Phylogeny, Variation, and Morphological Integration[1]

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SYNOPSIS. Studies of intra and interspecific variability of urodele mesopodia have revealed biases in the production of novel phenotypes; observed patterns of variability represent a small subset of the possible arrangements. The major trend in the phylogenetic diversification of the salamander limb is the reduction or loss of carpal or tarsal elements, and these patterns are often highly homoplastic. Mesopodial arrangements that are homoplastic are commonly encountered in studies of intrapopulational variation. Patterns of variation, when integrated with developmental biology, inform about the relationships between morphological integration and homology. The extensive conservation of primitive developmental and genetic interactions suggest that the individuation of structures may not be complete and that homologies, themselves, may be partial.

INTRODUCTION

In 1857, Agassiz proposed that a "threefold" parallelism between ontogeny, the fossil record, and comparative anatomy reveals the fundamental order of the natural world (Agassiz, 1962). The correspondence of morphological variation of these three types of data suggested a hierarchy of natural forms. As morphologists confront whole new types of comparative data, whether the result of genetic manipulation (*e.g.,* gene knockouts, targeted misexpression) or developmental teratology, Agassiz's methodology remains enlightening. The congruence between the phylogenetic distribution of characters, teratology produced by genetic and developmental perturbation, and patterns of intraspecific variability now can form the backbone for the formulation of hypotheses of homology, generative constraint, and morphological integration.

Morphological diversity can be described in several contexts, including, among others, synapomorphy, intrapopulational variability, and natural and experimentally induced teratology. Constraints on the production of variation are expected to be common to all of these; thus, analysis of internal constraints and morphological correlation is informed by the search for common patterns in diverse contexts (Alberch, 1989). The relationship between intraspecific variation, developmental morphology, and the phylogenetic distribution of characters suggests mechanisms are often reflected by predictable patterns of homoplasy (Hall, 1984; Wake and Larson, 1987; Wake, 1991; Shubin *et al.* 1995).

The evolution and developmental integration of the salamander limb skeleton has been the subject of experimental (*e.g.,* Alberch and Gale, 1985; Gardiner and Bryant, 1989), phylogenetic (*e.g.,* Schaeffer, 1941; Wake and Larson, 1987), and comparative morphological (*e.g.,* Hanken, 1983; Alberch, 1983; Wake, 1991; Shubin *et al.,* 1995) investigation. Studies of the intra and interspecific variability of urodele mesopodia have revealed biases in the production

of novel phenotypes (Alberch, 1983; Hanken, 1983; Vogl and Rienesl, 1991; Rienesl and Wagner, 1992). Observed patterns of variability represent but a small subset of the possible arrangements (based on fusions, separations, and losses). In this paper, we review the phylogeny of salamander limb structure, the embryological processes responsible for these phylogenetic patterns, and the intraspecific variation of the urodele limb. The parallels between these data reveal a range of possible morphological states; this biased variability generates nonrandom patterns of homoplasy and synapomorphy in urodele phylogeny.

THE SALAMANDER LIMB

Phylogenetic and developmental reduction of structure

Reduction, either through the loss or amalgamation of limb elements, is the major trend in both the origin and diversification of salamander limbs. Urodele outgroups, whether they be temnospondyls or other Paleozoic taxa, have more carpal and tarsal bones in the manus and pes than extant salamanders (Fig. 1). This general design (basal taxa, Fig. 1) consists of at least three proximal elements (proximal carpalia or tarsalia), one or more centralia (often as many as four), and a distal carpal and tarsal series. The number of elements in the distal series is highly variable and may include as many as six or seven individual elements (*Trematops*, Fig. 1).

All salamanders share synapomorphic patterns of reduction. In both the hand and the foot, the first and second distal carpals and tarsals are amalgamated to form a single element, the basale commune (bc); this enlarged element articulates with the first two digits. In addition, all urodeles have fewer than five digits in the hand. This reduction may be a more general tetrapod characteristic as it is seen in anurans and several Paleozoic tetrapods (*e.g., Colosteus, Amphibamus*).

