

ANALOGIES IN THE EVOLUTION OF COMBAT AND DISPLAY STRUCTURES IN ORNITHOPODS
AND UNGULATES

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ABSTRACT: The presence of a wide variety of cranial horns, frills and crests as well as caniniform teeth in various members of the Ornithopoda, and their derivatives, the Pachycephalosauria and the Ceratopsia, suggests analogy with various ungulates, especially artiodactyls. Suggestions that these cranial structures functioned in combat and display may be tested by comparing the actual structure with expectations or predictions derived from the hypothetical role of that structure. Such tests, while incapable of proving that the animals did in fact use these structures as suggested, could demonstrate that the structures either matched or did not match the expectations, and thus render more or less likely the suggested functions. Matching of such structures of psittacosaur, ceratopsians, pachycephalosaurs and some hadrosaurs with expectations shows that it is likely that the structures functioned in intraspecific combat and display. The sequence of evolution of these structures matches that suggested by Geist for ungulates, commencing with the use of teeth, progressing to lateral display and the striking of blows with the head and finally using various modes of frontal display and combat. It is suggested that early adoption of an herbivorous diet and later adoption of the head in striking blows controlled the development of this sequence.

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Introduction

Until recently speculation regarding dinosaur behavior was more easily found in the literature of science fiction (e.g. de Camp, 1956; Anthony, 1970) than in that of vertebrate palaeontology. Although Davitashvili (1961) had discussed the subject much of his work was ignored (translations from the Russian only recently having become available) and only in the last few years has this subject received attention (Farlow and Dodson, 1975; Hopson, 1975). This is due in part to the conservative attitude of many vertebrate palaeontologists with respect to speculation and deduction from fossil material which can never be proven or falsified.

Even though the specific function of a given structure of a fossil organism cannot be conclusively demonstrated, some indication of the likelihood of a suggested function can be obtained. This can be done by applying the method proposed by Rudwick (1961; 1964): comparing the actual structure with the optimal form of that structure for the suggested function. The closer the match of the actual structure with the expected optimal for any given function, the more likely that that suggested function did in fact occur.

The recent interest in ethological deduction from fossil material is due in part to the speculations of Geist (1966; 1971; 1972) about the function and evolution of horns and horn-like structures in ungulates. Working with sheep (*Ovis canadensis*) Geist (1971) showed that the horns are used in intraspecific combat, and because the horns are displayed after each clash and because horn size is related to the force delivered in the clash, the horns have taken on a display function in maintaining the dominance hierarchy.

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Before briefly reviewing Geist's speculations however, it is appropriate to discuss the various observed display functions. Three different types of displays seem to be confused in recent non-Russian literature relating to the possible existence of such behavior among dinosaurs. These are threat, dominance (or rank) and courtship displays (cf. Walther, 1974). Threat displays are those that express a readiness to fight and may involve structures that function as weapons, often drawing attention to these structures (Walther, 1974; also many ethology texts, e.g. Ewer, 1968). Dominance displays are those that indicate the strength of an individual and thus his (or her) position in a dominance hierarchy based on strength (Geist, 1971; Walther, 1974). Dominance displays also often involve weapons. Courtship displays communicate information about an individual's specific and sexual membership and state of sexual interest (Walther, 1974). Structures involved in such displays, and the displays themselves, tend to be most complex where a large number of closely related, sympatric species are found (e.g. Rand and Williams, 1970; Echelle, Echelle and Fitch, 1971). Structures involved in these displays (e.g. dewlaps) need not be related to any weapon function.

Rigorously distinguishing between these functions for a fossil organism is impossible at our present state of knowledge, nonetheless functions can be suggested if not proven. This is, after all, little worse than the situation with respect to the construction of phylogenies for fossil organisms, which also cannot be proven but only suggested. For purposes of such analysis intraspecific combat and display functions can be divided into three classes: combat itself; combat-related display (i.e. threat and dominance display); and, courtship display. The first of these involves the greatest number of constraints, for function as a weapon, once the type of weapon is specified, entails strong selection for the form optimal for that type of weapon. This does assume that the number of offspring (and hence the proportion of genes passed on to the next generation) is directly proportional to success in combat, an assumption which shall not be further pursued here. Thus a paradigm (in the sense of Rudwick, 1961) for the weapon should be specifiable and the match of the structure with this paradigm determinable. Weapons may reasonably be suggested to have functioned in combat-related displays as is often the case in living ungulates (Ewer, 1968; Walther, 1974). But other structures could also function in such displays with only the condition that they differ in some fashion from individual to individual (Smith and Parker, 1976): such structures would be subject to few obvious constraints and thus most difficult to identify in fossil vertebrates.

Courtship display structures similarly would be difficult to identify in fossil organisms. However, some suggestions have been put forth (Hopson, 1975): the structures would be expected to be distinctive to the species and sex; they would be expected to accompany an acute sense of vision; and their internal structure might vary independently of their external structure. To be rigorous, demonstration of the species and sexual membership of the specimen must not involve the form of the display structure, otherwise circularity would be introduced into the argument. An acute sense of vision cannot be demonstrated, but only suggested from fossil material.

Geist (1972) suggested a sequence in the evolution of combat and (combat-related) display mechanisms of ungulates and their ancestors. He presumes that the tail was typically used in intraspecific (and interspecific) combat among reptiles, and thus among those synapsids from which mammals ultimately arose. For reasons not clear the use of the tail was replaced by the use of the teeth. Although not explicitly stated, it may be assumed that development of canine teeth permitted the specialization of the remainder of the dentition in an adaptive fashion. Thus canine teeth or tusks came to be used in combat and possibly

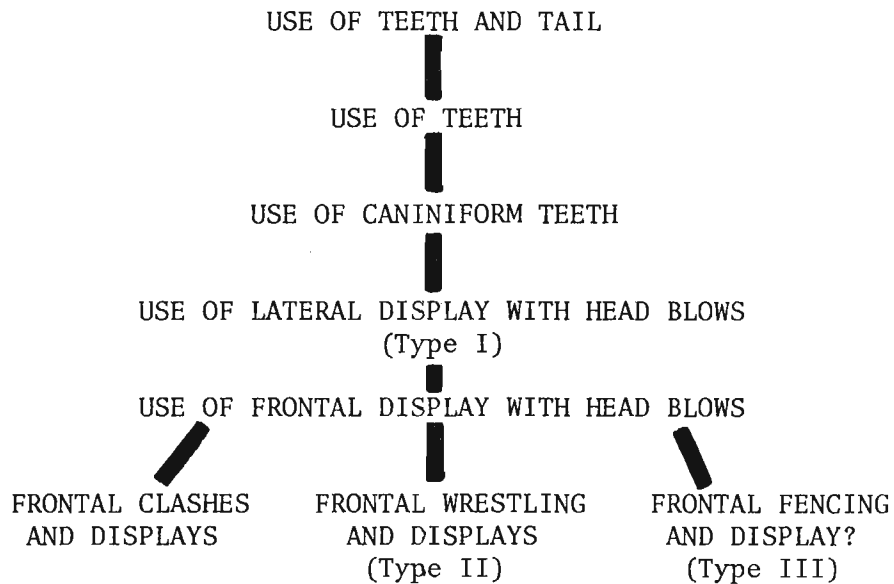


Fig. 1. Sequence of stages in the evolution of cranial combat and display mechanisms in ungulates. See text for further explanation.

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in related display, and this function persisted in forms that became herbivorous, such as the dicynodonts among therapsids and primitive cervids among artiodactyls. Geist suggests that weakness of the jaw joint, attributed to therapsids (Geist, 1972), became less of a liability in combat when combat style shifted to the use of the head to deliver blows (although the details of this shift are not elucidated). This latter style of combat involved lateral (or broadside) displays and the development of horns to concentrate the forces of the blows (Geist, 1966; 1971). Defensive considerations, the catching and deflecting of the blows of an opponent's horns, led to the development of frontal blows (and displays). From this combat style others differentiated, such as the frontal clashes of sheep, the frontal wrestling of antelope and antilocaprids and presumably the frontal fencing of rhinos. This scheme is presented, in outline, in Fig. 1.

