JOURNAL OF PALEONTOLOGY, V. 52, NO. 5, P. 964–971, 6 TEXT-FIGS., SEPTEMBER 1978

THE ORTHOMETRIC LINEAR UNIT

PHILIP J. CURRIE
Provincial Museum of Alberta, Edmonton, Alberta, Canada T5N 0M6

ABSTRACT—Romer and Price (1940) proposed a standard of unit measurement that they used in studying a group of fossil reptiles, the Pelycosauria. The basis for the system is the orthometric linear unit ($r^{2/3}$, where r is half the transverse width of a dorsal vertebral centrum). In a re-examination of the pelycosaurian genus *Haptodus*, it became apparent that it is necessary to restrict the use of the orthometric linear unit to linear dimensions of the skeleton that do not show interspecific allometry. Under this condition, differences in the unit measurements have quantitative, biological significance. Furthermore this system cannot be used directly with immature animals. Otherwise, unit measurement, based on the orthometric linear unit, would be a useful system within any group of animals where the backbone is encountering the same types of gravitational and propulsive forces.

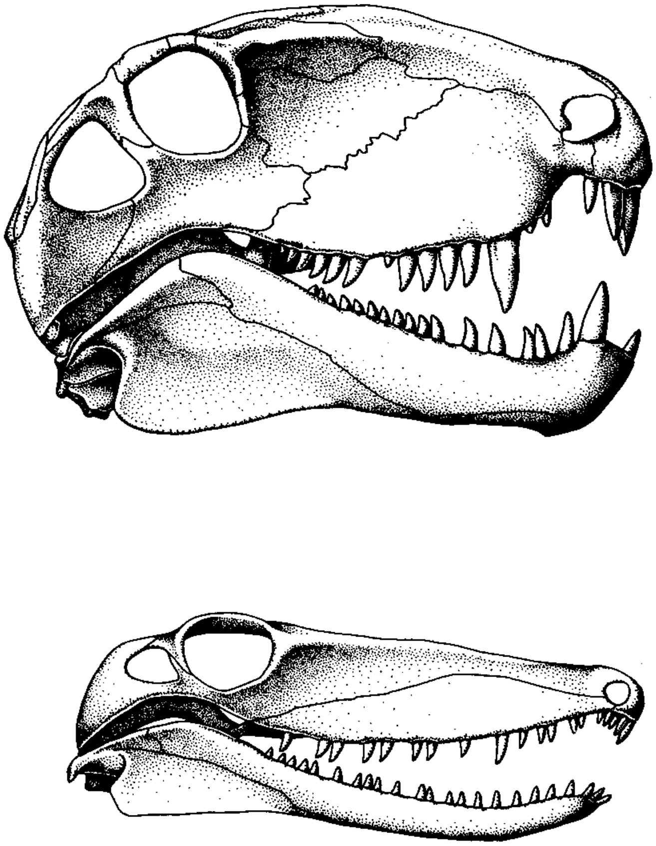
INTRODUCTION

IT IS DIFFICULT to compare objectively the relative dimensions of bones of mature animals of different sizes. Romer and Price (1940) found it necessary to develop a system whereby they could compare the relative lengths of various skeletal elements within and between genera of pelycosaurs (synapsid reptiles of Pennsylvanian and Permian times). Pelycosaurs exhibit a considerable range in mature size. For example, the total length of a femur of a mature specimen of *Dimetrodon natalis* never exceeds 150 mm in length, whereas in *D. grandis* the length of the same bone can be over 250 mm in a mature animal. The proportions of various elements are also diverse in pelycosaurs (for example, compare the skulls of *Dimetrodon* and *Secodontosaurus*, Text-fig. 1). The problem was to set up a standard of measurement that could be used to compare the linear dimensions of all pelycosaurs, regardless of absolute size at maturity. There is considerable variation in the relative lengths of the skull, limb bones and even the vertebral centra of pelycosaurs. As a consequence of this variability, none of these dimensions could be used as the basis for comparison with other skeletal elements.

