

Patterns of Regional Variation in the Vertebral Column of Terrestrial Salamanders

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ABSTRACT Regional variation in the vertebral column of several species of salamanders (families Ambystomatidae, Salamandridae and Plethodontidae) is analyzed. Measurements of three dimensions, centrum length, prezygapophyseal width, and transverse process length, provide the data. Ontogenetic, interspecific, intergeneric and interfamilial patterns of positional variation are diagrammed and discussed. Distinctive patterns of variation characterize the families, genera, and to a lesser extent, the species. The patterns of ambystomatid salamanders are the most generalized, and probably reflect derivation from a primitive ancestral stock. The most specialized conditions occur in the fully terrestrial plethodontids, a group generally considered to be highly derived. Data such as those presented here will aid in the identification of fossils.

The patterns described have functional significance. For example, species which have an aquatic larval stage and which return to aquatic breeding sites have vertebrae which taper in length and width behind the pelvis. This is a feature associated with production of a traveling wave in the tail which is necessary for propulsion in water. Fully terrestrial species do not have a tapering column. In them, standing waves, such as occur in the trunk region of all species, typically occur in the tail. The caudal vertebrae of terrestrial species are rather uniform in dimensions for some distance, and the tail is cylindrical in form. Other functionally important features include the narrowing and shortening of some anterior vertebrae, associated with the development of a neck in some species with tongue feeding mechanisms. In contrast, species which use their heads as wedges during locomotion have broadened anterior vertebrae which serve as sites of origin for hypertrophied neck muscles.

Regional variation in the vertebral column of salamanders has received scant attention, and the general assumption has been that little occurs. As recently as 1962, Mauger recognized but four regions in the column of *Pleurodeles*: a single atlas, 14 trunk vertebrae, a single sacral vertebra, and a number of caudal vertebrae. Comments concerning variation within these regions were limited to qualitative statements concerning relative degree of development of processes. Teege ('57) earlier recognized the same categories, but included some qualitative statements based on limited quantitative data (1 or 2 measurements per species, usually of centrum length of an unspecified posterior trunk vertebra). Papers by

other authors have tended to be even less specific.

Recently new interest has arisen in patterns of vertebral variation from workers concerned with the identification of fossil remains, and from those concerned with specific problems in functional and evolutionary morphology. Estes ('64), studying Cretaceous salamander remains, included some observations on variation in the anterior part of the column of recent and fossil salamanders. Wake ('63, '66) and Wake and Dresner ('67) drew attention to the tail base region, and the specializations of vertebrae related to patterns of locomotion and tail autotomy. Worthington ('68, '71) has been concerned with postmetamorphic changes in vertebral

proportions in *Ambystoma opacum*, and Wake and Lawson (unpublished) studied patterns of regional variation in the morphogenesis of the vertebral column of *Eurycea bislineata*.

We are concerned here with patterns of regional variation in ontogeny and at specific, generic and familial levels. One ontogenetic pattern of change (*Ambystoma opacum*), one set of interspecific comparisons (genus *Ambystoma*), two sets of intergeneric comparisons (two genera of salamandrids; four genera of plethodontids), and one set of interfamilial comparisons (ambystomatids, salamandrids, plethodontids) are presented. The study is limited to an analysis of three vertebral dimensions, centrum length, prezygapophyseal width and transverse process length. This analysis serves as a point of departure for more detailed studies, which we hope will be of value for the identification of fossil salamanders, for investigations of evolutionary relationships, and for functional morphological studies of locomotion, feeding, courtship and tail autotomy.

MATERIALS AND METHODS

Vertebrae were prepared by maceration of fresh specimens after passing a wire down the neural canal. Individuals of each species were selected from the same locality and matched (± 1.5 mm) in standard length (snout to posterior end of vent). Normally six, but occasionally five, specimens were used in each sample.

Three measurements were selected as being representative of much of the proportional variation observed throughout the vertebral column. Centrum length is the distance along the midventral line, including the condyle in those species which have opisthocoelous vertebrae. Prezygapophyseal width is the greatest distance across the prezygapophyses. Transverse process length is the maximum distance separating the distal tips of the transverse processes of a given vertebra; the measurement thus includes the length of two processes and the width of the neural arch. In species having separated rib bearers, the longer of the two was measured.

All measurements were taken to the nearest 0.1 mm under a dissecting micro-

scope fitted with an ocular micrometer. All vertebrae anterior to the fifth caudal, but excluding the atlas, were normally measured. The mean, standard deviation and 90% confidence interval of variation about the mean were calculated for each of the measurements taken for each vertebral position. Graphs (figs. 1–11) were constructed to aid analysis.

Species were selected from the families Ambystomatidae, Salamandridae, and Plethodontidae. In the Plethodontidae, representatives of the subfamilies Desmognathinae and Plethodontinae (and its three tribes Hemidactyliini, Plethodontini, and Bolitoglossini) (Wake, '66) were studied. The species examined, collection localities, standard length of the individuals, and sample sizes are as follows: Ambystomatidae — *Ambystoma opacum* (2.3 mi. SE of Largo, Prince George's County, Maryland; 33–35 mm, N = 5; 43–45 mm, N = 6; 64–65 mm, N = 6), *A. maculatum* (15 mi. W Hagerstown, Washington County, Maryland; 82–83 mm, N = 6; 1 mi. W Elkton, Howard County, Maryland; 90 mm, N = 6), *A. macrodactylum* (Skyway Park, King County, Washington; 51–52 mm, N = 6), *A. trigrinum* (2.5 mi. E Massey, Kent County, Maryland; 70–71 mm, N = 5), *A. jeffersonianum* (15 mi. W Hagerstown, Washington County, Maryland; 40–43 mm, N = 6; 81–83 mm, N = 5); Salamandridae — *Taricha granulosa* (Vashon Island, King County, Washington; 63–64 mm, N = 6), *Notophthalmus viridescens* (2.3 mi. SE of Largo, Prince George's County, Maryland; 41 mm, N = 6); Plethodontidae — Tribe Plethodontini, *Plethodon jordani* (0.9 mi. E and 0.5 mi. S top of White Top Mountain, Grayson County, Virginia; 51–52 mm, N = 6); Tribe Bolitoglossini, *Chiropterotriton multidentatus* (El Chico Park, Hidalgo, Mexico; 42–42.5 mm, N = 6); Tribe Hemidactyliini, *Eurycea bislineata* (Turkey Run State Park, Parke County, Indiana; 40–46 mm, N = 6); Subfamily Desmognathinae, *Desmognathus brimleyorum* (Little Missouri Falls, Montgomery County, Arkansas; 40–41 mm, N = 6).

Most of the samples were drawn from breeding populations and represent adults. There are some exceptions, including a sample of recently transformed individuals (33–35 mm *Ambystoma opacum*) and

three juvenile samples (43–45 mm *A. opacum*, 40–43 mm *A. jeffersonianum*, 70–71 mm *A. tigrinum*).

In some instances, a particular vertebra could not be measured because of damage. Damaged vertebrae were not measured, and a new sample size is recorded on the graph below the distribution; otherwise the sample sizes are as given above. Means were not calculated for less than four measurements.

The following notation is used: T = trunk vertebrae, S = sacral vertebra, CS = caudosacral vertebrae, C = caudal vertebrae.

Patterns of regional variation

In the following paragraphs data are presented and analyzed according to taxonomic divisions. Only the first treatment, of *Ambystoma opacum*, includes detailed information on ontogenetic changes.

Family Ambystomatidae

Ambystoma opacum

Centrum length. Patterns of variation in centrum length for samples of individuals in three size ranges are shown in

figure 1. The patterns are similar at all three sizes. In the anterior region of the column the vertebrae are relatively short. They increase in size posteriorly with the increase involving the first two trunk vertebrae in the smallest sample and the first three or four vertebrae in the samples of larger individuals. T 3 or 4 through T 14 show little variation in centrum length. Less than 0.1 mm separates the means of T 5 through T 14 in all three samples, with even greater uniformity in the smaller size ranges. Centrum length decreases regularly in the column from the sacral vertebra posteriorly. Slight decreases begin with T 13 and 14 in some individuals. The centrum of CS 3 is the first that is shorter than T 1. Means of centrum length (T 1 through C 4) differ by less than 0.4 mm (33–35 mm sample), to a little more than 0.5 mm (43–45 mm sample), to greater than 0.8 mm (64–65 mm sample).