Basal salamanders (*e.g.,* cryptobranchids and hynobiids) typically possess more elements in the limb than do other urodeles. No single carpal and tarsal design describes these taxa because interspecific variability

is very high; most cryptobranchids and hynobiids retain pleisiomorphic elements tha have been lost in the standard arrangement in other urodeles (Fig. 1). Some taxa retair the ancestral condition of two centrali (*Liua, Ranodon, Salamandra,* and *Cryptobranchus alleganiensis*) whereas others dc not. Other basal taxa retain a postminimu (a possible vestige of an additional digit *Liua, Ranodon Salamandrella* and *Andrias* and two taxa possess the ancestral prehallu) (*Cryptobranchus, Salamandrella*). Non-hy nobiid and cryptobranchid salamanders re tain no more than one centrale, and posses neither a postminimus nor prehallux in th standard tarsal pattern.

Patterns of limb reduction can be de scribed by their position within the limb Reductions of the proximal series consist o fusions of the intermedium (i) with the ul nare (u) in the hand and the fibulare in th foot (Fig. 1). This arrangement is the stan dard condition of some salamandrids, pro teids, amphiumids, and plethodontids (Fig 1). Reductions of the distal series are seei in a variety of basal (hynobiid) and neste (salamandrid and plethodontid) taxa. Com mon patterns of reduction consist of th amalgamation of neighboring elements (*i.e.* distal tarsal 4+5 (dt4+dt5) in some pleth odontids, salamandrids, and hynobiids an distal tarsal 3+4+5 (dt3+dt4) in *Necturus*) Interactions between the proximal and dis tal series typically occur at the junction o the centrale and distal series (*e.g.,* the fu sion of c and dt4 in *Thorius* and *Oedipina*)

