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Skull Evolution in the Rhinocerotidae (Mammalia, Perissodactyla): Cartesian Transformations and Functional Interpretations

Gerald S. Bales[1,2]

Cartesian transformation, applied as a landmark morphometric method, is used to investigate some of the evolutionary shape changes leading to the skulls of the modern rhinoceroses. The early Oligocene genus *Subhyracodon* serves as the primitive shape from which the extant genera (*Dicerorhinus, Rhinoceros, Diceros,* and *Ceratotherium*) have been transformed. Coordinate data for 21 landmarks, defined in lateral view, are analyzed by the computer program Thin-plate Splines. Each of the four transformations are interpreted separately as shape change from *Subhyracodon.* Computed results for *Rhinoceros* are also compared with previous results obtained by visual interpretation (the classic method). Among the extant genera, *Ceratotherium* and *Rhinoceros* have the most derived shapes and are opposites with respect to orientation of the occiput and relative size of the mandible angle. The significance of these foci of change is discussed in terms of the functions of the masseter and posterior temporalis muscles. In head positions associated with feeding on short vs. tall grasses, the two skull shapes are consistent with a role for these muscles in support of a large mandible against gravity. This common factor may help to explain both shapes.

KEY WORDS: Cartesian; transformation; splines; rhinoceros; skull; evolution.

INTRODUCTION

The four extant genera of Rhinocerotidae (*Dicerorhinus*, *Rhinoceros*, *Diceros*, and *Ceratotherium*) represent endpoints of a long evolutionary history in the Cenozoic (Prothero *et al.*, 1989). Rhinocerotids (rhinoceroses) arose in the Eocene as one of three familial clades comprising a superfamily (Rhinocerotoidea), and their phylogeny is recorded by one of the largest fossil collections available for large vertebrates. Recent phylogenetic studies (Prothero *et al.*, 1986) have recognized at least 26 genera (Fig. 1). The early Oligocene genus *Subhyracodon* is representative of the primitive rhinoceros skull condition. This long phylogeny with a well-characterized primitive taxon allows the study of shape evolution leading to the modern taxa.

One of the first attempts to characterize rhinoceros skull evolution in general terms was by Thompson (1917, p. 761). He included rhinoceros skulls as an example in a chapter on "comparison of related forms" where he introduced and formalized Cartesian

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[1] Department of Anatomy, Western University of Health Sciences, 309 E. Second Street College Plaza, Pomona, California 91766-1889.

[2] To whom correspondence should be addressed.

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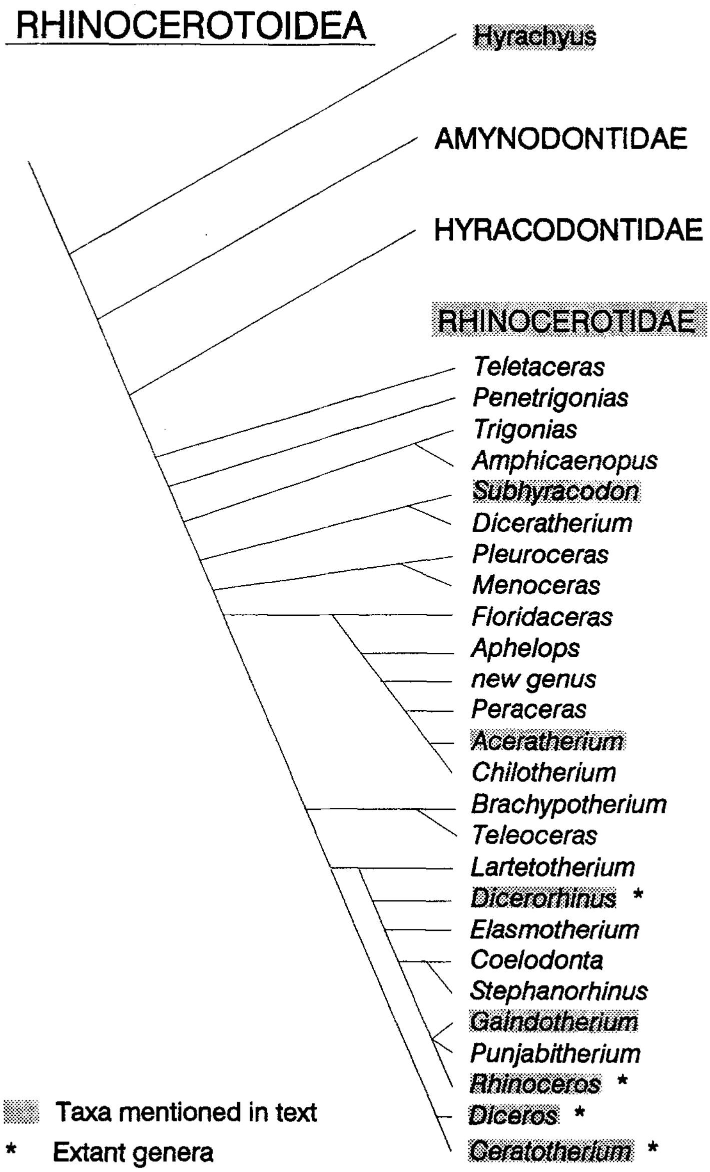

Fig. 1. Phylogeny of the Rhinocerotoidea showing genera of the Rhinocerotidae (after Prothero *et al.*, 1986). Shaded taxa are those mentioned in the text. Starred (*) taxa are extant.

transformation. The idea that evolutionary changes between closely related taxa could be summarized by geometric constructs was demonstrated by Thompson using a variety of animal and plant examples. Thompson's analyses of transformation in fishes were particularly elegant and convincing. In the rhinoceros example (Fig. 2), he examined the transformation from *Hyrachyus* (sister taxon of the three rhinocertoid families) to

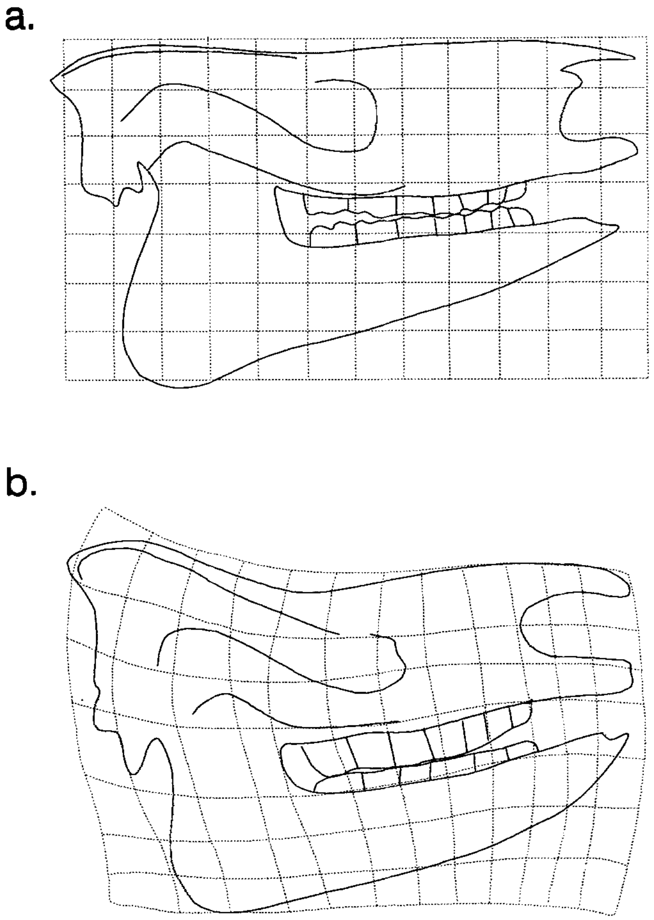

Fig. 2. Cartesian transformation of *Hyrachyus* to *Aceratherium* after Thompson (1917, p. 761). (a) *Hyrachyus* with superimposed, arbitrary rectangular (orthogonal) reference grid. (b) *Aceratherium* with grid lines deformed so as to pass across homologous points or areas, relative to *Hyrachyus*.