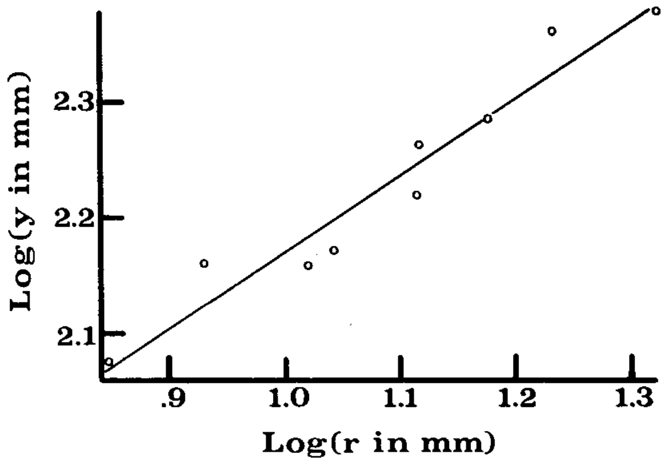
Romer and Price (1940, p. 7–9) propose a standard of measurement based on half the transverse width of a vertebral centrum (r) from the middle or posterior dorsal region. They selected r as the basis for comparison because it is proportional to the animal's weight, which in turn is proportional to volume. Volume is the three dimensional product of all linear measurements, and is therefore the ideal basis for comparison. The yardstick used for measuring pelycosaurian bones is $r^{2/3}$, which Romer (1948, p. 51) termed the orthometric linear unit (OLU). If the length of a bone is divided by the OLU, the resulting figure is called the unit measurement. This measurement should be constant for any bone in closely related adult animals, regardless of absolute size. Differences in unit measurements for the same bones in different genera of animals is expected. Romer and Price (1940, p. 8–9) and Romer (1948, p. 51, Table 2) give numerous examples of the usefulness of unit measurement.

Unit measurement, as envisioned by Romer, has not been widely utilized. Amadon (1943) used this system for birds, and Carroll (1970) employed it in comparisons of measurements of Paleozoic amphibians and reptiles. Otherwise, it has been used only in connection with pelycosaurs (Romer and Price, 1940; Romer, 1948, 1961; Lewis and Vaughn, 1965; DeMar, 1970). Olsen (1951, p. 523) has pointed out that this unit is applicable only to similar forms of animals. To the best of my knowledge, no other published criticism of the OLU has appeared. It would seem that unit measurement should have a much larger range of application than it has enjoyed up to now, and that it is probably applicable within any group of vertebrates where the backbone is mechanically serving the same function and is encountering the same types of gravitational and propulsive forces.

Although the OLU superficially appears to be the ideal standard of measurement, in a recent re-examination of the pelycosaurian ge-



TEXT-FIG. *1*—Lateral views of skulls of *Dimetrodon* (above) and *Secondontosaurus*. The relative lengths of both skulls are about the same. The elongate appearance of the skull of *Secodontosaurus* is caused by its low and narrow nature. ×⅕. (After Romer and Price, 1940.)



TEXT-FIG. *2*—Relationship between the length of the humerus (y) and half the transverse width of a thoracic centrum (r) in *Dimetrodon*. Each point represents the general averages of these measurements for a species. Data from Romer and Price (1940, Table 5).

nus *Haptodus* (pers. obs.), a number of problems arose with this system. Most significantly, it became evident that the OLU should not be compared with dimensions that are affected by the factors of weight and physiology. It is therefore necessary to reconsider the OLU and to place limitations on its usage to give it biological significance. These restrictions are presented here in the hope that unit measurement of this type may find wider application in the future.

