High incidence of limb skeletal variants in a peripheral population of the red-backed salamander, *Plethodon cinereus* (Amphibia: Plethodontidae), from Nova Scotia

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A single population of *Plethodon cinereus* from northwestern Nova Scotia shows a high incidence of limb skeletal variants, which is exceptional for this morphologically conservative species. Included are nine carpal patterns and five tarsal patterns, which result from the variable occurrence of 11 different combinations of fused adjacent mesopodial elements, and frequent absence of one or more ossified phalanges; one instance of increased phalangeal number also is noted. Primitive plethodontid carpal and tarsal patterns, which characterize *P. cinereus* from other parts of its range, occur in 69 and 71% of the carpi and tarsi examined, respectively. Modal phalangeal formulae also are those typical of *P. cinereus* generally. Several mesopodial variants resemble those seen in other plethodontid genera; they may have appeared independently in *P. cinereus*. Others are unique to this population. Both the genetic basis and geographical extent of this variation are unknown.

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Une population de *Plethodon cinereus* du nord-ouest de la Nouvelle-Ecosse semble être le siège de variations importantes des os des membres, phénomène exceptionnel chez cette espèce plutôt conservatrice morphologiquement. Neuf de ces variations affectent les carpes et cinq affectent les tarses, résultats de la fusion, selon 11 combinaisons différentes, d'éléments mésopodiaux adjacents et de l'absence fréquente de l'une ou de plusieurs des phalanges ossifiées; on a observé aussi un cas où le nombre de phalanges était plus grand que la normale. Des arrangements pléthodontidiens primitifs, caractéristiques de *P. cinereus* ailleurs dans sa répartition, ont été observées dans 69% des carpes et 71% des tarses examinés. Les modes des formules des phalanges sont également typiques des populations normales de *P. cinereus*. Plusieurs des variations mésopodiales rappellent celles qui existent chez d'autres genres de Plethodontidae; il est possible qu'elles soient apparues indépendamment chez *P. cinereus*. Certaines des variations sont particulières à cette population. Le fondement génétique et l'étendue géographique de ces variations demeurent inconnus.

[Traduit par le journal]

Introduction

The genus *Plethodon* is a morphologically generalized member of the tribe Plethodontini, one of two advanced lineages of terrestrial plethodontid salamanders with direct development (i.e., they lack a free-living aquatic larval stage). The most speciose temperate plethodontid genus, *Plethodon* perhaps also is the most conservative morphologically: except for relatively few characters, such as trunk vertebral number (Highton 1977), skeletal variation both between and within many species typically is so slight as to render osteology useless for taxonomic purposes (Wake 1963). This is especially true of so-called quasi-continuous variants (Grüneberg 1963), such as those which involve fusion or presence/absence of individual elements, which differentiate many other plethodontid taxa (Wake 1966; Wake and Elias 1983). In this paper I report extensive limb skeletal variation in a single population of the red-backed salamander, *P. cinereus*, the most widely ranging species in the genus, from the periphery of its range. In both its frequency and diversity, this variation may equal or exceed that previously reported for any population of plethodontid salamanders; included are several mesopodial and phalangeal patterns which are unique to this population.

Materials and methods

Nearly 100 *P. cinereus* were collected from a single locality on Glascow Mountain, 12 km northwest of Parrsboro, Nova Scotia (45°29′ N, 64° 26′ W), on 18 May 1982. The locality lies within an extensive deciduous hardwood forest (primarily sugar maple, *Acer saccharum*) on a northeast-facing slope beside a small stream (elevation ca. 100 m). Animals were distributed continuously within the locality and were collected along a 150-m section of the stream. Fifty adults (33 males, 17 females) were chosen randomly from the total sample and cleared and differentially stained for bone and cartilage (Hanken and Wassersug 1981). Each animal was scored on both sides for the presence of fused mesopodial elements, overall carpal and tarsal patterns, and phalangeal formulae.[2] Occasionally, adjacent cartilages appeared fused (i.e., contin-

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[2] The left forelimb of a single specimen was damaged during preparation. Complete phalangeal formulae were thus unavailable for this specimen.

uous), yet retained a median crease or suture; these instances were scored as fused. Mean standard length, in millimetres, measured from the snout to the posterior end of the vent, equaled 44.2 (males) and 47.5 (females).