Aceratherium, a Miocene rhinocerotid. Thompson concluded that the shape changes observed (an anterior-posterior "double curvature" and a dorsal-ventral "expansion") would produce the skull of an existing rhinoceros when extrapolated.

In a more advanced analysis, Colbert (1935, p. 190) used the Cartesian approach to demonstrate the intermediate position of *Gaindatherium* between *Subhyracodon* and *Rhinoceros*. He concluded that *Rhinoceros* is an extrapolation ("exaggerated accentuation") of *Gaindatherium* and is characterized by greater depth relative to length. *Dicerorhinus* was also included for comparison: Colbert pointed out that this skull has cheek teeth more forward in position and lacks a "strong forward inclination of the occiput." Colbert's transformation from *Subhyracodon* to *Rhinoceros* (Fig. 5) is discussed further below in comparison with computed results.

Neither Thompson nor Colbert analyzed their transformations in detail or discussed any functional consequences of the shape changes. The classical method used by both (here called Thompsonian transformation, TT) involves manual construction of a reference grid of orthogonal lines over the primitive (untransformed) shape. Corresponding lines, curved as needed, are then drawn on the evolved (transformed) shape such that they pass across comparable areas or through homologous points (landmarks). The overall effect is that of a deformation of the reference grid. The shape differences between primitive and derived taxa represent evolutionary changes in position and proportion of homologous structures. These structural changes in most cases will be accompanied by changes in the relative positions of landmarks. The shifts in landmark positions therefore contain information about the transformation. Recent advances in landmark morphometric methods have resulted in the Thin-plate Splines program (TPS), a computer implementation of the Cartesian method, but based on coordinate data for landmarks (Bookstein, 1989, 1990, 1992; Rohlf and Bookstein, 1990). Currently, the only available software for this procedure is that written by Rohlf (1990b). He continues to improve and expand his programs, including the addition of Windows versions, which are available through SUNY Stoneybrook WEB sites (http://life.bio.sunysb.edu).

The purpose of this study is to (1) generate landmark-based Cartesian transformation grids for the skulls of each of the extant rhinoceros genera in the context of their evolution from *Subhyracodon*, and (2) to biologically interpret the evolved shape differences in terms of skull functions.

MATERIALS AND METHODS

Thin-plate Splines

The method of Thin-plate Splines (TPS) was used to generate Cartesian transformation grids on a DOS 386 IBM PS2 microcomputer. The TPS method (Fig. 3a) uses x, y coordinate pair data derived from homologous landmarks on two different specimens (shapes). Each shape is represented by a matrix of x, y values listed in the same order. The order of operations on the data is as follows. First, TPS mathematically translates, rotates, and isometrically scales the "shapes" (datasets) to obtain the closest fit of the landmarks prior to deformation. This is a procrustes approach using a least squares criterion. Second, it analytically determines the deformations (in the form of interpolation functions) required to directly superimpose homologous landmarks from one shape on to the other. Last, the analytical functions are used to construct a grid representing the deformation(s). This deformation grid is the Cartesian transformation grid. An orthogonal reference grid, fundamental to the classical method, is not required. For more detailed analyses, TPS can factor the transformation grid into one affine and multiple nonaffine components. In relation to theoretically possible types of transformation (Fig. 3b), the affine component (as implemented by TPS) is a uniform global transformation. It is a special case in which all initially parallel lines remain parallel after transformation. The nonaffine components are generally local and nonuniform. It should be noted that, in terms of evolution, transformation grids represent net change between the primitive and derived forms. They do not necessarily provide information about the intervening pathway of change.

