

Morphometrics of the Skeleton of *Dermophis mexicanus* (Amphibia: Gymnophiona). Part I. The Vertebrae, With Comparisons to Other Species

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ABSTRACT Morphometric analysis of vertebral structure in caecilians (Amphibia: Gymnophiona) is presented. Ontogenetic variation in *Dermophis mexicanus* is analyzed through the 100+ vertebrae composing the column. Vertebral structure in adult *D. mexicanus* is compared with that in *Ichthyophis glutinosus* and *Typhlonectes compressicauda*. Centra of the atlas, second, tenth, 20th, and 50th vertebrae grow at allometrically different rates in *D. mexicanus*, though the 20th and 50th are not significantly different. Growth appears significantly slower in several dimensions of anterior and posterior vertebrae relative to mid-trunk vertebrae in all three species. Mensural patterns throughout the entire column are similar in the terrestrial burrowers *D. mexicanus* and *I. glutinosus*; patterns in the aquatic *T. compressicauda* differ substantially from those of the burrowing species and are strongly influenced by allometry. Of the 112 *D. mexicanus* examined, 13.4% had vertebral anomalies, usually fusions.

Some attention has been paid to vertebral structure in caecilians and to the development of vertebrae, particularly in attempts to understand variation among the three orders of Recent amphibians. A number of descriptions or figures of vertebrae occur in the literature, usually of only one or a few vertebrae from a single specimen to represent a species; for example, *Chthonerpeton indistinctum* (Wiedersheim, 1879), *Siphonops annulatus*, *Schistometopum thomensis*, *Uraeotyphlus oxyurus*, *Hypogeophis rostratus*, and *I. glutinosus* (Peter, 1894), *Hypogeophis rostratus* (Lawson, '63), anterior four or five vertebrae of 24 species (Taylor, '77), and the fossil *Apodops pricei* and six recent species (Estes and Wake, '72). More attention has been paid to development of vertebrae than to their adult structure by several authors: Marcus and Blume ('26), Marcus ('34, '37), and Lawson ('63, '66) on *H. rostratus*; Ramaswami ('58) on *I. "glutinosus"*; Mookerjee ('42) on an unidentified form, probably an *Ichthyophis*; Wake ('70) on *Gymnopsis multiplicata* and *T. compressicauda*, largely in analysis of amphibian ordinal relationships.

Regional variation throughout the vertebral column of caecilians has not yet been examined, nor has the comparative ontogeny of vertebrae. In contrast to most other elongate amphibians and reptiles, caecilians have an

atlas and 95–285 trunk vertebrae, lack a sacrum, and usually lack a tail (Taylor, '68). Two size samples of *D. mexicanus* (family Caeciliidae) plus an ontogenetic series of juveniles and adults were examined and compared to samples of *I. glutinosus* (Ichthyophiidae) and *T. compressicauda* (Typhlonectidae). Thus, three of the five families of caecilians were sampled; the species represent both terrestrial and aquatic ways of life.

This paper, and another in preparation on the morphometrics of the skull of *D. mexicanus*, provide information on osteological variation. It has been stated (see Lawson, '63) that there is no significant variation in structure and proportions of vertebrae following the atlas. I therefore wished to test the alternative hypothesis that there is significant variation among vertebrae in the column. I suspected that the structure of vertebrae in "neck," body, and posterior regions of the column might be significantly different, that growth pattern might also vary, and any differences might be correlated with locomotor (and, to some degree, feeding) functions. Further, since most work on caecilian vertebrae has been typological, it seemed useful to provide data on linear, ontogenetic, and population variation in vertebral structure. An understanding of regional, age-related, and populational varia-

tion allows more effective assessment of taxonomic comparisons in the literature, such as those of Peter (1894) and Estes and Wake ('72). It also provides a frame of reference for allocation of isolated vertebrae, such as fossils, to body regions and possibly to species. These data also provide a baseline for further work on the functional morphology of the vertebral column and assessment of regional, ontogenetic, and interspecific variation in function.

MATERIALS AND METHODS

For the study of ontogenetic and adult variation, material from a single population of *D. mexicanus* collected near San Rafael Pie de la Cuesta, San Marcos, Guatemala, was prepared. Five specimens from each of two size classes (total lengths 190 ± 5 mm and 370 ± 4 mm) were prepared by inserting nichrome wire through the neural arches of all vertebrae of freshly killed animals, then macerating and drying the bones. Vertebrae were thus maintained in order but freely movable. Measurements of neural arch length (NAL) and anterior (AW) and posterior widths (PW), width across transverse processes (TVPW), left parapophysis length (PPL), centrum length (CL), posterior centrum depth (CHK), depth of central keel at mid-vertebra (K), posterior vertebral height from neural arch rim to bottom of centrum (PVH), and height of neural (nuchal) keel (NK) were measured on an EPO1 microscope mounted with a digital micrometer which read to 0.001 mm. Means and 95% confidence limits were calculated for both samples. All measurements were taken on all 106 vertebrae of one specimen and plotted against vertebral number in sequence. It was thereby determined that variation could be adequately evaluated from measurements of each of the first 20 vertebrae, then every fifth vertebra to the 80th, and finally alternate vertebrae to the end of the column. Spinal nerve foramina were also examined. For comparison dried and strung vertebrae of an *I. glutinosus* (350 mm total length) of the primitive family Ichthyophiidae and two *T. compressicauda* (350 and 362 mm total length) of the aquatic family Typhlonectidae were also counted and measured. In addition, vertebrae were counted and length of the centrum of the atlas and second, tenth, 20th, and 50th vertebrae of each specimen was measured with a dial calipers on x-rays of 102 preserved specimens from 108 mm to 448 mm total length. These 102 specimens were selected from more than 300 x-rayed so

that the position of the vertebrae and the quality of the x-ray allowed careful measurement. Descriptive statistics were calculated using SPSS computer programs.

DESCRIPTION OF VERTEBRAE

Vertebral column

Vertebral counts in the population of *D. mexicanus* range from 100 to 112 ($\bar{x} = 106.19$, $s = 2.03$, mode = 105; Fig. 1). Contrary to Lawson's ('63) impression for *H. rostratus*, there is considerable regional variation in the features and proportions of vertebrae, although regions grade into one another, in all three species examined. The atlas is easily distinguished from other vertebrae. In addition, anterior vertebrae are characterized by the presence of a foramen (or pair of foramina) for the dorsal and ventral roots of the spinal nerves (these pass between vertebrae in the rest of the column beginning at the 15th to 21st vertebra in *D. mexicanus*, the fifth to 11th in *T. compressicauda*, and the fourth in *I. glutinosus*) and a nuchal keel. Posterior vertebrae have progressively reduced vertebral extensions such as the transverse processes, parapophyses, and the ventral keel so that posteriormost vertebrae are irregularly shaped rings of bone around the end of the spinal cord, composed only of neural arch and centrum. Descriptions of vertebrae are based primarily on the *D. mexicanus* sample, but apply to the three species examined, with exceptions as noted.

