Limb skeletal variation in the Jemez Mountains salamander, *Plethodon neomexicanus*

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We examine limb skeletal variability in *Plethodon neomexicanus*, a geographically isolated species of plethodontid salamander endemic to the Jemez Mountains of New Mexico, U.S.A. Data are derived from a series of 25 specimens prepared as whole mounts stained for bone and cartilage. Only 25% of hind limbs display the derived hind limb phalangeal formula 1-2-3-3-1, once considered characteristic of this species; two hind limb and one forelimb phalangeal formulae are reported for the first time. In addition, there are six variant carpal and tarsal patterns as well as the two predominant, primitive mesopodial patterns that are typical of most other species of *Plethodon* as well as of many other plethodontid genera. Limb skeletal variability in *P. neomexicanus* is among the highest recorded for urodeles and may represent an ancient and widespread polymorphism in the genus *Plethodon*.

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On trouvera ici les résultats d'une étude sur la variabilité du squelette des membres chez *Plethodon neomexicanus*, une espèce de salamandre pléthodontide isolée géographiquement, endémique dans les montagnes Jemez du Nouveau-Mexique, États-Unis. Les données proviennent d'une série de 25 spécimens dont les os et les cartilages ont été préparés entiers et colorés. Seulement 25% des membres postérieurs examinés ont la formule phalangienne 1-2-3-3-1 décrétée caractéristique de cette espèce; deux membres postérieurs et un membre antérieur ont des formules phalangiennes jamais rencontrées auparavant. De plus, l'examen de ces spécimens a révélé l'existence de six autres modèles de variations des carpes et des tarses en plus des deux modèles de mésopodes primitifs typiques de la plupart des autres espèces de *Plethodon* et des autres genres de pléthodontidés. La variabilité du squelette des membres chez *P. neomexicanus* est l'une des plus importantes jamais rencontrées chez un urodèle et représente probablement un polymorphisme ancien et répandu chez le genre *Plethodon*.

[Traduit par la revue]

Introduction

Among the most surprising discoveries to emerge from recent studies of limb development and evolution in urodeles is the often substantial intraspecific variation in skeletal patterning in natural populations of a variety of taxa (e.g., Ambystomatidae: *Ambystoma* (Worthington 1974); Hynobiidae: *Batrachuperus* (Reilly 1983); *Hynobius* (Maruyama 1977); Plethodontidae: *Bolitoglossa* (Alberch 1980), *Eurycea* (Potter and Sweet 1981), *Plethodon* (Hanken 1983), *Thorius* (Hanken 1982); Salamandridae: *Triturus* (Rienesl 1990), *Tylototriton* (Zhao et al. 1988). In many instances, alternative limb patterns in a given population are as different as those that distinguish species or even genera (Alberch 1983; Hanken 1982, 1985; Larson 1983). These data are relevant to a number of questions, ranging from the relation between morphological evolution and speciation to the role of developmental processes in constraining structural diversity. Especially surprising is the observation that the species that is perhaps the most variable, *Plethodon cinereus* (Hanken 1983; Hanken and Dinsmore 1986), is a member of a genus that is in many other respects among the most morphologically conservative vertebrate lineages (Highton and Larson 1979; Wake et al. 1983).

One species, however, in which limb skeletal variation has been known for some time is *Plethodon neomexicanus*, a geographically isolated species endemic to the Jemez Mountains of New Mexico, U.S.A. *Plethodon neomexicanus* possesses a variable hind limb phalangeal formula in which there may be one (the derived state) or two (the primitive state for the genus *Plethodon*) phalanges in the fifth toe (Wake 1966). Earlier studies of skeletal variability within *P. neomexicanus* assayed variation primarily from radiographs (Brodie and Altig 1967) or intact museum specimens (Stebbins and Riemer 1950; also see Stebbins 1962). Neither method, however, can effectively discern patterns among uncalcified, cartilaginous tissues which compose a substantial portion of the adult limb skeleton in plethodontid salamanders. Thus, there is a possibility that these studies may have failed to describe the full range or nature of limb skeletal variation in this species. Further complicating the situation is the fact that *P. neomexicanus* is designated a state endangered species (Schmitt et al. 1985), which makes it difficult to obtain additional specimens for scientific study.

