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Author(s): Edmund D. Brodie, Jr.

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Department of Zoology and Entomology, Auburn University,
Auburn, Alabama 36830

WESTERN SALAMANDERS OF THE GENUS *PLETHODON*:
SYSTEMATICS AND GEOGRAPHIC VARIATION

EDMUND D. BRODIE, JR.

ABSTRACT: Western salamanders of the genus *Plethodon* constitute three species groups: Vandykei group (*vandykei*, *larselli*), Vehiculum group (*vehiculum*, *dunni*, *gordoni* sp. nov.), and Elongatus group (*elongatus*, *stormi*). *P. gordoni* is described as closely related to *dunni*, and subspecies of *vandykei* are not recognized due to the discordant nature of geographic variation. Each species is described in detail and a key to the species is provided. A dendrogram of proposed evolutionary relationships is presented; *P. vandykei* is considered the most primitive and *elongatus* is considered the most specialized.

Character displacement is exhibited by sympatric *dunni* and *gordoni*. Character convergence occurs for *dunni* where it is sympatric with *larselli* and *elongatus*. Geographic variation in costal groove number, tooth numbers, limb length, pigment characters, and head shape was examined in each species. The number of maxillary plus premaxillary teeth was shown to be valuable in determining phylogenetic relationships. Significant geographic variation is present in *vandykei*, *larselli*, *vehiculum*, *dunni*, and *elongatus* but subspecific designations are not justified.

SALAMANDERS of the genus *Plethodon* Tschudi have been divided into three groups: eastern small plethodons, eastern large plethodons, and western plethodons (Grobman, 1944; Highton, 1962). Wake (1966) did not separate large and small eastern species but recognized their distinctness from western members of the genus. Highton examined interspecific variation in number of costal grooves and vomerine teeth but did not study geographic variation.

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Since Highton's revision, *P. stormi* Highton and Brame (1965) has been described, and a salamander which has previously been considered to be a melanistic *dunni* (Stebbins, 1951) is herein described as *P. gordonii*.

The western *Plethodon* can be placed into three species groups: Vandykei group (*vandykei*, *larselli*), Vehiculum group (*vehiculum*, *dunni*, *gordonii* sp. nov.), and Elongatus group (*elongatus*, *stormi*). Species groups indicate evolutionary relationships but are not meant to be recognized taxonomic units (Highton, 1962).

Stebbins (1951, 1954, 1966) discussed pigmentation, life history, and habitat of the western *Plethodon*. Brodie (1968) described mental glands and their value as a taxonomic character for this group. Numerous short papers presented range notations.

Most western *Plethodon* are restricted to the western parts of California, Oregon, Washington, and British Columbia, including Vancouver Island. One form is found in the Rocky Mountains of Idaho and western Montana. *Plethodon neomexicanus* is found in the Rocky Mountains of New Mexico and was considered by Highton (1962) to be an eastern small *Plethodon*. Thurow (1968) stated that *neomexicanus* is more closely related to *elongatus* than to the eastern *Plethodon*. *P. neomexicanus* is not considered in this study of the western *Plethodon*, but its relationship needs further investigation.

The type descriptions of the western *Plethodon* were based on small series (1-21 specimens) and were often superficial. No information is available on geographic variation, and evolutionary relationships are not well understood. The purpose of this study is to analyze intra- and interspecific variation within the western *Plethodon*.

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The following museums and individuals were kind enough to loan me specimens.

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ANSP, Academy of Natural Sciences of Philadelphia, J. E. Böhlke.
CA, Chicago Academy of Sciences, G. Iannarone.
CAS, California Academy of Sciences, A. E. Leviton.
CAS-SU, California Academy of Sciences: Stanford University
Collection, A. E. Leviton.
CWSC, Central Washington State College, P. Dumas.
EKT, E. K. Teberg.
FMNH, Field Museum of Natural History, H. Marx.
ISU, Idaho State University, A. D. Linder.
JLB, J. L. Briggs.
LACM, Los Angeles County Museum of Natural History, J. W.
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MCZ, Museum of Comparative Zoology, Harvard University,
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MVZ, Museum of Vertebrate Zoology, University of California,
Berkeley, R. C. Stebbins and R. B. Bury.
NMC, National Museum of Canada, F. R. Cook.
OSU, Oregon State University, R. M. Storm.
PLU, Pacific Lutheran University, J. W. Knudsen.
PM, Provincial Museum, Victoria, B. C., C. Carl.
PSU, Portland State University, R. Forbes.
RAN, R. A. Nussbaum.
SOC, Southern Oregon College, Dr. Sullivan.
SSC, Sacramento State College, R. L. Livezey.
UBC, University of British Columbia, I. McT. Cowan.
UI, University of Idaho, R. Wallace.
UMMZ, University of Michigan Museum of Zoology, C. F.
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UPS, University of Puget Sound, G. D. Alcorn.
USNM, United States National Museum, J. A. Peters.
WSU, Conner Museum, Washington State University, G. E.
Hudson.

Most of the specimens collected specifically for this study have been retained for further study (referred to as EDB) and will eventually be deposited in permanent museum collections.

MATERIALS AND METHODS

During this study 3518 specimens (Appendix I) were examined and analyzed; 1200 of these were seen alive and preserved by me. Several hundred other specimens were examined but not analyzed. Each species was divided according to geographic areas (= groups in Table 1). All existing holotypes except that of *elongatus* were examined.

TABLE 1.—Geographic groups of western *Plethodon*.

Species	Group	N	Locality
<i>Vehiculum</i>	1	105	Vancouver Island, B. C.
	2	55	British Columbia, mainland
	3	163	Western Olympic Peninsula, Wash.
	4	99	Eastern Olympic Peninsula, Wash.
	5	56	Willapa Hills, Wash.
	6	132	Washington Cascades
	7	48	Skamania Co., Wash.
	8	49	Clatsop & Columbia cos., Ore.
	9	76	Portland, Ore.
	10	54	Tillamook Co., Ore.
	11	153	Lincoln Co., Ore.
	12	153	Benton Co., Ore.
	13	49	Lane Co., Ore. (Coastal)
	14	22	Oregon Cascades
	15	55	Douglas Co., Ore. (Coastal)
	16	23	Coos Co., Ore.
<i>Dunni</i>	18	10	Washington
	19	69	Clatsop & Columbia cos., Ore.
	20	59	Portland, Ore.
	21	171	Multnomah & Hood River cos., Ore.
	22	59	Marion & Linn cos., Ore.
	23	48	Tillamook Co., Ore.
	24	42	Lincoln Co., Ore.
	25	90	Benton Co., Ore.
	26	58	Lane Co., Ore. (Cascades)
	27	56	Lane Co., Ore. (Coastal)
	28	51	Douglas Co., Ore. (Cascades)
	29	61	Douglas Co., Ore. (Coastal)
	30	22	Coos Co., Ore.
	31	112	Curry Co., Ore.
<i>Gordoni</i>	47	78	Benton Co., Ore.
<i>Elongatus</i>	32	185	Coos & Curry cos., Ore.
	33	35	Josephine Co., Ore.
	34	269	Del Norte Co., Calif.
	35	127	Humboldt (Inland) & Trinity cos., Calif.
	36	24	Humboldt Co., (Coastal)
<i>Stormi</i>	41	9	Paratypes
	42	130	Hutton G.S., Siskiyou Co., Calif.
	43	8	Western Jackson Co., Ore.
<i>Vandykei</i>	37	82	Olympic Peninsula, Wash.
	38	89	Willapa Hills, Wash.
	39	28	Washington Cascades
	40	154	Kootenai Co., Idaho
<i>Larselli</i>	44	58	Archer Falls, Skamania Co., Wash.
	45	15	Stevenson, Skamania Co., Wash.
	46	67	Oregon

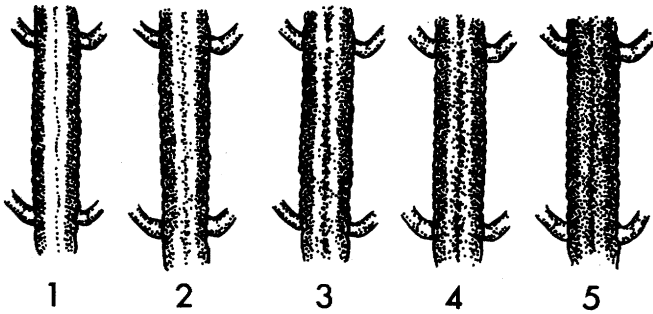
The following measurements and counts were made on preserved animals:

1. Snout-vent length (SVL), from the snout to the posterior margin of the vent.
2. Tail length (TL), from the posterior margin of the vent to the tip of the tail. Only specimens with complete, unre-generated tails were used.
3. Head width (HW), at the angle of the jaw.
4. Head length (HL), from the snout to the gular fold.
5. Stripe width (SW), at the widest point on the trunk.
6. Costal grooves were counted according to Highton (1957) who demonstrated that costal grooves total one less than the number of trunk vertebrae in 94% of the salamanders of the genus *Plethodon* he counted.
7. Costal folds between adpressed limbs were counted only on specimens freshly preserved in a uniform manner by me (fixed in 10% formalin for 24-48 hr, washed in water, stored in 30-35% isopropyl alcohol). This measurement made on uniformly preserved specimens has been shown to be valuable for demonstrating differences in leg length (Highton and Brame, 1965).
8. Total number of ankylosed vomerine teeth were counted. If one or both series were absent the specimen was not used in the calculations.
9. Maxillary plus premaxillary teeth were considered as one series; only ankylosed teeth were counted.
10. The degree of melanophore pigmentation within the dorsal stripe (black-in-stripe) was estimated on a one to five scale. Due to the nature of melanophore encroachment onto the stripe, it was necessary to use different scales for *dunni* and *vehiculum* (Fig. 1). The *vehiculum* scale was used for *larselli*. Melanophore increase is uniform in *elongatus* and *stormi* and could not be analyzed by this method.
11. Sex was determined by examination of the vent lining or internal examination. The vent of males is papillate and unpigmented; the vent of females is rugose and pigmented.

Measurements affected by injuries or abnormalities were excluded from calculations. Only costal grooves and teeth were counted on poorly preserved or desiccated specimens. Characters 1 through 5 were measured with Helios dial calipers, 1 and 2 to the nearest 1 mm and 3-5 to the nearest 0.1 mm.

Numbers of vomerine teeth and costal grooves were analyzed for each geographic group. Regression lines were fitted by the method of least squares for vomerine teeth vs. snout-vent length.

VEHICULUM



DUNNI

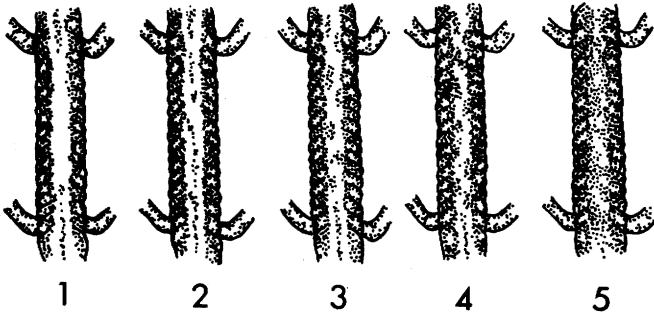


FIG. 1.—Standards used to analyze melanophore pigmentation within the dorsal stripe (black-in-stripe).

Means (\bar{x}), standard deviations (SD), standard errors (SE), and relative frequencies with 95% confidence intervals (normal approximation formula) were determined for costal grooves and black-in-stripe.

The following calculations were made on “large groups” ($N = 90+$) and “species” (all specimens of a species). Head width, head length, and stripe width were fitted by the method of least squares to snout-vent length; head width was regressed on head length. Vomerine teeth, maxillary-premaxillary teeth, HW, HL, HL/HW, SVL/TL, and black-in-stripe were separated into the following snout-vent length (mm) subgroups: 15–19, 20–24, 25–29, 30–34, 35–39, 40–44, 45–49, 50–59, 60–64, 65–69, 70+. All characters except black-in-stripe were also analyzed by sex; for each subgroup, \bar{x} , SD, and SE were determined. Unless otherwise stated, “significant differences” are at the 95% confidence level.

TABLE 2.—Geographic variation in number of costal grooves in the western *Plethodon*.

Species	Group	N	\bar{x}	SE	SD	Relative frequency and 95% confidence interval													
						13±	14±	15±	16±	17±	18±	19±	20±						
<i>Vehiculum</i>	1	99	16.172	.045	.453			.030 .033	.768 .082	.202 .078									
	2	51	15.921	.047	.337			.098 .080	.882 .080	.096 .080									
	3	147	16.150	.035	.428			.027 .025	.796 .064	.177 .063									
	4	88	16.011	.025	.239			.023 .031	.943 .049	.034 .037									
	5	56	16.393	.066	.493				.607 .127	.393 .137									
	6	123	15.984	.035	.384				.854 .063	.065 .043									
	7	47	16.085	.059	.408				.043 .049	.850 .108	.128 .094								
	8	48	16.187	.064	.445				.021 .041	.771 .119	.208 .116								
	9	65	16.081	.043	.348				.031 .041	.877 .078	.092 .067								
	10	53	16.284	.072	.524				.019 .037	.717 .121	.245 .116								
	11	140	16.136	.032	.383				.014 .020	.836 .061	.150 .059								
	12	148	16.027	.027	.329				.041 .031	.892 .049	.067 .041								
	13	49	15.490	.072	.505			.095 .125	.510 .130	.480 .139									
	14	55	15.200	.066	.487			.036 .049	.727 .118	.333 .200									
	15	52	15.855	.103	.486				.136 .143	.773 .174	.091 .120								
	16	17	15.990	.030	.340				1.000 0										
	17	66	14.939	.029	.321			.061 .055	.939 .055										
	18	59	14.949	.029	.321			.051 .057	.949 .057	.129 .049									
19	71	15.129	.026	.336				.871 .049	.949 .057	.051 .057									
20	59	15.051	.029	.321			.023 .043	.977 .043	.125 .102										
21	44	14.977	.023	.351				.875 .102	.125 .102	.012 .023									
22	40	15.125	.053	.335				.476 .108	.512 .108										
23	82	15.537	.058	.526				.891 .082	.091 .076										
24	55	15.073	.044	.325			.018 .035	.750 .114	.250 .114										
25	55	15.073	.044	.325				.823 .104	.157 .100										
26	56	15.250	.058	.437			.020 .039	.879 .084	.103 .078										
27	51	15.137	.056	.401			.017 .033	.181 .161	.181 .161										
28	58	15.086	.045	.339			.009 .017	.889 .059	.102 .055										
29	22	15.182	.084	.395				.645 .108	.355 .108	.028 .023									
30	108	15.093	.031	.322						.803 .057									
31	47	15.355	.055	.482						.857 .116									
32	183	18.147	.032	.439						.782 .049									
33	35	18.143	.060	.355						.008 .016									
34	260	18.038	.030	.479						.877 .059									
35	122	18.107	.030	.355						.708 .182									
36	24	18.292	.095	.464						.222 .272									
37	41	17.778	.147	.441						.778 .272									
38	118	17.186	.038	.412						.195 .071									
39	8	17.125	.125	.353						.875 .229									
40	75	14.400	.065	.569						.164 .053									
41	88	14.034	.038	.354						.857 .116									
42	28	14.036	.036	.188						.143 .116									
43	39	14.048	.022	.270						.123 .039									
44	147	14.048	.022	.270						.004 .008									
45	58	15.000	.043	.324						.115 .057									
46	15	15.133	.165	.640						.292 .182									
47	67	15.045	.054	.441						.052 .057									
48	67	15.045	.054	.441						.267 .223									
49	67	15.045	.054	.441						.119 .078									

Locality maps of examined specimens were prepared for each species. Specimens were examined from all regions of the known range of each species. The type locality of each species is designated by a triangle.

RESULTS

Costal Grooves.—The number of costal grooves varied inter-specifically and geographically (Table 2). Salamanders of each geographic group usually varied by only three grooves; the median was usually the mode (M). Usually sympatric populations have different modal numbers of costal grooves; exceptions are *vehiculum* and *dunni* (M = 16) in Benton County, Oregon and (M = 15) in Lane and Douglas counties, Oregon. In their zone of sympatry *larselli* and *dunni* both have a mode of 15 costal grooves. In decreasing order of number of costal grooves the species groups can be arranged as follows: *Elongatus*, *Vehiculum*, *Vandykei*. Intra-specific variation is discussed under each species.

Vomerine Teeth.—Highton (1962) suggested that the relationship of a regression of vomerine teeth on snout-vent length is linear for most *Plethodon* and that the regressions are useful in making speculations on phylogenetic relationships (Table 3).

Members of the *Vandykei* group have steep slopes, indicating a rapid increase in vomerine teeth with body size. Members of the *Vehiculum* group have flatter slopes, and members of the *Elongatus* group have slopes which do not vary significantly from zero, indicating little or no increase in tooth number with body size.