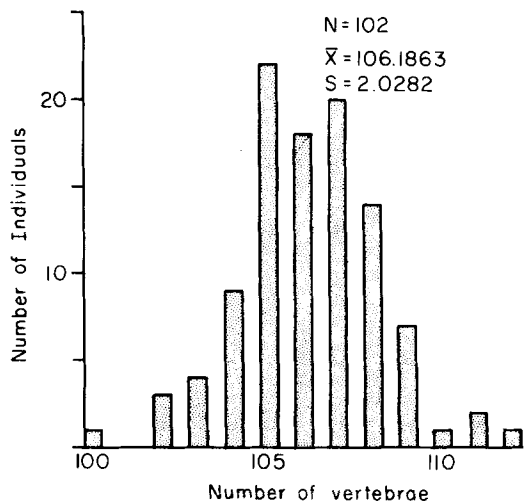


Fig. 1. Number of vertebrae vs. number of individuals in a sample of *D. mexicanus* from one population.

Atlas. The atlas is modified to provide large atlantal cotyles for articulation with the occipital condyles. The centrum and neural arch are significantly shorter ($p < .05$) than those of succeeding vertebrae (Figs. 2 and 4). The nuchal keel and ventral keel (except in *Ichthyophis*, which has a slight keel) are absent, as are transverse processes and elongate parapophyses. A small ventral spinal root foramen is present behind the rim of each cotyle. There is no indication of a tuberculum interglenoideum. Anterior width of the neural arch is significantly less than that of succeeding vertebrae, but posterior dimensions are not significantly different. The atlas and the terminal three to six vertebrae are the only ones in the column that do not bear ribs.

Second Vertebra. The second vertebra has a significantly longer centrum ($p < .001$, student's T test, Fig. 4) and neural arch than the atlas. The centrum is hourglass-shaped. The vertebra has well developed transverse processes, elongate, anteriorly curving parapophyses (the ventral transverse processes of Lawson, '63) with dorsal diapophyses, short postzygapophyses, a nuchal keel, a pronounced ventral keel that expands and bifurcates anteriorly to join the parapophyses, and paired spinal nerve foramina anterior to the transverse processes.

Tenth Vertebra. The tenth vertebra has a centrum longer than that of the second ($p < .1$, student's T-test, Fig. 4). Other processes, as described for the second vertebra, are present and larger than those of the second vertebra, except for the nuchal keel, which is smaller, having reached its greatest height in vertebrae four to six. Diapophyses of anterior vertebrae of *I. glutinosus* are more pronounced than those of the other species (Fig. 3). The spinal nerve exit shows substantial variation, being paired in three adults of *D. mexicanus*, single with a notch for the other root in one, and single (fused) in another; it is single in the juveniles of *D. mexicanus* examined. It is single in *T. compressicauda*, and in *I. glutinosus* the nerve passes between vertebrae after the fourth vertebra, which has paired anterior foramina (Fig. 3).

20th Vertebra. The centrum of the 20th vertebra is significantly longer than that of the tenth ($p < .01$) and of the second ($p < .001$), student's T-test, Fig. 4). Measurements of most components are still increasing (Figs. 5-9), except for posterior vertebral height,

which reaches its maximum at vertebra 13 to 16. The nuchal keel is absent, obliterated variously from vertebra 10 to 20, and having its greatest height in vertebra 4 through 9. Two of the large *D. mexicanus* retain an anterior notch through which the spinal nerve passes.

50th Vertebra. The centrum of the 50th vertebra is not significantly longer than that of the 20th ($p > 0.9$, student's T-test, Fig. 4). Most dimensions are diminishing slightly or have plateaued (Figs. 5-9).

Posterior Vertebrae. Most of the vertebral dimensions begin to decrease at about the 80th vertebra. By the 100th vertebra, transverse processes (and ribs), parapophyses, and the ventral keel are no longer present. The ventral keel is lost at about the 80th vertebra in juvenile *D. mexicanus* (Fig. 7) and *I. glutinosus*, the 90th in *T. compressicauda*. Posteriormost vertebrae are neural arch-centrum rings around the terminal fibers of the spinal cord. They are irregularly shaped and usually fused in sets of two or three vertebrae. Only the last two to five vertebrae extend posterior to the end of the vent (up to ten in *I. glutinosus*). There is no indication of a sacrum.

Ontogenetic variation in *D. mexicanus*

In adults, centrum length increases among the first three vertebrae, plateaus to the tenth then increases steeply to the 20th. Length stays about the same until the 60th, then begins to decline slowly, and precipitously after the 90th. Juvenile centrum length plateaus from the third to the 40th vertebra, then declines gradually to the 90th, then declines further to the terminal vertebra.

The neural arch length is proportionally similar in the second through tenth vertebrae of both juveniles and adults. There is a slight increase in length, in juveniles, of the tenth through 20th vertebra, a more precipitous increase in adults. Length then gradually declines in both samples (Fig. 5).

Widths of the neural arch show ontogenetic variation (Fig. 6). Posterior width increases slightly through the first 20 vertebrae, then declines in adults. Juveniles show a consistent decrease from atlas to terminal vertebra. Anterior width increases slightly in adults though the first 20 vertebrae, then declines, more precipitously in the final 20. Juveniles show nearly equal anterior widths among the first 20 vertebrae, then a gradual decrease through the entire column.