Worthington ('68, '71) compared the centrum lengths of T 1, 7 and 14 at 35, 55, and 70 mm standard length. T 1 is significantly shorter ($p < 0.01$) than T 7 and 14 at all three sizes. T 7 and 14 are not significantly different from one another. Worthington also found that the slope of the regression for centrum length

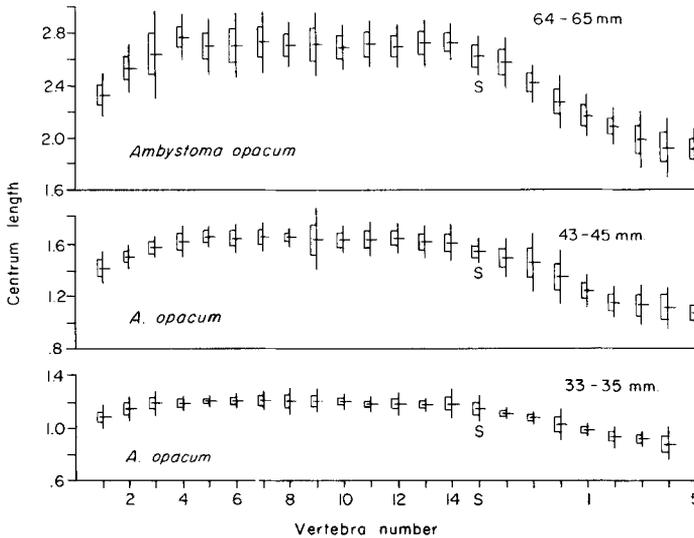


Fig. 1 Regional variation in centrum length in *Ambystoma opacum* at three different body sizes. Horizontal line: mean. Box: one standard deviation on either side of mean. Vertical line: 90% confidence interval for variation about mean. Even numbers: trunk vertebrae. S, sacral vertebra. Odd numbers: caudal vertebrae. Measurements in millimeters.

plotted against standard length for T 1 is significantly different ($p < 0.01$) from the slopes of T 7 and 14 (the slopes for T 7 and 14 are not significantly different from one another). This indicates that T 1 elongates more slowly than more posterior vertebrae.

To determine if any of the samples were more variable than the others, the coefficient of variability for each mean and standard deviation was calculated. An inspection of the graphs (fig. 1) indicates that with increase in size, variance also

increases. An inspection of the coefficients of variability, however, indicates that the smaller individuals are proportionally as variable as the adults.

Transverse process length. Patterns of variation for length of the transverse processes for three samples are shown in figure 2. The measurement is relatively large on the anterior trunk vertebrae, but decreases posteriorly. This trend involves T 1-5 in the 43-45 mm sample and T 1-4 in the 64-65 mm sample. In the 33-35 mm sample a plateau of less than 0.1 mm

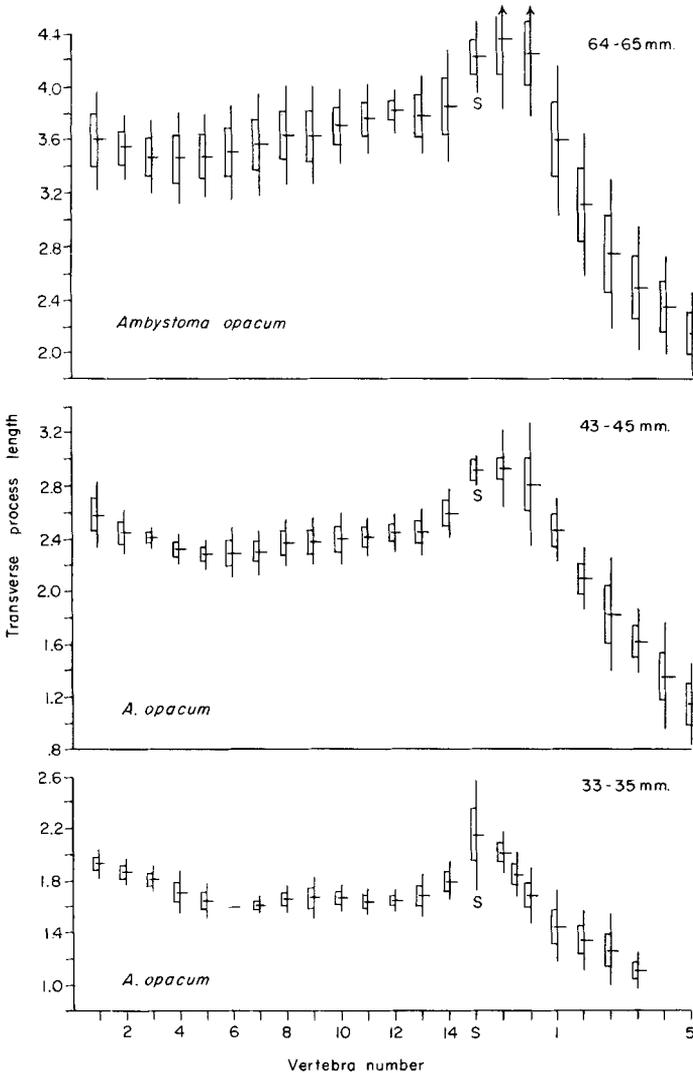


Fig. 2 Regional variation in transverse process length in *Ambystoma opacum* at three different body sizes. See figure 1 for explanation.

difference in means occurs from T 5 through 13. In the other samples the means gradually increase in size posteriorly, from T 4 or 5. The mean of the sacral vertebrae of all three samples is markedly larger than that of any of the preceding vertebrae. Processes of the caudosacral vertebrae all show a decrease in size posteriorly but exhibit a variable pattern. They are shorter than the sacral in the 33–35 mm sample; those of CS 1 are larger than those of the sacral in the 43–45 mm sample; and processes of CS 1 and 2 are larger than those on the sacral in the 64–65 mm sample. Processes of the caudal vertebrae exhibit a regular decrease in length posteriorly.

Worthington ('68, '71) measured both dorsal and ventral processes on T 1, 7, and 14. The slope of the calculated regression line for the measurements of the ventral rib bearer length of T 1 plotted against standard length is significantly different ($p < 0.01$) from that of T 7, but not from that of T 14. The difference in slopes is related to the angle the process makes with the body axis. On anterior vertebrae the ventral rib bearers project almost perpendicularly from the vertebra and body axis, whereas the dorsal rib bearers slant more posteriorly. With increasing body size the ventral rib bearers begin to project more posteriorly.

In most respects our results are in agreement with those of Worthington ('68, '71). He found that this dimension of T 1 is significantly larger ($p < 0.01$) than that of the seventh at 35 mm, but that the vertebrae are not significantly different at 55 mm. The dimension of T 7 is larger than T 1 at 70 mm ($p < 0.05$). The processes of T 14 are significantly longer than those of T 7 and T 1 at all three sizes (1% level). There is a point of disagreement with our data in comparing T 1 and T 14 at small sizes. Perhaps this is the result of some preparation artifact. There is agreement as far as adult conditions are concerned.

The transverse processes of caudosacral vertebrae usually lack ossified ribs (only a single ossified rib was found in this area in a series of 20 cleared and stained individuals). Caudosacral vertebrae of juveniles have a cartilaginous extension issuing from a single distal socket in the

transverse process. Rapid development of the transverse processes of the caudo-sacral vertebrae occurs by replacement of this extension by bone. Such a process cannot occur anteriorly, except perhaps on the last trunk vertebra, since ossified ribs appear early and presumably the flexible cartilage joints are required for functional reasons.

An inspection of the coefficients of variability for the 33–35 mm and 64–65 mm samples does not indicate any clear differences in variability. It is apparent, however, that the caudal vertebrae are more variable than anterior vertebrae (coefficients of variability average about twice those for anterior vertebrae). Because of our small sample size we cannot reject the possibility that the individuals in the smaller size range might be proportionally less variable.

Prezygapophyseal width. Prezygapophyseal width patterns are similar in the three samples studied (fig. 3). The anterior vertebrae are relatively broad and decrease in width posteriorly. This trend involves T 1–8 in the 33–35 mm sample, T 1–7 in the 43–45 mm sample and only T 1 and 2 in the 64–65 mm sample. In the samples of smaller individuals, less than 0.1 mm variation in means encompasses T 3–14 in the 33–35 mm group and T 2–13 in the 43–45 mm sample. In the posterior end of the column, means increase to the sacral, which is wider than neighboring trunk and postsacral vertebrae. Means increase from T 12 to S in the 33–35 mm sample, from T 11 to S in the 43–45 mm group, and from T 2 to S in those measuring 64–65 mm. A uniform decrease in size occurs from CS 1 posteriorly in all three samples. The sacral vertebra is the widest vertebra in the 64–65 mm sample, but is not as wide as T 1 in the 43–45 mm group, and is less wide than either T 1 or 2 in the 33–35 mm sample.

The slopes of the regression lines of prezygapophyseal width plotted against standard length for T 1 are significantly different ($p < 0.01$) from those of T 7 and 14 (Worthington, '68, '71). The slopes for T 7 and 14 do not differ significantly.