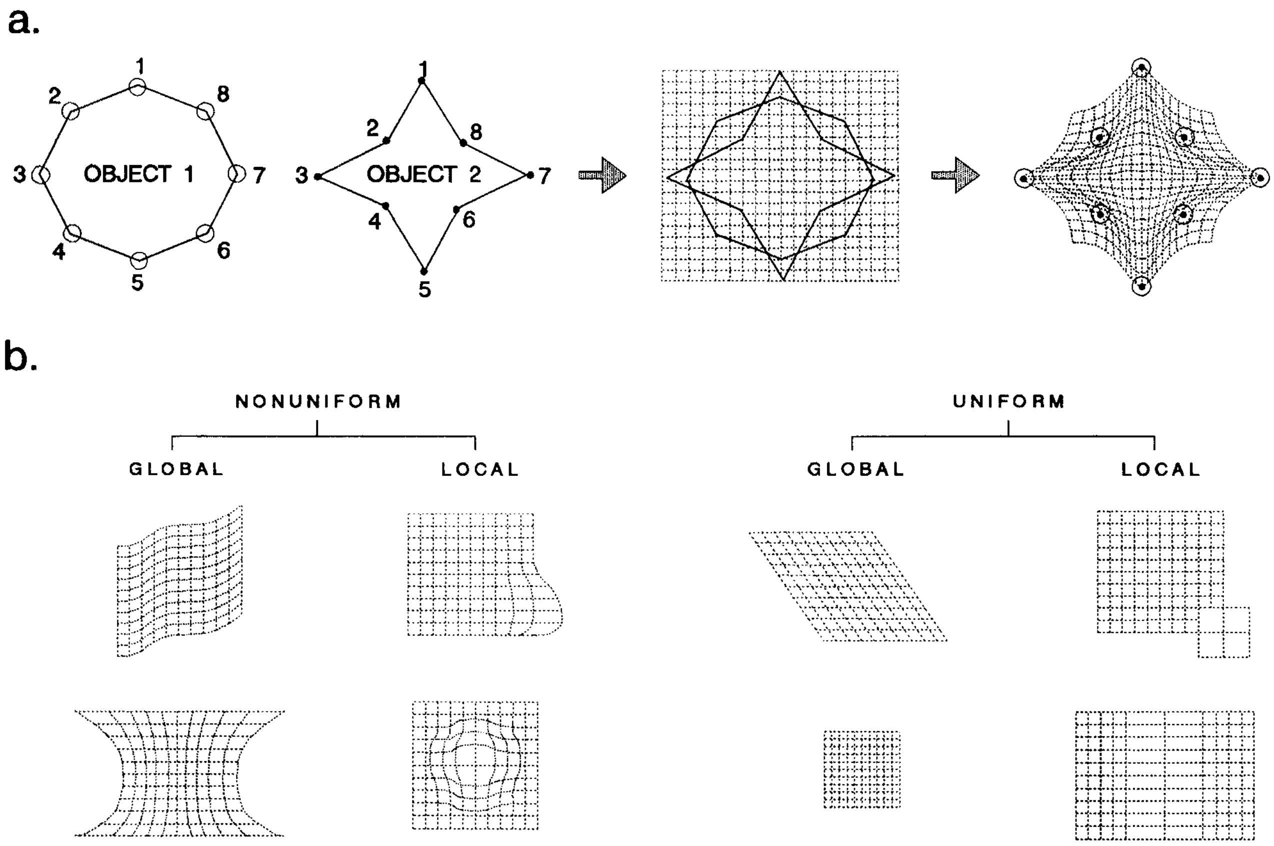

Fig. 3. Thin-plate Splines method and a classification of transformation types. (a) Nonbiological example of the Thin-plate Splines method where object 1 is transformed to object 2. (left) Homologous landmarks and coordinate data are determined for pairs of two-dimensional objects. (middle) Landmark sets are approximated by translation, rotation, and isometric scaling (as needed) to produce the best undeformed fit. Background is a hypothetical reference grid of squares. (right) Homologous landmarks are superimposed (mapped) one-to-one by calculating the necessary deformation(s). Background grid represents the deformation as applied to the reference grid. (b) A simple classification of "pure" transformation types. (left) Nonuniform transformations are those in which different reference squares are deformed in different ways. (right) Uniform transformations are those in which different reference squares are deformed similarly. In global transformations, all squares are deformed; in local transformations, only some squares are deformed.

Rhinoceros Landmarks

The primary data consist of line drawings of *Subhyracodon* (*S. occidentalis*) and each of the extant genera (see Figs. 5–7). Outline drawings of the five genera were derived from two sources. Drawings of *Subhyracodon*, *Dicerorhinus*, and *Rhinoceros* (*R. unicornis*) were adapted from Simpson *et al.* (1960), who reproduced Colbert's (1935) figures. These outlines were used to maximize comparability between Colbert's TT grid and the TPS grid. The drawings for *Diceros* and *Ceratotherium* were made by projection of photographs of representative specimens taken by the author. The visual perspective for comparison throughout is a lateral view with posterior on the left. Twenty-one landmarks were defined to capture shape information from the line drawings (Table I and Fig. 4). Thirteen landmarks may be considered "true" landmarks in that they are defined directly by morphological features. Eight landmarks are constructed by reference to the morphological landmarks. The constructed landmarks occur on the margin of the skull and are necessary to characterize shape details along a continuous curvilinear feature. Twelve of the 21 landmarks are peripheral and capture overall shape while nine landmarks capture internal detail, especially in the region of the tooth rows. Because the cheek teeth have not significantly changed and they define five of the internal landmarks, their influence may be weighted in determining the final transformation. That is, they may function as an area of "anchoring" in terms of the initial relative positions of the remaining landmarks before deformation.

Table I. Definitions of Landmarks Used for Thin-plate Spline Analysis of Rhinoceros Skull Outlines[a]

Morphological landmarks
1. Anteriormost point on the nasal bone (nasal tips).
2. Posteriormost point on the margin of the occipital crest.
3. Posteriormost point on the occipital condyle.
4. Superiormost point on the upper margin of the zygomatic arch.
5. Anteriormost point on the margin of the orbit.
6. Posteriormost point on the margin of the nasal notch.
7. Anteriormost point on the premaxilla.
8. Anterior margin of the second upper premolar at the alveolus.
9. Anterior margin of the first upper molar at the alveolus.
10. Posterior margin of the third upper molar at the alveolus.
11. Posterior margin of the third lower molar at the alevolus.
12. Anterior margin of the first lower molar at the alveolus.
13. Anteriormost point on the inferior margin of the mandible.

Constructed landmarks
14. Inferior margin of the nasals on the perpendicular bisector of 1 and 6.
15. Superior margin of the nasals on the vertical line through 14.
16. Posterior margin of mandible in the occlusal plane of the tooth row.
17. Inferior margin of mandible on vertical line midway between 10 and 16.
18. Margin of the mandible on the perpendicular bisector of 16 and 17.
19. Inferior margin of the mandible on the vertical line through 12.
20. Dorsal margin of the skull on the vertical line above 9.
21. Dorsal margin of the skull on the vertical line above 10.

[a] Morphological landmarks are defined by specific morphological loci. Constructed landmarks are defined by reference to morphological landmarks.

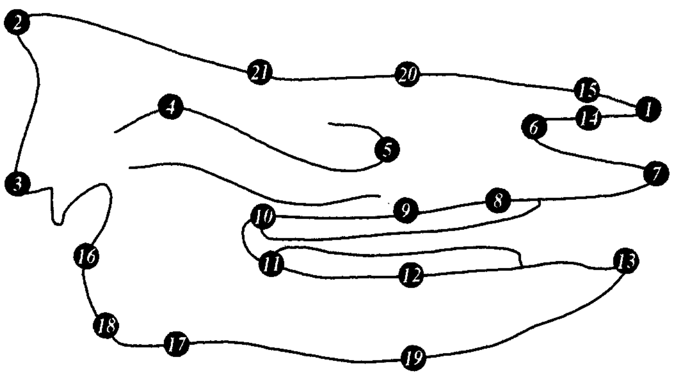

Fig. 4. Positions of landmarks used for Thin-plate Spline analysis. Landmarks are defined in Table I and shown on the outline of *Subhyracodon*.

Landmark coordinates were obtained from a Summagraphics Summasketch III tablet using DS-Digit software (Slice, 1990). Grids were generated by TPS and captured from the screen by Pizzaz Plus (1990). Pizzaz output was digitized into Freelance Graphics (Lotus, 1993) to produce the figures.

RESULTS

TT (Manual) and TPS (Computed) Grids

A comparison of Colbert's (1935) transformation from *Subhyracodon* to *Rhinoceros* with that of the TPS transformation is shown in Fig. 5. Features of the shape change shown by Colbert's grid (Fig. 5a, bottom) include (1) forward displacement of the occiput, (2) elevation of the nasal region, (3) relative broadening of the skull posteriorly, (4) shortening of the area between the orbit and nasal notch, and (5) a relative deepening of the skull overall (brachycephaly). The first two of these changes taken together produce a slight dorsal saddling effect in the grid. Generally, the grid seems to adequately reflect the major differences observed when the two skulls are inspected, especially the broadness of the posterior aspect of *Rhinoceros* relative to the anterior facial region. The TPS grid (Fig. 5b, bottom), representing the total deformation, shows both similarities and differences with Colbert's grid. Forward displacement of the occiput is well shown and is visually enhanced by the "compression" of the vertical lines through that region (as if the bone was squeezed to accommodate the displacement). Elevation of the nasal region is also indicated but in a somewhat different way such that the entire section of the grid is moved up and forward. Saddling is more evident within the grid than along the upper margin. Shortening of the distance between the orbit and nasal notch is also indicated by the smaller distances between vertical grid lines, and there seems to be a general counterclockwise rotation in this region. The TPS grid does not adequately reflect the posterior broadening or the overall relative deepening of the skull. Where Colbert (1935) shows dorsoventrally-elongated grid cells in the region of the angle of the mandible, the TPS shows paradoxically flattened grid cells. This might be explained by the