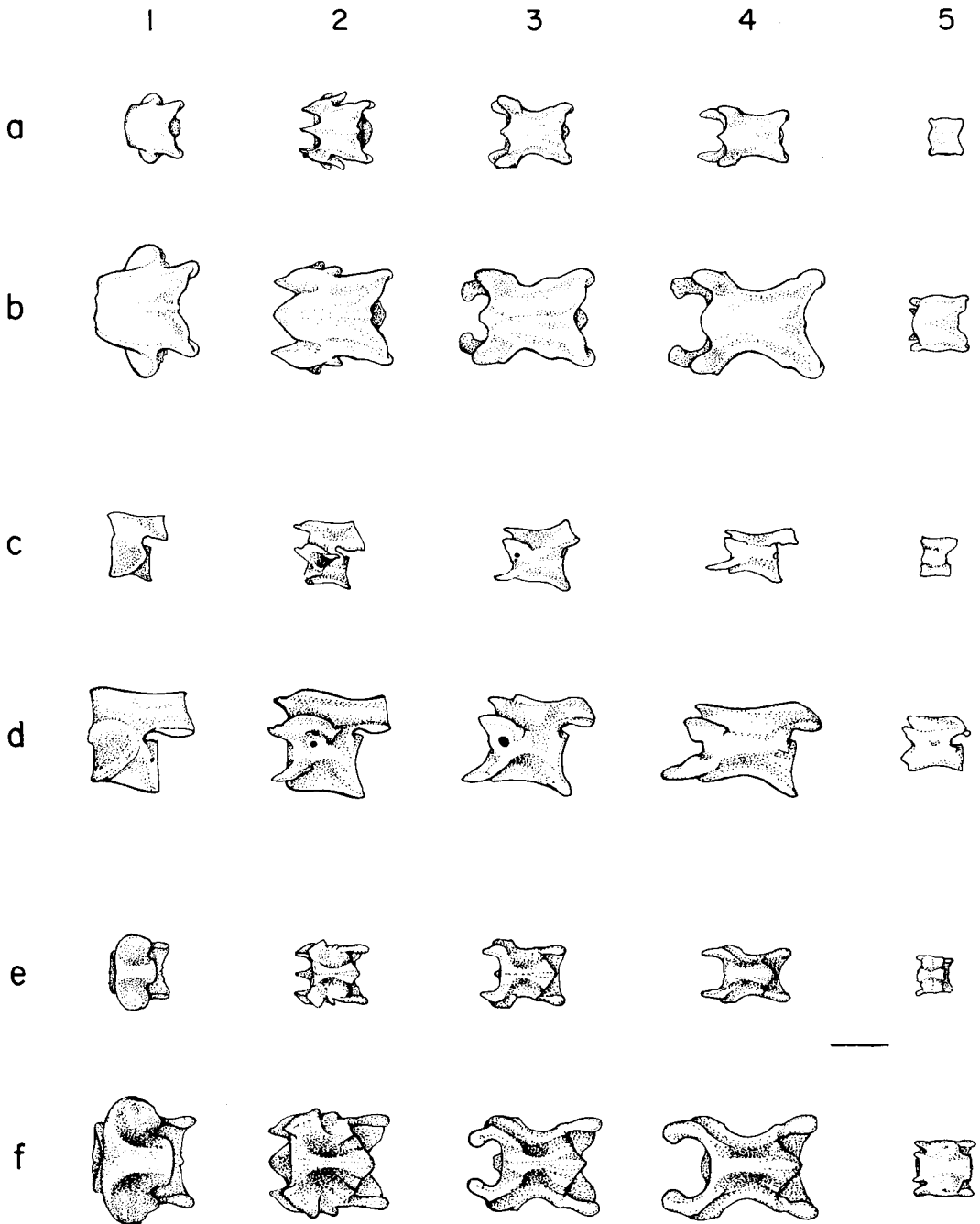


Fig. 2. Vertebral structure in juveniles and adults of *D. mexicanus*. Column 1, atlases; column 2, second vertebrae; column 3, tenth vertebrae; column 4, 50th vertebrae; column 5, near-terminal vertebrae. Row a, dorsal view, juveniles; row b, dorsal view, adults; row c, lateral view, juveniles; row d, lateral view, adults; row e, ventral view, juveniles; row f, ventral view, adults. Bar = 2.0 mm.

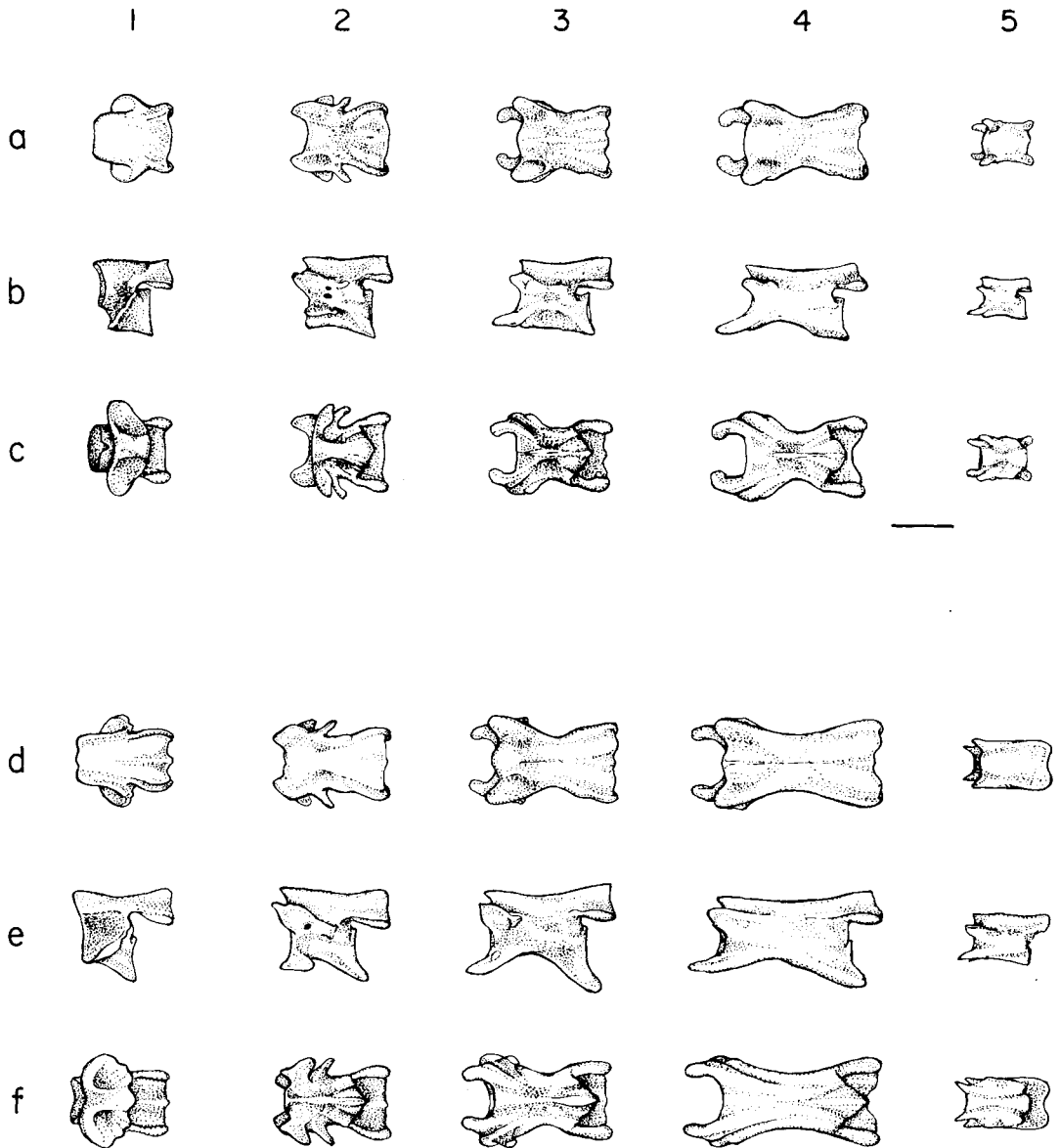


Fig. 3. Vertebral structure in *I. glutinosus* and *T. compressicauda*. Column 1, atlases; column 2, second vertebrae; column 3, tenth vertebrae; column 4, 50th vertebrae; column 5, near-terminal vertebrae. Rows a-c, dorsal, lateral, ventral views of *I. glutinosus*; rows d-f, dorsal, lateral, ventral views of *T. compressicauda*. Bar = 2.0 mm.