The relationship of vomerine tooth number to snout-vent length is not linear in some species. Separate regressions of juvenile and adult *vandykei* from the Willapa Hills show a rapid increase in tooth number in juveniles and no significant increase in tooth number after maturity (Fig. 2). Therefore the mean number of teeth in adults is a better indication of geographic variation. The regression for all individuals is still valuable for analysis of interspecific and evolutionary relationships.

There was no significant sexual dimorphism in this character. Intraspecific variation is discussed for each species.

Maxillary-Premaxillary Teeth.—The number of maxillary-premaxillary teeth increases with body size in juveniles, and males have significantly fewer teeth than females (Figs. 3, 4, 5). Wake (1966, p. 37) observed that premaxillary teeth of the more "primitive genera" of the *Plethodontidae* are only slightly modified and that "sexual dimorphism is more pronounced in advanced than in primitive genera." He further states in regard to species groups of *Aneides* that "reduction in maxillary dentition is a specialization encountered in highly specialized and advanced groups" (Wake,

TABLE 3.—Geographic variation in slope, Y-intercept, and correlation coefficient for number of vomerine teeth vs. snout-vent length in western *Plethodon*.

Species	Group	N	Slope	SE of slope	Y-int.	SE of Y-int.	Corr. Coef.
<i>Vehiculum</i>	1	105	.124	.016	2.952	.730	.610
	2	54	.142	.029	3.005	1.221	.565
	3	159	.127	.016	2.747	.684	.524
	4	96	.090	.021	3.757	.836	.405
	5	54	.120	.022	3.623	.975	.595
	6	131	.131	.017	3.651	.688	.558
	7	48	.127	.032	3.486	1.373	.511
	8	47	.085	.016	4.922	.633	.610
	9	75	.144	.016	3.182	.609	.722
	10	53	.115	.025	4.737	1.055	.541
	11	152	.102	.019	5.922	.769	.406
	12	149	.074	.018	5.905	.737	.324
	13	49	.090	.031	6.093	1.263	.389
	14	22	.159	.047	3.209	1.667	.604
	15	55	.122	.059	5.396	2.579	.274
	16	22	.003	.048	10.323	1.900	.015
<i>Dunni</i>	18	10	.116	.049	8.696	2.245	.643
	19	69	.165	.013	5.039	.425	.832
	20	58	.216	.028	5.459	.961	.721
	21	167	.151	.019	7.723	1.056	.496
	22	59	.133	.026	7.260	1.293	.561
	23	47	.215	.020	3.827	.899	.844
	24	41	.220	.043	5.512	1.750	.632
	25	90	.113	.016	7.011	.837	.601
	26	58	.189	.025	4.483	1.085	.717
	27	56	.124	.021	6.795	1.098	.629
	28	50	.175	.016	6.310	.771	.839
	29	59	.113	.022	6.636	1.147	.559
	30	22	.110	.039	5.629	1.953	.533
	31	112	.086	.013	6.726	.652	.516
<i>Gordoni</i>	47	78	.180	.019	4.040	.815	.741
<i>Elongatus</i>	32	185	.054	.010	7.166	.515	.355
	33	35	-.023	.022	11.916	1.116	-.176
	34	265	.038	.011	8.913	.512	.215
	35	126	.031	.017	9.150	.804	.160
	36	24	-.059	.041	14.195	2.151	-.293
<i>Stormi</i>	41	9	.074	.060	6.186	1.814	.426
	42	130	.035	.018	10.640	.839	.173
	43	8	.095	.060	4.863	2.777	.542
<i>Vandykei</i>	37	79	.358	.040	3.002	1.451	.716
	38	87	.278	—	5.55	—	—
	39	26	.212	.033	4.407	1.603	.791
	40	150	.252	.029	6.813	1.091	.585
<i>Larselli</i>	44	58	.332	.056	-2.080	2.307	.621
	45	15	.441	.081	-1.052	3.195	.833
	46	67	.333	.046	1.053	2.004	.671

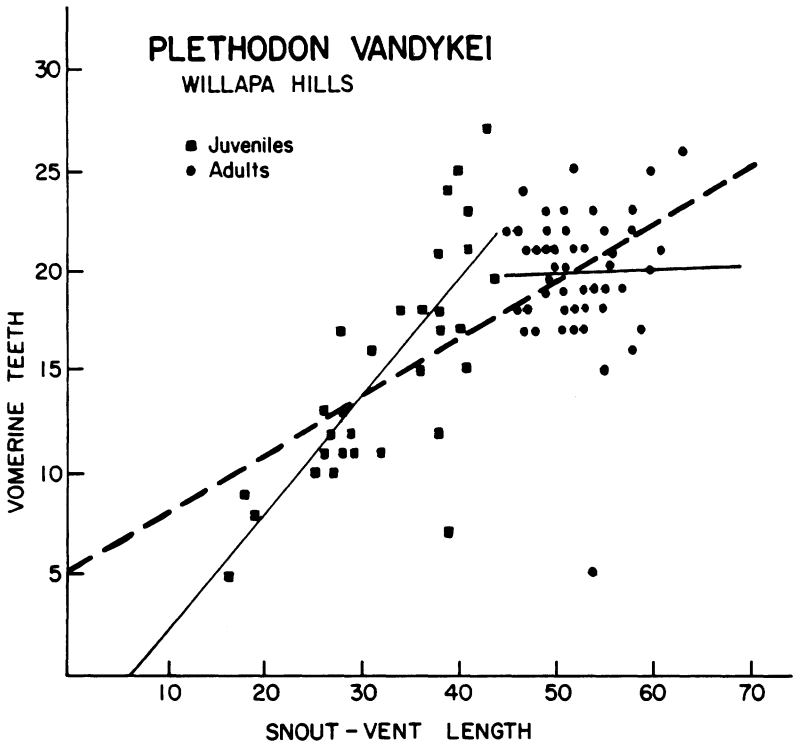


FIG. 2.—Relationship between number of vomerine teeth and snout-vent length in juvenile and adult *Plethodon vandykei*. Broken line is the regression for all specimens.

1966, p. 37). I suggest that these trends also hold true in the western *Plethodon*, i.e., primitive species have less sexual dimorphism and a higher number of maxillary-premaxillary teeth.

Each species of western *Plethodon* has a different mean number of teeth, although the ranges often overlap, and closely related species are similar. The ancestral condition would probably show a uniform increase; any reduction would indicate specialization. This condition is most closely approximated by members of the Vandykei group (*vandykei*, *larselli*). Male and female *elongatus* and *stormi* show a reduction in number of maxillary-premaxillary teeth as adults, which suggest that the *Elongatus* group is the most specialized in this character. Members of the *Vehiculum* group are intermediate. Changes in tooth number are probably more important than total number of teeth in indicating phylogenetic relationships since the changes are not necessarily dependent upon maximum body size.

Head Width and Head Length.—The relationship of head length

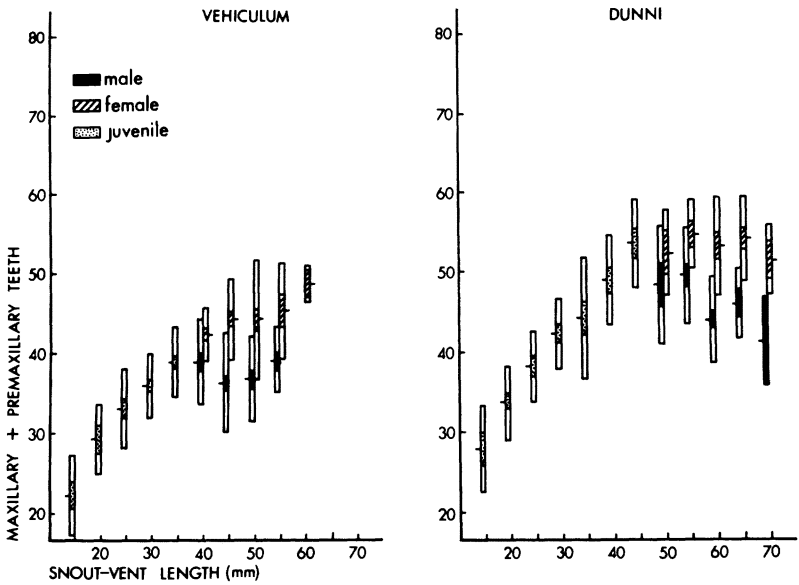


FIG. 3.—Interspecific variation in number of maxillary-premaxillary teeth in *Plethodon vehiculum* and *P. dunni*. Symbols: horizontal line = mean; solid bar = 2 SE \pm mean; open bar = 1 SD \pm mean.

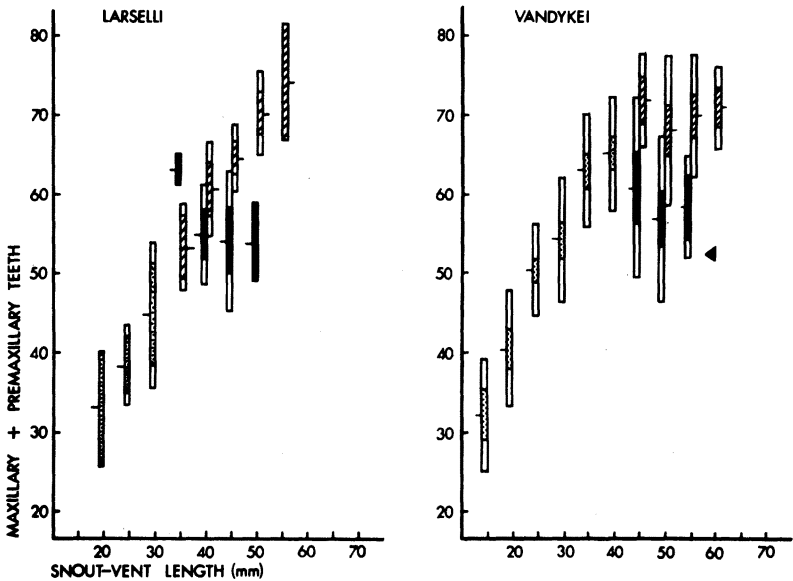


FIG. 4.—Interspecific variation in number of maxillary-premaxillary teeth in *Plethodon larselli* and *P. vandykei*. See Fig. 3 for legend.

TABLE 4.—Body proportions of a 60 mm SVL western *Plethodon* as calculated from regressions.

Species	Head width	Head length	Stripe width
<i>Vandykei</i>	8.7	12.9	4.6
<i>Larselli</i>	8.2	13.2	4.1
<i>Vehiculum</i>	7.4	12.3	4.3
<i>Dunni</i>	8.3	12.9	4.5
<i>Gordoni</i>	8.2	13.0	—
<i>Elongatus</i>	7.5	12.5	3.9
<i>Stormi</i>	8.4	13.6	3.7

or head width to snout-vent length is distinctive in only a few cases, but the relationship of head width to head length illustrates marked interspecific differences (Fig. 6). Within each species group there are members with short, wide heads and others with long, narrow heads. Steep slopes indicate short, wide heads.

In the Vandykei group, *vandykei* has a wide head and *larselli* has a narrow head. The Vehiculum group includes the wide-headed *dunni* and the narrow-headed *vehiculum* and *gordoni*. The Elongatus group includes the wide-headed *stormi* and the narrow-headed *elongatus*. The slope of head width on head length is the same for the narrow-headed forms and for the wide-headed forms. Only *dunni* has significant sexual dimorphism; males have longer, wider heads than females. Analysis of geographic groups by means for size classes indicates geographic variation in both head width and head length for *dunni* and *elongatus*. Table 4 compares body proportions on 60 mm SVL specimens as calculated from regressions.

Costal Folds Between Adpressed Limbs.—Few costal folds between adpressed limbs indicate long legs relative to body length. In decreasing order of leg length, the species groups can be arranged as follows: Vandykei, Vehiculum, Elongatus. Fig. 7 illustrates differences in leg length for *dunni* vs. *vehiculum* and *elongatus* vs. *stormi*. Relative length decreases with increased body size.

Tail Length.—Tail length was examined as a function of snout-vent length (SVL/TL); a small ratio indicates a relatively long tail. Tail length increases faster than snout-vent length in all species, and male *vehiculum*, *dunni*, and *gordoni* have longer tails than females. Fig. 8 illustrates sexual dimorphism for *vehiculum* and lack of sexual dimorphism for *elongatus*.

Plethodon larselli and *vandykei* have the shortest tails, followed by *vehiculum* and finally by *dunni*, *gordoni*, *elongatus*, and *stormi* which have tails of about the same length.

Stripe Width.—Dorsal stripe width of members of the Vandykei group is quite variable (Fig. 6), while other species have relatively

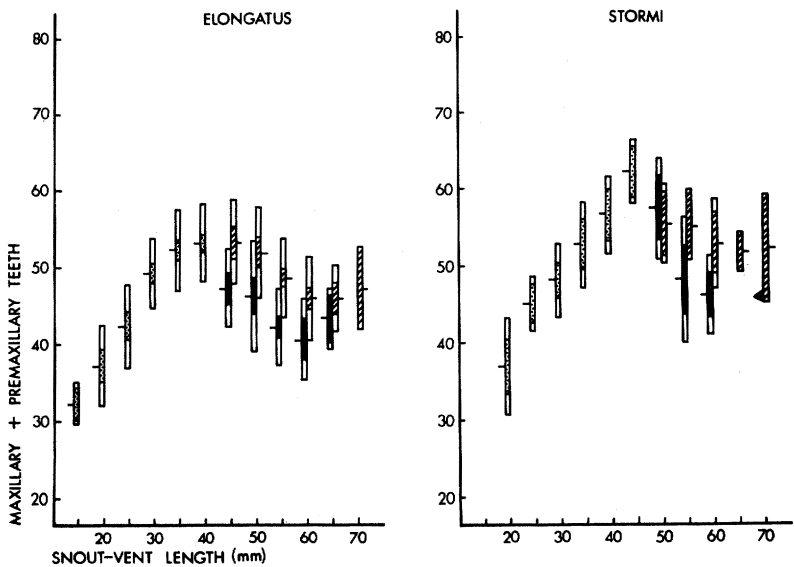


FIG. 5.—Interspecific variation in number of maxillary-premaxillary teeth in *Plethodon elongatus* and *P. stormi*. See Fig. 3 for legend.

consistent stripes. Members of the Vehiculum group have wider stripes than those of the Elongatus group (Table 4).

Black-in-Stripe.—Black-in-stripe (see Fig. 1) varies geographically (Table 5) and ontogenetically (Table 6), but intrapopulational variation rules out the diagnostic use of this character in most cases.

Black-in-stripe increases with size in all western *Plethodon* except *vandykei*. *P. elongatus* and *stormi* have an even network of melanophores that increases in density with age.

VANDYKEI GROUP

The Vandykei group (*vandykei*, *larselli*) possesses parotoid glands and short, slightly webbed toes. Members of this group have fewer costal grooves and vertebrae, more vomerine and maxillary-premaxillary teeth, wider heads, relatively longer legs, and shorter tails than other western *Plethodon*.

It could be argued that *larselli* should constitute a separate species group because adult male *larselli* lack mental glands which are found in all other western *Plethodon*. I prefer to leave *larselli* in the Vandykei species group to indicate its close relationship to *vandykei*. This relationship is especially apparent from high tooth counts, long legs and certain pigment characters, such as sparse melanic pigmentation on the venter; *P. larselli* has a reduced parotoid gland.

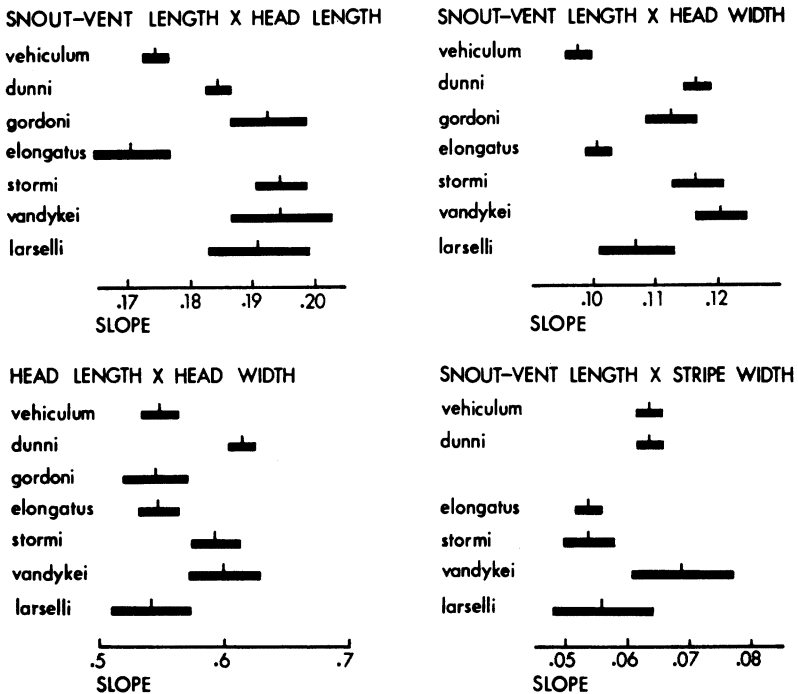


FIG. 6.—Interspecific variation in head width, head length, and stripe width vs. snout-vent length and head length vs. head width in the western *Plethodon*. Symbols: vertical line = slope; bar = $2 SE \pm$ mean.