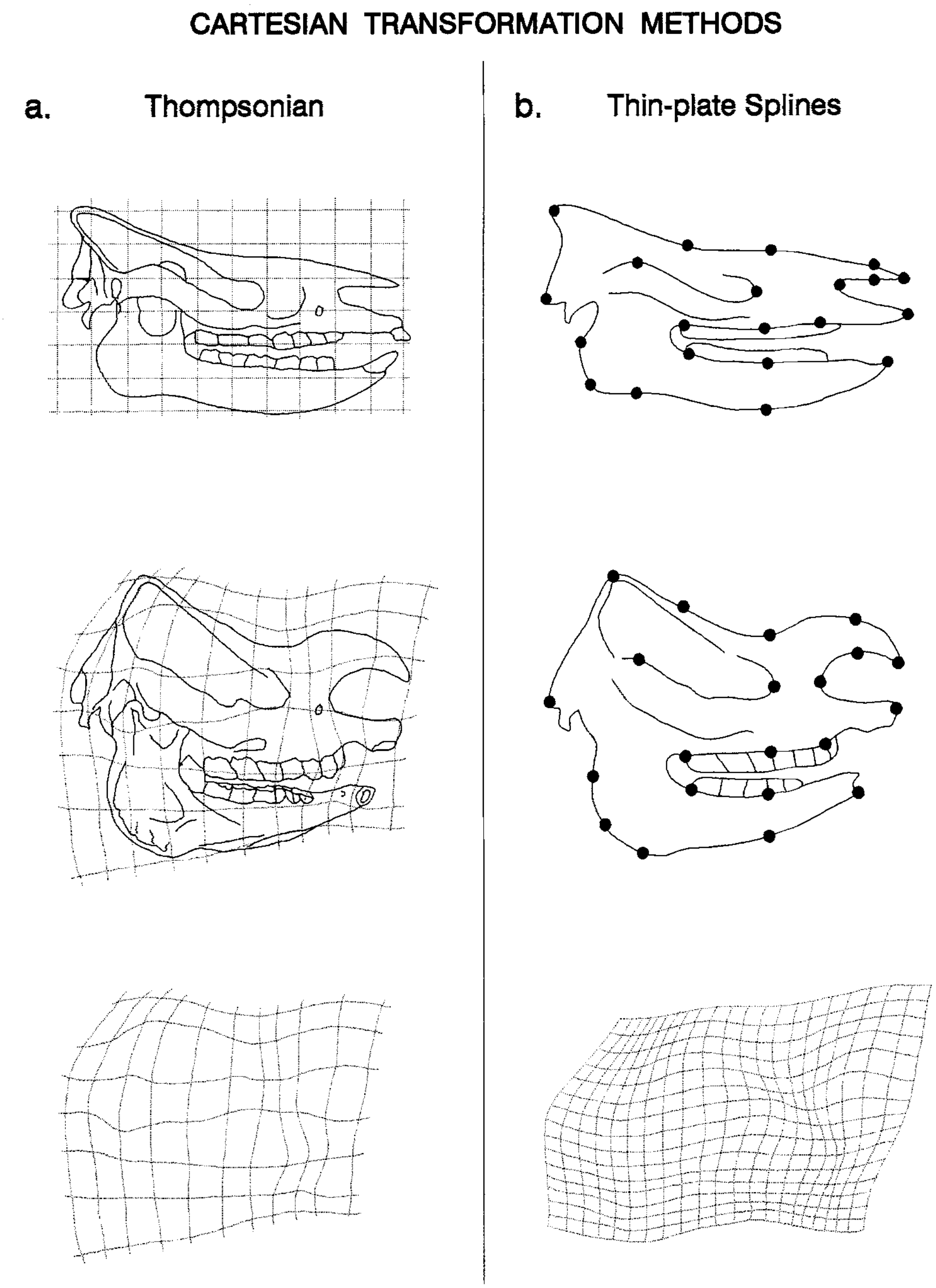

Fig. 5. Comparison of manual (Thompsonian) and computed (Thin-plate Splines) methods for the Cartesian transformation of *Subhyracodon* to *Rhinoceros*. (a) Replication of analysis by Colbert (1935). (top) Reference grid of squares is drawn over primitive specimen. (middle) Corresponding lines are drawn over derived specimen such that line-specimen relationships are maintained. (bottom) Resultant grid represents deformation of primitive to derived shape. (b) Comparable sets of landmarks are determined on primitive (top, *Subhyracodon*) and derived (middle, *Rhinoceros*) specimens. (bottom) Resultant grid represents the deformation necessary for a one-to-one superimposition of homologous landmarks (this result is the same as in Fig. 7b).

particular distribution of landmarks across the shape as well as the way landmarks are initially fit before superimposition. Undoubtedly, these factors influence the nature of the resulting local deformations which may turn out to be counterintuitive in some cases. Thus, deepening of the skull, as observed in Colbert's grid, is not evident in the TPS grid, although some of the cells in the occipital region (upper left) are vertically elongated. These observations emphasize potential limitations of TPS results and the care which must be used in their interpretation.

The affine and non-affine components of the transformation of *Subhyracodon* to *Rhinoceros* were investigated. Because of the scale of this study (whole skull) and the various limitations on landmarks, the nonaffine deformations were not found to be individually useful and are not reported. These may be of interest in more localized studies of individual bones or small regions, as in Swiderski (1993). The global uniform affine component (Fig. 6) is particularly interesting because it accounts for most of the transformation from dolichocephaly (long shallow skull of *Subhyracodon*) to brachycephaly (short, deep skull of *Rhinoceros*). However, it is only a suggestion of the elegant global transformations of fish demonstrated by Thompson (1917). The relationship between shape change, as observed in such global geometries, and the evolution of developmental programs remains to be determined.

TPS Transformations—Extant Genera

Figure 7 shows the skull outlines of the four extant genera to which *Subhyracodon* was transformed using the landmarks discussed above. The transformation results for each will be discussed in approximate phylogenetic order (top to bottom).