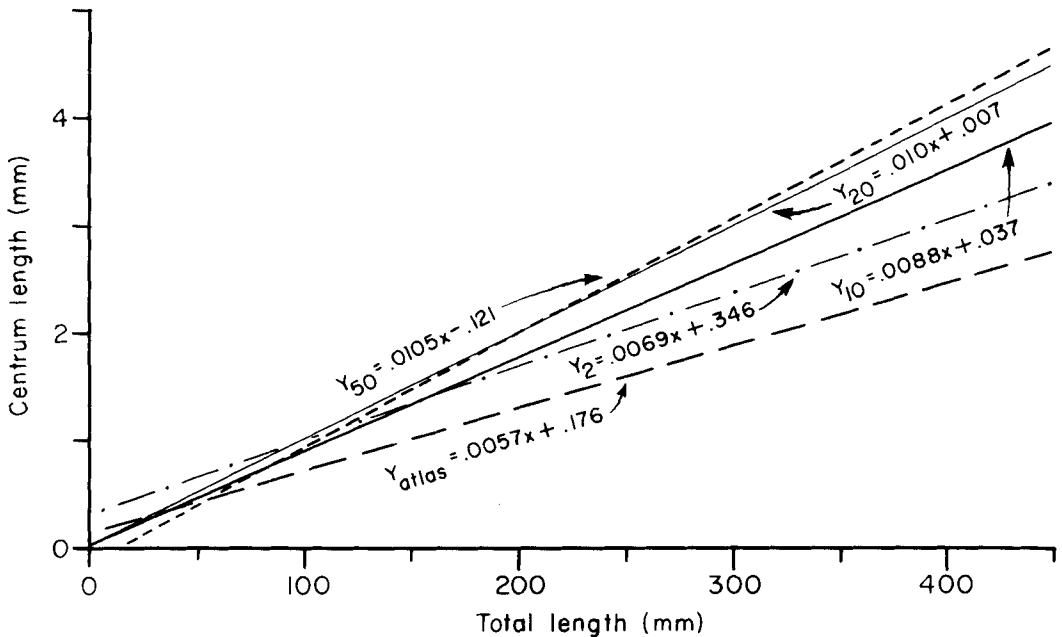


Fig. 4. Correlation slopes (principal axis) for centrum length of atlas (---), second vertebra (- - -), tenth vertebra (—), 20th vertebra (— · —), and 50th vertebra (.....) vs. total length of animal in an ontogenetic series of *D. mexicanus*. Differences in slopes indicate differences in growth rates, atlas slowest growing. Twentieth and 50th vertebrae have similar growth rates. This is predicted by their nearly equal lengths, as shown in Figure 5A.

Transverse process width in adults is approximately the same for the second through 20th vertebrae of adults, then diminishes, more precipitously after the 80th. Juveniles show a slight decrease in the anterior part of the column in that dimension, then a slightly increased diminution terminally, but not as pronounced as in adults (Fig. 6).

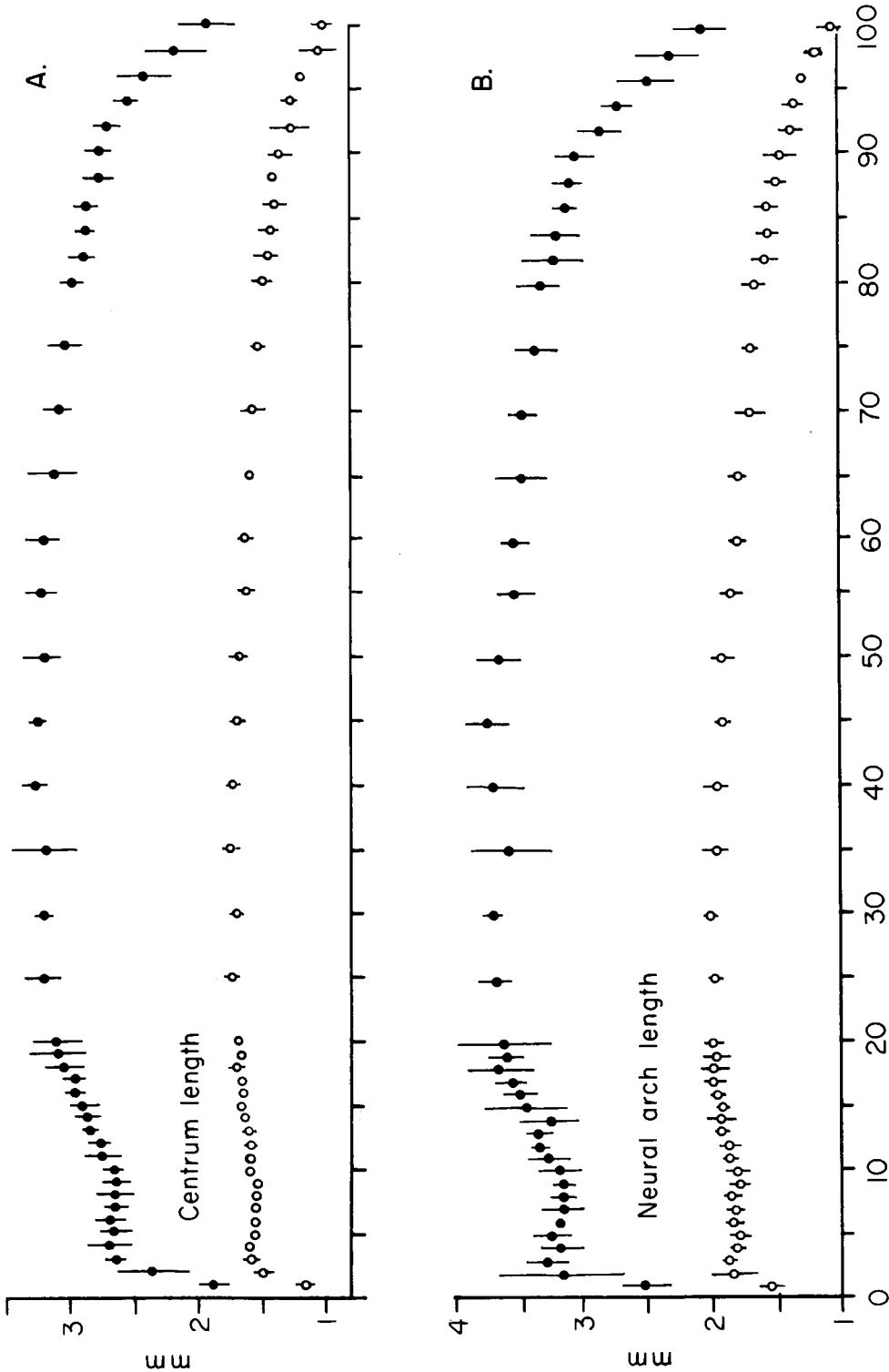
Posterior vertebral height increases from the first through the 17th vertebrae in both samples, much more in adults (increase in mean, 3.45 mm to 4.39 mm) than in juveniles (increase in mean, 2.10 mm to 2.41 mm) (Fig. 7), then gradually decreases in both.

