GROWTH PATTERNS IN THE CERATOPSIA

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ABSTRACT. The deformed coördinate system of D'Arcy Thompson is applied to both ontogenetic and phylogenetic series of ceratopsian dinosaurs. The results confirm the phylogeny of Lull, 1933, and the relative growth studies of Gray, 1946. An evaluation of the method and its relation to the relative growth formula is provided.

SIR D'Arcy Thompson in his book *On Growth and Form* showed, that, as a one to one relationship exists between homologous parts of the bodies of related animals, this relationship could be expressed in terms of a system of coördinate lines undergoing successive deformation. He suggested that this interpretation of relationship might provide a method for predicting unknown intermediate stages in the evolution of animal groups. He, himself, applied such a system to the phylogeny of the horse, comparing the actually known stages with those derived by deformed coördinates from beginning (*Hyracotherium*) and end (*Equus*) forms only. The agreement was very good. Colbert, 1935, used the method to show form changes but did not attempt to construct a phylogenetic system. Richards and Riley, 1937, used a modification of the method to show the differences between normal and abnormal growth in amphibian larvae. The method has been discussed in general by Woodger, 1945.

THE CERATOPSIA

The present study attempts to apply the deformed coördinate method to the phylogeny of the ceratopsian dinosaurs, a group of ornithischian reptiles from the Cretaceous. Growth of this group was previously studied by means of Huxley's relative growth equation by Gray, 1946, and it therefore seemed to be good material for testing the usefulness of the Thompsonian coördinates.

The specimens used were the series of skulls figured in Hatcher, Marsh, and Lull, 1907, and Lull, 1933. A few other sources supplied single specimens. Enlarged drawings were made from photographs, and coördinate lines were drawn directly upon them. The base grid was chosen arbitrarily for convenience although an attempt was made to have the evenly spaced lines cross as many definite landmarks as possible. Neither brow nor nasal horns were considered in the system as they are too frequently broken or distorted.

The first base selected was the Asiatic *Protoceratops andrewsi* described by Brown and Schlaikjer, 1942, because

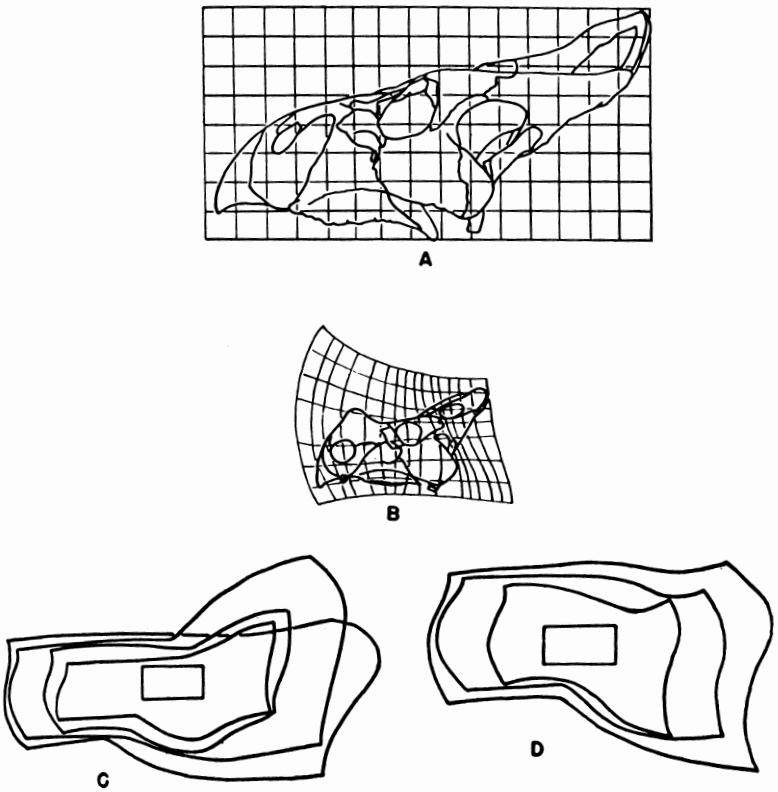

Figure 1. A. *Protoceratops andrewsi* with the basic rectilinear coördinate system. B. Same coördinate system deformed to fit *Leptoceratops cerorhynchus.* C. Same coördinate system (outlines only) for *P. andrewsi* (innermost), *Chasmosaurus belli, C. brevirostris, Pentaceratops sternbergii* and *Torosaurus gladius* (outermost). D. Same coördinate system (outlines only) for *P. andrewsi* (innermost), *Monoclonius flexus, Triceratops prorsus,* and *T. horridus* (outermost).

