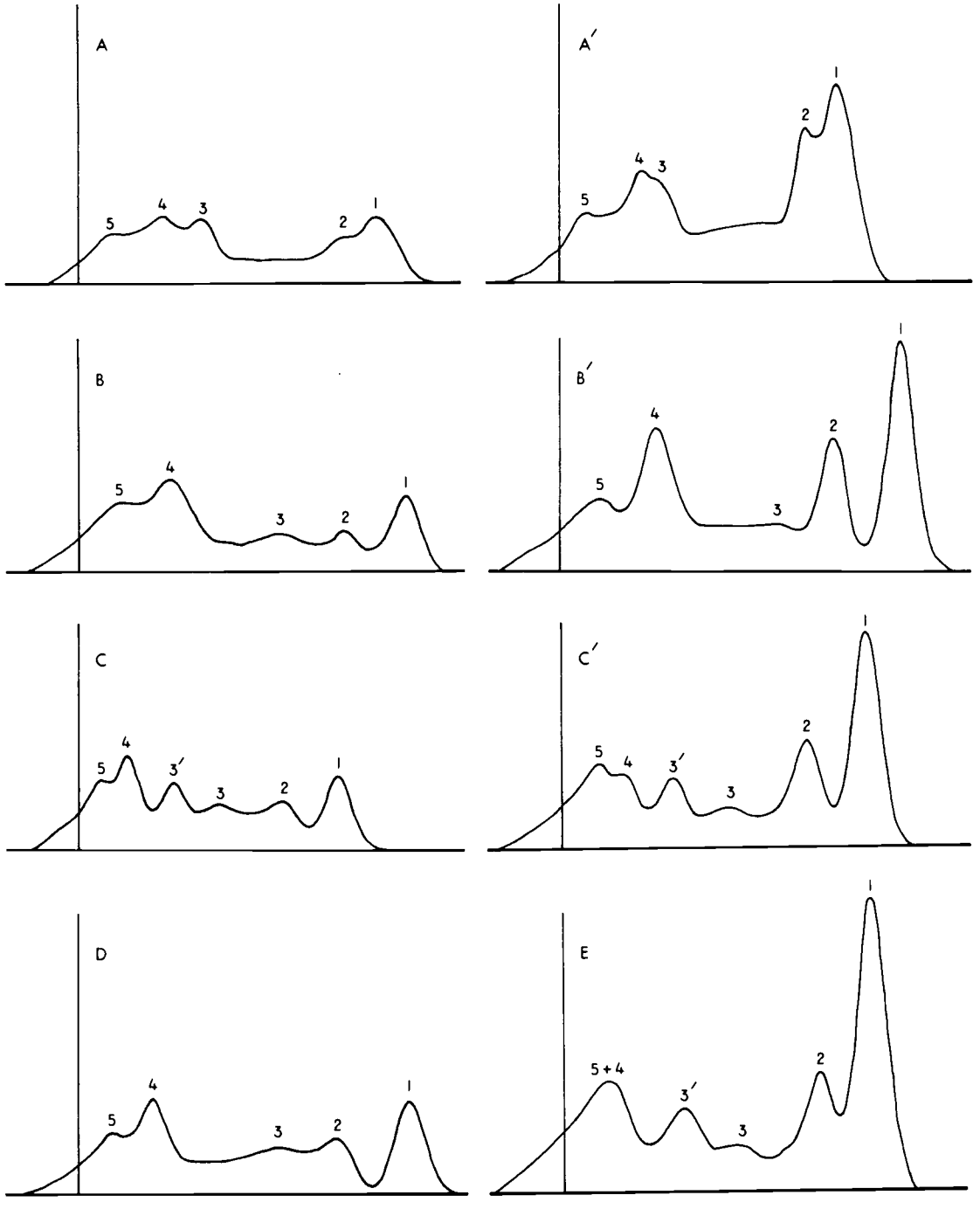


Figure 25. Ontogenetic changes in blood serum proteins of D. ensatus from Benewah Co., Idaho. A is the larval pattern, B is from a specimen in the process of metamorphoring, and C is from a completely metamorphosed individual. See text and Table 11.

Figure 26. Ontogenetic and phylogenetetic 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 adult D. ensatus from Maratta Creek; C and C' for D. ensatus from Mannering Creek, Latah Co., Idaho; D is the larval pattern for Mt. Pilchuck, Snohomish Co., Wash.; and E is the pattern for adults from Valley Co., Idaho.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2
1
D
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4
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1

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 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.

A comparison of the electrophorograms of larval Dicamptodon and their respective metamorphosed forms shows that there is an increase in the total amount of blood serum protein associated with metamorphosis (Figures 25 and 26), and that the increase is largely due to 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 11 to be significantly higher after transformation, for both D. copei and D. ensatus.

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 there is a phylogenetic correlation in vertebrates 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 11). 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 to those for D. ensatus shows that there are important differences between the two species (Figure 26). 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 (Figure 26A, 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 (Figure 25).

Other populations of D. ensatus from Washington and Idaho were sampled. Patterns for animals from Snoqualmie Pass, Kittitas County, Washington; Mount Rainier, Pierce County, Washington; Eldorado Gulch, Latah County, Idaho; and Roundhouse Gulch, Shoshone County, 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 Cos., 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 to 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 County, and Nine Foot Creek, Skamania County, 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 of larval D. ensatus of all sizes, including large neotenes, are cartilaginous; but that these elements 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 aging rather than 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; and contrary to

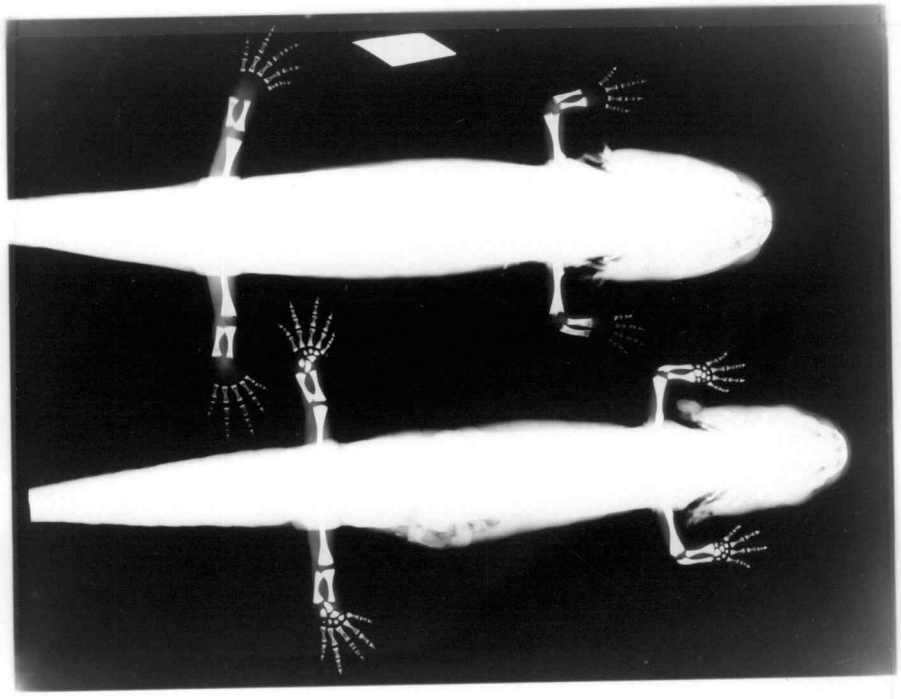
Hilton's results, many large, neotenic D. ensatus have bony carpals and tarsals. However, larval D. ensatus less than about 140 mm SVL seldom have these elements ossified. The mesopodial elements of D. copei are, by contrast, often ossified at sizes as small as 70 mm SVL (Figures 27 and 28).