The height of the nuchal keel in adults decreases from the seventh through the 20th vertebrae, with large 95% confidence intervals from the ninth on (since some adults lack the keel from that vertebra on). The height of the keel increases in juveniles in the first through fifth vertebrae, then decreases, but with much less variation. The ventral keel increases in depth slightly in adults among the first 18 vertebrae, then it diminishes, but more gradually posteriorly. The keel depth in the anterior column of juveniles is approximately the same, diminishing gradually through the 85th vertebra, then increases slightly before being lost (Fig. 7).

Other measurements show a characteristic increase among the first 20 vertebrae, a plateau or slight decrease from the 21st through the 80th, then a marked decrease. In general, the decrease in size in posterior vertebrae is much more precipitous in adults than in juveniles. Also, variance is greater in adults than in juveniles, as indicated by the greater 95% confidence intervals for most measurements on each vertebra in adults. This increase in variance with increase in size is similar to that reported by Worthington ('71) in salamanders.

Interspecific variation

The adult specimens of *I. glutinosus*, *T. compressicauda*, and *D. mexicanus* selected for study are of similar total length to make comparisons more direct, but the ranges in total lengths attained (*I. glutinosus*, 236–410 mm [Taylor, '60, '68]; *T. compressicauda*, 262–800 mm [Moodie, '78]; *D. mexicanus*, 108–487 mm in the population sampled, to 600 mm for the species [Taylor, '68]) suggest that though adult, individuals may not have been of equivalent ages. *I. glutinosus* (Ichthyophiidae) is a primitive egg-laying terrestrial burrower that lives near streams in Sri Lanka (Ceylon). *T. compressicauda* (Typhlonectidae)



Sequence of vertebrae

Fig. 5. A) Centrum lengths (CL) of five juvenile (190 ± 5 mm total length) (●) and five adult (370 ± 4 mm total length) (○) specimens of *D. mexicanus*. Means and 95% confidence limits are plotted, except when they include < 0.1 mm. Statistics for vertebrae past the 100th are not plotted because fusions, etc., distorted the data. B) Neural arch lengths plotted as in A.

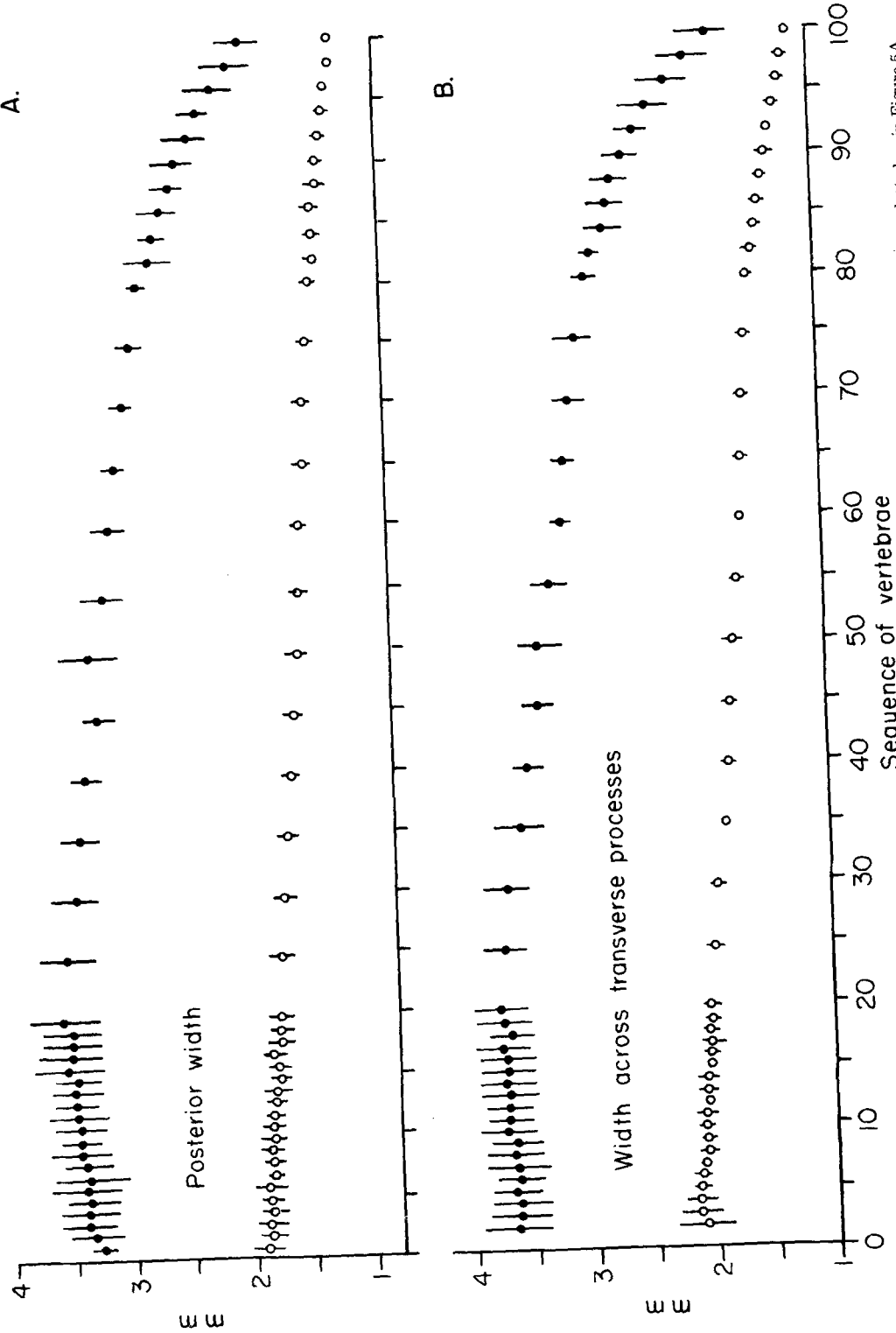


Fig. 6. A) Posterior neural arch widths in two samples of *D. mexicanus* plotted as in Figure 5A. B) Width across transverse processes plotted as in Figure 5A.

