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COMPARATIVE CRANIOLOGY OF THE CERATOPSIA

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ABSTRACT. The Ceratopsia or horned dinosaurs demonstrate great diversity of skull shape that makes them ideal subjects for morphometric investigation. Skulls of ceratopsians are subjected to landmark-based morphometric analysis using the robust mapping technique, RFTRA (resistant-fit theta-rho analysis). This technique elucidates morphological trends in skull shape in a series of pairwise comparisons. Morphological distance data among taxa from RFTRA comparisons are subjected to cluster analysis. Clusters formed by this technique compare favorably with higher taxa recognized by both classical and cladistic methodologies. Furthermore, deconstruction of the skull by elimination of horns, frill, and the facial region of the skull demonstrates that taxonomic cluster patterns remain substantially stable even when only selected regions of the skull remain intact. The correlation of display characters with functional complexes suggests that no characters of the skull are genuinely trivial. Major morphological trends in the skull involve reorganization of the cheek region, including forward rotation of the ventral end of the quadrate, caudal movement of the jugal, reduction of the quadratojugal, caudoventral expansion of squamosal caudal to the quadrate in centrosaurines, and further expansion of the squamosal at right angle to the previous growth axis in chasmosaurines. Muscles of mastication probably occupied the base of the frill but did not occupy the entire frill, where they would have been subject to injury during intraspecific combat. Ceratopsids may have consumed a woody diet, with small angiospermous trees a probable food source.

INTRODUCTION

The Ceratopsia represent one of the last and most successful evolutionary radiations of dinosaurs. At present some 18 genera and 26 species are recognized (Dodson and Currie, 1990). All except for *Psittacosaurus* are of Late Cretaceous age. Within a span of less than 50 my, these herbivores radiated from small bipedal forms less than 2 m long (Sereno, 1990) to become huge quadrupeds 8 m long with skulls up to 2.5 m long, the largest skulls of any terrestrial vertebrates. Early descriptions of horned dinosaurs based on fragmentary remains (Cope 1872, 1876) provided no insight into the nature of these remarkable animals. Indeed, the name *Monoclonius* (Cope, 1876) does not refer to "single horn" but rather to a tooth character that incorrectly contrasted the former with the hadrosaur *Diclonius* (Cope, 1876; personal communication, B. Creisler, 1991). Only with the description of complete skulls of *Triceratops* (Marsh, 1889) could a concept of horned dinosaurs emerge. Ceratopsid diversity was quickly uncovered, and valuable reviews (Hatcher, Marsh, and Lull, 1907; Lull, 1933) that still form the starting points for research today appeared. By 1951 our understanding of ceratopsid generic diversity was nearly complete (Sternberg, 1951). By contrast, diversity of more primitive ceratopsians in Asia has been uncovered recently (Maryanska and

Osmólska, 1975; Sereno and Chao, 1988; Sereno and others, 1988). Consensus has been reached about major patterns of ceratopsian phylogeny though not on all of its details (Lehman, 1990; Dodson and Currie, 1990).

With a mature data base for ceratopsians, studies progressed from taxonomic to broad paleobiological concerns. Fresh from his seminal studies of hadrosaur cranial anatomy, myology, and functional morphology, and by virtue of his curatorship of one of the great collections of ceratopsid skulls, John Ostrom naturally turned his attention to horned dinosaurs (Ostrom, 1964, 1966). In these papers Ostrom outlined a model for ceratopsid skull mechanics. Expanding on a study of *Protoceratops* by Haas (1955), he posited that the frill served as a framework for hypertrophied jaw adductor muscles, specifically M. adductor mandibulae externus. He drew attention to the mechanical significance of the elevated coronoid process, depressed mandibular articulation, and distally enlongated toothrow. He concluded that ceratopsids were capable of generating powerful occlusal forces characterized almost exclusively by shear. His characterization of ceratopsian mastication has both achieved acceptance (Weishampel and Norman, 1989) and has stimulated further work on ornithischian functional craniology (Weishampel, 1984; Norman and Weishampel, 1985).

Ceratopsians are an excellent group for morphometric analysis. They form an undoubtedly monophyletic assemblage (Sereno, 1986; Dodson and Currie, 1990; Forster, 1990), relatively restricted in both time and space. They are rich in taxonomic and morphological diversity and have one of the finest fossil records of any group of dinosaurs, with many complete skulls known (three ceratopsians, *Psittacosaurus, Protoceratops,* and *Triceratops* are among the ten most abundant dinosaurs—Dodson, 1990a). The goal of this study is to explore evolutionary trends in ceratopsian cranial morphology using quantitative methods that will permit functional insights.

The technique chosen for this study is RFTRA, resistant-fit theta-rho analysis (Siegel and Benson 1982; Benson, Chapman, and Siegel, 1982; Chapman, 1990a, b), a robust mapping method of landmark analysis. This is a valuable technique for both quantifying and visualizing transitions of form in a series of organisms. In this method, a series of homologous landmark points on a base specimen is mapped onto a second specimen. An optimal fit is produced by a series of geometry-preserving coordinate transformations that involve translation, rigid rotation, and scaling. For objects in which deformation is uniform, a least squares solution (LSTRA) is satisfactory. An appealing feature of RFTRA is that the use of repeated medians rather than least squares in the calculation of transformation factors produces a sensitivity to the localized deformations that prove to be of interest in evolutionary morphological series of complex objects such as vertebrate skulls. It has not yet enjoyed wide application. Early research applications were to ostracodes (Benson, 1982). Recent applications have been to dinosaurs, especially pachycephalosaurs and protoceratopsids (Chapman, 1990b), hadrosaurs (Chapman and Brett-Surman, 1990), and to salamanders (Reilly, 1990).

A practical aspect is that RFTRA is simple to use. The input is a series of landmark points digitized on a digitizing tablet from two-dimensional images (typically line drawings or photographs) of a series of specimens. The points chosen should represent stable anatomical landmarks that are homologous across a series of specimens. Three-way suture intersections are ideal but not always possible. For purposes of visualization (but not of calculation) specimen outlines may be stored, but this is somewhat costly in terms of data storage. The output is of two types, graphic and numerical. Graphic output is quickly produced on screen, and there is considerable flexibility of manipulation. Paired specimens are compared, represented as landmark points, vectors, outlines, user-constructed polygons, all of these or any subset thereof. It is a simple matter to atomize a whole skull into subunits of interest in order to highlight functional units or to test taxonomic hypotheses. For example, horns may easily be eliminated from analysis in order to test the dependence of taxonomy on possibly trivial characters.

The graphic output emphasizes pairwise comparisons and thus is potentially sensitive to phylogenetic bias in terms of pairs selected. However the numerical output consists of a matrix of distances among all specimens. The distance measure is the average of the squared magnitude of vectors and thus is a measure of the closeness of fit of two specimens. A purely phenetic clustering of the data may be compared with a cladistic analysis of the same taxa as an interesting exercise to determine empirically the information content of the morphological features examined.

ANALYSIS OF THE CERATOPSIA: MORPHOLOGICAL TRANSFORMATIONS

The taxa chosen for this analysis are recorded in table 1. Figures used were taken from the literature. The list includes all ceratopsian genera for which articulated cranial specimens permit reliable reconstruction of cranial sutures. Excluded are *Microceratops, Montanoceratops, Avaceratops, Brachyceratops, Pachyrhinosaurus, Anchiceratops,* and *Torosaurus.* Pachycephalosaurs are the sistergroup of the Ceratopsia, and the two groups form the Marginocephalia, the sistergroup of the Euornithopoda (Sereno, 1986). Although this study is comparative but not cladistic in emphasis, representatives of the two sistergroups were chosen, *Stegoceras* of the Pachycephalosauria and *Hypsilophodon* of the Euornithopoda. Neither represents a strictly satisfactory outgroup in a cladistic sense; no complete skull in the Pachycephalosauria does, and the cladistic position of taxa within the Hypsilophodontidae is not resolved (Sues and Norman, 1990). Nonetheless, *Hypsilophodon* is so well known anatomically (Galton, 1974) that it serves as a useful taxon for structural comparison with ceratopsians (Chapman, 1990b).

The problem of missing data deserves comment. Ceratopsid skulls typically measure between 1.5 and 2.5 m in length. It is not surprising