DISCUSSION

The system of unit measurement proposed by Romer and Price (1940, p. 7–9) is a derivation of the power equation $y = bx^k$. In this equation, y represents the magnitude of the element being studied, x represents that with which it is being compared (usually the total length or weight of the body), and b and k are constants over a specified range of x. Since volume is the three-dimensional product of all linear measurements, "the cube root of volume (less the part involved, if possible) is the ideal comparative unit to use for x" (Romer, 1948, p. 50).

$$L \text{ (length)} \propto V \text{ (volume)}^{1/3}$$

Because specific gravity is almost constant within any group of animals, weight is proportional to volume:

$$W \text{ (weight)} \propto V$$

and

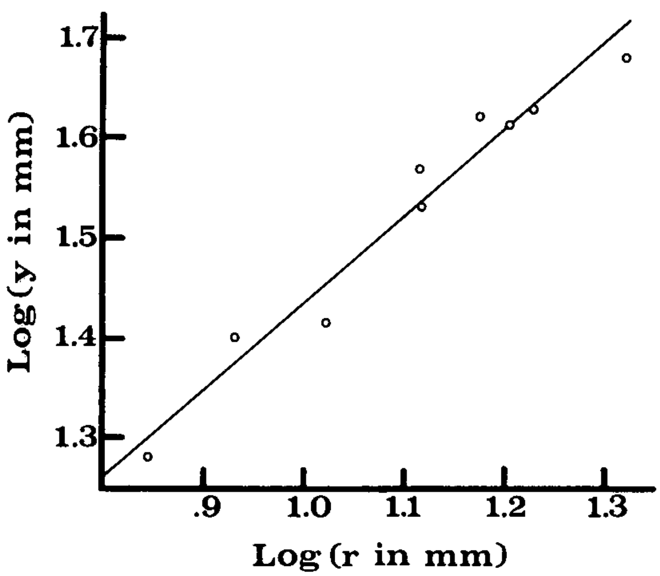
$$L \propto W^{1/3}$$

The weight of an animal is supported by the vertebral column. Therefore a cross-section of a trunk vertebral centrum (proportional to r^2, where r is arbitrarily chosen to be one half the posterior width of a dorsal centrum) will be proportional to weight.

$$L \propto (r^2)^{1/3}$$
$$L \propto r^{2/3}$$
$$L = br^{2/3}$$

The orthometric linear unit is $r^{2/3}$, and the unit measurement of an element of length L is b. Westoll (1950, p. 499) pointed out that $br^{2/3}$ should be multiplied by the cube root of the unit of linear measurement, i.e. $mm^{1/3}$.

The OLU can also be derived using empirical means. If the logarithm of the length (y) of the humerus is plotted against the logarithm of r (Text-fig. 2) for species of *Dimetrodon*, a



TEXT-FIG. 3—Comparison of the distal width of the radius (y) and *r* in *Dimetrodon*. Each point represents the general averages of these measurements for a species. k = 0.88 ± 0.12. Data from Romer and Price (1940, Table 5).

straight line results that can be defined by the equation

$$\text{Log}\, y = \text{Log}\, b + k(\text{Log}\, r)$$

The slope of the line, k, calculated by the least squares method, is 0.66 (95% confidence interval is ±0.18), which is not significantly different from the theoretical value of ⅔ (0.67).

$$\text{Log}\, y = \text{Log}\, b + (2/3)\text{Log}\, r$$
$$y = br^{2/3}$$
$$b = y/(r^{2/3})$$

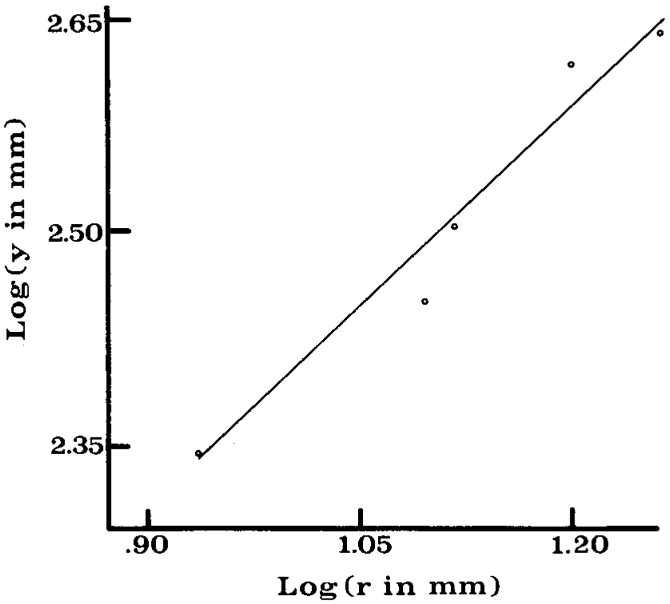
The final equation gives the unit length of the humerus. If the mean values of y and r are substituted into this equation, the average unit length of the humeri of the different species of *Dimetrodon* can be calculated.

