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Functional and ecological significance of relative growth in *Alligator*

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(With 1 plate and 5 figures in the text)

Allometric coefficients are calculated for 27 cranial and 39 postcranial measurements of a growth series of *Alligator mississipiensis* that spans a size range of an order of magnitude. Developmental patterns are quite-well canalized, as expressed in coefficients of variation of 8 to 10 for isometric variables. A multivariate expression of allometry is discovered using principal components analysis. A number of allometric coefficients have expression in known aspects of the life history of *Alligator*. Negative allometry of limb lengths and limb proportions shows an ontogenetic decrease in importance of the limbs throughout life, and observations show large animals to be more dependent on water than small ones. Isometry of skull length with respect to body length represents an adaptation to ever-increasing size of prey items as body size increases. Positive allometry of snout length and size of the upper temporal fenestrae finds parallel in the structure of the highly aquatic gavial.

Contents

Introduction

The study reported in this paper forms part of a larger project (Dodson, In press; In prep. *a*; *b*), the object of which is to apply principles of relative growth in ontogeny to a series of skulls of lambeosaurine hadrosaurs (duck-billed dinosaurs) that vary considerably in size and shape, to determine whether the 12 species currently recognized may possibly constitute an ontogenetic series of a single animal. The approach that is followed is explicitly morphometric, with large numbers of variables being measured in each case. The first requirement was to establish a standard of comparison for a taxonomically homogeneous growth series. *Alligator mississipiensis* seemed useful for this purpose, because it is a living animal, taxonomically well-defined, of large adult size (thus more similar to a dinosaur than would be a small lizard), and is represented in several museums by good numbers of specimens. *Alligator* is well-known osteologically (Mook, 1921*a*, *b*; Kälin, 1933); myologically (Romer, 1923; Lakjer, 1926; Poglayen-Neuwall, 1953; Iordansky, 1964); physiologically (Colbert, Cowles & Bogert, 1946; Spotila, Soule & Gates, 1972); and ecologically (McIlhenny, 1935; Neill, 1971). It thus provides an excellent opportunity to test which aspects of its form, as it changes through life, can be related to changes in function and ecology. How much variability does a continuously growing animal such as *Alligator* show, and how can this variability be expressed? Can multivariate methods provide insights into the function of the animal? Answers to these questions provide the basis for inferences about the interrelationships between form, function and ecology in ancient organisms, for which direct observations on life habits are impossible.

Life history of *Alligator mississipiensis*

General accounts of the life history of *Alligator* are given by McIlhenny (1935) and Neill (1971). Alligators hatch at a length of 200 to 220 mm and achieve a maximum reported length of about 5½ m. A growth rate of about 300 mm a year is sustained for the first 6 to 8 years. Sexual maturity may be attained at age 5, at a length of 1·8 m. After reaching a length of 2·4 to 2·7 m in about 8 years, they grow more slowly. The female is believed not to exceed 2·7 m, and a male requires 16 years to attain a length of 3·6 m. For the next 10 years, growth is very slow, and may all but cease after that. Signs of senility (failure of tooth replacement) begin to show at about age 30, and 50 years seems to be about the maximum lifespan. Growth rates of *Crocodilus niloticus* are sufficiently variable under natural conditions that year groups are blurred after three years (Cott, 1961).

It is quite clear that the ecological role of alligators changes continually through life, the size of the food obtained being a function of the body size of the individual. Hatchlings eat insects and small fish. At a length of 400 to 500 mm, they take crayfish, crabs, small fish, small reptiles and frogs, and insects. At a length of 900 to 1500 mm they add significant numbers of small mammals and birds to their diets: muskrat, rabbit, young duck and rail. Beyond 1·5 m, large mammals and birds are caught with regularity, although the bulk of the diet is supplied by garpike and other fishes, snakes, turtles, rabbit, muskrat, coot, rail and duck. Large alligators of 3·0 to 3·6 m are reported to catch deer, hogs and even cows on occasion (McIlhenny, 1935; Neill, 1971). Stomach analyses by Kellogg (1929), Giles & Childs (1949) and Fogarty & Albury (1968) emphasize that whatever food items are locally abundant are likely to be eaten in greatest proportion.

Cott (1961) has documented analogous food changes for *Crocodilus niloticus* from Uganda. The young of this species are said to be like insectivorous lizards on land, taking insects, spiders, frogs and toads. At a length of 2 m these food sources have fallen to a very low level, replaced by crabs, water snails and especially fish, the dominant component of their diet between 2 and 3½ m. At large size reptiles (half turtles, equal parts snakes and other crocodiles, and a tenth lizards) and mammals (half rodents, a third artiodactyls, the rest carnivores and primates) constitute the most important nutritional resources. *Varanus komodoensis* also begins life as an insectivore, adds small mammals and birds as it attains modest size, then switches to medium to large mammals as it reaches large size (Auffenberg, 1972). These large-bodied reptilian predators pass through the niches that are occupied by several different species of mammalian carnivores on their way to becoming adults. Thus interspecific niche differentiation by body size, such as occurs in mammalian carnivores (Rosenzweig, 1966) and possibly herbivores as well (Bell, 1969), cannot occur for these continuously growing reptiles. Their own young fill the niches that would otherwise be occupied by different species. In consequence, the level of sympatry among living crocodilians of the world is quite low, and is accompanied by obvious differences in snout structure, gross differences in size (there are a number of dwarf species), and major habitat differences.

Doubtlessly the young alligators constitute potential prey items for larger members of the species, and there is some ecological separation between young and old, but the nature of the separation is not well documented. The young remain in the vicinity of the nest for the first year of life at least, and if adverse conditions of low water prevail during the second year, they still remain there (Chabreck, 1966). Once they have left the nest, young animals have a much greater tendency to roam than do mature animals, that have established home ranges to defend.

Colbert *et al.* (1946) studied the temperature tolerances of a series of alligators that ranged in length from 275 to 1981 mm (47·5 to 24·5 kg) and discovered that body temperatures of small alligators rise much more rapidly than those of large ones. It takes only 1½ minutes for the body temperature of a 50 g animal to rise 1°C, while it takes a 13 kg animal 7½ minutes to do the same. Alligators elevate their body temperatures above ambient air temperatures to attain their thermal optimum of 32 to 35°C, and exposure to strong sun with an air temperature of only 30°C can cause the lethal temperature of 38°C to be reached. Spotila *et al.* (1972) have shown that the biophysical climate space (which defines the climatic conditions in which a physiological steady state is maintained) of small alligators includes greater tolerance to direct sun than does that of large alligators. Alligators of 2 cm trunk diameter can tolerate air temperatures of 30°C in direct sunlight with a wind of 5 m per second (or 21°C in still air), while an animal of 20 cm diameter can tolerate only 19°C with a breeze of 5 cm per second or 11°C in still air. Thus, large animals are more dependent on shade or the thermally buffering effect of water, than are small animals. It is true, however, that large alligators have a much greater capacity for heat storage, which can be radiated back into the water.

The studies of relative growth that follow will attempt to relate morphological changes to these aspects of the life history of *Alligator*.

Materials and measurements

Osteological specimens of *Alligator mississipiensis* located in the Peabody Museum of Natural History, Yale University; Museum of Comparative Zoology, Harvard University; the American Museum of Natural History and the United States National Museum were measured. Data were received from Dr Wann Langston Jr, University of Texas, on a further 16 skulls from the Field Museum of Natural History, Chicago and the University of Texas. Data on 52 skulls were thus obtained; these ranged in size from 35·3 mm to 632 mm. Twenty-eight skeletons, ranging from 197 mm to 3·13 m were also measured.

Measurements up to 180 mm were performed with dial calipers and recorded to the nearest 0·1 mm. A steel measuring tape was used for measurements greater than 180 mm, and readings were taken to the nearest millimeter. Measurements were taken at random on either side of the specimen, and the average of three determinations was recorded.

Which variables provide the most useful information and how many are enough? The empirical challenge is to select those variables that best reflect "alligatorness", the essential qualities that make *Alligator* unique. For studies that are frankly taxonomic or concerned with the development of centres of ossification, particular bones may be measured (e.g. nasal length, parietal width). In a functional study, measurements should reflect functional properties, and these may only incidentally coincide with individual bones (e.g. length of maxilla). A functional approach was taken in this study. Thus 27 variables were measured in the skull (Kälin (1933) recommended 12 cranial ratios) and 39 in the skeleton. Figures 1 and 2 illustrate cranial and skeletal measurements, and Tables I and II described the inferred significance of each.

The use of data from Langston requires justification. Only 15 of the full set of 27 measurements were measured on his skulls. The missing data did not present a problem (see discussion below). Potentially more serious is the variance resulting from two workers trying to measure the same thing. However, correlation between variables was so high (Tables III and IV), and Langston's data plotted so well within the trends defined by the other specimens (Fig. 3) that it is concluded that the allometric coefficients are not seriously affected by the heterogeneity of the data. The effect could be more significant in the multivariate analyses, but also was not identified.

Theoretical considerations of relative growth

The study of relative growth has been characterized by Gould (1966) as the study of size and its consequences. Relative growth denotes change of proportions as organisms increase in size. The size increase may be that which takes place in ontogeny, in phylogeny, or in a series of unrelated organisms, depending upon what kind of information desired. Whereas recognition of relative growth is very ancient, its modern treatment stems from Huxley (1932), whose conceptual tool in the bivariate study of organic form was the equation of simple allometry:

$$Y = bX^{a}$$

He recognized that the size of any part of an organism (Y) may be expressed as an exponential function of the size of the whole organism over a specified range of size, as in ontogeny or phylogeny. The validity of this approach was predicated upon the empirical observation that size of an organism and not its rate of growth is more important in determining the proportions of its parts (Moment, 1933; Outhouse & Mendel, 1933; Lerner & Gunn, 1938; Laird, Barton & Tyler, 1968). The value of the allometric coefficient (a) reveals whether a given part is increasing at a greater rate (positive allometry), a lower rate (negative allometry) or the same rate (isometry) as the whole organism.

Relative growth has been studied in many organisms for a variety of reasons (Gould, 1966). Initially it was regarded as a key to understanding embryonic morphogenesis (as in Moss, 1955; Moss; Noback & Robertson, 1955). Genetic significance of relative growth has been emphasized by Cock (1963, 1966). The evolutionary significance of relative growth in phylogeny has been reviewed and further exemplified by Gould (1966, 1967). Fundamental factors of constraints on vertebrate design in metabolism versus body weight in mammals have been discovered by Brody (1945) and Kleiber (1947) and in the relationship of body length and brain size to body weight in mammals by Jerison (1973).

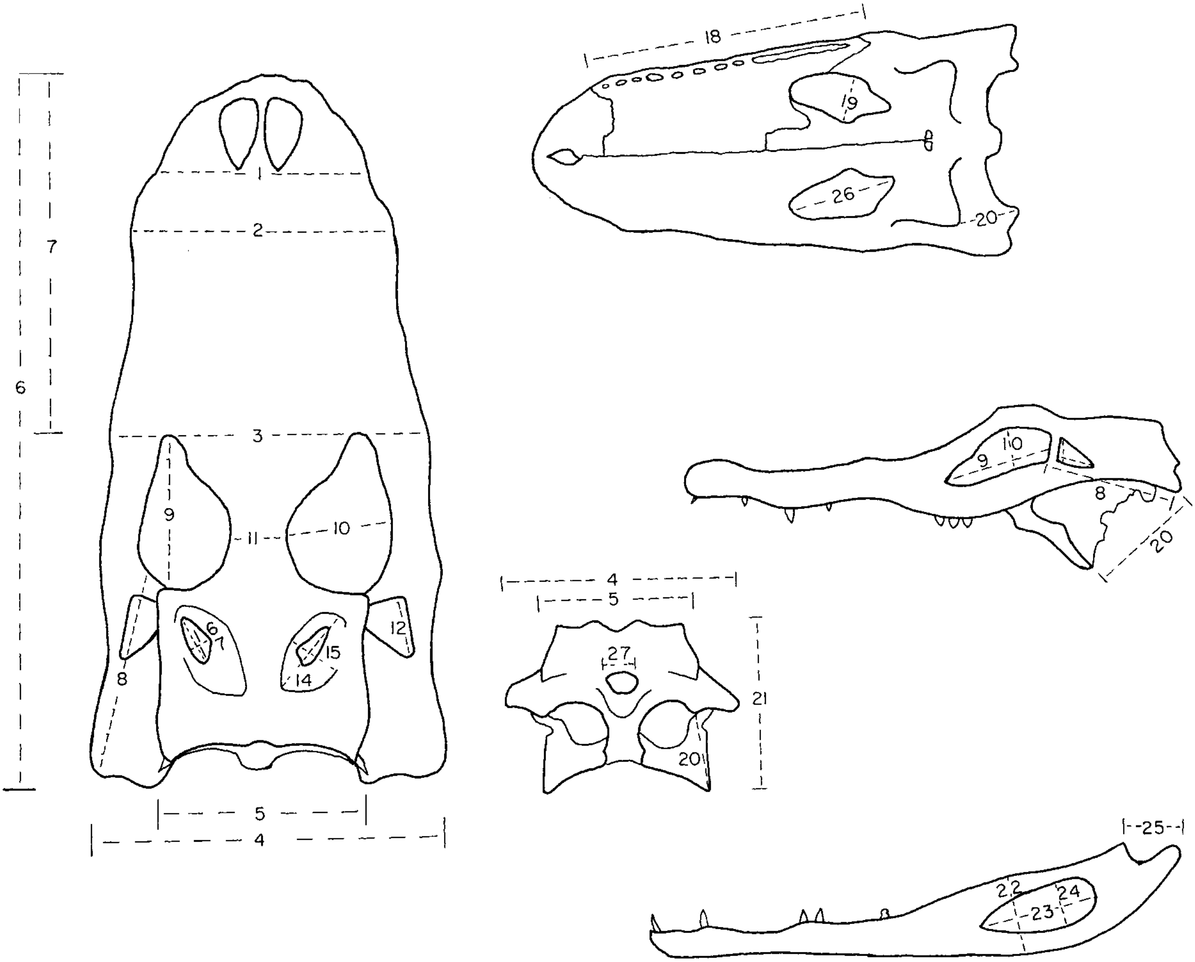

FIG. 1. Cranial measurements of *Alligator*.