While certain portions of this scheme may be criticised (e.g. Ewer, 1968) it does seem to reflect aspects not only of artiodactyl but also of ornithopod evolution. There is evidence to suggest that many ornithopods - as well as ceratopsians and pachycephalosaurs, usually considered to be late derivatives of the ornithopods (Galton, 1972; Thulborn, 1974; Maryanska and Osmolska, 1974) - used cranial structures in combat and display. The evolution of varied crests in hadrosaurs, recently discussed by Hopson (1975) is one example, and another is the massive thickening of the skull roof of pachycephalosaurs (Fig. 3) interpreted as relating to frontal clashes (Galton, 1971; Maryanska and Osmolska, 1974). Another is the exuberent development of horns, spikes and frills of ceratopsians (Fig. 4). Even the psittacosaur, probably ancestral to later ceratopsians, show indication of cranial combat mechanisms. It is also relevant to consider that there is evidence for cranial combat and display among theropods (saurischians): the lachrymal horns of Albertosaurus, Allosaurus and Daspletosaurus; the postorbital excrescences of Indosaurus and Tyrannosaurus; the nasal horns of Alioramus, Ceratopsaurus and Proceratosaurus; and possibly the crests of Dilophosaurus (Fig. 5). This emphasis on cranial "ornament" in

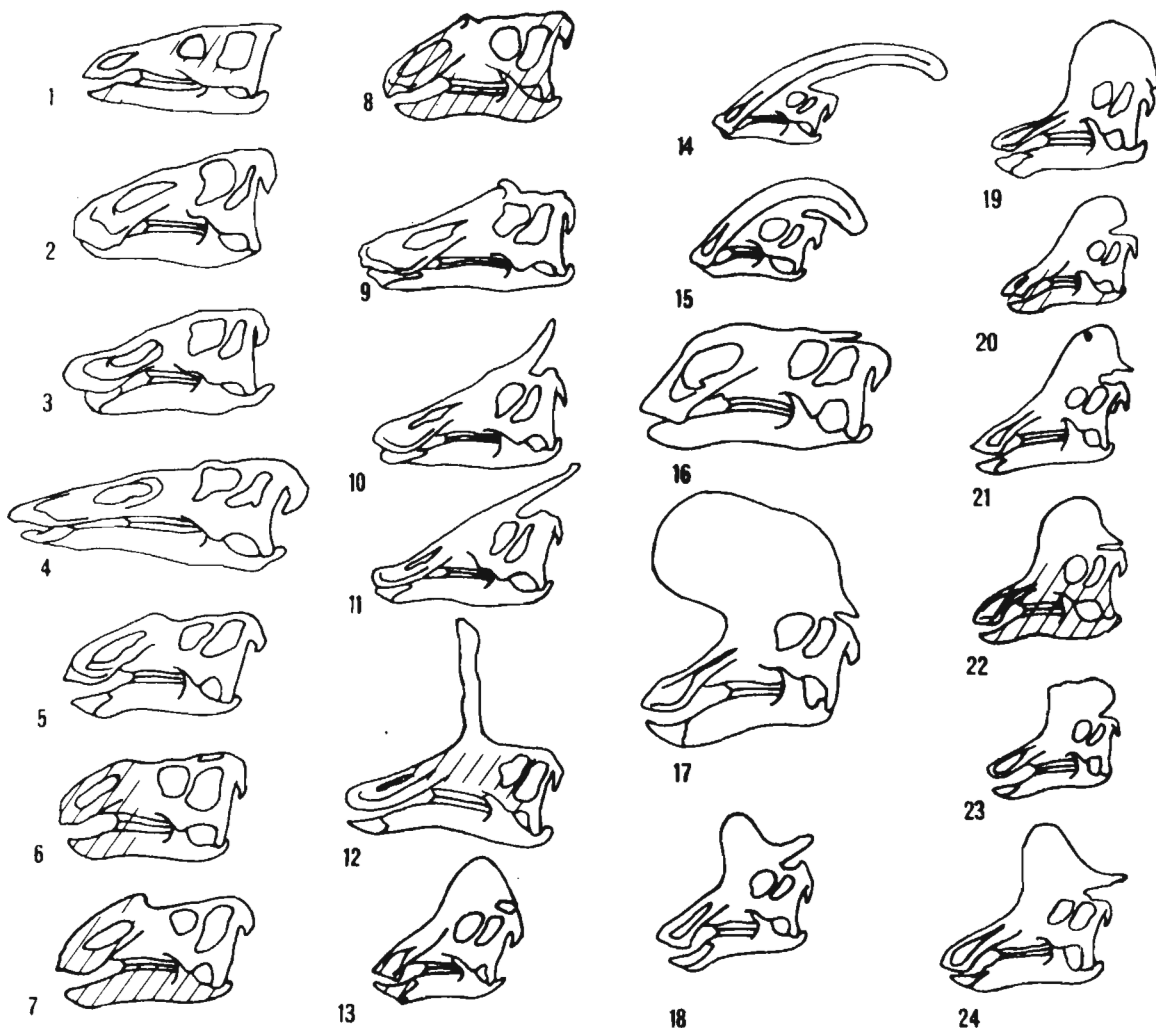


Fig. 2. Hadrosaur skulls showing the diversity of cranial "ornament". Not to scale. 1- Telmatosaurus transsylvanicus. 2- Edmontosaurus regalis. 3- Anatosaurus annectens. 4- Anatosaurus copei (crushed). 5- Kritosaurus notabilis. 6- Kritosaurus incurvimanus. 7- Aralosaurus tuberiferus. 8- Lophorhynchon atopus. 9- Prosaurolophus maximus. 10- Saurolophus osborni. 11- Saurolophus angustirostris. 12- Tsintaosaurus spinorhinus. 13- Hypacrosaurus altispinus. 14- Parasaurolophus walkeri. 15- Parasaurolophus cyrtocristatus. 16- Brachylophosaurus canadensis. 17- Lambeosaurus magnicristatus. 18- Lambeosaurus lambei, presumed male. 19- Corythosaurus casuarius, presumed male. 20- C. casuarius, presumed male (Corythosaurus "brevicristatus"). 21- C. casuarius, presumed female (Corythosaurus "intermedius"). 22- C. casuarius, presumed female (Corythosaurus "excavatus"). 23- C. casuarius, presumed female (Corythosaurus "bicrocristatus"). 24- Lambeosaurus lambei, presumed female (Lambeosaurus "clavinitialis"). Diagonal lines represent reconstructed portions. (After various authors, many after Steel.)

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bipedal dinosaurs, and the apparent lack of such emphasis in most quadrupedal forms other than ceratopsians suggests a relation between bipedality and cran-

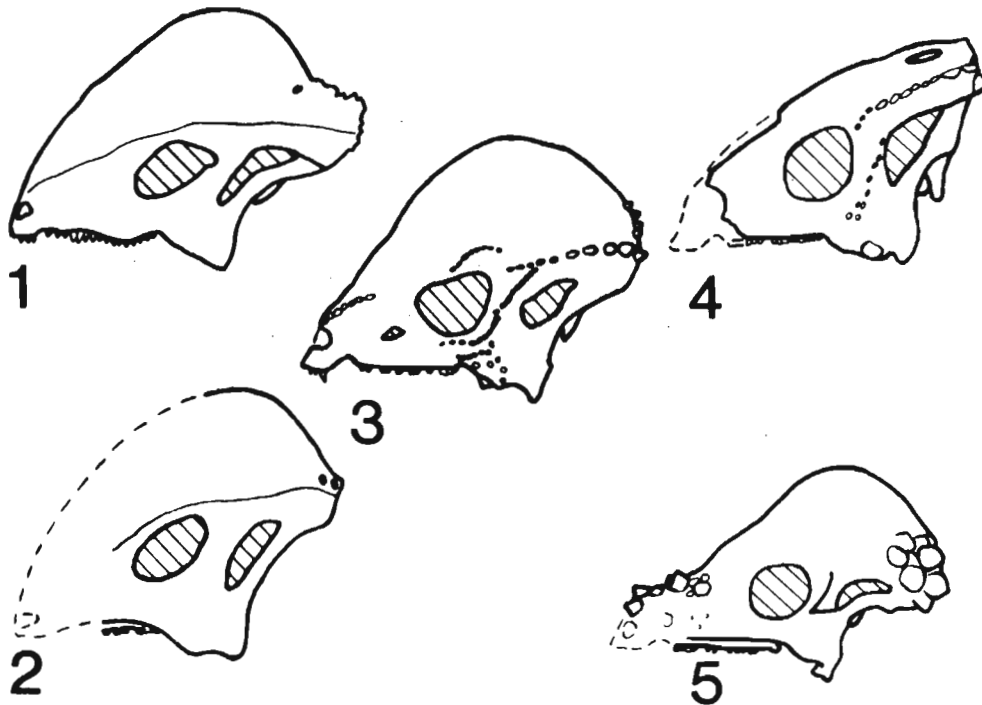


Fig. 3. Pachycephalosaur skulls, Not to scale. 1- Stegoceras validus. 2- Tylocephale gilmorei. 3- Prenocephale prenes. 4- Homalocephale calathocercos. 5- Pachycephalosaur grangeri. (After Maryanska and Osmolska.)

ial combat and display mechanisms in ornithopods not found in ungulates.