Because of the relationship between body weight and r, the length of a bone, compared with r, is isometric with respect to differences in absolute size in interspecific comparisons when $k = 2/3$.

It is not always possible with pelycosaurs to determine whether a bone increases isometrically with respect to size changes in closely related species. Some genera are monospecific, while the species of other genera such as *Haptodus* were all about the same size when mature. It is reasonable to assume that if the length of an element increases isometrically with respect to linear size differences among species of *Dimetrodon* (which has the largest sample size of all pelycosaurian genera) that it also increases isometrically above the species level in other pelycosaurs. Although this is not always true (for example, neural spine length of primitive pelycosaurs seems to increase isometrically in relation to changes in size of mature animals, but exhibits positive allometry in several advanced lineages), the fact that division of actual measurements by the OLU usually produces results of consistent magnitude for any genus demonstrates that the relationship holds true in most cases. If k is the same in each genus being compared, then differences in the magnitude of b between genera are biologically significant (White and Gould, 1965), and the objectives for establishing this standard of measurement are fulfilled.

There are, however, several problems involved in the use of unit measurement that restrict its application as a biologically significant standard.

The orthometric linear unit represents a special case of the power (allometric) equation, $y = br^k$, where $k = 2/3$. When k does not equal two thirds, the use of the OLU must be restricted, because differences in the unit measurements are no longer significant. Romer developed the system of unit measurement as a means of comparing linear measurements that are independent of weight and other physiological considerations. Division of the length of the humerus or other limb bones of *Dimetrodon* by the OLU will produce a measurement whose magnitude is consistent for the genus, even though animals of different species differ greatly in weight and total linear dimensions. Measurements made perpendicular to the longitudinal axes of supporting bones (such as the distal width of the radius, Text-fig. 3) however increase with positive allometry as the absolute length of the animal increases. This occurs since larger animals carry a proportionally greater weight and must compensate for this in the skeleton (see Gould, 1967, p. 392). Division of such measurements by the OLU will therefore produce numbers of greater magnitude in larger animals. Unit measurement can therefore be used to demonstrate allometric size changes with respect to the linear measurements of the animal. In dealing with allometric size changes, unit mea-



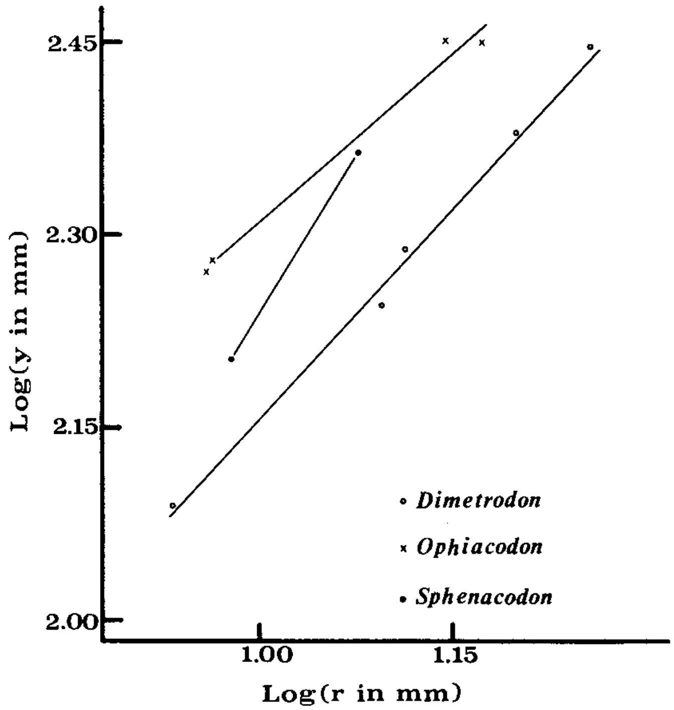
TEXT-FIG. 4—Comparison of skull length (y) and r in *Dimetrodon*. Each point represents a single animal. Data from Romer and Price (1940, Tables 1 and 3).