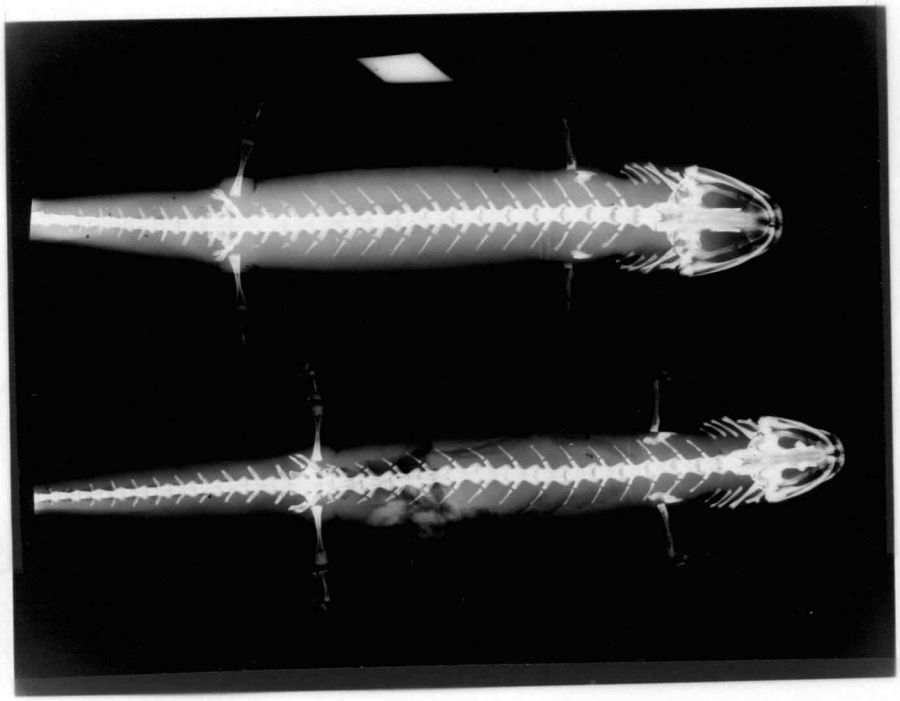
The pubic portion of the pelvic girdle is cartilage in larval D. ensatus smaller than 140 mm SVL, whereas two separate centers of ossification are usually present in D. copei larger than 75 mm SVL. In the larger specimens of D. copei, mineralization has spread, rod-like, anteriolaterally along each pubic half (Figures 27 and 28).

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 (Figures 27 and 28), and the first ceratobranchials are also ossified over much of their length. These latter elements are ossified in some extremely large, neotenic D. ensatus.

Other parts of the skeleton of D. copei seem to be in advanced stages of ossification compared to larval

Figure 27. Radiographs, taken at two different exposures, of a larval D. ensatus (upper in both radiographs, RAN 9861, SVL = 99 mm, immature male) and a larval D. copei (lower, RAN 9845, SVL = 97 mm, 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 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.





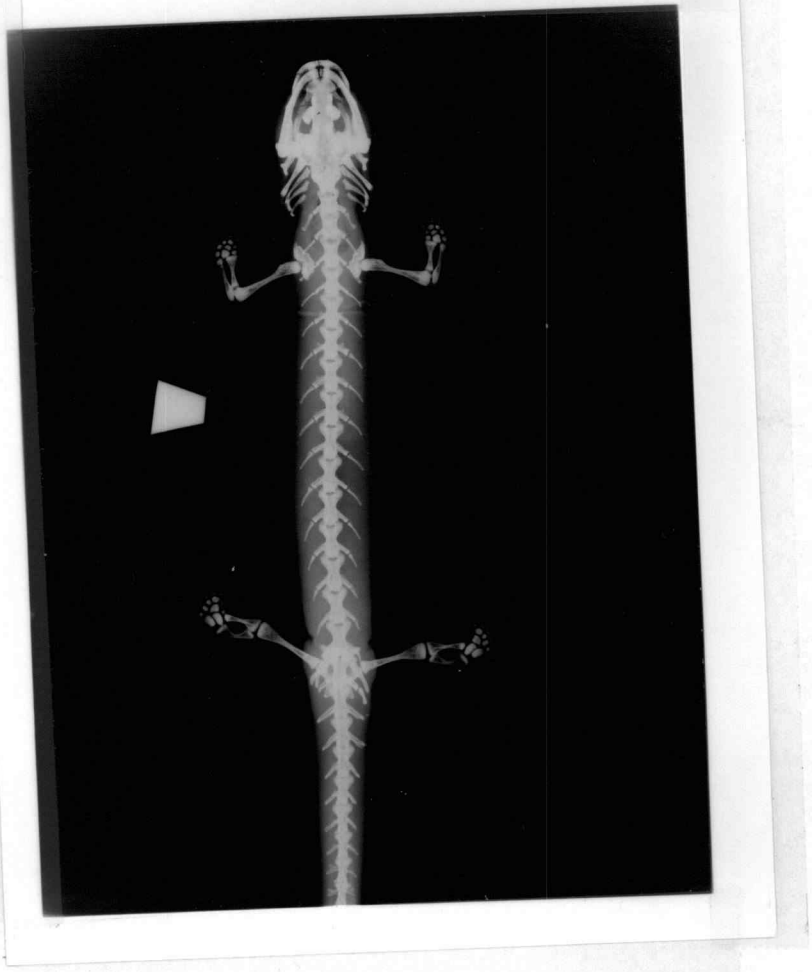


Figure 28. Radiograph of larval D. copei from Nine Foot Creek, Skamania Co., Washington (RAN 8710, SVL = 105 mm, mature males). Note that the degree of ossification is even greater in this specimen than in the smaller D. copei of Figure 27. Especially note the coracoids, long bones, mesopodials, and angularity of the skull. Two small tuberosities can be seen projecting laterally from each squamosal.

D. ensatus of similar size. For instance, the scapula is the only portion of the pectoral girdle which is ossified in D. ensatus, while a large part of the coracoid cartilage in the regions around the glenoid fossae have additionally become mineralized in D. copei (Figures 27 and 28). Inspection of Figure 27 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 (Figure 28). 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, neotenic D. ensatus.

Multivariate Comparisons of OTU's

Comparison of Populations of Larvae

Figure 29 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, number of max-premax teeth, number of vomerine teeth, and number of gill rakers on each of the six rows. At