Current emphasis (Gould, 1966, 1967, 1968, 1970, 1971*a*) centres upon the functional and adaptive significance of relative growth, particularly upon the necessity of organisms to maintain functional constancy of processes whose requirements are determined by the volume of the animal (e.g. weight support, metabolism) but that are mediated by surface areas (cross-sections of limbs, respiratory surfaces) that decrease in proportion to volume if size increases and isometry is maintained. If relative growth has adaptive as well as developmental significance, it may provide an excellent tool to describe the adaptation of an organism to its particular niche (Mosimann, 1958), although this approach has not been commonly followed. Notable efforts to describe adaptation by means of relative growth have been made by Needham (1935) on long-jawed fishes; Butler (1941) on two species of *Hemicentetes*; Gould (1971*b*) on scallops; and Goldstein (1972) on burrowing rodents.

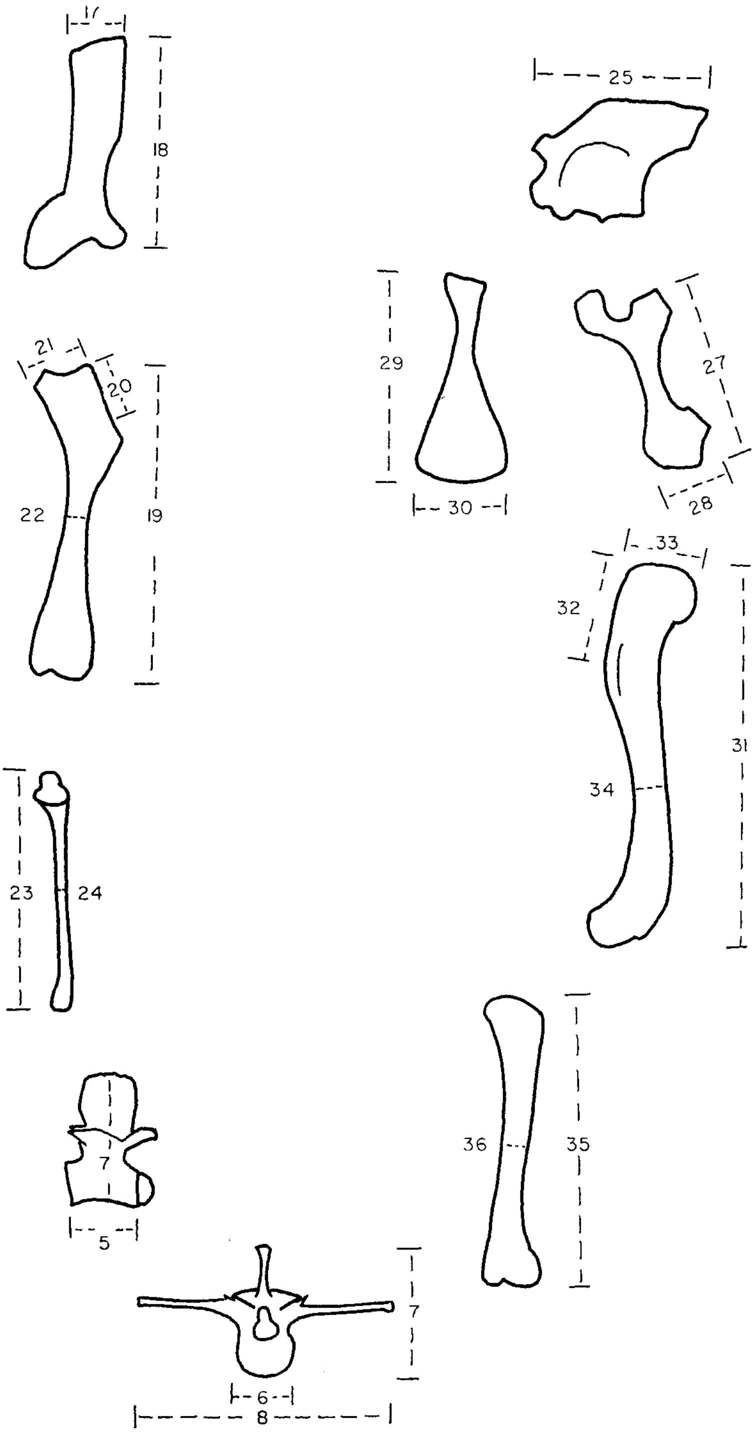

FIG. 2. Postcranial measurements of *Alligator*.

TABLE I
Alligator skull measures and their significance

1 skull width at posterior border of external nares	a shape parameter, potentially sensitive to mode of life
2 skull width at 4th maxillary tooth	as above
3 skull width at anterior border of orbit	as above
4 skull width at posterior border of quadratojugals	as above
5 skull width across exoccipitals	a measure of the bulk of the axial measure from the neck inserting on the back of the skull: relates to head orientation (Lundelius, 1957); but also includes jaw depressor muscles
6 skull length from tip of snout to quadrates	a measure of standard skull length; basal length (to occipital condyle) may have been preferable for comparative purposes (Kälin, 1933; Kramer & Medem, 1955), but this measurement is easier to make
7 skull length from tip of snout to anterior border of orbits	snout length is an indicator of the relative importance of the food gathering apparatus in the alligator design
8 skull length from posterior border of orbit to external condyle of quadrate	a crude indicator of the relative importance of the "Adduktorapparat" of Kramer & Medem in the alligator design
9 orbit length	size of the orbit, a feature widely known to be negatively allometric in vertebrates (of descriptive interest only)
10 orbit height	as above
11 orbit separation	measures relative strength of this region of the skull
12 lateral temporal fenestra length	of descriptive interest, as for orbits; unlike orbits, its allometric behaviour is not well known; may also relate to superficial mandibular adductor muscles, though in a manner not clearly understood (Frazzetta, 1968).
13 lateral temporal fenestra height	as above
14 external upper temporal fenestra length	of interest for descriptive and allometric reasons, as above; relates to region of origin of deep external adductor muscles (Lakjer, 1926; Iordansky, 1964).
15 external upper temporal fenestra width	as above
16 internal upper temporal fenestra length	of interest for descriptive and allometric reasons, as above; relates to maximum cross-section of deep external adductor muscles
17 internal upper temporal fenestra width	as above
18 maxilla length	the principal tooth-bearing element, an indicator of the relative importance of the toothrow in the alligator design
19 palatal fenestra width	may relate to the action of the pterygoid muscles (parts B and D of Lakjer)
20 distance from the tip of the posterolateral corner of the pterygoid to the medial condyle of the quadrate	may relate to the bulk of the pterygoid muscles, particularly parts A and B; an indicator of the relative importance of the pterygoid muscles with respect to the vertical adductors

TABLE I *continued*

21 height of skull from extremeties of pterygoid processes to dorsal surface of skull, perpendicular to long axis of snout	of descriptive interest; also, another indication of the importance of the pterygoid flanges, and by inference, the muscles arising from them, as above
22 maximum depth of the jaw	of descriptive importance; may relate to the relative importance of the vertical adductor muscles
23 external mandibular fenestra length	of descriptive interest; may relate to the action of the vertical adductor muscles
24 external mandibular fenestra width	as above
25 retroarticular process length, from crest of ridge posterior to articular cotylus to tip of process	the lever used in depressing the jaw, possibly relating to the gaping behaviour; site of insertion of depressor mandibulae and pterygoid A and B muscles
26 palatal fenestra length	may relate to the action of the pterygoid muscles (parts B and D of Lakjer), as for 19 above
27 foramen magnum width	of descriptive interest, a well-known negatively allometric feature of vertebrates

TABLE II
Alligator skeletal measures and their significance

1 trunk length, measured from the front of the axis to the neural spine of the first sacral vertebra	the standard measure of body length, more or less equivalent to snout to vent length; because tails were often incomplete, axis-tail length could not be used; in many cases measured by articulating isolated vertebrae into a complete series
2 tail length, from posterior surface of second sacral neural arch to tip of tail	preservation of small vertebrae beyond the 30th variable, although a maximum of 41 was found in one specimen
3 skull length	
4 axis-tail length	not used for standard measure of length as observed above
5 thoracic vertebra length, measured along ventral margin of centrum as exposed in an articulated series, thus excluding posterior hemisphere that is received by procoelous cavity of next vertebra	the 16th presacral vertebra was selected as a representative thoracic vertebra
6 thoracic vertebra width, measured across the midportion of the centrum, just ventral to the transverse process	
7 thoracic vertebra height, measured from ventral margin of midportion of centrum to top of neural arch	
8 thoracic vertebra transverse process	
9 lumbar vertebra length	the 20th presacral vertebra was selected as a representative lumbar vertebra
10 lumbar vertebra width	
11 lumbar vertebra height	

TABLE II *continued*

12 lumbar vertebra transverse process	
13 caudal vertebra length	the 4th caudal vertebra was selected as a representative caudal vertebra
14 caudal vertebra width	
15 caudal vertebra height	
16 caudal vertebra transverse process	
17 scapula width of proximal end	
18 scapula length from proximal end to coracoid contact in glenoid fossa	
19 humerus length	
20 humerus length to deltopectoral crest	this defines the moment arm of the humerus with respect to the insertion of the powerful posteroventral pectoralis muscles
21 humerus width at proximal end	in sprawling animals this measure reflects the weight-bearing function of the humerus (e.g. Gould, 1967 on pelycosaurs)
22 humerus width minimum, measured distal to the deltopectoral crest	this is the width measure of a column used for weight support
23 ulna length	
24 ulna width	
25 ilium length, measured along dorsal border	may reflect the strength of the couple of the hindlimbs with the body
26 ilium, separation of blades across sacrum	a descriptive measure of width of the pelvis
27 ischium length, measured from contact with ilium in acetabulum to tip	
28 ischium width across distal expansion	reflects relative size of muscles arising from this surface
29 pubis length	reflects relative size of muscles arising from this surface (slips of the puboischiofemoralis) used in femoral protraction (Charig, 1972)
30 pubis width	as above
31 femur length	
32 femur length to 4th trochanter (mid-point of muscle scar)	defines the moment arm of the femur with respect to insertion of the powerful caudifemoralis muscle of femoral retraction
33 femur width at proximal end	as for comments concerning 21 above
34 femur width minimum	as for comments concerning 22 above
35 tibia length	
36 tibia width	
37 calcaneum length	defines lever arm in tarsus
38 2nd digit of manus: length including metacarpal and ungual	selected as a representative measure of the length of the manus
39 2nd digit of pes: length including metatarsal and ungual	selected as a representative measure of the length of the pes

Quantitative techniques

Allometric equation

It is advantageous to use the logarithmic form of the allometric equation:

$$\log Y = \log b + a \log X$$

If the data are converted to logs, curvilinear relations become linear, and the powerful line-fitting techniques may be used. Use of the regression model, which assumes that all of the error of measurement is associated with the dependent variate X and none with the independent variate Y, has been strongly cautioned against by Kermack & Haldane (1950), Kermack (1954), Zar (1968) and Sacher (1970). If it be assumed that biological variability is far more significant than error of measurement, and that this variability is likely to be distributed between both variables, use of another technique is indicated. That selected for this study is Bartlett's best fit (well described in Simpson, Roe & Lewontin 1960), an unbiased and efficient method of representing the general trend of a set of observations recommended by Kidwell & Chase (1967). The method is very simple, and a computer program was easily developed to determine both the line of best fit and the confidence interval about the slope, the latter involving the Student's t statistic.

Fitting the allometric equation as the first step in analysis is not universally recommended; Olson (1951); Olson & Miller (1951); McIntosh (1955); Lundelius (1957); and Simpson *et al.* (1960) are among those who recommend against it. Their arguments are unconvincing for several reasons. The eye is not particularly sensitive to departures from linearity on graphic plots (Lundelius failed to report the curvilinearity of a plot whose allometric coefficient was 2·47!), and this would seem a poor criterion for deciding whether to look for allometry. Using the allometric equation does not prevent isometry from being discovered; while few coefficients have a value of 1·00, calculation of confidence intervals (Tables III and IV) shows some variables to be essentially isometric. Conversely, the same procedure shows some coefficients as close to isometry as 0·98 to be significant for *Alligator*.

Biometric considerations dictate that the choice of X, the measure of size, while mathematically arbitrary, should be made carefully. It should correspond to some intuitive concept of size, such as basal length or total length of a skull, snout to vent length or overall length of a skeleton. Another criterion is that it be the measurement with the greatest absolute magnitude or range of size. McIntosh (1955) recommended that it be the measure that is least variable. A multivariate concept of size that incorporates the contributions of all variables is possible (Teissier, 1960; Jolicoeur, 1963). An obstacle to deducing the functional implications of allometry is that the relationships studied are based on linear measurements that define lever systems in two dimensions but fail to account for quantities such as area and mass, which scale as the second and third powers, respectively, of length. It is just these changes that provide the basis for our current understanding of the adaptive meaning of allometry. Thus the use of weight or volume as a standard of size, while descriptively less useful, is justifiable on functional grounds. Cube root of weight or volume can provide a useful standard, particularly for comparisons of animals of dissimilar shape. A relationship is allometric only with respect to a specified standard (X); a given variable may be positively or negatively allometric or isometric, depending upon which variable is chosen for X. This suggests that a well chosen measure of size is one that constrains a significant number of coefficients to fall upon both sides of

1·00; if most are positive or negative, as in Butler (1941), the standard chosen is not representative of the growth of the whole.