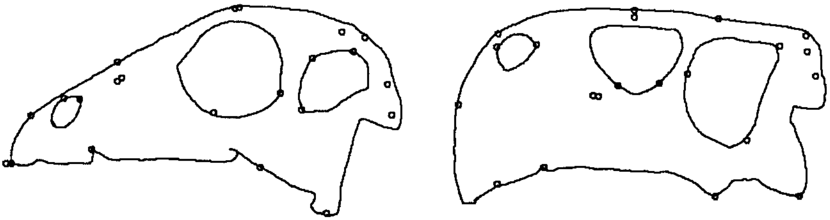
TABLE 1

Selected Taxa for analysis of Ceratopsia

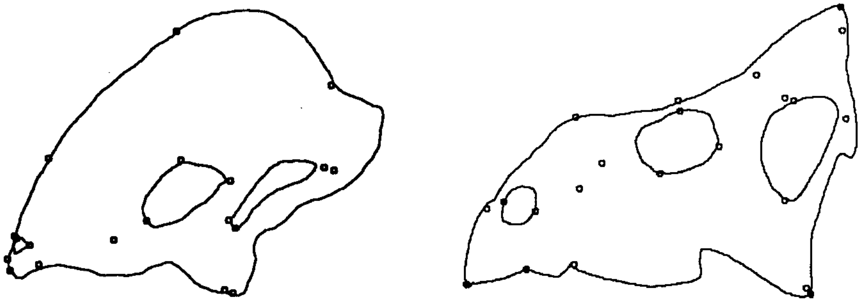
Taxon	Source	Specimen
Ornithopoda		
family Hypsilophodontidae		
1. *Hypsilophodon foxii*	Galton, 1974, fig. 3	BM R2477
Marginocephalia		
Pachycephalosauria		
family Pachycephalosauridae		
2. *Stegoceras validus*	Maryanska and Osmólska, 1974, fig. 1	UA 2
Ceratopsia		
family Psittacosauridae		
3. *Psittacosaurus mongoliensis*	Sereno and others, 1988, fig. 5	AMNH 6254, 6534
family Protoceratopsidae		
4. *Leptoceratops gracilis*	Russell, 1970, fig. 1	NMC 8887, 8889
5. *Bagaceratops rozhdestvenskyi*	Maryanska and Osmólska, 1975, fig. 6c	ZPAL MgD-I/126
6. *Protoceratops andrewsi*	Lull, 1933, fig. 32	AMNH 6408
7. *Protoceratops andrewsi*	Brown and Schlaikjer, 1940, fig. 4D	AMNH 6466
family Ceratopsidae		
subfamily Centrosaurinae		
8. *Centrosaurus apertus*	Lull, 1933, fig. 4	YPM 2015
9. *Centrosaurus apertus*	Lambe, 1915, pl. VI	NMC 348
10. *Styracosaurus albertensis*	Lambe, 1915, pl. VI	NMC 344
subfamily Chasmosaurinae		
11. *Arrhinoceratops brachyops*	Tyson, 1981, fig. 1	ROM 796
12. *Chasmosaurus belli*	Lambe, 1915, pl. VIII	NMC 2280
13. *Chasmosaurus canadensis*	Lull, 1933, fig. 38	AMNH 5401
14. *Pentaceratops sternbergii*	Lull, 1933, fig. 39	AMNH 6325
15. *Triceratops horridus*	Hatcher, Marsh and Lull, 1907, fig. 10	YPM 1821
16. *Triceratops horridus*	Forster, 1990, fig. 1-1	composite

that many of them are imperfectly preserved, particularly in terms of loss of extremities such as horn tips, rostral bone, and portions of the parietal, or in terms of crushing of intact structures. The problem of incomplete data has been approached in two ways. One way is to use multiple specimens of the same taxon where possible (*Protoceratops, Centrosaurus, Chasmosaurus, Triceratops*). The latter three remain together in all analyses, suggesting that vagaries of preservation of individual specimens do not necessarily invalidate the information content of a specimen. The two specimens of *Protoceratops* plot separately in two of three analyses, but this is not surprising in view of the fact that one is a juvenile and the other an adult. The second way to approach the problem is by the technique of cranial deconstruction, as described below, by which horns and face are sequentially removed from the analysis. Again, the substantial stability of the results obtained encourages the conclusion that the results are robust to loss of certain features. An imperfect specimens provides incomparably more information than no specimen at all.

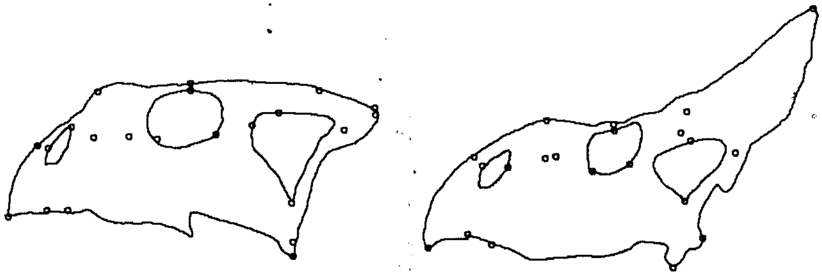
Lateral skull profiles of 12 genera selected from the published literature were digitized (figs. 1 and 2), with 21 landmark points for each



Hypsilophodon Psittacosaurus

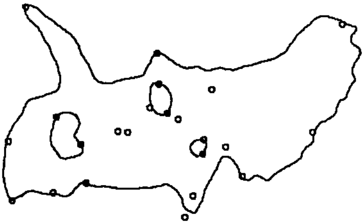


Stegoceras Leptoceratops

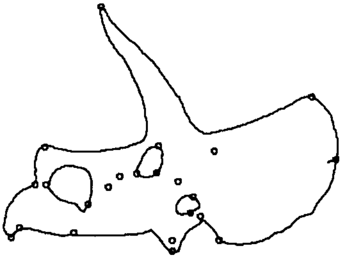


Bagaceratops Protoceratops

Fig. 1. Skull profiles of *Hypsilophodon, Stegoceras,* and protoceratopsids used in study. Landmark points illustrated.



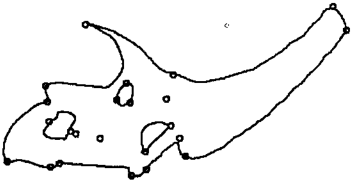
Centrosaurus



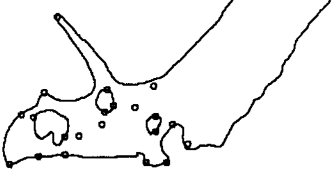
Triceratops

Styracosaurus

Chasmosaurus



Arrhinoceratops



Pentaceratops

Fig. 2. Skull profiles of centrosaurines and chasmosaurines used in study.

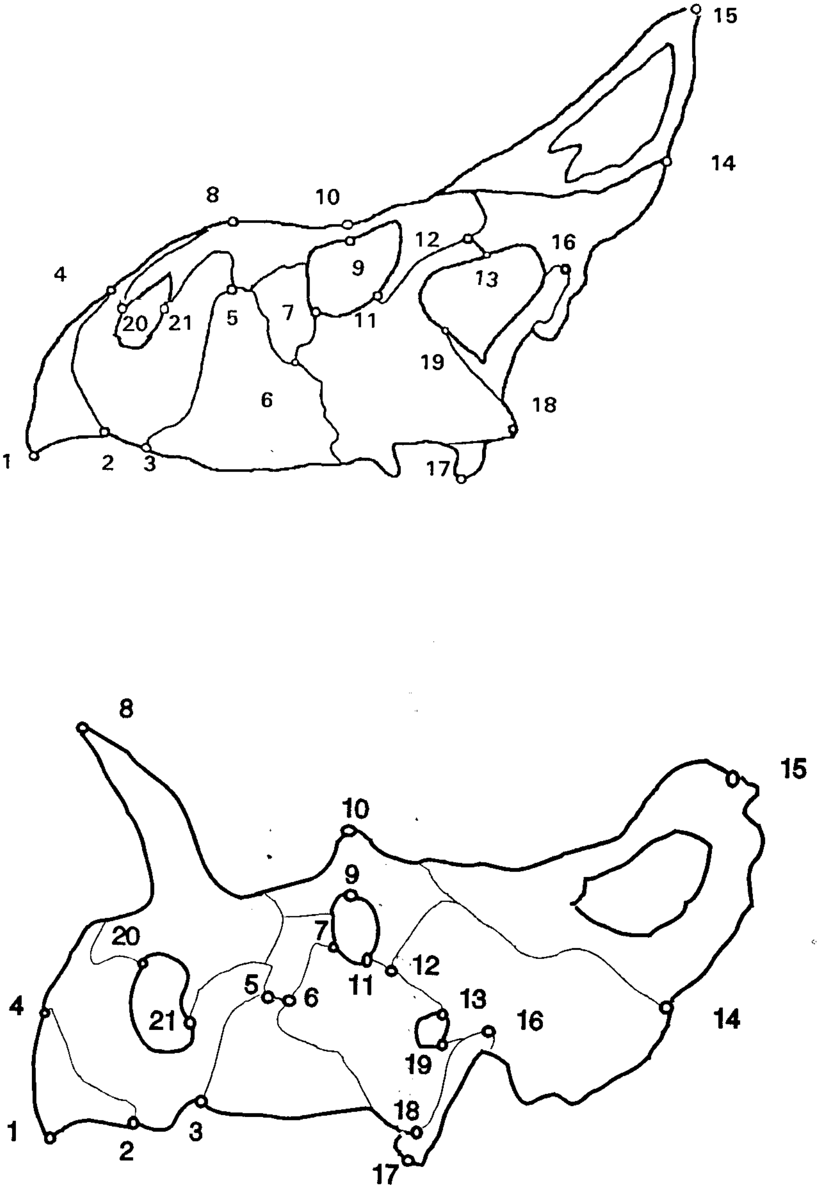


Fig. 3. Landmark points on *Protoceratops* (above) and *Centrosaurus* (below).

TABLE 2

Landmark Points

1. tip of rostral
2. rostral-premax suture-(ventral)
3. premax-max suture (ventral)
4. rostral-premax suture (dorsal)
5. dorsal contact: premax-max
6. max-lac-jugal
7. lac-jugal suture at orbit
8. apex of horn/nasal midpoint*
9. apex of orbit*
10. apex of orbital horn/postorbital*
11. postorbital-jugal at orbit
12. postorbital-squamosal-jugal
13. jugal at infratemporal fen-dorsal prong
14. squamosal-parietal: caudal
15. parietal-caudal margin at midline*
16. quadrate-dorsal end
17. quadrate-ventral end
18. jugal-ventral apex
19. jugal at infratemporal fenestra-ventral
20. premax-nasal in rostrodorsal external naris
21. premax-nasal in caudal external naris

*denotes pseudolandmarks of Bookstein and others, 1985. These points are not constrained by three-way anatomical sutures but represent extreme points.

specimen. The landmarks selected (fig. 3, table 2) were anatomically-constrained descriptors of shape, with some emphasis on cheek region, including position of the quadrate, the jugal, and the squamosal relative to the orbit and the infratemporal fenestra. Reorientation of the cheek region is a major feature of ceratopsian evolution (Dodson and Currie, 1990). The parietal occupies a large area of the skull in ceratopsids but presents few landmarks; consequently there are fewer landmarks and less statistical weight given to the back of the skull; this could conceivably bias the results of the first analysis presented below. It is possible to complement a study of lateral views with dorsal views, as Chapman (1990b) did; however, as the emphasis in this study is on the masticatory functional complex, only lateral views were used. When taxa are examined *seriatim* (from primitive to highly derived), vectors highlight the morphological changes observed. Selected examples are shown in figures 4 to 8.