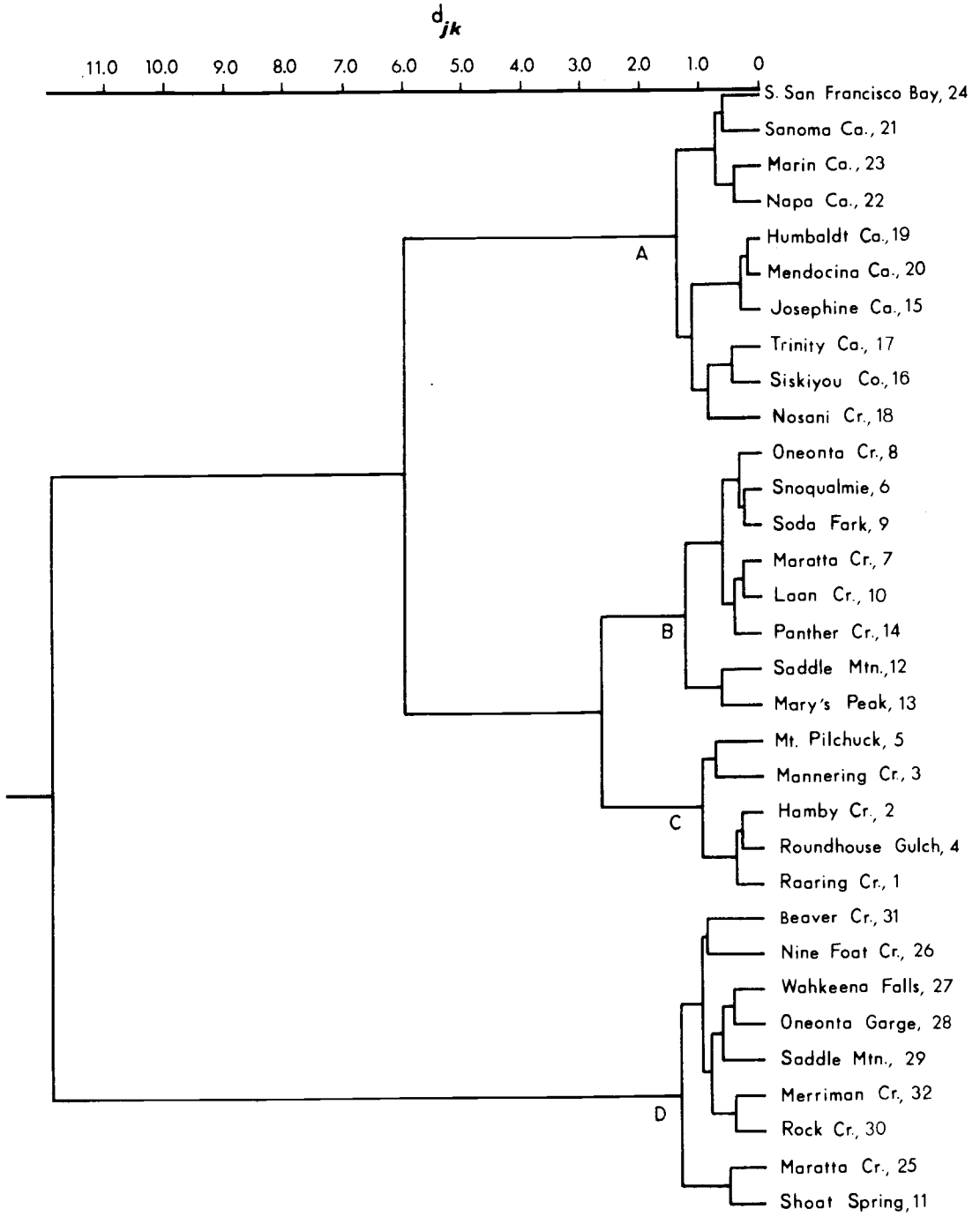


Figure 29. Phenogram of larval OTU's based on HGroup cluster analyses of the d_{jk} matrix.

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 (OTU's 21, 22, 23, and 24) and a northern subgroup which are geographically divided at about the level of southern Mendocino County.

Group B may be described as a Cascade and Oregon Coast Range group of D. ensatus. Two northern, Coast Range populations (OTU's 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 comingling of the Coast and Cascade Ranges in southerwestern 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 closely related to each other than to the other groups.

Group D is widely separated 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 Michner, 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 30 and 31).

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; and R-technique was used with projection of the larval OTU's onto the component axes. (For a description of the matrix algebra involved in determining the position of individuals (OTU's) on component axes see any good text on multivariate statistics, e.g., Cooley and Lohnes (1971).) The first three principal components accounted for 92 percent of the total variance in the multivariate system, and only the first three components were used in subsequent analysis.

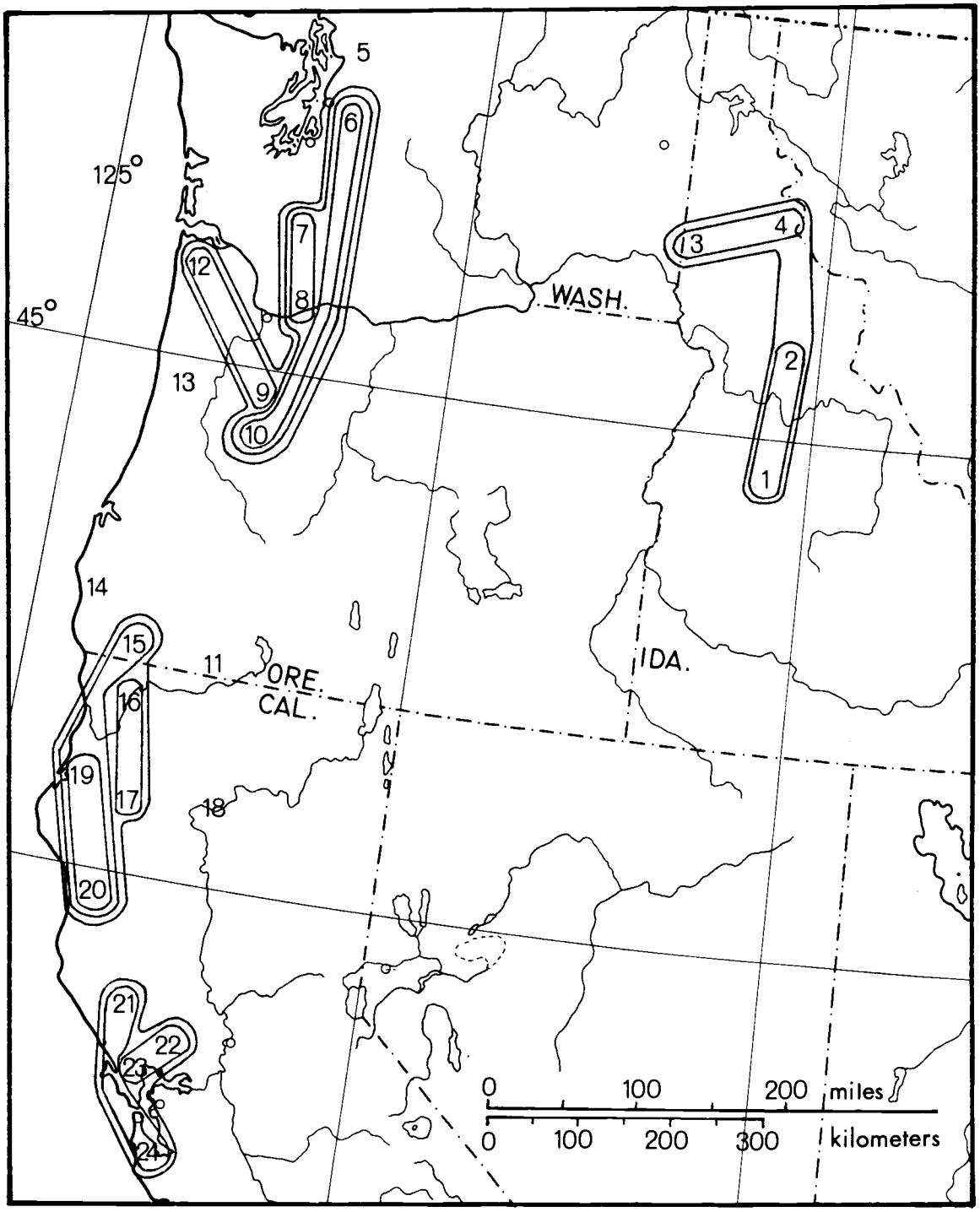


Figure 30. Clusters of OTU's of larval D. ensatus shown in relation to geography. UWPG clustering of the r_{jk} matrix (see text). Successive rings indicate more inclusive groupings. Results of first 15 cycles shown.