We recently obtained a reasonably large sample of 25 *P. neomexicanus* legally collected under the auspices of the New Mexico Department of Game and Fish. In this paper we describe limb skeletal variability (mesopodial patterns and phalangeal formulae) in this sample, which we prepared as whole mounts cleared and differentially stained for bone and cartilage, a method that is much more effective for resolving skeletal patterning than methods used earlier. In addition to clarifying the nature and extent of skeletal variation in this species, we use the data in a preliminary analysis of the patterns of limb skeletal evolution within the genus *Plethodon* and to address recent hypotheses concerning developmental constraints on limb patterning in urodeles.

Materials and methods

Twenty-five specimens (1 adult male, 8 adult females, 16 subadults) were collected by Dr. Cynthia Carey from Pony, Hay, and Oat canyons, Rio Cebolla drainage, Jemez Mountains, Santa Fe National Forest, Cibola County, New Mexico, on 13–16 August 1986. They were maintained alive in the laboratory for periods lasting up to several months, at which time they were preserved in 10% neutral-buffered formalin, measured (mean snout–vent length (SVL) 51.2 mm; range 42.5–62.3 mm), and prepared as cleared whole mounts differentially stained for bone with alizarin red S and for cartilage with Alcian blue

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(Dingerkus and Uhler 1977; Hanken and Wassersug 1981). None of the limbs bore any sign of regeneration, such as a vestige of a regeneration callus on the stylopod or zeugopod, and all were fully formed. A few limbs were damaged while being skinned in preparation for staining; they were not used to derive the frequencies of skeletal variants. Similarly, only specimens with both of the forelimbs or hind limbs intact were used in calculations of the frequency of right–left asymmetry in mesopodial pattern or phalangeal formula. All specimens will be deposited in the permanent collection of the Museum of Vertebrate Zoology, University of California, Berkeley.

Mesopodial pattern and phalangeal formula in each limb were determined from the array of distinct cartilages, regardless of degree of ossification. The numbering of individual mesopodial fusion combinations (Arabic numerals), as well as overall carpal and tarsal patterns (Roman numerals), follows Hanken (1983) and Hanken and Dinsmore (1986). For ease of presentation, "fusion" is used in instances in which adjacent mesopodial elements that are separate in one limb pattern are not separate in another (joined elements retaining a visible suture are considered fused). However, as pointed out by Shubin and Alberch (1986), many supposed instances of fusion likely represent the failure of cartilage primordia to separate during early stages of limb development.

Results

Phalangeal variation

As previously reported (Brodie and Altig 1967; Stebbins and Riemer 1950; Wake 1966), the hind limb phalangeal formula in *P. neomexicanus* is highly variable (Table 1). Although approximately two-thirds of the hind limbs examined had the predominant formula for *Plethodon*, 1-2-3-3-2 (Wake 1966), four additional patterns were observed. The formula originally described as predominant in *P. neomexicanus,* 1-2-3-3-1 (Stebbins and Riemer 1950; Stebbins 1962), was the most common variant, characterizing about one-fourth of all the limbs. The three remaining variants (1-2-3-2-2, 1-2-2-2-2, and 1-2-3-2) were seen only once, each in a different specimen. Virtually all the forelimbs had the typical formula for the genus, 1-2-3-2 (Wake 1966); a variant formula, 1-2-2-1, was found in only one limb (Table 1). Typically, each variant phalangeal formula was asymmetric with respect to the contralateral limb. In 10 of these 12 cases of asymmetry the complete formula of the opposite limb was determined, and it was the predominant formula. The single instance of right–left symmetry of a variant formula was one specimen that had the most common variant, 1-2-3-3-1, in both hind limbs.

Mesopodial variation

Carpus

The so-called primitive plethodontid carpal pattern, which comprises eight separate cartilages (ulnare, intermedium, radiale, centrale, centrale 1, and distal carpals 1–2, 3, and 4 (Wake 1966) was present in 80% of the forelimbs (Table 2; Fig. 1, pattern I). Most remaining carpi (18%) displayed a second pattern that is distinguished by fusion of the ulnare and intermedium (Fig. 1, pattern II). An additional pattern, characterized by fusion of the ulnare, intermedium, and centrale, was found in only one limb (Figs. 1 and 2, pattern XII). This last pattern and its distinctive fusion combination have never before been reported in *Plethodon*. Eight of the nine limbs with variant pattern II were symmetrical, i.e., they were found in four specimens that had the pattern on both sides. The carpus opposite the ninth limb with pattern II, as well as that opposite the lone limb with pattern XII, bore pattern I.