This paper will therefore concentrate on two aspects: first, discussion and evaluation of claimed cranial adaptations for combat and display; and second, the general pattern seen among the ornithopods and their late derivatives, and analogous patterns among ungulates. It is recognised that even among ungulates with well-developed horns or antlers, other, non-cranial structures are used both in display and combat (cf. Franklin, 1974; Lott, 1974; Walther, 1974), and this was probably true of ornithopods as well. An obvious example is the manual spike of Iguanodon.

Heterodontosaurs

A remarkable and unexpected feature of at least some Triassic ornithopods (Abriktosaurus, Geranosaurus, Heterodontosaurus and Lycorhinus) was the possession of caniniform teeth. This was unexpected because there is no evidence for such teeth among the later ornithopods (with a single exception) nor among those thecodonts, such as Euparkeria, from which the ornithopods were apparently derived (Bonaparte, 1975). Thulborn (1974) described an apparently female skull, now referred to Abriktosaurus, that did not possess the caniniform teeth, but did have the associated diastema. This suggested to him that the caniniform teeth were a sexually dimorphic character in that species. Steel (1969) and later Thulborn (1974) suggested a display function for these teeth. While this may have been true it would seem likely that they were also useful in biting combat, as among suids (Frédérich, 1974) and primitive cervids (Ewer, 1968; Geist, 1966). If this were the case, then one would expect: 1- strengthening



Fig. 4. Ceratopsian skulls showing the diversity of cranial "ornament". Not to scale. 1- Chasmosaurus belli. 2- C. brevirostris. 3- C. kaiseni. 4- C. russelli. 5- Arrhinoceratops brachyops. 6- Torosaurus latus. 7- Pentaceratops fenestratus. 8- P. sternbergii. 9- Anchiceratops longirostris. 10- Monoclonius flexus. 11- Centrosaurus apertus. 12- Monoclonius nasicornus. 13- M. lowei. 14- M. longirostris. 15- Styracosaurus parksi. 16- S. albertensis. 17- Pachyrhinosaurus canadensis. 18- Triceratops horridus. 19- T. brevicornus. 20- T. prorsus. 21- T. hatcheri. 22- T. obtusus. 23- T. eurycephalus. 24- T. elatus. 25- T. calicornis. 26- T. flabellatus. 27- T. albertensis. 28- T. serratus. 29- Protoceratops andrewsi. 30- P? kozlowskii. 31- Montanaceratops cerorhynchus. 32- Leptoceratops gracilis. 33- Bagaceratops rozhdestvenskyi. Diagonal lines represent reconstructed regions, heavy lines indicate probably pathological openings in the frills. (After various authors, mainly Steel.)

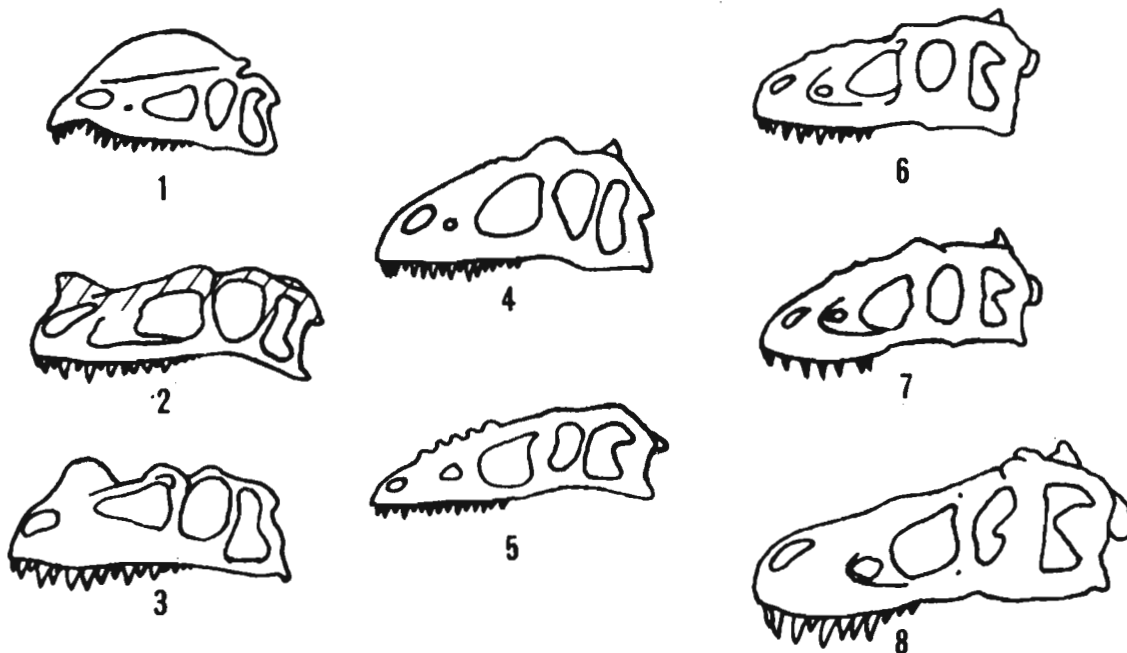


Fig. 5. Various theropod skulls showing the presence of cranial "ornament". Not to scale. 1- *Dilophosaurus wetherilli*. 2- *Proceratosaurus bradleyi*. 3- *Ceratosaurus nasicornus*. 4- *Allosaurus fragilis*. 5- *Alioramus remotus*. 6- *Albertosaurus libratus*. 7- *Daspletosaurus torosus*. 8- *Tyrannosaurus rex*. Diagonal lines represent reconstructed portions. (After various authors, 1 drawn from photo in Welles, 1972.)

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of the atlanto-occipital joint and of the associated cervical musculature; and 2- strengthening of the jaw joint. Unfortunately the published information does not permit a test of the first expectation. The jugal bar, however, of these forms is deeper than that of such thecodonts as *Euparkeria* and this may reflect adaptation to resist increased anteriorly directed forces impressed on the quadrate by the jaw. Such would be expected as a result of adoption of a biting mode of combat with associated holding of the opponent's jaw.

The possession of caniniform teeth by the most primitive (known) members of an extensive terrestrial herbivore radiation prompts comparison with primitive ungulates which also possess prominent canine teeth although herbivorous, and which use these teeth in combat and threat display (Portmann, 1952; Ewer, 1968). Had ungulate evolution been used as a model for that of ornithopods, the possession of caniniform teeth by primitive members of the latter group need have come as no surprise (Fig. 6).

Accepting for the moment Geist's suggestion of the tail as the major combat weapon among reptiles, and assuming that this was also true of Permian as well as modern forms, some consideration about why the tail ceased to be used as a weapon is necessary. This may have resulted from the increasing function of the tail as a balancing organ in bipedal locomotion. *Hypsilophodon*, apparently representative of primitive ornithopods, has a tail made more or less rigid by numerous ossified tendons (Galton, 1974). This suggests that such constraint to lateral flexibility of the tail developed early in ornithopod evolution. Recently, ossified tendons have been described in the tail of *Heterodontosaurus tucki* (Santa Luca, Crompton and Charig, 1976). Thulborn (1972), in a specimen referred (probably incorrectly) to *Fabrosaurus australis*, found the caudal zygapophyseal surfaces to be nearly vertical, an adaptation that would also reduce lateral mobility of the tail. This implies that at least two mechanisms were developed to increase rigidity of the tail, and indicates the importance of a reasonably rigid tail for such forms.



Fig. 6. A primitive cervid (*Archaeomeryx optatus*) skull (A) and a primitive ornithomimid (*Heterodontosaurus tucki*) skull (B). Both show canine or canini-form teeth in a dentition adapted for an herbivorous diet. (A after Colbert, B after Galton).