Starting with *Hypsilophodon* as a base specimen external to the Ceratopsia, vectors document elevation of the face and external nares, expansion of the infratemporal fenestra, and the repositioning of the quadrate into an erect position in *Psittacosaurus* (fig. 4). From *Psittacosaurus* to *Leptoceratops* (fig. 4) the largest vectors are associated with ventral migration of the external nares, caudodorsal migration of the caudodorsal process of the jugal, and elevation of the parietal into a modest crest. In *Bagaceratops* the crest seen in *Leptoceratops* is absent, and the caudodorsal process of the jugal is more rostroventral in position. The biggest change in *Protoceratops* compared with either *Leptoceratops* or *Bagaceratops* (fig. 5)

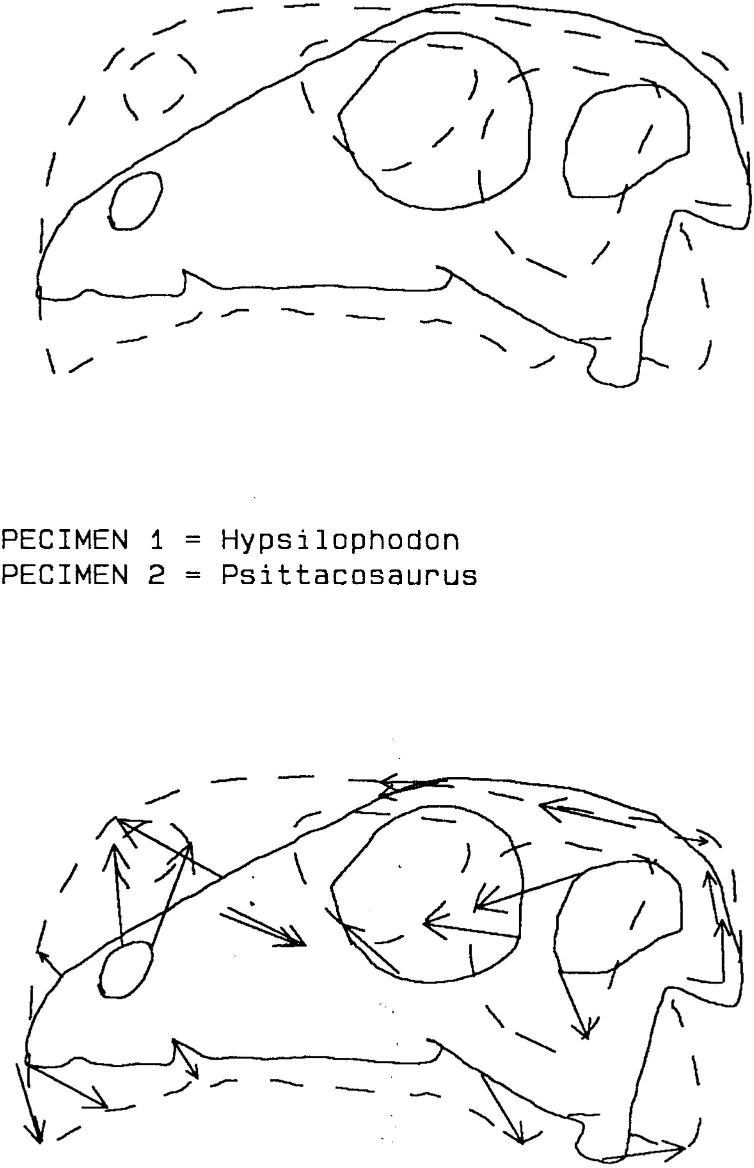


Fig. 4. RFTRA comparisons of *Hypsilophodon* with *Psittacosaurus* (left) and of *Psittacosaurus* with *Leptoceratops* (right). On the left a simple comparison is shown, with outlines of the base specimen (solid) and of the second specimen (dashed line) superimposed. Vectors highlight migration of homologous landmarks in the hypothetical transformation of a *Hypsilophodon* to a *Psittacosaurus*. On the right an additional option removes the outlines and highlights only the vectors of change themselves.

SPECIMEN 2 = Psittacosaurus
SPECIMEN 3 = Leptoceratops

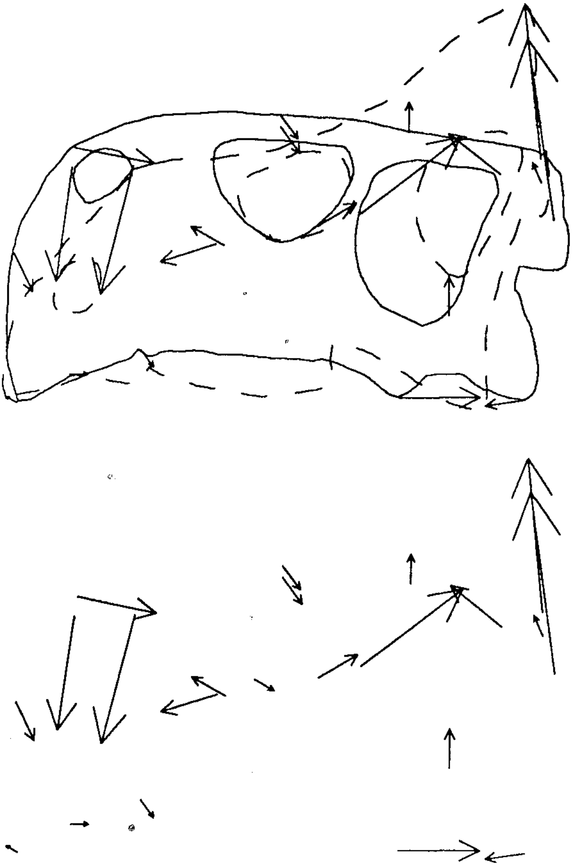


Fig. 4 (continued)

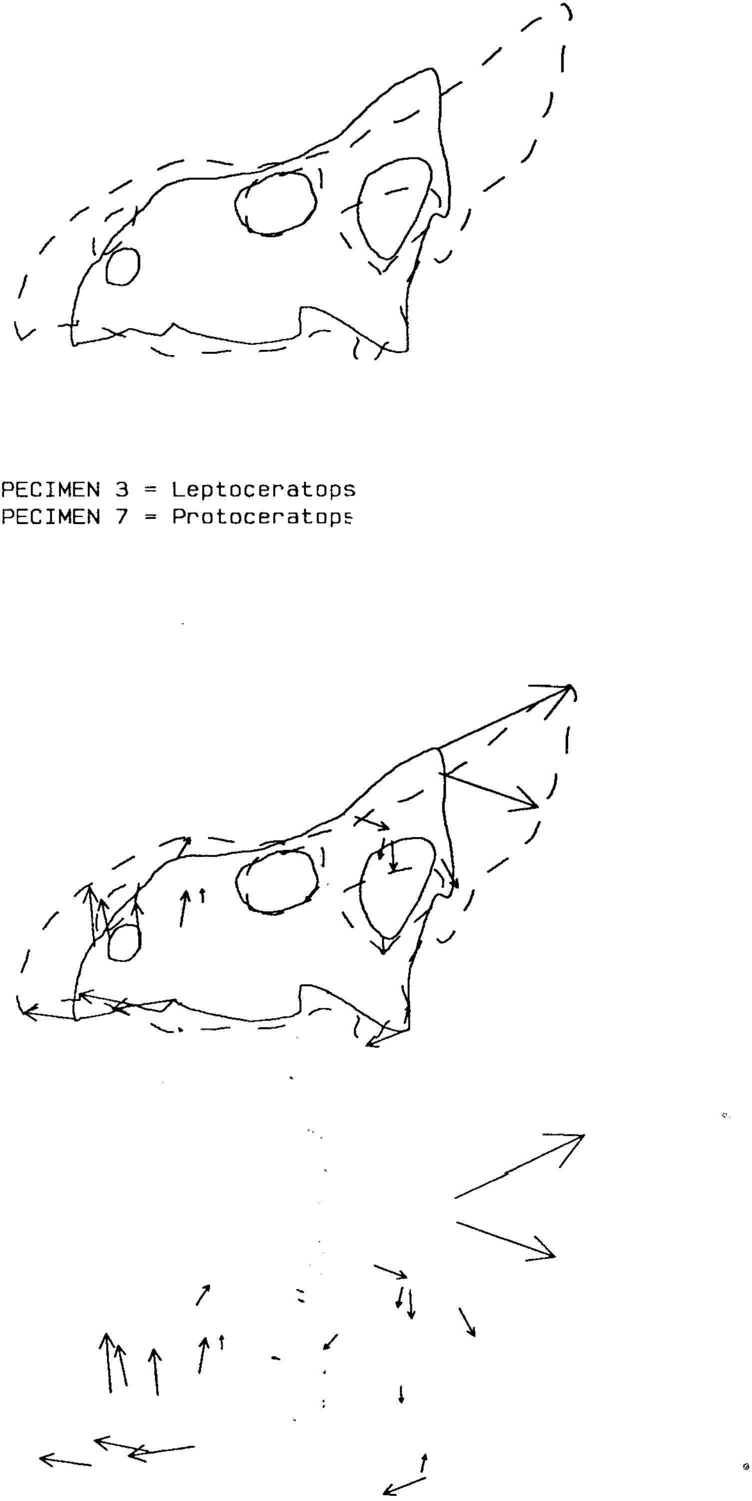
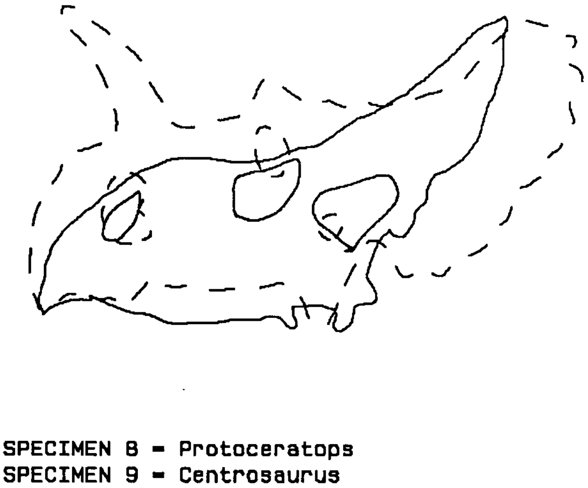


Fig. 5. RFTRA comparisons of *Leptoceratops* (left) and *Bagaceratops* (right) with *Protoceratops*.