Results

Mesopodial elements

Carpus

Typically, the carpus of *Plethodon* consists of eight separate elements (Wake 1966; Fig. 1, pattern I): ulnare, intermedium, radiale, centrale, centrale 1 (mediale of some authors, e.g., Alberch 1980), distal carpals 1–2, 3, and 4. This pattern was seen in 69% of the carpi examined (Table 1). In the remaining carpi (31%), these elements were fused in any one of five different combinations: (1) intermedium, ulnare; (2) distal carpals 3 and 4; (3) distal carpal 4, centrale; (4) distal carpals 3 and 4, centrale; (5) intermedium, centrale. Combination 1 was most frequent (18%); two combinations (4 and 5) each were observed in single specimens on one side only.

Variable occurrence of these five fusion combinations yielded seven additional overall carpal patterns (Fig. 1, II–VIII; Table 1), each containing as few as five, and as many as seven, separate carpal units. Two patterns each were found in 10% of the carpi. All of the five remaining patterns were found at lower frequency; three occurred in single specimens on one side only. Thirteen specimens (26%) exhibited different carpal patterns on right and left sides.

Tarsus

Nine separate tarsal elements are characteristic of *Plethodon* (Fig. 2, pattern I): fibulare, intermedium, tibiale, centrale, centrale 1 (or mediale, as above), distal tarsals 1–2, 3, 4, and 5. This pattern was observed in 71% of the tarsi examined (Table 2). The remaining tarsi (29%) displayed six different fusion combinations: (1) intermedium, centrale; (2) tibiale, centrale 1; (3) distal tarsals 1–2 and 3; (4) distal tarsals 3 and 4; (5) distal tarsals 1–2, 3, and 4; (6) distal tarsals 4 and 5. Combination 6 occurred at a high frequency (26%), those remaining were rare: combinations 1, 2, 4 and 5 all were found in only a single specimen; combination 3 occurred on one side of two other specimens.

Variable occurrence of these fusion combinations in a given tarsus yielded four additional overall tarsal patterns (Fig. 2, II–V; Table 2); each pattern contains as few as five, and as many as eight, separate tarsal units. Only one pattern (II) was common (25%); patterns IV and V were seen only on opposite sides of a single specimen. Ten specimens (20%) exhibited right–left asymmetry in tarsal pattern.

Digits

The primitive plethodontid phalangeal formulae are 1-2-3-2 (hand) and 1-2-3-3-2 (foot). They characterize most plethodontid genera and all but two species of *Plethodon*; *P. larselli* and *P. neomexicanus* typically lack one phalange from the fifth toe, giving a reduced foot formula of 1-2-3-3-1 (Wake 1963, 1966). The primitive formulae were found in 92% (hand) and 94% (foot) of the limbs examined in this study. Remaining limbs displayed the following variants. Hand: 2-2-3-2 (1%), 1-2-2-2 (1%), 0-2-3-2 (5%), 1-2-2 (1%); in the latter case, metacarpals 3 and 4 articulate along their entire length and support two abnormally wide phalanges which appear to represent fused phalanges of digits 3 and 4. Foot: 1-2-3-3-1 (2%), 1-2-2-3-1 (1%), 1-2-3-2-1 (1%), 1-2-3-2-2 (1%), 0-0-1-3-2 (1%). Some digits with a reduced number of phalanges possess a terminal cartilaginous rudiment that may correspond to a missing phalange; in such cases, phalangeal absence was judged by the lack of a distinct, ossified element. Additional, more subtle variation that did not affect phalangeal formula included one hand in which the penultimate phalange of digit 4 articulates with metatarsals 3 and 4; one foot with abnormally short phalanges in digit 3; and two feet with the penultimate phalange of digit 4 so reduced that it barely or only partly separates adjacent proximal and distal elements (Fig. 2, IV).