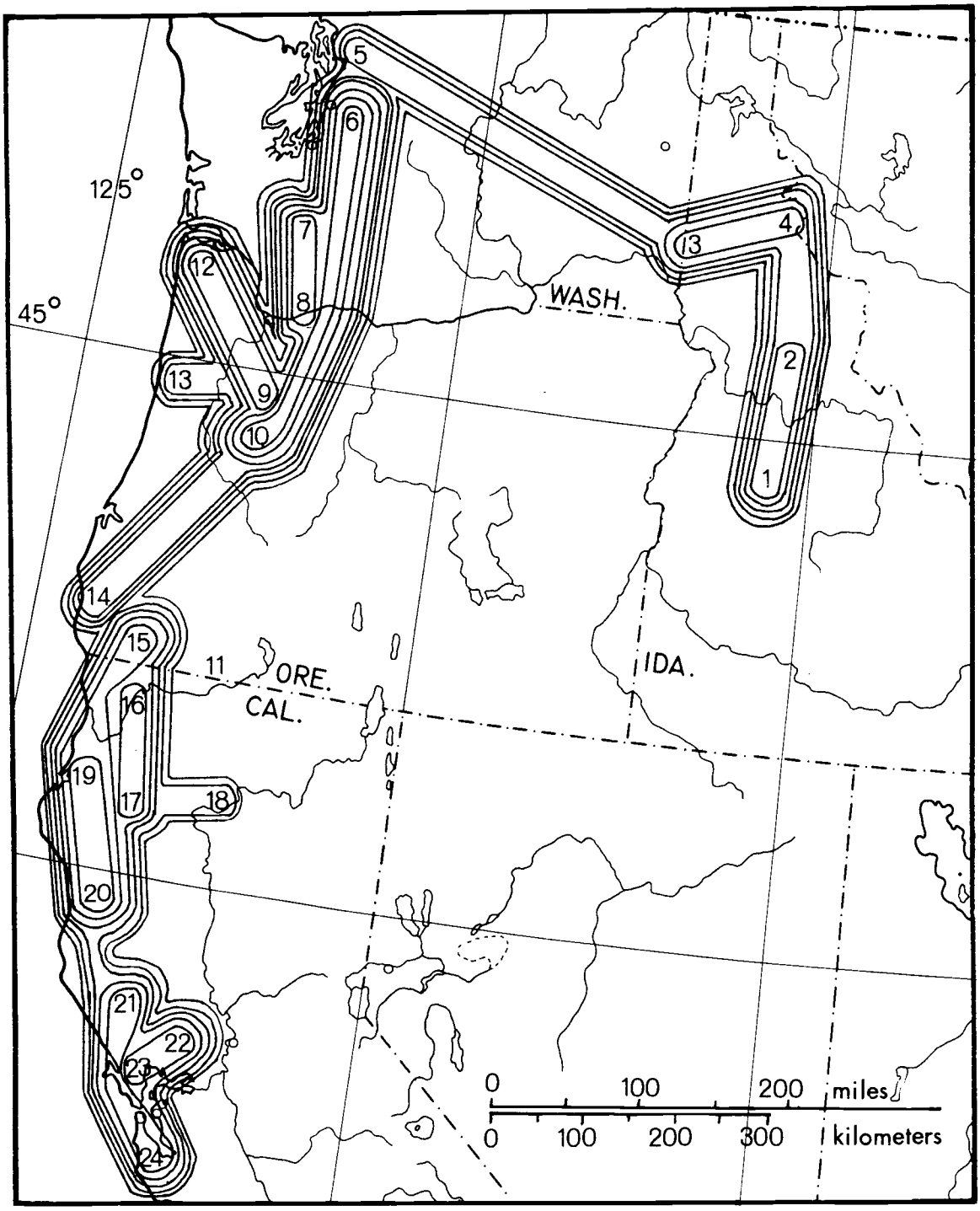
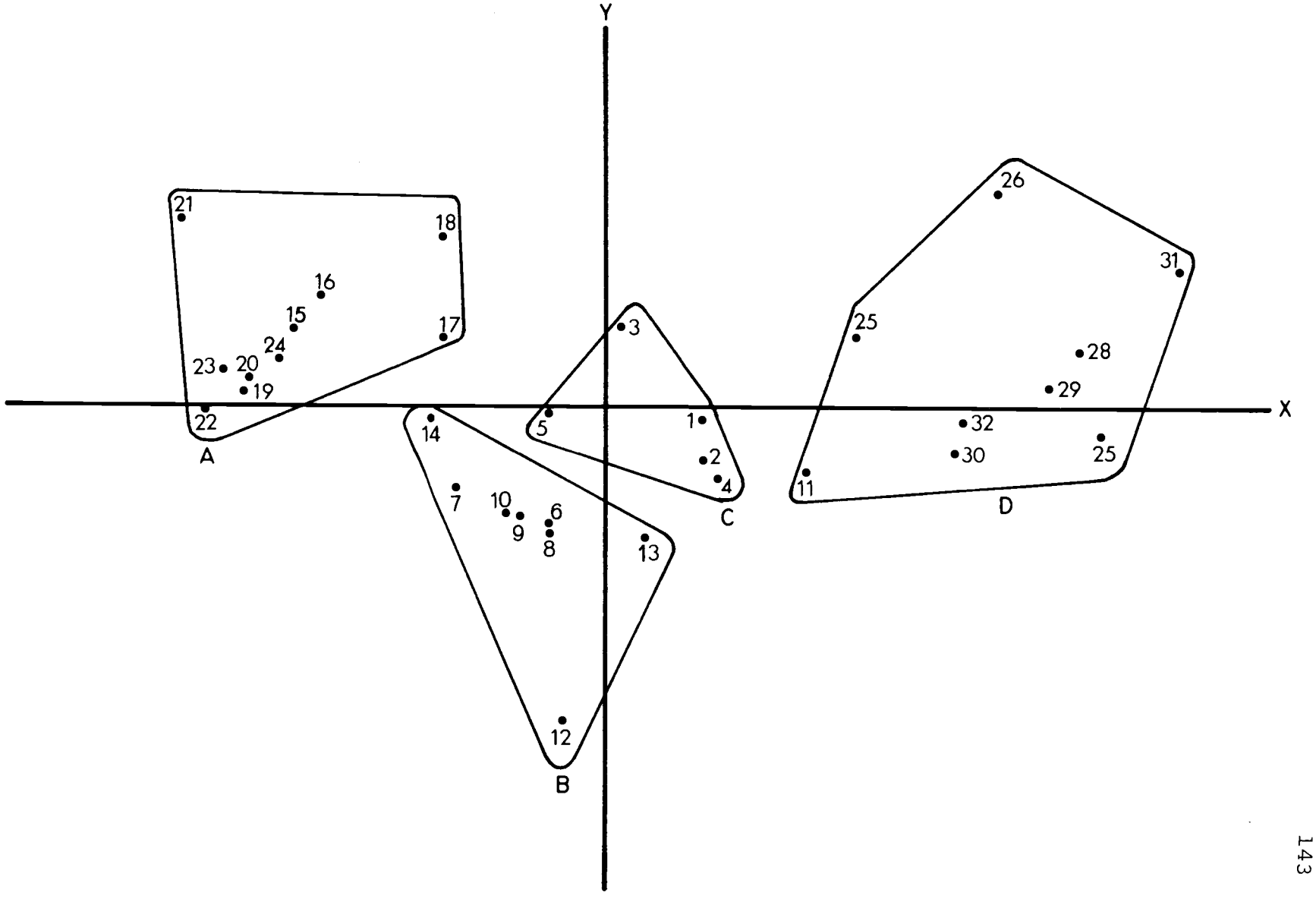


Figure 31. Complete clustering of OTU's of larval D. ensatus. See Figure 30 for explanation. OTU 11 is shown not clustered because it clustered with D. copei.

Ordination of the larval OTU's on the first two and three principal axes is illustrated in Figures 32 and 33. In Figure 32, lines have been drawn around the OTU's which formed the four major groups in HGroup and UWPG cluster analysis; and 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 groups, based on these two, new, uncorrelated variables, correlates well with the relative degree of isolation of the four groups indicated by the linkage pattern of HGroup analysis, based on 25, correlated characters (see Figure 29). Therefore, the results of cluster analysis are largely confirmed by component analysis.