Dicerorhinus (Figure 7a) is the most plesiomorphous living rhinoceros and this is

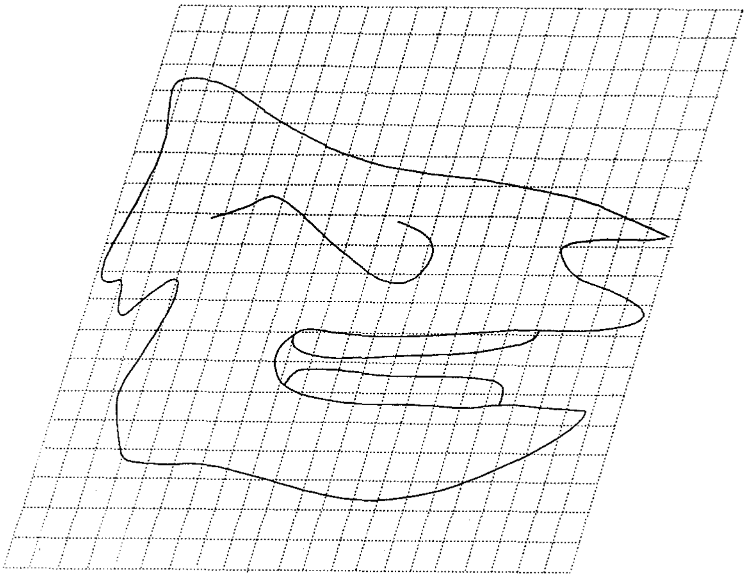

Fig. 6. Affine (global uniform) component of TPS factoring of *Subhydracodon* to *Rhinoceros* transformation. Outline represents deformed *Subhyracodon*.

reflected in its skull shape and transformation grid. In overall shape, it is the most dolichocephalic of the living forms and thus is most like *Subhyracodon* (see Fig. 4). TPS emphasizes small changes: (1) some shortening of the orbitonasal distance, (2) some expansion of the nasals, and (3) a small amount of forward occipital rotation. The first two effects are seen in all of the extant forms. Expansion of the nasal region is correlated with the evolution of keratinous epidermal horns (*Subhyracodon* was hornless) and does not appear to have any other obvious functional significance.

Rhinoceros (Fig. 7b) represents a derived phylogenetic endpoint in terms of skull shape but is closely related to *Dicerorhinus* (closer than to the African taxa). The details of the TPS transformation to *Rhinoceros* are discussed in the preceding section where it is compared to Colbert's TT grid.

Diceros (Fig. 7c) appears to be the less derived of the two African genera from a morphological view, but it is nevertheless distinct from *Subyracodon.* Several aspects of its skull shape stand out in the TPS transformation. Expansion and elevation of the nasal region ''pushes'' the grid significantly upward such that the upper right corner of the grid is much higher than the upper left corner. This effect is contrary to the actual skull where the occiput remains higher than the nasals. However, by doing this, the grid emphasizes where significant change has occurred between the two forms. Another anterior feature shown is the reduction of the dentition associated with the premaxilla, producing lines which have become compressed together in that region. The occipital region of *Diceros* is little changed over *Subhyracodon*, with the tip of the occiput and the occipital condyle approximately in line vertically in both. What is emphasized posteriorly occurs in the region of the mandibular angle of *Diceros*. The rightward curvature of the vertical grid lines in the lower left corner suggests that the mandibular angle has shifted anteriorly, been reduced, or otherwise changed shape. Because the body of the mandible does not appear to be shifted, a relative reduction or shape change is indicated. Inspection of the mandibular angle in *Subhyracodon* shows it to be more squared while in *Diceros* it is more rounded. The grid therefore emphasizes this shape difference which may or may not represent a change in relative area. The mandible of *Diceros*, like that of *Rhinoceros* is deeper relative to its length than is that of *Subhyracodon*, but this is not reflected by TPS.

Ceratotherium (Fig. 7d) is similar to the other extant genera with respect to nasal enlargement, and similar to *Diceros* with respect to reduction of the anterior dentition. Two features of this transformation stand out from the others. The distortion of the grid lines near the upper middle of the grid shows the backward and upward shifting of the orbit relative to the tooth row (only slight in the other taxa). Most importantly is the posterior displacement of the occiput relative to the occipital condyle. As seen in the grid, the upper left corner is to the left of the lower left corner, an effect distinctly different from the other grids. The relatively small area of the mandibular angle (compare outline with *Rhinoceros*) is somewhat obscured by the displacement of the occiput, but it can be seen in the grid as a moderate compression of the vertical lines.

In summary, the TPS approach to Cartesian transformation emphasizes the following net changes between *Subhyracodon* and one or more of the extant genera: (1) enlargement and elevation of the nasal region, (2) changes in orbitonasal length and orbital position, (3) relative orientation of the occiput (forward in *Rhinoceros*, backward in *Ceratotherium*), and (4) shape and position of the mandibular angle (relative enlarge-