Forty-three of 49 specimens (88%) had the primitive phalangeal formula in both hands; 2 animals (4%) had the same variant formula on both sides; the remaining 4 specimens (8%) were asymmetric. Forty-four of 50 specimens (88%) showed the primitive foot phalangeal formula on both sides; 1 specimen (2%) had the same variant formula on both sides; the remaining 5 specimens (10%) were asymmetric.

Discussion

Twelve carpal and twelve tarsal patterns have been described in plethodontid salamanders, each pattern comprising a particular combination of fused adjacent elements (Alberch 1980, 1981, 1983; Hanken 1982; Lynch and Wake 1975, 1978; Potter and Sweet 1981; Wake 1963, 1966). Of these, five carpal and three tarsal patterns were observed in the sample of *P. cinereus* considered in this study (see below). This leaves an additional three carpal (V, VI, VIII) and two tarsal (IV, V) patterns in *P. cinereus* that have never been reported before in the Plethodontidae. Larson *et al.* (1981) and Wake (1980) cited a particular rearrangement of the fusions involving distal tarsals 4 and 5 and the centrale as one of two "key innovations" (sensu Liem 1974 and Miller 1949) that characterized the evolution of the arboreal genus *Aneides* from *Plethodon*. This tarsal pattern was not seen in *P. cinereus*. However, in terms of fusions several observed patterns differ from pattern I as much, if not more so, than that seen in *Aneides*. Thus, a polymorphism of discrete character states as different