SPECIMEN 5 = Bagaceratops
SPECIMEN 7 = Protoceratops

Fig. 5 (continued)



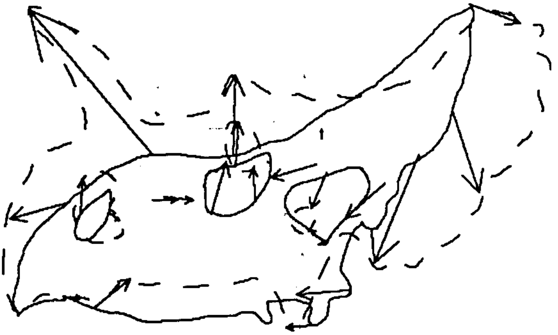
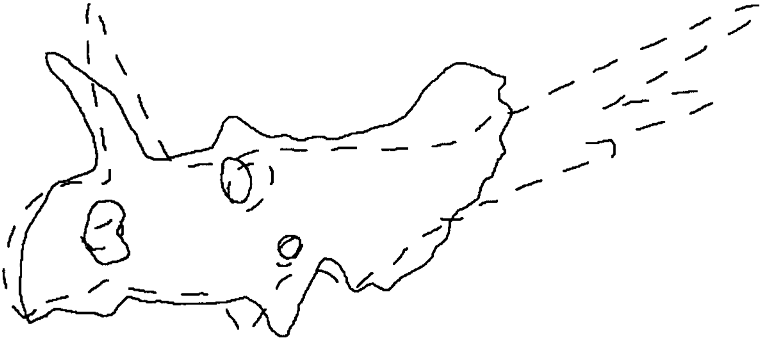


Fig. 6. RFTRA comparisons of *Protoceratops* with *Centrosaurus* (left) and of *Centrosaurus* with *Styracosaurus* (right). In the latter analysis, the outlines have been removed (bottom), and a skeletal polygon has been selected.



SPECIMEN 9 = Centrosaurus
SPECIMEN 10 = Styracosaurus

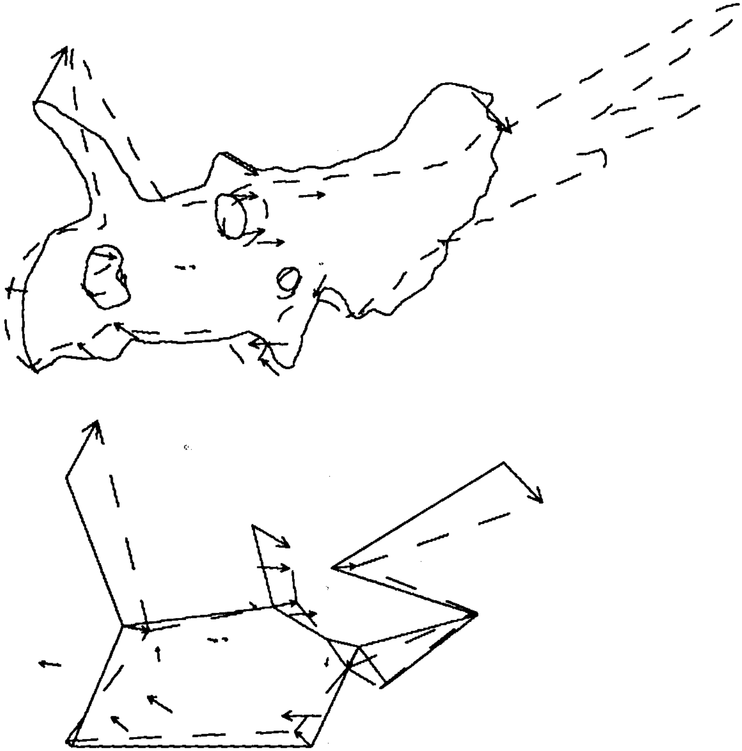


Fig. 6 (continued)

reflects elevation of the parietal into a substantial frill, with a modest contribution from the squamosal. There is a small rostral migration of the ventral end of the quadrate and a prolongation of the rostral bone.

The reorientation of the skull between *Protoceratops* and the ceratopsid *Centrosaurus* (fig. 6) is profound. In addition to the development of true horn cores and anticipated allometric reduction in size of fenestrae, the orbit is repositioned dorsally and the infratemporal fenestra more ventrally. The ventral end of the quadrate moves farther rostrally, and the quadrate decreases in relative height by dorsal shortening. The squamosal increases in length caudal to the quadrate and is reoriented along a caudoventral axis. The parietal is drawn farther caudad. Differences in horns and frills between *Centrosaurus* and *Styracosaurus* are very striking, but the vectors of change in the landmarks chosen are quite modest (fig. 6). The spikes in the frill of *Styracosaurus* were not selected as landmarks for comparison. It is clear in this analysis as elsewhere (Dodson, 1990b; Dodson and Currie, 1990) that *Centrosaurus* and *Styracosaurus* are very closely related, possibly even congeneric.

In a hypothetical transformation between *Protoceratops* and *Arrhinoceratops* vectors highlight the development of the orbital horns, the ventral movement of the proximal portion of the squamosal, and the caudodorsal migration of the frill. In a transformation from *Centrosaurus* (subfamily Centrosaurinae) to *Arrhinoceratops* (subfamily Chasmosaurinae), there is a change of horn pattern but also continued rostral migration of the ventral end of the quadrate (fig. 7). The most striking changes are shown by the strong vectors of elongation of the parietal and squamosal; the squamosal shows the primary caudoventral axis of centrosaurines plus a distinctive secondary dorsal bend. Apart from difference in horn pattern, *Chasmosaurus* has a slightly more erect quadrate, a lower, more attenuated face, and a slightly longer frill (fig. 8). The match between *Chasmosaurus* and *Pentaceratops* is quite close, but the frill is slightly longer and more elevated in the latter. Compared to *Arrhinoceratops* the frill of *Triceratops* is shorter and lower, and the orbital horns are far more massive (fig. 8).

TAXONOMIC IMPLICATIONS

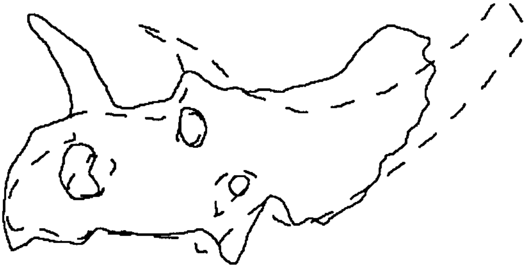
These data based on 21 landmark points may be used for several purposes. Their content of phylogenetic information may be examined, or they may be used to highlight functional transformations. Both uses are investigated. The phylogeny of the Ceratopsia is known to some extent (Sereno, 1986; Dodson and Currie, 1990; Forster, 1990; fig. 9). Disagreement surrounds the question of whether the Protoceratopsidae are monophyletic (Dodson and Currie, 1990) or paraphyletic (Sereno, 1986; Forster, 1990). The matrix of distance data generated by RFTRA is subjected to cluster analysis (fig. 10) using the algorithm UPGMA (unweighted pair group method using arithmetic average; Sneath and Sokal, 1973). The Ceratopsidae break into one cluster, with subclusters corresponding to the Centrosaurinae and the Chasmosaurinae. *Tricera-*

tops occupies an isolated position within the Chasmosaurinae, consistent with the historical problem of its systematic placement (Sternberg, 1949; Ostrom, 1966; Lehman, 1990). It is noteworthy that a specimen of *Chasmosaurus canadensis* pairs with *Pentaceratops* rather than with *C. belli;* a case could be made for uniting the two in one genus (but see Lehman, 1989). There is a clear separation of the Protoceratopsidae plus the outgroups from the Ceratopsidae. The separation is consistent with the view that no member of the Protoceratopsidae is closer than any other to the Ceratopsidae. *Stegoceras* is separate from all other protoceratopsids plus *Hypsilophodon*. Although the pachycephalosaurians are apparently the sister group of the Ceratopsia (Sereno, 1986), all known members are already highly specialized in features quite unlike ceratopsians. *Hypsilophodon* pairs with *Psittacosaurus,* consistent with the cladogram, and the remaining protoceratopsids form a cluster, with juvenile *Protoceratops* pairing with the primitive (and very small) *Bagaceratops,* and adult *Protoceratops* pairing with *Leptoceratops,* which is more derived than *Bagaceratops* in the frill.

Using RFTRA it is an easy matter to "deconstruct" the morphology of the skull. For instance, in the next analysis the nasal (landmark 8) and postorbital horns (10) and parietal frill (15) are removed. When the cluster analysis is performed (fig. 11), overall stability is maintained, but several interesting features emerge. Without horns and parietal, *Triceratops* clusters with the centrosaurines, a position it has long enjoyed (Hatcher, Marsh, and Lull, 1907; Lull, 1933; Colbert, 1948; Ostrom, 1966) but a position that is almost certainly incorrect (Sternberg, 1949; Lehman, 1989; Dodson and Currie, 1990; Forster, 1990). The shortness of the *Triceratops* squamosal is like that of centrosaurines. When the chasmosaurine horns and parietal are removed, the superficial resemblances of *Triceratops* to centrosaurines causes *Triceratops* (but only *Triceratops*) to be misclassified. Another change is that *Psittacosaurus* occupies a more isolated position than *Hypsilophodon,* consistent with its autapomorphies (Sereno, 1990); it is not "almost" a protoceratopsid. In this analysis, the two species of *Chasmosaurus* come together. The uncharacteristically long horns of AMNH 5401 caused separation previously.