Worthington ('68, '71) compared vertebrae at three different sizes. At 35 mm, T 1 has a significantly wider prezygapophyseal width ($p < 0.01$) than T 7 and 14,

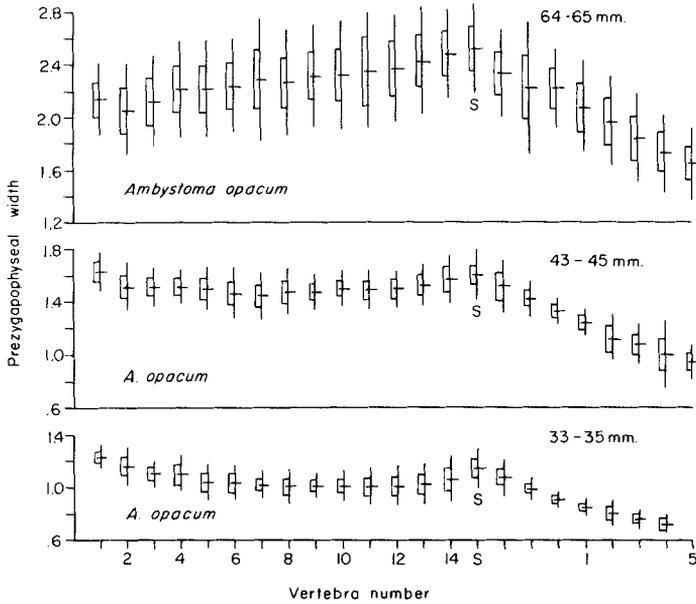


Fig. 3 Regional variation in prezygapophyseal width in *Ambystoma opacum* at three different body sizes. See figure 1 for explanation.

and T 14 is significantly wider than T 7 ($p < 0.01$). At 55 mm T 1 and 7 do not differ significantly, but T 14 is wider than both ($p < 0.01$). At 70 mm T 1 is narrowest, T 7 is wider than T 1, and T 14 is widest (all differences significant at 1% level).

An inspection of the coefficients of variability for prezygapophyseal width indicates that the sample of smaller individuals may be less variable. Coefficients of variability for the 33–35 mm sample fall between 3.3 and 6.9 whereas at 64–65 mm they range from 6.2 to 12.1.

Comparison of *Ambystoma opacum* patterns

Centrum measurements in the 33–35 mm sample average slightly larger than the prezygapophyseal width means on corresponding vertebrae, except in the neck region (T 1–2), where the vertebrae tend to be widened and shortened, and in the sacral and caudosacral regions, where the means are similar. Transverse process length means are much larger than those of the other two measurements, except in the caudal region where the dimension decreases rapidly. The pattern of the

means for transverse process length resembles that of prezygapophyseal width in that the anterior trunk and sacral region means are the broadest. The centrum length pattern is consistently different from the others in that the means are greatest throughout most of the trunk, decreasing from the level of the last trunk or sacral vertebra posteriorly, and at the anterior end of the column.

The combined patterns of the 43–45 mm sample are little different from the patterns of the 33–35 mm group. Centrum length means are larger than prezygapophyseal width means throughout most of the trunk and in the caudal region. Means of the two measurements are similar in the sacral and caudosacral regions whereas the prezygapophyseal width means are larger in the anterior end of the trunk. Means for transverse process length are consistently larger than the means of the other two measurements. The pattern of transverse process lengths is almost identical to that of prezygapophyseal widths. The means of all three measurements are most similar in the caudal region and show the greatest divergence in the anterior end of the column and in the sacral and caudosacral regions.

Centrum length means in the 64–65 mm sample are all larger than the prezygapophyseal width means on corresponding vertebrae. This differs from the other samples in that the vertebrae in the anterior end of the column have longer centrum lengths than prezygapophyseal widths. Centrum length and prezygapophyseal width are most similar in the sacral and immediate postsacral areas. The prezygapophyseal width pattern very closely matches that for transverse process length, but some minor differences can be noted. Only T 1 has a wider prezygapophyseal width than more posterior vertebrae whereas T 1–3 show this trend in transverse process length. Both prezygapophyseal width and transverse process length show a gradual increase throughout the trunk to the level of S. This trend continues to CS 1 in the pattern of the transverse process length. The increase in length in the trunk region is different from the relatively uniform measurements found in the same regions of the smaller samples, although a hint of this posterior increase is in evidence in the transverse process of the 43–45 mm sample. The area of greatest divergence in the combined patterns of the 64–65 mm sample is the caudosacral region, while in the 33–35 mm sample it is at the level of the sacral vertebra. A high degree of divergence is also found in the anterior end of the column, as is the case in the other samples. The greatest similarity in the means of the three measurements of the 64–65 mm sample is in the caudal region.

Worthington ('68, '71) studied patterns of positional variation of other measurements in the vertebral column of *A. opacum*. Height (measured from the posterior midventral tip of the centrum to the dorsal portion of the bony part of the neural spine) of the atlas, trunk, sacral and first two caudosacral vertebrae decreases posteriorly throughout the trunk region to the sacral vertebra, with a slight increase in the caudosacral region. The maximum height of the caudal vertebrae (measured from the ventral tip of the haemal spine to the dorsal tip of the neural spine) decreases regularly from C 1 posteriorly. Vertebral length (measured from the anterior tip of a prezygapophysis to the posterior tip of a postzygapophysis)

and neural arch length (measured mid-dorsally) have patterns almost identical to that of centrum length.

Patterns in other species of *Ambystoma*

Centrum length. Similar patterns of regional variation in centrum length occur in all species of *Ambystoma* examined (figs. 1, 4). A region of shortened vertebrae at the anterior end of the column includes from one to three vertebrae. Mean lengths steadily increase on the first three (*A. macrodactylum*, *A. maculatum*) to eight (*A. jeffersonianum*) vertebrae. A 0.1 mm plateau, including from six vertebrae, in *A. maculatum*, to fifteen, in *A. macrodactylum*, is conspicuous in most species. A steady decrease in mean length begins with T 13 (*A. macrodactylum*) to

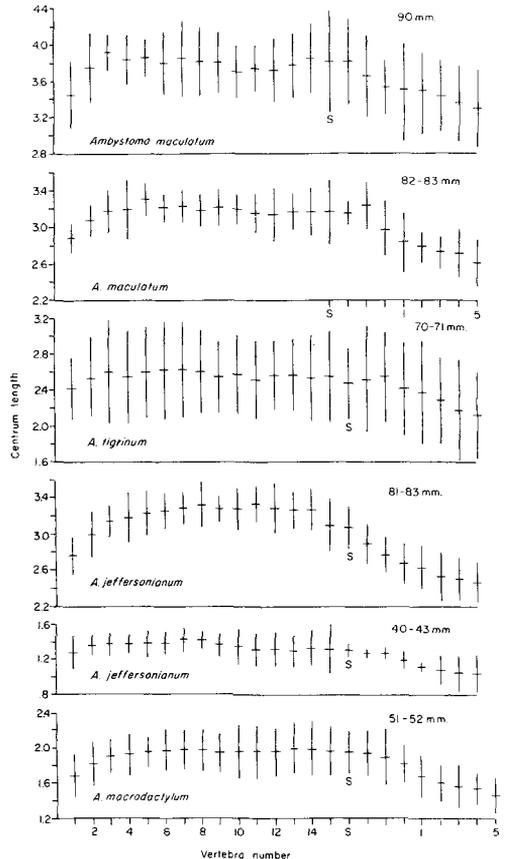


Fig. 4 Regional variation in centrum length in different species of *Ambystoma*. See figure 1 for explanation.

CS 2 (*A. tigrinum*) and extends into the tail. The total range of mean lengths is from less than 0.5 mm (*A. tigrinum*) to over 0.8 mm (large *A. jeffersonianum*). T 1 is always the shortest of the trunk series. The first postsacral vertebra shorter than T 1 may be as far forward as CS 3, (*A. jeffersonianum*, *A. tigrinum*) or as far backward as C 3 (large *A. maculatum*). The longest vertebra is variable in position, from the front part of the column in *A. maculatum* and *A. tigrinum* to nearer the middle in *A. macrodactylum* and *A. jeffersonianum*. The patterns are relatively flat over most of the column in *A. macrodactylum* and *A. tigrinum* and most curved in *A. jeffersonianum*.

Transverse process length. All *Ambystoma* examined are roughly similar to *A. opacum* in the general pattern of regional variation (figs. 2, 5). Transverse processes are relatively long on T 1 and means then decrease for from one (*A. maculatum*) to four (*A. tigrinum*) vertebrae before beginning a general increase that continues to CS 1. From slight (*A. macrodactylum*, *A. tigrinum*) to marked (larger *A. maculatum* and *A. jeffersonianum*) decreases in mean length occur in the trunk region immediately in front of the sacrum. Mean length decreases from CS 1 posteriorly. The magnitude of this decline, through the level of C 4, is from about 1.5 mm in the sample of small *A. macrodactylum* to nearly 2.5 mm in *A. tigrinum*. The longest processes in the trunk series are found on T 1 in small *A. jeffersonianum* and in *A. tigrinum*, in the middle of the trunk in large *A. jeffersonianum* and *A. maculatum*, and at the posterior end of the trunk in *A. macrodactylum* and the largest *A. maculatum*. The variation in the position of the longest processes of the trunk series reflects the different ontogenetic states of our samples. The patterns of the small *A. jeffersonianum* and the *A. tigrinum* (at 70–71 mm standard length they have grown little since metamorphosis) are most similar to the patterns for recently metamorphosed and small *A. opacum* (figs. 2, 5). The patterns of *A. macrodactylum* and *A. maculatum* (90 mm sample) are almost identical to the pattern for large adult *A. opacum*. The remaining patterns for adult *A. jeffersonianum* and *A. maculatum* (82–

83 mm) are similar to the pattern for adult *A. opacum*, but probably reflect slightly earlier ontogenetic stages.