Plethodon vandykei Van Denburgh
Washington Salamander

Plethodon vandykei Van Denburgh, 1906:61.

Plethodon idahoensis Slater and Slipp, 1940:38. Holotype, (USNM 110504) adult male, collected at the northeast corner of Coeur d'Alene Lake, Kootenai County, Idaho (elev. ca. 2160 ft) by James R. Slater, 13 September 1939.

Plethodon vandykei vandykei: Lowe, 1950:93.

Plethodon vandykei idahoensis: Lowe, 1950:93.

Holotype.—CAS 6910 collected at Paradise Valley, Mt. Rainier National Park, Washington, by Dr. E. C. Van Dyke, 15–31 July 1905; destroyed by the 1906 San Francisco fire. A neotype (CAS 47495) was designated by Slevin and Leviton (1956:535) but should not be recognized (Highton, 1962).

Diagnosis.—*Plethodon vandykei* can be distinguished by: a modal number of 14 costal grooves, distinct parotoid glands, an irregular dorsal stripe, two phalanges in the fifth toe of the hind foot, and a mental gland in males.

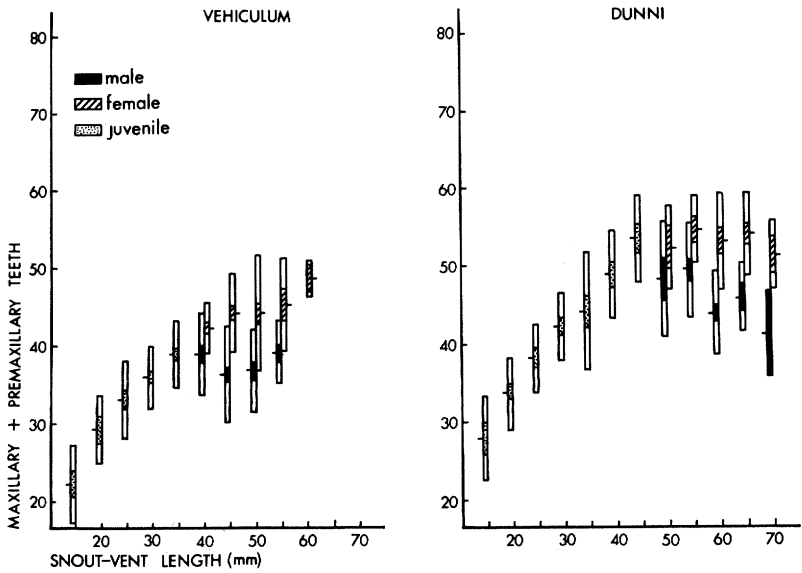


FIG. 3.—Interspecific variation in number of maxillary-premaxillary teeth in *Plethodon vehiculum* and *P. dunni*. Symbols: horizontal line = mean; solid bar = $2 SE \pm$ mean; open bar = $1 SD \pm$ mean.

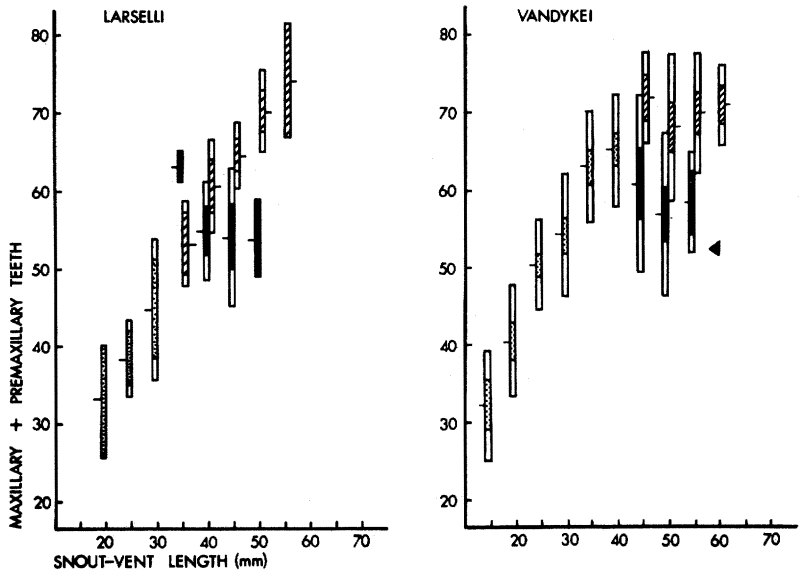


FIG. 4.—Interspecific variation in number of maxillary-premaxillary teeth in *Plethodon larselli* and *P. vandykei*. See Fig. 3 for legend.

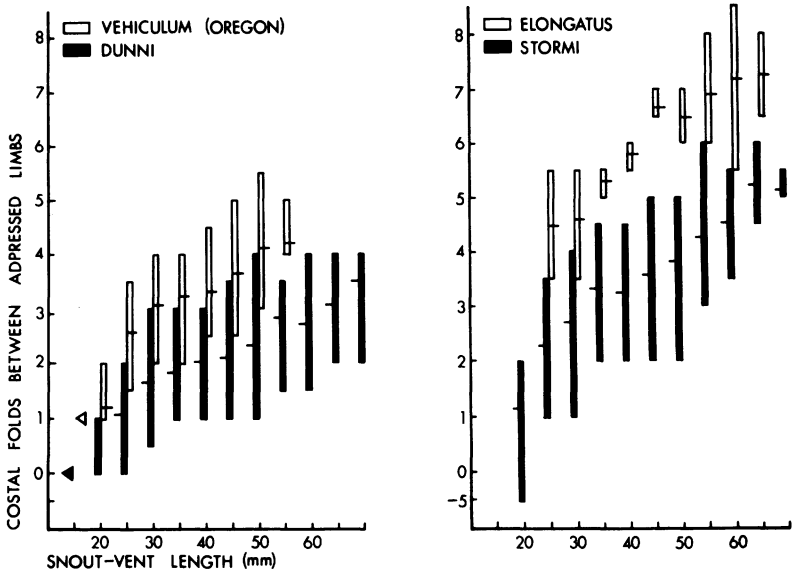


FIG. 7.—Interspecific variation in costal folds between addressed limbs (limb length) in *Plethodon vehiculum*, *P. dunni*, *P. elongatus*, and *P. stormi*. Symbols: horizontal line = mean; bar = range.

specimen from Skamania County, Washington (Slater, 1964) is apparently lost and collection data were incomplete, thus this record is questionable.

Savage (1952) discussed the possibility of *vandykei* having a continuous range along the Canadian border. Due to the relatively low rainfall in this area as compared to the known range of *vandykei*, I think it is unlikely that the range is continuous at present.

This is the most aquatic *Plethodon*. It is usually found in seepages and under rocks along streams in moist coniferous forests. Several times I have seen *vandykei* enter fast-moving water and escape upstream when uncovered. It is sometimes found under objects away from water but in moist conditions. Where sympatric with *vehiculum*, it is found in moist habitats; in Idaho where it is the only plethodontid salamander, it occupies a wider range of conditions from stream-sides to talus slopes and leaf litter.

Description.—Three color phases are present: light-phase, rose-phase and dark-phase. The dark phase is characterized by a black or dark brown dorsal ground color and a black venter usually interrupted by a light gular patch. The gular patch is due to an absence of melanophores and may be reduced to flecking. A transverse row of light-colored blotches occurs posterior to the gular fold. The dorsal stripe may be yellow, green, orange or red and is usually

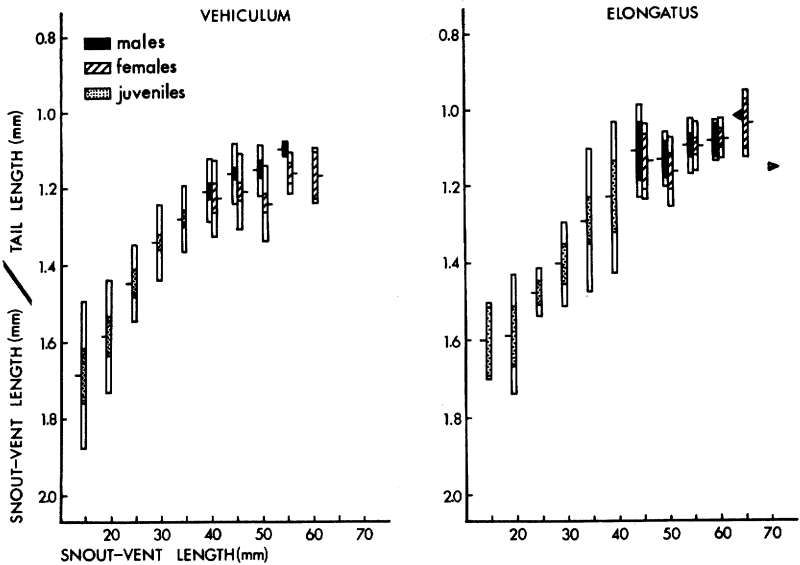


FIG. 8.—Sexual dimorphism in tail length in *Plethodon vehiculum* and *P. elongatus*. Symbols: horizontal line = mean of SVL/TL; filled bar = 2 SE \pm mean; open bar = 1 SD \pm mean.

partially obscured on the head by melanophores. The stripe has an irregular edge that becomes more regular, but seldom straight, in adults. The snout pigment is similar to the stripe and is not obscured by melanophores.

Light-phase specimens have a tan or yellowish ground color which is often indistinguishable from the dorsal stripe; the ground color in juveniles is usually light brown. The venter of light-phase individuals is yellow, without markings, and the snout is lighter than the rest of the dorsum.

Rose-phase specimens, except for red instead of yellow stripes, ground color, and venters, are similar to light-phase animals. I examined a single orange specimen intermediate in color between the light and the rose phases. The light, uniform color of light-phase and rose-phase animals is due to a reduction in melanophores. The light and rose phases are thus probably derived from the dark phase. Apparently this is a case where reduced melanism has become the normal condition.

Large white iridophore flecks and small gold iridophore flecks are usually present in dark specimens; sometimes only white flecks are present. Flecking is heaviest along the side of the body and neck and on the dorsal surfaces of the limbs. Sparse flecking is present on the head and venter. The iris of the eye is heavily flecked

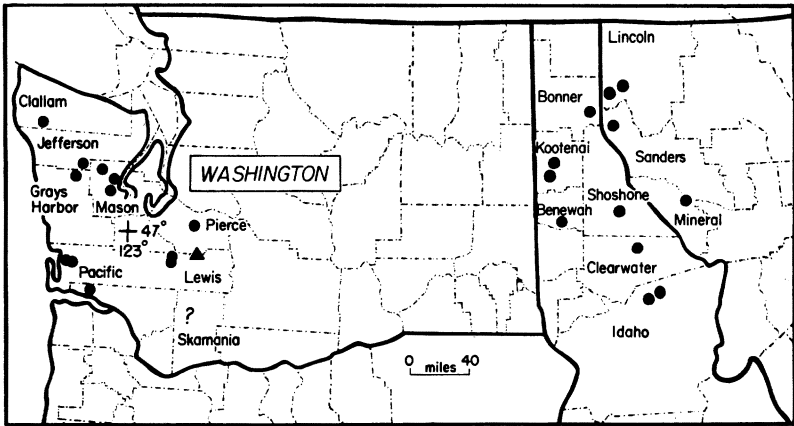


FIG. 9.—Range map of *Plethodon vandykei*.

with brassy iridophores above the pupil and sometimes lightly flecked below the pupil. Light-phase individuals usually lack iridophores but may have a few along the side.

Plethodon vandykei has 13–16 ($M = 14$) costal grooves, 14–17 ($M = 15$) trunk vertebrae, and 0.5–3.0 (usually 1.5–2.0) costal folds between adpressed limbs in adults. The smallest known specimen is 15 mm SVL (RAN 5132). Adults may have 5–41 (usually 11–31) vomerine teeth. Adult males and females have 19–84 ($\bar{x} = 58.7$) and 32–89 ($\bar{x} = 69.7$) maxillary–premaxillary teeth respectively.

Males have a mental gland, more maxillary–premaxillary teeth, and elongate nasolabial cirri. Poorly developed vent lobes are usually present in males. Sexual maturity is reached at about 45 mm SVL.

Geographic Variation.—Most populations of *vandykei* have a modal number of 14 costal grooves. The mean number of grooves is also 14 (14.03–14.05) for populations in the Willapa Hills and Cascade Mountains, Washington and Coeur d'Alene Lake, Idaho; the range in groove counts for these groups is 14–15 or 13–15. Populations from the Olympic Mountains, Washington or Montana have mean counts of 14.4 and 14.5 (13–16). The relative frequency of 14 grooves is much lower in the latter two populations. Three of seven animals from Idaho County, Idaho have 14 grooves, the other four have 15. In number of costal grooves the two populations at opposite ends of the range are most similar.

In decreasing order of vomerine teeth number, geographic groups can be arranged as follows: Montana ($\bar{x} = 23.5$), Olympic Mountains ($\bar{x} = 20.7$), Willapa Hills ($\bar{x} = 19.9$), Coeur d'Alene Lake

TABLE 6.—Ontogenetic variation in degree of melanophore pigmentation within the dorsal stripe in *P. vehiculum*, *P. dunni*, and *P. larselli*.

Group	Snout-Vent Length (mm)												
	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70+	
<i>Vehiculum</i>													
1	1.000	1.000	1.000	1.000	1.400	2.000	2.278	2.548	3.200	2.750	—	—	—
3	1.000	1.000	1.250	1.450	2.333	1.867	2.522	2.522	2.000	3.500	—	—	—
4	—	1.000	1.000	1.182	1.524	1.647	1.846	2.273	2.000	—	—	—	—
6	1.000	1.000	1.000	1.200	1.500	1.857	2.375	1.933	3.500	1.000	—	—	—
11	1.000	1.000	1.200	1.563	1.821	2.250	2.300	2.640	3.000	3.000	—	—	—
12	1.250	—	1.364	1.769	1.720	2.192	2.111	2.440	2.667	—	—	—	—
<i>Dunni</i>													
21	1.000	1.500	1.250	1.333	1.667	1.750	2.167	1.917	2.389	2.778	3.093	—	3.000
25	—	2.000	4.000	3.625	2.000	3.250	3.600	3.500	3.400	3.857	4.412	—	4.500
26 & 28	1.000	1.417	1.600	2.071	2.751	2.555	2.857	2.273	2.941	3.118	3.200	—	—
31	1.000	1.111	1.500	2.200	2.125	2.571	2.600	2.545	2.842	3.320	3.444	—	—
<i>Larselli</i>													
44	—	—	3.250	3.800	4.571	4.667	4.643	4.000	—	—	—	—	—
46	—	2.000	2.000	2.125	2.375	2.375	2.941	3.444	3.000	—	—	—	—

(\bar{x} = 19.1), Cascade Mountains (\bar{x} = 15.2). The tail is relatively longer in the Coeur d'Alene population than in Washington populations but the difference is slight.

Pigmentation is variable and the subspecies were distinguished by pigment characters. Populations from Washington have stripes that extend to the tip of the tail, while the stripe of Idaho and Montana specimens stops short of the tip of the tail. Animals from Idaho have more irregular and slightly narrower stripes than Washington animals. The stripe color ranges through green, orange and red in the Coeur d'Alene population; green is the most common. Animals from Washington have yellow or red stripes. Melanophore pigmentation is often present within the dorsal stripe of Idaho and Montana specimens but is rarely found in Washington animals. Washington animals have light-colored limb bases with dark flecks; Idaho and Montana animals have dark limb bases with light flecks.

All specimens from Idaho and Montana and many from the Cascades are dark phase. Light-phase and rose-phase animals are found in all Washington populations. The rose phase is common in the Willapa Hills and rare in the Olympic and Cascade Mountains.

Animals from the Olympic Mountains are smaller than those from the other areas. The largest animals from each population are: Olympic, 57 mm SVL (CAS 55340); Willapa Hills, 63 mm SVL (RAN 5097); Cascades, 65 mm SVL (UPS 7180); Coeur d'Alene Lake, 60 mm SVL (RAN 710, 719; EKT 530); Montana, 64 mm SVL (CWSC, no number).

Each geographic group of *vandykei* is distinct from the other groups by a unique combination of tooth number, costal groove number and pigmentation. The discordant nature of this variation does not allow the recognition of previously described subspecies.

Plethodon larselli Burns
Larch Mountain Salamander

Plethodon vandykei larselli Burns, 1954:83.

Plethodon larselli: Burns, 1962:177.

Holotype.—USNM 134129, adult male, from the north slope of Larch Mountain, 3 miles from summit on the Multnomah Falls Trail, Multnomah County, Oregon. Collected by Douglas M. Burns, 24 May 1953.

Diagnosis.—*Plethodon larselli* can be distinguished by: a modal number of 15 costal grooves, reduced parotoid gland, one phalanx in the fifth toe of the hind foot and no mental gland in males.