The centrale (c), dt4, and dt5 exhibit hig levels of homoplasy in salamander phylog eny (Wake, 1991; Shubin *et al.* 1995). Th primitive amphibian tarsus (represented b: Paleozoic temnospondyls) is similar to tha of basal salamanders (represented by hy nobiids and cryptobranchids, Fig. 1) in th possession of five toes and separate dista tarsals 4 and 5 (Schaeffer, 1941). In addi tion, most salamanders (ambystomatids, di camptodontids, basal plethodontids, man salamandrids, rhyacotritonids, and dicamp todontids) possess separate distal tarsals and 5. In these taxa, distal tarsal 4 extend proximally into the central region of th limb and is larger than distal tarsal 5 (Fig 1). Departures from this condition are see
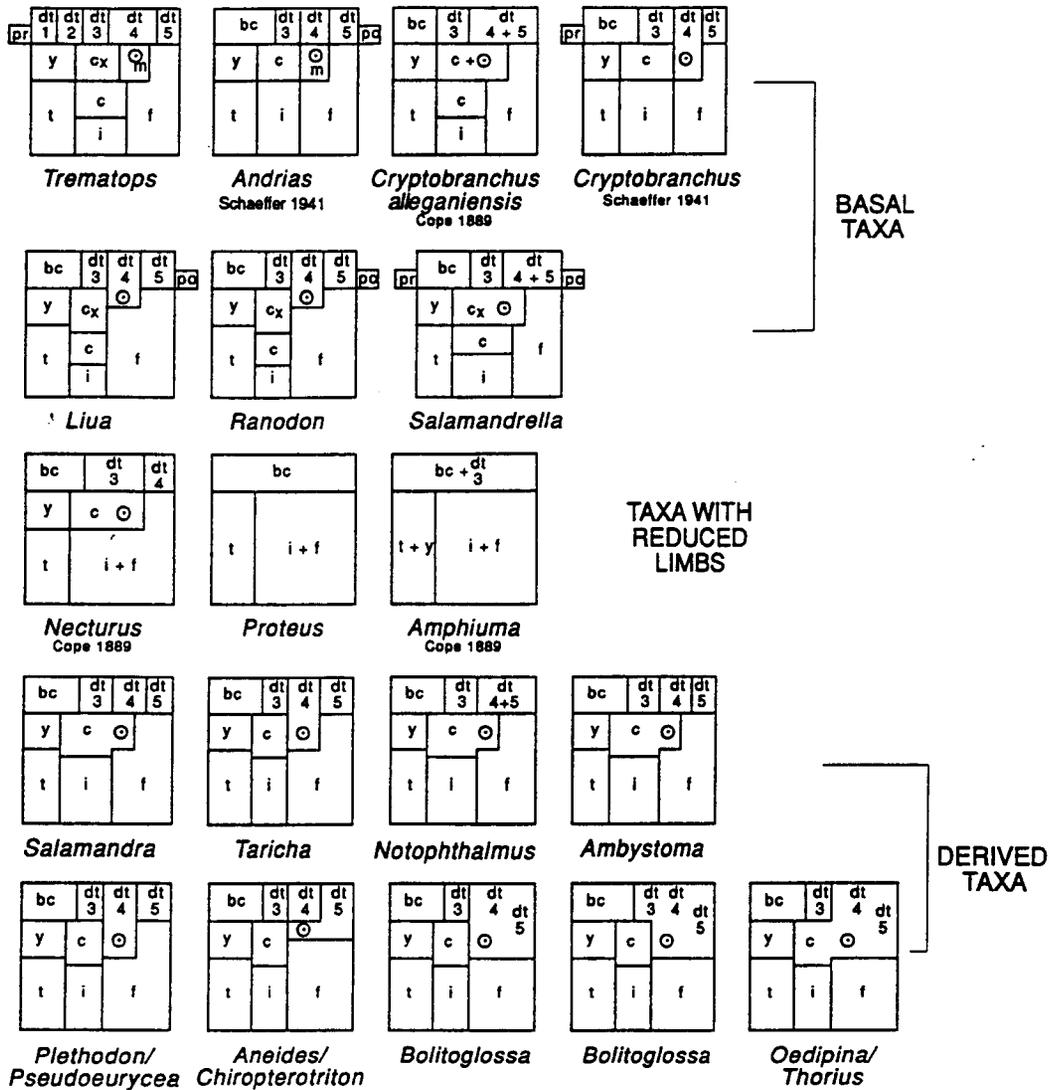
FIG. 1. Geometric interpretation of standard tarsal patterns for diverse urodele taxa. The tarsus is considered to be a bounded domain, illustrated by a box, and the space within the box accommodates all tarsals. Two elements, pr and po, lie outside this domain; they have been considered by some authors to be rudiments of supernumerary digits (Jarvik, 1965). The dot enclosed by a circle represents the position of m in each tarsus. Basal groups have higher numbers of mesopodial elements and they typically retain the "external elements" pr and po. Taxa with reduced limbs lose digits and have a highly reduced mesopodium. In all salamanders, y and t may be independent or combined, f and i may be either separate or fused, and adjacent distal tarsals can combine with one another. The space in the central region can be filled by: an independent m (in basal taxa), a combined c and m, an extension of dt4 (dt4 + m), an extension of dt5 (dt5 + m), or an extension from combined distal tarsals (e.g., dt4 + 5 + m or dt4 + 5 + c + m). Our interpretation is based on inspection of specimens in the collections of the Museum of Comparative Zoology, Harvard University, and the Museum of Vertebrate Zoology, University of California at Berkeley. Abbreviations: bc, basale commune; c, centrale; cx, supernumerary centrale; dt 1–5, distal tarsals 1–5; i, intermedium; f, fibulare; pr, prehallux; po, postminimus; t, tibiale; y, element y.
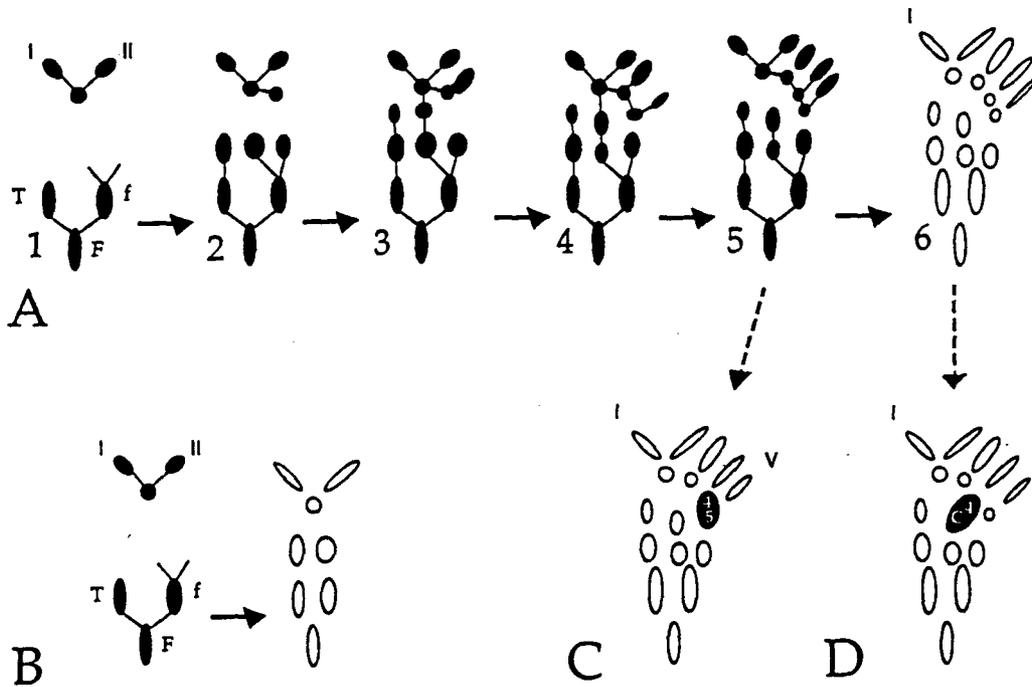
Fig. 2. Major developmental modes of limb reduction. A) Developmental sequence of the tarsus of *Amby. toma mexicanum* (1–6). 1. Digits one, two appear relatively earlier than in other tetrapods. Digital developmei continues in a general anterior to posterior sequence. Generally, new cartilage condensations arise connected t differentiated elements. These connections are cleaved at different stages of development to produce a tarst with a full complement of nine distinct mesopodial elements (6). B) Global truncations of the development sequence can produce greatly reduced patterns of limb structure (as in *Proteus*, shown). C) The retention c local connections can produce enlarged, amalgamated elements (as in distal tarsal 4 and 5 shown). D) Separai elements occasionally fuse during chondrogenesis and/or osteogenesis as in the fusion of c and distal tarsal ∢ shown.