In the third analysis, deconstruction is carried further. Morphology is atomized with the goal of concentrating on a specific functional complex concerned with the jaw adductors, the maxillary and the mandibular masticatory system: landmarks focusing on the face and nostrils (1, 2, 4, 20, 21) in addition to the horns (8, 10) are removed (figs. 12, 13). However, parietal midline length is reinstated due to the postulated involvement of the frill in mastication (Ostrom, 1966). Interestingly, in these "stripped down" skulls the taxonomic signal emerges with clarity (fig. 14). *Triceratops* is restored to its position within the Chasmosaurinae but once again differs from the other members of the clade. *Pentaceratops* resolutely remains outside the *Chasmosaurus* pair. *Hypsilophodon* clusters with *Psittacosaurus* and the primitive *Bagaceratops,* but *Stegoceras* clusters with the more derived, frilled *Protoceratops-Leptoceratops* pair. This empha-

Fig. 7. RFTRA comparison of *Protoceratops* with *Arrhinoceratops* (left) and of *Centrosaurus* with *Arrhinoceratops* (right).



SPECIMEN 9 - Centrosaurus
SPECIMEN 11 - Arrhinoceratops

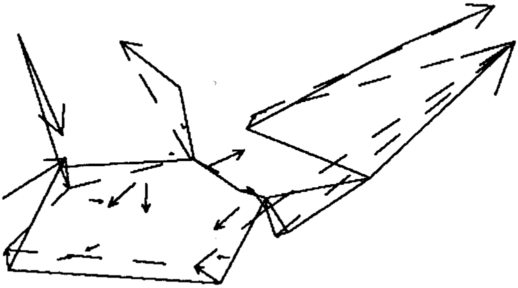


Fig. 7 (continued)

SPECIMEN 11 = Arrhinoceratops
SPECIMEN 13 = Chasmosaurus

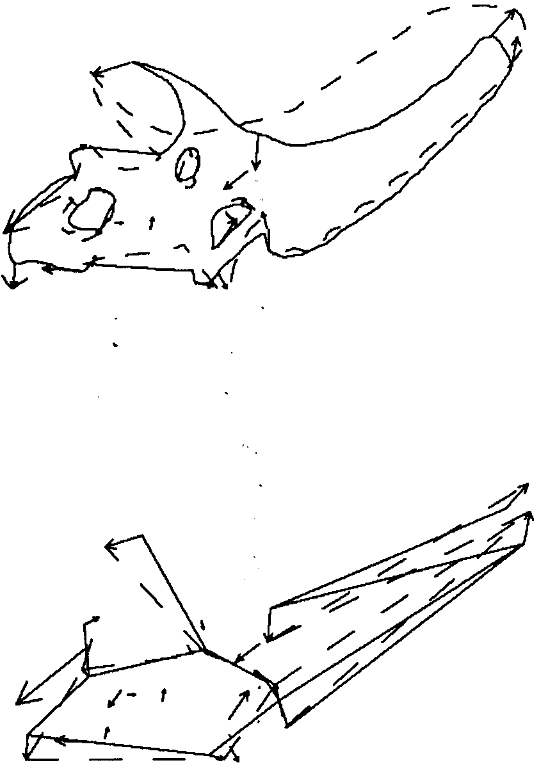
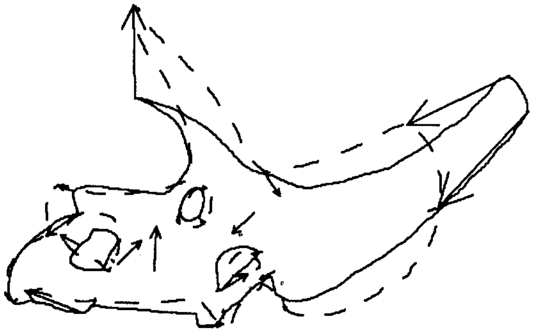


Fig. 8. RFTRA comparison of *Arrhinoceratops* with *Chasmosaurus* (left) and with *Triceratops* (right).

SPECIMEN 11 = Arrhinoceratops
SPECIMEN 12 = Triceratops



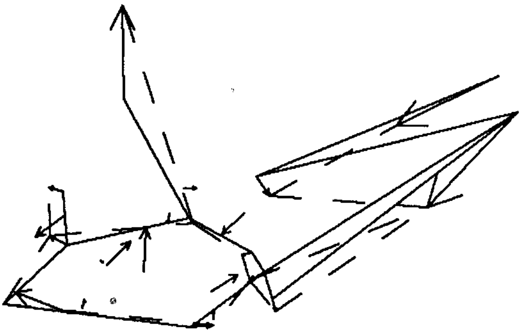


Fig. 8 (continued)

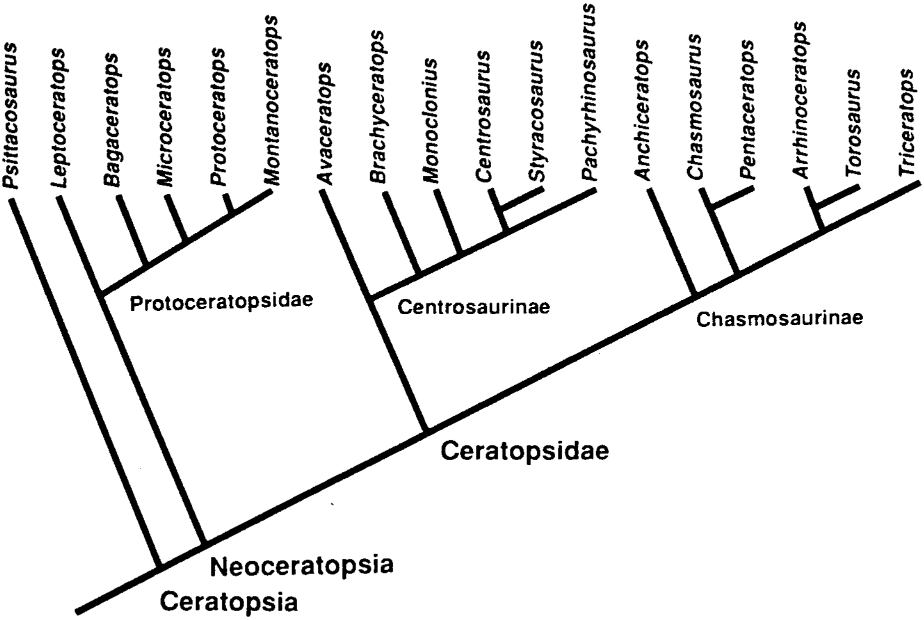


Fig. 9. Cladogram of the Ceratopsia (from Dodson and Currie, 1990).

sizes that resemblance of pachycephalosaurs to ceratopsians is concentrated in the cheek region and may reflect a limited functional convergence, although their dentitions and jaw mechanics are very unlike one another.

MORPHOLOGICAL TRENDS IN CERATOPSIAN CRANIAL EVOLUTION

Morphological trends can be recognized in the phylogenetic series. In *Hypsilophodon,* the jugal is relatively small, the infratemporal fenestra is smaller than the orbit and is dorsal in position; the quadratojugal is large and is completely exposed in lateral view between the jugal rostrally and the quadrate caudally; the squamosal forms a simple cotylus for the head of the quadrate. In *Psittacosaurus* (fig. 15) the very large infratemporal fenestra extends ventral to the orbit, the jugal is enlarged caudally, the quadratojugal lies caudal to the jugal and covers the ventral end of the quadrate, which is erect and robust. In the adult *Bagaceratops* the jugal is the major structural element of the ventral cheek, and the jugal "horn" largely covers the quadratojugal in lateral view; the ventral end of the gracile quadrate is rotated forward slightly, giving a modest rostroventral-caudodorsal tilt to the quadrate. However, a juvenile skull of *Bagaceratops* shows the linear rostral-caudal arrangement of the jugal-quadratojugal-quadrate (Maryanska and Osmolska, 1975). In *Protoceratops* the inclination of the quadrate is a little more pronounced, and the squamosal

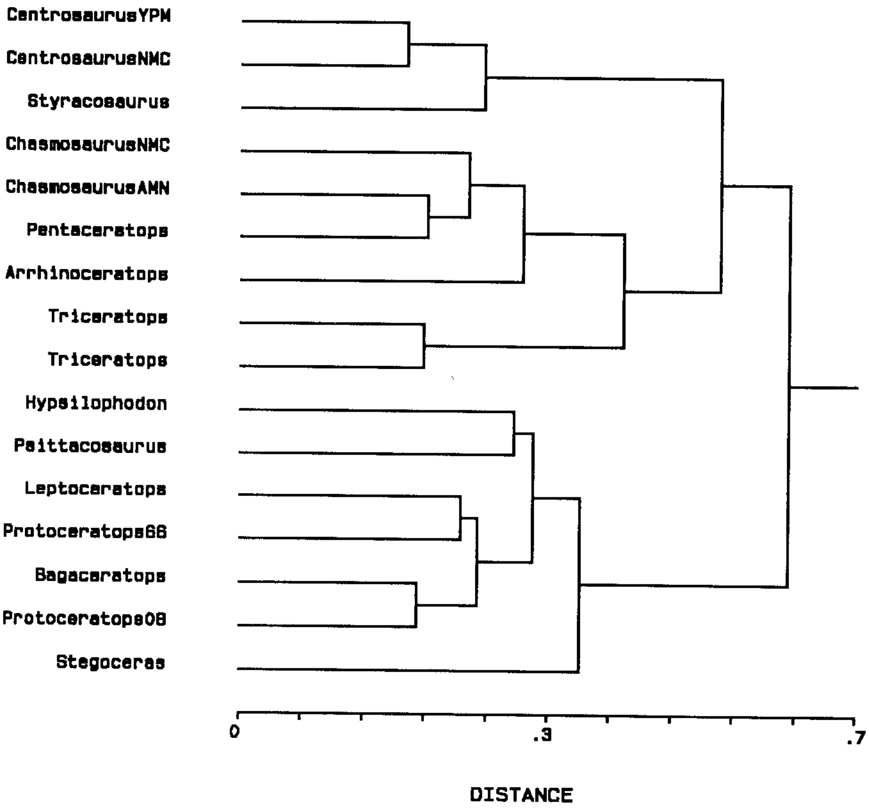


Fig. 10. UPGMA cluster analysis of the Ceratopsia. The data set includes all 21 landmark points for 16 specimens of 12 taxa. See text for discussion.