The first postsacral vertebra with longer processes than any trunk vertebra is CS 1, which has the largest mean of any in the column. The first postsacral vertebra that has shorter processes than any trunk vertebra is C 1, except in *A. macrodactylum*, where it is CS 3.

Prezygapophyseal width. The patterns for prezygapophyseal width exhibit considerable variation among the species of *Ambystoma* (fig. 6). Yet when ontogenetic state is considered, the patterns are essentially similar to those of *A. opacum* (fig. 3). The patterns for *A. jeffersonianum* (40–43 mm sample) and *A. tigrinum* are almost identical to those of recently metamorphosed and small *A. opacum*. Comparisons of the patterns of *A. jeffersonianum* (40–43 mm sample), *A. tigrinum*, and the 43–45 mm sample of *A. opacum* reveal that prezygapophyseal width decreases to T 7, remains relatively uniform throughout the posterior half of the trunk, increases slightly in the immediate presacral region to a wide point on the sacral (but not wider than on the first vertebrae), and then progressively decreases in the tail region. The patterns of prezygapophyseal width for *A. maculatum* (both samples), *A. macrodactylum* and large *A. jeffersonianum* (fig. 6) show marked similarities to the pattern for adult *A. opacum* (fig. 3). In all the sacral has the greatest prezygapophyseal width. In all but *A. jeffersonianum* T 1 is wider than the next one or two, and all show a posterior increase in prezygapophyseal width throughout most of the trunk. In the immediate presacral area of large *A. jeffersonianum* and both *A. maculatum* samples, a slight decrease in prezygapophyseal width is evident before an increase at the sacrum. A similar trend was noted in transverse process length of some species. In both samples of *A. maculatum*, CS 1 has a prezygapophyseal mean width that is slightly smaller than those of S and CS 2. In all other species of *Ambystoma* a regular decrease in mean width occurs from S into the tail. The first postsacral vertebra to have a smaller mean than any trunk vertebra (the narrowest trunk vertebra is T 1 in large *A. jeffersonianum*

and as far posteriorly as T 7 in small *A. jeffersonianum* and other species) is from CS 2 (*A. tigrinum* and small *A. jeffersonianum*) to C 2 (*A. maculatum*).

Summary of patterns in *Ambystoma*

When comparisons among the samples of *Ambystoma* are made with a knowledge of ontogenetic state, the patterns of regional variation are found to be remarkably similar in all the species. Centrum length patterns show relatively little ontogenetic change, being short in the anterior region of the trunk, relatively uniform and longest throughout most of the posterior two-thirds of the trunk, and decreasing posteriorly from the sacral region.

Transverse process length patterns

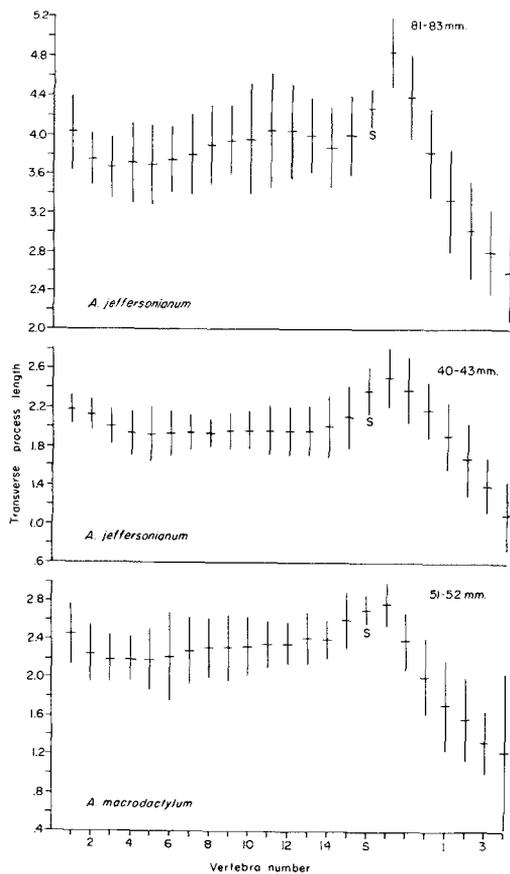


Figure 5a

change ontogenetically. In small *Ambystoma*, mean lengths are large anteriorly, progressively decreasing to about the middle of the trunk. Lengths then increase rapidly at the posterior end of the trunk to a maximum on CS 1 (the sacral vertebra is widest in the smallest sample of *A. opacum*) then regularly decrease posteriorly into the tail. In adult *Ambystoma*, only T 1 to 3 show a posterior decrease in length and most of the trunk region is characterized by increase which is pro-

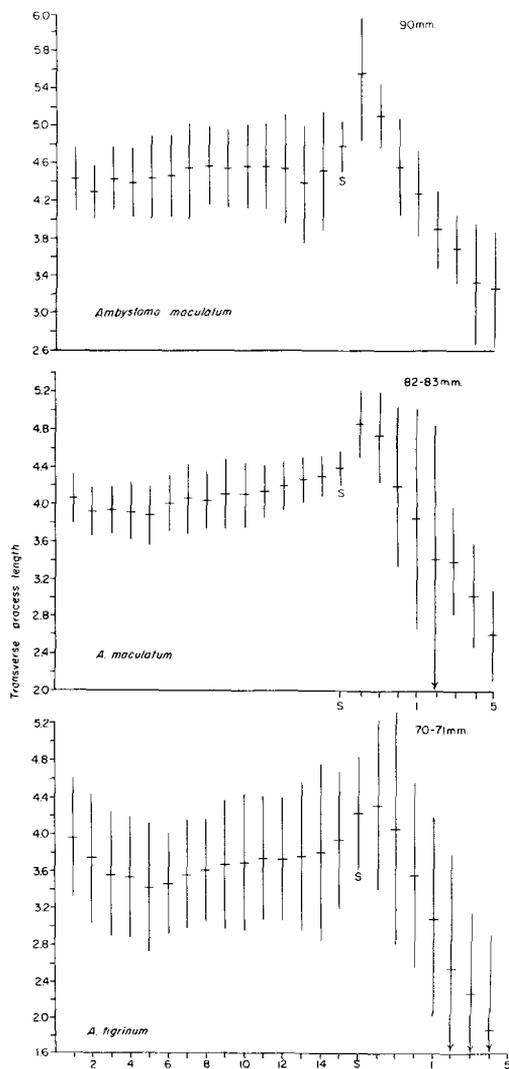


Figure 5b

Fig. 5 Regional variation in transverse process length in different species of *Ambystoma*. See figure 1 for explanation.

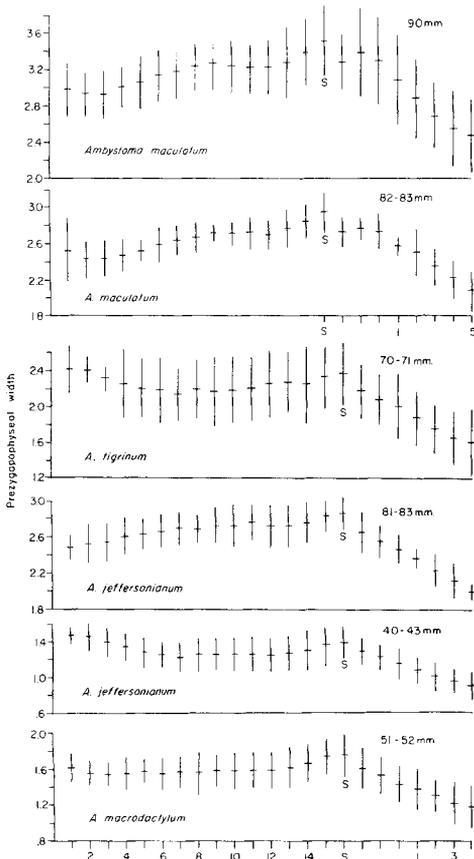


Fig. 6 Regional variation in prezygapophyseal width in different species of *Ambystoma*. See figure 1 for explanation.

nounced in the sacral and caudosacral regions. CS 1 has the longest transverse processes, and they shorten precipitously beyond that point.