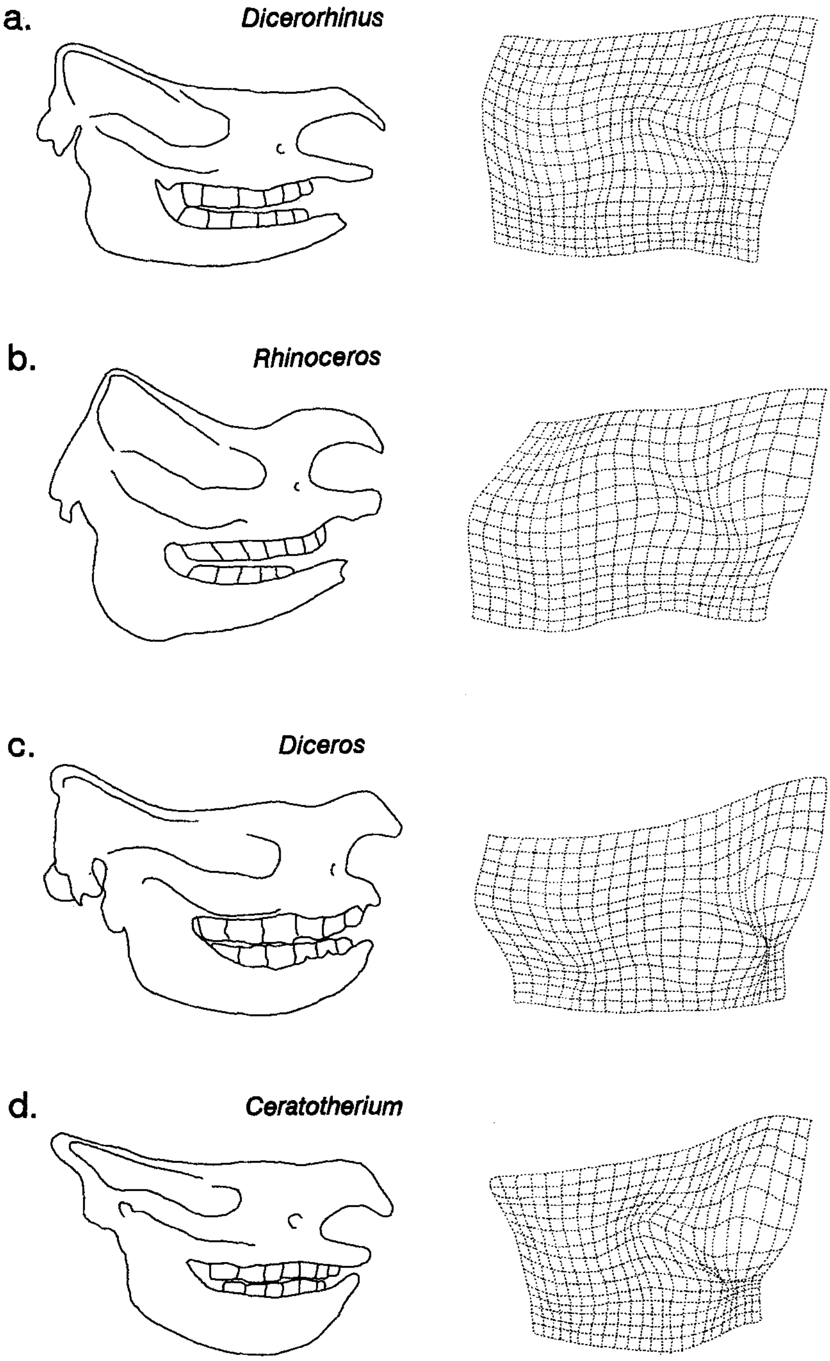

Fig. 7. Thin-plate Spline transformations from *Subhyracodon* to each of the extant rhinoceros genera. Specimen outlines (left, landmarks not shown) and corresponding deformation grids (right). (a) *Dicerorhinus*, (b) *Rhinoceros* (same transformation as in Fig. 5b, bottom), (c) *Diceros*, (d) *Ceratotherium*.

ment in *Rhinoceros* and reduction in *Ceratotherium*). TPS did not emphasize relative differences along the dolichocephaly-brachycephaly spectrum or the actual shapes of the skulls. These results suggest that TPS should be viewed as supplementary and/or complimentary to the classic (visual) method.

Functional Interpretations

The rhinoceros skull, like all skulls, is a complex composite whose structure is determined by multifactorial influences. Natural selection sorts out the relative contributions of these influences to the functioning whole. Because most structures are multifunctional, they will tend to represent compromises between competing functions and mechanical requirements. Determining these intercorrelations among structures, functions, and mechanics is one of the goals of functional and comparative evolutionary morphology. Here, it is hypothesized that the differences in occipital orientation and mandibular angle size described above may be influenced, in addition to other factors, by the need to support a large mandible against gravity.

Figure 8 shows comparisons of *Rhinoceros* and *Ceratotherium* with *Subhyracodon* relative to common reference frames. It is clear in Fig. 8a that the posterior portion of the temporalis muscle in *Ceratotherium* has a greater posterior pull on the coronoid process, while in *Rhinoceros* it has a greater vertical pull. From this perspective, the differences would be attributable to differences in masticatory function (mandibular motion and occlusal forces), for example, in providing differential proportions of elevation versus retraction relative to the skull itself. Similarly, the differences of the mandibular angles would most likely reflect qualitative and/or quantitative differences in masseter function during mastication. Figure 8b shows another potential effect of the two extremes in occiput position. All other things being equal, *Rhinoceros* can extend its head further. This correlates well with its habit of feeding on tall grasses (see below). *Ceratotherium*, on the other hand, is a grazer of low grasses and does not utilize head extension during feeding. Although these interpretations are reasonable given a common reference frame, it is of further interest to examine the role of functionally important head positions, especially with respect to gravity, on the skull shape differences.

The living rhinoceroses are megafauna and their mandibles accordingly contribute a substantial amount of weight to the skull. Because the mandible is a separate element suspended below the craniofacial skull, at least some aspects of its associated musculoskeletal morphology may reflect a weight bearing function. Further, the predominating position of the head will influence the details of the gravitational and countergravitational forces acting on the mandible. As large herbivores, rhinoceroses spend much of their daily activity schedule in foraging (Owen-Smith, 1988). Thus, forces acting on and within the skull while in the feeding position can be expected to be influential on skull shape. *Subhyracodon*, probably a browser, was small by comparison (Great Dane-sized) and the weight of its scaled-down mandible would be much less of a factor in the function of attached muscles. The evolution of large size in *Diceros* and *Ceratotherium* would require some adjustment to compensate for the scaling of mandibular weight.

Kurten (1968) briefly discussed head positions in *Diceros*, *Ceratotherium*, and *Rhinoceros* in the context of inferring feeding habits for Pleistocene fossil rhinos. He explicitly correlated forward occipital position with head held up (*Rhinoceros*) but did not