shows distinct elongation caudal to the dorsal head of the quadrate. In *Centrosaurus* (fig. 15) the squamosal is expanded both caudally and rostroventrally to become, along with the jugal, a key structural element of the cheek. The infratemporal fenestra is very reduced in size and is pushed ventrally by the ventral expansion of the postorbital and by the broad sutural contact among the postorbital, the squamosal, and the jugal. The long axis of the squamosal is directed caudoventrally. The quadratojugal is a small thick element usually covered in lateral view that serves as a spacer between the jugal laterally and the ventral end of the quadrate medially. The quadrate is relatively short. In chasmosaurines the squamosal is greatly elongate in an interesting pattern. The caudoventral orientation of the centrosaurine squamosal is still evident, but the caudal extremity is attenuated caudodorsally resulting in a distinctive

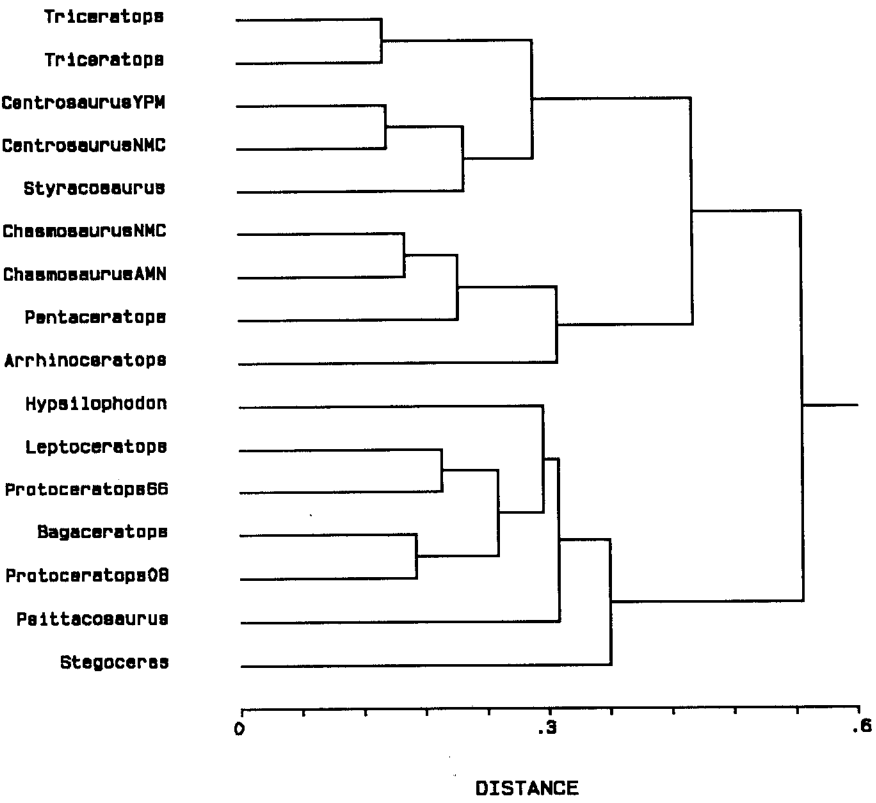


Fig. 11. UPGMA cluster analysis of "hornless ceratopsians." The data set has been modified by elimination of the landmarks points for nasal horn (8), orbital horn (10), and parietal midline length (15).

kink or bend of the dorsal or medial border, a trait by which chasmosaurine squamosals may be immediately recognized.

DISCUSSION

Reorientation of the cheek region is a major feature of the evolution of the Ceratopsia. Hypertrophy of the infratemporal fenestra and increase in the size of the adductor chamber in *Psittacosaurus* suggest increase in mass of the mandibular adductor musculature. The adductor chamber may be conceptualized as the space lateral to the braincase bounded rostrally by the orbit and caudally by the quadrate. The distance from the orbit to the dorsal end of the quadrate provides a rough proxy for a transect across the adductor muscle mass. In *Hypsilophodon* this measures for about 27 percent of the basal length of the skull, while the comparable span in *Psittacosaurus* amounts to 35 percent of skull length. As the quadrate in *Psittacosaurus* is erect, the adductor chamber is uncompressed. In *Protoceratops* the dorsal line across the adductor chamber accounts for 30 percent of skull length. However, due to the rostral rotation of the ventral end of the quadrate, the distance from the ventral end of the quadrate (the mandibular articular condyle) to the vertical line dropped from the caudal border of the orbit is but 8 percent of the basal skull length. In ceratopsids, similar compression of the adductor chamber ventrally is also seen. For instance, in *Centrosaurus* the dorsal line accounts for 27 percent of basal skull length, the ventral line 11 percent of skull length; in *Triceratops* the dorsal line is 18 percent and the ventral line is 11 percent.

The increase in size of the jugal and squamosal and their firm connection may also reflect increased muscular strength. The telescoping of the jugal, quadratojugal, and ventral end of the quadrate so that these elements come to lie side-by-side rather than rostral-to-caudal shortens the adductor chamber ventrally. It shortens the jaw relative to basal skull length by an average of about 20 percent compared to skull with a vertical quadrate (in *Arrhinoceratops* the rostral rotation of the ventral end of the quadrate is extreme, resulting in a 30 percent shortening of the jaws). This shortening especially causes decrease in the moment arm of the jaw adductors. Ostrom (1966) interpreted the elevated coronoid process and depressed jaw point as increasing the moment arm of ceratopsids. These changes may be viewed as compensation for ventral shortening of the adductor chamber. The jaw adductor muscles assumed a dominantly oblique orientation parallel to the strongly sloping quadrate and inserted on a robust elevated coronoid process. An elevated coronoid process has evolved repeatedly in vertebrate evolution; in synapsids it evolved in connection with carnivory (DeMar and Barghusen, 1973), but it is also common in herbivores (for example, hadrosaurs—Ostrom, 1961). Combined with decrease in relative height of the postorbital region of the skull and reduction of the infratemporal fenestra, the adductor chamber was reduced in size. In consequence the adductor muscles evidently emerged from the adductor chamber and occupied at least the base of the parietal frill (Haas, 1955; Ostrom, 1964, 1966).

But did the entire frill of ceratopsids serve as a platform for muscle origin? Objections to the concept of the parietal frill as serving primarily for muscle origin are several. Functionally, it is unclear why adductor musculature should increase enormously in bulk, especially in length. Increase in length of muscle fibers does not increase the force of muscle contraction, although increase in complexity of muscle fiber architecture by means of pinnation could have had this effect, depending on the outcome of vector resolution of the contractile fibers. Squamosals of ceratopsids often show adventitious unilateral fenestrae that have been interpreted as puncture wounds, indicative of intraspecific aggression

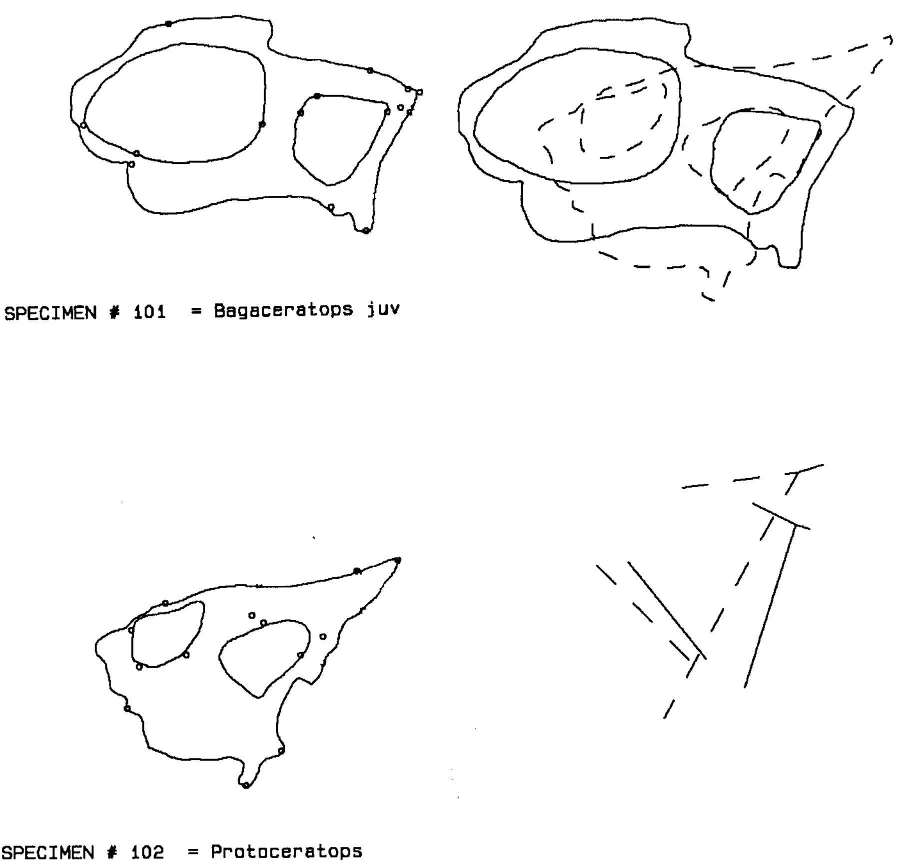
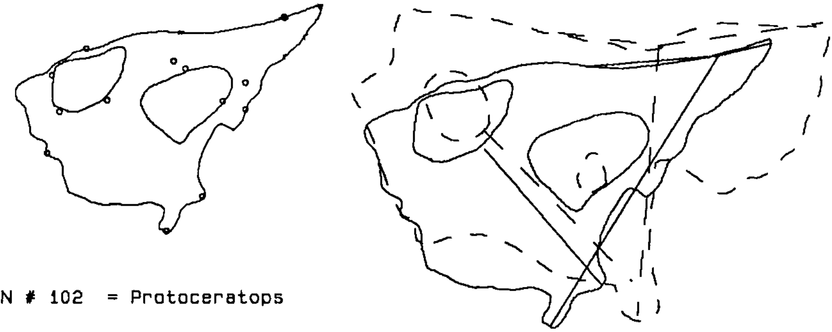