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A complete absence of lateral mobility of the tail need not be hypothesized, just a significant reduction correlated with the development of the ossified tendons (cf. Ostrom, 1964). Such a development would restrict the ability of the tail to deliver blows. In quadrupedal ornithischians other than ceratopsians (which show indication of bipedal ancestry) there is little indication of cranial involvement in combat or display. There is, however, considerable evidence of caudal involvement which may or may not be primitive, e.g. the caudal spikes of stegosaurs and caudal clubs of ankylosaurs. Nor is there any indication of such emphasis on the head in sauropods (saurischians), where the tail also may have been used in combat (Holland, 1915; von Huene, 1929). Thus it seems reasonable to suggest that, assuming the tail had a primitive role in interspecific combat among the ancestors of the ornithomimids, reduction of the mobility of the tail associated with its function of maintaining balance during bipedal locomotion terminated that role.

Hypsilophodonts and iguanodonts

The Hypsilophodontidae may be considered as the "central" family of the ornithomimids and appear to include, or be close to, the ancestors of the iguanodontids, the hadrosaurids, the psittacosaurids (and hence the ceratopsians) and the pachycephalosaurs (Galton, 1972; 1974). Hypsilophodontids exhibit no obvious evidence of cranial specializations for combat or display. If heterodontosaurids were ancestral to hypsilophodontids then the caniniform teeth were early lost in the main line of ornithomimid evolution. They did, however, persist in one, probably aberrant, line represented only by *Echinodon* (Owen, 1884, Pl. 11, Fig. 1).

The jugal boss of *Heterodontosaurus* (Crompton and Charig, 1962) suggests the possible existence of a second mode of combat in that form involving swinging of the head, the jugal boss acting like a horn to deliver blows. Such blows would presumably be delivered to the flanks of an opponent, with the two animals standing parallel (or antiparallel). Such a mode of combat might be related to the development of the palpebral as a partial bar across the orbit in *Heterodontosaurus* (Coombs, 1972) and, if the mode were retained by hypsilophodontids, in that group as well. Such a partial bar could act to protect the eye during such combat. On the other hand, were that mode retained by the hypsilophodontids a strong jugal boss would be expected. None is known in members of that family, although such processes do appear in the psittacosaurids.

Recently Barrette (1977) has proposed a model for the transition from the use of canines to the use of antlers (or horns) in artiodactyls based on study of the muntjac. The antlers are used, and hence are suggested to have developed, to fend off blows delivered with the canines. The direct application of this model to the heterodontosaurids would predict the development of horns in that group or its descendents, which apparently did not occur. This suggests that either the caniniform teeth were not used as weapons by the heterodontosaurids, or that they were countered in some other fashion not obvious from the fossil record. It would seem unlikely that the jugal boss could easily be used in a fashion to counter blows delivered with the caniniform teeth, so that both the transition from the possible use of the caniniform teeth to the possible use of the jugal process, and the mode of combat used by the hypsilophodontids are unclear and represent a weak point in the analogy between the evolution of combat and display mechanisms of the ornithopods and the ungulates.

Until recently the possible mode of combat of the iguanodontids was also unclear, but the discovery and description of Ouranosaurus (Taquet, 1975) permits the suggestion that that form at least used a form of frontal combat. Because of the similarity and possible relation of Ouranosaurus to the hadrosaurids, it will be discussed along with that group.

Pachycephalosaurs

Galton (1970a; 1971) has convincingly argued that the thickened skull roof of the pachycephalosaurs was used in frontal clashes during intraspecific combat. Having previously shown that many ornithopods probably habitually carried the vertebral column in a nearly horizontal attitude (Galton, 1970b), Galton presented several arguments in favour of the function of the skull roof to strike blows in frontal clashes much like those of Geist's sheep. These include the orientation of the trabeculae within the bone of the skull roof, the fusion of the bones of the roof, the position of thickened bone in relation to the occipital condyle, the structure of the vertebrae and possible sexual dimorphism. Galton's exposition is thorough and requires little comment.

Galton (1971) also described the skull roof of a small Lower Cretaceous ornithopod, Yaverlandia, which represents a primitive pachycephalosaur. In Yaverlandia two low dome-like thickenings of the frontals (much like those found in Ouranosaurus) foreshadow the massive fronto-parietal thickenings of later forms. This double dome would permit operation during clashes of the self-correcting mechanism described by Stanley (1974; and Barghusen, 1975), and strongly suggests that Yaverlandia indulged in frontal clashes. Since presumably there would be no selection for increasing the thickness of the skull roof without clashes, this in turn suggests that some pre-Yaverlandia hypsilophodontids also engaged in frontal clashes. Unfortunately this development appears to have occurred much too late in time (Lower Cretaceous) to be a result of a mechanism for countering blows of the caniniform teeth (which almost entirely disappeared at the end of the Triassic).

Maryanska and Osmolska (1974), in their description of new Mongolian pachycephalosaurs, accept Galton's suggestion as to the role of the fronto-parietal thickening in frontal clashes, but are unconvinced by his suggestion of sexual dimorphism. They argue that were Galton's hypothesis correct then the single specimen of Prenocephale prenes and that of Homalocephale calathocercos, the former domes and the latter not, would have to be interpreted as male and female respectively. Since the two specimens show several differences in other portions of the skull and postcranial skeleton they conclude that such is un-

likely. However other portions of the osteology might be expected to show sexual dimorphism, and with so few specimens (one each) it cannot be decided if Galton's hypothesis is endangered.

Psittacosaurids

Psittacosaurus had an elongate, laterally directed jugal projection (Osborn, 1924) which may have functioned as a horn during lateral swinging of the head. Osborn (1923) also reported a thin dermal armor in the gular region of this form which may have acted to protect the neck from such blows. The jugals were quite long in some species, such as Psittacosaurus sinensis (Young, 1958) and P. youngi (Chao, 1963), prominent enough to have possibly taken on a display function. Were this the case, acute vision would be expected and the large orbit suggests a large eye and hence a good visual sense. The form of the endocranial cavity is unknown so nothing can be said about the development of the optic lobes of the brain. The jugal projections are borne on deep infratemporal bars composed of the jugal and quadratojugal, so that the projections were buttressed against laterally applied forces. Such a mode of combat suggests parallel or antiparallel orientation of two individuals in combat.

Some psittacosaurids (P. youngi) have in addition an incipient nasal horn core (Fig. 7). This horn core is reinforced below by the ascending processes of the maxillae just behind the external nares.

If psittacosaurids delivered blows by swinging the head to strike with either the jugal or nasal projection, exceptional development of the cervical musculature would be expected. Such development is suggested by the relatively large muscle scars of the occipital face of the skull (Fig. 7), approximately as large relatively in Psittacosaurus mongoliensis as the corresponding scars of Stegoceras (which muscles were presumably not used for swinging the head). These scars for epaxial cervical muscles are about twice as large in P. youngi as in P. mongoliensis (Fig. 7). While it is possible that Osborn's specimens of P. mongoliensis represent juvenile individuals, which when mature resembled P. youngi, it must be borne in mind that the figured skull of P. mongoliensis is twenty-five per cent longer in its linear dimensions than that of P. youngi. This in turn suggests a trend from the P. mongoliensis to the P. youngi condition during which the supraoccipitals and opisthotics (and with them the squamosals) became enlarged as a result of the increasing size of the cervical musculature. This together with the posteriad enlargement of the supratemporal fenestrae, may have initiated the trend which eventually resulted in the ceratopsian frill.

The existence of adaptations in the cervical column for increased lateral flexibility, which would be expected from the suggested function of the jugal projections, cannot be verified or falsified from the published descriptions.

Ceratopsians

The ceratopsian frill may have been initiated in part by enlargement of the cervical muscles, but already among the protoceratopsids its evolution was seemingly influenced by a display function. Both Kurzanov (1972) and Farlow and Dodson (1975) consider the frill to have been used in both threat and courtship displays. If so the following would be expected: 1- some evidence for the possession of acute vision; 2- evidence of sexual dimorphism in frill size or shape; and 3- progressive increase in size and ornamentation of the frill during evolution. Taking these in order, the endocranial mold of Protoceratops shows no