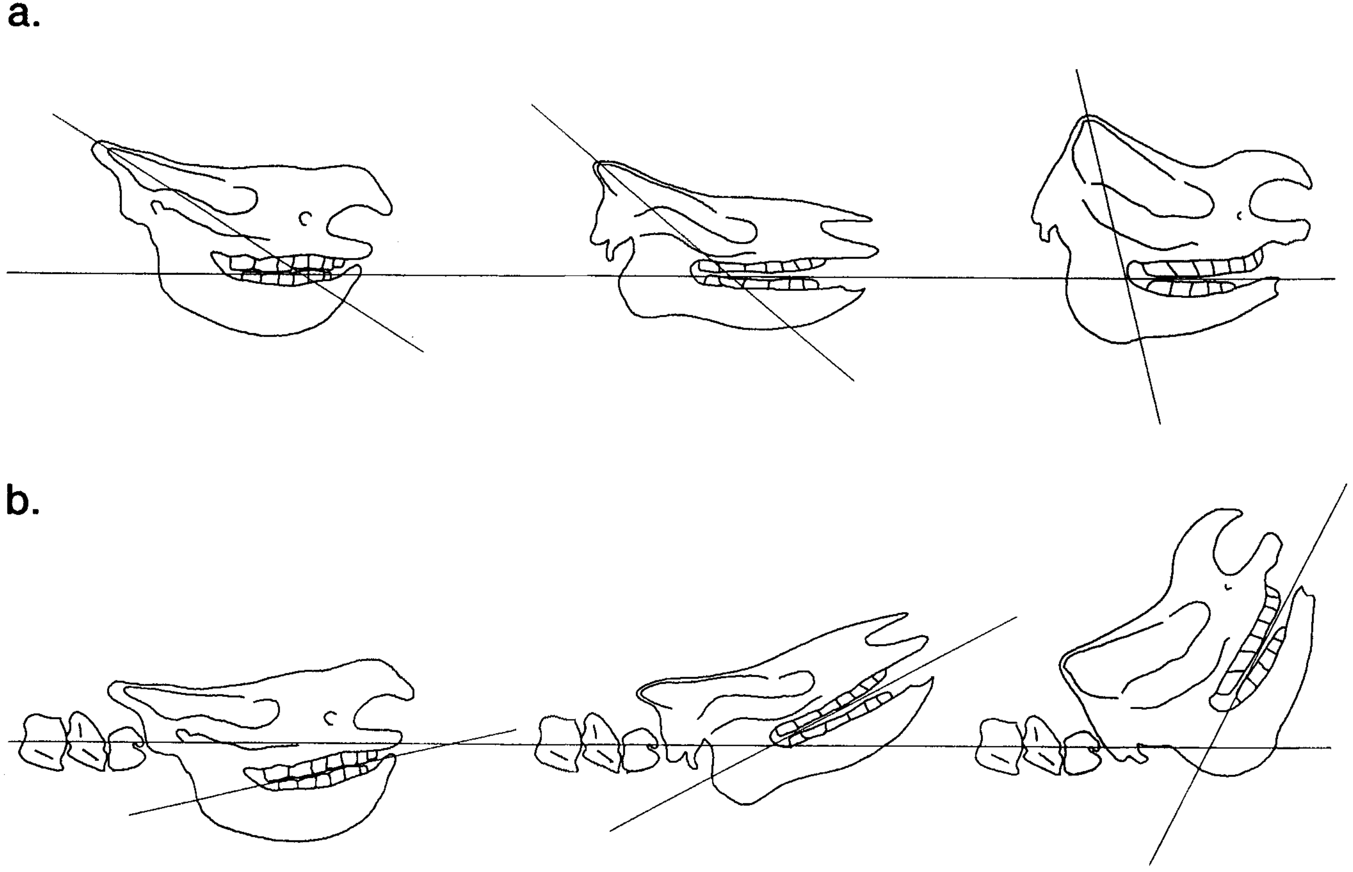

Fig. 8. Some functional consequences of occipital orientation among rhinoceroses. (a) Comparison of orientation of posterior temporalis muscle fibers relative to horizontal tooth rows in *Ceratotherium* (left), *Subhyracodon* (middle), and *Diceros* (right). (b) Comparison of head extension relative to a horizontally-fixed cervical vertebrae in *Ceratotherium* (left), *Subhyracodon* (middle), and *Diceros* (right).

correlate head held down (*Ceratotherium*) or head held level (*Diceros*) with occipital positions. In a section headed "general trends," Heissig (1989) stated that occipital plate orientation deviates in both directions from a right angle, and that the deviations reflect normal skull position which in turn is dependent on feeding position. Figure 9 shows an analysis of posterior temporalis and masseter muscle orientation relative to head position and gravity in *Ceratotherium* and *Rhinoceros*. The head position of *Ceratotherium* (Fig. 9a, top) is shown in a lowered position as would be expected during grazing on short grass. Owen-Smith (1988) reported white rhino dietary grass height averaging 200 mm or less over the year. As shown, the head could be held higher or lower and thus represents an arbitrary, but reasonable, choice. Decomposition of the muscle force vectors (Fig. 9, bottom) into their rectangular components shows the relative pull of each muscle against gravity. In the lowered position of *Ceratotherium*, the posterior portion of the temporalis (PT_C) has a large vertical (antigravity) component while the masseter (M_C) has a small vertical component. In contrast, the head position of *Rhinoceros* (Fig. 8, top) is shown in a raised position, as would be expected during feeding on tall grasses. The predominant year-round dietary vegetation of Indian rhinos consists of tall cane-like grasses (Laurie, 1982; Owen-Smith, 1988). Again, the position shown is arbitrary but within the range of expected positions during feeding. For *Rhinoceros* (Fig. 9b, bottom), the force components of the posterior part of the temporalis (PT_R) are approximately equal, while the pull of the masseter (M_R) is entirely vertical.

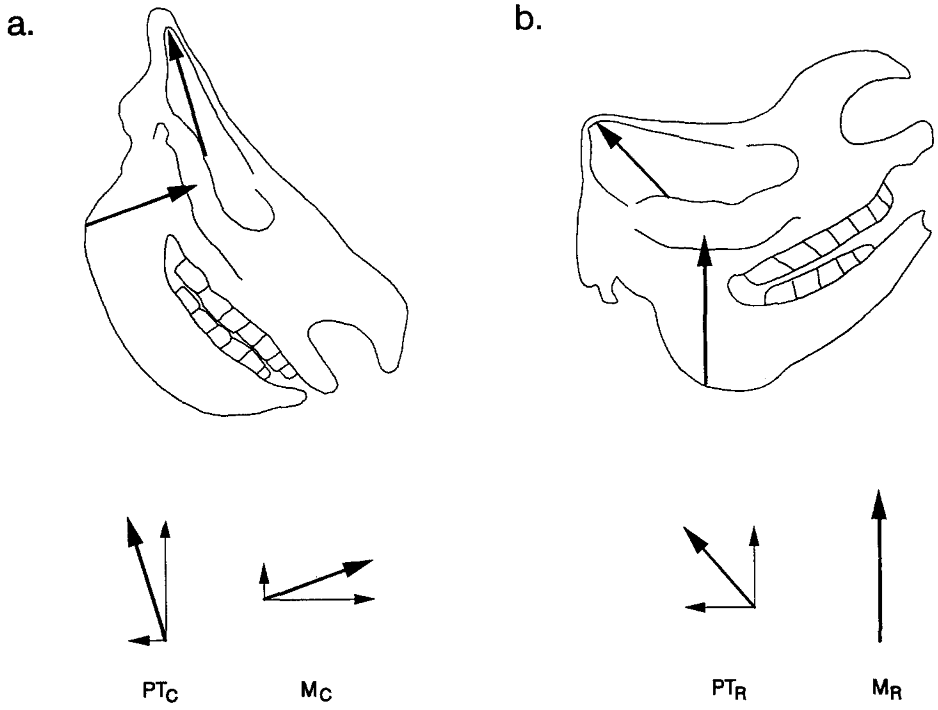

Fig. 9. Masticatory muscle orientations (lines of action) relative to feeding positions of the two extreme skull shapes. (a) *Ceratotherium* and (b) *Rhinoceros*. Thick arrows: posterior temporalis (PT) and masseter (M) muscle orientations. Thin arrows: perpendicular force components for *Ceratotherum* (PT_C; M_C) and *Rhinoceros* (PT_R; M_R) muscles.

The occipital and mandibular angle differences between the two derived taxa *Ceratotherium* and *Rhinoceros* may be partially explained by the force components of the two masticatory muscles discussed. In *Ceratotherium*, the masseter does little work supporting the mandible against gravity (in a still lower position, the masseter would provide even less and the posterior temporalis fibers would provide more support). The masseter's size, therefore, should be correlated mostly with swinging the mass of the mandible forward and providing bite force. The *Rhinoceros* masseter, in addition to overcoming masseter inertia and providing bite force, must provide extra force to counteract gravity. Thus, the relatively larger mandibular angle of *Rhinoceros* may reflect a larger masseter required to provide the extra force during feeding (by analogy, it requires more force to lift a refrigerator than to push one). The posterior temporalis fibers, acting on the same bony element, should be expected to correlate with the masseters to some degree, if support is a significant function. The vertical component of PT_C, for example, appears to compensate for a lack of that component in M_C. It may be hypothesized that occipital position in *Ceratotherium* (i.e., backwardly-rotated relative to the ancestral condition) is at least partly explained by the need for this compensation in the lowered feeding position. Of course, relative to the skull itself, it is providing a retractive force on the mandible. It must also be remembered that anterior fibers of the temporalis play a role but are not associated here with observed morphological differences. The PT_R has less of its pull directed vertically but is still significantly synergistic against gravity with M_R (anterior temporalis fibers, not shown, must also be pulling against gravity). The horizontal component of PT_R is providing retraction. These observations suggest that the forward rotation of the occiput in *Rhinoceros* has helped maintain a vertical component to the action of posterior temporalis fibers in a raised feeding position.