Figure 33 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 OTU's 1, 2, 3, 4, and 5, which together form the Rocky Mountain Group. OTU 5 is shown in Figure 32 to be closer to other Cascade OTU's than to Rocky Mountain OTU's, but its value for the third component places it in an intermediate position between Groups B and C.

Figure 32. Ordination of larval OTU's 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 total). Lines have been drawn around the OTU's which correspond to the 4 major stems of HGroup cluster analysis (A, B, C, and D). See text.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25
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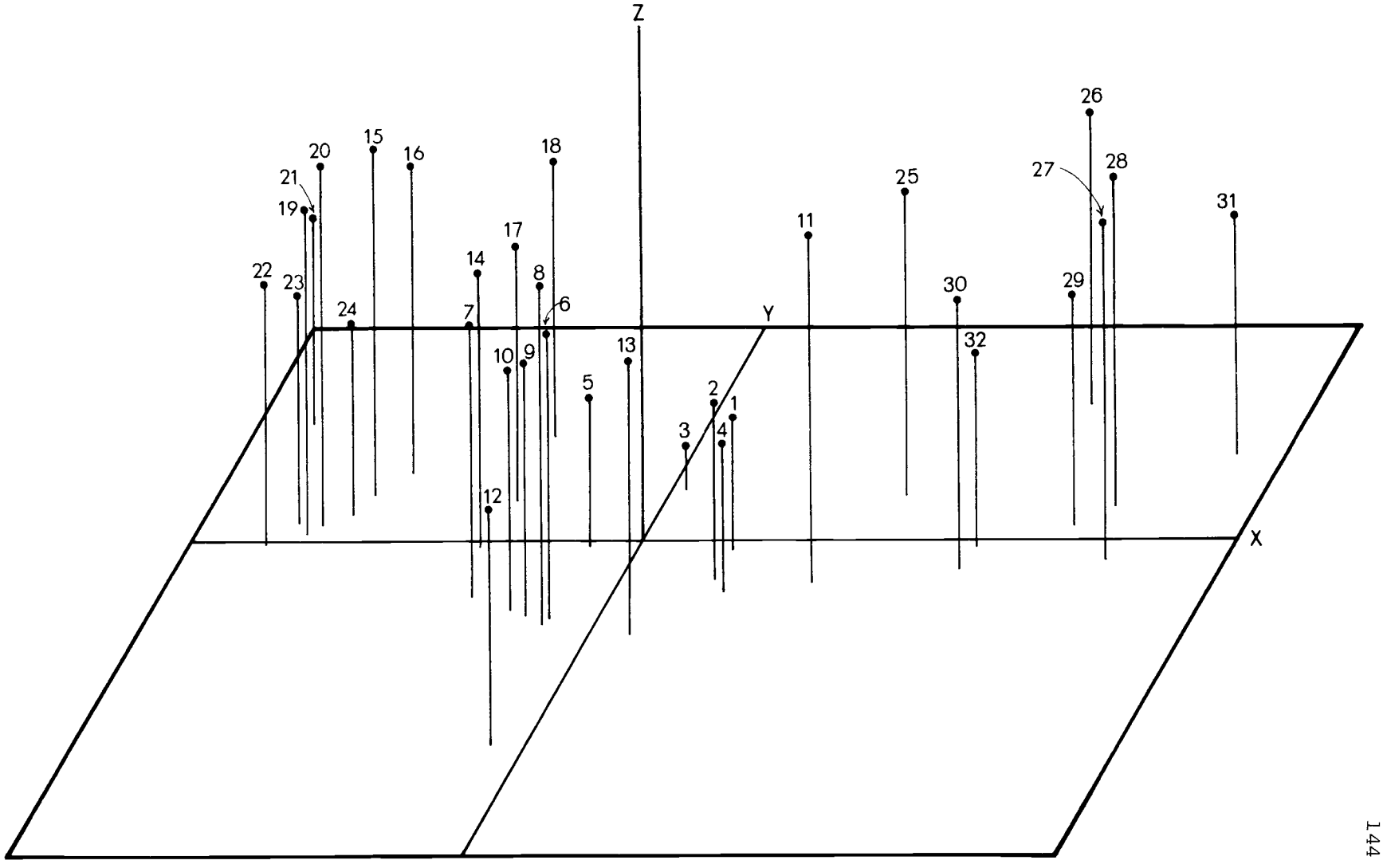
D

Figure 33. Ordination of larval OTU's 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. See text.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32

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

Factor analysis of larval OTU's (Q-technique, 25 by 32 matrix) was done with various criteria for rotation. The results of these analyses are given in Tables 12 and 13, with the criteria for rotation defined in the respective table legends. 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 (Figure 29).

Under the conditions of Table 12, the five OTU's of Stem C all load high on Factor III, thus Factor III defines a Rocky Mountain Group of D. ensatus. The eight OTU's of Stem B all load high on Factor II, which is then a Cascade-Oregon Coast Range Factor. OTU 5C loads second high 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 population on Factor II. Rather, OTU 11 loads high on Factor V. The only other OTU which

Table 12. Rotated factor scores for larval OTU's, based on 25 characters (see text); maximum absolute row values in diagonal; the number of factors rotated was equal to the number of positive eigenvalues; only the highest score for each OTU is listed in most cases, but the numbers in parentheses are the second highest scores; letters correspond to stems in Figure 29.

OTU	Stem	Factor Preserved for Rotation									
		I	II	III	IV	V	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									

Table 13. Rotated factor scores for larval OTU's, based on 25 characters (see text); unities in diagonal; the number of factors preserved for rotation was equal to the number of eigenvalues equal to or greater and than +1; only the highest loading for each OTU is listed in most cases, but numbers in parentheses are second highest scores; letters correspond to stems in Figure 29.

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		

correlates relatively high with Factor V is OTU 25, a D. copei OTU; and it is significant that OTU's 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 OTU's of Stem (Group) D all load high on Factor I, which then 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 County, 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 abberrant morphologically. Notice, however, that OTU's 16 and 17, Siskiyou and Trinity Counties, also have their highest loadings on Factor IV. Siskiyou, Trinity, and Shasta County are geographically close, and hence this relationship might be expected. These three OTU's also form a separate substem of Group A in 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 abberrant member (OTU 18), an artifact of the criteria for rotation, or a combination of these possibilities.

A different picture emerges with the rotation criteria of Table 13. 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 conditions of Table A is now well defined 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 OTU's by the fact that it is the only one with a negative highest loading. It's two highest loadings are, however, on Factors II and IV, the two factors over which the D. copei OTU's (D's) have their highest loadings. Examination of the distribution of the second highest loadings of Stem C OTU's suggests the Rocky Mountain Group of D. ensatus may be broken into three subgroups. The first would be a Central Rocky Mountain Subgroup (OTU's 1 and 2), the second a Northern

Rocky Mountain Subgroup (OTU's 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 Michner's (1958) weighted-pair-group method (WPGM). Nine characters, including the seven predicted $\overline{Y}$'s (Table 8) and the mean numbers of max-premax teeth and vomerine teeth (Table 10), were used in one case, and 19 characters, including 17 mean ratios of Table 7 and the two 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 34. 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 County, California, clusters with the Northern Group in both phenograms. However, other, less easily quantified