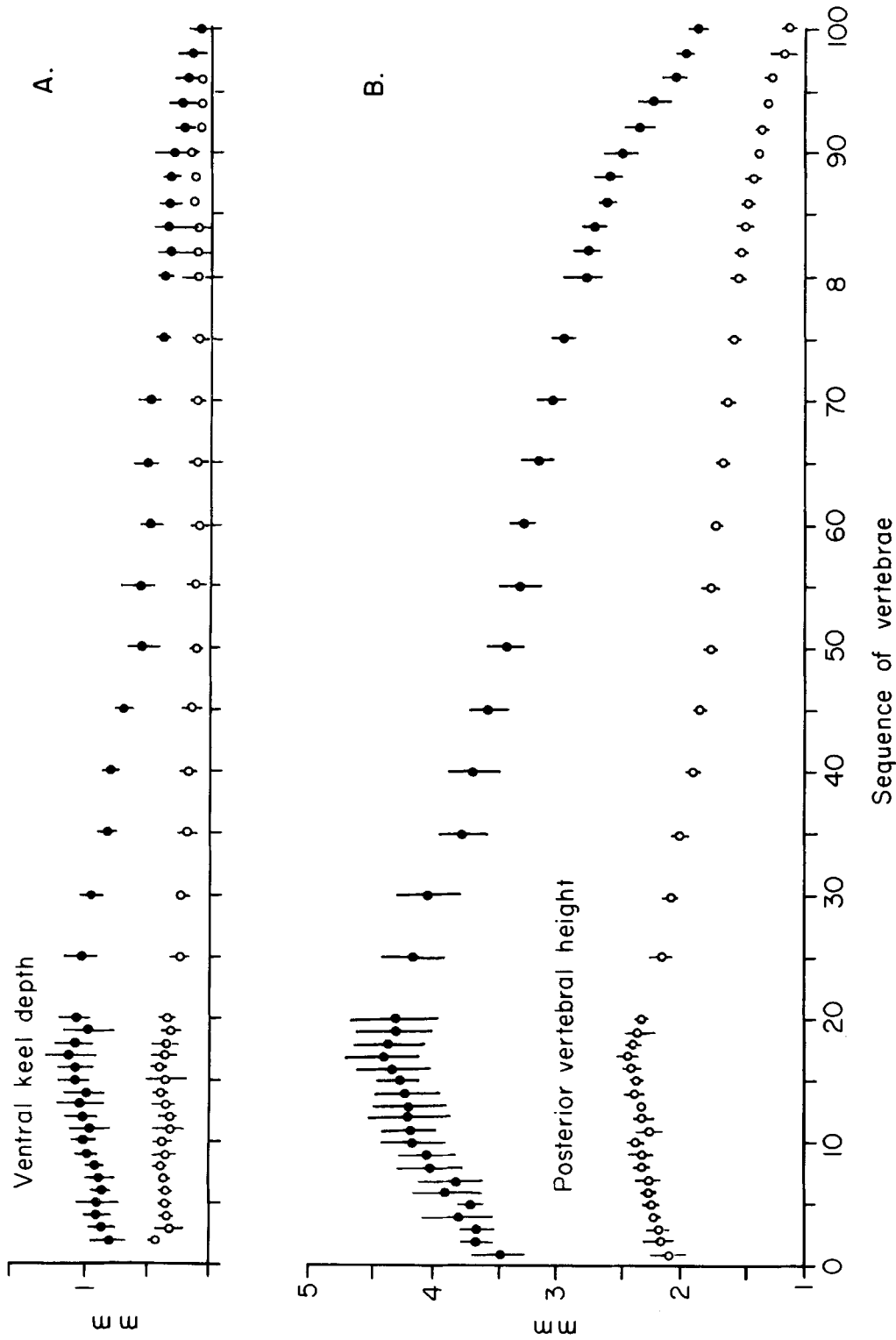


Fig. 7. A) Depth of ventral keel in two samples of *D. mexicanus* plotted as in Figure 5A. B) Height of vertebra at its posterior end plotted as in Figure 5A.

is a viviparous, aquatic species of the Amazon basin, while *D. mexicanus* (Caeciliidae) is a viviparous terrestrial burrower inhabiting lowland northern Central America.

Four sets of measurements are compared, for they are representative of the patterns for all measurements in each species. Centrum lengths show considerable variation among adults of nearly the same size in the three species. The curves that this measurement describes for each vertebral column have markedly different shapes (Figs. 5, 8, 9). The atlas of *T. compressicauda* is shortest of the three, yet mid-body centra reach substantially greater lengths (4.0–4.5 mm, 25th to 60th vertebrae) than those of the other two species (*I. glutinosus*, 2.5–2.85 mm, 15th to 90th vertebrae; *D. mexicanus*, 3.03–3.25 mm, 18th to 75th vertebrae). The range in size in this series is 0.5 mm in *T. compressicauda*, 0.35 mm in *I. glutinosus*, 0.25 mm in *D. mexicanus*, over 35 of 98 mid-body vertebrae in *T. compressicauda*, 75 of 111 in *I. glutinosus*, and 57 of 110 in *D. mexicanus*. The slopes of the increase and decrease in centrum lengths of the first and last 20 vertebrae are much greater in *T. compressicauda* than the other two

species, with the slope of anterior increase in *I. glutinosus* slightly less steep than in *D. mexicanus*. Both species decrease centrum length posteriorly in comparable patterns. It appears that *T. compressicauda* increases centrum length, though in progressively slighter increments, to a vertebra at about mid-body or just posterior, then decreases centrum lengths consecutively. In contrast, both *I. glutinosus* and *D. mexicanus* increase centrum length in anterior vertebrae, but have centra of very similar lengths through the 60 mid-body vertebrae, then centrum lengths decrease posteriorly. There is a step in the increase in length of anterior vertebrae at the seventh to 10th vertebrae in all three species, then the slope of the curve rises. Thus, the curve described by centrum length throughout the vertebral column in *T. compressicauda* is rounded, whereas those of the other two species are flattened except at the extremes.

The length of the neural arch through the column follows a pattern very similar to that of the centrum for all three species (Figs. 5, 8, 9). Neural arches are approximately 0.5 mm longer than centra for all vertebrae in *I. glutinosus* and *D. mexicanus*, except for the atlas,