TABLE III
Allometric coefficients for ***Alligator*** *skull*

X=Snout-quadrate length (variable 6) Y	N	R	V_D	a	Significance	b
1 width at nose	39	0·995	8·9	1·07	***	0·189
2 width at 4th tooth	41	0·997	6·7	1·01	no	0·331
3 width at orbit	39	0·996	6·5	0·98	*	0·470
4 width quadratojugal	39	0·995	7·8	0·99	no	0·533
5 width exoccipital	30	0·992	11·2	0·96	**	0·407
6 snout-quadrate length	52	1·000		1·00	no	1·000
7 snout-orbit length	35	0·998	11·2	1·10	***	0·311
8 orbit-quadrate length	35	0·999	5·3	1·02	***	0·251
9 orbit length	39	0·981	28·0	0·69	***	0·984
10 orbit height	38	0·972	34·4	0·60	***	1·172
11 orbit separation	34	0·990	12·8	1·07	***	0·046
12 lat. temp. fen. length	35	0·993	11·2	1·01	no	0·078
13 lat. temp. fen. height	35	0·990	12·5	0·91	***	0·141
14 ext. up. fen. length	51	0·986	31·9	0·67	***	0·531
15 ext. up. fen. width	50	0·976	17·5	0·88	***	0·117
16 int. up. fen. length	35	0·989	14·7	0·90	***	0·093
17 int. up. fen. width	34	0·989	30·4	1·32	***	0·0051
18 maxilla length	29	0·998	4·8	0·98	*	0·596
19 palatal fenestra width	36	0·956	21·2	0·77	***	0·305
20 quadrate-pterygoid	20	0·996	10·4	1·10	***	0·135
21 skull height	32	0·996	8·7	0·99	no	0·361
22 jaw depth	40	0·972	21·9	1·07	**	0·130
23 jaw fenestra length	41	0·994	8·6	1·04	***	0·173
24 jaw fenestra height	41	0·990	11·5	1·04	**	0·068
25 retroarticular process	51	0·994	11·8	1·08	***	0·083
26 palatal fenestra length	37	0·976	13·9	0·98	no	0·377
27 foramen magnum	28	0·962	30·7	0·64	***	0·410

N = number of specimens
R = correlation coefficient of variable with X, skull length, using the natural logarithm instead of the raw measurement
a = allometric coefficient
b = intercept in allometric equation
* indicates that a is significantly different from 1 at p=0·05
** indicates that a is significantly different from 1 at p=0·02
*** indicates that a is significantly different from 1 at p=0·01
V_D coefficient of dynamic variability, as defined in text.

Principal components analysis

Multivariate analysis has as its goal the parsimonious summary of large numbers of observations into a small number of axes (Gould, 1967). The most generally applicable technique for multivariate study of a homogeneous growth series is principal component analysis. The mathematical model is well treated by Seal (1964) and many examples are

TABLE IV

*Allometric coefficients for **Alligator** skeleton*

X=Axis-sacrum length (variable 1) Y	N	R	V_D	a	Significance	b
2 tail length	21	0·990	12·7	0·99	no	1·796
3 skull length	23	0·997	6·9	0·98	no	0·580
4 axis-tail length	20	0·996	8·3	0·99	no	2·874
5 thoracic vert. length	19	0·995	7·0	0·94	***	0·060
6 thoracic vert. width	20	0·979	13·9	1·02	no	0·032
7 thoracic vert. height	20	0·990	17·4	1·17	***	0·033
8 thoracic vert. tr. pr.	25	0·983	17·6	1·20	***	0·049
9 lumbar vert. length	21	0·996	6·5	0·96	**	0·058
10 lumbar vert. width	20	0·982	12·2	1·08	*	0·024
11 lumbar vert. height	21	0·993	10·3	1·06	*	0·063
12 lumbar vert. tr. pr.	25	0·991	19·0	1·23	***	0·036
13 caudal vert. length	22	0·984	11·6	0·96	no	0·055
14 caudal vert. width	22	0·944	22·2	0·95	no	0·024
15 caudal vert. height	22	0·988	11·8	1·11	***	0·043
16 caudal vert. tr. pr.	23	0·983	21·6	1·23	***	0·027
17 scapula width	21	0·988	15·8	1·14	***	0·025
18 scapula length	25	0·993	9·6	1·03	no	0·112
19 humerus length	26	0·996	7·1	0·98	no	0·252
20 deltopec length	25	0·973	20·0	1·08	*	0·021
21 humerus prox. width	26	0·993	14·0	1·12	***	0·027
22 humerus min. width	25	0·989	23·8	1·24	***	0·005
23 ulna length	27	0·993	9·4	0·96	***	0·216
24 ulna width	26	0·986	18·2	1·17	***	0·004
25 ilium length	28	0·995	9·2	1·05	***	0·080
26 ilium separation	18	0·995	11·6	1·08	***	0·118
27 ischium length	27	0·994	12·4	1·08	***	0·075
28 ischium width	27	0·988	16·4	1·04	no	0·058
29 pubis length	25	0·958	20·0	1·08	no	0·066
30 pubis width	24	0·989	15·2	1·12	***	0·031
31 femur length	26	0·996	7·4	0·97	***	0·312
32 femur len. to 4th troc.	25	0·991	13·3	1·09	***	0·050
33 femur prox. width	25	0·995	10·9	1·09	***	0·033
34 femur min. width	25	0·989	13·6	1·09	***	0·013
35 tibia length	28	0·995	9·2	0·91	***	0·348
36 tibia width	26	0·977	16·7	1·01	no	0·016
37 calcaneum length	26	0·985	15·7	1·15	***	0·021
38 2nd digit manus	16	0·995	9·8	0·94	***	0·198
39 2nd digit pes	19	0·996	11·1	0·90	***	0·427

N = number of specimens
R = correlation coefficient of variable with X, skull length, using the natural logarithm instead of the raw measurement
a = allometric coefficient
b = intercept in allometric equation
* indicates that a is significantly different from 1 at p=0·05
** indicates that a is significantly different from 1 at p=0·02
*** indicates that a is significantly different from 1 at p=0·01
V_D coefficient of dynamic variability, as defined in text.

reviewed in Blackith & Reyment (1971). Although the principal components analysis by Jolicoeur & Mosimann (1960) on a growth series of turtles included only three variables, their lucid explanation and interpretation of the results makes it an important study.

Principal components analysis is a variance preserving technique that performs rigid rotation of a matrix of correlations or variance-covariance into a system in which the covariance between all factors is reduced to zero (geometrically, all factors are mutually orthogonal in multidimensional space), so that the entire variance is preserved in the diagonal elements of the matrix produced by the rotation (the off diagonal elements are zeroes). The elements of the diagonalized matrix are the eigenvalues, and the matrix that affected the rotation of the original matrix is the matrix of eigenvectors, which convey the coordinates of the orthogonal axes in multidimensional space. The first principal component is the axis that best describes the trend of the cloud of the observations in multidimensional space (absorbs the maximum amount of variance); the second principal component describes the next best trend, perpendicular to the first axis (absorbs the maximum amount of the residual variance). Subsequent components are determined in a similar fashion, always perpendicular to the preceeding ones. Eigenvalues, usually expressed as a percentage of the total variance, describe the amount of information accounted for by each component. The first has the greatest value, and the rest have successively lower values. In a "good" analysis, most of the information is conveyed by the first few components, the remainder of the eigenvalues being very small. Each principal component is a linear compound of all the original variables. Interpretation of each component is based on those variables that have strong positive or negative weightings (factor loadings); those variables with factor loadings of low magnitude contribute little to the particular component and are ignored.

The purpose of principal components analysis is to partition the variance of a homogeneous series of objects into identifiable factors; that is, to analyze why members of a series of objects differ from one another. If the objects were identical with respect to the variates measured, the variance in the system would be zero and no analysis could be performed. If they differ only in size, all the information would be conveyed by one component. If the objects differed in size and shape, as is usually the case, several components would be required, the first usually being a size axis.

The magnitude of the first eigenvalue is a function of the size range of the objects studied. When the size range is great, the first axis may account for more than 95% of the variance, and size literally swamps out shape factors. The size axis in a growth series is of little biological interest; consequently major interpretative effort is directed towards the "shape" axes, which are, at least mathematically, independent of size.

Principal components analysis was carried out using the program Factor, unrotated factor solution option, from the Statistical Programs for the Social Sciences (SPSS) package. The program was desirable because of the pairwise deletion method of handling missing data, as discussed below.

Morphological integration

Morphological integration is a pre-computer age technique of multivariate analysis developed by Olson & Miller (1958). Essential to its conceptual foundation is the belief that anatomical structures that are highly correlated with one another represent true functional groups; that is, that degree of association of measurements is a sensitive indicator of biological processes; and that dimensions within a functional system co-vary more than dimensions between systems.

A correlation matrix is constructed based on all the measurements available. The operation of morphological integration consists of specifying an arbitrary high level of correlation above which no measurements are intercorrelated, then lowering the level of correlation by successive increments, causing the formation of groups of intercorrelated variables. As the level of correlation is progressively lowered, the groups increase in size, often coalescing at lower levels. The groups have in some cases interpretable significance in terms of the organization and function of the organism.

Despite the apparent significance of the technique (Van Valen, 1965), it has been used infrequently (Pohlo, 1964, on a mactrid bivalve; Gould & Garwood, 1969, on dentitions of two mammals). At least part of the reason for this stems from the laborious nature of the work, which entails repeated searches of large correlation matrices by hand. A computer program was written for this purpose, and so the method was tried so that the results could be compared with those of principal components analysis. Modifications recommended by Gould & Garwood, following criticism of the original method by Bock (1960), were incorporated. Raw correlation coefficients were used instead of the upper confidence limit, because the former is the best estimate of the parameter p. And the basic pair criterion recommended by Olson & Miller was eliminated because of the possibility of losing functionally significant measurements while preventing redundancy. These modifications also had the effect of simplifying the calculations.

Missing data

The problem of incomplete data sets is an obvious one in the study of fossils, but even for modern animals significant numbers of specimens in museums could not provide complete data. For instance, certain specimens have been partly dissected to expose deep anatomical structures, or thin-sectioned for histological investigation; small elements from skeletal extremities were lost, or juvenile skulls covered with integument. The number of specimens used in the calculation of bivariate statistics such as the allometric coefficient varied from variable to variable (Tables III and IV), and the width of the confidence interval varied accordingly.

For multivariate methods, the only practical problem lies in composing the matrix upon which the analysis is based. Once formed, there are no gaps in the matrix and operations are performed as usual. Because the elements of the matrix are based on different numbers of specimens, the rank of the matrix is uncertain, which prevents significance testing. Inasmuch as the calculations are based upon the best estimates the data will permit, this pragmatic procedure is perfectly justifiable.

Computer programs treat missing data in various ways. The method that makes maximum use of the available data is that of pairwise deletion: in calculating a bivariate statistic for a series of specimens, if a data field is blank for a particular specimen, the field for the other variable is ignored so that the particular specimen does not contribute to the calculation of this coefficient only. A second procedure is estimation, which has the effect of reducing the variance in the system (often the subject of investigation) and so is not recommended. The most severe alternative is simply to eliminate the whole specimen if any data are missing.

The amount of missing data that can be tolerated is an empirical problem. Principal coordinates analysis is reported to tolerate up to one third missing data (Pilbeam, 1969). Fewer points are needed to define a correlation coefficient reliably when the size range is great than when it is small (Gould & Garwood, 1969).

Correlation and variation

Correlation between variables in the logarithmic bivariate plots (Fig. 3) is remarkably high, the majority of the coefficients being greater than 0·98 (Tables III and IV). This reflects first and foremost the size range of the series, spanning more than an order of magnitude in both skulls and skeletons. Unfortunately size tends to swamp out other types of potentially interesting variation, so it is necessary to discover procedures that allow real biological variation to be expressed.

In mammalian dentitions, there is no ontogeny and a definitive adult size characterizes the teeth; correlations are generally much lower, in the range of 0·4 to 0·7 (Olson & Miller, 1958; Gould & Garwood, 1969). For mammals a coefficient of variation (Simpson *et al.*, 1960) expresses a biologically meaningful concept of variation:

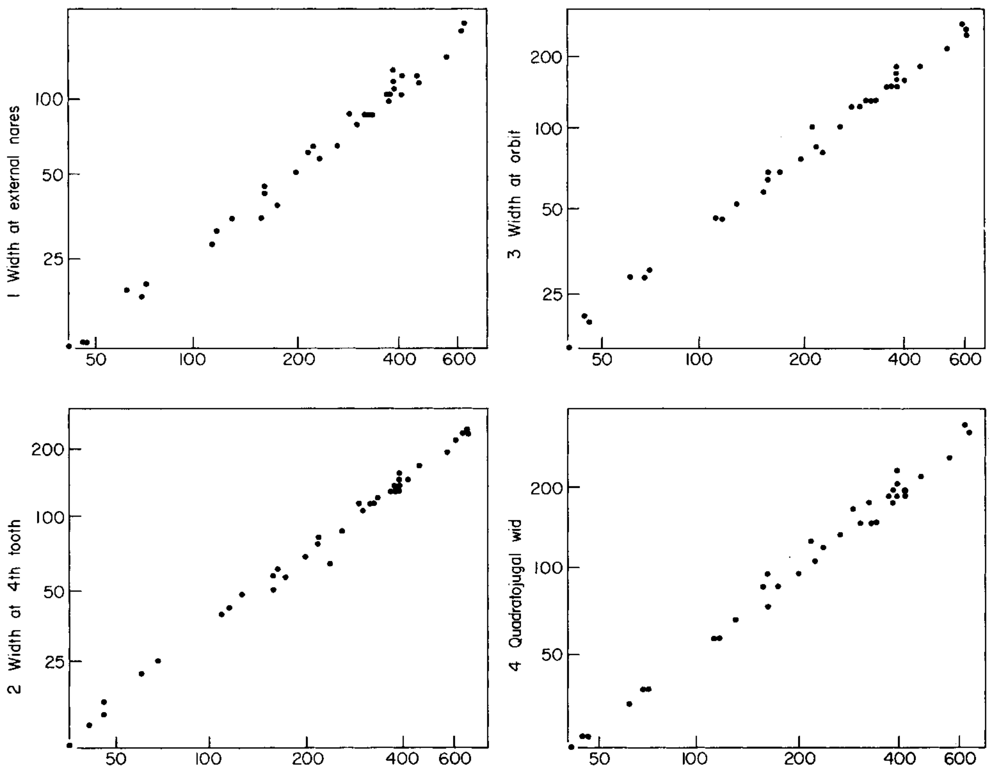

FIG. 3. Bivariate plots of the skull of *Alligator*. The scale on both axes is logarithmic, and the measurements are given in mm. In each plot, the X axis is standard skull length (variable 6); the Y axis is as given.