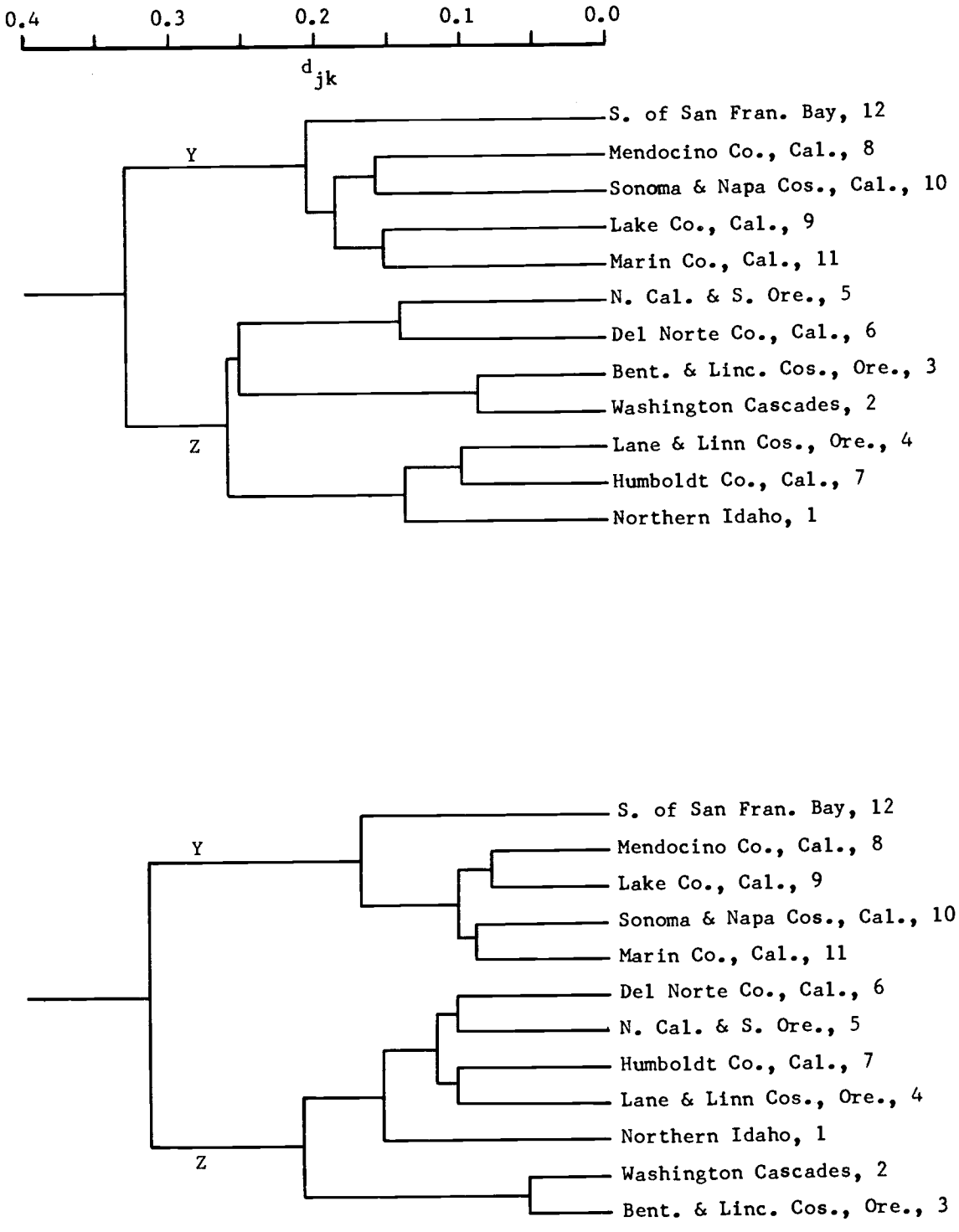

Figure 34. Phenogram of OTU's of transformed D. ensatus, based on WPGM clustering of the d_{jk} matrix. Upper phenogram based on 19 characters and the lower on 9 characters. See text.

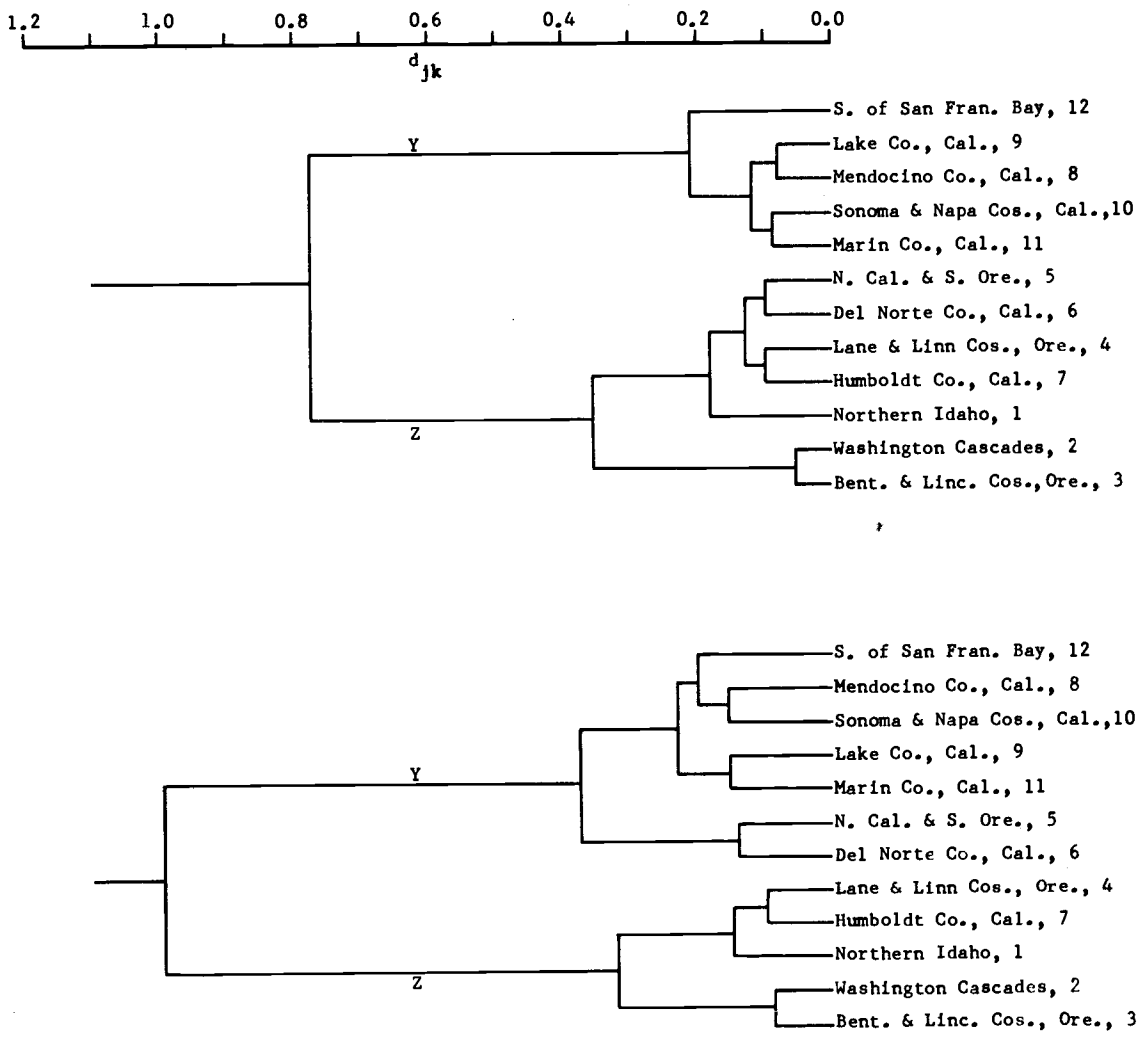

Figure 35. Phenogram of OTU's of transformed D. ensatus, based on HGroup clustering of the d_{jk} matrix. Upper phenogram based on 9 characters, lower on 19 characters. See text.

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 am certain the Humboldt County population would cluster with the Southern Group, although it would remain a somewhat abberrant OTU.

The results of the two HGroup analyses are shown in Figure 35. Again, a Southern Group (Y) and a Northern Group (Z) are evident. It is of interest that in the upper phenogram of Figure 35, the subgroup composed of OTU's 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 OTU's.