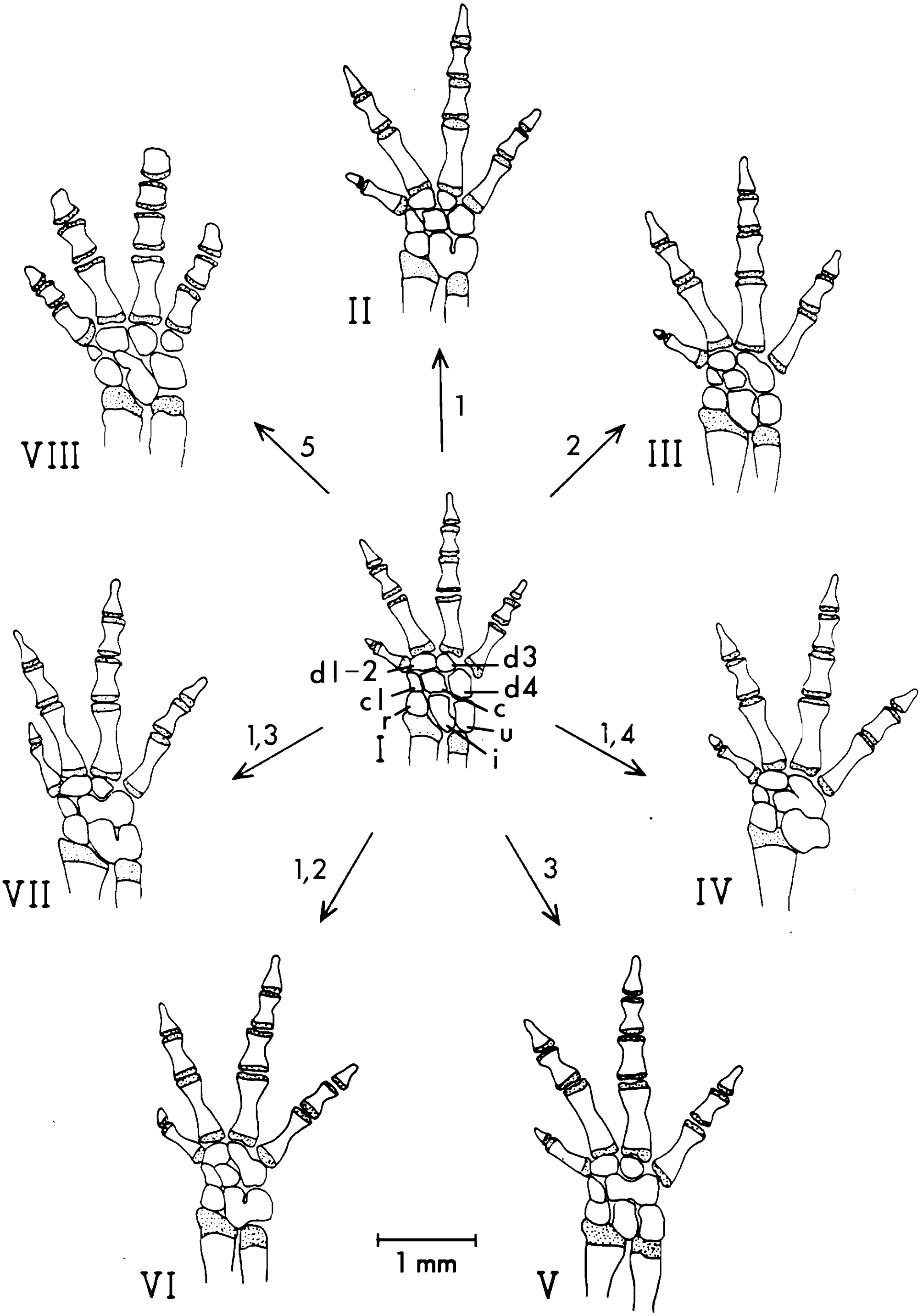

FIG. 1. Alternate carpal patterns I–VIII in *Plethodon cinereus* (dorsal view). All patterns are drawn as right carpi, although two (III, VIII) were observed in the left carpus only; III and IV occurred in the same specimen (ulna was removed from IV during staining). Arabic numerals identify the carpal fusion combination(s) (described in text) that distinguish patterns II–VIII from I. Abbreviations: *r*, radiale; *u*, ulnare; *i*, intermedium; *c*, centrale; *c*1, centrale 1; *d*1–2, distal carpals 1–2; *d*3, distal carpal 3; *d*4, distal carpal 4. Cartilage is stippled, except in carpals which have been left unshaded. Note excessively broad phalanges in VIII, which includes an additional element in digit 1.