in arboreal salamanders that possess the opposite pattern; distal tarsal 5 extends into the central region and is larger than distal tarsal 4 (*e.g.*, *Chiropterotriton, Aneides*, Fig 1). Several taxa (*e.g.*, *Cynops, Triturus, Nototriton, Bolitoglossa, Parvimolge*) display the derived condition of a combined distal tarsal 4 and 5 (Fig. 1) that articulates with metapodials IV and V. This amalgamation has occurred several times independently and would be homoplastic in any of the hypotheses of urodele phylogeny presented by Larson and Dimmick (1993). Some bolitoglossines possess the highly derived amalgamation of distal tarsals 3, 4 and 5. (Fig. 1). In these taxa, distal tarsal 3+4+5 extends into the central region of the tarsus (Fig 1).

Several major developmental events underlie the phylogenetic reduction of limb structure (Fig. 2). Cartilage anlagen typi cally arise as extensions of existing carti lage elements that later separate from on another (Fig. 2A). Three major patterns o developmental connectivity occur: bifurca tion, segmentation, and de novo condensa tion (Oster *et al.*, 1988). Bifurcation occur when two analgen arise within a '"y' shaped extension from an existing element whereas segmentation occurs when a singl element divides from an existing extension An element which arises in isolation is con sidered to be a "de novo condensation." Two axes of differentiation are observed: ∢ proximodistal axis includes the humer us(forelimb)/femur(hindlimb), radius/tibia ulna/fibula and the proximal mesopodials while an antero-posterior (digital) axis aris es on the anterior (preaxial) border and dig ital-distal mesopodial development pro

gresses posteriorly (postaxially). The two axes of development terminate in the region of the centrale and ulnare/fibulare, where they converge.

The forelimb includes a proximal humerus (H) which extends distally to a bifurcation that contains the anlagen of the radius (R) and the ulna (U). The anlage of R in turn extends distally and segments the radiale (r) and a more distal element (variously termed a mediale or a centrale; we refer to it as y). The anlage of U extends distally and postaxially to a bifurcation that contains the anlagen of the intermedium and the ulnare; i then segments a centrale. C may bifurcate, segment or both; but, in the more derived urodele lineages (most families), it neither bifurcates nor segments. The anlage of the basale commune (bc) forms as a de novo condensation that is distal to and separated from the other carpal rudiments. The bc and metapodials one and two are the first elements of the digital arch to appear. The digital arch segments and bifurcates in a postaxial sequence to produce the distal carpals (dc), normally two in number, and the metacarpals (mc), four in number. Each metacarpal segments to produce the final phalangeal formula of 1-2-3-2 (from pre- to postaxial).

The hindlimb includes a proximal femur (F) which extends to a bifurcated, y-shaped zone that contains the anlagen of the tibia (T) and the fibula (Fi). The anlage of T extends distally and segments a tibiale (t) and then y. The anlage of Fi bifurcates postaxially to form i and the fibulare (f); i later segments to form c. The anlage of bc gives rise to the digital arch, which segments and bifurcates to produce the series of distal tarsals (dt), normally three, and the metatarsals (mt), normally five. Each metatarsal segments to produce the final phalangeal formula of 1-2-3-3-2.