Prezygapophyseal width patterns also change ontogenetically, in much the same way as do those of transverse process length. Small *Ambystoma* show a decrease in prezygapophyseal width behind the middle of the trunk. Most of the trunk is characterized by little change in this dimension. Width increases at the posterior end of the trunk (widest at sacral) and then regularly decreases in the caudosacral and caudal regions. In adults only T 2 to 3 show an initial decrease in size (large *A. jeffersonianum* are an exception), and most of the trunk is characterized by an increase to the sacral (widest), followed by a regular decrease posteriorly

through the caudosacral and caudal regions. Prezygapophyseal width and transverse process length patterns are conspicuously different in the caudosacral region.

The means of transverse process length are much greater than the other means for a given vertebral position. The means of centrum length are generally more similar to those of prezygapophyseal width. Means for transverse process length and centrum length tend to converge in the anterior part of the tail. Means of centrum length and prezygapophyseal width tend to converge at the anterior end of the column and in the sacral region.

Family Salamandridae

Notophthalmus viridescens and *Taricha granulosa*

Centrum length. Considerable positional variation is evident (figs. 7, 8) with means of trunk vertebrae differing by nearly 0.5 mm in *Notophthalmus* and by almost 1.0 mm in *Taricha*. Mean lengths regularly increase posteriorly from T 1 (shortest) through T 9 (longest) in both genera. The relative shortness of the vertebrae near the anterior end of the column is marked. The mid-trunk plateau of less than 0.1 mm variation in means includes T 5 through 13 in *Notophthalmus* and T 7 through 12 in *Taricha*. Centra regularly decrease in length posteriorly from T 12 (*Notophthalmus*) and T 9 (*Taricha*).

Transverse process length. Means decrease regularly on T 1-5 of *Taricha* and less regularly on T 1-4 of *Notophthalmus* (figs. 7, 8). A plateau of less than 0.1 mm variation in means includes T 1-12 in *Notophthalmus*, but only T 6-10 in *Taricha*. Mean lengths increase abruptly from the last trunk to the sacral vertebra (more than 0.25 mm in *Notophthalmus* and over 0.5 mm in *Taricha*), and the largest means are those for CS 1. From that point means decrease rather abruptly until well into the tail. The decrease between CS 1 and C 4 is more than 1.0 mm in *Notophthalmus* and nearly 1.8 mm in *Taricha*. The three caudosacrals in *Notophthalmus* and the first caudosacral in *Taricha* are the only postsacral vertebrae with longer processes than any trunk vertebrae (the longest trunk processes are

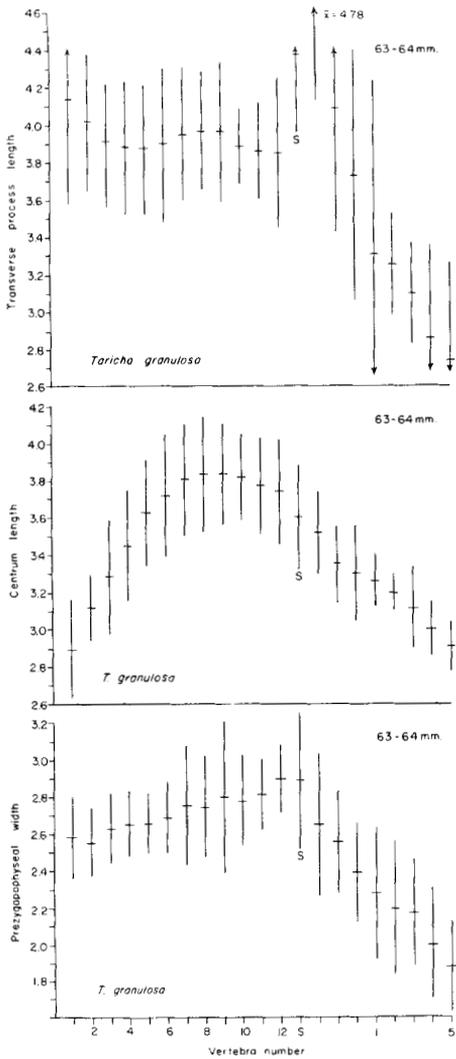


Fig. 7 Regional variation in three vertebral dimensions in *Taricha granulosa*. See figure 1 for explanation.

the first and thirteenth in *Notophthalmus* and the first in *Taricha*). The first postsacral vertebra with shorter processes than any trunk (shortest on T 4 of *Notophthalmus* and T 12 of *Taricha*) is C 1 of *Notophthalmus* and CS 3 of *Taricha*. Patterns are similar in the two genera despite the differences noted above. Positional variation includes initial decrease, then slight increase of means, followed by a slight (*Notophthalmus*) to marked (*Taricha*) presacral decrease and an abrupt sacral and caudosacral increase. This is

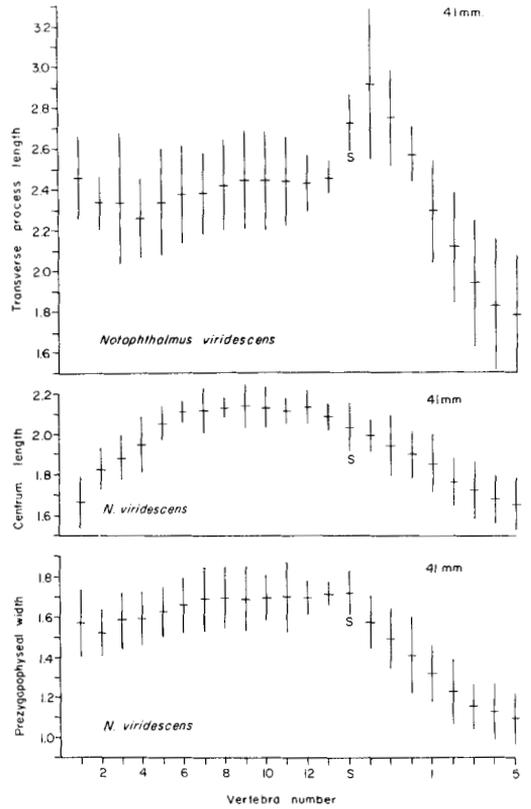


Fig. 8 Regional variation in three vertebral dimensions in *Notophthalmus viridescens*. See figure 1 for explanation.

followed by regular decrease in means posteriorly through the caudal region.

Prezygapophyseal width. Patterns are generally similar in the two genera (figs. 7, 8). T 2 has a smaller mean than T 1, then means regularly increase through T 8 in *Notophthalmus* and T 12 in *Taricha*. A plateau of less than 0.1 mm variation of means extends from T 5 through T 13 of *Notophthalmus*. No plateau as such occurs in *Taricha*, although the means of T 3-6 differ by less than 0.1 mm. The sacral mean is greater than any trunk mean in *Notophthalmus*, but is slightly less than the mean for the last trunk vertebra (T 12) in *Taricha*. CS 2 is the first postsacral mean equal to or smaller than any trunk mean (smallest on the T 2).

Summary of the salamandrid patterns

While the individual dimensional pat-

terns of *Notophthalmus* and *Taricha* are very similar, the overall or combined patterns are distinct. Means of transverse process length are greater than means of other dimensions except in the tail of *Taricha*. However, means of centrum length in *Taricha* approach those of transverse process length in the middle and posterior part of the trunk, while those of *Notophthalmus* tend to be more nearly equidistant between means of prezygapophyseal width and transverse process length. *Taricha* has one less vertebra than *Notophthalmus*. Possibly the increased length of some vertebrae is a compensation for a reduction in vertebral number. The means for centrum length converge with those of prezygapophyseal width in the neck, and with the transverse process width means in the mid-trunk and tail base regions. The greatest area of divergence is between the means of transverse process width and centrum length in the neck and sacral-caudosacral regions.

Family Plethodontidae

Chiropterotriton multidentatus, *Desmognathus brimleyorum*, *Eurycea bislineata*, and *Plethodon jordani*

Centrum length. Positional variation is moderate in these genera, and maximum difference between means is from less than 0.2 mm in *Plethodon* to over 0.5 mm in *Desmognathus* (fig. 9). The *Desmognathus* pattern is rather similar to that of *Eurycea* and that of *Plethodon* is similar to *Chiropterotriton*. In both *Eurycea* and *Desmognathus* means increase regularly at the anterior end of the column, from T 1 through T 7 in the former and through T 9 in the latter. Midtrunk means are the largest in the column in both genera (T 7 through T 9 in *Eurycea*, T 9 in *Desmognathus*). Means increase abruptly from T 1 to 2 in both *Chiropterotriton* and *Plethodon*, and the mean of T 2 is as large as, or larger than, that of any other vertebra. Means decrease from T 2 to T 4 (*Chiropterotriton*) or T 5 (*Plethodon*), then increase slightly in the midtrunk region reaching a maximum by about T 9 as in *Eurycea* and *Desmognathus*. The midtrunk means relative to that of T 1 are greater in *Chiropterotriton*

(as in *Desmognathus* and *Eurycea*) than in *Plethodon*. In *Desmognathus* and *Eurycea* means steadily decrease from the last two or three trunk vertebrae to the sacral, then increase slightly on CS 1 (*Eurycea*) to considerably on CS 1 and 2 (*Desmognathus*). In *Plethodon* and *Chiropterotriton*, by contrast, the means increase on the last two trunk vertebrae through the sacral (where they reach a maximum for that region in *Chiropterotriton*). In *Plethodon*, the means continue to increase through CS 2. A plateau of less than 0.1 mm variation of means includes T 6–15 of *Desmognathus*, T 6–14 in *Eurycea*, T 5–CS 1 in *Chiropterotriton*, and T 3–S in *Plethodon*.