Distribution and Habitat.—Specimens were examined from all known localities (Fig. 10). Two unreported localities in Skamania County, Washington extend the range of *larselli* about 30 miles east;

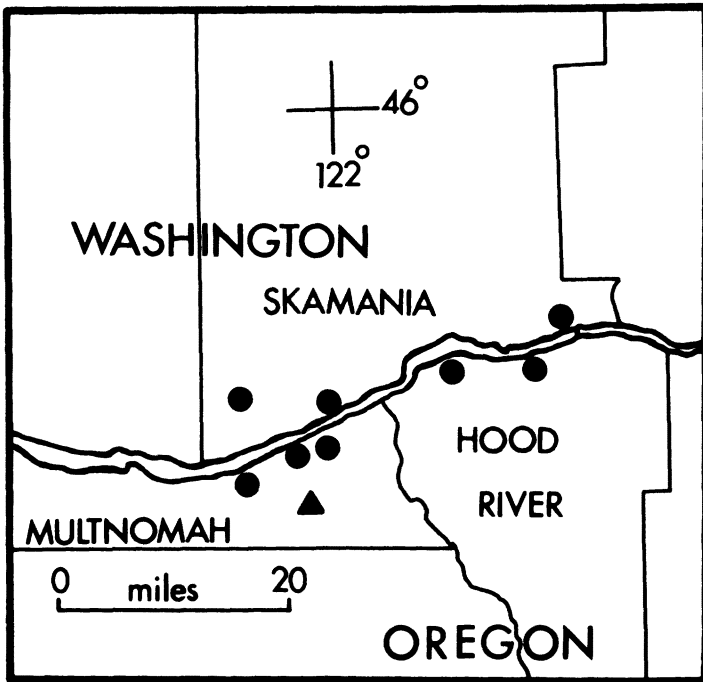


FIG. 10.—Range map of *Plethodon larselli*.

these localities are Beacon Rock State Park (RAN 1574-5) and 12.8 miles E Stevenson (RAN 1540-54, EDB 2986-8).

This species is closely associated with outcrops of basaltic rock. It is most commonly found at the base of these outcrops where chunks of basalt are in contact with soil. Salamanders may also be found under logs or leaf litter but are seldom found in association with seepages or streams; it appears to be the most terrestrial of the western *Plethodon*. *P. larselli* is sympatric with *vehiculum* in Washington and *dunni* in Oregon.

When disturbed, *larselli* typically coil tightly, sometimes coiling and uncoiling rapidly several times; they lose this behavior quickly in captivity. This behavior is possibly an example of mimicry between *larselli* and the numerous millipedes in the area.

Description.—Indistinct parotoid glands and a short (one phalanx) fifth toe on the hind feet characterizes this smallest of western *Plethodon*. The ground color is black but is evident only in a narrow, distinct stripe below the dorsal stripe. The black color of the sides is largely obscured by heavy iridophore concentrations. Gold iridophores are present on the dorsal half of the sides and the dorsal surfaces of the limbs; white iridophores are present on the ventral

half of the sides and the ventral surfaces of the limbs and chin but are absent from the venter. The dorsal stripe has a moderate amount of gold flecking on the trunk and heavy concentrations on the head. The tail stripe usually has few iridophores. The brown iris is heavily flecked with gold or white iridophores above the pupil and sometimes lightly flecked below.

The dorsal stripe appears eroded along the edges and usually extends to the tip of the tail. The degree of black-in-stripe is geographically variable, but in most individuals at least the middorsal area is black. This condition sometimes gives the appearance of two dorsolateral stripes which join at the base of the tail. The stripe is obscured on the head and brightest on the tail. Stripe color is present as small flecks on the sides and as blotches on the dorsal surfaces of the limb bases.

The ventral surfaces of the body, tail, limbs and feet of adults are red-orange covered with a melanic network of varying intensity. The chin is cream colored with a tinge of red-orange.

Dorsal pigmentation of juveniles is basically the same as adults but with less black-in-stripe. The venter is black with flecks or blotches of red pigment which enlarge with age.

This species has 14–16 ($M = 15$) costal grooves, 15–17 ($M = 16$) trunk vertebrae, and 0–3 costal folds between adpressed limbs in adults. The smallest specimen examined was 20 mm SVL (EDB 3008). Burns (1964) reported a specimen 29 mm TL; if this animal had a complete tail, it must have been less than 20 mm SVL. The largest specimens from each of the three areas were: Archer Falls, 51 mm SVL (EDB 1884); Stevenson, 53 mm SVL (RAN 1542); and Oregon 57 mm SVL (EDB 790). Adults have 5–31 vomerine teeth. Adult males and females have 33–68 ($\bar{x} = 54.4$) and 51–83 ($\bar{x} = 65.4$) maxillary-premaxillary teeth respectively.

Sexual dimorphism is as described for *vandykei* except that male *larselli* lack a mental gland. Sexual maturity is reached at about 40 mm SVL.

Geographic Variation.—Three groups of *larselli* were analyzed: Oregon; Stevenson, Skamania County, Washington; and Archer Falls, Skamania County, Washington. Geographic variation was detected for number of teeth, black-in-stripe, and size.

Archer Falls *larselli* have a significantly greater amount of black-in-stripe than those from the other two areas (Table 5); Stevenson animals were intermediate in this character. Washington adults (Archer Falls and Stevenson) are darker dorsally than Oregon adults because of a more intense melanophore network.

Regressions of vomerine teeth vs. snout-vent length were not significantly different for any of the three groups (Table 3), but the ranges and means for adults are different. Archer Falls adults

have 6–18 (\bar{x} = 12.5) teeth, Oregon adults have 13–31 (\bar{x} = 16.6), and Stevenson adults have 17–24 (\bar{x} = 19.8). The number of maxillary-premaxillary teeth is variable only in males. Archer Falls males have 33–63 (\bar{x} = 53.4), Oregon males have 40–68 (\bar{x} = 59.1), and Stevenson males have 43–50 (\bar{x} = 49.0). Stevenson *larselli* resemble Oregon populations in vomerine tooth counts and the Archer Falls population in maxillary-premaxillary tooth counts, but they are not intermediate in either character.

Fewer Washington adults (3 of 51) than Oregon adults (30 of 48) were over 50 mm SVL. In addition to being larger, it appears from inspection of gonads that Oregon *larselli* mature at slightly over 40 mm SVL and Washington *larselli* mature at just under 40 mm SVL.

The recently discovered population near Stevenson suggests that there may be additional isolated and variable populations elsewhere along the Columbia River. Although Washington and Oregon populations of *larselli* are significantly different in a number of characters and the Columbia River is probably an effective barrier, I do not believe subspecific recognition is warranted.

VEHICULUM GROUP

The species of this group are intermediate between those of the *Vandykei* and *Elongatus* groups in costal groove number, number of vomerine and maxillary-premaxillary teeth, leg length, head width, and head length. The toes are unwebbed and longer than those of the other two species groups. Males of this species group have slightly longer tails than females.

Plethodon vehiculum (Cooper) Western Red-backed Salamander

Ambystoma vehiculum Cooper, 1860:pl. 31, Fig. 4. Only a figure was published. Although the salamander figured by Cooper has only 13 costal grooves, a count known only for *vandykei*, there is no doubt that the salamander was *vehiculum*. The evenness of the dorsal stripe and the degree and distribution of melanophores within the stripe eliminate *vandykei*, *larselli*, and *dunni*, which are closer to the costal groove count of Cooper's figure than *vehiculum*. Apparently Cooper was careless in determining costal groove number, as the *Batrachoseps attenuatus* (18–21 grooves) figured on the same plate had 14 grooves.

Plethodon intermedius Baird, in Cope, 1867:209. Holotype, (USNM 4732-a) adult female, collected by J. Xantus. The type locality (Fort Tejon, California) is obviously in error.

Plethodon vehiculus: Bishop, 1934:171.

Plethodon vehiculum: Slater, 1940:43.

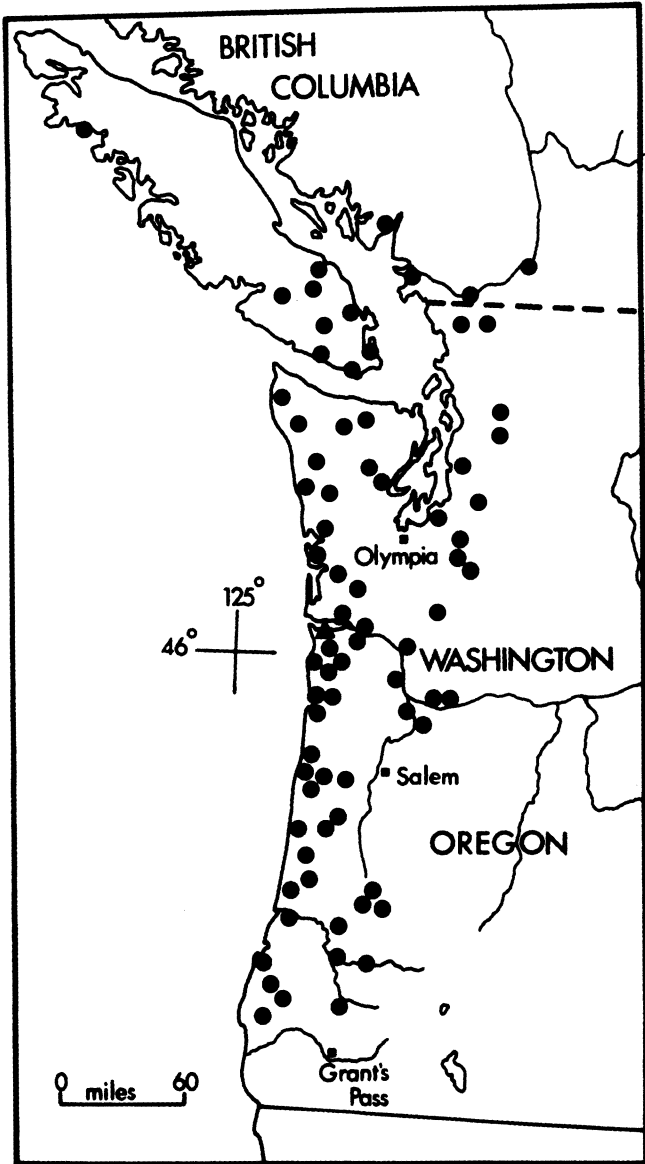


FIG. 11.—Range map of *Plethodon vehiculum*.

Holotype.—No type was designated by Cooper. Type locality is Astoria [Clatsop County], Oregon.

Diagnosis.—*Plethodon vehiculum* can be distinguished by: usually a modal number of 16 costal grooves and an even-edged dorsal

stripe which extends to the tip of the tail. Males have mental glands with straight posterior edges.

Distribution and Habitat.—*Plethodon vehiculum* ranges from southern Oregon to British Columbia; its northern limits, especially along the coastal strip, are uncertain (Fig. 11). The southernmost records from Oregon are 3 miles SW Powers, Coos County (OSU 3680-1); 5.7 miles SE Remote, Coos County (OSU 3693-4); 2 miles S Canyonville, Douglas County (EDB 2329-30); and near Steamboat, Douglas County (EDB 2547, 2550). It is found from the crest of the Cascade Mountains to the coast, but it is absent from the Oregon Cascades north of an area east of Eugene, Lane County. This species was reported from Fernwood (Fernview) Forest Camp on the South Santiam River, Linn County, Oregon (Graf, Jewett, and Gordon, 1939). Confusion existed as to the distinctness of *dunni* and *vehiculum* at that time (K. Gordon, pers. comm.), and since Graf's specimens could not be located and further collecting at the locality produced only *dunni*, I believe this record is a case of misidentification.

The occurrence of *vehiculum* at Portland, Multnomah County, 3 miles S Boring, Clackamas County, and 2 miles E Carver, Clackamas County in northern Oregon places it immediately adjacent to the range of *larselli* in the Cascades. No apparent physical barrier accounts for the absence of *vehiculum* in this area. Sympatry with *larselli* directly across the Columbia River in Washington rules out competitive exclusion as the sole reason for their allopatry in Oregon.

Near Steamboat, Douglas County, Oregon, *vehiculum* occurs to an elevation of 4100 ft. In other areas it seldom occurs above 2500 ft. It occurs on several offshore islands of Washington (Brown and Slater, 1939; Slater and Brown, 1941).

This is the most common *Plethodon* throughout its range, and it occurs in a variety of habitats. In Oregon and Washington it is commonly found in talus slopes or under surface objects. It may also be found under bark of rotting logs or in piles of leaves. It is usually not found in situations as wet as is common for *dunni* (Dumas, 1956).

Description.—As well as being the most wide ranging and numerous western *Plethodon*, *vehiculum* displays the most intrapopulational variation. In some populations both melanism and reduced melanism are common; these two conditions sometimes make up 50% or more of the sample. Reduced melanism usually results in a salamander largely the color of the dorsal stripe, i.e., erythristic. The stripe may be shades of red, orange, yellow, olive, or tan.

The stripe extends from the snout, where it is not obscured, to the tip of the tail and has an even edge throughout. Black pigmentation in the stripe is concentrated along the middorsal line and is

absent or light on the tail. An irregular blotch of stripe color on the limb bases is flecked with melanophores and iridophores. Distal limb segments, sides of the head, and ventral surfaces are sprinkled with stripe color. Flecking encroaches onto the sides from the venter to a point corresponding with the top of the iridophore network.

Heavy white iridophore concentrations on all ventral surfaces give a salt and pepper effect. This network extends onto the side as far as half-way to the dorsal stripe in some specimens. Iridophores are absent from the upper half of the side, leaving a solid strip of dark brown to black ground color. A few iridophores are present on the head and scattered on the dorsal stripe. The dark brown iris is heavily flecked with brassy iridophores above the pupil and usually lightly flecked below; in a few specimens the iris color is obscured by brassy iridophores.

Plethodon vehiculum has 14–18 costal grooves ($M = 15$ or 16 depending on locality), 15–19 trunk vertebrae ($M = 16$ or 17) and 2.5–5.5 (usually 3.5–4.5) costal folds present between adpressed limbs in adults. The smallest specimen examined was 13 mm SVL (UMMZ 54366). The largest specimens are from island populations (see Geographic Variation); a more common maximum size is 55–59 mm SVL. Adults have 2–20 (normally 5–17) vomerine teeth. Adult males and females have 9–57 ($\bar{x} = 37.6$) and 18–58 ($\bar{x} = 44.2$) maxillary-premaxillary teeth respectively.

Size at sexual maturity varies geographically from 40–50 mm SVL. Males have vent lobes (1 of 300 lacked vent lobes) and squarer snouts than females. Mental glands are present in males but are usually not evident by external examination.

Geographic Variation.—The majority of the 16 geographic groups had mean costal groove counts between 15.95 and 16.17 (Table 2). Two series of groups varied from this norm. Groups 5, 8, and 10 from southwestern Washington and northwestern Oregon were higher (16.39, 16.19, and 16.26); group 5 from southwestern Washington was significantly higher than all groups except 8 and 10. Groups 13, 14, and 15 from Lane and Douglas counties, Oregon were significantly lower (15.20–15.40) than all other groups and have 14–16 costal grooves ($M = 15$). All populations from the Oregon Cascade Mountains have low costal groove counts. The only coastal animals with low groove counts are those adjacent to the populations in the Cascade Mountains suggesting that there is now or was recently gene exchange across the southern end of the Willamette Valley. Populations of *vehiculum* further south, in Coos County, have the usual number of costal grooves.

No significant variation in tooth counts was detected. The flat slope obtained for vomerine teeth vs. snout-vent length for group 16 may be due to the small sample size (Table 3).

Animals from Washington and Oregon have legs of the same length. Salamanders from Vancouver Island have proportionately longer legs than the other two areas; this character was not examined in specimens from mainland British Columbia.

The degree of black-in-stripe is variable geographically. Coastal populations of *vehiculum* generally have a higher degree of melanophore encroachment onto the dorsal stripe and a higher incidence of melanistic individuals. The relative frequency of Type 5 (Table 4) indicates the percentage of melanistic specimens for each geographic area. The only noncoastal groups with melanistic individuals were those from the Washington Cascades and Portland, Oregon. Groups with melanistic salamanders usually also had many individuals with reduced melanism. Melanism and reduced melanism are similar in that the entire animal is fairly uniform in pigmentation. Some intermediate individuals are uniformly brown. In coastal groups many Type 1 salamanders have reduced melanism (e.g., 12.6% of group 11 have reduced melanism). A female *vehiculum* and seven hatchlings (15–17 mm SVL) collected together on 20 May 1956 all have reduced melanism (OSU 4162). Populations from the western Olympic Mountains, Washington have 10.8% melanistic individuals, but melanistic animals were lacking from the eastern Olympics.

A series from Wheeler, Tillamook County, Oregon (OSU 5100–2, 5105–7) has one individual with reduced melanism, two with normal pigmentation, and three that are piebald. The piebald salamanders are light with dark blotches and lack definite stripes.