Reductions of limb structure can be produced by three different processes. One very common mode of reduction is when skeletal elements simply remain connected throughout chondrogenesis (Fig 3C). This non-fission often results in an enlarged amalgamated element that incorporates the rudiments of several foci. This type of reduction lends a developmental predictabil-

ity to anatomical diversity (Shubin et al., 1995) because common patterns of reduction can be expected, or predicted, from a knowledge of developmental patterns. Neighboring skeletal elements may also fuse after separation. The fusion of elements results in combinations of elements that develop within different connection tracks (Fig. 2D). The fusion of distal carpal 4 and the centrale (in several plethodontids; Hanken, 1983, 1985) is an example of this mode of transformation. The final mode of developmental reduction is global truncation of a primitive developmental program. The development of the paedomorphic salamander, Proteus, is a case in point. Proteus has a hindlimb with only 2 digits. Digits III, IV, and V and never appear. The developmental trajectory of Proteus is a truncated version of the primitive urodele developmental plan (Fig. 2B).

Variation and homology

The use of intraspecific variation in the analysis of homology has a long history. Schmalhausen (1917) analyzed variation in the hand of Ranodon sibiricus, a hynobiid salamander. Schmalhausen (and Wake, 1966; 1991) noted that variation in this species is strikingly congruent to that of other species for which he had data. He described three "states" of the hynobiid tarsus consisting of different configurations of the centralia, distal tarsal four, and distal tarsal five. Change in any one of these elements usually involves reciprocal changes in other elements within this region of the foot because dt4, c, and dt5 interact with one another during ontogenesis. These interactions suggest underlying morphological identities. A major player in this interaction is a small element that Schmalhausen called m3 (known as "m" by other authors). This element m (m3) can be independent, it can merge with dt4, or dt5, or it can form an amalgamation with dt4 and dt5 (Fig. 1; Wake 1991). Many fossil amphibians possess an independent m, a small rudimentary bone between the centralia and the distal tarsals (Fig. 1). This bone is not part of the standard morphology of any extant salamander and has, presumably, been lost during the evolution of urodeles. Schmalhau-
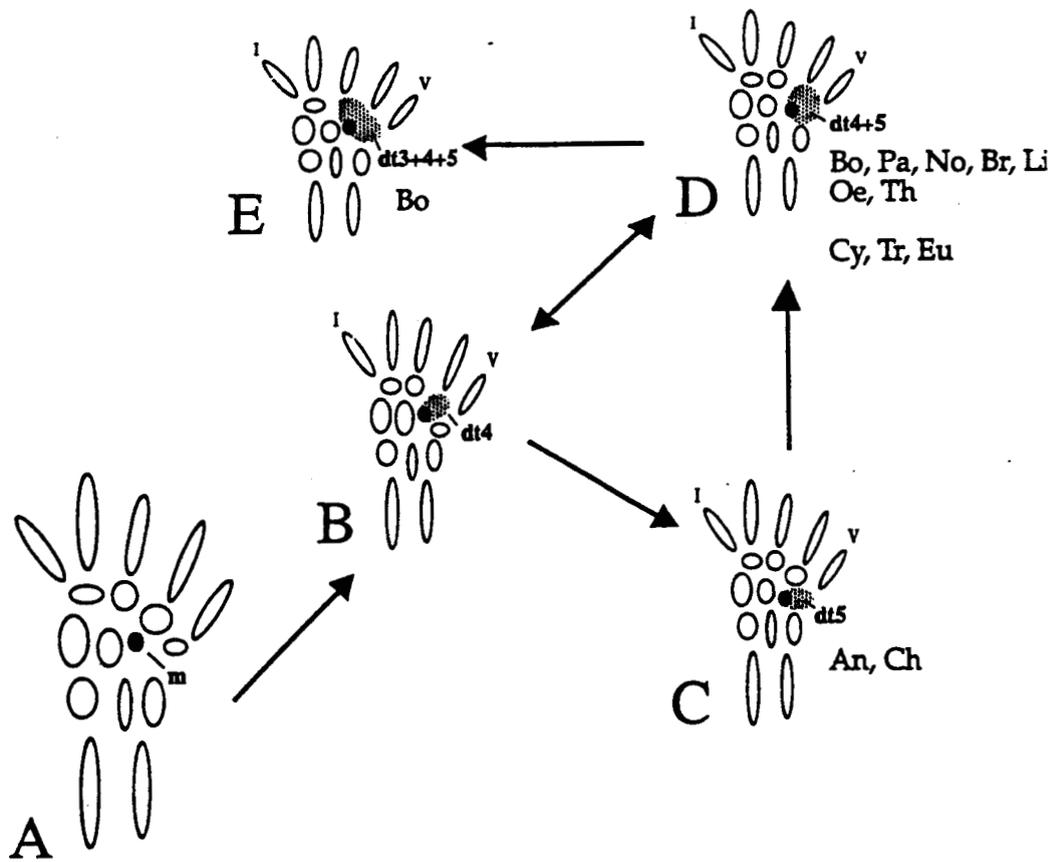
FIG. 3. Major transformations of salamander limb structure, exclusive of major digital losses seen in am-
phiumids, sirenids, and proteids. A) An independent m (bold) is the ancestral condition for the urodele tarsus
The exact number of centralia of the ancestral tarsus is greater than two. B) The generalized non-hynobiid and
cryptobranchid tarsus consists of an enlarged distal tarsal 4 (stipple) that extends towards the centrale. C
Arboreal salamanders (*Aneides, Chiropterotriton*) convergently acquire a tarsus distinguished by a reduced distal
tarsal 4 and a distal tarsal 5 that extends into the central region. D) The amalgamation of distal tarsals 4 and 5
is seen in a variety of plethodontid and salamandrid taxa (Bo: *Bolitoglossa*, Pa: *Parvimolge*, No: *Nototriton*, Li
Lineatriton, Oe: *Oedipina*, Th, *Thorius*, Br: *Bradytriton*, Cy: *Cynops*, Tr: *Triturus*, Eu: *Euproctus*). E) The
amalgamation of distal tarsals 3, 4, and, 5 is seen in several different bolitoglossines (Bo). Atavisms are fre-
quently encountered: *e.g.*, salamanders standard for dt3 + 4 + 5 contain variants with dt4 + 5; salamanders
with dt4 + 5 contain variants with separate dt4 and dt5 (Alberch, 1983). Most taxa contain variants with the
atavistic restoration of an independent m (bold).