Means decrease into the tail in *Eurycea* and *Desmognathus*, but in *Plethodon* there is a slight decrease from CS 2 through C1, then a slight increase through C 4. C 4 has a slightly larger mean than CS 2 and is equal to the longest trunk centrum (T 2). Means decrease regularly posterior to C 4 in *Plethodon*. In *Chiropterotriton* means decrease from S to CS 1, then decrease abruptly from CS 1 to CS 2 and slightly to C 1. Means increase abruptly on C 2, and slightly on C 3 and 4. C 4 has a mean just slightly less than that of the sacral and of the longest trunk vertebra. The marked and abrupt decrease in centrum length at the tail base in *Chiropterotriton* contrasts with patterns of the other three genera.

Transverse process length. Means decrease steadily on the first four (*Chiropterotriton*) to six (*Eurycea*) vertebrae in a regular pattern (fig. 10). From that point, means increase slightly or remain nearly stable throughout most of the trunk region. A plateau of less than 0.1 mm variation of means includes from 7 (*Chiropterotriton*) to 12 (*Plethodon*) trunk vertebrae. The greatest mean is that of the CS 1 in all genera, but an abrupt increase in means occurs between the next to last and last trunk vertebrae (between the last trunk and sacral in *Eurycea*). Means steadily increase on the last eleven trunk vertebrae of *Chiropterotriton* and on the last three of *Plethodon*. The abruptness of change at the end of the trunk series is greatest in *Chiropterotriton*, in which the means of the next to last and last trunk vertebrae differ by over 0.4 mm.

brae which we measured in *Plethodon* have longer processes than any trunk vertebrae.

The patterns in these four genera are generally similar, and positional variation is rather regular except in the sacral-caudosacral region. The pattern involves initial increase on the anterior vertebrae, a period of little change throughout most of the trunk vertebrae, then abrupt increase and decrease in the sacral-caudosacral region, followed by a steady decline.

Prezygapophyseal width. Patterns differ considerably in the plethodontid genera (fig. 11). In *Eurycea* means are relatively uniform throughout the series, with marked sacral widening. In *Desmognathus* the largest mean is on the first vertebra, and the pattern is one of general decrease posteriorly. Means increase markedly in the sacral region. In *Plethodon* and *Chiropterotriton* the pattern is one of small anterior means and a general increase behind that point. *Desmognathus* and *Chiropterotriton* represent opposite ex-

tremes. The patterns are relatively regular in all four genera.

A plateau of less than 0.1 mm variation of means includes from eleven (*Plethodon* and *Chiropterotriton*) to fourteen (*Eurycea*) of the trunk vertebrae, excluding mainly the anterior ones. The sacral mean is greater than any trunk mean in *Plethodon*, *Chiropterotriton*, and *Eurycea*, but in *Desmognathus* the mean of T 1 is the greatest. In *Desmognathus* C 2 is the first postsacral mean that is smaller than any trunk mean (the smallest are T 4 and T 13). None of the postsacral vertebrae measured have smaller means than the smallest trunk means in *Chiropterotriton* (T 1) and *Plethodon* (T 2), but the mean measurement of C 2 (the last measured) of *Eurycea* is equal to the smallest mean of the trunk series (T 4). Means of all postsacral vertebrae measured (through C 4) are equal to or greater than all trunk

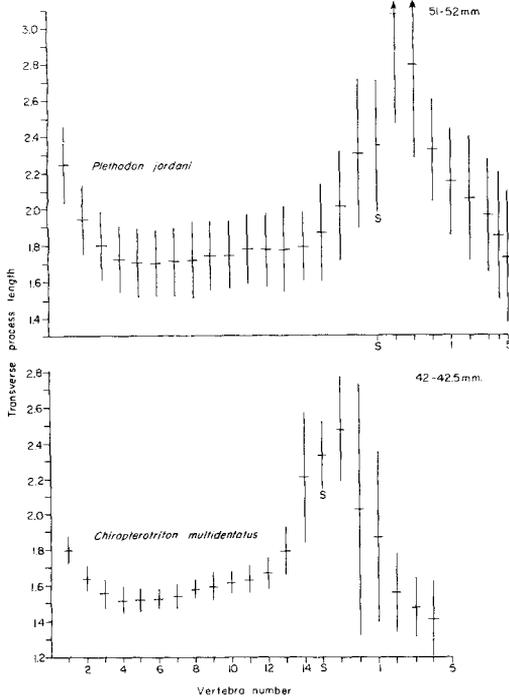


Figure 10a

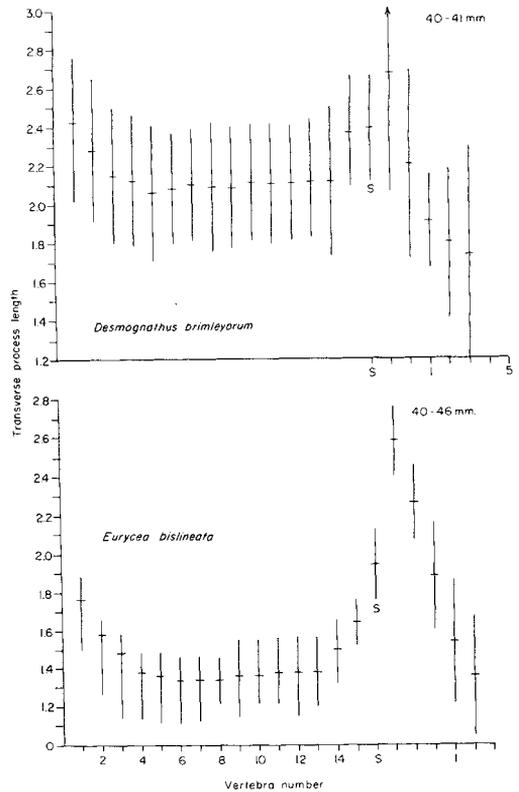


Figure 10b

Fig. 10 Regional variation in transverse process length in four species of plethodontid salamanders. See figure 1 for explanation.

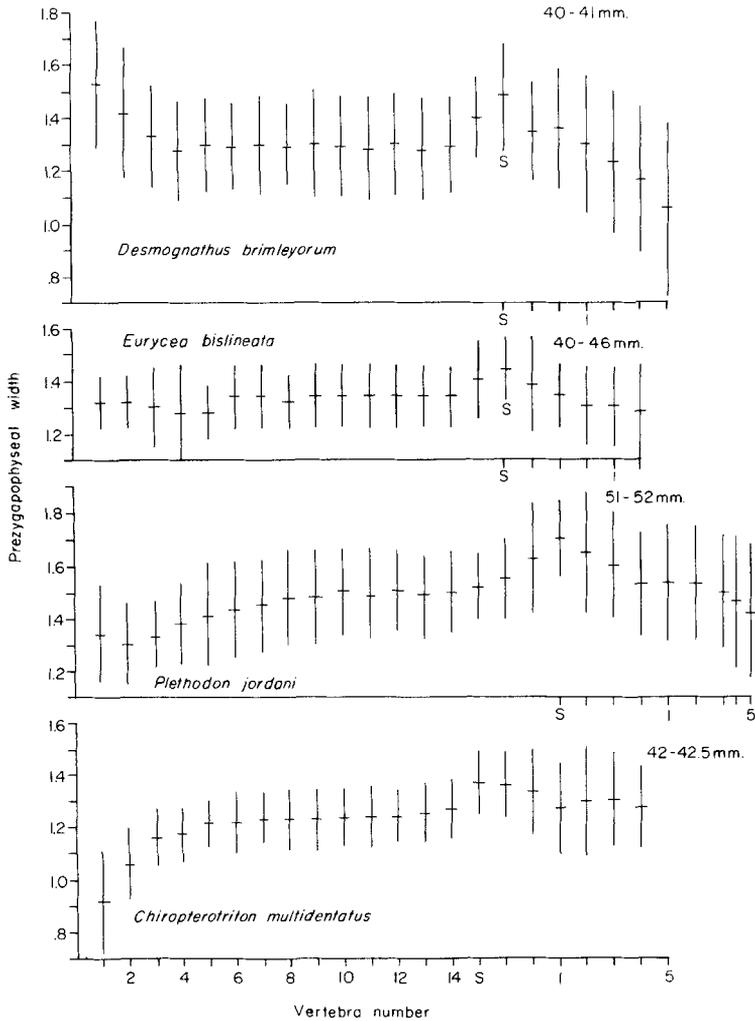


Fig. 11 Regional variation in prezygapophyseal width in four species of plethodontid salamanders. See figure 1 for explanation.

means in *Chiropterotriton*. The mean of C 5 of *Plethodon* is larger than that of the first five trunk vertebrae.