surement must be used with great care. For example, the lengths of vertebrate skulls, including those of pelycosaurs (Text-fig. 4), often exhibit positive allometry among the adult forms of groups of closely related animals. In this case, the relative size is a "secondary result of a single common growth-mechanism, and therefore is not of adaptive significance" (Huxley, 1932, p. 214). Therefore, one cannot say that a large species of *Dimetrodon* is more advanced than a small species of the same genus, if the only basis for saying that is a difference in the unit lengths of the skulls.

Changes in the magnitude of b can be independent of k, so it is biologically valid to compare differences in the size of b if k is the same in the animals being compared. If the magnitude of k is the same in two genera, but not equal to ⅔, although differences in b are biologically significant, differences in unit measurements between the two genera are not usually meaningful. In this case, unit measurements are defined by the equation

$$y/r^{2/3} = br^{k-2/3}$$

Comparisons of differences in unit measurements between genera should only be made when r is the same in the animals considered, unless k is close to being ⅔. The size dependence of the unit measurement increases directly with increased difference between k and ⅔.



TEXT-FIG. 5—Relationship between facial length (y) and r in ophiacodontid and sphenacodontid pelycosaurs. Each point represents a single animal. ○ = *Dimetrodon*, × = *Ophiacodon*, ● = *Sphenacodon*. Data from Romer and Price (1940, Tables 1 and 3).

A change in k produces a correlated modification of b (White and Gould, 1965). Therefore if the relative lengths of an element are being compared in different animals, and k is not the same in each, then differences in b are not significant. In Text-fig. 5, the logarithm of preorbital length of the skull has been plotted against the logarithm of r for *Ophiacodon Sphenacodon* and *Dimetrodon*. It can be seen from the scatter diagram that at a value of r shared by *Ophiacodon* and *Dimetrodon*, *Ophiacodon* has a relatively longer facial region than the latter genus. Similarly, the preorbital lengths of species of *Sphenacodon* are relatively longer than they are in *Dimetrodon*. Calculation of b however gives somewhat different results. *Ophiacodon* has the highest b-value at 27.1, correlated with the lowest value of k (.88). The next highest b-value, 11.9, belongs to *Dimetrodon*. *Sphenacodon*, on the other hand, which actually has a greater preorbital length than *Dimetrodon*, has a low b at 4.6 because of a relatively high value of k.

Romer and Price (1940, Table 6) compared cranial measurements by dividing the actual lengths in millimeters by the OLU. The reliability of using unit measurements to compare the skulls of pelycosaurs is poor. Since $k \neq 2/3$, cranial unit measurements are size dependent. Furthermore, because k is not the same for each genus, differences in the magnitude of b are not biologically significant.

Juvenile and sub-mature specimens represent a further complication that was largely overlooked by Romer and Price, probably because they had little juvenile material to work with. If two animals are the same size, and one is a juvenile of one species, and the other is a mature representative of a different species, the juvenile will have relatively thicker bones. This occurs because juveniles anticipate their adult form to a large extent in the length to width proportions of their bones. As a result, the centra of juveniles are relatively thicker than those of an adult form of the same absolute size, and the value $r^{2/3}$ is relatively higher and the unit measurements are relatively lower.

The pelycosaurian genus *Haptodus* is represented by specimens of eight species ranging from juveniles to adults (pers. obs.). Almost all individuals of *H. longicaudatus* preserved were small juveniles when they died. The largest specimens of *H. saxonicus* appear to be fully mature animals showing ossification of the ends of the limb bones, co-ossification of limb girdle elements, etc. The single specimen, an isolated maxilla, of *H. grandis* represents an individual that could have been as much as fifty percent longer than any other haptodontine known. This suggests that *Haptodus* was capable of growth throughout its life, although individuals of the length seen in *H. grandis* were probably exceptional. *Alligator mississipiensis* can be cited in comparison. Individuals seldom surpass 3.5 m in length, although lengths of 5.5 m have been recorded for this species (Neill, 1971). Other species of *Haptodus* are intermediate in size and degree of ossification between specimens of *H. longicaudatus* and *H. saxonicus*. In the absence of even a single diagnostic feature to distinguish any of the Early Permian species of this genus from each other, and considering the correlation of size with the degree of ossification in all specimens concerned, it is profitable to consider all specimens of this genus as representatives of a single growth series.