DISCUSSION AND CONCLUSIONS

On the Validity of D. copei

The ranges of the two species of Dicamptodon (Figure 1) will suggest to some taxonomists that they are really only subspecies. However, the cross-hatching on the range map indicates an area of complete sympatry, and there is no evidence for intergradation or hybridization. Therefore, unless we allow the ranges of subspecies to overlap, the two forms must be given specific status.

The possibility that the two species of Dicamptodon are morphs of a single, polymorphic species is a more difficult problem to resolve and 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 both slender-bodied, small-headed and compact-bodied, large-headed forms were found within single populations. The parallel between D. copei and larval D. ensatus is obvious. However, as will be shown, the situation described by Powers for A. tigrinum is unique and entirely different from that which attains 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" (my quotes) of these factors. Therefore an array of possible body forms exists, and, indeed some of the extreme forms described and figured by Powers seem almost teratological.

This type of "continuous polymorphism" 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.

Two lines of evidence indicate that the variation found in Dicamptodon is not attributable to polymorphism. First, the known ranges of the two forms are not consonant with the idea of polymorphism. D. copei is found throughout the Olympic Peninsula, where, as yet, D. ensatus is not known to occur; and D. copei is not found over most of the range of D. ensatus. Thus, if the two forms were morphs of a single species, it would be a remarkable case of polymorphism in which the two morphs are largely allopatric with only a narrow zone of overlap. It is difficult to imagine how such a form of polymorphism could be maintained.

Second, the two species of Dicamptodon seem to breed true to type. Nineteen broods of D. copei and 11 broods of D. ensatus have been reared from the egg 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. Furthermore, species characteristics were observable even in the hatchlings, and there was no divergence of body form, within a brood, during development as noted by Powers (1907) for A. tigrinum.

From 1933 until the description of D. copei in 1970, the genus Dicamptodon was considered monotypic, and all museum specimens were labeled as D. ensatus. Specimens of D. copei were available, but because D. copei and larval D. ensatus are not readily distinguishable by cursory examination, D. copei went un-noticed. 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, and now the two species are readily discriminated on the basis of morphology alone.

Geographic Variation

Major Patterns of Variation

As might be 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 more northerly counties of California. Larvae and adults from these southern counties have the largest heads and highest numbers of max-premax and vomerine teeth of all larval and adult Dicamptodon. Larvae lack palatopterygoid teeth, and this is surprising because the populations with the highest percentage of larvae with palatopterygoid teeth occur just north in Mendocino County. Larval OTU's from this area have FLL + HLL/AGL values which are significantly higher than for all other OTU's, except possibly for larvae from Siskiyou County, California (OTU 16). Colorwise, the larvae are white-ventered and not so mottled dorsally as larvae from northern California, especially when compared to larvae from the interior highlands of northern California. The color of adults from these southern counties is distinctive. They have white venters, inherited from the larval form, and a light, reddish-brown, dorsal ground color with coppery-tan marbling. Marbling on the chin is most prominent in

adults from this area.

The distinctness of D. ensatus in these Bay Area populations may partly reflect the uniqueness of the local habitat. The coastal, redwood forest which covers much of this region is the oldest, most stable forest ecosystems 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, call it the "North Coast Divide", and 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 seems to correspond with the break in variation between southern and northern populations of D. ensatus in California, and such a geographic feature might be expected to have a strong influence on gene flow and disperal in a salamander like D. ensatus with stream-dwelling larvae.

The North Coast Divide seems to 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 are closely associated in the same habitats with 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 drainages which are still north of the North Coast Divide. Other

amphibians which are characteristic of the Northwestern Herpetofauna may also be effected 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 partly 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 apparently 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. Adults on the south side have the most extensive chin and throat marbling of all adult D. ensatus; and both larvae and adults from the south side have higher numbers of max-premax and vomerine teeth. But these features represent only an extreme of the condition found just north of

the Bay, and in a sense, represent the tail end of a north-south cline for these characteristics when the entire range of D. ensatus is considered.

Populations of D. ensatus in the more northern counties of California and in extreme southern Curry, Josephine, and Jackson Counties, Oregon seem to form a natural group, at least based on measured characteristics. On a finer scale, color and pattern, especially of larvae, varies considerably within this area. Populations in the humid coastal region of northern California seem to form a subgroup within this northern group, and populations in the drier interior highlands seem to form a second subgroup (see Figure 29). In color, larvae and adults from the humid coastal subgroup appear to be intermediate between larvae and adults from the interior highlands subgroup and larvae and adults from south of the North Coast Divide. Perhaps these circumstances may be explained by the following reasoning. 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 up and down this humid

corridor, and selection pressures along the corridor should not differ greatly because of similarities in climate and substrate. In the northern, interior highlands, a different and unique phenotype, especially in larval coloration, is maintained by strong 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 higher 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 of Figure 29). The Siskiyou-Klamath Region marks the area of most rapid change in overall appearance of both larval and adult D. ensatus. Populations in northern Curry, central Josephine, and southwestern Jackson Counties, Oregon are in an area of most rapid change (for instance, note the positions of larval OTU's 14 and 15 in Figure 3).

The Klamath-Siskiyou Region has had an important influence on distribution and variation in many other northwestern herptiles. The ranges of some species seem to be limited by this major topographic feature. 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 range on both sides of the Klamath-Siskiyou Region 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 are the closely related Del Norte and Siskiyou Mountain salamanders (Plethodon elongatus and Plethodon stormi). Many other plants and animals are similarly effected by the distinctive geographic position and complex ecology of the Klamath-Siskiyou Region (Stebbins and Major, 1965; Remington, 1968; Whittaker, 1961).

With minor, local aberrations, 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. It appears that 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 could also be an important dispersal route between the two mountain ranges.

The Willamette Valley appears to be only a weak barrier for most species of amphibians and reptiles. Only the Oregon slender salamander, Batrachoseps wrighti and the Cascades frog, Rana cascadae appear to be limited to one side of the Willamette Valley (the Cascade side), and the Cascades frog is a high elevation form which

probably could not find suitable habitat in the Coast Range. No form of raciation or major variation appears to be associated with the Willamette Valley.

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 may result from the complex intermingling of the Coast, Siskiyou, and Cascade Mountains in southwestern Oregon; and two major rivers, the Rogue and Umpqua, which head in the Cascades and cross into the Coast Range could provide 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 seems to be hardly a barrier at all, because populations on either side of the Gorge are nearly identical for most characteristics. Storm (1966b) summarized evidence which shows that the Columbia River Gorge has had little effect on the distribution or variation of other northwestern amphibians and reptiles.

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 adults and the fine-grained marbling of the adult. Individuals from these populations also show close relationship in various measurements and counts, as indicated by the larval phenogram (Figure 29). Furthermore, the electrophoretic pattern of blood serum proteins is distinct for Rocky Mountain D. ensatus, at least by comparison to populations which occur in the Cascade Mountains of Washington.

Variation between populations in the Rocky Mountains is slight, but the dorsal color pattern of adults from the Central Rocky Mountains in Valley County, Idaho is even finer grained than the pattern found in adults in 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 gine-grained patterns in the south. Unfortunately it is not yet known whether populations in the Northern Rocky Mountains and in the Central Rocky Mountains of Idaho are truly disjunct. Two

intriguing sight records near the old mining camp of Dixie, Valley Co., suggest that the populations are at least not as widely separated as present range maps show.

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 OTU's (Figures 29 and 31). Adults 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. Adults from the northern Cascades have coarser marbling than adults from Idaho, but in general, not as coarse as the marbling of adults from south of the Klamath-Siskiyou Region.