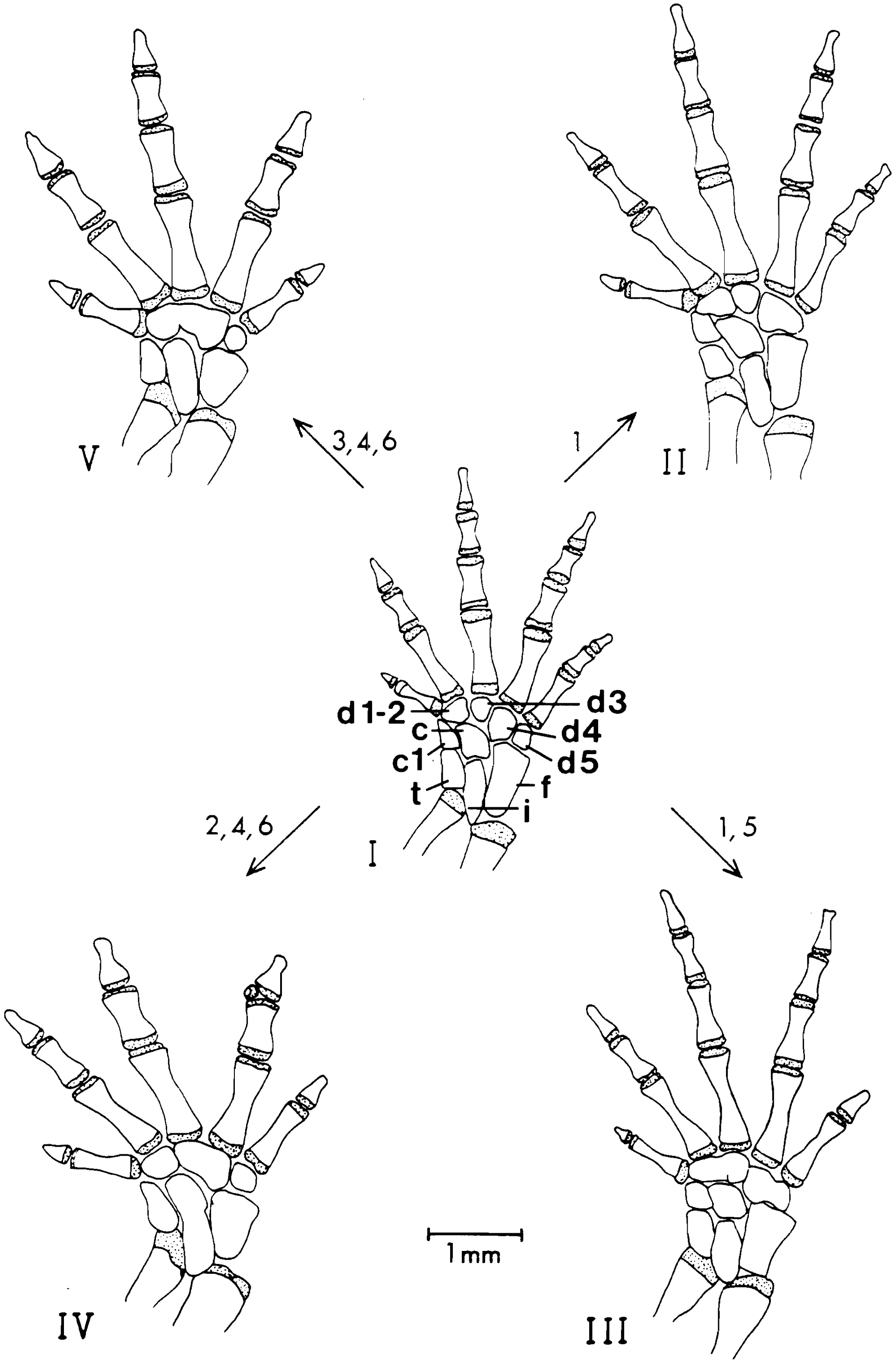

FIG. 2. Alternate tarsal patterns I–V in *Plethodon cinereus* (dorsal view). All patterns are drawn as right tarsi, although one (V) was observed in the left tarsus only; IV and V occurred in the same specimen. Arabic numerals identify the tarsal fusion combination(s) (described in text) that distinguish patterns II–V from I. Abbreviations as in Fig. 1, also: *t*, tibiale; *f*, fibulare; *d*1–2, distal tarsal 1–2; *d*3, distal tarsal 3; *d*4, distal tarsal 4; *d*5, distal tarsal 5. Cartilage is stippled, except in tarsals which have been left unshaded. Note reduced phalangeal formula in III, IV, and V; IV includes an abnormally short phalange in digit 4 that fails to completely separate adjacent phalanges.

TABLE 1. Frequency of five carpal fusion combinations and eight overall carpal patterns in 50 adult *Plethodon cinereus*. Frequency of right–left asymmetry in carpal pattern was 26%

Fusion combinations	% frequency[a]	Carpal pattern[b]	% frequency[a]
(1) Intermedium, ulnare	18	I	69
(2) Distal carpals 3, 4	3	II	10
(3) Distal carpal 4, centrale	16	III	2
(4) Distal carpals 3, 4, centrale	1	IV	1
(5) Intermedium, centrale	1	V	10
		VI	1
		VII	6
		VIII	1

[a] Frequencies were first calculated separately for the right and left sides and then averaged to yield a single value.

[b] I: *i, u, r, c, c1, d1–2, d3, d4*; II: *i–u, r, c, c1, d1–2, d3, d4*; III: *i, u, r, c, c1, d1–2, d3–d4*; IV: *i–u, r, c1, d1–2, d3–d4–c*; V: *i, u, r, c1, d1–2, d3, d4–c*; VI: *i–u, r, c, c1, d1–2, d3–d4*; VII: *i–u, r, c1, d1–2, d3, d4–c*; VIII: *i–c, u, r, c1, d1–2, d3, d4*.

TABLE 2. Frequency of six tarsal fusion combinations and five overall tarsal patterns in 50 adult *Plethodon cinereus*. Frequency of right–left asymmetry in tarsal pattern was 20%

Fusion combination	% frequency[a]	Tarsal pattern[b]	% frequency[a]
(1) Intermedium, centrale	2	I	71
(2) Tibiale, centrale 1	2	II	25
(3) Distal tarsals 1–2, 3	2	III	2
(4) Distal tarsals 3, 4,	1	IV	1
(5) Distal tarsals 1–2, 3, 4	1	V	1
(6) Distal tarsals 4, 5	26		

[a] Frequencies were first calculated separately for the right and left sides and then averaged to yield a single value.