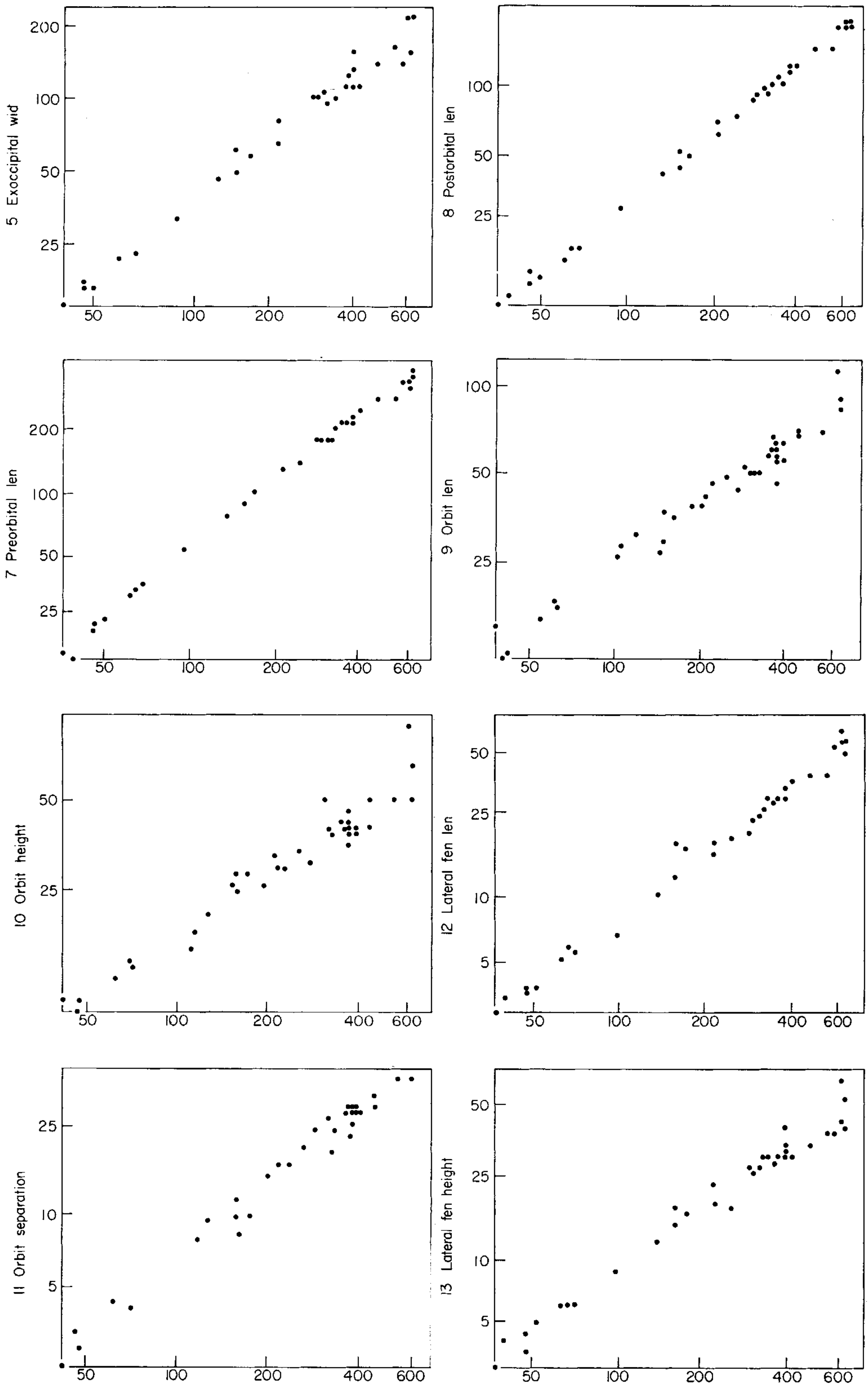

FIG. 3. *continued*

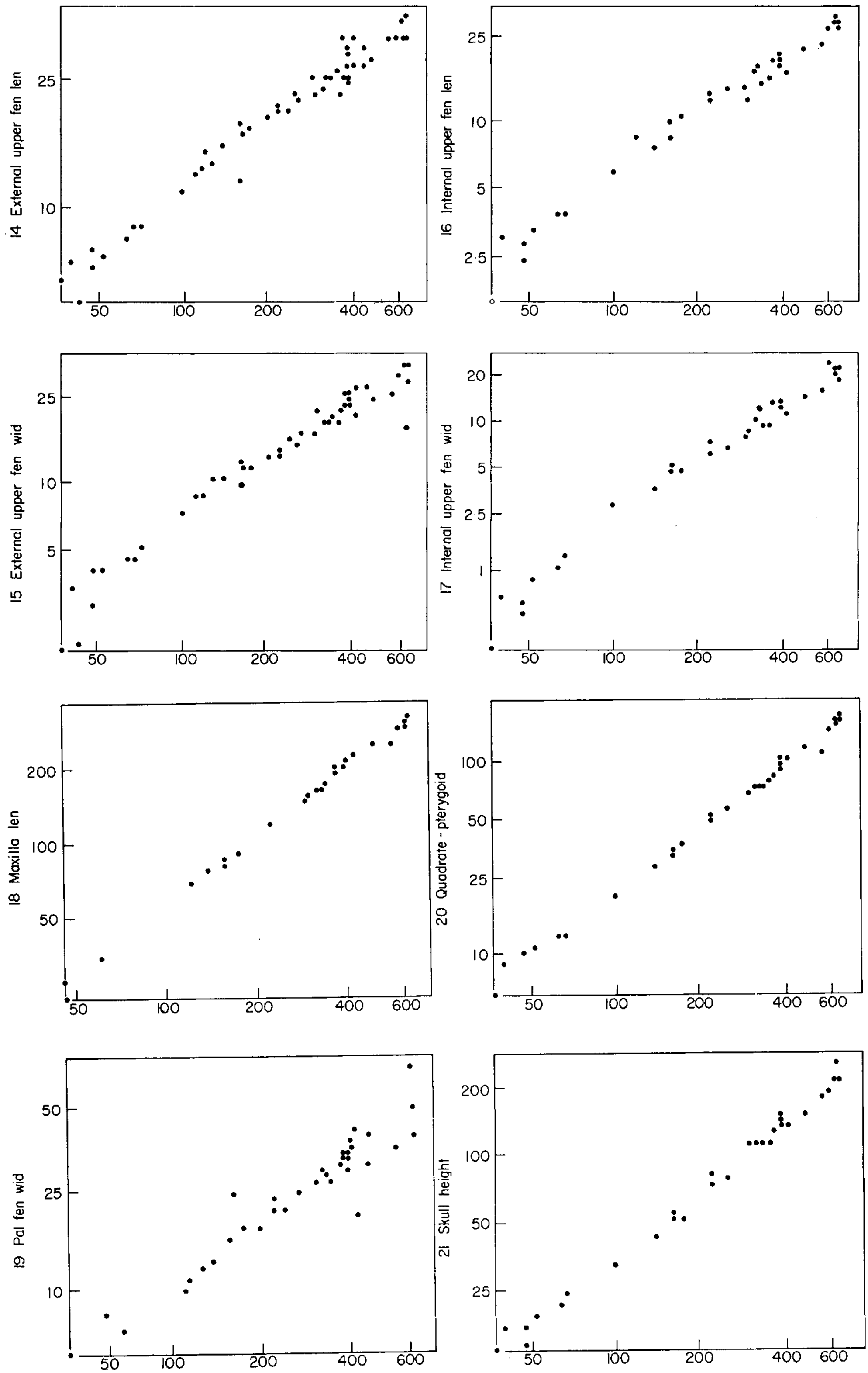

FIG. 3. *continued*

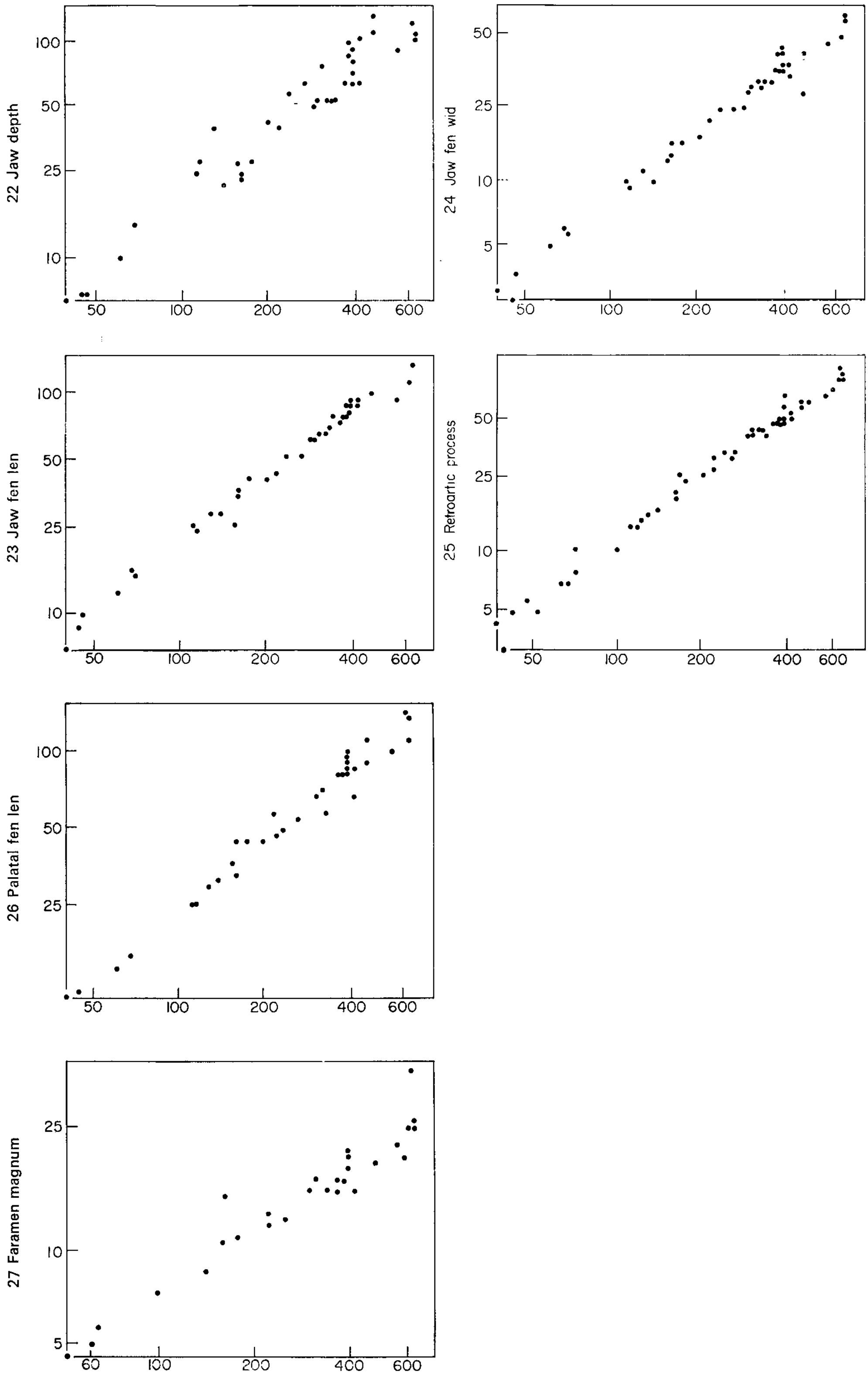

FIG. 3. *continued*

$$V = \frac{100}{\bar{X}} s$$

where $\bar{X}$ is the sample mean and s is the standard deviation. V is found to range between 4 and 10, and especially 4 to 6, in samples that are taxonomically homogeneous at specific or lower level. But to attempt their calculation on the sample of *Alligator* would give

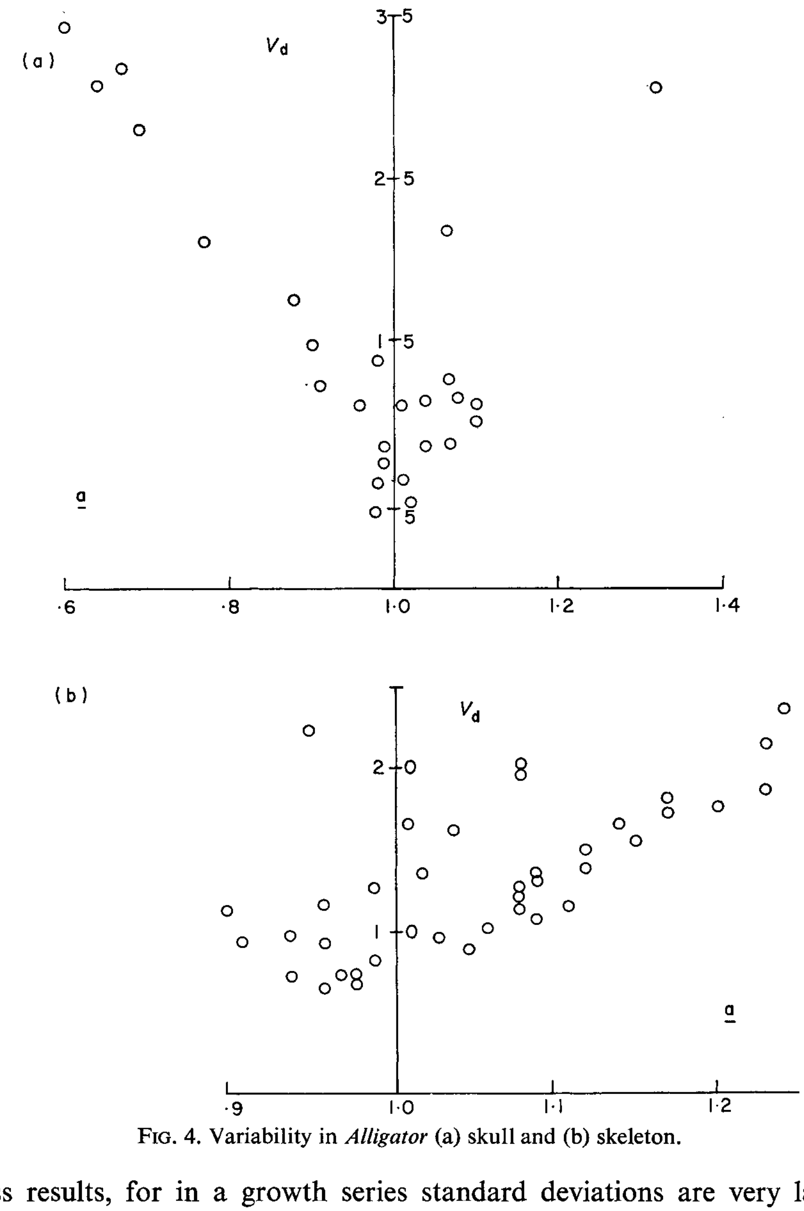

FIG. 4. Variability in *Alligator* (a) skull and (b) skeleton.

meaningless results, for in a growth series standard deviations are very large. Aware of this difficulty, Olson (1951) in a study of a large growth series of the fossil amphibian, *Diplocaulus*, took a rather pessimistic view of the possibility of discovering a method to

TABLE V
*Summary of principal components analysis of raw cranial data in **Alligator***

Component 1	97·9%	size
Component 2	0·8%	foramen magnum–palatal fen wid–orbit height VS jaw fen length–orbit sep
Component 3	0·6%	palatal fen wid–pal fen len–orbit height VS jaw depth–width internal and external up fen
Component 4	0·3%	jaw depth VS palatal fen wid–external up fen wid
Total variance	99·6%	

express the biological variability of continuously growing organisms. He tried to accomplish this by standardizing each specimen to unit length. But even so, he found that for the relationship, distance from orbit to snout versus skull length, V was 29·2 in *Diplocaulus*. For the same relation in the living anuran, *Bufo marinus*, V was 18·8, or 10·0 for adults only. Olson correctly concluded that V was still not measuring biological variability, but did not surmise the reason.