TABLE 1. Phalangeal variation in *Plethodon neomexicanus*

	Formula	Frequency (%)
Forelimb (*N* = 24, 22)	1-2-3-2	97.8
	1-2-2-1	2.2
Hindlimb (*N* = 21, 20)	1-2-3-3-2	68.3
	1-2-3-3-1	24.4
	1-2-3-2-2	2.4
	1-2-2-2-2	2.4
	1-2-3-2	2.4

NOTE: Each frequency value denotes the number of limbs with a particular phalangeal formula divided by the total number of fore- or hind-limbs examined. Frequency of right–left asymmetry in phalangeal formula equals 4.8% in the forelimb (*N* = 21 specimens) and 50.0% in the hind limb (*N* = 20 specimens). Sample sizes are given for right and left limbs, respectively.

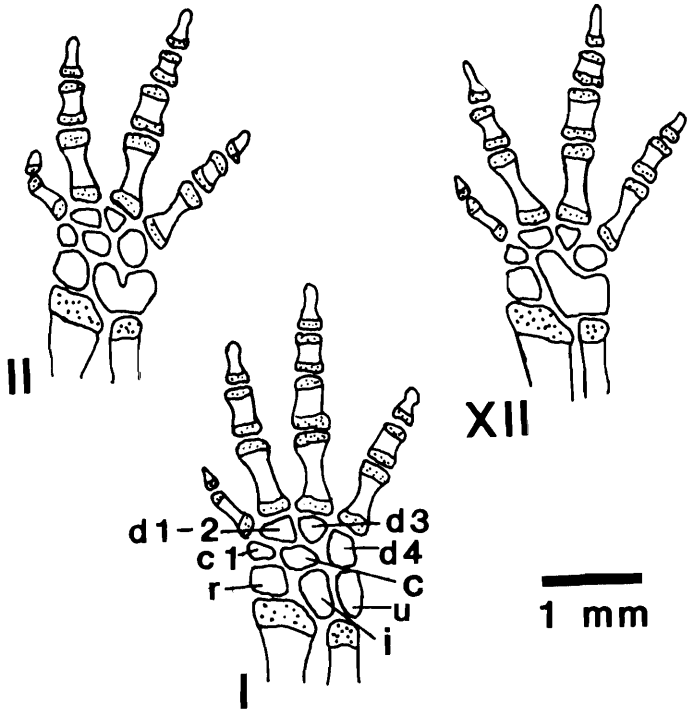

FIG. 1. Carpal variation in *P. neomexicanus*. All patterns are drawn from right limbs; cartilage is stippled. *r*, radiale; *u*, ulnare; *i*, intermedium; *c*, centrale; *c*1, centrale 1; *d*1–2, *d*3, *d*4, distal carpals 1–2, 3, and 4.

Tarsus

The primitive plethodontid tarsal pattern of nine separate elements (tibiale, intermedium, fibulare, centrale, centrale 1, and distal tarsals 1–2, 3, 4, and 5 (Wake 1966)) was found in nearly 90% of the specimens (Table 2; Fig. 3, pattern I). Remaining specimens together displayed four additional patterns, each with a distinct arrangement of tarsal cartilages and each found in only one or two limbs (Table 2; Figs. 2 and 3, patterns II, VII–IX). Homologies could be readily identified between the discrete tarsal cartilages of two of these variant patterns and those in the primitive plethodontid pattern. Thus, in pattern II, distal tarsals 4 and 5 are fused (fusion combination 6), whereas in pattern VII, distal tarsals 1–2 and 3 (combination 3) and tibiale and centrale 1 (combination 2) are fused; all of these elements are separate in pattern I. Patterns VIII and IX both have fewer separate tarsal cartilages (six) than pattern I, but neither can be described simply with respect to the fusion of separate, adjacent cartilages in the primitive plethodontid