[b] I: *i, t, f, c, c1, d1–2, d3, d4, d5*; II: *i, t, f, c, c1, d1–2, d3, d4–5*; III: *i, t, f, c, c1, (d1–2)–d3, d4–d5*; IV: *i–c, f, t–c1, d1–2, d3–d4, d5*; V: *i–c, t, f, c1, (d1–2)–d3–d4, d5*.

as that proposed as a key innovation in other salamanders is present in *P. cinereus*.

Carpal patterns I, II, III, IV, and VII occur in other plethodontid genera. Pattern I represents the primitive plethodontid pattern (Wake 1966); its presence in *Plethodon* presumably represents the retention of a primitive character. There are at least two explanations for the presence of the remaining patterns in *P. cinereus*. First, they have appeared independently in *Plethodon*, and thus represent instances of convergent evolution. Pattern II, for example, which differs from I in the fusion of ulnare and intermedium, is present in several genera in the tribe Bolitoglossini (*Batrachoseps*, *Parvimolge*, *Oedipina* (Wake 1966); *Chiropterotriton* (Lynch and Wake 1978); *Thorius* (Hanken 1982)) yet within the Plethodontini is found elsewhere only in *Aneides hardii* and rarely in *A. ferreus* (Wake 1963, 1966). Alternatively, a low frequency polymorphism of carpal variants may have appeared early in the Plethodontidae and be retained in many genera, yet remain undetected in most instances due to limited sample sizes typically used to estimate natural variation in osteological characters (see below). Neither alternative can be accepted unconditionally at the present time. Similar arguments apply to those rare tarsal patterns that are also found in other genera (I, II, III).

The predominant carpal (1) and tarsal (6) fusion combinations are the same two combinations that Wake and Elias (1983) found most effective in differentiating neotropical plethodontid genera. Alberch (1980, 1983) cited similar observations in the genus *Bolitoglossa* as evidence of a developmental "constraint" which favors the appearance of certain combinations over others and which may influence long-term trends of morphological evolution in that genus. The *Plethodon* data are consistent with this interpretation as regards the appearance of these combinations in other genera. Furthermore, this suggests that the constraint may be a fundamental, conservative feature of limb development that is shared by at least two major plethodontid lineages, the tribes Plethodontini and Bolitoglossini. Interestingly, this potential constraint has exerted little influence over the direction of change within *Plethodon*: all species share the same modal carpal and tarsal patterns.

Quantitative estimates of intraspecific variation in mesopodial patterns in a variety of other plethodontid salamanders are required in order to fully evaluate the origin and magnitude of that observed in the population of *P. cinereus* from Parrsboro. At present such estimates are available for only a handful of species in relatively few genera (e.g., *Bolitoglossa* (Alberch 1980, 1983); *Eurycea* (Potter and Sweet 1981); *Thorius* (Hanken 1982); *Typhlomolge* (Potter and Sweet 1981)). Nevertheless, from these studies it is clear that the variation in *P. cinereus* is extreme. Species of two neotropical genera, *Thorius* (Hanken 1982) and *Oedipina* (Wake 1966), are considered to have exceptionally high levels of intraspecific variation, yet the range of variation (e.g., number of mesopodial patterns) in the Parrsboro population of *P. cinereus* exceeds even these levels. In this study 9 of the 13 carpal and tarsal patterns were detected at frequencies of 10% or lower; many were observed only in single specimens. Presumably, most of these would have gone unnoticed in a smaller sample of adults. Similarly rare variants may exist in other species, yet remain undetected due to relatively small sample sizes. However, studies which have included samples larger than that included here have not revealed comparable levels of variation. Alberch (1980), for example, found but two tarsal patterns in a survey of 126 tarsi of two neotropical species, *Bolitoglossa rostrata* and *B. subpalmata*.