In fact, even though size is theoretically eliminated by standardizing the data, it is reconstituted in the variability associated with the changes of proportion that accompany growth. Even without reference to scale, a juvenile alligator is recognizably different from an adult in having relatively large orbits and foramen magnum and narrow slit-like upper temporal fenestrae. It turns out that high coefficients of variation are associated with strong allometric coefficients ($a = 1·17$ for Olson's relation), and low coefficients of variation are associated with near isometry, so that a plot of characteristic "V" shape is formed (Fig. 4). For *Alligator* minimum values of V are in the vicinity of 8 to 10. While these are still moderately high when compared with those of mammals, it is nonetheless suggested that these minimum values provide the basis for estimating the variability of a growing species. A V calculated in this fashion might be called a coefficient of dynamic variation. The greater the size range of the sample, the greater will be the apparent variability for a given coefficient of allometry, and thus the steeper will be the "V"-shaped plot' The estimation of variability of a series of continuously growing organisms must be based on a

TABLE VI
*Summary of principal component analysis of cranial ratios in **Alligator***

Component 1	32·0%	preorbital len–internal up fen wid VS foramen magnum–orbit height–external up fen len–orbit len
Component 2	19·6%	width at quadratojugals–skull height–width at orbit–width across exoccip–width at 4th tooth–quadrate to pterygoid distance
Component 3	11·6%	lateral fen len–postorbital len VS maxilla len–jaw fen len–external up fen wid
Component 4	8·9%	pal fen len–retroarticular proc–width at external nares VS jaw depth–external up fen wid
Component 5	7·0%	jaw fen len–lateral fen len–external up fen wid VS orbit sep–skull height
Total variance	79·1%	

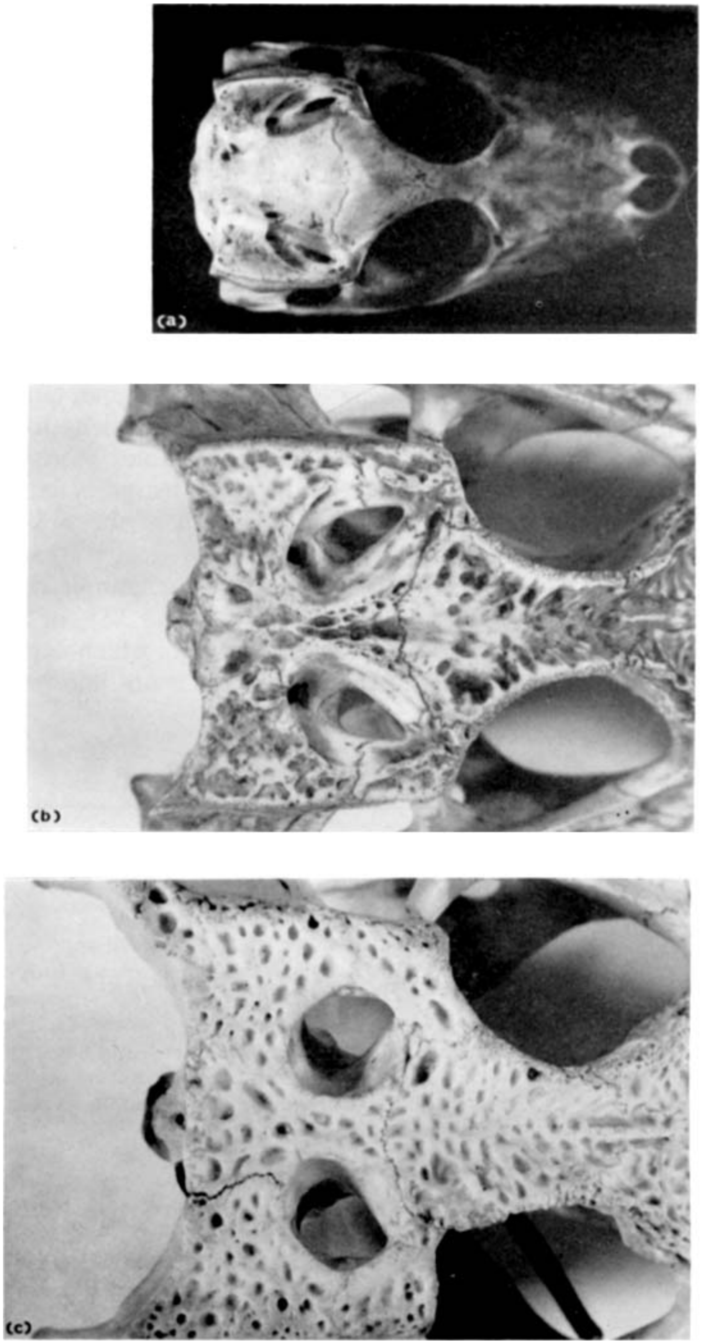

PLATE I. Ontogeny of the upper temporal fenestra of *Alligator*. (a) A very young specimen, YPM 1890. Length of the skull 42 mm; width of the internal portion of the upper temporal fenestra (variable 17) 0·6 mm. (b) YPM 573. Skull length 158 mm; width of the upper fenestra 5·1 mm. (c) YMP 759. Skull length 410 mm; width of the upper fenestra 14·7 mm.

series and not a single determination of V, for it must be verified that V is a function of the allometric coefficient to validate this interpretation.

Principal components analyses (Tables V, VI and VIII) bear directly on the problem of variation. The first axis of a principal components analysis is often found to be a size axis, with factor loadings of about the same size and of the same sign. This was the case for analyses of the raw data of both skull and skeleton of *Alligator*, in which the first eigenvalues accounted 97·9% and 95·2% of the variance, respectively. This indicates that only 2·1% and 4·8% of the variance, respectively, results from factors other than size, and may provide a crude multivariate analogue of V.

In analyses based on ratios (standardized lengths) instead of raw data, quite another aspect of variation is discovered. The first principal components in these cases turn out to be size axes again, but in an unusual fashion. This time contrasts are formed between positively allometric variables (preorbital length, width of the upper temporal fenestra for the skull; proximal width of the femur, length of the ischium, length of the fourth trochanter for the skeleton) and negatively allometric variables (width of the foramen magnum, length and width of the orbit, length of the upper temporal fenestra for the skull; lengths of the second digits of the hand and foot, length of the tibia in the skeleton). The first components thus measure the variability associated with size-related changes of shape. If growth in *Alligator* were isometric, size would be completely eliminated from the principal components analysis by the use of ratios. About 32% of the variance in the skull and 38% in the skeleton is due to size-related change, which explains why juvenile alligators are so obvious in photos (Plate I), even if scale is not known.

TABLE VII

Morphological integration of the skull of ***Alligator***

Level 1 0·997 or greater	
2–7–18	wid 4th tooth–preorbital len–maxilla len
6–7–18	skull len–preorbital len–maxilla len
Level 2 0·995 or greater	
1–2–3–18	wid nose–wid 4th tooth–wid orbit–maxilla len
2–3–6–7–8–18	wid 4th tooth–wid orbit–skull len–preorbital len–postorbital len–maxilla len
2–3–6–8–21	wid 4th tooth–wid orbit–skull len–postorbital len–skull height
2–6–8–20–21	wid 4th tooth–skull len–postorbital len–quadrate to pterygoid–skull height
3–4–6–8–21	wid orbit–wid qjugal–skull len–postorbit len–skull height
4–6–8–20–21	wid qjugal–skull len–postorbit len–quadrate to pterygoid–skull height
8–21–22	postorbit len–skull height–jaw depth
Level 3 0·993 or greater	
1–2–3–4–6–7–20	all width measures except exoccipital–skull length–preorbit len–quadrate to pterygoid
1–2–3–4–6–20–21	as above, but omit preorbit len, add skull height
1–2–3–6–7–18–20	anterior width measures, total, preorbit & maxilla lengths–quadrate to pterygoid
1–2–3–6–18–20–21	as above, but omit preorbital len, add skull height
2–3–4–6–7–8–20	posterior width measures except exoccipital, all length except maxilla–quadrate to pterygoid
2–3–4–6–7–8–25	as above, but omit quadrate to pterygoid, add retroarticular process
2–3–4–6–8–20–21	as second above, but omit preorbit len, add skull height

TABLE VII *continued*

2–3–6–7–8–18–20	wid 4th tooth and orbit–all lengths–quadrate to pterygoid
2–3–6–8–18–20–21	as above, but omit preorbit len, add skull height
3–4–5–21	three posterior widths–skull height
5–21–22	exoccipital wid–skull height–jaw depth
6–7–18–23	skull len–preorbit len–maxilla len–jaw fen len
6–8–12	skull len–postorbit len–lat fen len
7–8–18–20–22	preorbit, postorbit and maxilla lengths–quadrate to pterygoid–jaw depth
8–18–20–21–22	as above, but omit preorbit len, add skull height
Level 4 0·990 or greater	
1–2–3–4–6–7–8–18–20–21–25	all width measures except exoccipital–all lengths–quadrate to pterygoid–skull height–retroarticular process
1–2–3–6–7–8–18–23	anterior width measures–all lengths–jaw fen len
2–3–16	wid 4th tooth–wid orbit–internal upper fen len
3–4–5–6–8–20–21–25	three posterior widths–skull length–postorbit len–quadrate to pterygoid–skull height–retroarticular process
4–25–26	wid qjugal–retroarticular process–palatal fen len
5–8–13–21–22	wid exoccipital–postorbit len–lat fen height–skull height–jaw depth
5–8–20–21–22	as above, but omit lat fen len, add quadrate to pterygoid
6–7–8–12–20–21	all length measures except maxilla–lat fen len–quadrate to pterygoid–skull height
6–7–8–18–23–24	all length measures–jaw fen len and height
6–7–11–18–21	length measures except postorbit–orbit separation skull height
7–8–12–20–21–22	pre and postorbit len–lat fen len–quadrate to pterygoid–skull height–jaw depth
7–8–18–20–21–22	as above, but omit lat fen len, add maxilla len
8–12–13–21–22	postorbit len–lat fen len & height–skull height–jaw depth
Level 5 0·985 or greater	
1–2–3–4–5–6–7–8–11–18–21	all widths and lengths–orbit separation–skull height
1–2–3–4–5–6–7–8–18–20–21–24–25	all widths and lengths–quadrate to pterygoid–skull height–jaw fen height–retroarticular process
1–2–3–4–6–7–8–18–20–21–23–24–25	as above, but omit exoccipital width, add jaw fen len
1–2–3–4–18–25–26	width measures except exoccipital–maxilla len–retroarticular process–palatal fen len
2–3–4–5–6–7–8–12–13–20–21–25	widths except nose–skull, pre and postorbit lengths–lat fen len and height–quadrate to pterygoid–skull height–retroarticular process
2–3–4–5–6–7–8–12–18–20–21–25	as above, but omit lat fen height, add maxilla len
2–3–4–6–7–8–13–16–20–21	posterior width except exoccipital, lengths except maxilla–lat fen height–int upper fen len–quadrate to pterygoid–skull height
2–3–4–6–7–8–16–18–20–21	as above, but omit lat fen height, add maxilla len
2–6–7–8–16–17–18–21	wid 4th tooth–all lengths–int upper fen len and wid–skull height
2–6–7–8–17–18–21–24	as above, but omit int upper fen len, add jaw fen height
5–7–8–12–13–20–21–22	exoccipital wid–pre and postorbital len–lat fen fen len and height–quadrate to pterygoid–skull height–jaw depth
5–7–8–12–18–20–21–22	as above, but omit lat fen height, add maxilla len
6–7–8–14–21–23	lengths except maxilla–ext upper fen len–height skull–jaw fen len
7–8–13–16–20–21–22	pre and postorbital len–lat fen height–int upper fen len–quadrate to pterygoid–skull height–jaw depth
7–8–16–17–18–21–22	lengths except skull–int upper fen len and wid–skull height–jaw depth
7–8–16–18–20–21–22	as above, but omit int upper fen wid, add quadrate to pterygoid

Relative growth in *Alligator*

Allometric data for the skull of *Alligator* are summarized in Table III. Allometric coefficients range from 0·60 to 1·32. Length and height of the orbit, width of the foramen magnum, and length of the external portion of the upper temporal fenestra have strongly negative allometric coefficients; these structures are relatively large in juveniles and decrease in proportion throughout life. The greatest positive allometry is shown by width of the internal portion of the upper temporal fenestra, which begins as a very narrow slit and achieves moderate width later in life (Plate I). The length of the snout increases in proportion throughout life, but at a much more modest rate than width of the upper temporal fenestra. Many features of the skull change relatively little in shape during ontogeny, but only five cannot be shown to have even slight change. The fact that coefficients as close to isometric as 0·98 or 1·02 can be shown to differ from 1·00 at $p=0{\cdot}02$ or even $p=0{\cdot}01$ is indicative of the high correlation between variables, partly conditioned by the great size range of the specimens. Because measurements of skull width and height change only slightly relative to length, the overall shape of a hatchling alligator already resembles that of an adult.