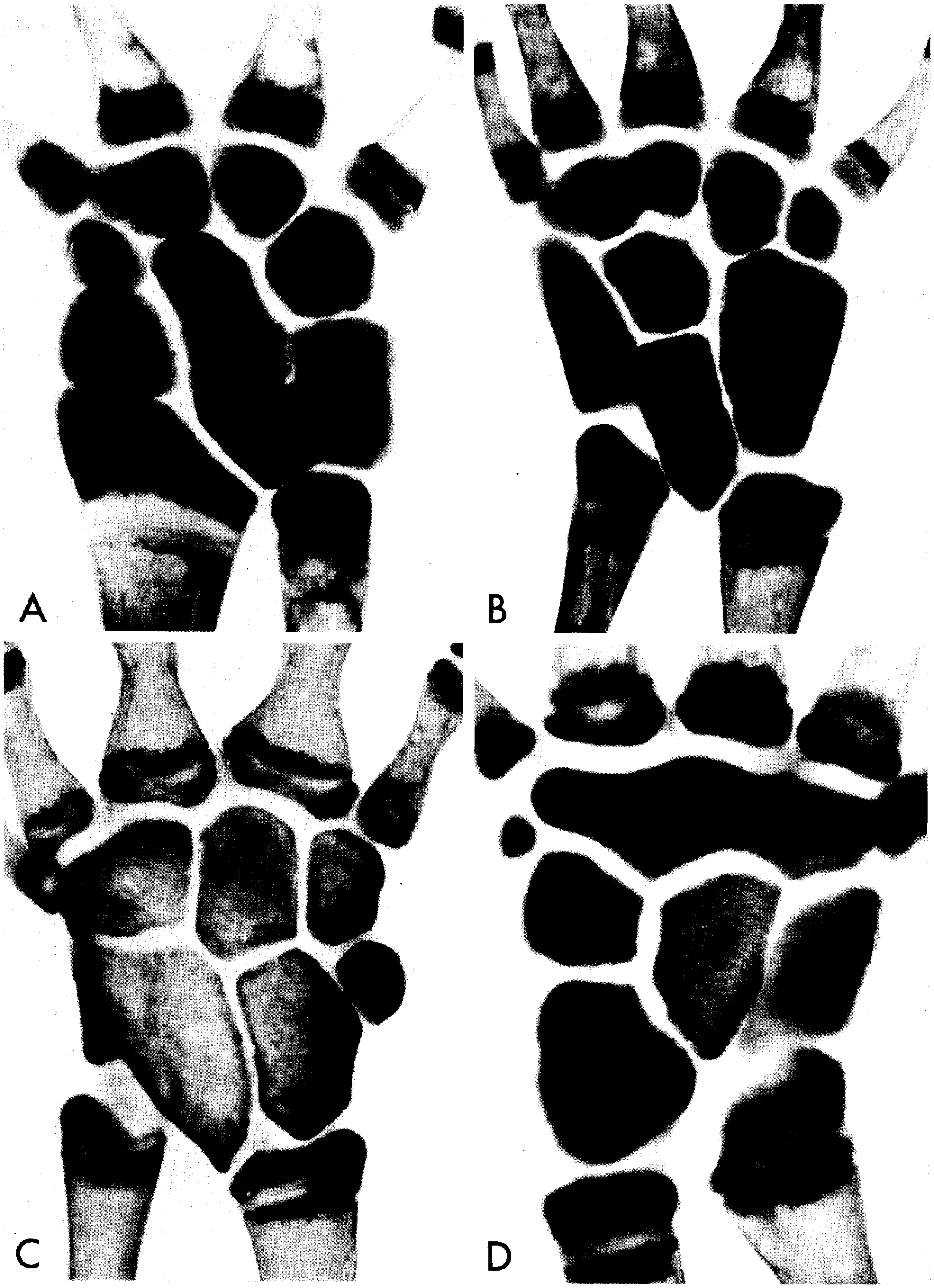

FIG. 2. Photographs of four mesopodial patterns in *P. neomexicanus*, previously unreported for the genus *Plethodon*. (A) Carpal pattern XII (J. Hanken cleared and stained (CS) tag no. 94). (B) Tarsal pattern VII (CS 94). (C) Tarsal pattern VIII (CS 93). Tarsal pattern IX (CS 114). A–C are right limbs; D is a left limb. Note fused ulnare, intermedium, and centrale in A, and fused distal tarsals 1–2 and 3, and tibiale and centrale 1 in B (elements are identified in Figs. 1 and 3). Specific homologies of fusion combinations involved in C and D are uncertain.