of its small size, moderate crest development and absence of horns (fig. 1A). Previous studies of the ceratopsian material, Gray, 1946, had shown that there was a discontinuity between the relative dimensions of *Protoceratops* and those of the remainder of the group (fig. 1). This discontinuity resolved itself into a nearly constant deformation of the rectilinear coördinates in all of the higher forms when *Protoceratops*

was used as a base. There is a downward displacement of the post-orbital region superficially apparent from the consistently inferior location of the temporal opening. This displacement is more marked in the ventral than in the dorsal contour lines.

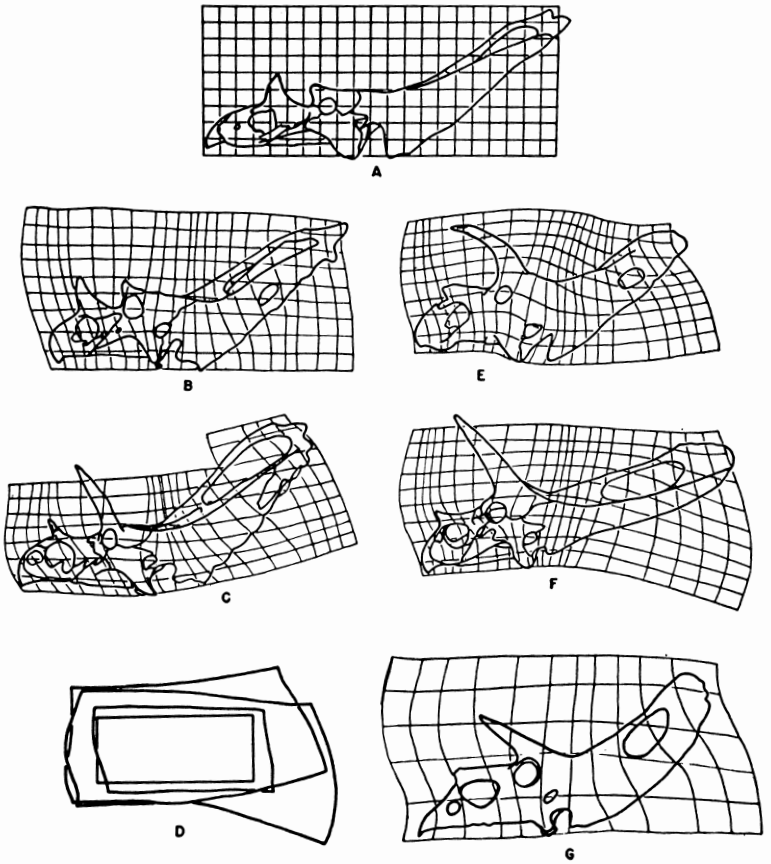

Figure 2. A. *Chasmosaurus belli* with basic rectilinear coördinate system. B. Same system deformed to fit *C. brevirostris*, C. *P. sternbergii*, D. Superimposed outlines of A, B, C, E and F, E. *Arrhinoceratops brachyops*, F. *Torosaurus gladius*, G. *T. latus*.

While it is slightly more prominent in the *Monoclonius-Triceratops* series (the "short-crested" line of Lull) it is present in all of the forms examined, showing neither a constant increase nor decrease as one goes up the series (figs. 1C and D). It is, however, a smooth deformation and *may be drawn with unbroken lines.*

Leptoceratops cerorhynchus (AM 5464), as reconstructed

by Brown and Schlaikjer, does not show any trace of this deformation found in the higher forms but instead shows a quite different pattern of its own (fig. 1B). The extent of reconstruction renders judgment difficult but it does not seem to lie between *Protoceratops* and the other Ceratopsia.

This constant deformation of the Ceratopsia with respect to the base, *Protoceratops*, obscures other changes which may have taken place. New series were therefore constructed. For the "long-crested" line of Lull, *Chasmosaurus belli* (AMNH 5402) was selected as the base form (fig. 2). This skull, from the Belly River formation of the upper Cretaceous has been considered the earliest member of the series culminating in the giant *Torosaurus* of the Lance formation. The only marked deformation in the series is in the angle which the crest makes with the rest of the skull. Both *T. gladius* and *T. latus* from Yale show considerable downward bending of the crest but it should be noted that the skull from the Hell Creek formation of South Dakota assigned to *T. latus* by Colbert, 1947, shows no such deformation with respect to *Chasmosaurus belli* (fig. 2G). It is probable that the crest was easily distorted during preservation and not impossible that its angle with the remainder of the skull was somewhat variable from one individual to another during life. Neglecting this angular deformation of the crest, the phylogenetic growth in the *Chasmosaurus-Torosaurus* line, is very nearly uniform, with a slightly accelerated increase in the posterior lateral edges of the crest.