Reduction and variation in digital phalangeal formula are common in some or all species of several genera in the tribe Bolitoglossini, including *Batrachoseps*, *Bolitoglossa*, *Lineatriton*, *Thorius*, and *Oedipina* (Wake 1966). In most instances, reduction and variation are associated with overall decrease in relative limb size and (or) paedomorphic limb morphology (Alberch 1980, 1981, 1983; Wake 1966). Neither characteristic is typical of the limb morphology of *Plethodon*. This, and the absence of comparable phalangeal reduction and variation in other plethodontine genera, implies that the digital variants in the Parrsboro population of *P. cinereus* are derived independently with respect to those of the bolitoglossine genera. Interestingly, the foot formula that characterizes most *P. larselli* and *P. neomexicanus*, and which distinguishes these species from all other *Plethodon*, was one of the variants observed in *P. cinereus*. One variant hand formula (2-2-3-2) represents an increase in the number of phalanges in digit 1 (Fig. 1, VIII); this has not been reported previously in the Plethodontidae, although this formula is typical of genera in some other urodele families (e.g., *Ambystoma*).

Substantial limb skeletal variation in *P. cinereus* from Nova Scotia is particularly surprising in view of the previous history of populations in this area. Maritime (Atlantic) Canada and adjacent regions of northeastern United States were under ice during the last Pleistocene glaciation; subsequent colonization of this region by *P. cinereus* is inferred to be a post-Pleistocene event (see Fig. 1 of Highton and Webster 1976). Highton and Webster (1976) established near identity in electrophoretic characters among populations from glaciated regions (Nei's $\bar{I} = 0.99$) and documented reduced genic heterozygosity in these populations compared to those from unglaciated regions. Therefore, the variants either arose in situ, and relatively recently, or they were carried along with the colonizing *P. cinereus* from unglaciated populations to the south and have been maintained since that time. One study of a large series of adult *P. cinereus* from Indiana detected no variants (D. B. Wake, personal communication), and thus lends support to the former hypothesis. Final determination of the geographical extent and age of these polymorphisms awaits further study.

The genetic basis of this variation is unknown. In a similar study of increased limb skeletal variation in a geographically peripheral (southern) population of the spotted salamander, *Ambystoma maculatum*, Worthington (1974) proposed that the novel variants may be induced by relatively high pond water temperatures during embryonic and (or) larval development. He further suggested that this "intolerance" to high temperatures may be one factor that prevents this species from extending its range further south. The Nova Scotia population of *P. cinereus* is geographically peripheral with respect to the main body of the species. However, if increased skeletal variation is environmentally induced, the specific agent is unclear. Summer and winter temperatures are moderate when compared with parts of the range further inland (e.g., northcentral Quebec); if extreme temperatures are responsible, then increased variation is more likely to be found in inland populations for which data are not available. Furthermore, unlike the limb anomalies described by Worthington which are extremely malformed or teratological, most of the limb variants described above, while different, are not malformed. This is especially true of several mesopodial pattern variants which closely resemble those characteristic of other plethodontid taxa. Van Valen (1974) suggested that in instances in which phenotypic variance primarily is environmentally induced, the mode of expression and sensitivity to the environmental agent nevertheless is a function of the genome. Applying this concept to the present example, even if much of the variation in *P. cinereus* is environmentally induced, genetic or epigenetic factors are regulating skeletal development to produce an ordered expression of limb variation.

This study documented abundant phenotypic polymorphism of relatively discrete alternative character states (e.g., cartilaginous elements fused or unfused) in a single population and in many cases within a single individual. Such phenomena are not uncommon in vertebrates (for example, the so-called trophic polymorphisms exhibited by several diverse fishes which involve substantial differences in jaw morphology and (or) dentition (see references in Kornfield *et al.* 1982)), yet they have received surprisingly little attention from the standpoint of the evolution of morphology. Nevertheless it is likely that these examples, especially when combined with greater consideration of the nature and extent of naturally occurring variation, offer much to the eventual resolution of fundamental aspects of morphological evolution, such as the nature of morphological transitions and the origin of morphological discontinuity during phylogeny.

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