TABLE 2. Mesopodial variation in *Plethodon neomexicanus*

Fusion combination	Frequency (%)	Mesopodial pattern	Frequency (%)
Carpus (N = 25, 25)			
(1) Intermedium, ulnare	20	I	80
(9) Intermedium, ulnare, centrale	2	II	18
		XII	2
Tarsus (N = 24, 24)			
(2) Tibiale, centrale 1	4	I	89.6
(3) Distal tarsals 1–2, 3	4	II	4.2
(6) Distal tarsals 4–5	4	VII	2.1
		VIII	2.1
		IX	2.1

NOTE: Each value denotes the number of limbs with a particular fusion combination or mesopodial pattern divided by the total number of fore- or hind-limbs examined. Frequency of right–left asymmetry in carpal and tarsal pattern equals 8% (N = 25 specimens) and 16.7% (N = 24 specimens), respectively. Carpal fusion combinations 2–8, carpal patterns III–XI, tarsal fusion combinations 1, 4, 5 and 6–8, and tarsal patterns III–VI, all originally described in *P. cinereus* (Hanken 1983; Hanken and Dinsmore 1986), were not observed in *P. neomexicanus*. *Carpus*: I: *i*, *u*, *r*, *c*, *c*1, *d*1–2, *d*3, *d*4; II: *i–u*, *r*, *c*, *c*1, *d*1–2, *d*3, *d*4; XII: *i–u–c*, *r*, *c*1, *d*1–2, *d*3, *d*4. *Tarsus*: I: *i*, *t*, *f*, *c*, *c*1, *d*1–2, *d*3, *d*4, *d*5; II: *i*, *t*, *f*, *c*, *c*1, *d*1–2, *d*3, *d*4–5; VII: *i*, *t–c*1, *f*, *c*, (*d*1–2)–*d*3, *d*4, *d*5. Fusion combinations contained in tarsal patterns VIII and IX are not listed because of their uncertain homologies with the primitive pattern (see text). Sample sizes are given for right and left limbs, respectively.