Arrhinoceratops brachyops (*ROM* 5135), placed doubtfully between the long- and short-crested lines by Lull, 1933, has been shown to belong to the long-crested series on the basis of relative dimensions and the deformed coördinates confirm this conclusion. The deformation with respect to *Chasmosaurus* indicates that, while it is closer to this line than to the *Monoclonius-Triceratops* series, it shows a certain downward bending in the post-orbital region which is reminiscent of that seen in all of the forms when deformed to the *Protoceratops* base.

In the short-crested line, *Monoclonius flexus* (YPM 2015) provided the base for the coordinate system (fig. 3). In general, even less distortion appeared than in the *Chasmosaurus-Torosaurus* series. There was, however, much more trace of the deformation seen with respect to *Protoceratops*. In other words, the downward bending of the post-orbital region noted

between *P. andrewsi* and *M. flexus* was still continuing in the higher forms although to a much smaller extent.

Both this study and the previous one with relative growth seem to indicate that no better classification of the group can be made than that of Lull in 1933.

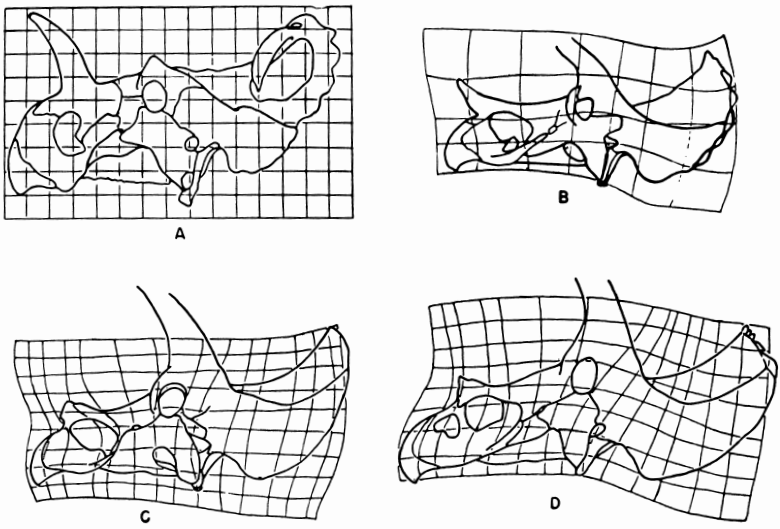

Figure 3. A. *Monoclonius flexus* with basic coördinate system. B. same system deformed to fit *Triceratops prorsus,* C. *T. elatus,* D. *T. calicornis.*

An attempt was made to follow the deformation of both phyletic lines backward in time by extrapolation from *T. prorsus* through *M. flexus* (fig. 4A). It was found impossible to continue the change at the same rate to a point as far "below" *M. flexus* as *T. prorsus* is "above" it. Before reaching such a stage, parts of the deformation become geometrically impossible, that is, the figure begins to buckle and fold. It is possible to reach a stage about three quarters of the way and this is shown in fig. 4A. This completely hypothetical skull shows some resemblance to *Protoceratops* in its small crest and high nasal region, but the position of the temporal opening in relation to the orbit is like that in the higher forms. This character shows no sign of approaching the protoceratopsian condition.

The similar extrapolation from *Pentaceratops sternbergii* through *Chasmosaurus belli* does not at all resemble either of the protoceratopsian skulls. It, in fact, looks like nothing more than a smaller specimen of *Chasmosaurus.* There is no trace

of a tendency to approach *Protoceratops* in the long-crested line.