The lengths of skeletal elements of the largest specimen of *H. saxonicus* are approximately five times the lengths of the equivalent elements in the smallest specimen of *H. longicaudatus*. In modern reptiles of approximately the same size (between one and two meters in total length at maturity) as *Haptodus*, a size magnification from birth to maturity of this magnitude would be possible, but low. For example, the ratio of adult to hatchling length is seven to one as an average for six species of *Varanus*, and nine to one for *Caiman sclerops*. In general, the magnitude of the ratio varies directly with the mature size of a reptile. If we assume that the largest specimen of *H. saxonicus* represents the average adult size of the genus, then it might be concluded from the low ratio that the smallest specimens of this genus had not just emerged from their eggs when they died. However, since reptiles under normal conditions generally double their hatching length within the first year of life, it seems probable that the smallest specimens of *Haptodus* were less than a year old. This would give an adult to hatchling length ratio of between five and ten to one.

The power formula can be adapted to describe growth in *Haptodus*. Simpson, Roe and Lewontin (1960, p. 407) point out that the relative growth rate of two dimensions is a basic characteristic of a species, and in some cases can be extended to apply to closely related species in a genus, or even closely related genera. In studies such as this, individual specimens could have had different rates of growth, but a random sample of individuals can give measurements that represent a simple power equation of growth.

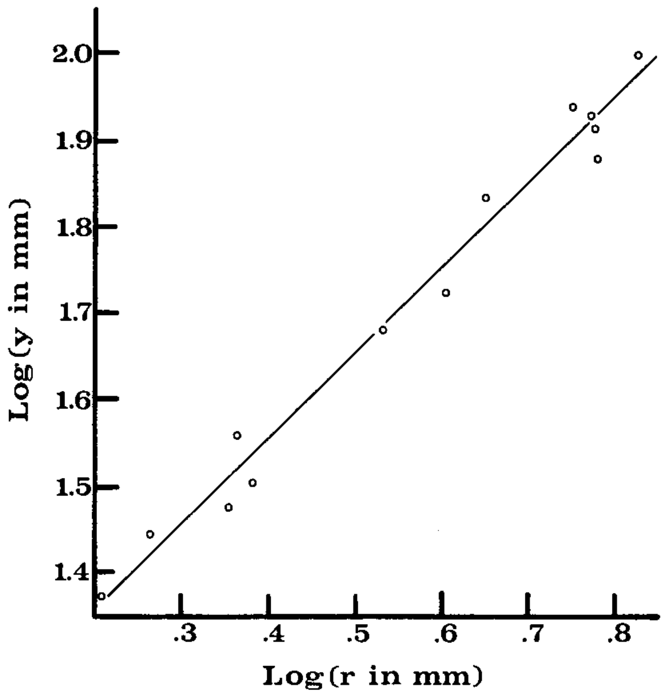
Let $y = b'r^{k'}$, where y is the length of the element being considered, r is one half the transverse width of a trunk centrum, and b' and k' are constants. The thickness of the centrum is not dependent on weight in ontogenetic development (see above), and therefore r, like y, increases at the same rate as the linear measurements of the animal during growth. Therefore growth is isometric when $k' = 1.0$. The logarithm of the length of the humerus has been plotted against the logarithm of r for thirteen specimens of *Haptodus* where both these dimensions are known (Text-fig. 6). The points on the scatter diagram are amazingly consistent in their alignment, the correlation coefficient being 0.99. The 95% confidence interval of k_{yx}' (calculated by the least squares method) is 0.99 ± 0.09. Comparisons of other dimensions during growth of this genus produce results that in most cases are as significant as those of the humerus (pers. obs.). The ossified lengths of most limb elements increase isometrically with growth. The length of the skull shows significant negative allometry, and several dimensions (such as the length of the pubis and the height of the neural spines) show significant positive allometry of growth.