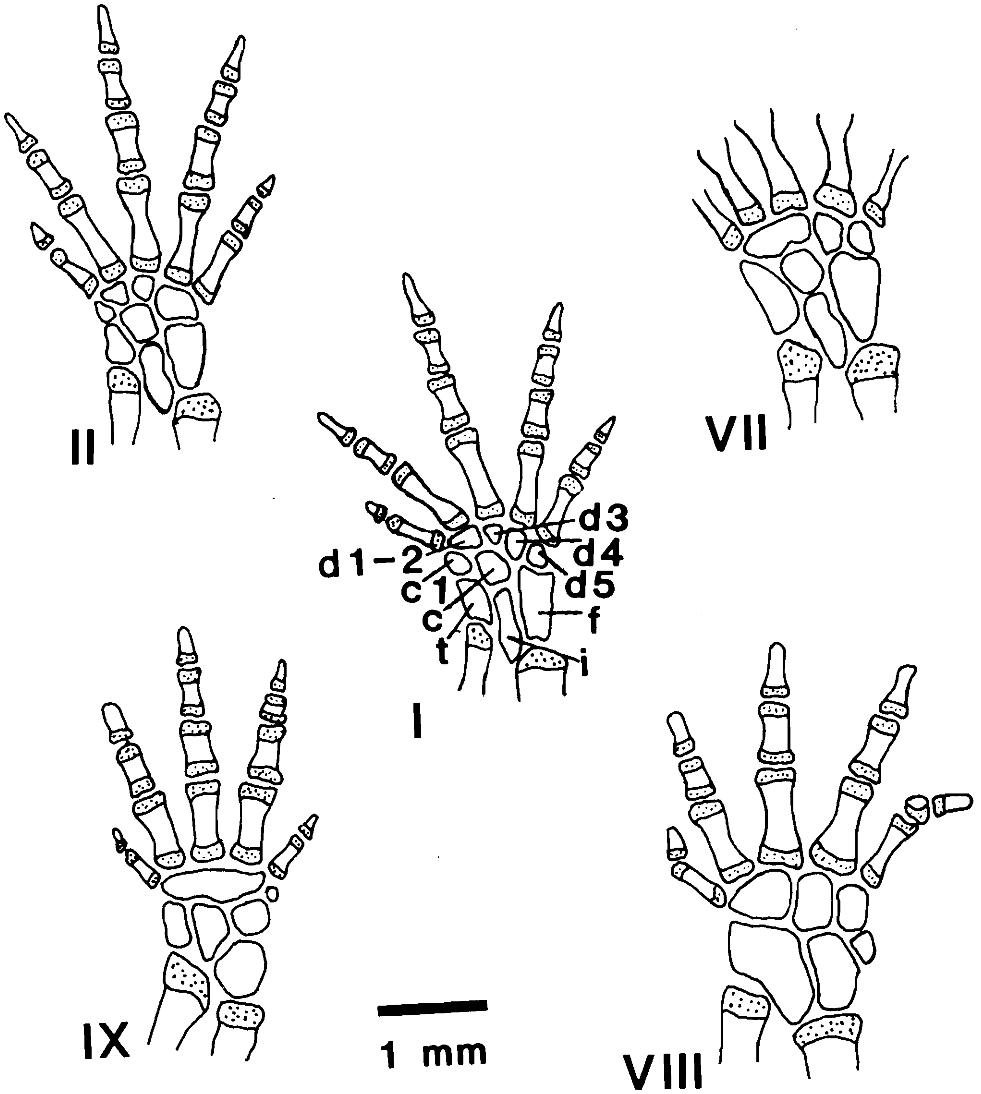

FIG. 3. Tarsal variation in *P. neomexicanus*. All patterns are drawn as right limbs, although IX was observed only on the left side of a single specimen; cartilage is stippled. Note variant phalangeal formulae in VIII (1-2-2-2-2) and IX (1 2-3-3-1); phalanges in pattern VII were lost during preparation. *t*, tibiale; *c*, centrale; *c*1, centrale 1; *i*, intermedium; *f*, fibulare; *d*1-2, *d*3, *d*4, *d*5, distal tarsals 1–2, 3, 4, and 5.

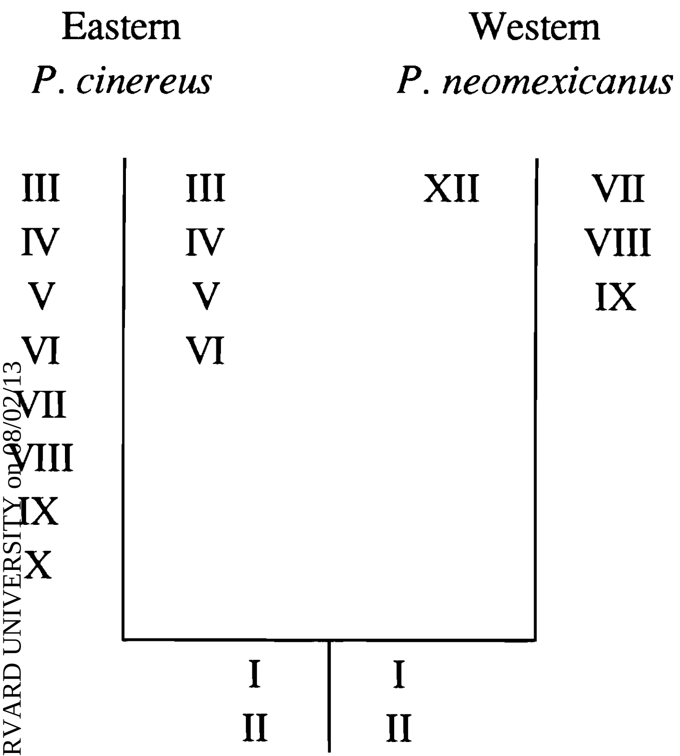

FIG. 4. Comparison of mesopodial variation between *P. neomexicanus* (this study) and *P. cinereus* (Hanken 1983; Hanken and Dinsmore 1986). Carpal and tarsal patterns found in each species are listed to the left and right of each vertical branch, respectively; patterns I and II are present in both species.

pattern. Tarsal patterns VII, VIII, and IX have never before been reported in *Plethodon*. All variant tarsal patterns involved cases of right–left asymmetry. In three cases, the contralateral limb had the predominant pattern, I. The two remaining variant hind limbs (patterns II and VII) were on opposite sides of the same specimen, which also had a variant carpal pattern (XII) on one side.