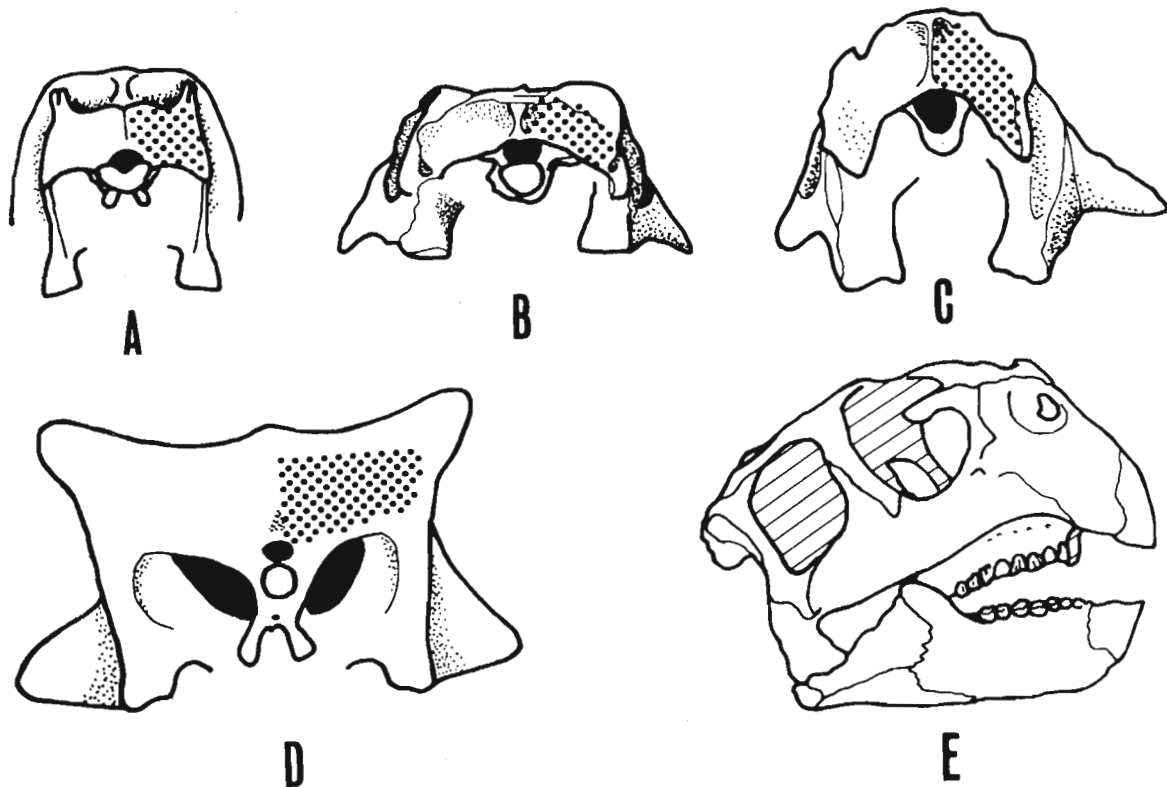


Fig. 7. Occipital aspects of *Hypsilophodon foxii* (A), *Psittacosaurus mongoliensis* (B), *P. youngi* (C), *Bagaceratops rozhdestvenskyi* (D). Presumed attachment areas for epaxial cervical musculature stippled. A and B one-half natural size, C and D two-thirds natural size. Lateral aspect of *P. youngi* skull (E). (A modified after Galton, B after Osborn, C and E after Chao, D after Maryanska and Osmolska.)

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 special development of the optic lobes (cf. Brown and Schlaikjer, 1940), but the orbits are large and in some specimens a sclerotic ring is preserved. This indicates large eyes and presumably good vision (Hopson, 1975).

Both Kurzanov (1972) and Dodson (1976) have demonstrated likely sexual dimorphism in frill size and shape.

Increase in the relative size of the frill during ceratopsian evolution has been shown by Colbert (1948) and Lull and Gray (1949), while increasing elaboration of the frill ornament has been shown by Lull (1933) and Colbert (1948).

Thus the evidence is consistent with a display function for the frill, at least in part: Haas (1955) and Ostrom (1964), among others, have strongly suggested a role for the jaw musculature in the evolution of the frill.

Farlow and Dodson have suggested that the frill ornament, the spikes and epoccipitals, functioned in display pointing out that these structures have no obvious defensive function. The epoccipitals are short and blunt, while the spikes parallel the surface of the forequarters and are thus poorly placed for the delivery of blows (Russell, 1935).

Considering that dominance display implies the existence of individual variation in the display structure (Geist, 1971) it is interesting that Lull (1933) described the variation of these structures in *Triceratops* as "infinite". While some workers have expressed belief that these structures were not of adaptive significance (a recent example being Steel, 1969), others have maintained a more conservative attitude, but expressed uncertainty as to the exact nature of the

adaptive significance (e.g. Colbert, 1948; 1961).

Early speculation about horn function is summarized by Hatcher, March and Lull (1907) and somewhat later by Lull (1933). The major function of the horns was assumed to be defence against predation, and while intraspecific combat was not overlooked it was given less attention. Lull (1933) for example pointed to the apparent absence of sexual dimorphism in ceratopsid horn form and related this absence to the necessity for defensive structures in both sexes in the face of potential predation by the tyrannosaurids. The view of Tait and Brown (1928) that the horns were used to collect fodder never gained acceptance (cf. Nopcsa, 1929; Lull, 1933). Later work (e.g. Colbert, 1948; Lull and Gray, 1949) concentrated on the evolution of form with little interpretation, or else was purely descriptive. Only recently (Davitashvili, 1961; Farlow and Dodson, 1975) has serious attention been given to possible intraspecific combat and display function.

Farlow and Dodson have given the most detailed interpretation of ceratopsian horns and frills in these terms. They applied a model of Geist (1966; 1971) modified by themselves to the Ceratopsia. Three types of intraspecific combat likely to have been used among ceratopsians are described: type I, involving anti-parallel orientation of the bodies of the combatants with blows delivered by relatively small horns (as in *Oreomnos*); type II, derived from type I, involving frontal contact and wrestling (as in antelope); and type III, presumably also derived from type I, and involving frontal fencing with elongate horns (as in rhinos). This is the scheme diagrammed in Fig. 1. Protoceratopsids (Fig. 4, 29 to 33) are considered to have used type I combat, the short-frilled ceratopsids, other than *Triceratops* (Fig. 4, 10 to 17), to have used type II, and the long-frilled forms together with *Triceratops* (Fig. 4, 1 to 9 and 18 to 28) to have used type III combat.

Suggesting these correlations, Farlow and Dodson stop short of explicitly comparing the structures of each group with expectations derived from consideration of the combat style. Delivery of blows in living ungulates that engage in type I combat (e.g. *Giraffa*, *Oreomnos*) involves bending and twisting the neck in order to orientate the head for delivery of blows and some indication of flexibility in the neck would be expected in protoceratopsids if they also used this combat style. It would also be expected that the nasal horn core be firmly supported by the snout and not placed over the external nares where the forces impressed by the blow might fracture the supporting elements. Some specimens might exhibit puncture wounds. Development of armor to protect against blows might also be expected, but since this need not involve osseous elements (*Oreomnos* simply has a thickened skin: Geist, 1971) such armor may not be determinable from fossil remains.

Taking these in order, the ability to twist the vertebral column is often associated with low zygapophyses having nearly horizontal facets (Grant and Basmajian, 1965). The literature indicates that the cervical zygapophyses of the protoceratopsids tended to be high with the facets strongly inclined to the horizontal (Brown and Schlaikjer, 1940; 1942; Sternberg, 1951), suggesting restricted rotation in the cervical column. The figures of Brown and Schlaikjer (1940) however show that the ball-and-socket atlanto-occipital joint characteristic of later ceratopsians was already present in *Protoceratops*. This would allow rotation of the skull without the necessity for twisting the cervical column.

In all cases in which the horn core is preserved it is firmly supported below by the nasals, maxillae and premaxillae (Brown and Schlaikjer, 1940: 1942; Maryanska and Osmolska, 1975). In no case known to me is it placed on the arch over the nares.

No puncture wounds (nor armor) are known in protoceratopsids, but their dis-

covery would be of interest. The previous expectations do not differentiate between blows struck during intraspecific and those of interspecific combat. The evidence suggests that the horns of protoceratopsids were used to strike blows, hardly a novel conclusion, but the existence of wounds would suggest that at least some of these blows were struck in intraspecific combat.

Use of type II combat generates the following expectations: 1- firm buttressing of the brow horn cores; 2- projection of the brow horns anterolaterally beyond the snout (so that they rather than the snout would come into contact with the opponent); 3- protection of the eye and ear; 4- restriction of the adductors attaching to the frill, to the medial portion of the frill, where they would be less likely to be struck and injured; 5- some mechanism to stiffen the cervical column and thus help resist the forces impressed at contact (cf. Galton, 1971); and, 6- puncture wounds in the skull.