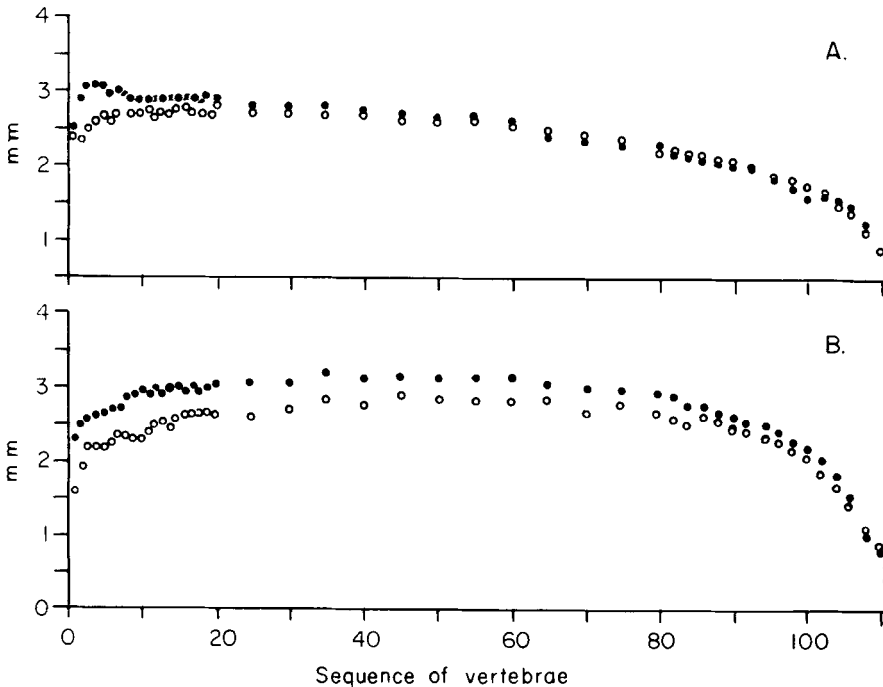


Fig. 8. A) Posterior width of neural arch (•) and width of vertebra across the transverse processes (○) through the column of a specimen of *I. glutinosus*. B) Neural arch length (•) and centrum length (○) in *I. glutinosus*.

in which the neural arch is 0.75 mm longer, and for the posterior 20 vertebrae, for which the difference diminishes so that neural arches are nearly the same length as centra. In *T. compressicauda* neural arches through mid-body are 0.5–0.9 mm longer than centra. The difference diminishes posteriorly.

Width across transverse processes (Figs. 5, 8, 9) reaches its greatest extent at the 20th vertebra in *T. compressicauda* and *D. mexicanus*, then gradually declines. In posterior-most vertebrae the processes are barely discernable, so the measurement (for all vertebrae) is also one of vertebral width just anterior to mid-vertebra. In *I. glutinosus*, however, the greatest width is that of the third and fourth vertebrae; length of anterior vertebrae diminishes to the tenth vertebra, remains about the same through the 20th, then gradually declines through the posterior vertebrae. The processes in posterior vertebrae, as in other species, are barely discernable. The posterior 3–7 vertebrae in each species do not bear ribs; ribs are rudimentary in the three to five vertebrae immediately anterior to these.

The posterior width of the neural arch in *D. mexicanus* increases through the tenth vertebra, plateaus through the 20th, then diminishes (with some variation) to the 92nd vertebra. The 93rd to 95th vertebra increase in width 0.25 mm, then width precipitously decreases posteriorly. Posterior width is consistently less than that at the transverse processes, usually 0.25 mm, except anterior to the 19th vertebra, where the difference is less. The pattern in *T. compressicauda* is very similar to that of *D. mexicanus* (Figs. 6, 9), but with a more gradual decline in width in posterior vertebrae. The pattern found in *I. glutinosus* differs substantially from that of the other two species. Posterior width of the neural arch is greater than that at the transverse processes in the first 20 vertebrae, and about the same width through the rest of the column. Greatest width is attained by the third and fourth vertebrae, then it progressively diminishes with a plateau from the ninth through the 20th vertebra (Fig. 8). There is no indication that the "tail" vertebrae of *Ichthyophis* (a few post-vent vertebrae are seen in x-rays,

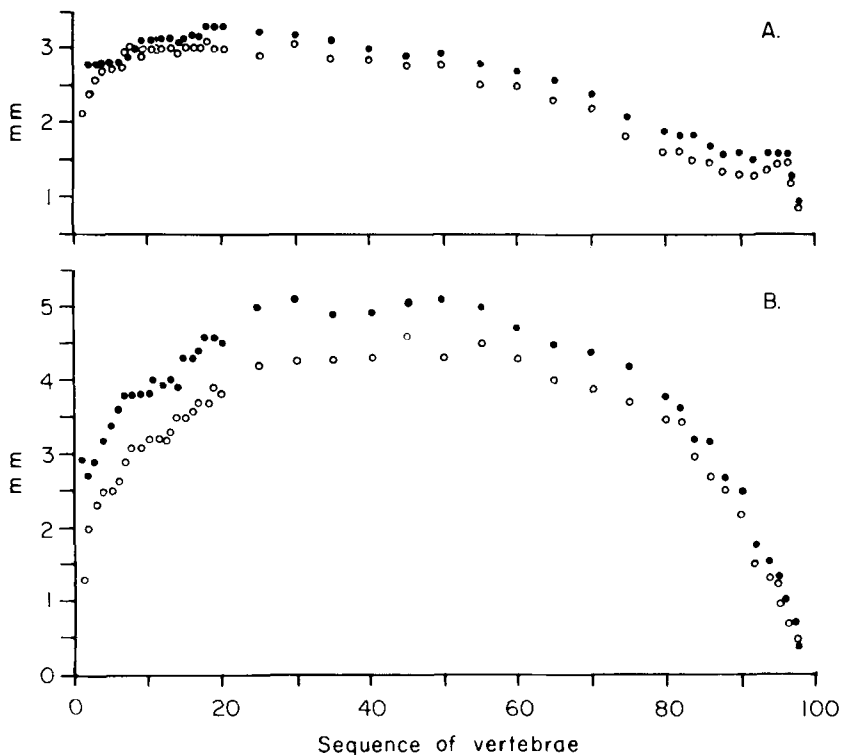


Fig. 9. A) Posterior width of neural arch (○) and width of vertebra across the transverse processes (●) through the column of a specimen of *T. compressicauda*. B) Neural arch length (●) and centrum length (○) in *T. compressicauda*. Compare with *D. mexicanus* (Figs 5–7) and *I. glutinosus* (Fig. 8).

whereas these are not characteristic of non-ichthyophiids) are significantly different from posteriormost vertebrae of the other two species, except perhaps the absence of *any* indication of transverse processes. Functional implications of these inter-specific differences are discussed below.

Anomalies

The most characteristic structural anomaly seen in the caecilian vertebral column involves fusion of vertebrae (see Table 1). While this appears a normal state for posteriormost vertebrae (of 112 *D. mexicanus*, 106 had two or more fused vertebrae among the last six), fusions more anteriorly are rare. Of the 112 *D. mexicanus*, 13 had more anterior fusions. These were primarily among vertebrae in the posterior half of the body, though two had fusions among the 20th to 24th vertebrae. Two to four vertebrae were usually fused; only one specimen had fusions in two body regions. The most marked situation was a small specimen (111 mm total length) that had its posterior 40 vertebrae truncated and fused (possibly contributing to its small size). In one instance, the right half of a vertebra was fused to the preceding vertebra.

Two other anomalies were observed. In one specimen, an anterior vertebra was significantly shorter than those surrounding it. In three specimens, instances of two pairs of ribs per vertebra occurred. The transverse processes of these vertebrae were broadened and diapophyses either expanded or duplicated.

Anomalies are summarized in Table 1. Of the 15 specimens from the population with anomalies, ten were specimens with total lengths greater than 320 mm; five were juveniles 201 mm or smaller.