D. copei shows little variation within its relatively small range. It may be of some significance that the three populations which occur in Oregon (OTU's 27, 28, 29) cluster with each other (Figure 29) before clustering with populations from north of the Columbia River in Washington; but in general, variation between OTU's is slight and appears to be simply a function of geographic distance. For instance, the two most similar populations are OTU's 27 and 28, and they are less than six km apart.

D. copei from the Olympic Mountains seem to be more sensitive to thyroxine than D. copei from other areas. This fact is intriguing in light of the occurrence of a transformed specimen supposedly collected in the Olympic Mountains (USNM 64320). This specimen is the only transformed Dicamptodon I know of from the Olympic Peninsula, and if the locality is not in error, it may be the only know, naturally-transformed D. copei; or it could mean that D. ensatus occurs on the Olympic Peninsula. Unfortunately, the specimen is old and very poorly preserved. However, it appears to have the attenuate characteristics of artificially-transformed D. copei, and I am inclined to believe it is a valid record and represents good evidence that D. copei is capable of natural metamorphosis, at least in the Olympic Mountains. Additional field work on the Olympic Peninsula is needed to resolve this question.

The Effects of Isolation

A population of D. ensatus is isolated at Oak Springs, Wasco Co., Oregon (see Figure 1). The site is in the Upper Sonoran Life-zone, with the typical aspect of northern, cold deserts. The temperature of the spring

is constant at 12.5 C and the volume of flow never fluctuates. The surrounding habitat is totally unfavorable for 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 (o.5 to 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 adults 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.

An 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 fluctuation 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, 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, allows the population to exist.

As noted earlier, larvae from Shoat Spring are similar to D. copei for some characteristics. However, for reasons outlined below, I am convinced the OTU 11 properly belongs to D. ensatus, and that its similarity to D. copei is superficial and is the 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 is somewhat intermediate between D. copei and D. ensatus (e.g., see Figures 3 and 4). OTU 11 has fewer max-premax and vomerine teeth than D. ensatus, and is in the range

of D. copei for these characters. But earlier I showed there is a strong phylogenetic correlation between head size and tooth number, so that the relatively small heads of OTU 11 would account for fewer teeth.

Neoteny at small size is another 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 full adults 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 neoteny are different between the two.

Short, weak limbs, relative to body length, and small heads are characteristic of many aquatic salamanders, as of course is neoteny 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, giving them a triangular, webbed appearance.

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 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. Adults obtained by treating larvae from Shoat Spring with thyroxine have coarse marbling, similar in pattern and hue to adults from the Siskiyou-Trinity-Shasta Region.

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 an aberrant 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 unhampered by gene flow from other populations; and the extreme environmental conditions have produced strong selection pressures which led to the neotenic mode of reproduction and aquatic, morphological adaptations.

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 so.

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 paeloecological 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 Northwest during the Paleocene Epoch. Royse (1965) described the Paleocene, Pipestone flora of northcentral Washington as a warm-temperate phase of the Arcto-Tertiary Geoflora; and fossil redwoods are know 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 is 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^{o} 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 boreal 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, summer-wet forest, dominated by redwoods. Many fossil floras of the period are known from the 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 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 life-zones 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 life-zones 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, which lasted from about 7,000 to 4,000 years B.P. During this period, life-zones 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, summer-wet 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 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 relict 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 primitive features of these southern populations are large heads, high numbers of max-premax and vomerine teeth, and high gill raker counts. Individuals with the extreme expression of these primitive characters are found in the Bay Area, south of the "North Coast Divide", and it is here where the lowest percentage of neotenes are found. The primitive generalized Dicamptodon would not be expected to be highly neotenic; nor would such a specialization be suitable in a stable forest ecosystem, with humid, equable climates, where the terrestrial habitat is highly productive and predictable.

Another primitive feature of populations from the Bay Area is the propensity for adults 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 other naturalists. California specimens can easily be induced to vocalize in captivity, but I have never heard vocalization in adults 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 characteristics 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, neoteny was selected for because of the hostile terrestrial environ-

ment 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 neotenous, 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, Fryxell, Neff, Weis, 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 neotenic habit, evolution toward fixation of neoteny and the associated, attenuate body form proceeded rapidly. The glacial streams and lakes of the region were essentially "aquatic deserts" with limited food resources; and the evolution of small body size would be favored as an energy conserving measure. Limited food sources would also place a selective premium on the neotenic mode of reproduction.

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. 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 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 life-zones. 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" that 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 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, genetically and historically, to northern populations of D. ensatus than to southern populations; and this seems to be the case, both from the standpoint of morphology and life history. The theory also requires that inland D. ensatus show affinity to northern Cascade D. ensatus and this has been abundantly shown.

Taxonomic Conclusions

Arguments could be made for subspecific recognition of some populations of D. ensatus. The Rocky Mountain Group is distinctive, but related to the Cascade and Oregon Coast Group. The populations south of the Klamath-Siskiyou Region are distinctive on one level, but on a finer scale 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 seems to be a function of geographic distance; and therefore no subspecies are recognized.

The genus Dicamptodon as defined by Tihen (1958) consists of two closely related species, D. ensatus and D. copei; and the diagnostic features are given by Nussbaum (1970).

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APPENDICES

APPENDIX A

Larval OTU's (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, summer-dry; 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, summer-dry; 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 (?), summer-dry; 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, summer-wet; 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, summer-dry; 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, summer-dry; precip. 210; FFS 120; primary; RAN 3223, 3243, 3260, 3292-3, 3304, 3309, 3311, 3322, 3439, 3395, 3397, 3402, 3405, 3409, 3410, 3442, 3448, 3458, 3465; n = 20.

8. Oneonta Gorge, Multnomah Co., Oregon; Douglas fir, summer-dry; 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 County, Oregon; Douglas fir, summer-dry; 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, summer-dry; 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, summer-dry; precip. 60; FFS 120; primary; RAN 8082-3, 8089-91, 8127-9, 8134-6, 8138-9, 8142-3, 8145-8, 8150-2, 8154-6; n = 25.

12. Saddle Mountain, Clatsop Co., Oregon; Douglas fir, western hemlock, summer-wet; 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, summer-dry; 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 summer-dry 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 summer-dry; secondary; RAN 4485-7, CAS-SU 7408, WSU 56108, LACM 40795-6; n = 7.

16. Siskiyou Co., California; western half of country; generally summer-dry; secondary; MVZ 18335, 18339, SSCMNH 20, CAS 85424, CAS-SU 2074-5, 2081; N = 7.

17. Trinity Co., California; ponderosa and digger pine, summer-dry; 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, summer-dry; 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, summer-wet; secondary; MVZ 38741, LACM 10674-8, 29418, 29422, CAS-SU 7386-7, 1600; n = 11.

20. Mendocino Co., California; redwood, summer-wet; 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, summer-wet; secondary; MVZ 76723, 76726, LACM 10683, CAS-SU 17946, 17949, 18096; n = 6.

22. Napa Co., California; redwood, summer-wet; secondary; MVZ 36212-3, CAS-SU 7356-8; n = 5.

23. Marin Co., California; redwood, summer-wet, secondary; CAS 44143-4, 63722-7, 93736; n = 9.

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

Larval OTU's (*D. copei*)

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

26. Nine Foot Creek, Skamania Co., Washington; Douglas fir, short summer-dry 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 summer-dry periods; precip. 240; FFS 220; primary; RAN 6114-5, 6117-9; n = 5.

32. Merriman Creek, Grays Harbor Co., Washington; Douglas fir, western hemlock, summer-wet; precip. 280; FFS 300; primary; RAN 4082, 4084, 4098, 4101, 4103-4, 4111-4, 4116, 4118-21; n = 15.

Adult OTU's (D. ensatus)

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

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

3. Benton and Lincoln Cos., 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 Cos., 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 Cos., Cal. and parts of southern Josephine and Jackson Cos., 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 Cos., 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, 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.

Appendix B Localities for populations of D. copei by OTU number (see Appendix A).