Summary of the plethodontid patterns

The combined patterns are distinctive for each of the four plethodontid genera. Means of transverse process length are greater than means of other dimensions throughout the column in *Desmognathus*, and on all but C 5 of *Plethodon*. However, these means are greater only on T 1 and 14, S, CS 1 and 2, and C 1 of *Chiropterotriton*, and on T 1, S, and CS 1-3 of *Eury-*

cea. Centrum length has the smallest mean on 16 of 21 vertebrae measured for *Eurycea* (including only 2 caudals) and on 15 of 21 vertebrae measured for *Chiropterotriton* (including 4 caudals).

Centrum length means more or less parallel prezygapophyseal means in the neck of *Chiropterotriton*, but the patterns converge strongly in both *Eurycea* and *Desmognathus*. In *Desmognathus* prezygapophyseal width is greater than centrum length. In *Plethodon* means of the two dimensions converge on T 1 but diverge on T 2. These two means tend to converge again in the sacral region of all genera,

and especially in the tail base region of *Chiropterotriton*. These means diverge in the midtrunk region of *Eurycea* and *Desmognathus*, but are more parallel, or tend to converge, in *Chiropterotriton* and *Plethodon*.

Means of transverse process length and prezygapophyseal width tend to parallel one another in patterns of positional change in *Desmognathus*, except for a disproportionate increase in transverse process length in the caudosacral region and its subsequent disproportionate decrease in the tail. Different patterns occur in the other species, where these means converge strongly in the midtrunk region (especially in *Eurycea*) and again in the anterior part of the tail.

Two marked patterns of divergence occur between the means of centrum length and transverse process width in the neck of *Desmognathus*, and between the means of transverse process width and prezygapophyseal width in the neck of *Chiropterotriton*.

DISCUSSION

Interfamilial patterns of regional variation

Although we have sampled only five species of ambystomatids, two of salamandrids, and four of plethodontids, it seems evident that certain features of regional variation are characteristic of each family. In ambystomatids the trunk, sacral and caudosacral regions differ in transverse process length and prezygapophyseal width. The means for centrum length lie between the other two means, and tend to be closer to those of prezygapophyseal width, especially in the posterior part of the trunk. The postsacral region is characterized by a rapid and abrupt decline in the means of all measurements.

The salamandrid patterns are quite distinctive and are characterized by very long centra, absolutely and relative to other vertebral dimensions and size. As a result, the means for centrum length lie closer to those of transverse process length than to those of prezygapophyseal width, especially in the middle of the trunk. Transverse processes are very long, relative to prezygapophyseal width, as in ambystoma-

tids. The postsacral region is characterized by a relatively rapid decrease in mean measurements, though less dramatic for centrum length than for the other dimensions. This, again, is similar to the ambystomatid patterns.

The only plethodontid pattern even roughly comparable to the salamandrid and ambystomatid conditions is that seen in *Desmognathus*. Here means for transverse process length and prezygapophyseal width are much less than in *Ambystoma opacum* and *Notophthalmus viridescens* of comparable size. Means for centrum length are slightly greater than in *Ambystoma*, but much less than in *Notophthalmus*. Postsacral decline in means of all measurements is less than in members of the other two families.

The remaining plethodontids display patterns that are very different from the patterns of other families and of *Desmognathus*. The transverse processes of trunk vertebrae are much shorter relative to the other dimensions. As a result the trunk means of all dimensions of *Plethodon* are very close to one another. In *Eurycea* and *Chiropterotriton* means of centrum length are from slightly to greatly larger than means of transverse process length on most trunk vertebrae.

In all plethodontids prezygapophyseal measurements are relatively uniform and do not demonstrate the marked postsacral decline that is seen in ambystomatids and salamandrids.

The relative relationship of the three dimensions in the anterior part of the trunk of *Chiropterotriton*, *Eurycea* and *Plethodon* differs considerably from that seen in *Desmognathus* and in the other families. In *Chiropterotriton* and *Eurycea* the means of centrum length and transverse process length reverse their relative positions between T 1 and 3, and this pattern is not seen elsewhere.

Functional and evolutionary implications

The techniques and approaches utilized in this paper are likely to be most useful in interpretations within single families, where greater comparability exists between taxa. We view this paper as an initial effort and hope to extend these studies to more detailed analyses of the families Ambystomatidae and Plethodon-

tidae. However, even at the level of the present survey, certain functional interpretations are possible.

Centrum length is related directly to size and number of vertebrae. For example, two species of identical size with different numbers of vertebrae would have centra of different lengths, assuming head length remains constant. The patterns of regional variation may or may not be identical. All of the vertebrae could be longer in the species with fewer vertebrae, or certain of the vertebrae could be longer. Inspection of our sample provides some illustrative examples of the relation between trunk length, vertebral number and pattern of regional variation in centrum length.

Centrum length measurements are not strictly comparable throughout our sample because of differences in the morphology of the joint region. *Taricha*, *Notophthalmus* and *Desmognathus* have anatomically opisthocoelous vertebrae (but see Wake, '63, '65, '70) with persistent and protrusive condyles on the anterior ends of the vertebrae. Thus the lengths of their centra are increased relative to the other species which are anatomically amphicoelous.

At the anterior end of the column in all species there is a distinct shortening of the centra relative to midtrunk regions, and a similar decline occurs in the post-sacral centra. These differences appear to be directly attributable to differences in growth rates throughout the column. Some data which are available for *Ambystoma opacum* support this conclusion. Slope values (mm increase in centrum length per 1.0 mm increase in standard length) at various points in the column are as follows: T 1, 0.038; T 7, 0.046; T 14, 0.046; S, 0.044; CS 1, 0.047; CS 3, 0.042; C 5, 0.035, (Worthington, '68). Thus anterior trunk and caudal vertebrae increase in length more slowly than do other vertebrae, and this fact is reflected in the centrum length profiles of adults. The differences are likely greater in *Taricha*, where differences between anterior and midtrunk vertebrae are the greatest in our sample. In *Taricha* the relatively great length in the midtrunk vertebrae is a compensation for the very short trunk series of but twelve vertebrae. In this

genus, and to a lesser extent in *Notophthalmus*, trunk lengthening is primarily the result of higher growth rates of the midtrunk vertebrae relative to other vertebrae.

Centrum length increases regularly on the first few trunk vertebrae, but there are some exceptions. In *Plethodon* and *Chiropterotriton* centrum length increases abruptly from T 1 to T 2, and the latter is the longest of all trunk vertebrae. In both, T 1 is by far the shortest of any trunk vertebrae. It is possible that this phenomenon is related to the evolution of a neck in *Plethodon* and *Chiropterotriton*. Both genera rely on vision and tongue feeding to a large degree. In such a situation, the short atlas and T 1 produce an area of constriction between the skull and the long T 2, which allows greater flexibility. The head is seemingly more movable in these strictly terrestrial genera than in the other somewhat more aquatic genera utilized in this study. It is impossible for more than the atlas and T 1 to be involved in a neck in salamanders because of the severe design constraints imposed by the architecture of the shoulder. The second rib, on T 2, is the dominant support of the shoulder girdle, and serves as the site of attachment of two major parts of the serratus musculature. T 1 is involved to a lesser degree in shoulder support, and is thus subject to some modification under selection for a flexible neck.

Salamanders use different patterns of lateral bending during locomotion, depending on whether they are on land or in the water. When in the water, a traveling wave is propagated which passes down the body and tail, providing the major propulsive force. On land, the limbs serve as relatively fixed points, and the main function of lateral bending is to supplement the limb muscles. It has been shown that standing rather than traveling waves are propagated during salamander locomotion on land, with nodes of virtually no bending located at about T 6 (just behind the shoulder region), in the caudosacral region, and at about C 7 (Roos, '64; Daan and Belterman, '68). In locomotion of this sort, Roos ('64) calculates that half of the progress of the fore limb originates in body undulation. The importance of body undulation in the hind limb, which is di-

rectly attached to the vertebral column, is much less.

The above considerations may aid in interpretation of the caudal patterns of positional variation seen in our sample. Note that in the species in which aquatic locomotion is utilized during part of the life (all except *Plethodon* and *Chiropterotriton*) centrum length decreases sharply and rather regularly posterior to the sacrum, or even anterior to that point in some species. This results in a tapered tail well suited for the propagation of muscular waves.

Breder ('26) classified fish in three categories according to body movements, and each has a typical body form, with a characteristic tail-body ratio and degree of tail flexibility. While salamanders can by no means be compared directly with fish as far as overall locomotion is concerned, we believe that certain comparisons related to tail form and function can be made. Salamanders with aquatic locomotor patterns are closest to Breder's carangiform pattern (tapering tails of medium length), but differ in lacking a terminal fin expansion. Precise analysis of motion requires consideration of several factors, including maximum degree of rotation of the fin, the amplitude of its transverse movement, and the phase relationship between the rotational and transverse movements (Gray, '68). We restrict our comments to the transverse movements because rotational movements seem less important than in fishes and are beyond the scope of this study.