Vertebral growth

In *D. mexicanus* there is a highly significant correlation between increase in centrum length and increase in total length (principal axis correlation: atlas, $r = .95$; second vertebra, $r = .97$; tenth, 20th, and 50th vertebrae, $r = .98$ for each; $N = 102$). The correlation slope for the atlas is low relative to other vertebrae, and the slopes for the second, tenth, and 20th increase proportionately to the atlas and to each in succession, suggesting increasing growth rates for these vertebrae. The slope for the 50th vertebra is similar to that of the 20th, suggesting little difference in growth rate (Fig. 4). This agrees with the pattern shown in Figures 5, 8, and 9, which show differences in centrum length among anterior vertebrae, but little difference between the 20th and 50th vertebrae, indicating size differences at one point in time that reflect the differences in growth rates suggested in Figure 4. This also indicates allometric increase in size due to greater differential growth of mid-body vertebrae relative to anterior (and doubtless posterior) vertebrae. Functional implications of these differences are discussed below.

There have been suggestions that vertebrae number might increase with size (and age)

TABLE 1. Vertebral Anomalies*

Total length of specimen	Vertebral number	Anomaly
367	14	Truncate
366	20-21	Fused (2)
195	23-24	" (2)
163	52-53	" (2)
327	54-55	" (2)
201	68-72, 74-75	" (2 sets, 1 of 4, 1 of 2 vertebrae)
387	77-78, 88-90	" (2 sets, 1 of 2, 1 of 3 vertebrae)
373	81-82	" (2)
329	88-89	" (2)
190	90-91	" (right 1/2)
380	94-95	" (2)
384	98-99	" (2)
111	60-100	" (40); multiple ribs
327	54	"
387	62	"

* Size (total length) of specimens having vertebral anomalies, location of anomaly in the sequence of vertebrae in the column, and nature of the anomaly are presented. $N = 112$; 13.4% have anomalies.

(Wiedersheim, 1879) or with the influence of the "crawling" locomotion (Marcus [34], in a curiously Lamarckian explanation of increased vertebral number and internal organization in limbless amphibians and reptiles). I suspect that the former question may have arisen as morphologists observed the marked cephalization of development in caecilian embryos, for posterior somites differentiate much later than more anterior ones. In the sample of 102 *D. mexicanus*, there is no correlation of vertebral number with size ($r = 0.1274$).

DISCUSSION

There are functional implications to the regional differences in vertebral structure and to the interspecific differences in pattern. The anterior 20 vertebrae in all three species and in all sizes of *D. mexicanus* differ in several respects from those of the rest of the column. The atlas is modified for articulation with the skull and lacks ribs. Most of the anterior vertebrae have a longitudinal nuchal keel, apparently produced according to the stress of the dorsal head musculature that attaches in the midline of these vertebrae. Parapophyses are short and widespread on these vertebrae, and pre- and postzygapophyses are broader and flatter than those of more posterior vertebrae. Observations of caecilians beginning to burrow suggest that they stiffen the anterior part of the column and position the head for use as a trowel. The head is moved in an up-and-down burrowing motion, with the anterior vertebrae transmitting forces from resistance of a more posterior body coil placed on the surface of the substrate, and the resistance of the substrate to the head. There is little side-to-side motion of the head, and it is usually due to movement of the entire anterior part of the body. Hence, the structure of the anterior vertebrae permits little rotation of atlas on second vertebra, provides for "fixing" vertebrae as a rod because of the association of zygapophyses and parapophyses of adjacent vertebrae during burrowing, and the dorsal longitudinal head musculature attaching to the nuchal keel provides for forceful elevation of the head during burrowing. Positioning of the head is also important within the burrow. Observations of three species at rest in burrows (under red light in glass containers) indicate that much of the "resting time" is spent with the head in a slight enlargement of the burrow. The head is held elevated from the floor of the burrow by contraction of the dorsal longitudinal head musculature and the fixed position of the anterior vertebrae. This facilitates buccal respiration. Thus, Taylor

('77) was correct in saying that caecilians have a "cervical" region and that the region is modified to accommodate the stresses of burrowing. However, the cervical region includes many more vertebrae than the four or five Taylor considered, and the region is not modified for pivotal movements of the cranium in a general sense. If Taylor meant that "cervical" vertebrae represent an adaptation for movement of the cranium in a single plane and positioning the anterior end of the body, I concur.

Differences in slopes of the anterior and posterior vertebral dimensions in juveniles and adults of *D. mexicanus* appear to be the result of differences in growth. Anterior and posterior vertebrae appear to grow more slowly (Fig. 4) than mid-body vertebrae. In adults, mid-body vertebrae have grown more relative to anterior and posterior vertebrae by exploiting these differential growth rates over a longer time than juveniles have had. The adult curves are thus more pronounced for several meristic features.

Mid-body vertebrae, their ribs, and associated musculature are involved primarily in locomotion, as discussed by Marcus ('34), von Schnurbein ('35), Gaymer ('71), and Gans ('73), and are modified for flexibility in controlling movement on (or in) the substrate by having well extended rib-bearers (less so in *I. glutinosus* than others), confined zygapophyses, and greater length, making for longer positional segments. Posterior vertebrae appear to have more limited locomotor function, but provide a positioning effect, especially in the aquatic forms such as *Typhlonectes*, in which the posterior part of the body has a dorsal "fin" which may act as a rudder. Positioning of the posterior part of the body is also important in copulation.

Major differences in pattern among these three species appear to be related to differences in growth rate of mid-body vertebrae and degree of extension of rib-bearing processes. The primitive, burrowing *Ichthyophis* has the least accelerated midbody growth rate; the highly derived, aquatic *Typhlonectes*, the greatest rate (Figs. 8-9). In fact, *Typhlonectes* appears to increase the growth rate to actual mid-body, then decrease it slowly, rather than having an extended mid-body region composed of vertebrae of equivalent size. This may be an adaptation for aquatic locomotion and sine-wave generation in a surrounding medium.

The rib-bearers of *Ichthyophis* are not as extended as those of the other two species (Figs. 2, 3, 6, 8, 9). X-rays show that the ribs of *I. glutinosus* are held more perpendicular

to the vertebral axis than in the other species and are shorter, broader structures. The mensural data on transverse processes of *Typhlonectes* relative to *Dermophis* are somewhat misleading, since the dimension is smaller in *Typhlonectes*. Though the measurement from tip to tip of the processes is less in *Typhlonectes* than in *Dermophis*, the processes are at least equivalently extended. The centra and neural arches of *Typhlonectes* are much more slender than those of *Dermophis*, as can be evaluated by inspecting the measurements of the posterior width of the neural arch (Figs. 6, 9).

It is probable that these several differences have to do with differences in the fine-tuning of locomotion. These conjectures await the test of rigorous analysis using living animals representing several species and of various sizes within species. Yet, the meristic data for entire vertebral columns provide insight into the nature of ontogenetic and phylogenetic structural variation.

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