TABLE VIII
Summary of principal components analysis of skeletal ratios in ***Alligator***

Component 1	37·7%	2nd digit pes–2nd digit manus VS femur prox wid–ischium len–4th trochanter–humerus prox wid–ilium sep–ilium len
Component 2	21·2%	tibia len–femur len–lumbar vert len–2nd digit pes–thoracic vert len–humerus len–ulna len VS calcaneum–caudal vert trans proc–thoracic vert trans proc–lumbar vert trans proc–ulna wid
Component 3	9·7%	axis to tail len–tail len–tibia wid–pubis wid VS caudal vert wid–lumbar vert wid–thoracic ver len–deltopectoral len
Component 4	6·8%	femur min wid–skull len–axis to tail len VS thoracic vert trans proc–calcaneum–2nd digit manus–caudal vert trans proc–lumbar vert trans proc
Component 5	5·6%	ulna wid–thoracic vert wid–2nd digit manus VS caudal vert wid–skull len–caudal vert height–thoracic vert height
Total variance	81·0%	

The range of allometric coefficients of the skeleton of *Alligator* (Table IV) is smaller than that for the skull, being only 0·90–1·24. More coefficients are greater than 1·00 than are less; the asymmetry of distribution of coefficients (Fig. 4(b)) is reflected in the first principal component of the skeletal ratios, in which negatively allometric coefficients have weak negative or positive factor loadings, rather than strong negative loadings. Selection of another standard of length may result in a more symmetrical distribution of allometric coefficients, but it is difficult to discover a better one among the data that would have this effect. Lengths of the second digits of the hand and foot, and of the tibia, become relatively shorter during ontogeny, while widths of vertebral transverse processes and width of the humerus are among those features that increase in size the most relative to length.

The recognition of proportional changes during the growth of crocodilians is not new. Mook (1921*c*) and Kälin (1933, 1955) observed such changes in a number of species, presenting their data in the form of ratios. The use of the allometric equation in this paper makes it practical to use a larger number of characters than Mook and Kälin could use. A single allometric coefficient replaces a whole series of ratios in conveying the sense of the change of a relationship during growth. In addition, the allometric equation can be used to predict the size of any body part for any specified body size. Mook and Kälin did not attempt to relate changes of shape that they observed to function or behavior of crocodilians. This will be a major goal of the remainder of this report.

Discussion

Skull

Isometry of skull length with respect to body length is of interest, because negative allometry of the skull is widespread among vertebrates (Rensch, 1960) and even among other reptiles (e.g. Dodson, in press, on *Sceloporus* lizards). Vertebrate skulls are typically well-developed at birth, and strong negative allometry of the brain often results in a similar decrease in relative size of the skull. However, brain size constitutes a rather insignificant architectural factor in the design of crocodilian skulls; the food-gathering function instead is the design factor. Continued isometric growth of the skull and positive allometry of the snout implies that, as ever larger body size is attained, larger and larger prey items may be captured (e.g. deer, hogs and cows for 3 metre alligators). Lack of dietary specialization is implied. *Caiman sclerops* ($a=0{\cdot}95$) is somewhat similar in strategy, but for the long-snouted crocodilians, *Gavialis* and *Tomistoma*, positive allometry early in life declines sharply later (for *Tomistoma*, $a=0{\cdot}78$ for snout length of 40 to 60 cm) (Kramer & Medem, 1955), implying a tendency to specialize on a particular size class of prey items later in life.

Measurements of skull width (but excluding width at the nose) are highlighted by the second principal component of the skull ratios (Table VI). The component expresses the tendency of some skulls to be narrower and lower and others to be wider and higher, irrespective of size. This apparently refers to morphs noted by McIlhenny (1935) and Neill (1971) that are neither sexual nor geographic, but that appear in the same sex at the same locality. The addition of quadrate to pterygoid distance to the complex of characters implies that the broader higher skulls have stronger adductor muscles. The exclusion of the anterior width measurement is interesting, for it alone of the five width measurements showed significant positive allometry ($a=1{\cdot}07$). It obviously reflects selection for a different purpose, possibly olfaction, whose requirements prevent it from varying according to the pattern described. Measurements of skull width appear at very high levels of correlation in morphological integration (Table VII) in association with skull length. This indicates that the configuration of the skull, and of the snout in particular, is an essential feature that characterizes *Alligator* among crocodilians.

Whereas the ontogenetic pattern of strong negative allometry of the orbits and foramen magnum is well-known, and virtually universal to all vertebrates, a similar level of knowledge about the behaviour of the cranial fenestrae does not exist. In *Alligator*, the development of the various temporal, palatal and mandibular fenestrea ranges from very strong positive allometry (width of the internal portion of the upper temporal fenestra) to strong negative allometry (length of the external portion of the upper fenestra). The function of cranial fenestrae is by no means clear (recently reviewed by Fox (1964) and Frazzetta (1968)), and probably varies from position to position within the skull. The traditional view is that the fenestrae are related to the bulging action of the muscles underneath, allowing the muscles to expand outward as they contract. Fox developed the idea that openings occur in regions of low stress in the skull, while Frazzetta emphasized the relations of muscle origins to the fenestrae. Aspects of the various cranial and mandibular fenestrae were measured in the hope that bivariate and multivariate studies would illuminate their functional properties, and dissection of several specimens of *Alligator* was undertaken to clarify the relationships of muscles to fenestrae.

Dissection has partly verified the assumption that ontogenetic changes of the fenestrae have interpretable significance. The upper temporal fenestra in crocodilians is the site of origin of a slip of the M. adductor externus profundus (Lakjer, 1926; Iordansky, 1964), so its development provides a direct indication of the size of the muscle during ontogeny. The external portion of the fenestra (Fig. 1) is a relatively shallow depression, almond-shaped in larger animals (Plate I), in the postorbital, parietal and squamosal bones, and is the actual site of origin of the muscle. The internal portion of the fenestra consists of a well-defined, smooth-sided canal, subcircular in cross-section in animals of moderate size, that is located anteriorly within the outer portion of the fenestra. The canal is bounded by the postorbital, parietal, squamosal and quadrate bones, and communicates with the adductor chamber of the skull lateral to the braincase. It defines the course of the fibres of the adductor profundus as it passes from the dorsal surface of the skull through the adductor chamber to insert on the mandible via the stem tendon (Iordansky, 1964). No fibres originate within the canal (*contra* Iordanksy), and its dimensions accurately define the cross-section of the adductor profundus at that level.

The shape of both portions of the upper temporal fenestra changes dramatically during ontogeny (Plate I). The upper fenestra begins as a long narrow slit in hatchlings. Both dimensions of the external portion of the fenestra decrease in larger animals, but length decreases at a greater rate than width, so that the fenestra becomes subrounded later in life. By contrast, the internal portion increases greatly in relative size, and the allometric coefficient for width of the fenestra is the highest found in the body. The adductor profundus thus changes from a feeble, strap-like muscle early in life to have a respectable fleshy belly later on. The functional significance of this change is not clear, for the size of the muscle is still smaller than that of more superficial portions of the adductor externus and to M. pterygoideus. But it has an interspecific parallel, for long-snouted crocodilians (*Alligator* becomes longer snouted in onotgeny), including both living gavials and a variety of extinct Mesozoic crocodilians, show strong emphasis on the adductor profundus, as expressed in hypertrophy of the upper temporal fenestrae.

Only one edge of the triangular lateral temporal fenestra serves for muscle attachment. Fibres of M. adductor externus superficialis arise from the postero-dorsal edge of the opening, from the quadratojugal and the quadrate. The ventral margin of the fenestra is entirely free from muscle, as is usually the case in reptiles (Haas, 1955). The adductor externus superficialis is a fairly large muscle, and its insertion on the dorsal surface of the jaw is clearly demarcated by a flat surface on the surangular. Isometry of the length of the lateral temporal fenestra and negative allometry of its height may indicate decrease in the relative importance of the adductor externus superficialis during growth.

The palatal fenestrae are completely surrounded by the bulky pterygoideus anterior muscles (pterygoideus D of Lakjer), whose fibres originate suborbitally and antorbitally on the ectopterygoid, pterygoid, palatine, maxilla, prefrontal, lacrimal and jugal bones. This long muscle is a very important adductor of the jaw, and its cross-section roughly equals that of all the vertical adductors combined. Its length must give the muscle considerable endurance (the work performed by a muscle is a function of its volume; e.g. Hill, 1950). The palatal fenestra decreases markedly in relative width, indicating a decrease in the relative importance of the pterygoideus anterior in ontogeny. The length of the palatal fenestra is isometric, but the origin of the muscle extends considerably anterior to the fenestra in *Alligator*.

The jaws show a modest tendency to deepen during ontogeny and the mandibular fenestra shows a similar modest but significant tendency to increase in both dimensions. The insertion of the adductor musculature on the jaw is principally tendinous (Iordansky, 1964), so the jaw fenestra is filled with M. intramandibularis and not with mandibular adductor muscles. The role of the M. intramandibularis is unusual. It apparently serves to fix the jaws in a gaping position by manoeuvring the stem tendon beneath the pterygoid flange so that the skull is effectively maintained in a gaping position. Gaping is a very characteristic aspect of crocodilian behaviour, quite possibly related to thermoregulation (Cott, 1961), although this has apparently not yet been tested.

Besides the fenestrae, several other osteological features were measured to estimate aspects of the musculature. Although the distance from the pterygoid flange to the quadrate was used to estimate the bulk of M. pterygoideus posterior (pterygoids A and B of Lakjer), dissection revealed that length of the retroarticular process should be added to the former to make the estimate more proper; as the two measurements are positively allometric to about the same degree, the muscle increases with positive allometry during growth.

The principal components analyses make abundant references to the various fenestrae, and by inference, to the muscles associated with them. The second principal component in the analysis of the raw data (Table V) points to variation in width of the palatal fenestra accompanied by variation in the opposite direction of the length of the jaw fenestra. As the M. pterygoideus anterior and M. intramandibularis insert on the stem tendon as antagonists, the factor may be referring to their opposing actions as jaw adductor and agent of gaping, respectively. Also there is reciprocal variation between height of the orbit and interorbital distance, a trivial geometric factor that is nonetheless true.

The third component of the analysis of the raw data and the third and fourth components of the analysis of ratios (Table VI) refer to contrasts between the deep vertical adductors and either the superficial vertical adductors or the horizontal pterygoid muscles. The reciprocal relationship between the pterygoid muscles and the superficial vertical adductors on the one hand and the deep vertical adductors on the other has already been noted in the comparison of *Alligator* with *Gavialis*, and it is interesting to find the basis for the contrast between long-snouted and short-snouted forms within *Alligator* itself.

In contrast to the principal components analyses, morphological integration did not attribute a high level of importance to the fenestrae. The lateral temporal fenestra, whose structural relationship to muscle is less intimate than that of the other fenestrae, appeared at a higher level of correlation than the other fenestrae. Only the most general reference to muscles appeared at a very high level of correlation (0·995): height of the skull, with its reference to the condition of the pterygoid muscles, and distance from the pterygoid process to the quadrate.

M. depressor mandibulae inserts on the retroarticular process that lowers the jaws. Positive allometry of the retroarticular process results from the resistance to opening the jaws in the watery medium in which crocodilians live and feed. The short moment arm of the lever defined by the retroarticular process is very close to the jaw joint. This imparts a high velocity ratio and a low mechanical advantage to the jaw abducting moment, and the modest size of M. depressor mandibulae and its slight decrease in ontogeny (inferred from the decrease in relative width of the skull across the exoccipitals), insure that the effective jaw opening force is quite weak. With the lower jaw fixed against the ground, contraction of the depressor mandibulae will exert a force tending to elevate the skull. But the mass of the skull is much greater than that of the jaw, and the mechanical arrangement described would seem inadequate for this .task. The much greater mass of the M. spinalis capitis inserting on the occiput operates at the same or a better mechanical advantage than the depressor mandibulae, but with three to four times the force. Thus it is concluded (*contra* Watson (1951) on abduction of the jaws in *Cyclotosaurus*) that the principal force for elevating the skull in gaping is supplied by the cervical epaxial muscles.

Postcranial skeleton

As noted above, the range of allometric coefficients for the postcranial skeleton (Table IV) is not as great as that for the skull. The suite of changes that the skeleton undergoes during growth is therefore less dramatic than that for the skull.

The powerful sculling tail of crocodilians is an extremely important locomotor organ, and lack of any detectable change of proportion of the tail makes it difficult to conclude that the role of the tail in swimming changes during the life of *Alligator* (in *Caiman sclerops* the tail is a somewhat negatively allometric feature). However, fore and hind limbs decrease in relative size in *Alligator* (generally true among crocodilians—Kälin, 1955), and this provides one line of evidence that juveniles are better adapted to efficient terrestrial locomotion than are adults. Cursorial animals (Gregory, 1912; Howells, 1944) are characterized by shortened propodials and elongate epipodials and metapodials, while in graviportal animals propodials are long and epipodials and metapodials are short. For *Alligator*, not only do the limbs as a whole become relatively shorter, but their proportions become less cursorial and more graviportal. The proximo-distal gradient in the fore limb, from humerus to ulna to digit, declines $a=0{\cdot}98$, 0·96, 0·94; and in the hind limb, from femur to tibia to digit, $a=0{\cdot}97$, 0·91, 0·90. Increasing the relative length of the proximal segment of the limb has the effect of moving the appendicular muscle mass farther from the centre of rotation (hip joint) and increasing the moment of inertia of the limb. This adversely effects the speed of both protraction and retraction. Decreasing the relative length of both the hand and foot also decreases the length of the stride for a given arc of rotation of the proximal segment of the limb. Increase in length of the obliquely inclined proximal segment also increases the torque exerted by the weight of the body that tends to collapse the limb at the elbow or knee joint.

The strategy of limb growth has an interesting adaptive basis. Precocious development of limbs, with ensuing decrease in cursorial proportions characterizes certain ungulates (e.g. antelope, moose, horses) that run effectively within a few hours of birth (Howells, 1944). In altricial birds (Huggins, 1940), rodents (Green & Fekete, 1933; MacArthur & Chiasson, 1946) and man (Moss, 1955), all of which are helpless after birth and are sustained by parental care, postnatal limb growth is positively allometric. *Alligator*, which certainly must depend on its own resources after hatching, fits into the precocial pattern. However, positive allometry of limbs does not constitute sufficient grounds for inferring postnatal care, as it obtains, for instance, in the lizard *Sceloporus* (Dodson, In press).

Knowledge of the weights of individual animals would permit further investigation into the functional implications of changes in limb shape. Live weights are seldom included in museum records. Fortunately, however, data on the weights of more than 100 individuals, ranging in length from 230 mm to 3·68 m and in weight from 47·5 g to 267 kg are given in McIlhenny (1935) and Colbert *et al*., 1946), so it was possible to determine the relationship between length and weight in *Alligator*. As axis to sacrum length, not overall length, is the standard of length for this study, it was necessary to use the sum: skull length+axis to sacrum length+ilium length+tail length, then solve for axis to sacrum length. It was thus found that weight varies as length to the power of 3·18 ($b=0{\cdot}00000097$), which differs from isometry (3·00 for this relationship) at $p=0{\cdot}01$. This means that long alligators are relatively heavier than short ones. Coulson, Coulson & Hernandez (1973) found that alligators raised under laboratory conditions grew more rapidly and were relatively heavier than wild animals; they found an allometric coefficient of 3·35 for the relationship between length and weight. Using the equation developed from the data of McIlhenny (1935) and Colbert *et al*. (1946), weights were assigned to animals of specified lengths (Table X).