Discussion

Limb skeletal variation in Plethodon neomexicanus

The variant hind limb phalangeal formula 1-2-3-3-1 was first reported in the original description of *P. neomexicanus* by Stebbins and Riemer (1950), who considered it to be the predominant formula in this species, based on examination of two dried skeletons and manipulation of several preserved specimens. (Stebbins' later account of only "3 exceptions in 20 animals" (1962, p. 76) is presumably based on his earlier study.) Brodie and Altig (1967) later assayed variability from radiographs of 27 additional specimens and reported a much lower incidence (35%) of the supposedly "diagnostic" formula. They further implied that their estimate was more reliable than that of Stebbins and Riemer because of the difficulty of detecting the highly variable second phalanx on the fifth toe simply by manipulating preserved specimens. Our value of approximately 25%, derived from cleared and double-stained specimens, is even lower than that of Brodie and Altig. The difference between our estimate and that of Brodie and Altig may represent nothing more than sampling error or slight geographic variation among collection localities. On the other hand, it may be a function of the greater resolving power afforded by cleared and differentially stained whole mounts versus radiographs. For example, a hind limb containing an unossified second phalanx on the fifth toe likely would be scored as a variant limb when examined in a radiograph, whereas it would be scored as a typical limb in a whole mount. In any event, it is clear, as was pointed out by Brodie and Altig, that the variant formula 1-2-3-3-1 is not diagnostic, or even predominant, in *P. neomexicanus*. At the same time, phalangeal variability is more extensive than has been recognized previously, as evidenced by the several additional variants, in both the forelimb and the hind limb, which occur at very low frequencies (Table 1).

In contrast to the considerations of phalangeal variation discussed above, mesopodial variability has never before been reported in *P. neomexicanus*. In this study, we have described six variant carpal and tarsal patterns in addition to the two predominant, primitive patterns that are typical of most other species of *Plethodon* as well as numerous other plethodontid genera (Wake 1966). Two of these variant patterns are present in *P. cinereus* (see below); the remaining four have been found only in *P. neomexicanus* within the genus *Plethodon*. Thus, far from being absent, mesopodial variability in this species is extensive. In fact, in terms of the total number of carpal or tarsal patterns, limb skeletal variability in *P. neomexicanus* is the second-highest reported for any species of salamander (see earlier references), behind only *P. cinereus* (Hanken 1983; Hanken and Dinsmore 1986).

As in other instances of intraspecific variability in limb skeletal pattern, the causes of the variation in *P. neomexicanus* are obscure. Several possible factors, however, can be excluded. First, as was mentioned earlier there is no indication from gross morphology that any of the limbs is regenerated (Dinsmore and Hanken 1986). Second, there is little likelihood of any ontogenetic effect, as our sample includes only fully grown or nearly fully grown specimens. (The mean adult SVL for *P. neomexicanus* is 54–56 mm (Williams 1973), compared with our sample mean of 51.2 mm.) Though variation in limb patterning (particularly mesopodial fusion) according to body size or age remains a possibility, to our knowledge this phenomenon has never been reported for any urodele in either natural or laboratory situations. Third, there is no obvious association between any variant phenotype, or variation in general, and sex or sexual maturity. Because of the high incidence of right–left asymmetry, there is a strong possibility that many of the limb skeletal variants are environmentally induced. Yet asymmetry of paired features may also reflect an underlying genetic predisposition, or liability, towards the variation, as seen in "threshold characters" (Falconer 1981). Thus, not even the relative contributions of environmental and genetic components of variation can be discerned from the data now available.