sen noted that an independent m is a com-
mon variant condition in the foot of *Rano-
don, Cryptobranchus,* and *Onychodactylus*
(Table 1). When an independent m is pres-
ent in these limbs, dt4, and dt5 are both
reduced in size. These observations sug-
gested a "latent" homology of m, whereby
it is lost from the standard conditions of
extant taxa, but the developmental interac-
tions that form it are retained; hence it is
retained in the natural variation of extant
taxa. These studies imply that dt4, dt5, c,

and m are the product of interaction during
ontogeny that serves to integrate and reg-
ulate their phenotypic expression.

Recent analyses of urodele limb variation
extend and amplify Schmalhausen's (1917)
observations (Table 1; Fig. 3). The parallel
between patterns of intrapopulational vari-
ability and homoplastic characters is so
common as to be the expected situation in
urodele limb diversity (Shubin *et al.,* 1995).
Studies on the intra and interspecific vari-
ability of urodele mesopodia have revealed

TABLE 1. *List of variant conditions observed in urodeles.*

Plethodontidae
Plethodon neomexicanus (Dwyer and Hanken, 1990)
 f: i + u, i + u + c
 h: t + y, bc + d3, dt4 + dt5
Plethodon cinerus (Hanken and Dinsmore, 1986)
 f: i + u, d3 + d4, d4 + c, i + c, bc + d3, bc + d3 + d4, r + y
 h: d4 + d5, d3 + d4 + d5
Plethodon cinerus (regenerative anomalies, Dinsmore and Hanken, 1984)
 f: r + y, c + i, d3 + d4, d4 + u, bc + d3 + d4
 h: t + y, c + i, d3 + d4, d4 + d5, c + i, d3 + d4 + d5, bc + d3
Plethodon cinerus (Hanken, 1983)
 f: i + u, d3 + d4, d4 + c, d3 + d4 + c, i + c
 h: i + c, t + y, bc + d3, d3 + d4, bc + d3 + d4, d4 + d5
Bolitoglossa rostrata (Alberch, 1983)
 f: u + i
 h: i + f, d4 < d5, d3 + d4 + d5
Bolitoglossa subpalmata (Alberch, 1983)
 h: bc + d3, d5 > d4, d3 + d4 + d5
Bolitoglossa adspersa (Alberch, 1983)
 h: d3 + d4.+ d5
Bolitoglossa platydactyla (Alberch, 1983)
 h: d3 + d4 + d5
Bolitoglossa dofleni (Alberch, 1983)
 h: d4 + d5
Bolitoglossa occidentalis (Alberch, 1983)
 h: d3 + d4 + d5