Changes in the ontogenetic series of skulls of *Protoceratops andrewsi* from Brown and Schlaikjer, 1940, were examined

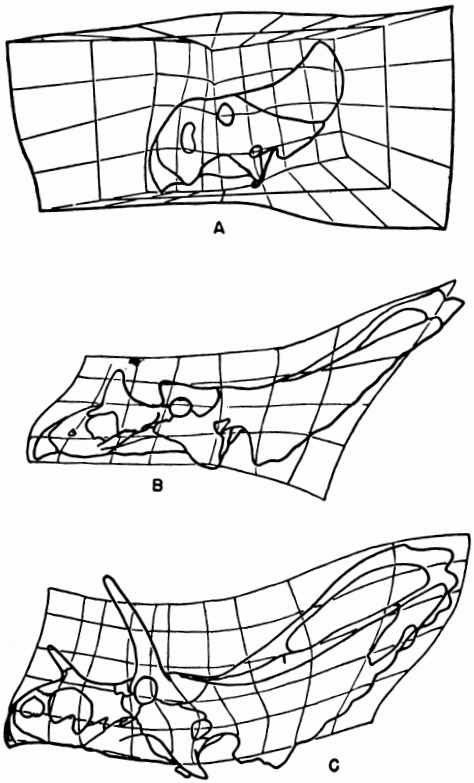

Figure 4. A. Hypothetical skull resulting from extrapolating coördinate system based on *Monoclonius* from *T. prorsus* (outermost) through *M. flexus* backward in phylogenetic time (see Text). B. coördinate system based on *M. flexus* deformed to fit *C. belli.* C. coördinate system based on *T. prorsus* deformed to fit *P. sternbergii.*

from a series of deformed coördinates based upon the youngest specimen (AM 6419) (fig. 5). A series of five skulls shows an excellent set of progressive deformation culminating in the "Old Male" (AM 6432). The greatest change is in the great increase in the depth of the nasal region with age. This is not similar to the condition in the higher Ceratopsia where the nasal region remains relatively undisturbed, all of the growth being localized in an actual horn instead of the more diffuse involvement of the surrounding bone.

In no way does the development of the young *Protoceratops* resemble the phylogenetic changes of the sub-order as a whole. There is no tendency for the temporal opening to shift toward the position found in the higher forms and the increase in the size of the crest hardly forecasts the great crests of the future. The specimens tentatively called females by Brown and Schlaikjer proved to fit the deformation at all points but the nasal region. There is no doubt that these skulls are slightly but consistently different from the other five and this difference may well represent sexual dimorphism (fig. 5A).

DISCUSSION

The Thompsonian grid, being constructed so that lines pass through homologous points in a series of skulls, it follows that

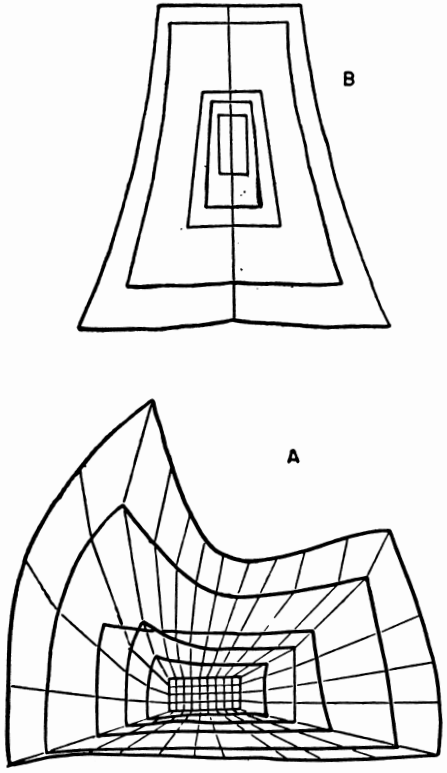

Figure 5. A. Ontogenetic series of outlines of successive deformations of coördinate system taking place in the growth of *Protoceratops andrewsi.* The grid is based on the youngest specimen (AM 6419). The fourth outline from the inside is that of a putative female. B. Similar outlines for dorsal aspect of skull of *P. andrewsi.*

the distance between two points of intersection on one skull is homologous with the distance between the equivalent two points on another skull in the same series. It has been shown in a previous paper (Gray, 1946) that many dimensions on the ceratopsian skulls follow the Huxley equation $y = bx^k$ in both phylogeny and ontogeny. It should follow from this that any pair of line segments in the Thompsonian grid will be similarly related to the homologous pairs of line segments of the same grid distorted to pass through homologous points of another skull of the series. If this "distortion" is simple, uniform growth without bending, and the line segments remain straight, the resulting patterns are capable of ready analysis. If the growth rate in all directions be equal, and the initial dimensions be equal, then b in the Huxley formula equals 1.0 and K equals 1.0. The resulting Thompsonian series will have straight lines connecting all equivalent points of the series (fig. 6D). If b remains equal to one and K becomes greater than one the midpoints of the line segments alone will lie in a straight line and the remaining equivalent points will fall on logarithmic curves concave toward the segment chosen as x. Should K become less than unity the curves will become concave toward the segment chosen as y. This expresses the fact that the value of K becomes its reciprocal if the dimensions chosen as x and y are interchanged (fig. 6C and E).