All series seen alive, except those from Vancouver Island, had many color phases, i.e., yellow, red, and tan stripes. Of 44 live *vehiculum* from Vancouver Island, 43 had red stripes and one had an olive-tan stripe; none were melanistic. The ratio of each stripe color varies geographically but must be studied from live specimens.

Salamanders from Vancouver Island are larger than those from mainland populations. This may be correlated with a greater size at maturity or a greater life span. The four *vehiculum* (MVZ 34939–34942) from Destruction Island, Jefferson County, Washington are larger than those from Vancouver Island. The two largest are a female (64 mm SVL) and a male (62 mm SVL); both are larger than individuals of the same sex from other populations.

Plethodon dunnii Bishop
Dunn's Salamander

Plethodon dunnii Bishop, 1934:169.

Holotype.—USNM 95196, an adult female, collected just outside the city limits of Portland, Oregon in Clackamas County by Stanley G. Jewett, Jr., 13 January 1934.

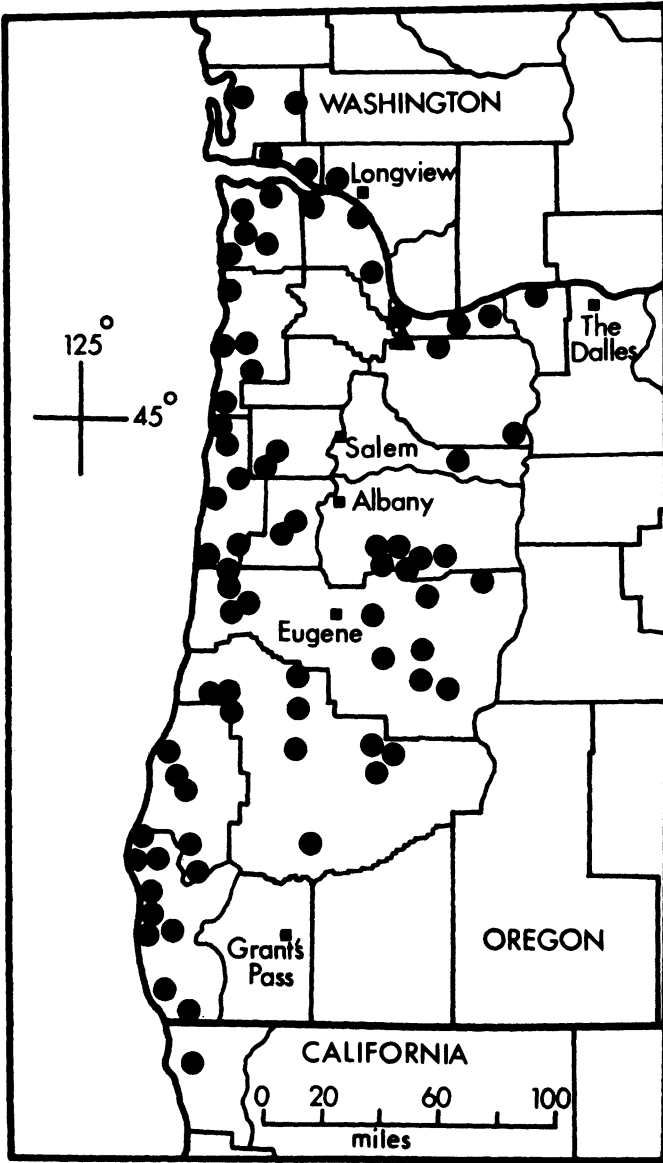


FIG. 12.—Range map of *Plethodon dunni*.

Diagnosis.—*Plethodon dunni* can be distinguished by: a modal number of 15 costal grooves, an uneven, greenish-yellow dorsal stripe, and blotches of stripe color along the sides. Males have a mental gland with posterolateral processes.

Distribution and Habitat.—*P. dunni* occurs throughout the Coast Range from Fort Smith, Del Norte County, California to South Bend and Frances, Pacific County, Washington (Fig. 12). It occurs in the Cascade Mountains of Oregon from the North Umpqua River, Douglas County, to the Columbia River. South of the North Umpqua River *dunni* is restricted westward by xeric conditions.

P. dunni is associated with rocky substrates, particularly talus slopes, in moist conditions. It is most abundant in seepages and along streams and commonly enters the water when disturbed; it is a strong enough swimmer to move upstream (Stebbins, 1951). It appears to be similar to *vandykei* in moisture preferences which might account for the narrow zone of sympatry of these two species.

Description.—The dark brown or black ground color encroaches upon the edges of a dorsal stripe which extends from the snout onto the tail but does not reach the tip. The stripe appears eroded along the edges, is usually obscured on the head, and is broken on the tail. Blotches of stripe color are abundant along the sides and on the dorsal surfaces of the limbs. The venter is dark with scattered small blotches of yellowish pigment and iridophores. Concentrations of iridophores are medium to heavy along the sides and on the head but are sparse on the trunk. The iris is dark brown with scattered brassy flecking heavier above the pupil than below.

P. dunni has 14–17 costal grooves ($M = 15$), 15–18 trunk vertebrae ($M = 16$), and 1–4 (usually 3) costal folds between adpressed limbs. The smallest specimens examined were 17 mm SVL (EDB 1350, 2305; OSU 4161); Dumas (1955) reported 16 mm SVL near-hatching embryos. The largest individual examined was 75 mm SVL (EDB 2326). Adults may have 4–31 (usually 7–25, but varies geographically) vomerine teeth. Adult males and females have 30–61 ($\bar{x} = 45.6$) and 38–69 ($\bar{x} = 53.6$) maxillary-premaxillary teeth respectively. Size at sexual maturity is 50–55 mm SVL. Males have vent lobes, mental glands, and wider heads than females.

Geographic Variation.—Most of the 14 geographic groups were too small for analysis of characters which vary ontogenetically.

Group 25 shows significant variation in costal groove number. Mode (16), range (15–17), mean (15.54) and relative frequencies of each groove count were different from other groups.

No consistent geographic variation was evident from the regressions of vomerine teeth on snout-vent length. It appears that southern populations have flatter slopes than northern populations (Table 3), indicating less increase in tooth number with size in southern salamanders. Adult *dunni* from Multnomah County had more vomerine teeth (8–27, $\bar{x} = 16.2$) than those from Benton County (8–20, $\bar{x} = 13.7$), and Curry County adults had the fewest teeth (7–17, $\bar{x} = 11.7$). Juveniles less than 30 mm SVL yielded the fol-

lowing data: Multnomah County (5–15, \bar{x} = 9.7), Benton County (5–10, \bar{x} = 8.7), and Curry County (5–13, \bar{x} = 8.1).

The number of maxillary-premaxillary teeth varied geographically. Males from Multnomah County (37–55, \bar{x} = 48.3) had the most teeth, those from Benton County (35–55, \bar{x} = 45.3) were intermediate, and those from Curry County (30–53, \bar{x} = 40.0) had the fewest teeth. The same held true for females: Multnomah County (43–69, \bar{x} = 56.2), Benton County (45–58, \bar{x} = 52.3), and Curry County (41–57, \bar{x} = 49.1). Tooth number appears to increase clinally from south to north, but more large samples are needed to illustrate this with certainty.

P. dumni from Curry County have narrower heads than those from Multnomah County; Benton County salamanders are intermediate. This parallels the variation in tooth number and holds true for all sizes and both sexes. Differences in head length are less clear; Multnomah County salamanders might have longer heads than others but the difference is not significant.

A pattern of character convergence in head shape and tooth number is exhibited by *dumni* where it is sympatric with *larselli* and *elongatus*. Populations of *dumni* sympatric with *larselli* have wide heads and more teeth; those sympatric with *elongatus* have narrow heads and fewer teeth. This convergence is probably due to environmental factors acting on each species independently.

Benton County *dumni* have proportionately shorter legs than Multnomah County animals as shown by more costal folds between adpressed limbs. Other populations resemble the Multnomah County series.

Populations of *dumni* can be divided into light and dark groups based on black-in-stripe. Groups from the Oregon Cascades and Lane County south along the coast average 2.75–3.06. Groups from Benton County and Lincoln County north are significantly darker (\bar{x} = 3.75–4.00). Light groups are also characterized by larger and more numerous blotches of stripe color along the sides and on the gular region.

A third species of the Vehiculum group has previously been considered a melanistic color phase of *dumni* (Stebbins, 1951). I am pleased to name this species after Dr. Kenneth L. Gordon, Professor Emeritus of Zoology at Oregon State University.

Plethodon gordoni, new species
Mary's Peak Salamander

Holotype.—USNM 166687, adult female, collected 9 April 1969 by E. D. Brodie, Jr. and R. A. Nussbaum; preserved 19 May 1969. Type locality, Dinner Creek, (T13S, R7W, Sec. 1, NW quarter), Benton County, Oregon.

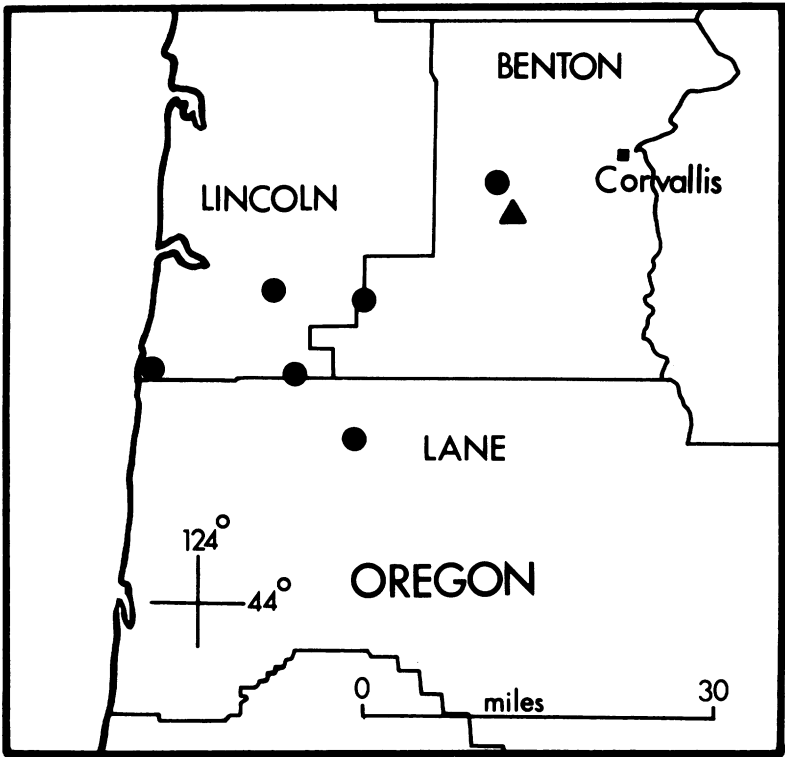


FIG. 13.—Range map of *Plethodon gordonii* sp. nov.

Paratypes.—BENTON COUNTY: Dinner Creek, T13S, R7W, Sec. 1, NW quarter (EDB 3095–3100); Wells Creek, 7 miles SW Philomath (EDB 3094, OSU 195, 199, 214–7, 1658–9, 5361, 10458); Hyde (Hide) Creek, T13S, R6W, Sec. 6 (EDB 527, 582–4, 684, 759, 788, 1326, 2981–2, OSU 5218, 5959–63, 10455–7, USNM 166695–702); 2 miles up Mary's Peak road from Hwy 34 (EDB 682–3, 747); Rock Creek road (OSU 207–8, 210, 212–3); 6 miles S, then 8 miles W Philomath (OSU 3282); Alder Creek, on Mary's Peak road, T13S, R7W, Sec. 3 (USNM 166692–3); 1 mile up road 121 off Rock Creek road, T12S, R6W, Sec. 19, SW quarter (EDB 1081, 1326–47, 1355–7, 1930–1, 2014, 2306–10, 3104–16, USNM 166703–7); 3 miles W Hwy 34 on Klickitat road, T13S, R7W, Sec. 16, NW quarter (USNM 166694); 10.3 miles SW Alsea (LACM 30641–2). LINCOLN COUNTY: 12 miles from Hwy 34 on Klickitat road, T13S, R8W, Sec. 1 (USNM 166688–91); 20 miles E Alsea on Hwy 34 (OSU 10459); Cape Perpetua (OSU 10461–2). LANE COUNTY: Fisher (OSU 10452–4); 7 miles S Fisher (OSU 10460, 10463).

Diagnosis.—*Plethodon gordonii* can be distinguished by: a modal



FIG. 14.—Habitat at Dinner Creek, the type locality of *P. gordonii*.

number of 15 costal grooves, no dorsal stripe, and usually 2–2.5 costal folds between adpressed limbs.

Distribution and Habitat.—*Plethodon gordonii* occurs in Benton, Lincoln, and Lane counties, Oregon (Fig. 13). Throughout its range it is sympatric with *dunni* and *vehiculum*. *P. gordonii* is found in rocky outcrops and talus slopes, usually near seepages (Fig. 14). During wet times of the year, *gordonii* may be found under surface objects. There are no obvious differences between the habitat preferences of *gordonii* and *dunni*.

Description of Holotype.—The holotype is an adult female with a snout–vent length to the anterior margin of vent of 63 mm; snout–vent length to the posterior margin of the vent is 68 mm. The tail is 67 mm long and complete. Head width is 8.6 mm, head length is 14.1 mm. Forelimb length is 13.5 mm (both right and left); hindlimb length is 16.8 mm on the right and 17.2 mm on the left. The axilla–groin length is 37 mm. It has 16 costal grooves; 2.75 costal folds are present between adpressed limbs on the right side and 3.0 on the left side. There are 15 vomerine teeth, 55 maxillary–premaxillary teeth, and 55 dentary teeth. The length of toes from longest to shortest is 3-2-4-1 on the forefeet and 3-4-2-5-1 on the hindfeet.

In life the dorsum of the holotype was chocolate brown and the venter was light purplish-grey. The eye was dark brown with silver

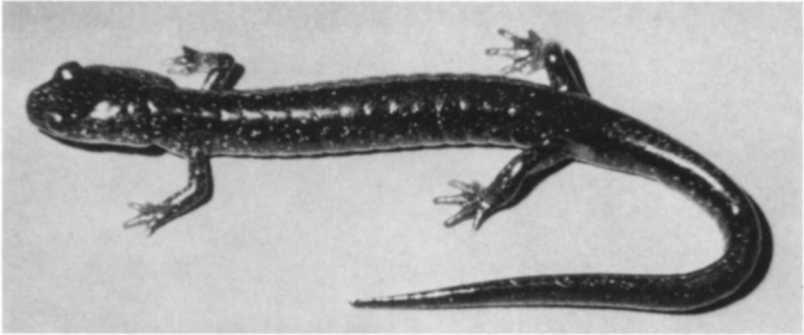


FIG. 15.—*Plethodon gordonii* sp. nov. Holotype, USNM 166687.

and gold flecking above and below the pupil. A few brassy pigment flecks were present along the dorsum and on the posterior one-third of the head, but no dorsal stripe was present.

Iridophore flecking was heavy ventrally, laterally, on the head dorsum and on the anterior one-third of the tail dorsum. Flecking was medium on the body dorsum and very heavy on the gular region. Dorsal iridophores were small and white; ventrally they were larger and yellowish. No greenish pigment was present in life.

Description.—This dark grey or brown salamander (Fig. 15) lacks a dorsal stripe in adults. In life juveniles have a faint pinkish dorsal stripe formed by underlying gold, brassy and reddish iridophores. In adults a melanic network covers the dorsum entirely; occasionally animals have breaks in the melanic network resulting in flesh-colored areas over deep brassy iridophores. Numerous small white iridophores are scattered over the entire animal in juveniles. In adults, the white iridophores are found on the dorsum; yellowish iridophores are present along the lower sides and venter. The dark brown iris has gold and/or silver iridophores present. No green pigment flecks or blotches were seen on *gordonii*.

There are 15–16 costal grooves ($M = 15$), 16–17 trunk vertebrae ($M = 16$), and 1.5–3.5 (usually 2–2.5) costal folds between adpressed limbs. The smallest specimen examined was 18 mm SVL (EDB 1338) and the largest was 72 mm SVL (OSU 10459). Adults may have 11–22 vomerine teeth. Adult males and females have 37–53 ($\bar{x} = 45.9$) and 46–60 ($\bar{x} = 53.1$) maxillary-premaxillary teeth respectively. Size at sexual maturity is about 50 mm SVL. Males have vent lobes and mental glands which resemble those of *dunni*.

Comparison with P. dunni.—Structural features of *gordonii* and *dunni* from the same area (Hyde Creek and the Corvallis Water Shed, Benton County, Oregon) were compared. In general appearance, *gordonii* is more slender than *dunni*. The mean costal groove count is different at the 80% level and the modal groove count is

different: *dunni* = 16, *gordoni* = 15. All other populations of *dunni* have a mode of 15.

Slopes for vomerine teeth vs. snout-vent length for *gordoni* and *dunni* are different at the 90% level. Juvenile *gordoni* have fewer teeth than *dunni* of the same size; adult *gordoni* have more vomerine teeth than *dunni*. There are no apparent differences in number of maxillary-premaxillary teeth but the samples are small.