The supraorbital horn cores of ceratopsids uniformly are reinforced below by the anterior wall of the orbit and the skull roof. Certain forms, e.g. Pentaceratops, Torosaurus and Triceratops, apparently had the supraorbital horn cores so oriented that their axes were directed through or nearly through the occipital condyle (Fig. 8). This would be of obvious benefit in the transmission of forces from the horns to the vertebral column. It is not clear that this was true of all specimens of Triceratops, but to judge from the illustrations of Hatcher, Marsh and Lull (1907) it was clearly true for T. flabelatus and probably for T. brevicornus, T. hatcheri, T. obtusus, T. prorsus and T. serratus. Possible distortion of the specimens affecting the orientation of the horn cores cannot always be judged from illustrations alone, so that the actual prevalence of this trait cannot be determined from the literature.

When held horizontally the brow horn cores must project beyond the snout to contact an opponent; nonetheless this is not obviously true of all ceratopsids. In some forms, e.g. Anchiceratops (Fig. 4, 9), it is easy to believe that the horn cores were sufficiently lengthened by sheathes to project beyond the snout and contact an opponent, even though the cores themselves do not project beyond the snout (cf. Lull, 1933, Pl. X). For other forms, especially Chasmosaurus belli and C. brevirostris (Fig. 4, 1 and 2), it would seem that a lengthy extension was necessary. In these forms however the nasal horn core is longer than those of the brow horns, and thus these forms may have retained type I combat: development of the brow horns and transition to type II will be discussed later.

The orbit of ceratopsids was usually protected by a raised rim of bone. The external ear (tympanic membrane) would also have been protected being located in the jugal notch, a deep slot between the quadrate and squamosal.

Assuming that the brow horns were held horizontally in each of the contestants during the conflict, the tips of the horns would be able to strike and injure the adductors attaching to the frill (Fig. 9). Restriction of the adductors to the medial portion of the frill would reduce their vulnerability, placing them behind the brow horns which could parry a thrust at them. From the work of Ostrom (1964) it appears that an injury to these muscles could seriously disadvantage an individual's feeding ability. The expectation of medial restriction is borne out by examination of the frills (Fig. 10), and also implicitly suggested by Russell (1935). In Triceratops these adductors may have been reduced in size and thus in that fashion have come to be restricted (Russell, 1935; but also see Ostrom, 1964).

There are no special adaptations for strengthening or stiffening the cervical column, other than the fusion of the first three cervicals (Hatcher, Marsh and Lull, 1907; Lull, 1933). Fusion of more posterior cervicals is reportedly

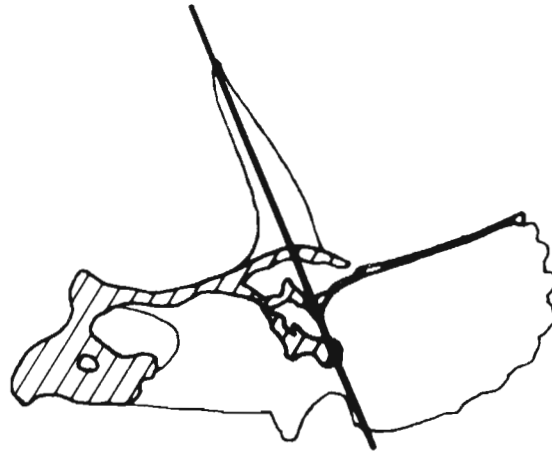


Fig. 8. Cross-section of the skull of Triceratops flabellatus, showing that the axes of the brow horn cores pass through the occipital condyle. (Modified after Marsh).

* * *
 common in ceratopsians (Brown and Schlaikjer, 1940), and it is interesting that such fusion may result from injury sustained by local buckling of the column under compressional forces (Winsberg, 1971; Rooney, 1974), although it can also result from other causes.

Ceratopsids seem to exhibit more abundant cranial injury than other dinosaurs although this may be due to the relative abundance of ceratopsian cranial material. Much of this damage is such as would be expected from blows inflicted by the horns (Swinton, 1970). Possible puncture wounds have been reported in Triceratops elatus (Hatcher, Marsh and Lull, 1907), T. hatcheri, T. serratus, Pentaceratops fenestratus and Arrhinoceratops brachyops (Lull, 1933). Although not mentioned in the text plate VIIA of Lull (1933) shows a probably pathological opening in the frill of Chasmosaurus brevisrostris, much like that of A. brachyops. All of these wounds are represented by anomalous openings usually in the lateral portion of the frill. Other apparent wounds, fractures of the mandible and horn cores, are also known (Moodie, 1930; Swinton, 1970).

Of the six expectations the first four are met, the last two possibly but not clearly met, and none contradicted. The first two expectations suggest only that the horns were used to deliver blows, while the third, fourth and sixth suggest that the blows were delivered, at least sometimes, in intraspecific combat.

Like some bovids certain ceratopsians, especially Triceratops, possessed chambers in the skull immediately beneath the supraorbital horn cores. These seem analogous to the frontal sinuses of bovids which are thought to cushion the brain during clashes (Schaffer and Reed, 1972). The chambers of Triceratops (Fig. 11) are not true sinuses but were formed by the growth of the postfrontals over the frontals and supraoccipitals (Lull, 1933). They may also have functioned as a cushion.

Several expectations are also generated by the hypothesis of the use of type III combat by certain ceratopsians, some of which are similar or identical to those suggested previously. These expectations are: 1- possession of a sharp, and probably long straight, nasal horn core; 2- firm buttressing of this horn core; 3- protection of the eye and ear; 4- absence of restriction of the adductors attaching to the frill; and 5- possible existence of puncture wounds.

In Styracosaurus the nasal horn core, and hence probably the nasal horn, is long and straight. This is true of Centrosaurus apertus, Monoclonius flexus and

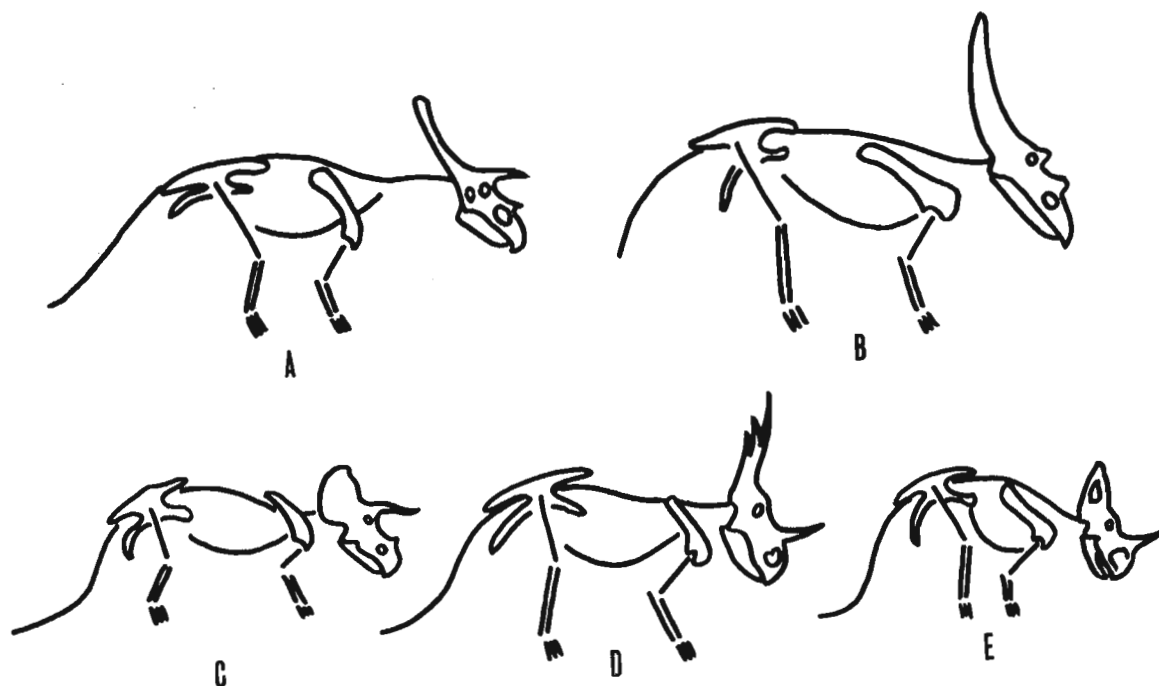


Fig. 9. Posture of various ceratopsians probably adopted for delivery of blows. A, Anchiceratops longirostris, B, Chasmosaurus belli, and C, Triceratops horridus presumably used type II combat and the supraorbital horns are so placed as to easily contact the frill and associated musculature. D, Styracosaurus parksi and E, Monoclonius nasicornis presumably used type III combat and the nasal horns are well below the frill and associated muscles. (Modified from Lull, 1933, and Brown and Schlaikjer, 1937.)