But such simple growth systems as these are not common, and in practice, in the Ceratopsia, one finds that the axes are deformed and that many varying rates of growth are involved so that rarely do the equivalent points lie in a straight line. In addition to this, the skull is not homogeneous and will resist deformation more in one direction than in another and thus the increase in length of a region due to growth may appear, chiefly, at that end least firmly attached to more slowly growing structures. When, in addition to these complications, it is considered that certain growth rates may change during the phylogeny of a group while others remain constant, it is impossible accurately to analyze the deformed series into its factors without a nearly perfect set of specimens. For this reason it has seemed best to treat most of these lines as being straight. Similarly, while it is possible to analyze the patterns of angular change in the direction of a line in the Thompsonian grid, there is insufficient material to be sure that the skull actually obeys such laws as this analysis might indicate.

When progressive deformations are carried far enough there usually appears a point at which further deformation is no longer possible on a plane surface. Simply expressed, the

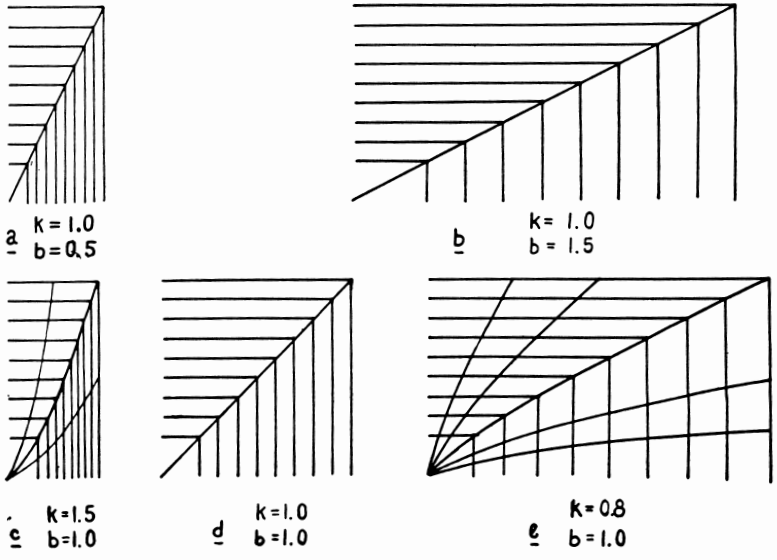

Figure 6. Appearance of quadrants of deformed coördinate systems showing the effects of varying b and k in the Huxley equation.

condition is usually that in which three points form a triangle, one of whose sides grows fast enough to exceed the total of the other two. Such a condition is geometrically impossible and biologically absurd. It was reached during the attempt to extrapolate backward in time in both the *Monoclonius-Triceratops* line and the *Chasmosaurus-Pentaceratops* series. Long before such a condition occurred in nature the forces involved would produce a bending effect upon some one of the structural members involved. An indication that this is already happening in the "Old Male" *Protoceratops* appears in figure 5A. The slow growth of the frontal bones above the orbit with the great increase of the vertical height in the nasal region has produced the elevated nasal prominence. Nevertheless, this growth has placed a strain on the lower portion of the skull so that there is a tendency for it to give in a downward direction and thus produce a more hooked beak. To what extent such rapid growth of one region may affect the history of a group such as the ceratopsia is not clear. They remained well within the bounds of geometrical possibility but had

they not become extinct, and had they continued to increase in size with their same relative skull growth rates they would have reached this interesting stage. As Simpson, 1944, has pointed out, this would affect only the oldest animals first and, even though the resulting stresses might prove fatal, through warping of the upper jaw with resulting mal-occlusion, for example, it would exercise no selective effect until it had progressed far enough to make itself felt in animals of breeding age. Thus, the impending phylogenetic crisis might be first apparent in a decreasing individual life-span.

From these considerations it would appear that there are real limitations to the extent with which orthogenetic or "straight-line" evolution may operate. An increasing dimension need not reach the bizarre and inefficient size necessary to become an impossible burden upon the animal but need only grow to such a point that it can no longer be fitted with other, more slowly growing dimensions. This might well occur in a structure of no great absolute size.