Salamandridae
Taricha granulosa (Shubin et al., 1995)
 f: +2c, +c, +dc, +u, bc + d3, bc + d3 + d4, bc + d3 + c, bc + c, d3 + d4, d4 + c, i + c, m, po, r + i + u,
  r + r, sep u/i, u + i + c, u + u, y + r, y + r + c
 h: +2c, +c, +y, −d5, bc + d3, bc + c, d3 + d4, d4 + d5, d5 + m, f + i, m, +c
Triturus carniflex (Zaffaroni et al., 1992)
 f: r + y, c + i, c + i + u, bc + d3, d3 + d4, bc + d3 + d4, y + bc
Triturus cristatus (Rienesl and Wagner, 1992)
 f: d3 + d4, r + y, r + i + u, sep 1, 2
 h: extra y, m?
Triturus marmoratus (Rienesl and Wagner, 1992)
 f: d3 + d4, r + y, r + i + u
 h: Bc + 3, d3 + d4 + d5, r + y, extra y

Rhyacotritonidae
Rhyacotriton variegatus (Good and Wake, 1992)
 f: sep i/c
 h: bc + d3, d4 + d5, −d5
Rhyacotriton olympicus (Good and Wake, 1992)
 f: sep i/c

Hynobiidae
Cryptobranchus sp. (Schmalhausen, 1917)
 h: po, m
Onychodactylus sp. (Schmalhausen, 1917)
 h: po
Salamandrella sp. (Schmalhausen, 1917)
 h: m
Ranidens sibiricus (Schmalhausen, 1917)
 h: m
Siredon pisciformis (experimental manipulation, Schmalhausen, 1925)
 h: t + y, i + c, d3 + d4 + d4, d3 + d4, d4 + d5, f + d5, F + f, c + d2 + d3 + d4 + d5, F + f + d3 + d4 + d5,
  T + t + y, y + t + i + c

biases in the production of novel phenotypes (Alberch, 1983; Hanken, 1983; Vogl and Rienesl, 1991; Rienesl and Wagner, 1992). Observed patterns of variability are often predictable from a combination of developmental and phylogenetic considerations (Shubin et al., in press). Mesopodial arrangements that are homoplastic are commonly encountered in studies of intrapopulational variation. Distal tarsal 4+5 is found in the intrapopulational variation of salamanders with different standard patterns, in particular: 1) taxa that normally retain separate distal tarsal 4 and distal tarsal 5 (Table 1; e.g., Plethodon cinerus, Taricha granulosa) and 2) species that are standard for a combined distal tarsal 3+4+5 (Table 1, e.g., Bolitoglossa dofleni). Variation in the former parallels homoplastic conditions of highly nested plethodontids, whereas variation in the latter reflects atavistic restoration of an ancestral condition. Other types of atavism also occur; in Triturus cristatus (a species that normally possesses a joined distal tarsal 4+5) the ancestral pattern of two elements appears in natural patterns of variation (Rienesl and Wagner, 1992).

Analysis of variation reveals atavisms that restore conditions at different hierarchical levels of urodele phylogeny. The most commonly observed variants (those characteristic of the patterns of intraspecific variation of many different clades) often reflect the atavistic restoration of highly general characters of Paleozoic taxa and/or hynobiids and cryptobranchids (po, pr, m, supernumerary centralia). Variants of highly nested clades (e.g., bolitoglossines) often correspond to less general characters (Table 1, e.g., dt3+dt4+dt5 in B. adspersa; d4+d5 in B. dolfleni; independent dt5 larger than dt4 in B. subpalmata).