* * *
M. sphenocerus as well (Hatcher, Marsh and Lull, 1907; Lull, 1933). But other forms had distinctly curved nasal horn cores, anteriorly directed in Centrosaurus longirostris, Monoclonius flexus and M. recurvicornis and posteriorly in M. lowei and M. dawsoni. It seems unlikely that either of these latter forms could strike a blow with the tip of the nasal horn if the horn core accurately reflects its form. Anterior curvature of the nasal horn core suggests that a blow could be struck without the necessity of inclining the head as strongly to the horizontal as was necessary, e.g. for Styracosaurus (Fig. 9D). Evidently this expectation is not met by all forms, and some differentiation of combat styles may have occurred.

The skulls sufficiently well preserved all show reinforcement of the nasal horn core below by the nasals and maxillae (cf. Lull, 1933).

As among those ceratopsids suggested to have used type I combat, the orbits and otic regions were protected by a raised rim and the jugal notch respectively.

There is no evidence from the frills of these forms to suggest much restriction of the adductor mass to the medial portion of the frill (Fig. 10A).

No evidence is known to me of puncture wounds in the skull or jaws of these forms, although as with the protoceratopsids such evidence would be of interest.

Of the five expectations four are met, and one of those (the first) incompletely. True, the fourth expectation is a negative one in the sense that it would be equally well met in the absence of intraspecific combat involving the head, so this further reduces the match between expectation and observation. That the first expectation is not more widely met is disturbing, and suggests that type III combat was more restricted among ceratopsids than appeared at

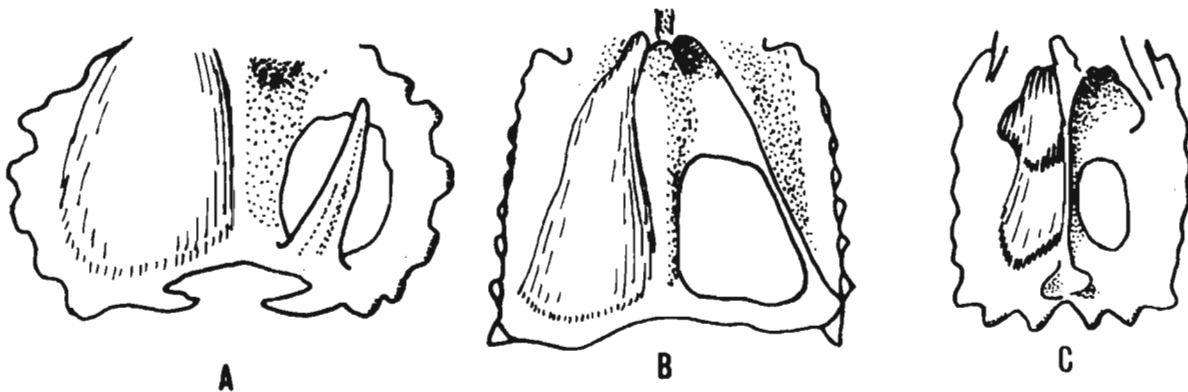


Fig. 10. Ceratopsian frills with adductors reconstructed on the left halves of each. Centrosaurus apertus (A) is suggested to have used type III combat, and Chasmosaurus belli (B), and Anchiceratops longirostris (C), to have used type II combat. The posterior and medial restriction of the adductors can be seen. (B and C after Russell.)

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first sight.

One genus, Pachyrhinosaurus, was singled out by Farlow and Dodson as probably not having exhibited any of these three modes of combat. They suggested that this form engaged in shoving matches, presumably similar to those of many artiodactyls (Ewer, 1968) or those suggested by Barghusen (1975) for some dinocephalians. The nasofrontal boss of Pachyrhinosaurus is of course thickened as are the bones of the snout which buttress it, and the cranial bones in general are firmly fused together (Langston, 1975). All of these would be expected for a form engaging in shoving matches or clashes.

It seems quite reasonable to interpret the horns of ceratopsians as analogous to those of many ungulates, and the frills as display structures in part. There may, however, have been more diversity in combat style than suggested by Farlow and Dodson. It is tempting to analogize the later protoceratopsids (e.g. Montanaceratops) with the surviving primitive bovids and the ceratopsids with the larger, more advanced bovids in terms of horn development. Because such primitive bovids are usually forest-dwelling forms, and the more advanced ones plains-dwelling (Estes, 1974) such an analogy would suggest similar habitats respectively for the later protoceratopsids and ceratopsids.

Hadrosaurs

Contemporaneous with the later ceratopsians, hadrosaurs developed a great variety of solid and hollow crests and "Roman noses". The early hadrosaurs are unfortunately poorly known, so that the existence of such cranial ornament among them is problematic (Steel, 1969). These various crests have recently been linked to a combat and display function by Hopson (1975), who has thoroughly summarized earlier thought on their function.

Hopson has proposed, following Abel (1924) and Davitashvili (1961), that hadrosaur crests were visual and acoustic display structures, functioning in threat and courtship and possibly dominance displays. From this hypothesis he predicts: 1- hadrosaurs had well-developed eyes and ears; 2- the external characters of the crests could vary independently of the internal structure; 3- crest form was species-specific and sexually dimorphic; 4- distinctiveness of the crest should correlate with species diversity; and 5- crest size increased

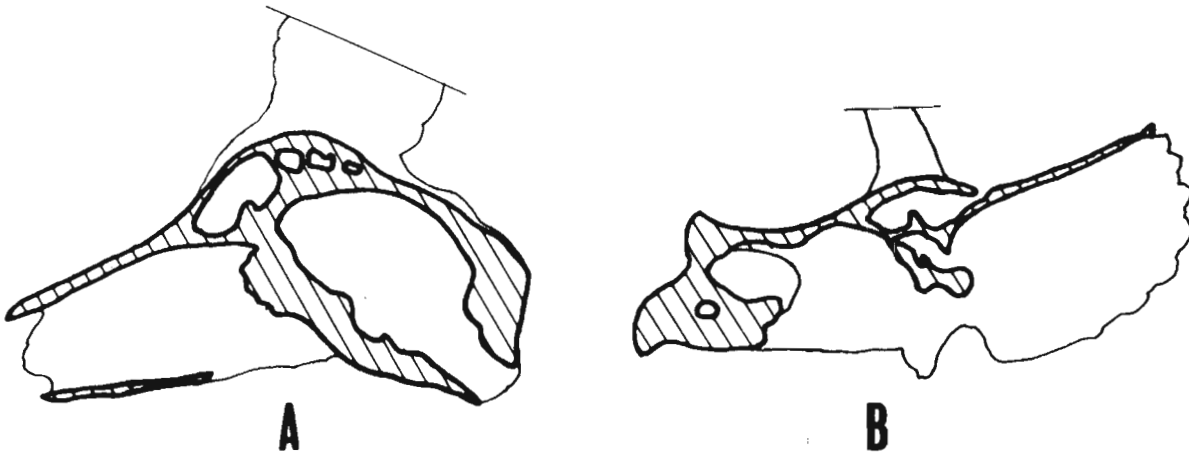


Fig. 11. Parasagittal sections of the skulls of Capra ibex (A) and Triceratops flabellatus (B) to show the chambers beneath the supraorbital horns. (A from photograph in Schaffer and Reed, B after Marsh.)

* * *
 with time. Hopson also suggests that the nasal projections of the kritosaurs functioned as horns. In time these became associated with inflatable nasal diverticula, which took on an acoustic and later a visual display function. In the lambeosaurs these diverticula became surrounded by sheets of bone growing out from the premaxillae and nasals to form hollow crests, while in the saurolophs the diverticula were supported by solid crests growing posteriorly from the nasals. Hopson thus proposes that the kritosaurs are primitive hadrosaurs from which the lambeosaurs, saurolophs and edmontosaurs evolved. His hypothesis has the distinction that it is the first single hypothesis to account for all hadrosaur cranial "ornament".

Although Hopson's argument is reasonable and well set forth, certain criticisms can be made especially concerning his third to fifth predictions and certain suggested relationships. These do not invalidate the hypothesis as a whole. In the discussion of his third prediction, Hopson emphasizes that signal (display) structures used in courtship act as genetic isolating mechanisms. Thus it is logical to expect his third prediction to be met. This prediction involves a double correlation between crest form and species membership on the one hand and crest form and sexual membership on the other. To demonstrate this assertion, determination of the sexual and specific membership of the specimens must be carried out without using crest form, for otherwise no correlation can be made. Unfortunately this has not been done, Hopson citing Dodson (1975) to show that the observed data substantiate the prediction. Dodson however studied cranial characters only, and found that the differences "are confined to several parameters of the bony crest" (1975, p. 50). Thus the data are interpretable in terms of the prediction but strictly speaking do not verify it.