Orthogenesis can operate, then, only within the framework of a Thompsonian grid having line segments of positive sign. Overgrowth of one region may imply that a distant dimension become negative ("folding" or "buckling"), and, while the other side of zero holds no terrors for the mathematician, it is a land closed to dinosaurs.

In summary it may be said that the deformed coördinate system should, under careful analysis, yield, at one stroke, the same information to be obtained from a large series of relative growth measurements. The relationship of ontogeny to phylogeny within such a group as the Ceratopsia may be illustrated both in terms of relative growth of single dimensions and the deformed coördinates in figures 7 and 8. In practice, the required accuracy in the identification of homologous points is not easily achieved and the use of the system is thus markedly limited. It should also serve to indicate probable lines of evolution within the series, and, indeed, will no doubt succeed where more perfect material is available. At present, it seems to be rather less useful, despite the striking nature of its results, than the method of comparing single pairs of measurements which may be available even when the material is fragmentary. With either method it is possible to produce totally spurious relationships; for two points may always be connected by a straight line although evolution may have pro-

ceeded quite differently. Thus, there is a perfectly possible transformation between *Protoceratops* and *Monoclonius* which may or may not be the actual change which took place. There

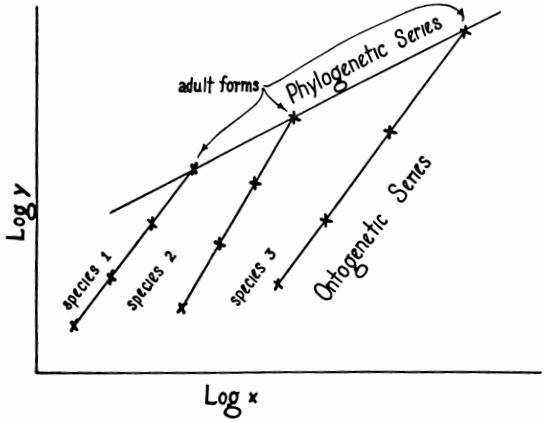

Figure 7. Generalized relation between ontogenetic and phylogenetic relative growth. Where two dimensions, x and y, are compared, each species has its own growth curve with values of b and k peculiar to it. The phylogenetic curve of the *adult* forms intersects each ontogenetic curve with independent values for the variables.

is a deformation of coördinates based upon *Monoclonius* and applied to *Torosaurus* which represents a change which did not occur at all, yet, in neither case would the data alone give one the clue to this. Both methods tell us only that in the case

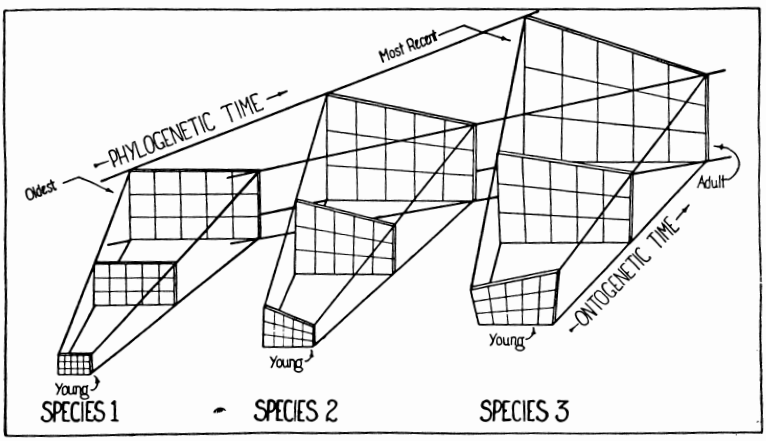

Figure 8. Generalized relation between deformed coördinate systems for three species. As in Figure 7, each ontogenetic series culminates in an adult form which falls into line with other adult forms to create the phylogenetic series.

of two different forms there are certain differences and, *if* the forms are related, it is in a certain way. In spite of these drawbacks, the analysis of the Ceratopsia confirms the relationship previously suggested and further emphasizes the great gap between the Protoceratopsidae and the Ceratopsidae.

Even a casual glance at the deformations produced by this method shows that boundaries between bony elements of the skull are in no sense boundaries of growing systems. The crest behaves as a unit without reference to the boundary between the parietals and squamosals. The orbital region is not the result of a ring of bones growing at different rates but acts as if the whole region were under a single control. Even such units as the crest and the orbital region are so smoothly integrated with one another that one feels that the true "field" can be no less than the entire skull. It is possible that this integration can be broken down into growth centers of some sort, each under some overall control by the entire animal.

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