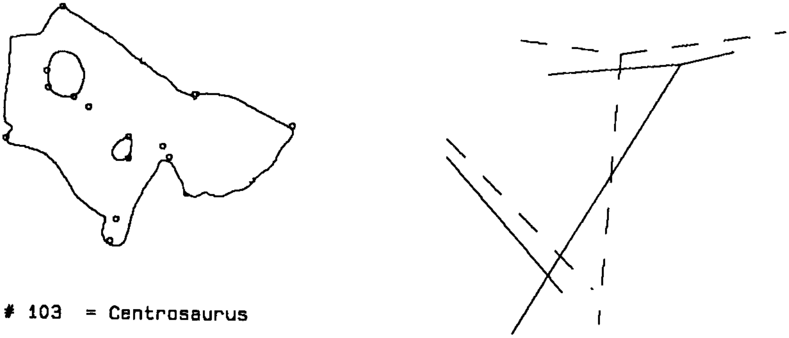
Fig. 12. RFTRA analysis of "deconstructed" skulls. With the removal of horns and face, this analysis focuses on functionally significant aspects of cranial anatomy. Left is a comparison of a juvenile specimen of *Bagaceratops* with *Protoceratops;* on the right is a comparison of *Protoceratops* with *Centrosaurus*. The stick figures compare three structural units of the skull, the axis from the orbit to the ventral tip of the jugal, the axis of the quadrate, and the axis of the prequadrate portion of the squamosal and the postquadrate portion of the squamosal. As above, the solid indicates the first specimen of the pair (base specimen), and the dotted lines indicate the second specimen.

(Dodson and Currie, 1990); soft tissues on the exposed frill would be very susceptible to injury, a poor risk for the jaw muscles.

Ceratopsians had a unique dental mechanism. They were herbivores with a vertical occlusal plane (Ostrom, 1964, 1966; Weishampel and Norman, 1989). In shearing, masticatory forces are concentrated along a continuous edge rather than broadly distributed over a grinding surface. The mere fact of elevating the angle of the occlusal surface from a low-angle compressional grinding surface to a high-angle shearing surface must have the mechanical effect of increasing the occlusal pressure



SPECIMEN # 102 = Protoceratops



SPECIMEN # 103 = Centrosaurus

Fig. 12 (continued)

per unit of tooth area. This strategy is also correlated with high rate of tooth wear and runs counter to the evolutionary trend of mammalian herbivory (Rensberger, 1986a, b). It is difficult to conceive of the ceratopsian mechanism as representing any paradigm of dental efficiency; it seems that effectiveness is the best that can be said. Grouping hadrosaurs with ceratopsids on the basis that they both possess dental batteries seems inappropriate. Whereas the hadrosaur dental battery represents one of the peaks of vertebrate dental evolution (Edmund, 1960; Ostrom, 1961; Weishampel, 1984), the ceratopsid dental battery may simply represent a mechanism for increased rate of tooth replacement due to the excessive wear caused by its shear-dominated masticatory system.

Was still further increase in occlusal pressure by elongation and hypertrophy of adductor muscles really necessary? Was the jaw joint strong enough to support hypertrophied adductor muscles? The quadrate-articular joint appears to be very strong (ventral end of the quadrate

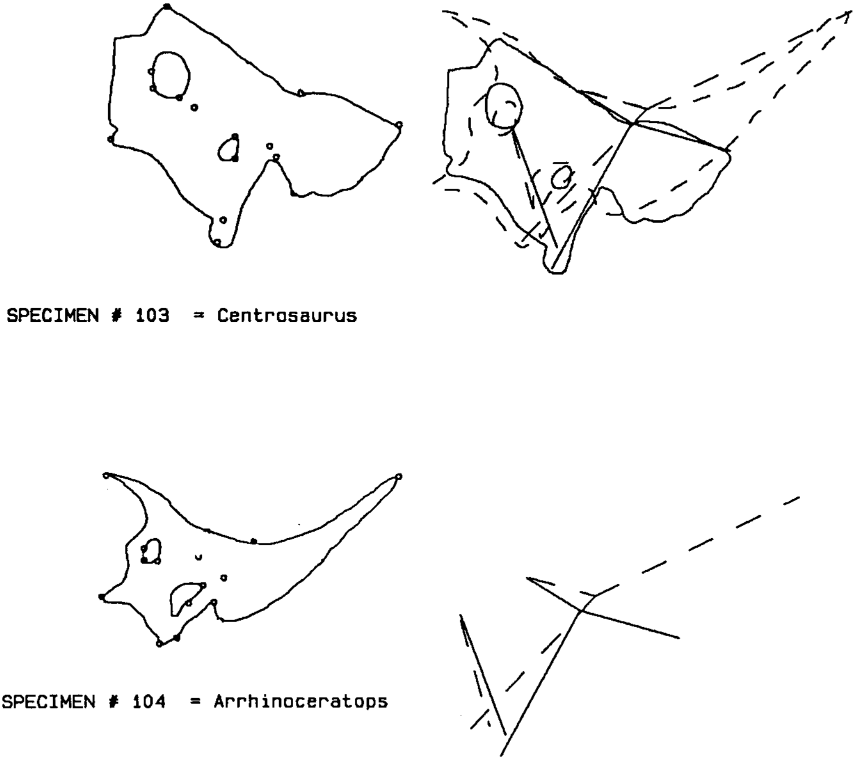
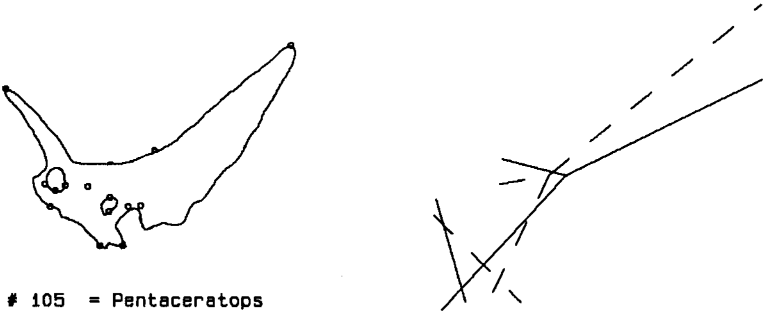


Fig. 13. RFTRA comparison of deconstructed skulls as above. Left, comparison of *Centrosaurus* with *Arrhinoceratops;* right, comparison of *Arrhinoceratops* with *Pentaceratops.*

may exceed 100 mm in width in a large ceratopsid skull), and the quadrate is also supported by the pterygoid, jugal, and quadratojugal, all of which distribute stresses. However the dorsal end of the quadrate is thin and was somewhat loosely connected to a shallow cotylus on the medial surface of the squamosal. Quadrates are often lost from skulls, and isolated ceratopsid quadrates are almost always broken dorsally. This suggests that while the quadrate was well designed to provide stability to the jaw, it was probably not designed to resist extraordinary levels of stress.

Were chasmosaurines more effective at mastication than centrosaurines by virtue of longer muscle bellies? Parietal frills provided large surface areas for potential muscle origin, but large parietal fenestrae are common among ceratopsians, and these fenestrae are hypertrophied in *Chasmosaurus* and *Pentaceratops.* The parietal fenestrae themselves and the thinness of the surrounding bone suggest that structural stresses were typically low over large areas of the parietal. In the case of *Protocera-*

SPECIMEN # 104 = Arrhinoceratops



SPECIMEN # 105 = Pentaceratops

Fig. 13 (continued)

tops the parietal is so thin as to be translucent. In general bone that serves for origin of muscle fibers has a smooth texture; it may be assumed that bone with a pattern of vascularization or ornamentation had a tightly adherent dermis with no skeletal muscle fibers. The texture of ceratopsian parietal bone is a highly distinctive feature. Rigby (1989) has gone so far as to suggest that the frill of ceratopsians, especially *Triceratops,* was primarily thermoregulatory in function. Without subscribing to this argument, it may nonetheless be accepted that at least for those ceratopsids with textured parietals (*Centrosaurus, Monoclonius, Brachyceratops, Chasmosaurus, Anchiceratops, Arrhinoceratops, Triceratops, Torosaurus*) jaw adductor muscles did not occupy those areas of the parietal that were so textured. In all protoceratopsids, by contrast, the parietal is smooth. Thus it is possible to make the argument that the parietal frill of protoceratopsids resulted from selective pressures to increase muscle mass by dorsal expansion. However, it is clear that by the level of derived protoceratopsids such as *Protoceratops* the frill had already assumed a sexual dimorphic display function in addition to presumed muscle sup-

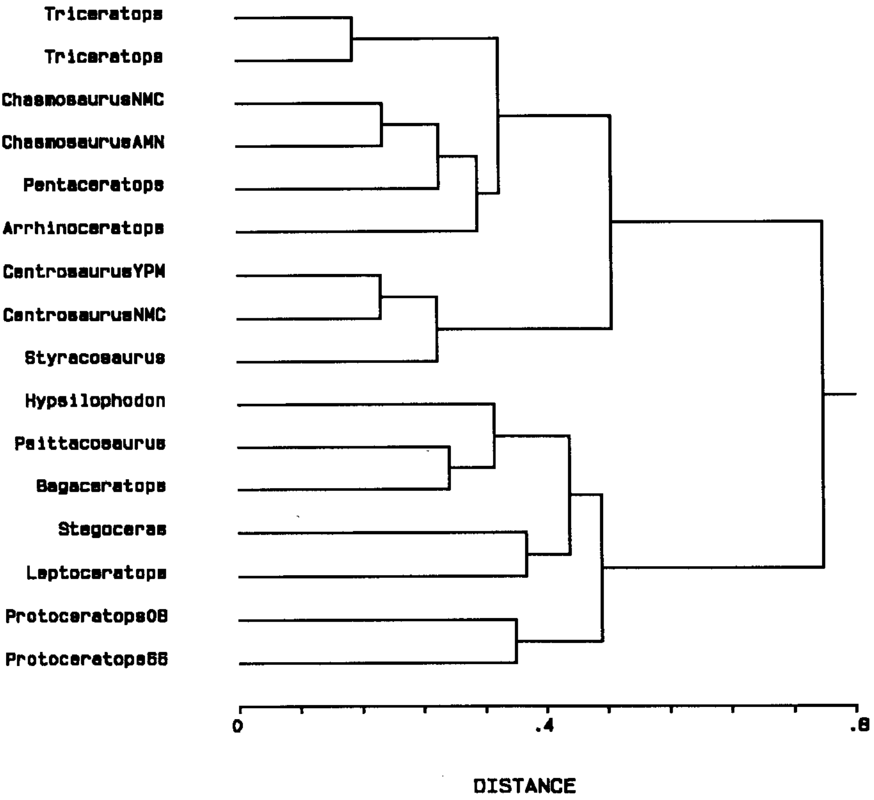
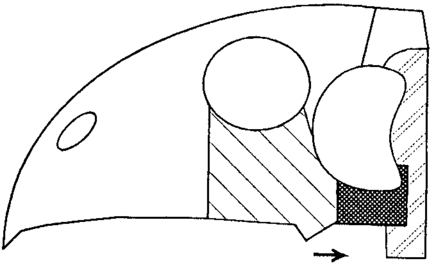


Fig. 14. UPGMA cluster analysis of deconstructed ceratopsian skulls with horns and face removed. See text for discussion.