Since r is not directly dependent on weight in ontogenetic size increase, but is dependent on weight in interspecific size changes, its relationship to other bones might be used to indicate whether a large series of specimens of different sizes represents an ontogenetic series or an interspecific size range of mature animals. For example in *Dimetrodon*, an interspecific comparison of the length of the humerus with r produces a k of ⅔. However, for each species of *Dimetrodon*, one would expect an ontogenetic series where $k' = 1$. In terrestrial reptiles it is usually possible to tell whether or not the specimens are fully mature by the degree of ossification. In amphibians and aquatic reptiles however, it is not as easy to distinguish mature and immature forms since the extent of ossification can be almost the same throughout the animal's life. In cases such as these, differences in the magnitude of k and k' could be useful in distinguishing ontogenetic from interspecific series.

The largest specimen in the *Haptodus* growth series studied is *H. saxonicus* #6, which seems to be a fully mature animal. Because unit measurement is valid only when adult forms are compared, the unit measurements of *H. saxonicus* #6 only should be used in comparisons with other pelycosaurs. Unfortunately, only the skull, part of the presacral vertebral column, ribs and part of the pectoral girdle are preserved in this specimen. However, if the power equation for growth is known for any element in *Haptodus*, an estimated mean value of y and the confidence limits can be calculated from the known value of r of *H. saxonicus* #6. For example, the estimated length of the humerus is

$$y = b'r^{k'} = (14.69)(7.70)^{0.99} = 110.25 \text{ mm}$$

The unit length can then be calculated by dividing the estimated length by the OLU of *H. saxonicus* #6 (3.90), and this can be compared with the unit lengths of the same element in other pelycosaurs.



TEXT-FIG. 6—Relationship between the ossified length of the humerus (y) and r in *Haptodus*.

A simpler calculation can be used to obtain the approximate unit length of some bones. The lines defined by the equations

$$y_1 = b'r_1^{k'} \quad \text{(ontogenetic power equation)}$$

and

$$y_2 = br_2^{k} \quad \text{(interspecific power equation)}$$

intersect when (y_1, r_1) coincides with (y_2, r_2). This occurs at the adult stage. At the intersection,

$$y = b'r^{k'} = br^{k}$$

Therefore

$$b = (b'r^{k'})/r^{k} = b'r^{(k'-k)}$$

When there is no allometry in either ontogenetic or interspecific size increases, $k' = 1$ and $k = ⅔$. Therefore the unit measurement, equivalent to b, is equal to $(b'r^{1/3})$.

The degree of allometry can change between ontogenetic and interspecific levels. For example, the pubis of *Haptodus* exhibits positive allometry in its ontogenetic development. Interspecific comparisons within the genus *Dimetrodon* show that the length of the pubis increases isometrically with respect to size. If the adult length of an element is known for a species, it is valid to use unit measurement to compare the length of that element, even if it acquired that length through allometric growth, provided that that element is isometric in interspecific size differences.

SUMMARY

Volume is the three-dimensional product of all linear measurements. Because r, one half the transverse width of a vertebral centrum, is proportional to the volume of an animal, it can be used as the basis for a standard of measurements. Romer and Price (1940) proposed that actual measurements of bones be divided by the orthometric linear unit ($r^{2/3}$) to give a unit measurement that is independent of the absolute size of the animal.

Romer's system of unit measurement is a derivative of the power, or allometric, equation, $y = bx^k$, where y is the linear length of a bone, b is the unit measurement, and x^k is $r^{2/3}$. In its derivation, it concerns only isometric interspecific size changes in the length of bones, and should therefore be restricted to these same dimensions in its application. Here differences in unit measurement have biological significance.