We may now enquire into the functional significance of the fourth trochanter migrating down the shaft of the femur. M. caudifemoralis arises from the centra and transverse processes of the third through the 16th caudal vertebrae, at which point the transverse processes die out on the tail. It inserts on or beside the fourth trochanter on the medial (ventral) surface of the femur, and leaves a broad rugose impression at the site. It was verified by dissection of specimens 50 cm and 130 cm long that the cross-section of the muscle may be estimated from the width of a proximal caudal transverse process. As the force of a muscle is proportional to its cross-section, the changes (though not the absolute magnitude) of force that the muscle undergoes in life may be followed by tracing the change in the square of the width of the transverse process. The width of the transverse process of the fourth caudal vertebra is subject to strong positive allometry ($a=1{\cdot}23$). However, as weight varies as length to the 3·18 and not length to the 2·46, it is evident from the relation $A=\frac{\mathrm{F}}{\mathrm{M}}$ that, assuming no change in the lever system, constancy is not being maintained but that the accelerational increment provided by each stroke of femoral retraction must decrease through life; an allometric coefficient of 1·59 for growth of the transverse processes would have to be sustained for constancy to be maintained. The lever system does not remain the same, however, but the site of insertion of M. caudifemoralis moves distally during ontogeny ($a=1{\cdot}09$), achieving a progressively more advantageous position.

Does migration of the fourth trochanter down the shaft of the femur suffice to compensate for the insufficient allometry of the muscle itself? To answer this, static analysis of forces was performed by taking moments about the femur to calculate the force delivered at its distal end (details in Table X). Even though the moment arm defined by the insertion of the caudifemoralis on the femur increases from 0·22 times the length of the femur in the smallest specimen to 0·38 in the largest ones, accelerational increments do not remain constant but decrease with increasing size (Fig. 5).

To test how much migration of the fourth trochanter would be required to maintain the level of acceleration calculated for the smallest animal, a further calculation was performed (Table X). It was found that the fourth trochanter would have to move distally at a rate of femur length to the power of 1·58. At such a rate, the insertion would extend beyond the femur at a body length of 2·6 m. Even before such an extreme configuration were attained, morphological changes would be highly disruptive (Charig, 1972, discussed theoretical problems of muscle configurations).

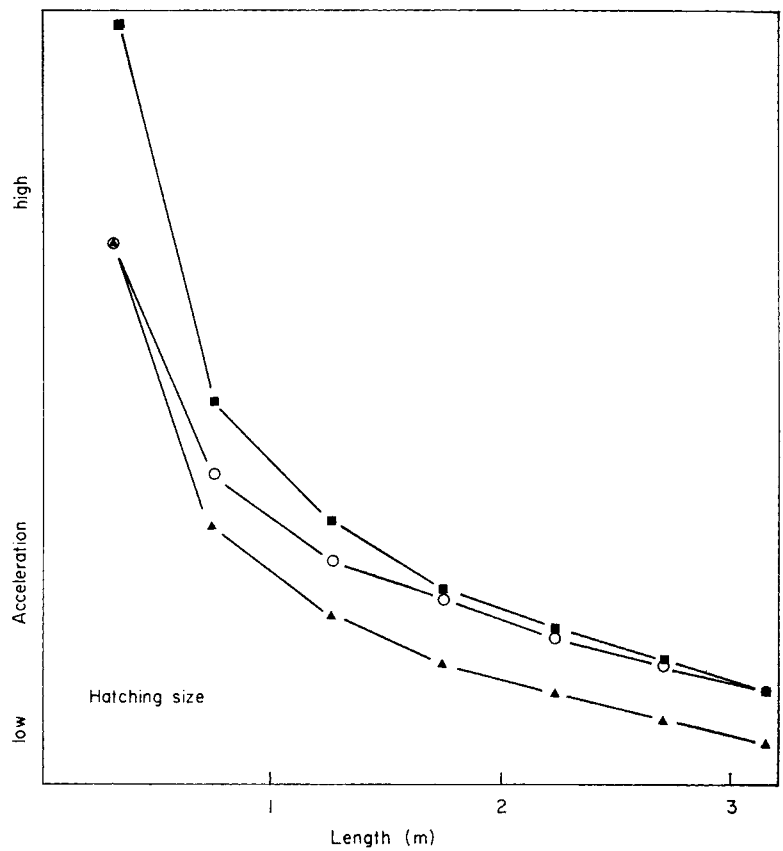

FIG. 5. Acceleration in ontogeny. (■) Adult form; (O) actual form; (▲) juvenile form.

There seems to be no feasible morphological configuration to prevent decrease in acceleration in *Alligator*. Compensation could occur by increasing the number of femoral strokes per unit time, but morphological changes already described are directed away from swiftness of limb movement. Perhaps there is no need for *Alligator* to maintain potential for constant speed through life, but the course of development is such that the requirements of adulthood are adequately met (large crocodilians have no natural enemies). Decrease in acceleration becomes very low after a certain size is reached (Fig. 5).

If there is no need for functional constancy, why does the position of the fourth trochanter change at all? If the adult configuration of the femur were maintained through life, hatchling alligators would experience some 30% greater acceleration per femoral stroke than they actually do, and this acceleration would decrease at a greater rate than is actually the case. High juvenile acceleration might be energetically wasteful, and the higher rate of change of acceleration undesirable. If the juvenile configuration were maintained, the larger the animals became, the more sluggish they would be, clearly an inadaptive course. The course followed by *Alligator* lies between lack of morphological change, which maximizes functional changes in life, and morphologically impossible changes that would maintain functional constancy. The change that actually occurs achieves an adaptive compromise that satisfies the functional requirements of its adaptive zone while at the same time preserving developmental harmony.

Principal components analysis did not illuminate any aspects of the function of the limbs, but morphological integration did. The level of integration (*sensu* Olson & Miller, 1951) of the hind limb and girdle is considerably higher than that of the fore limb. Lengths of the femur, tibia and toe formed an integrated unit at the highest level studied (0·998, Table IX), and at successively lower levels, further aspects of its operation were added. The origin of M. pubo-ischio-femoralis internus from the lumbar vertebrae (Romer, 1923), and its role of femoral protraction were alluded to at the level 0·997. Femoral abduction (length of the ilium, site of origin of M. ilio-femoralis) and adduction (length of the ischium, site of origin of M. pubo-ischio-femoralis externus, in part) also enter consideration at this level. Femoral retraction, with participation of the fourth trochanter, appears only at the lowest level of integration studied. The fore limb becomes integrated with its girdle only at the lowest level of integration investigated. At this level it was simultaneously bonded with the hind limb—the fore limb association had no discrete existence. The fore limbs are subsidiary to the hind limbs and tail in the production of thrust, and crocodilian body structure prevents them from playing a role in the acquisition or manipulation of food.

Limbs are charged with the role of weight support, but none of the six measurements of limb width even approached the predicted value of 1·5 for constancy of cross-sectional area of limbs to body weight. Instead, allometric coefficients range from 1·01 for width of the tibia to 1·24 for minimum width of the humerus. This indicates that the relative strength of the limbs decreases during ontogeny for *Alligator*. In fact, there seem to be no examples among any vertebrates of an allometric coefficient of 1·5 for limb thickening (Goldstein, 1972). The value of 1·41 for the femur of *Dimetrodon* (Romer, 1948) is apparently one of the highest coefficients reported.

Several explanations have been advanced for the failure of limb widths to behave as predicted. Romer noted that structural strengthening could achieve the desired effect without differential thickening (light coelurosaurian dinosaurs had hollow bones while large heavy theropods had solid bones). Juveniles may have a wider margin of safety than adults (Gould, 1968), or it may simply be true that large animals are more subject to limb breakage than are small ones. McMahon (1973) suggested that the problem lies in the application of a static concept of strength to limbs that are obviously adapted to dynamic torsional stresses; trees do not thicken according to the 1·5 rule but follow a law that takes into account bending stresses produced by the wind. Allometric coefficients of humerus width in rodents vary according to mode of life (Goldstein, 1972). Thus there are a variety of reasons why the predicted value of 1·5 is not found.

TABLE IX
*Morphological integration of the skeleton of **Alligator***

Level 1 0·998 or greater	
19–31–35	humerus len–femur len–tibia len
23–31–35	ulna len–femur len–tibia len
31–35–39	femur len–tibia len–2nd digit pes
Level 2 0·997 or greater	
5–19–31–39	thoracic vert len–humerus len–femur len–2nd digit pes
8–9–11	thoracic vert trans proc–lumbar vert len–height
9–19–31–35–39	lumbar vert len–humerus len–femur len–tibia len–2nd digit pes
19–23–26–31–35–39	humerus len–ulna len–ilium sep–femur len–tibia len–2nd digit pes
21–26–33	humerus prox wid–ilium sep–femur prox wid
23–27–31–35	ulna len–ischium len–femur len–tibia len
25–26–31–35	ilium length and sep–femur len–tibia len
Level 3 0·995 or greater	
1–3–4–9–31–35–39	axis to sacrum–skull len–axis to tail–lumbar vert len–femur len–tibia len–2nd digit pes
1–3–4–25–31–35–39	as above, but omit lumbar vert len, add ilium len
1–3–9–19–31–35–39	as above, but omit axis to tail and ilium len, add lumbar vert len and humerus len
1–4–9–31–35–38–39	axis to sacrum–axis to tail–lumbar vert len–femur len–tibia len–2nd digit manus and pes
1–5–19–25–31–35–39	axis to sacrum–thoracic vert len–humerus len–ilium len–femur len–tibia len–2nd digit pes
1–9–19–31–35–38–39	axis to sacrum–lumbar vert len–humerus len–femur len–tibia len–2nd digit manus and pes
2–4–30	tail len–axis to tail–pubis wid
3–4–23–25–27–31–35–39	skull len–axis to tail–ulna len–ilium len–ischium len–femur len–tibia len–2nd digit pes
3–4–28	skull len–axis to tail–ischium wid
3–19–23–25–27–31–35–39	skull len–humerus len–ulna len–ilium len–ischium len–femur len–tibia len–2nd digit pes
4–9–11–31	axis to tail len–lumbar vert len–height–femur len
4–18–25–27–31–35–39	axis to tail–scapula len–ilium len–ischium len–femur len–tibia len–2nd digit pes
4–23–25–27–31–33–35–39	as above, but omit scapula len, add ulna len, femur prox wid
4–23–31–35–38–39	axis to tail–ulna len–femur len–tibia len–2nd digit manus and pes
5–12–16	thoracic vert len–lumbar vert trans proc–caudal vert trans proc
5–12–31	as above, but omit caudal vert, add femur len
5–18–25–31–35	thoracic vert len–scapula len–ilium len–femur len–tibia len
5–19–25–26–31–35–39	thoracic vert len–humerus len–ilium len–ilium sep–femur len–tibia len–2nd digit pes
8–9–10	thoracic vert trans proc–lumbar vert len–wid
8–9–11	as above, but omit wid, add height
15–31–39	caudal vert height–femur len–2nd digit pes
19–21–23–26–31–33–35	humerus len–prox wid–ulna len–ilium sep–femur len–prox wid–tibia len
19–23–25–26–27–31–32–33–35	humerus len–ulna len–ilium len and sep–ischium len–femur len–4th troch–prox wid–tibia len
19–23–25–26–27–31–33–35–39	as above, but omit 4th troch, add 2nd digit pes
19–23–31–35–38–39	humerus len–ulna len–femur len–tibia len–2nd digit manus and pes

TABLE XI *continued*

Level 4 0·993 or greater	
1–3–4–5–19–23–25–26–27–31–33–35–39	axis to sacrum–skull len–axis to tail–thoracic vert len–humerus len–ulna len–ilium len and sep–ischium len–femur len–prox wid–tibia len–2nd digit pes
1–3–4–9–19–23–31–35–39	axis to sacrum–skull len–axis to tail–lumbar vert len–humerus len–ulna len–femur len–tibia len–2nd digit pes
1–3–4–19–21–23–25–26–27–31–33–35–39	axis to sacrum–skull len–axis to tail–humerus len–prox wid–ulna len–ilium len and sep–ischium len–femur len–prox wid–tibia len–2nd digit pes
1–4–5–18–19–23–25–26–27–31–33–35–39	as above, but omit skull len and humerus prox wid, add thoracic vert len and scapula len
1–4–5–19–23–25–27–31–33–35–38–39	as above, but omit scapula len and ilium sep, add 2nd digit manus
1–4–9–19–23–31–35–38–39	axis to sacrum–axis to tail–lumbar vert len–humerus len–ulna len–femur len–tibia len–2nd digit manus and pes
1–4–18–19–21–23–25–26–27–31–33–35–39	axis to sacrum–axis to tail–scapula len–humerus len–prox wid–ulna len–ilium len–sep–ischium len–femur len–prox wid–tibia len–2nd digit pes
2–3–4–5–23–25–27–33–35–39	tail len–skull len–axis to tail–thoracic vert len–ulna len–ilium len–ischium len–femur prox wid–tibia len–2nd digit pes
2–4–9–11–35–39	tail len–axis to tail–lumbar vert len–height–tibia len–2nd digit pes
2–4–30	tail len–axis to tail–pubis wid
2–4–33–34	tail len–axis to tail–femur prox wid–min wid
3–4–5–19–23–25–26–27–31–32–33–35–39	skull len–axis to tail–thoracic vert len–humerus len–ulna len–ilium len and sep–ischium len–femur len–4th troch–prox wid–tibia len–2nd digit pes
3–4–5–28	skull len–axis to tail–thoracic vert len–ischium wid
3–4–9–19–23–31–32–33–35–39	skull len–axis to tail–lumbar vert len–humerus len–ulna len-femur len–4th troch–prox wid–tibia len–2nd digit pes
3–4–19–21–23–25–26–27–31–32–33–35–39	as above, but omit lumbar vert len, add humerus prox wid–ilium len and sep–ischium len
3–15–19–31–39	skull len–caudal vert height–humerus len–femur len–2nd digit pes
4–5–18–19–23–25–26–27–31–32–33–35–39	axis to tail–thoracic vert len–scapula len–humerus len–ulna len–ilium len and sep–ischium len–femur len–4th troch–prox wid–tibia len–2nd digit pes
4–9–11–19–31–32–35–39	axis to tail–lumbar vert len–height–humerus len–femur len–4th troch–troch–tibia len–2nd digit pes
4–18–19–21–23–25–26–27–31–32–33–35–39	axis to tail–scapula len–humerus len–prox wid–ulna len–ilium len and sep–ischium len–femur len–4th troch–prox wid–tibia len–2nd digit pes
4–26–33–34	axis to tail–ilium sep–femur prox wid–min wid
5–12–16	thoracic vert len–lumbar vert trans proc–caudal vert trans proc
5–12–25–26–31–35–39	thoracic vert len–lumbar vert trans proc–ilium len and sep–femur len–tibia len–2nd digit pes
6–26–32–33	thoracic vert wid–ilium sep–4th troch–femur prox wid
8–9–10–11	thoracic vert trans proc–lumbar vert len–wid–height
9–10–11–32	lumbar vert len–wid–height–4th troch
11–13–35	lumbar vert height–caudal vert len–tibia len
21–22–26–33	humerus prox wid–min wid–ilium sep–femur prox wid
22–26–33–34	humerus min wid–ilium sep–femur prox wid–min wid