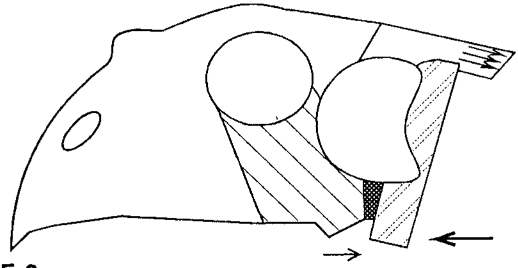
port function (Kurzanov, 1972; Dodson, 1976). It is also evident that ornamentation of the parietal and squamosal such as spikes, hooks, and scallops cannot have enhanced muscle function but can only be explained in terms of behavioral display (Farlow and Dodson, 1975; Molnar, 1977; Spassov, 1979; Dodson and Currie, 1990).

Fig. 15. Levels of structural evolution within the ceratopsian skull, emphasizing rearrangement of the cheek region and development of the squamosal. In stage 1, represented by *Psittacosaurus,* an incipient "horn" is seen on the jugal (single right hatch). In stage 2, represented by *Bagaceratops,* the ventral end of the quadrate (double left hatch) is rotated forward while the jugal horn is directed backward, resulting in restriction of the quadratojugal (dark stipple); caudal growth of the squamosal is incipient. In stage 3, represented by *Centrosaurus,* the backward movement of the jugal and forward movement of the ventral end of the quadrate has resulted in structural linkage of these elements. The quadratojugal (light stipple) is not visible in lateral view but is juxtaposed as a spacer between the ventral end of the quadrate and the jugal horn. The primary axis of the squamosal is caudoventral in orientation, and the postquadrate portion of the squamosal is hypertrophied. In stage 4, represented by *Pentaceratops,* a secondary growth axis nearly perpendicular to the primary axis elevates the distal end of the squamosal and results in a characteristic bend in the chasmosaurine squamosal.



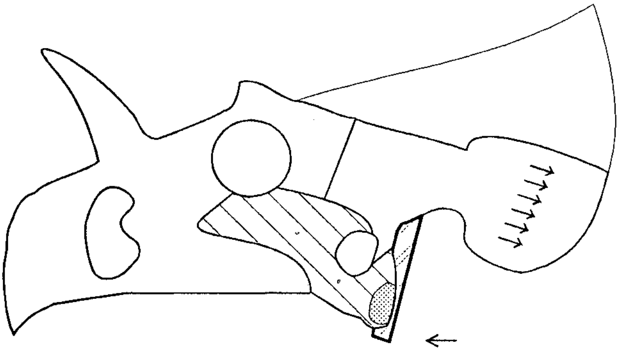
STAGE 1

PSITTACOSAURUS



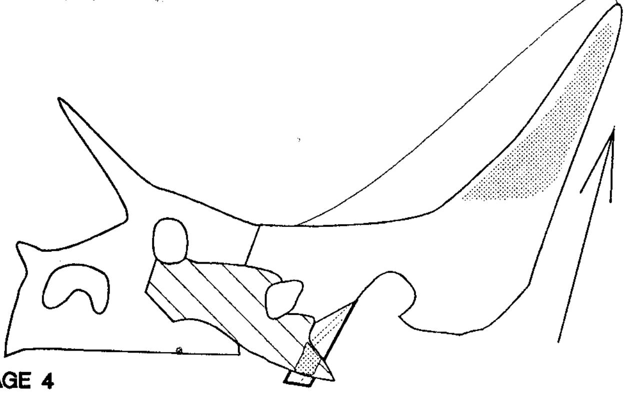
STAGE 2

BAGACERATOPS



STAGE 3

CENTROSAURUS



STAGE 4

PENTACERATOPS

Figure 15

It is by no means self-evident that ceratopsid masticatory systems co-evolved with succulent new angiosperm food sources. Ostrom (1966) postulated that ceratopsians consumed tough fibrous foods inaccessible to herbivores lacking their specializations. He suggested cycads and palms as potential food sources. Neither seems particularly probable food sources for Campanian or Maastrichtian ceratopsians, especially from those of Montana and Alberta. Cycads had dwindled strongly by the Campanian, and palms were not important at mid-latitudes until the Maastrichtian (Crane, 1987). The ecological success of ceratopsians suggests they were not dependent on either group of plants. Furthermore, large herbivores are generally unselective in their foraging (Coe and others, 1987). I interpret their masticatory machinery as suitable for simply a coarser, woodier angiosperm diet than that of hadrosaurs, which preferentially consumed herbaceous angiosperms and gleaned foliage and small stems (Coe and others, 1987; Wing and Tiffney, 1987; Weishampel and Horner, 1990). Late Cretaceous angiosperm tree trunks were mainly less than 10 cm in diameter (Crane, 1987) and thus were of a size that they could have easily been knocked over by ceratopsids.

CONCLUSIONS

The Ceratopsia are a group rich in taxonomic and morphological diversity. They have also served as a substrate for pioneering work in dinosaurian functional morphology (Ostrom, 1964, 1966). The present work is stimulated by my association with the author of these studies. The purpose of the present study is to apply a new technique of multivariate morphometric analysis, resistant-fit theta-rho analysis or RFTRA (Benson, Chapman, and Siegel, 1982; Chapman, 1990a,b) to a series of ceratopsian skulls to examine taxonomic questions and functional questions. The study used 21 homologous landmark points on the skulls of 16 specimens of 12 taxa, including *Hypsilophodon,* representing a generalized ornithopod, and *Stegoceras,* a member of the putative sistergroup of the Ceratopsia, the Pachycephalosauria (Sereno, 1986). The output of RFTRA is a cluster analysis, which is frankly phenetic in content. Because the Ceratopsia have already been analyzed cladistically (Sereno, 1986; Dodson and Currie, 1990; Forster, 1990), it is possible to compare the results of the phenetic analysis with those of the cladistic analysis in order to determine what validity (if any) the former may have. Three separate analyses were performed, one using the entire data set, and two using progressively smaller sets (with 18 and 14 landmarks respectively). This technique of cranial deconstruction, whereby first the nasal and orbital horns and the parietal, and then these characters plus the face were eliminated, allowed a test of the hypothesis that dinosaur systematists rely too heavily on trivial, possibly sexually dimorphic characters in recognizing taxa and reconstructing phylogenies. The analysis demonstrates that taxonomically significant characters are distributed throughout the skull; it falsifies the hypothesis that horn characters are trivial. Horn characters are congruent with the pattern established by other morphological and functional characters.

In the first analysis, a clear Ceratopsidae with Centrosaurinae and Chasmosaurinae emerged. A second fundamental group included the Protoceratopsidae plus the outgroups, although *Stegoceras* segregated from all other members of this cluster; *Hypsilophodon* paired with *Psittacosaurus*. Although Sereno (1986) and Forster (1990) are convinced that cladistically the Protoceratopsidae are a paraphyletic assemblage of primitive forms, this analysis suggests there is a qualitative discontinuity between protoceratopsids and ceratopsids as previously maintained (Maryanska and Osmólska, 1975; Dodson and Currie, 1990). An unexpected finding is that the fundamental taxonomic structure of the dendrogram is unaffected by the elimination of horns and face. It is evident that features of the cheek region and the adjacent frill that are central to the masticatory system are intrinsic to the evolution of the Ceratopsia, and whether studied cladistically or by careful morphometric analysis, these features convey a strong reliable taxonomic signal. The congruence of the horns and frill with the functional complex leads to the conclusion that display features are in no sense trivial characters that are inherently unreliable taxonomically.

Morphological trends in the Ceratopsia include enlargement of the jugal, rotation of the ventral end of the quadrate forward, telescoping of the jugal, quadratojugal and quadrate so that these elements lie in a transverse plane, reduction in size and ventral migration of the infratemporal fenestra, compression of the adductor muscle chamber ventrally, caudoventral growth of the squamosal from the dorsal end of the quadrate, and finally tremendous elongation of the squamosal at a high angle to the caudoventral axis. These changes produced a strong cheek region anchored by the jugal and squamosal. A sequela of compression of the adductor muscle chamber was spread of muscles onto the base of a parietal frill. As Ostrom (1964, 1966) elegantly described, elevation of the coronoid process and oblique orientation of the line of muscle action followed. Ceratopsians developed a unique dental shearing mechanism that permitted the slicing of fibrous woody stems, quite possibly small angiosperm trees. Their occlusal mechanism chopped fibrous material into chunks but did not permit efficient grinding. They were not quadrupedal equivalents of hadrosaurs in masticatory efficiency or metabolic rate. The frills of ceratopsids played a modest role in muscle origin and a much greater role in behavioral biology.

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