The long narrow head of *gordoni* is indicated by a flatter slope for HW vs. SVL and a steeper slope for HL vs. SVL (Fig. 6). Neither of these slopes is different from *dunni* above the 70% level. The difference in head shape is demonstrated in a flatter slope for HW vs. HL. The HW vs. HL slope for *gordoni* is the same as that for *vehiculum* but is significantly lower than sympatric *dunni* at the 99% level. From calculated regressions, the head of a 60 mm SVL *gordoni* would be 8.1 mm wide and 13.0 mm long. These figures for a *dunni* from the same area are 8.4 mm and 12.8 mm.

Most (85%) adult *gordoni* have 2–2.5 costal folds between adpressed limbs and most (72%) sympatric *dunni* have 3 or more folds. Sympatric *dunni* have shorter legs than other populations.

Samples of these animals were collected at the same times and places, and all salamanders collected were preserved and analyzed; in these samples, *dunni* was commonly larger than *gordoni*. Animals 50–59 mm SVL made up 19% of each sample, while 38% of the *dunni* and 18% of the *gordoni* were 60 mm SVL or over.

The dark gray or brown ground color of *gordoni* is lighter than the black or dark brown of *dunni*. Lighter ground color suggests that *gordoni* does not represent a melanistic phase of *dunni*. No *gordoni* had green pigment although several specimens had a few tan or colorless blotches of various sizes on the dorsum.

P. gordoni is more similar to some allopatric populations of *dunni* than it is to sympatric populations of *dunni*. This is true for leg length, modal number of costal grooves, head shape, and tooth counts. This suggests that *gordoni* and *dunni* do not interbreed at the present time and that character displacement may be taking place in the zone of sympatry.

ELONGATUS GROUP

The *Elongatus* group includes *elongatus* and *stormi*. These salamanders are characterized by more costal grooves, shorter legs and fewer teeth than other western *Plethodon*. The toes are partially webbed.

Plethodon elongatus Van Denburgh Del Norte Salamander

Plethodon elongatus Van Denburgh, 1916:216. Highton (1962) pointed out the validity of this name even though Duméril, Bibron,

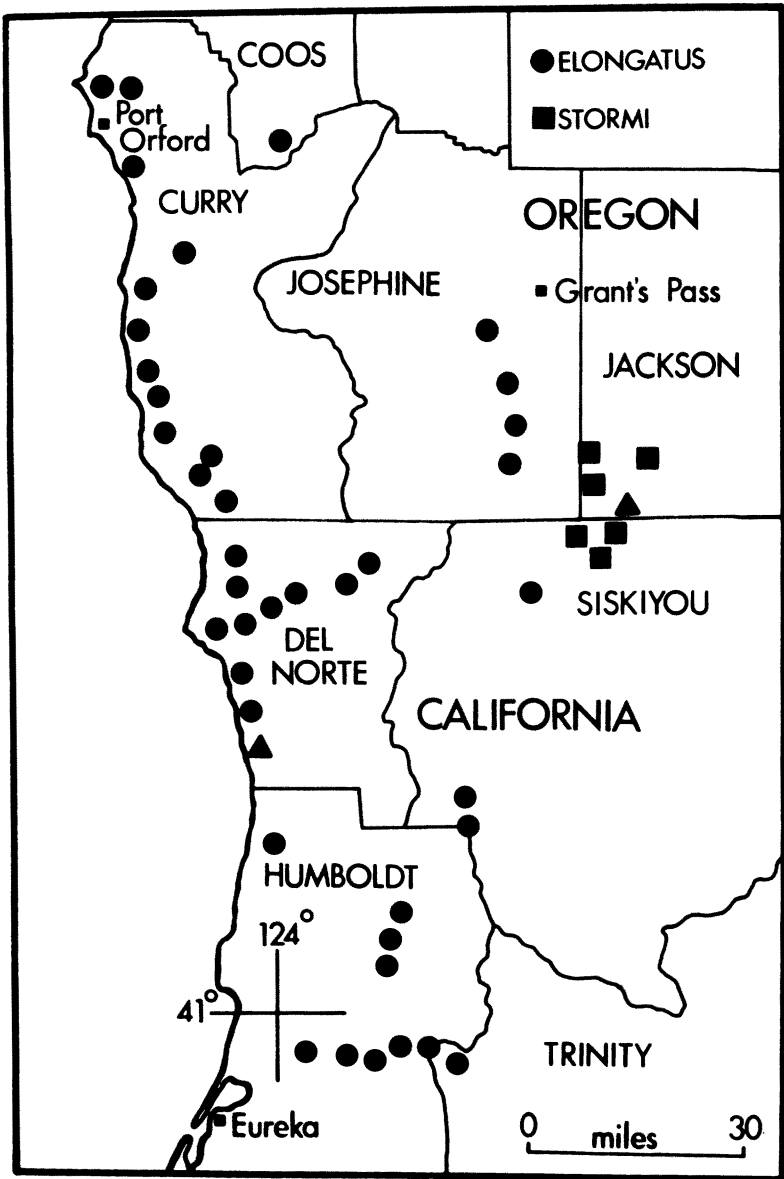


FIG. 16.—Range map of *Plethodon elongatus* and *Plethodon stormi*.

and Duméril (1854) first published the manuscript name *Salamandra elongata* Valenciennes which Dunn (1926) placed in synonymy with *Plethodon glutinosus*. Since *Salamandra elongata* Valenciennes was never proposed validly according to the International Code of Zoo-

logical Nomenclature, *P. elongatus* remains the valid name of the Del Norte Salamander.

Holotype.—CAS 29096 from Requa, Del Norte County, California collected by J. R. Slevin, 22–26 May 1911.

Diagnosis.—*Plethodon elongatus* can be distinguished by: a modal number of 18 costal grooves, reddish dorsal stripe, and usually 6.5–7.5 costal folds between adpressed limbs in adults.

Distribution and Habitat.—*P. elongatus* occurs in southwestern Oregon and northwestern California (Fig. 16). It is found in stabilized talus, under surface objects, and occasionally in decaying logs. The best sites, especially along the coast, are under dense Douglas fir or redwood cover. This species is not commonly found in seepages or very moist situations. The range of *elongatus* is allopatric and adjacent to the range of *vehiculum*. These two species appear to be nearly identical in habitat preferences.

Description.—This is the most attenuate of the western *Plethodon*. The ground color is dark brown or black and the reddish dorsal stripe is overlain with an even network of melanophores. Many adults, especially those from coastal populations, have the dorsal stripe completely obscured. The stripe has an even edge and extends at least three-fourths the length of the tail, usually to the tip. Stripe color is present in small flecks along the side and occasionally on the venter. The venter is dark and the gular area is light gray and often mottled.

Heavy concentrations of white and yellow iridophores occur along the sides of the head and body, on limb dorsums, and in the gular area. Lighter concentrations are present on the venter and head dorsum; a few iridophores are occasionally present on the body dorsum. The dark brown eyes usually lack iridophores but some animals have a few flecks on the iris.

P. elongatus has 17–20 ($M = 18$) costal grooves, 18–21 ($M = 19$) trunk vertebrae, and 5.5–8.5 (usually 6.5–7.5) costal folds between adpressed limbs in adults. The smallest hatched specimens examined were 18 mm SVL (CAS 80033, MVZ 81848); ten pre-hatching embryos (Livezey, 1959) averaged 12 mm SVL. The largest specimen was 73 mm SVL (MVZ 74431). Adults may have 5–21 (usually 6–16) vomerine teeth. Adult males and females have 30–57 ($\bar{x} = 42.3$) and 34–64 ($\bar{x} = 47.6$) maxillary-premaxillary teeth respectively. Size at sexual maturity is about 55 mm SVL. Males have mental glands; vent lobes are absent or poorly developed.

Geographic variation.—As first noticed by Stebbins (1951), inland *elongatus* more often have dorsal stripes, have a somewhat lighter ground color, and have less elongate heads than coastal animals from California. Oregon coastal animals are like inland ani-

mals in respect to head shape. These differences are not sufficient to recognize inland animals as a distinct subspecies.

There is no significant geographic variation in tooth number or costal groove count. One population of *elongatus* (9 miles W Seiad Valley, Siskiyou County, California) is different from other known populations. They are larger than other *elongatus* and resemble *stormi* in vomerine tooth number (adults, \bar{x} = 13.6), maxillary-premaxillary tooth number (male, \bar{x} = 47.5; female, \bar{x} = 55.1), and leg length (adults, 4.5–6 costal folds between adpressed limbs). The head is wider and longer than other *elongatus* or *stormi*. The shape of the head is proportionally narrower than other populations of *elongatus*. For this reason and because the pigmentation is always that of *elongatus* rather than intermediate between *elongatus* and *stormi*, I believe this population of *elongatus* has paralleled or converged toward *stormi* due to similar environmental conditions.

Plethodon stormi Highton and Brame
Siskiyou Mountains Salamander

Plethodon stormi Highton and Brame, 1965.

Holotype.—USNM 149964, adult male, collected 1.25 miles S Copper, Jackson County, Oregon, by James Riggs, 11 May 1963.

Diagnosis.—*Plethodon stormi* can be distinguished by: a modal number of 17 costal grooves, an olive-tan dorsal stripe in juveniles and usually 4–5.5 costal folds between adpressed limbs in adults.

Distribution and Habitat.—Fig. 16 indicates all known localities for *stormi*. Two unreported localities along Carberry Creek (Indian Creek and Sturgis Guard Station) were analyzed as “western Jackson County, Oregon.” This group is geographically situated between the paratype series and the closest known population of *elongatus* at Oregon Caves National Monument, Josephine County, Oregon. Highton and Brame (1965) reported one *stormi* from near the Oregon Caves (OSU 7319) which would mean *elongatus* and *stormi* are sympatric. The specimen is *stormi*, but it was collected on a trip to both Oregon Caves and the type locality of *stormi*; since both species were collected on the trip, and all salamanders were preserved and stored together without tags, it is likely that the collectors erred in assigning locality to this specimen. Since additional trips to the Oregon Caves area by me have produced only *elongatus*, this area is excluded from the range of *stormi*.

Additional localities for *stormi* in Siskiyou County, California between known populations of *stormi* and *elongatus* are 1.4, 3, 4.7, 5.2 miles E and S Hutton Guard Station (T48N, R11W, Sec. 20, 21, 28, 33, 34); Cook and Green Campground, .25 mile S Cook and Green Guard Station (T48N, R12W, Sec. 36); and 1.4 miles W Cook and Green Guard Station on Middle Fork of Applegate River, then 0.2 mile S (T48N, R12W, Sec. 35). *Plethodon stormi* is com-

monly found in loose rubble or under surface objects on north slopes or in heavily shaded areas.

Description.—This is a short-limbed, long-bodied form closely resembling *elongatus*. The ground color is black in small juveniles and lightens to chocolate brown or light purplish-brown in adults. The venter is black or dark brown in juveniles but changes to purplish in subadults, then to lavender or purplish-gray in adults. The gular region is cream-colored.

The dorsal stripe has an even edge and extends as far as one-half the length of the tail but not to the tip. The olive-tan or yellowish-tan stripe present in juveniles often appears light brown in adults due to an overlying network of melanophores. Coppery iridophores are present beneath the stripe pigment, and in 3 of 53 *stormi* on which careful color notes were taken, the stripe appeared pink or orange due to these underlying iridophores. The pigment in the dorsal stripe appears to be in four layers in order from innermost: coppery iridophores, stripe pigment, melanophores, and white iridophores. About one-half of the *stormi* examined had small flecks of stripe color along the sides.

Both white and yellowish iridophores are present in adults; usually only white ones are present in juveniles. When both are present, the white ones are confined to the dorsal surfaces and the yellowish ones occur ventrally and laterally. Iridophore flecking is heavy on the anterior three-fourths of the head dorsum, the sides of the body and head, and on the limbs. Flecking is lighter in the gular area and on the dorsal stripe; flecking is light or absent along the midventral line. A few gold iridophores may occur (2 of 53 specimens) on the dark brown iris above the pupil.

P. stormi has 16–18 ($M = 17$) costal grooves, 17–19 ($M = 18$) trunk vertebrae, and 3–6 (usually 4–5.5) costal folds between adpressed limbs of adults. The smallest known specimens are 21 mm SVL (USNM 152775, EDB 3059); the largest is 76 mm SVL (EDB 3066). Adults may have 7–25 (usually 8–18) vomerine teeth. Adult males and females have 37–65 ($\bar{x} = 47.4$) and 42–62 ($\bar{x} = 53.9$) maxillary-premaxillary teeth. Size at sexual maturity is about 55 mm SVL; sexual dimorphism is similar to *elongatus*.

Geographic Variation.—Although *stormi* occurs in a small area, it varies markedly in costal groove count. Salamanders from Hutton Guard Station have a modal number of 17 grooves (79.7%) while the paratype series (less than 2 miles away) has a modal number of 18 grooves (81.0%). Animals from western Jackson County resemble the Hutton Guard Station series. No other character appears to vary geographically.

The type series of *stormi* (Highton and Brame, 1965) is closer to *elongatus* in costal groove count (higher than other *stormi*) and

in pigmentation (occasional red stripe) than other populations of *stormi*, but the type locality of *stormi* is farther than other *stormi* populations from existing populations of *elongatus*. Populations of *stormi* in Siskiyou County, California and from Sturgis Guard Station, Jackson County, Oregon are 11 and 9 miles respectively from known populations of *elongatus*. These populations of *stormi* are more distinct from *elongatus* than is the type series. From this geographic variation it seems most likely that *elongatus* and *stormi* were last in contact along the Applegate River. This could well have been a rassenkreise that was broken by warm and dry conditions along the Applegate River during an interglacial period. This resulted in *elongatus* and *stormi* being distinct and noninterbreeding entities.

PHYLOGENY

Dunn (1926) and Wake (1966) considered *yonahlossee* (an eastern large *Plethodon*) as the most primitive member of the genus. Highton (1962) suggested that the eastern small and western *Plethodon* resemble the generic ancestor more closely than the eastern large *Plethodon*. He considered *yonahlossee* as one of the most specialized members of the genus. Thurow (1968) speculated that the western members of the genus have the most primitive characters.

Low numbers of trunk vertebrae and high numbers of teeth are considered to be primitive characters in the tribe Plethodontini (Wake, 1966). He also stated that primitive species of the genus *Plethodon* have long legs. Reduction in numbers of maxillary teeth was considered to be a specialized condition. Thurow (1968) listed large heads as a primitive character. My data indicate the number of teeth is generally correlated directly with the head width in western *Plethodon*.

Fig. 17 illustrates my concept of evolutionary relationships of the western *Plethodon*. The most primitive species is on the left, the most advanced on the right. I consider *vandykei* to be most similar to the ancestral type since it has the longest legs, widest head, fewest vertebrae, and highest number of both vomerine and maxillary-premaxillary teeth (all considered primitive traits). The *Vandykei* and *Vehiculum* groups are closely related and this line was probably separated from the *Elongatus* group early in the development of the genus.

There are primitive members (*vandykei*, *dunni*, and *stormi*) and specialized members (*larselli*, *vehiculum*, *gordoni*, and *elongatus*) in each species group. The primitive members have wider heads, longer legs, more teeth, and fewer vertebrae than their more specialized counterparts. Possibly this parallel evolution of each group

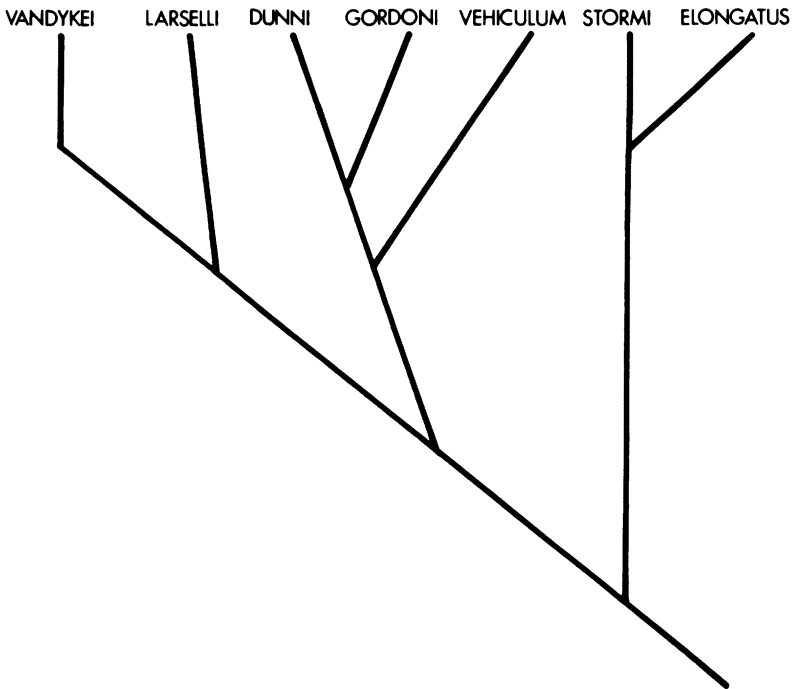


FIG. 17.—Dendrogram of a suggested phylogeny of the western *Plethodon*.

in regard to head shape is due to feeding specializations, but few comparative data on food habits are available to substantiate this. Dumas (1956) demonstrated that *dunni* ate larger food items and a greater variety of food than sympatric *vehiculum*; Altig and Brodie (unpubl.) found similar relationships between *dunni* and sympatric *larselli*. This could be due to different head widths or to the larger size of *dunni*.