TABLE
Acceleration of

Length axis to sacrum	Length Total	Weight	Transverse process width	Femur Length	4th Trochanter	4th Trochanter (hypothetical)
70 mm	230 mm	31·8 g	1·8 mm	19·2 mm	5·1 mm	5·1 mm
220	719	1178	8·1	58·5	17·7	28·3
370	1205	6111	15·9	96·8	31·2	63·1
520	1690	17912	24·6	134·6	45·2	107·6
670	2173	39894	34·0	172·7	59·6	160·6
820	2657	75537	44·0	209·4	74·3	220·0
970	3139	135607	54·4	246·5	89·2	

Total length, weight, width of transverse process and lengths of femur and fourth trochanter (Y's) calculated from generated by M. caudifemoralis retracting the femur is proportional to the cross-section area of the muscle, estimated muscle times the length of the moment arm (length of the fourth trochanter from the acetabulum) equals length of retraction is thus calculated at intervals during the ontogeny of *Alligator* (force actual). Knowing force (F) and relative (unitless) quantity, because its actual magnitude is not known. Using the calculated value for the actual increasing size, and the length of the fourth trochanter in such a hypothetical system, are computed. Alternatively, values for F and A are calculated.

In the multivariate analyses of *Alligator*, widths of limbs and vertebrae are most readily interpreted in the context of weight support. At the level of 0·995 in morphological integration, proximal widths of both propodials sort with their own lengths, plus lengths of their epipodials and separation of the ilia in a locomotor group that is influenced by the requirement for weight support. At the level 0·993, length of the body, width across the pelvis and proximal and minimum widths of the femur form a weight support association. In a similar group, length of the body and minimum width of the femur are replaced by width of the thoracic vertebra and length of the fourth trochanter. The vertebral and pelvic widths refer to weight support, as perhaps does proximal width of the femur; however, the association of proximal width with the fourth trochanter may indicate that part of the width of the femur is conditioned by the attachment of M. caudifemoralis. Several groups contain propodial width measurements and width across the ilia; humerus proximal and minimal widths cluster with femoral proximal width, or proximal and minimum widths of the femur with minimum width of the humerus. The mutually exclusive relationship between femoral minimum width and humeral proximal width is curious, perhaps alluding to the different roles that fore and hind limbs play in locomotion and weight support; but in either case, the association emphasizes the relative independence of widths and lengths of limbs, which was also observed by Gould (1967) in an oblique factor analysis of pelycosaurs.

The sorting together of limb lengths and vertebral lengths independent of limb widths and vertebral widths, as in pelycosaurs, is a conspicuous feature of the second principal component. Both propodial lengths, both epipodial lengths and length of the second digit of the foot, plus two vertebral lengths, thoracic and lumbar, are set in contrast to the transverse processes of all three vertebrae, length of the calcaneum and width of the ulna (tentatively regarded as an indicator of weight). The contrast is drawn between the role of the limbs in locomotion and the role of lateral undulations of the body, as expressed

X
***Alligator** in ontogeny*

Force for constant acceleration	Force actual	Acceleration actual	Force: juvenile shape	Acceleration juvenile shape	Force: adult shape	Acceleration: adult shape
0·86	0·86	0·0270	0·86	0·0270	1·2	0·0367
31·8	19·9	0·0169	17·5	0·0148	23·8	0·0202
165	81·7	0·0133	67·3	0·0110	91·7	0·0150
484	209	0·0117	161	0·0090	219	0·0122
1077	401	0·0101	307	0·0077	418	0·0105
2040	687	0·0091	514	0·0068	700	0·0093
	1072	0·0079	788	0·0058	1072	0·0079

allometric equations relative to the specified standard length (X). Other entries calculated as follows. The force by the square of the width of the transverse process. As a third class lever system, the product of the force of the the resistance arm (length of the femur) times force delivered at the end of the femur. The force produced by femoral weight (M), acceleration due to one femoral stroke (A) is calculated ($A=F/M$). Acceleration is expressed as a acceleration of the hatchling (70 mm standard length), the force required to maintain constant acceleration with if the relative length of either the hatchling or the terminal adult trochanters are used, correspondingly different

in development of the axial musculature of the trunk and tail. This represents a comparison, independent of size, between individuals that are more terrestrial and those that are more aquatic in adaptation (a similar contrast obtains in ontogeny). The appearance of length of the calcaneum within the "aquatic" group seems contradictory unless development of the calcaneal lever compensates for relative atrophy of the limbs.

The reflection of weight in the various structures of the body probably depends heavily on the locomotor habitus of the animal. High correlation between proximal end of the femur and weight is regarded as a function of sprawling posture (Gould, 1967). The poor participation of vertebral width measurements in weight support may result from the aquatic habits of *Alligator*, and its belly-resting tendencies while on land. Thus the vertebral column habitually bears less weight than the cantilever model attributes to it.

Vertebral widths, which have also been suggested to follow the 1·5 rule in vertebrates (Romer & Price, 1940; Romer, 1948) on the basis of the cantilever model of weight support between the limbs, show no greater attendency to observe the rule of 1·5 than do limb widths for *Alligator*. Allometric coefficients in *Alligator* range from 0·95 to 1·08. Neural spines have an important role in weight support by resisting bending between adjacent vertebrae. The neural spines of all three vertebrae measured in *Alligator* show significant positive allometry. The longer the neural spine, the greater the torque produced by the intraspinous ligaments acting between the tips of adjacent spines to prevent bending.

Increased emphasis on the epaxial and hypaxial muscles is reflected in the strong positive allometry of the transverse processes, with allometric coefficients ranging from 1·20 to 1·23. Lateral undulations of the body and especially of the tail are particularly important in propelling *Alligator* through the water. At the level 0·995 in morphological integration, several small groups refer to aspects of vertebral function. Two triplets collect together length of the thoracic vertebra and transverse process of the lumbar vertebra with either transverse process of the caudal vertebra or length of the femur. The former relates to lateral undulation of the body, while the latter reflects the origin of M. pubo-ischio-femoralis internus acting from the lumbar vertebra. Length of the thoracic vertebra also bonds with lengths of scapula, ilium, femur and tibia, showing the role of the vertebrae in stabilizing the appendicular girdles. One triplet relates lengths of hindlimb elements to height of the neural spine of the proximal caudal vertebra, and reflects stresses on the tail caused by contraction of M. caudifemoralis. At a level of 0·993, length of the thoracic vertebra and transverse process of the lumbar vertebra bond with two ilial measurements and the hind limb group, indicating a lower level of integration of limb action and the vertebral column. In a sense, the vertebral column of crocodilians is less important than that of lower vertebrates that throw their backs into serpentine waves while walking or that of cursorial mammals that flex their backs in a dorsoventral plane in running.

Conclusions

This study of *Alligator mississipiensis* was undertaken in a paleontological context, to determine characteristics by which a taxonomically homogeneous growth series can be recognized. Another goal was to test the extent to which function can be deduced from changes in form. The developmental pattern of *Alligator* is well canalized, as expressed by the very high correlations among variables (Tables III and IV) and the linearity of the bivariate plots (Fig. 3). Measurement of variability in a growth series is difficult, but a coefficient of dynamic variation (V_d) was developed, which is analogous to the standard statistic V, and it indicated variabilities in the range of 8 to 10 for *Alligator*. This compared favourably with values of V for taxonomically homogeneous samples of mammals. *Alligator* lacks strong secondary sexual characters that contribute significantly to the variability of the characters measured.

By and large, the qualitative changes in shape that occur in the ontogeny of *Alligator* may be expected to take place in phylogeny as well. For instance, the relative size of the orbits and foramen magnum may be expected to be smaller in larger species of crocodilians, and the snout longer, etc. No changes have been recognized in ontogeny by which it may be unequivocally identified. There is nothing about a 150 mm skull of *Alligator* that marks it as a small individual of a large species rather than a large individual of a small species. Its bone texture does not have a particularly "juvenile" appearance. Its sutures are well-defined, but this is not a character of ontogenetic significance, because in continuously growing lower vertebrates, the sutures are always open. The best method to assess the status of a particular specimen is to test its morphometric properties with those of a known (or inferred, if fossil) growth series. If the specimen falls in with the bivariate trends of the growth series, the specimen is conspecific with the series. When the specimen is distinct from some of the trends, particularly for strongly allometric relationships that are size limiting, it is fair to conclude that it represents a separate species. When no ontogenetic series for reference exists, as is very often the case for fossils, it may be impossible to solve the problem definitively, although geographic and stratigraphic considerations are relevant.

The problem of the inference of function and ecology from form yielded somewhat more positive results, for many allometric changes proved to be interpretable. Allometric features of the limbs, both as a whole and of their parts, and of the mechanical properties of their muscles, all point to the ontogenetic decrease in locomotor ability of the limbs of

Alligator. Such an inference is supported by mark and recapture studies (Chabreck, 1966) that show small animals to have a much greater tendency to roam than large ones, and from biophysical studies (Spotila *et al.*, 1972) that show small alligators to be better able to tolerate direct sun, and thus less dependent on the thermally buffering effect of water, than larger ones. Both bivariate and multivariate studies emphasize the poor correlation between body weight and widths of the limbs and vertebrae. The inappropriateness of the cantilever model of weight support may be an indicator of the aquatic habits and sprawling posture of *Alligator*.

Isometry of the length of the skull with respect to body length and positive allometry of the jaws is an adaptation to ever increasing size of prey, which is known to occur in *Alligator*. The jaw muscles of broad-snouted *Alligator* are dominated by the pterygoid muscles with a more or less horizontal position. The posterior pterygoid muscles, whose development is probably indicated by the size of the pterygoid processes, act close to the jaw joint and adduct the jaws with a high velocity ratio. In sharp-snouted *Crocodilus acutus*, the pterygoid flanges are slightly lower than in *Alligator*, and by inference, the posterior pterygoid musculature is slightly less developed. In *Gavialis* (and also in several groups of Mesozoic crocodilians of aquatic nature), which has a very long narrow snout, the pterygoid processes are very weak, and the upper temporal fenestrae much enlarged. The M. adductor externus profundus that occupies the upper temporal fenestra inserts farther from the jaw joint and thus operates with greater strength but lower velocity than the pterygoid. Its narrow snout is an adaptation for decreasing resistance as the jaws close through a viscous medium, but evidently a mechanical arrangement for greater strength is required too. In view of the more aquatic nature of larger alligators, it is interesting to find both bivariate (positive allometry of the snout and the upper temporal fenestra) and multivariate (contrast of the pterygoid muscles and superficial vertical adductors with the deep vertical adductors) analyses that point to variation in the direction of *Gavialis*.

The use of multivariate techniques, frankly experimental in this study, appears to be moderately successful in providing functional and morphological insights. The detection of the broad and narrow skull morphs by the principal components analysis, and of the subtle relationship between the lumbar vertebra and the femur by morphological integration and good examples. Other examples are the finding, as did Gould (1967), of the independence of limb widths and lengths, and the poor relationship between body weight and limb and vertebral widths. The property of the first principal component in analysis of specimens of a growth series standardized to unit length of functioning as a size axis by setting positively and negatively allometric variables in contrast to each other has not been reported before.

It is unfortunate that the ecology of the crocodilians of the world is not better understood today. There exists among living (and fossil) crocodilians a great variety of shapes of snout, temporal and other fenestrae, and pterygoid process development. Although the functional interrelationships of these structures and the muscles related to them are not yet completely understood, it is quite probable that morphometric study of ontogenetic series of the other living crocodilians would provide deep insight into the functional and ecological similarities and differences among these animals, and would permit a more sophisticated assessment of the role of crocodilians in ancient communities than has been possible until now.

Summary

A series of studies of relative growth and ontogeny in reptiles designed to help recognize growth series in the fossil record, was begun with *Alligator mississipiensis*. A large number of variables (27 in the skull, 39 in the skeleton), designed to be functionally interpretable, were measured on 52 skulls and 28 skeletons that spanned more than an order of magnitude of size. The data were subjected to bivariate allometric analysis and two kinds of multivariate analysis, principal components analysis and morphological integration.

Correlation coefficients among variables are very high, indicating rather narrow canalization of developmental trends that is necessary when growth spans such a large size range. A coefficient of variation for a growth series was developed that indicated minimum variation of the order of 8 to 10.

No ontogenetic changes in *Alligator* that are not also likely to be encountered in phylogeny were recognized. The distinction of small specimens of large species from large specimens of small species in lower vertebrates depends on careful biometric analysis rather than on the existence of qualitative characteristics.

A number of allometric features of *Alligator* were interpretable in terms of function and ecology. Negative allometry of limb lengths and relative decrease in the mechanical properties of the femoral retractor muscles correspond very well with physiological and behavioural observations showing that small alligators are more mobile than large ones. Isometry of skull length and positive allometry of snout length appear to be adaptations to ever increasing prey size, and anecdotal observations on the diet of *Alligator* corroborate this. Superimposed on the *Alligator* jaw adductor system that is predicated upon the massive development of the pterygoid muscles, there is an ontogentic trend towards the enlargement of M. adductor externus profundus, such as characterizes *Gavialis*; multivariate analyses confirm variation in the direction of *Gavialis*.

It is concluded that study of the patterns of relative growth and its functional significance would provide very useful insights into the ecological relationships of modern crocodilians and their relatives in the fossil record.

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