In dealing with allometric interspecific size changes, a difference in unit measurements is a combination of both interspecific proportional differences of the animals concerned, and a size dependent factor ($r^{k-2/3}$). If the animals being compared are approximately the same size, and the coefficient of allometry (k) is the same in both, then the size dependent factor is negligible, and the unit measurement is a reasonable estimate of proportional differences. The greater the difference in the absolute sizes of the animals being considered, the less significant is the difference in the unit measurements. A better estimate of proportional differences in this case would be obtained by dividing the linear measurements by r^k.

If k is not the same in animals being compared, a further complication is introduced. The magnitude of b is determined to an extent by the measure of k. An increased distinction in the b-values of the same dimension in different animals occurs with the augmentation of differences in the coefficients of allometry. The unit measurement is also affected by the size dependent factor considered in the previous paragraph. In this situation, unit measurement cannot accurately show differences in proportions. When k is variable, the simplest way to compare proportions is by examination of scatter diagrams such as Text-fig. 5.

The orthometric linear unit should not be used in studying sub-mature specimens because the coefficient of allometry is not the same in ontogenetic and interspecific series when r is used as the basis for comparison. This occurs because r is weight dependent in an interspecific series, but not in an ontogenetic one. If the magnitude of r is known for a mature specimen, unit measurements for the genus can be calculated indirectly by using the growth series of that animal.

Differences in the unit measurements of different genera are significant provided interspecific size changes are isometric, even though the dimensions may have been attained by allometric growth.

The orthometric linear unit is a useful basis for comparing differences in the proportions of linear dimensions within any group of animals where the backbone is encountering the same types of gravitational and propulsional forces. Caution should be taken however in assessing differences in unit measurements whenever growth or interspecific allometry are involved.

ACKNOWLEDGMENTS

This paper is the result of work done at the Redpath Museum of McGill University. I would like to thank Dr. Robert L. Carroll of McGill University and Dr. Stephen Jay Gould of the Museum of Comparative Zoology for reading this paper and offering useful suggestions.

REFERENCES

Amadon, D. 1943. Bird weights as an aid in taxonomy. Wilson Bull. 55:164–177.

Carroll, R. L. 1970. The ancestry of reptiles. Philos. Trans. R. Soc. Lond. B 257:267–308.

DeMar, R. 1970. A primitive pelycosaur from the Pennsylvanian of Illinois. J. Paleontol. 44:154–163.

Gould, S. J. 1967. Evolutionary patterns in pelycosaurian reptiles: a factor-analytic study. Evolution. 21:385–401.

Huxley, J. S. 1932. Problems of Relative Growth. Methuen, London, 276 p.

Lewis, G. E. and P. P. Vaughn. 1965. Early Permian vertebrates from the Cutler Formation of the Placerville area, Colorado. U.S. Geol. Surv. Prof. Pap. 503-C, p. 1–46.

Neill, W. T. 1971. The Last of the Ruling Reptiles. Alligators, Crocodiles and their Kin. Columb. Univ. Press, New York, 486 p.

Olsen, R. 1951. Size relations in the limb bones of *Buettneria perfecta*. J. Paleontol. 25:520–524.

Romer, A. S. 1948. Relative growth in pelycosaurian reptiles. R. Soc. S. Afr., Spec. Publ. Robert Broom Comm. Vol., p. 45–55.

——. 1961. Synapsid evolution and dentition, p. 9–56. *In* International Colloquium on the Evolution of Lower and Non Specialized Mammals. Kon. Vlaam. Acad. Wet. Lett. Sch. Kunsten Belg., Brussles.

—— and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Am. Spec. Pap. 28, p. 1–538.

Simpson, G. G., A. Roe and R. C. Lewontin. 1960. Quantitative Zoology. Harcourt, Brace and World, New York, 440 p.

Westoll, T. S. 1950. Some aspects of growth studies in fossils. Proc. R. Soc. Lond. 137:490–509.

White, J. F. and S. J. Gould. 1965. Interpretation of the coefficient in the allometric equation. Am. Nat. 99:5–18.

MANUSCRIPT RECEIVED NOVEMBER 29, 1977
REVISED MANUSCRIPT RECEIVED FEBRUARY 23, 1978