KEY TO THE WESTERN *PLETHODON*

1. Outer (fifth) toe on the hindfoot with one phalanx (Fig. 18C); venter reddish; males without a mental gland *larselli*
 Outer (fifth) toe on the hindfoot with two phalanges (Fig. 18A, B); venter usually not reddish; mental glands present in males 2
2. Parotoid glands present (Fig. 18D); modal number of 14 costal grooves *vandykei*
 Parotoid glands absent (Fig. 18E); modal number of costal grooves 15 or more 3
3. Modal number of 17 – 18 costal grooves; short toes (Fig. 18B); little or no iridophore flecking on the iris of the eye 4

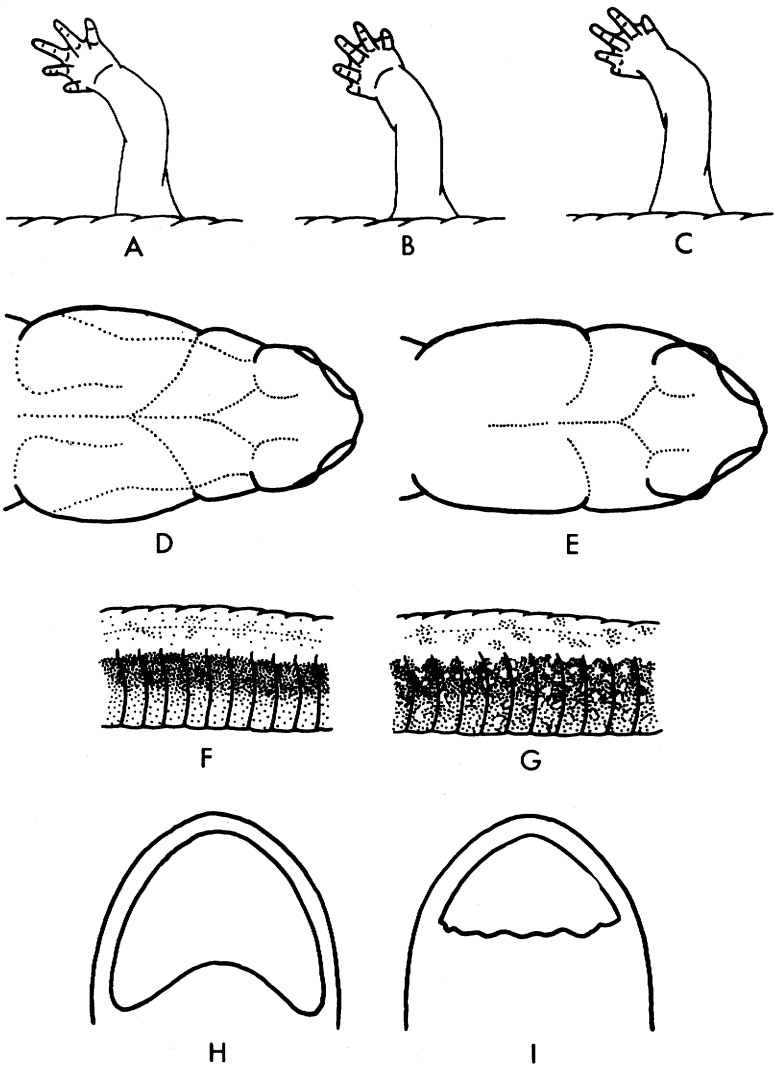


FIG. 18.—Key characters in the western *Plethodon*. Symbols: A,E,G,H, *dunni*; B, *elongatus*; C, *larselli*; D, *vandykei*; F,I, *vehiculum*.

- Modal number of 15 – 16 costal grooves; long toes (Fig. 18A);
 iridophore flecking heavy on the iris of the eye, at least
 above the pupil 5
4. Modal number of 18 costal grooves; reddish dorsal stripe
 extends at least three-fourths down the tail, usually to the

- tip; 5.5 – 8.5 costal folds between adpressed limbs, usually
 6.5 – 7.5 *elongatus*
- Modal number of 17 costal grooves; olive-tan dorsal stripe
 extends at least to the base of the tail, usually half way
 to the tip; 3 – 6 costal folds between adpressed limbs, usu-
 ally 4 – 5.5 *stormi*
5. Dorsal stripe absent in adults 6
 Dorsal stripe present, sometimes heavily covered with
 melanophores 7
6. Flecks of color usually present on the dorsum; usually 3.5 –
 4.5 costal folds between adpressed limbs; mental gland in
 males without posterolateral tips (Fig. 18I) – *vehiculum* (part)
 Usually lacks light flecks on dorsum, if present they are color-
 less; usually 2 – 2.5 costal folds between adpressed limbs;
 mental gland in males with posterolateral tips (Fig. 18H) –
 *gordoni*
7. Dorsal stripe variable in color, extends to tip of tail; stripe
 not encroached upon along margins by the ground color
 and flecks of stripe color not present along upper sides of
 body (Fig. 18F); modal number of 16 costal grooves in
 most areas (modal count in Lane and Douglas counties,
 Oregon = 15); mental gland in males without postero-
 lateral tips (Fig. 18I) *vehiculum* (part)
 Olive dorsal stripe extends onto tail but not to tip; stripe
 appears eroded along the edges with an interdigitating of
 stripe and ground color; flecks and blotches of stripe color
 present along upper sides of body (Fig. 18G); modal num-
 ber of 15 costal grooves (16 in Benton County, Oregon);
 mental gland in males with posterolateral tips (Fig. 18H) –
 *dunni*

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Zoology Section, Clemson University, Clemson, South Carolina 29631

APPENDIX I

Specimens Examined

Plethodon vehiculum

Group 1.—VANCOUVER ISLAND, BRITISH COLUMBIA: Goldstream Provincial Park, EDB 2276-88, 2596-616, PM 76-80; 2.5 miles W Cameron Lake, EDB 2289-98; Ladysmith, UBC 200; Berkley Stream, NMC 3187; Victoria, UBC 193; Miracle Beach, NMC 8272; Brentwood, UBC (10 specimens, no numbers), PM 87-106; Sooke, PM 74; Union Bay, USNM 29616, 52108; Renfrew, PM 75; 8 miles WNW Qualicum Beach, CAS-SU 9584-5; Cowichan Lake, PM 81-6, 638, 798-800; Kyuquot, PM 922.

Group 2.—BRITISH COLUMBIA: Cultus Lake, UBC 194-5; Cultus Lake Provincial Park, NMC 7204 (16 specimens), 7205 (25 specimens); East Shore, Cultus Lake, UMMZ 123959 (5 specimens); North Vancouver, UBC 877; Vancouver, UBC 855, 1079; Lake Haney, NMC 10148; UBC Forest, Haney, UBC 871; McNab Creek, Howe Sound, UBC 872; Hope, NMC 1114.

Group 3.—JEFFERSON COUNTY, WASHINGTON: 13.9 miles NE Quinault, EDB 2757-97; Hoh River, CAS 47509-13, 47700, FMNH 105749; 4-5.6 miles from Hwy 101 up Hoh River, MVZ 46188-97, 46218-27; 9 miles from Hwy 101 up Hoh River, MCZ 26158-63. GRAY'S HARBOR COUNTY, WASHINGTON: Quinault, CAS 29950-8, 29960-2, 39227, 39229-36, 39238-41, FMNH 92900-1, 92903; 2 miles S Quinault River, CAS-SU 9282; 3.6 miles SSW Quinault, MVZ 46216-7; Montesano, CAS 24104; Melbourne, CAS 24105; Humptulips, CAS 29998-9, 39244-5; Hoquiam, CAS 39207, 39210-1, 39214, 39216, 39219, 39221, 39224, FMNH 92904-6, AMNH 14470-3. CLALLAM COUNTY, WASHINGTON: nr Forks, MVZ 46198-200, 46228-33, CAS 48904-13, FMNH 92892-6, 93423; Ozette, WSU 40-95 to 40-103; Ozette Lake, AMNH 45940; Sol Duc Hot Springs, CAS 78716-7, 78748-51.

Group 4.—MASON COUNTY, WASHINGTON: Skokomish River Valley, UMMZ 54349-69 (49 specimens); Lake Cushman, UMMZ 48414-8, 52078, 52080-2, 52514 (2 specimens), FMNH 92911-3, 93424, AMNH 15325-7, 17848, 17853, 17855, 20596 (2 specimens); 8 miles S Sheldon, FMNH 92882-9; 3 miles N Staircase Camp, MVZ 27291; Tripletrip, AMNH 20740-1, 20755, 20757 (3 specimens), 20760, 50802, 59818; Hoodspout, AMNH 35841-4, 36955-9.

Group 5.—PACIFIC COUNTY, WASHINGTON: South Bend, CAS 29890-901; 5-6 miles S South Bend, EDB 992-1004, 1079, 2743-56, LACM 31200-5; 11.4 miles S South Bend, MVZ 46214-5; 4 miles ENE Frances, LACM 31194-8. WAHAKIUM COUNTY, WASHINGTON: Gray's River, MVZ 41385; 6.3 miles SE Cathlamet, MVZ 46212. COWLITZ COUNTY, WASHINGTON: 3 miles E Mouth of Kalama River, MVZ 36844.

Group 6.—SNOHOMISH COUNTY, WASHINGTON: Mt. Pilchuck, CA 12742-3, LACM 31265-9, FMNH 41280-1; Monrow, CAS 6907-9; 4 miles NW Monrow, AMNH 65182. KING COUNTY, WASHINGTON: Green River Gorge, FMNH 36874-9, 69492-525, 92869-81, 92908-10; Seattle, FMNH 105223, MVZ 41382-3, CAS-SU 1647-51; 0.5 mile S Paradise Lake, MVZ 41322-6. PIERCE COUNTY, WASHINGTON: Tacoma, FMNH 92914-6,

LACM 31243-4; 2 miles SW Eatonville, LACM 31206-12; 1 mile SW Carbonado, LACM 31213-42; Green River Gorge, CAS 63062-8. LEWIS COUNTY, WASHINGTON: Cowlitz River, near Randle, FMNH 92890-1; West Fork, Tilton River, MVZ 46238.

Group 7.—SKAMANIA COUNTY, WASHINGTON: Archer Falls, EDB 706-11, 794-9, 1065-77, 2705-7, LACM 31246-64; 2.5 miles E Stevenson, MVZ 37359.

Group 8.—CLATSOP COUNTY, OREGON: Elsie, OSU 4162 (7 specimens); Jewell, OSU 4195; Saddle Mt. Road, OSU 4166-86; Young's River, CAS-SU 5223; Clatsop Beach, CAS 63834-5; Olney, CAS 29879; Hwy 30, Columbia River, LACM 31185-6; 4.9 miles SE Westport, MVZ 46208-11, 46187; 3.2 miles NW Clatskine, MVZ 46184-6, 46207; Cannon Beach, CAS 55292. COLUMBIA COUNTY, OREGON: 2.8 miles S Scappoose, MVZ 46204.

Group 9.—MULTNOMAH COUNTY, OREGON: Portland, EDB 1832-5, 1864-8, OSU 144-9, 155-7, 160-1, 166-74, 180-1, MVZ 61652-4, 61656-80, 74480-2, CAS-SU 5250-3. CLACKAMAS COUNTY, OREGON: 3 miles S Boring, EDB 1851-2; 2 miles E Carver, MVZ 61655.

Group 10.—TILLAMOOK COUNTY, OREGON: Wheeler, EDB 2273-5, 2318-25, OSU 5100-2, 5105-7, 9120; Manhattan, OSU 9147; Neskowin Forest Camp, OSU 5362-6; 7.9 miles NW Vernonia Jct., OSU 4160; 5.2 miles E Hemlock, UMMZ 125404 (7 specimens), 125405 (20 specimens).

Group 11.—LINCOLN COUNTY, OREGON: Cape Perpetua, EDB 1009, OSU 1137-41, 1328-32, 1338-41, 4048-9, 4318-64, 4901, 4991, 6425, 8731-4; Nelscott, OSU 737; Yaquina Bay, OSU 2756-9; Denzer, MVZ 25263-4, 25266-70; Fogarty Creek, MVZ 42430-5, 42437-41, 61681-93; 5 miles E Siletz, OSU 7790; 9 miles N Siletz, LACM 31180-4; 11 miles N Siletz, LACM 31173-9; 10.3 miles SW Alsea, LACM 30643, 31155-6, 31159-70; 12.3 miles ENE Tidewater, LACM 31187-92; Logsdens, OSU 3817-26; Maple Forest Camp, OSU 1372.

Group 12.—BENTON COUNTY, OREGON: Hyde (Hide) Creek, EDB 528-81, 605-74, 691-746, 760-2, 847.

Group 13.—LANE COUNTY, OREGON: Lobster Valley, EDB 849; nr Fisher, EDB 863-6, 868, 1080; 5-8 miles E Mapleton, EDB 1107-47.

Group 14.—LANE COUNTY, OREGON: Shady Dell Forest Camp, OSU 4032, 4294-7; Fall Creek, LACM 31171-2; 9 miles NW Oakridge, OSU 3848-52; 6 miles E Oakridge, CAS 85020-1; 13 miles SE Dexter, MVZ 46239; Dorena Reservoir, EDB 2727-9. DOUGLAS COUNTY, OREGON: near Steamboat, EDB 2547, 2550; 2 miles S Canyonville, EDB 2329-30.

Group 15.—DOUGLAS COUNTY, OREGON: 16.3 miles E Scottsburg, OSU 5591-602; 1 mile E Scottsburg, EDB 869; 7-11 miles E Reedsport, EDB 964-5, 2233-42, 2491-3, 2617-26, 2686-96, MVZ 46183, 46202, 56104; Loon Lake, EDB 2271-2, OSU 5604.

Group 16.—COOS COUNTY, OREGON: Charleston, OSU 3909; Coos Bay, AMNH 55329; 2 miles W Coquille, OSU 4904-11; 2.6-7.2 miles SW Coquille, MVZ 42201, 46181-2, 56067, 56103, 56105; 4 miles SE Myrtle Point, EDB 2259-61; 5.7 miles SE Remote, OSU 3693-4; 3 miles SW Powers, OSU 3680-1.

Plethodon vehiculum examined but not analyzed with a group. WASHINGTON. WHATCOM COUNTY: Lynden, OSU 8585-6; 5.3 miles SE Glacier, WSU 59-338. JEFFERSON COUNTY: 3 miles S, 3.5 miles W Quilcene, AMNH 71524-6; Destruction Island, MVZ 34939-42. CLALLAM COUNTY: Elwha Ranger Station, CAS-SU 9281; $\frac{3}{4}$ mile S Elwha, FMNH 92897-9; Lake Crescent, FMNH 27109-10, MVZ 46234-7; Snider Ranger Station, MVZ 41379-81. OREGON. POLK COUNTY: 1 mile S, 10 miles W Peedee, EDB 724; 2 miles W Falls City, OSU 4996; 7 miles SW Falls City, OSU 3815-6; $7\frac{3}{4}$ miles

E Valsetz, OSU 3811-4, 3827. LANE COUNTY: Wohink Lake, OSU 1009; Lane-Douglas County Line, OSU 5606-12. DOUGLAS COUNTY: 11 miles W Sutherlin, OSU 10101-4; 4.8 miles NW Umpqua, MVZ 46203; Tsiltcoos (Siltcoos) River, CAS-SU 1640. "*P. intermedius*" holotype, USNM 4732a.

Plethodon dunni

Group 18.—PACIFIC COUNTY, WASHINGTON: 5 miles S South Bend, EDB 991; 7 miles SW South Bend, OSU 9338-40; 4 miles ENE Frances, LACM 30663, 31199. COWLITZ COUNTY, WASHINGTON: 5.4 miles E Wahkiakum County Line, EDB 1880; 2 miles E Stella, MVZ 37358. WAHAKIUM COUNTY, WASHINGTON: 6.3 miles SE Cathlemet, MVZ 46157; 8 miles NW Skamokawa, LACM 30664; 12 miles NE Cathlemet, PLU A-0364.

Group 19.—CLATSOP COUNTY, OREGON: 10 miles NE Elsie, EDB 2326-8; 2 miles W Elsie, OSU 4161 (46 specimens); 4.5 miles NW Jewell, OSU 4196-7; Cannon Beach, CAS 55291, 55293; Young's River, CAS-SU 4934-9, 5222. COLUMBIA COUNTY, OREGON: 2.8 miles S Scappoose, MVZ 46154, 46173-5; 4.5 miles SSE Rainier, MVZ 46155-6, 46176-7; 2.3 miles NW Clatskanie, MVZ 46178.