The amplitude and speed of lateral displacement increases in a tapered tail as the muscular contraction waves pass posteriorly (Gray, '68). Those species which depend most on lateral tail displacement as a means of locomotion in aquatic situations have the greatest degree of tapering, as reflected in the progressive decline in mean centrum length posterior to the pelvic region. Those species which do not demonstrate such a pattern (*Plethodon* and *Chiropterotriton*) are not aquatic at any stage of their life history, but are terrestrial to arboreal. In them, the tail has gained new functions, including fat storage, prehension (*Chiropterotriton*), cutaneous respiration (both are lungless and rely to a large degree on skin and buccal

regions for respiration), and protection (e.g., tail autotomy in *Chiropterotriton*). In addition such primitive non-locomotor functions as involvement in courtship are retained for the tail of these genera. There is an advantage to the organism in several regards for a tail of greater length than in more primitive species, and it seems that one means of accomplishing this end has been a departure from the growth pattern of primitive species. In these two genera mean centrum length increases progressively from the anterior end toward the middle of the tail. Whether this results from an increased growth rate relative to more anterior vertebrae or to initially larger segments we cannot say with our data, but we think the former is the likeliest explanation. Only one vertebra (T 2) has a mean centrum length as great as those in the anterior end of the caudal series in these two genera.

The pattern of *Chiropterotriton* stands out from all other genera studied in the tail base region, where CS 2 and C 1 (especially the latter) vertebrae have mean lengths that are much shorter than those of neighboring vertebrae. This produces a constriction at the base of the tail related to tail autotomy. The constriction is a superficial indication of a suite of internal morphological specializations (Wake and Dresner, '67).

Transverse process patterns are complicated by several factors. Means increase on the anterior end of the column in all species. This is due in part to an increase in the diameter of the spinal cord, and hence the vertebral canal, and in part to a tendency for the transverse processes to be oriented at right angles to the vertebral axis on the anterior vertebrae. On more posterior vertebrae the processes tend to be oriented at an angle of less than 90° to the vertebral axis. Thus, the anterior increase in process length is more apparent than real. Other areas of pattern irregularity are in the immediate presacral, sacral, and caudosacral regions. The last trunk, and sometimes the last two trunk vertebrae, lack ribs in some species. Unfortunately, we do not have reliable data on variation in presence or absence of ribs on the last trunk vertebra, but we do know that they are usually present in *Taricha* and usually absent in

Plethodon. Means of transverse process length on the last trunk relative to the sacral vertebra are much higher in *Plethodon* than in *Taricha*. Apparently the intermyotomal tissue that gives rise to ribs on most trunk vertebrae has the potential of being added to the transverse process when ribs are absent. Ribs are usually absent posterior to the sacrum in salamanders, but they are present in the caudosacral region of some salamandrids and ambystomatids. None of the species that we have used in this study have caudosacral ribs, but all of the species have very long transverse processes on these vertebrae, especially the first. It is known that rib materials appear independently of these vertebrae and later become incorporated into the transverse processes in *Eurycea* (Wake and Lawson, Ms.). Clearly the caudosacral region is one in which selection has favored a less flexible intermyotomal support than in anterior regions, and the rib material of more anterior vertebrae has been added to the transverse processes, lengthening them. These long processes provide attachment for the caudal musculature at the base of the tail which functions in propagating the sinuous waves important in locomotion. In all genera but *Notophthalmus* and *Eurycea* variation is greater in both the last trunk and first caudosacral than in the sacral vertebra, and variation is typically greater in the caudosacral region than in the trunk region.

There are great differences in the relative length of transverse processes among genera. They tend to be very long in the ambystomatids, and shorter (*Desmognathus*) to very much shorter (*Eurycea*, *Chiropterotriton*) in the plethodontids. The processes tend to be relatively shorter in slender forms with more terrestrial habits. Ideally ribs and transverse processes are considered together, but we do not have quantitative data on rib length. An additional consideration is the degree of separation of the dorsal and ventral rib bearers, which vary from nearly complete continuity (some of the *Ambystoma*) to very wide separation (*Eurycea*). Until more is known concerning rib relationships and the functional significance of rib-transverse process units in locomotion, we cannot make further comments.

Patterns of regional variation in prezygapophyseal width are more regular than are those of other dimensions. One consistent feature is the increased mean of the sacral vertebra relative to surrounding vertebrae. The sacral vertebra plays an important functional role as the sole axial support of the pelvic girdle. While it is not longer than neighboring vertebrae, it is more massive, and this is reflected in the increased value of the mean for prezygapophyseal width relative to the other vertebrae.

Means of prezygapophyseal width steadily decline in the postsacral region, including the tail base, in all genera, but the decline is more regular and steep in ambystomatids and salamandrids than in plethodontids, except *Desmognathus*. This is a reflection of the general tapering effect seen in the laterally compressed tails of the majority of salamanders studied, and of the more nearly cylindrical tails of such plethodontids as *Plethodon* and *Chiropterotriton*.

While detailed functional analysis must await the availability of more material within families and genera, at least one set of functional interpretations is possible from the comparative data assembled thus far. Means for prezygapophyseal width tend to increase steadily near the anterior end of the column in most species. This is probably directly related to the fact that the spinal cord is tapered as it nears the brain, and steadily increases in diameter as it passes through the anterior end of the vertebral column, nearing the skull. However, the increase in size is greater in *Desmognathus* than in other genera and includes the first three vertebrae rather than just the first one or two, as in most of the other genera. *Desmognathus* and its close relatives are unique among salamanders in the manner in which the skull articulates on the atlas and the way in which the head is used in feeding and locomotion (Wake, '66). A stout ligament extends from the atlas to the mandible, restricting the downward motion of the mandible. Strong throat muscles pull the head down to the point at which the temporal ligament becomes taut, and the head, bent sharply downward, is used as a wedge by the organisms, to allow them to squeeze under rocks and

into burrows. In order to function effectively, the head must be raised, and this task is accomplished mainly by the dorsal spinal muscles, which are greatly hypertrophied in desmognathine salamanders. These muscles originate over the dorsal surfaces of the anterior trunk vertebrae. The increased breadth of these vertebrae is probably related to the requirement for muscle attachment space, and an increase in vertebral mass associated with the requirement to absorb the forces transmitted to the vertebral column from the skull during burrowing activities.

A sharp reversal of the typical pattern of other genera is encountered in *Chiropetrotriton*. Here means of prezygapophyseal width steadily decrease near the anterior end of the column. The first four vertebrae have means less than those of the other vertebrae which were measured. This narrowing of the vertebrae, together with the shortened T 1 previously noted, is related to the evolution of a functional neck in this genus. All of the neotropical genera utilize a specialized tongue feeding mechanism (Wake, '66). Correlated with tongue feeding is a tendency toward arboreal habits. These two phenomena result in organisms which dwell in a more fully three dimensional world than do other salamanders. In such a way of life, with an organism searching for food and catching it by tongue propulsion, head mobility on the vertebral column is highly desirable. *Chiropetrotriton* gives evidence of morphological specializations in the vertebrae of the anterior trunk region which suggest that a more flexible neck is evolving in the group.

CONCLUSION

Patterns of positional variation in vertebral columns of salamanders have diagnostic value at several taxonomic levels. Extension of studies reported here will enable paleontologists to more accurately identify fossil remains than is now possible. The patterns also have value for analysis of phylogenetic relationships. Although our sample is limited, certain conclusions seem warranted.

On the basis of the structure and development of vertebrae, ambystomatids are closer to hypothesized ancestral con-

ditions than are salamandrids and plethodontids (Wake, '70). The large, amphicoelous vertebrae of ambystomatids have a large, persistent notochord and close-set rib bearers. These are primitive features. Opisthocoelous vertebrae with rather widespread rib bearers characterize most salamandrids. The notochord frequently is not persistent. Much variety is seen in plethodontids, but usually the vertebrae have a modified form of amphicoely and a small, persistent notochord. In some the rib bearers are very widespread, but in others they are closely placed and may fuse. This latter condition is specialized. Ambystomatids also have more generalized ways of life than the salamandrids and plethodontids used in this study. In view of these considerations, it is likely that patterns of positional variation in ambystomatids are more like ancestral conditions than are those of the other two families. Perhaps this is another way of saying that ambystomatids are more conservative in locomotor specialization than are the other groups. The various species of salamandrids and plethodontids studied all have distinctive patterns, but the kinds of specializations are in different directions in the two families. The extremes of specialization occur in plethodontids, and usually involve specialized behavior, and feeding and locomotor mechanisms that are associated with ecological shifts. In future studies we hope to explore these suggestions in greater detail.

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