In summary, evolved shape differences in the posterior skull regions of the two most divergent extant rhinoceroses are consistent with a role for the masticatory muscles in supporting large mandibles in the two different feeding positions.

DISCUSSION

The evolution of large size in terrestrial vertebrates is accompanied by musculoskeletal changes which can be correlated with mechanical needs. For example, the limbs of large animals generally have greater relative diameter and decreased joint angulation (graviportal limbs) than smaller animals (Alexander, 1985). Mechanically, the linear limb elements become progressively dominated by the need for columnar support of a volumetric mass (presumably in a grossly compressive environment). Within a skull, it is predictable that increasing mandible mass would proportionately increase the need for suspensory support (presumably, in a grossly tensional environment). The increasing need for suspension would require compromises with other functions of the masseter and temporalis (Smith, 1993). The results of two-dimensional shape analysis in this paper, correlated with direction of muscle pull and corresponding bony features, suggest that mandible suspension has evolved as an important function in the large extant rhinoceros skulls. Further, the function is tracked in two divergent genera with different feeding postures. Thus, the rhinoceroses may be an example where a relatively simple mechanical requirement has had a strong influence on skull shape, and can be relatively simply correlated with feeding behavior. It is interesting to speculate how the muscle fiber types and motor units might be apportioned, because the support must be a continuous function of the muscles in contrast to intermittant, heterogeneous chewing functions (Herring *et al.*, 1979).

In the light of current research interest and advances in the evolution and development of the vertebrate skull (see Hanken and Hall, 1993a,b), and the predominance of cladistic character analysis in systematics and phylogeny reconstruction (Maddison, 1994; Padian *et al.*, 1994), it is useful to briefly discuss the present results in those two contexts.

With respect to rhinoceros skull ontogenetic evolution, some fundamental questions include: when do the generic or specific shape differences appear; what are the proportions of genetic versus epigenetic factors on shape; what are the epigenetic factors (e.g., what is the tensional/compressional "history" of the skull); and how does behavioral ontogeny correlate with morphological ontogeny? In terms of postnatal epigenetic mechanical effects, the suckling offspring of both species probably have approximately the same head orientation at least some of the time. It is especially important to determine the relationship between the time course of weaning to vegetation and differences in skull shape during this period when they begin to behaviorally diverge and the skull and mandible become more massive. Unfortunately, descriptive and experimental rhinoceros embryology is nonexistent. Some inferences can be made based on the craniological literature (Emerson and Bramble, 1993; Herring, 1993; Russell and Thomason, 1993; Smith, 1993).

First, occiput orientation (shape) does not seem to have been developmentally or evolutionarily constrained. Rather, orientation evolved in opposite directions according to functional-mechanical needs. This would not be the case, for example, if brain growth/evolution were significantly controlling occiput shape (a study of rhinoceros endocranial volume and shape would be interesting). Next, it is reasonable to assume that at least some of the occiput shape and mandible angle size are regulated by proximate effects of associated muscles (Herring, 1993). Groves (1982) noted examples of plastic deformation in the skulls of captive rhinos, usually feeding under unnatural conditions. Finally, because the occiput serves multiple functions (e.g., for nuchal and temporal musculature attachments and for brain encasement), it must represent a compromise between multiple functional matrices (Moss, 1968). In the view of Moss, a functional matrix evolves and the skeleton responds. For this example, evolution of different behavioral orientations changes muscle needs which in turn provides the environment (matrix) within which the occiput "responds." Interestingly, the forward inclination of the occiput in *Rhinoceros* seems to be an example of synergism among functional matrices, because it allows greater head extension ("nuchal matrix") as well as support ("mandible matrix") at the same time.

With respect to systematics and phylogeny reconstruction, it may be asked: to what extent have the occipital and mandibular angle differences between *Rhinoceros* and *Ceratotherium* been correlated with, or used as, taxonomic characters (especially in more recent cladistic analyses)? Skull shape is clearly an important aspect of what these two divergent species are and what they do. And clearly, the occipital differences are derived characteristics (autapomorphies) distinguishing the two genera from *Subhyracodon* and from each other. However, it might be argued that any rhino lineage achieving large size and feeding in the same way might convergently have similar features. The black rhino (*Diceros*), for example, is known to be a closer relative of *Ceratotherium* (Prothero *et al.*, 1986; Morales and Melnick, 1994), yet its occipital orientation is intermediate to slightly-rotated forward, consistent with its characterization as a ''horizontal'' browser (Kurten, 1968). It is well known that gross features resulting from mechanical causes, such as graviportality or fusiform shape, are not necessarily useful for determining monophyly because of convergences. The relationship between cladistics and morphometrics has only recently begun to be investigated as a result of the maturing of the former and the advances of the latter (e.g., Warheit, 1992; David and Laurin, 1996).

Differences of mandibular angle among rhinoceros taxa have not been important systematically. Differences of occipital shape (position) have been cited historically, but not universally. Cuvier (1834) was probably the first to note occipital differences (implied in Flower, 1876). Flower cited occipital crest position as a feature separating the Indian and Javan rhinos (*Rhinoceros*) from the Sumatran rhino (*Dicerorhinus*). Osborn (1903) mentioned the ''high forward-sloping occiput'' in *Rhinoceros* but not the opposite condition in *Ceratotherium*. Pocock (1945) discussed the forward inclination of the occiput in *Rhinoceros* as a well known difference separating it from *Didermocerus* [*Dicerorhinus*]. Meester and Setzer (1971) relied heavily on the backward position of the occiput as a feature distinguishing *Ceratotherium* from *Diceros*. In an analysis of the interrelationships of the living genera, Groves (1983) used occipital crest orientation to differentiate the Asian from African rhinos. His implication that the occiput slopes backward in *Diceros* is contradicted by the Cartesian results. The most recent and comprehensive character analysis of rhinoceroses is that of Prothero *et al.* (1986) which provides a phylogeny based on shared derived characters. Neither occipital nor mandibular angle features are cited as characters distinguishing the black and white rhinos (subtribe Dicerotina) from each other, or distinguishing them from *Rhinoceros* (subtribe Rhinocerotina). Each subtribe contains a less derived member (*Diceros* and *Dicerorhinus*, respectively). Thus, the shape differences have occurred relatively recently, and entirely within the respective generic lineages. It seems that behavioral-physiological canalization for vegetation preferences in the two lineages determined which direction skull shape would adapt to accommodate a massive mandible in different orientations.

This paper presents a ''postcladistic'' analysis of shape change in two lineages of a mammalian phylogeny with fairly high confidence. Analyses of shape change in such cases should be valuable in understanding the causes and consequences of character evolution within the phylogenies. Further craniological analyses of *Rhinoceros* and *Ceratotherium* may provide an opportunity for some integration of evolution, biomechanics, development, behavior, ecology, systematics, and phylogeny within an ancient mammalian clade. This I hope will stimulate research on the rhinoceroses, and in turn, broaden and deepen interest in conserving these deserving representatives of the Age of Mammals.

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