Limb skeletal variation in the genus Plethodon

The genus *Plethodon* comprises at least 27 species (Frost 1985) which are divided into distinct "eastern" and "western" groups; as revealed by a phylogenetic hypothesis derived from molecular data, separation of these two lineages may have occurred more than 40 million years ago (Larson et al. 1981; Highton and Larson 1979). *Plethodon neomexicanus* belongs to the western group, whereas *P. cinereus*, the only other species for which there are comparable data concerning the extent and nature of limb skeletal variation (Hanken 1983; Hanken and Dinsmore 1986), is in the eastern group. Several hypotheses concerning limb skeletal variation in the genus emerge from a comparison of the mesopodial patterns found in these two species (Fig. 4).

First, the same carpal and tarsal patterns (Fig. 1, pattern I, and Fig. 3, pattern I, respectively) predominate in both species. As these patterns are also characteristic of all other species of *Plethodon* as well as many other plethodontid genera (Wake 1966), their presence in *cinereus* and *neomexicanus* most likely represents the retention of patterns present in the common ancestor of all living species in the genus.

Second, carpal pattern II and tarsal pattern II both occur as moderate- to low-frequency variants in each species. (In *P. cinereus,* each pattern is found in widely separated localities from Virginia to Nova Scotia at frequencies of 3–17%.) One explanation for this distribution is that each pattern has been retained from the common ancestor of eastern and western groups in at least these two descendant species. This would imply that limb skeletal variability, involving patterns I and II in both the carpus and the tarsus, is an ancient phenomenon in *Plethodon*. Alternatively, each pattern II may have appeared independently and more recently in the two lineages that gave rise to *neomexicanus* and *cinereus*.

Third, the several remaining carpal or tarsal patterns are found in one or the other species, but not in both. Each of these patterns arose either after the two species last shared a common ancestor, or arose once in the common ancestor and was subsequently lost or remained undetected in one or the other group.

Finally, carpal patterns II and XII and tarsal pattern II are found in the distantly related bolitoglossine genus *Thorius* from southern Mexico; indeed, pattern II is the predominant tarsal pattern in several species (Hanken 1982, 1985). Unless these patterns have been retained from the remote common ancestor of *Plethodon* and *Thorius*, their distribution indicates the independent appearance of several identical, derived limb patterns in two plethodontid tribes.

We wish to emphasize that many of these hypotheses represent little more than conjecture in the absence of additional data from other species of *Plethodon* and from additional samples of *P. neomexicanus* and *P. cinereus*. Thus, it is not possible to distinguish between the several alternative scenarios at this time. This is especially true for those that address the distribution of several extremely rare variants (e.g., carpal pattern XII, tarsal patterns VII, VIII, and IX), each of which has been observed to date in only a single limb. The significance of these variants to long-term trends of limb evolution in *Plethodon* remains to be established.

Developmental constraints

Shubin and Alberch (1986) have recently proposed a model of vertebrate limb development in which pattern results from three primary processes of cartilage development: de novo condensation, segmentation, and branching. According to their model, each major tetrapod group, such as the urodeles, has a characteristic combination of these three processes; within each group, variation results from minor perturbations of this basic theme, which constrains the overall array of realized patterns.

One prediction that follows directly from Shubin and Alberch's model of limb patterning as applied to urodeles is that there should not be fusion between any element of the distal "digital axis" (*d*1–2, *d*3, *d*4, *d*5) and any of the more proximal "stem" elements (e.g., *t, i, f, c, c*1), as these two areas form from separate condensation events. The data for *P. neomexicanus* are consistent with this prediction. Despite the diversity of mesopodial patterns, all individual fusion combinations are either among stem elements (e.g., *t*–*c*1) or among digital elements (e.g., *d*1–2–*d*3). One possible exception is tarsal pattern VIII, in which the unusually large distal elements seemingly incorporate some of the cartilage that ordinarily contributes to proximal elements (Fig. 3). However, because of the difficulty in resolving the exact homologies of the component tarsal elements in this pattern, this interpretation cannot be considered reliable. Interestingly, a fused distal carpal 4 – centrale, which is not "permitted" according to the model but which is common in many plethodontid salamanders (e.g., *Thorius*, Hanken 1982, 1985; and *P. cinereus*, Hanken 1983), is absent in *P. neomexicanus*. Thus, limb skeletal variation in *P. neomexicanus,* although extensive, is clearly ordered.

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