Group 20.—MULTNOMAH COUNTY, OREGON: Portland, EDB 1817-31, 1836-45, 1856-63, OSU 147, 150, 178-9, 712, 714-5, 717-22, 724-7, MVZ 61645-51, 74479, CAS 71405.

Group 21.—MULTNOMAH COUNTY, OREGON: Ainsworth State Park, EDB 719-23, 789, 1012-5, 2015-23, 2055-108, 2336-9; Multnomah Falls, EDB 814-21; Wahkeena Falls, EDB 2148-87, LACM 30646-58; Oneonta Gorge, EDB 2130-43, 2347-51; Latourelle Falls, LACM 30659; Washtucna Falls, LACM 30660-2. HOOD RIVER COUNTY, OREGON: Starvation Creek Falls, EDB 1025-32.

Group 22.—MARION COUNTY, OREGON: 3-4 miles W Detroit, LACM 10816-7; North Santiam River, OSU 176; between Niagara and Detroit Dam, OSU 8086-8. LINN COUNTY, OREGON: Cascadia, OSU 745, 980, LACM 30631-6; Foster, OSU 773, 3287-8; 4.8 miles E Foster, OSU 1709-10; 7.9 miles ESE Foster, MVZ 46150-3; Fall Creek, OSU 1006; Moose Creek, OSU 1643-4; House Rock Forest Camp, OSU 5129-30; Trout Creek Forest Camp, OSU 6071-80; Fernwood Forest Camp, OSU 6081-4, 6435, 6451-3; Crabtree Creek, OSU 7093, 7094-5, 7103.

Group 23.—TILLAMOOK COUNTY, OREGON: Wheeler, EDB 2311-7; 1 mile SW Wheeler OSU 9118-9, 9148; Tillamook, OSU 787-9; 7 miles E Tillamook, OSU 1321-6; Neskowin Forest Camp, OSU 5367; 5.2 miles E Hemlock, UMMZ 125401 (6 specimens), 125402 (20 specimens).

Group 24.—LINCOLN COUNTY, OREGON: Cape Perpetua, EDB 1010-1, OSU 1142-3, 1833, 1835-7, 4368-76, 8730; Yaquina Bay, OSU 1099, 1395-6; 5 miles E Siletz, OSU 7789; Sugar Bowl Creek, OSU 2716; 10.3 miles SW Alsea, LACM 30616, 30644-5, 31154, 31157-8; 12.3 miles ENE Tidewater, LACM 30637-40, 31193; 23.8 miles N Hwy 20 from Hwy 299, LACM 10807-15.

Group 25.—BENTON COUNTY, OREGON: Hyde (Hide) Creek, EDB 516-26, 585-604, 685-90, 731-46, 807-11, 876-80, 886; Corvallis Water Shed, EDB 893-4, 897-9, 1348-52, 1932-8, 2302-5.

Group 26.—LANE COUNTY, OREGON: Shady Dell Forest Camp, OSU 3699-702, 4033-8, 4298, LACM 10818; 9 miles NW Oakridge, OSU 3853-5; 6 miles E Oakridge, CAS 85013-9, 85022-3; Fall Creek, OSU 7943-5, LACM 30628-30; 8.9-13.0 miles SE Dexter, MVZ 46158-9; 4 miles E Creswell, OSU 3971-3; 13 miles E Eugene, OSU 3981, 4259-70; 0.5 mile SSE McKenzie, OSU 6211-2; 1 mile E Vida, OSU 3943, 4045-6; Emile Creek, CAS 85048-52.

Group 27.—LANE COUNTY, OREGON: nr Fisher, EDB 851-2, 858-61, 867; 5-8 miles E Mapleton, EDB 1148-92; 1 mile above Swisshome, OSU 8034-7.

Group 28.—DOUGLAS COUNTY, OREGON: nr Steamboat, EDB 2554-72, 2574-84, 2588-95; Canyon Creek, OSU 192-3, CAS 85032-41, 86696.

Group 29.—DOUGLAS COUNTY, OREGON: 12.5 miles NW Drain, OSU 8431; 16.3 miles E Scottsburg, OSU 5603; 4 miles SW Scottsburg, OSU 1302-4; 8 miles W Scottsburg, MVZ 52092; 11 miles E Reedsport, EDB 962-3, 2243-9, 2490, 2494, 2627-43, 2697-704, 2712-5, MVZ 56044-57; Loon Lake, EDB 2270.

Group 30.—COOS COUNTY, OREGON: Charleston, OSU 3881-90; 2 miles E Coquille, OSU 4912; 2 miles W Coquille, OSU 4903; 2.6-3.5 miles SW Coquille, MVZ 56058-9, 56064-6, 56199; 6 miles E Powers, OSU 6688, 6700; 18 miles S Powers, OSU 7846-8.

Group 31.—CURRY COUNTY, OREGON: Sixes, LACM 30622-4, OSU 2944; 4.5 miles E Sixes, LACM 30625; Humbug Mountain, EDB 763, 977-84, 2229-30, 2268, LACM 30626-7, OSU 2875, 2895-902, 2918-25, 8075; Floras Creek, OSU 7849-55; 5 miles SW Rogue River, OSU 7879-80; 11 miles above mouth of Rogue River, MVZ 18565-81; Rogue River, CAS 71960; Lobster Creek, MVZ 46147-9, 46160, 46162-9, 46179-80, CAS-SU 4731, 4735, 4761-7, 4769-73; 7 miles N Pistol River, MVZ 56060-3; 11.2 miles S Carpenterville, MVZ 56038-43; Westmore Guard Station, OSU 5526-31, 5559.

Plethodon dunni examined but not analyzed with a group. OREGON. CLACKAMAS COUNTY: "near Portland," USNM 95196 (holotype); 3 miles S Boring, EDB 1846-50; Eagle Creek, LACM 30617-21; Collawash River at confluence with Clackamas River, OSU 7276-82. POLK COUNTY: 1 mile S, 10 miles W Peedee, EDB 676-9, 725-30. DOUGLAS COUNTY: 4.8 miles NW Umpqua, MVZ 46170-2. CALIFORNIA. DEL NORTE COUNTY: Fort Smith, EDB 1309.

Plethodon gordoni

See text, specimens listed as paratypes.

Plethodon elongatus

Group 32.—COOS COUNTY, OREGON: 14.5 miles S Powers, OSU 6691, 6699. CURRY COUNTY, OREGON: 1 mile E Sixes, LACM 30692-3; 4.5 miles E Sixes, LACM 30687-91; Humbug Mountain, EDB 968-76, 2231-2, LACM 30677-86, OSU 2870-4, 2876-94, 2933, 8060-73, FMNH 131279-80; Winchuck River, EDB 764-87, 834-43, 966-7, LACM 30697-8, OSU 5537-58, 5579; 8 miles up Chetco River, OSU 8004-7; 14.1 miles up Chetco River, EDB 2254-7; 14.7 miles N Brookings, OSU 5655-61; 11 miles up Rogue River from mouth, FMNH 71358-60, 71363-71, MVZ 18550; Lobster Creek, MVZ 46119-21, CAS-SU 4710-3, 4733-4; Carpenterville, FMNH 36872-3, 92453-8; 11 miles S Carpenterville, MVZ 56077; 1 mile E Pistol River, LACM 30694-6; 7.5 miles N Pistol River, MVZ 56097-101.

Group 33.—JOSEPHINE COUNTY, OREGON: 4 miles E Wilderville, OSU 2336-56; 13.6 miles up Deer Creek from Hwy 199, EDB 3026-30; near entrance to Oregon Caves, OSU 4761-8, 4.2 miles up Grayback Road from Hwy 46, EDB 3012-7; Grayback Forest Camp, EDB 987-90, 3018-9; 1 mile E Cedar Guard Station, EDB 2534-6; 10 miles E, 3 miles S Cave Junction, SOC 32-3, 55.

Group 34.—DEL NORTE COUNTY, CALIFORNIA: Fort Smith, EDB 812-3, 2251-3; Smith Redwoods State Park, SSC 619, FMNH 71355-7, LACM 10799-804; 1 mile W Smith State Park, MVZ 81837; 3 miles E Smith State Park, MVZ 73245-55; Smith River, FMNH 71355-7; 2.9 miles E Smith River, SSC 408-9; Smith River Bridge on Hwy 199, MVZ 74427-31, 80834-9, 81388; 2 miles W Hiouchi Bridge, MVZ 80857-82; 5 miles S Gasquet, EDB 985-6; 3 miles SW, 14.1-20.3 miles NE Gasquet, OSU 2303-7, 2309-20, 2323; 14.1 miles

up Smith River from Gasquet, MVZ 63806-8, 63810; Requa, CAS 29094, 29101, 71325-6, LACM 30665-76; 5 miles SE Requa, FMNH 31863-8, ANSP 23060, MVZ 19141, 32563; Klamath, MVZ 32562; 2 miles E Klamath, CAS 80124-31; 8 miles N Klamath, CAS 80025-42, 80044, 80047-68; 13.6 miles N Klamath, OSU 2292, 5673; 3.4 miles N Humboldt, OSU 5828; Elk Valley Forest Camp, OSU 8011; Turnwar Creek Bridge, CAS-SU 4690; 1 mile E Hwy 101 on Hunters Creek Road, MVZ 73256-60; ½ mile E, ½ mile N Fort Dick, MVZ 56095; 2¼ miles E, 2¼ miles S Fort Dick, MVZ 56072-6, 56082-94, 56200-3, 66215; 2¼ miles N, 6½ miles E Crescent City, MVZ 56069-71, 56078-81, 56096; 3.2 miles NE Crescent City, MVZ 77017-9; 6 miles NE Crescent City, MVZ 73239-44, 74501; 8 miles NE Crescent City, CAS 80148-54; 6 miles E Crescent City, FMNH 31870-2; 5 miles S Crescent City, CAS 81857-9; 7 miles S Crescent City, MVZ 44037; 5 miles SE Crescent City, CAS 81260-91; 10 miles SE Crescent City, CAS 81833-5.

Group 35.—HUMBOLDT COUNTY, CALIFORNIA: Boise Creek, LACM 10798, MVZ 44376-82, 45836-41, 46122, 56174-6, 70329-34; 10.2 miles W Boise Creek, MVZ 54459-61, 56177; Low Gap Creek, SSC 571 (5 specimens), MVZ 77020-1, 81841-51; 3 miles N Hoopa, MVZ 80808-12; 5.5 miles NW Hoopa, SSC 572 (5 specimens); 4.9 miles S Weitchpec, MVZ 80884-919, 81839-40, 81861-74; 6 miles NE Weitchpec, MVZ 80798-803; Bluff Creek, EDB 2731-5, MVZ 81838. TRINITY COUNTY, CALIFORNIA: 0.4 mile W Salyer, MVZ 80883; 1 mile E Salyer, MVZ 81755-6, 81758; 4 miles ESE Salyer, MVZ 45843, 81754, 81757.

Group 36.—HUMBOLDT COUNTY, CALIFORNIA: Prairie Creek, CAS 81922; 4 miles NNE Orick, MVZ 44368-75, 56068, 81852-60; 3.1 miles E Blue Lake, MVZ 66531-4; 5.5 miles E Blue Lake, MVZ 45842.

Plethodon elongatus examined but not analyzed with a group. CALIFORNIA. SISKIYOU COUNTY: Seattle Creek, 9 miles W Seiad Valley, JLB 191-5, MVZ 5584-93, 84836, 84847-60.

Plethodon vandykei

Group 37.—CLALLAM COUNTY, WASHINGTON: Forks, UPS 1154-7, FMNH 92825-6, CAS 47493-4, 47496-9. JEFFERSON COUNTY, WASHINGTON: 16 miles W Jackson Ranger Station, UPS 5608; 13.9 miles NE Quinalt, EDB 2935-41, RAN 1512-20. GRAY'S HARBOR COUNTY, WASHINGTON: 3 miles SE Ox Bow Ranger Station, UPS 2584. MASON COUNTY, WASHINGTON: Olympic Mountains, AMNH 20531 (3 specimens), 20585 (6 specimens), 20591 (5 specimens), 20599 (6 specimens); Tripletrip, AMNH 20596, 20749-50, 20758, 20772; Lincoln Ranger Station, UPS 5900; Mt. Cushman, AMNH 17100; Lake Cushman, MVZ 41384; 6 miles above Lake Cushman, MCZ 6607-8; Staircase Camp, CAS 55340, AMNH 17842; Hoodspport, AMNH 35831-6, 36960, 37592-5, 37597-8; Skokomish River Valley, UMMZ 54213-4, 54215 (3 specimens), 54218-31, 54233.

Group 38.—PACIFIC COUNTY, WASHINGTON: 5-7 miles S South Bend, EDB 2709-10, OSU 9336-7, FMNH 131284, PLU A-0379-89, A-0621-7, UPS 1414, 9412-4. WAHKIACUM COUNTY, WASHINGTON: nr Skamokawa, RAN 5093-132, 3297-316, 5351, 5355, 5358, 5360.

Group 39.—PIERCE COUNTY, WASHINGTON: Cataract Creek, CAS-SU 9721-2, FMNH 59239-40; 7 miles NNW Mt. Rainier, MVZ 52120-1; Carbon River, UPS 7178, 7180-3, 7190, 7197-8, 7408, 7410, 7412, 7415-6. LEWIS COUNTY, WASHINGTON: west fork Tilton River, EDB 2960, 3128, OSU 4933-4, FMNH 37194-5, MVZ 46123-4, PLU A-0216, UPS 1631, 2129.

Group 40.—KOOTENAI COUNTY, IDAHO: Wolf Lodge Bay, Coeur d'Alene Lake, EDB 2664-85, 2730, 2934, RAN 684-770, FMNH 92827, ISU 3309 (7 specimens), MVZ 46125, 46127, 46129-46, USNM 11054-5, 129406-8, AMNH 53902-3, 55112-3, OSU 8178-80, UI 62, 68, 116, 308.

Plethodon vandykei examined but not analyzed with a group. IDAHO. BENEWAH COUNTY: 5.5 miles SW Ennida, UI 212. BONNER COUNTY: Wellington Creek, EKT 722 (2 specimens). IDAHO COUNTY: 16 miles E Lowell, EKT 685 (6 specimens); 21 miles E Lowell, EKT 710. MONTANA. LINCOLN COUNTY: Troy, EKT 537-8; 8 miles E Troy, CWC (17 specimens, no numbers); 5.5 miles SE Troy, EKT 717 (2 specimens), 718; Hoodoo Mountain, EKT 530. SANDERS COUNTY: 2 miles W Noxon, EKT 750. MINERAL COUNTY: 6.5 miles S Paradise, EKT 676-7.

Plethodon stormi

Group 41.—JACKSON COUNTY, CALIFORNIA: ½ mile N California state line, OSU 7316-8; 1½ miles S Copper, USNM 149964-6; 3 miles S McKee Bridge, USNM 152773-8; Copper, SOC 42, 46.

Group 42.—SISKIYOU COUNTY, CALIFORNIA: 0.5–5.2 miles E and S Hutton Guard Station, EDB 844-5, 903-61, 1895-1903, 2495-528, 2644-8, 2650-63, 2716-22, 3031-59.

Group 43.—JACKSON COUNTY, CALIFORNIA: Indian Creek, EDB 900-2; Sturgis Guard Station, EDB 2529-33.

Plethodon stormi examined but not analyzed with a group. CALIFORNIA. SISKIYOU COUNTY: Cook and Green Guard Station, EDB 3065; 1.4 miles W, 0.2 mile S Cook and Green Guard Station, EDB 3066.

Plethodon larselli

Group 44.—SKAMANIA COUNTY, WASHINGTON: Archer Falls, EDB 712-8, 791-3, 1033-64, 1321-3, 1883-94, 2711, 2942-3.

Group 45.—SKAMANIA COUNTY, WASHINGTON: Dog Creek, 12.8 miles E Stevenson, EDB 2986-8, 3008, RAN 1540-54.

Group 46.—MULTNOMAH COUNTY, OREGON: Ainsworth State Park, EDB 790, 1016-24, 2024-9, 2047-54, 2340-4, MVZ 79132; Oneonta Gorge, EDB 2109-23, 2345-6, 2537-46; Wahkeena Falls, EDB 2299; North Slope Larch Mountain, USNM 134129-30. HOOD RIVER COUNTY, OREGON: Starvation Falls, EDB 2970-2, 2983-5, MVZ 74473, 74475-8; 1.5 miles N, 2.5 miles E Cascade Locks, PSC 92-3.

Plethodon larselli examined but not analyzed with a group. WASHINGTON. SKAMANIA COUNTY: Beacon Rock State Park, RAN 1574-5.

DEFENSIVE DISPLAYS IN SOME AUSTRALIAN
DENISONIA (SERPENTES: ELAPIDAE)

CLIFFORD RAY JOHNSON

ABSTRACT: Defensive displays in two Australian elapid snakes, *Denisonia maculata devisii* and *D. daemeli*, are described from field and laboratory observations.

ALTHOUGH certain aspects pertaining to defensive behavior (mostly flattening of neck) have been reported for several genera of Australian elapids, detailed accounts of this behavior are lacking.

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