Basal clades reveal a great diversity of homoplastic conditions (Fig. 1) each of which reflects part, but not all, of the ancestral condition. Paleozoic temnospondyls possess a postminimus, prehallux, supernumerary centralia, and an independent m (m3, Schmalhausen, 1917). No single hynobiid or cryptobranchid possesses all of these primitive elements; individual taxa are often standard for different ones (basal

taxa, Fig. 1). This early flexibility of c, dt4 dt5 and m is reflected in the variation o more nested clades of urodeles; all of these conditions are observed variant condition: (Table 1). As comparative data from uro dele limb variation emerge, it is becoming increasingly apparent that urodeles share homologous patterns of variation with homoplastic patterns of fixation on standarc structural designs. The limitations imposec by developmental processes then, can play an important role in phylogenetic diversification. Significantly, no new carpal or tarsal elements have evolved during urodele phylogenesis; limb diversification is characterized by the fixation on patterns that are seen in the variation of related taxa.

Homology and Developmental Integration

The formulation of hypotheses of homology relies, in part, on the developmental individuation of organs (Wagner 1989a, b). Often, however, different (supposedly nonhomologous) structures share developmental and genetic interactions (Zuckerkandl, 1994). Hox genes, for example, appear to play a role in the development of a wide variety of different structures from the body axis to the limbs. Recent genetic and developmental investigation has given increasing support to Jacob's (1982) broad notion of "tinkering." New structures, in fact whole new body plans, do not necessarily involve new batteries of genes; their evolution often relies on the expansion and modification of existing regulatory and epigenetic networks (Carroll, 1994; Zuckerkandl, 1994). Widely different morphological structures can share similar mechanisms of genetic regulation, and these shared developmental mechanisms define ancestral patterns of integration and derived patterns of parallel evolution (Zuckerkandl, 1994).

The combined analysis of variation and morphological integration has important consequences for the notion of homology. If different organs, or elements within the same organ, share similar genes or developmental processes, then homology may be "incomplete", or fractional (sensu Zuckerkandl, 1994) if structures are not complete-

ly individuated. Morphological identity can exist at different structural and phylogenetic levels. Thus, element m of a cladistic outgroup may be seen as a homologue of different components of the tarsus in derived taxa (Fig. 3; *e.g.*, dt4 in *Plethodon*, but dt5 in *Aneides*; Wake, 1991)

This notion of fractional, or partial, homology can be used to portray variation and development of the postaxial mesopodium. The urodele tarsus is a bounded domain that is filled by different numbers of bones and differently shaped tarsals (Fig. 1). The space between the centrale and the distal tarsus can be filled by either an expanded centrale, independent m, or expanded distal tarsalia. These condensations interact during development as their condensations lie in close proximity during phases of cellular aggregation and differentiation. The development of any single condensation depends on the interaction between local developmental events (localized gradients, patterns of gene expression, and intercellular communication) and more global organismic phenomena (developmental gradients across the whole organism, DNA content per cell, cell size, rates of mitotic division). In this context, the development of the postaxial tarsus can be viewed as the outcome of a hierarchy of processes acting at different temporal and spatial scales. These developmental interactions have important consequences for the recognition of homologous elements. The homology of distal tarsal 4 can be viewed in two different ways; both carry different assumptions of developmental and morphological integration. The expanded distal tarsal 4 of most salamanders can be interpreted as a completely individuated element, homologous to the reduced distal tarsal 4 of some arboreal salamanders (Fig. 1). Likewise, the expanded distal tarsal 4 can be viewed much as Schmalhausen proposed in 1917; as a distal tarsal 4 + m (Fig. 3). This notion suggests that the expanded distal tarsal 4 is partially homologous to the expanded distal tarsal 5 and expanded centralia seen in basal taxa (Figs. 1, 3) because each of these would also result from different combinations with m.

Analysis of intraspecific variation can provide a test between these alternatives.

The intraspecific variation of m, the distal tarsus, and c defines range of observed morphological conditions and transformations (Fig. 3). An independent m is default state, one that is observed in the variation of many distantly related taxa (Table 1). Both basal and nested taxa contain m within their natural patterns of variation; all taxa appear capable of reverting to this ancestral condition. The "identity" of each of the postaxial elements is reflected in their variation. The appearance of an independent m appears to be correlated to a change in the distal tarsus or alteration of the central region. An independent m was never seen to coexist with an enlarged distal tarsal 4, expanded distal tarsal 5 or expanded c. These observations support Schmalhausen's (1917) proposal that the developmental integration of the distal tarsus and centralia is reflected by m.

Agassiz's "three-fold" parallelism is now "many-fold"; "many," because new types of comparative data continually emerge. As comparative morphology becomes enlightened by new data on variation, whether by genetic manipulation or intraspecific variation, the search for congruence remains paramount in the exploration of the hierarchy, integration, and homology of natural forms.

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