Hopson's fourth prediction involves a similar problem. How is species diversity to be determined for lambeosaurs (and saurolophs) without reference to crest form? In fact much of the diagnoses have rested on crest form (Lull and Wright, 1942; Dodson, 1975). Again Hopson's prediction is a reasonable interpretation of the data. What is needed is thorough investigation of the postcranial anatomy of hadrosaurs in an effort to determine both specific and sexual membership independently of cranial form (perhaps by pelvic form).

To test increase in crest size with time Hopson has relied on the sauroloph lineage (since the lambeosaurs do not seem to exhibit such a trend, the latest known member, Hypacrosaurus, having a smaller crest than its predecessors). Hopson assumes a lineage in which Tsintaosaurus represents the most advanced

form. Tsintaosaurus clearly possessed the largest crest of the saurolophs (Fig. 2, 12) and such a lineage forms a sensible morphological series. Hopson suggests a Maestrichtian age for this genus, but Rozhdestvenskii (1971; 1974) claims a much earlier, pre-Campanian age. If this is true then there is no clear evidence in support of Hopson's fifth point.

No predictions are presented for Hopson's hypothesis that the nasal projections of the kritosaurs acted as horns. Some may however be stated: 1- the nasal projection (like ceratopsian horns) would be firmly buttressed below; 2- some protection for the eye and ear might have been developed; 3- the occipital condyle and atlas would be strengthened to resist the shock of contact (as in sheep, Geist, 1971).

The kritosaur nasal projection is indeed reinforced below by the lachrymal, jugal and maxilla (Lull and Wright, 1942; Lanston, 1960; Rozhdestvenskii, 1968).

Unlike ceratopsians, hadrosaurs did not develop any obvious bony protection for the eye or ear.

Information about the occipital condyles and atlas was available from the literature only about Kritosaurus and Lophorhodon (Lull and Wright, 1942; Langston, 1960). Together with these was considered Ouranosaurus even though an iguanodont because it also possesses a frontal projection roughly (but not in detail) like those of kritosaurs (Fig. 12). Also Taquet (1975) suggested that this genus is close to the ancestry of the hadrosaurs. These forms were compared with Camptosaurus and Hypsilophodon representing more conservative (and earlier) ornithopods, and Edmontosaurus and Iguanodon representing a flat-headed hadrosaur and iguanodontid. Comparison of the development of the occipital condyle and atlas was ambiguous, Lophorhodon (and Iguanodon) had relatively large condyles, while Kritosaurus and Ouranosaurus did not. Edmontosaurus had a relatively small condyle. Such results do not clearly support the hypothesis.

Nor was there any indication of a more robust atlas-axis complex in Kritosaurus or Ouranosaurus than in any of the others.

Only one of the three expectations is clearly suggested by the data.

The existence of the inflatable diverticulum is suggested by the nasal excavations found in hadrosaurs (and also in ceratopsians for whom such a diverticulum has not yet been suggested). Clearly some more, independent evidence is needed.

This last suggestion seems to run into some difficulty (like many others that have been proposed) with the saurolophine lineage. Accepting for the sake of the argument Hopson's suggested lineage (Lophorhodon to Prosaurolophus to Saurolophus to Tsintaosaurus) the trend is from the function of the frontal projection ("Roman nose") as a weapon to gradual replacement of the weapon function by a display function of the diverticulum. This presumably took place by a process like that described by Smith and Parker (1976). If the weapon reduced its significance and use, it would be expected to be reduced in size. This does not occur and Saurolophus has a slender, well-developed crest. Hopson argues that this crest was too slender to effectively function as a weapon, but it is as robust as those of Oreamnos and Rupicapra, and more robust than that of Nesotragus, all of which do function as weapons. Because the nasal excavations associated by Hopson with the diverticulum extend up onto the crest, it would be expected that this diverticulum might interfere with any weapon function of the crest, and these excavations and diverticula would be reduced or lost. This seems to be the case for Tsintaosaurus has a crest onto which the nasal excavations do not intrude (Young, 1958). All of this suggests that while the nasal diverticulum may have been present, it may not have relieved the crest of a weapon function. Or else Tsintaosaurus may not be a descendant of Saurolophus.

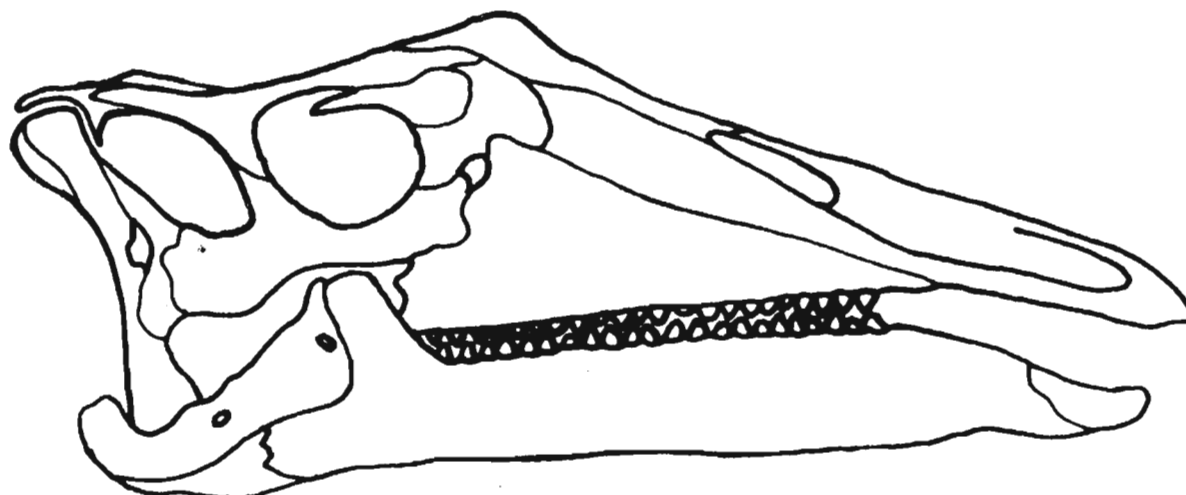


Fig. 12. Skull of *Ouranosaurus nigeriensis*. (After Taquet.)

In spite of these criticisms, Hopson has shown that it is reasonable to view the cranial crests of hadrosaurs as possible display structures. He has also suggested that the preorbital projections of certain hadrosaurs functioned as weapons in combat. Given the inherent limitations of work with fossil material this is perhaps as much as can reasonably be expected. Little discussion of the selective pressures responsible for such structures is given, especially concerning the origin of these combat and display styles. Rather than perfecting the preorbital "horn", selection in the hadrosaurs apparently resulted in the evolution of display structures and the abolition of the weapon function largely or entirely in some lines. The saurolophs and *Brachylophosaurus* presumably used their crests as weapons, at least to some extent, the latter form engaging in shoving matches analogous to those hypothesized for *Pachyrhinosaurus* (Hopson, 1975). How the weapon function came to be lost in some lines and the display function emphasized needs explanation, as some combat function should have been necessary from time to time to reinforce the effect of the display.

Nothing like this is known to me to have occurred among ungulates, other than in very general terms, and thus the hadrosaurs show the limitations of the comparison between ornithischians and ungulates.

Summary of evolution of combat and display in ornithopods

The following pattern can be made out for ornithopods and their derivatives. Adoption of an herbivorous diet by one group of thecodonts, ultimately ancestral to the ornithischians, led to selection for a dentition suited to such a diet. This in turn interfered with the use of the dentition in combat (and possibly, related display). Adoption of bipedal locomotion by this same group of thecodonts, quite likely prior to the adoption of the herbivorous diet led to selection for a rigid tail and hence interfered with a caudal role in combat. If bipedal locomotion were adopted after the herbivorous diet, it might be expected that the teeth would not have taken on a role in combat, hence the suggestion that bipedal locomotion came first. Evolution of caniniform teeth allowed the dentition to function both in combat (and possibly display) and in preparation of the vegetable food. Further selection for a more efficient dentition led to the loss of the caniniforms in most lines and the development of some mode of display (possibly lateral) and some mode of combat involving the head. One line eventually developed frontal ramming, thickening the frontals and parietals and becoming the pachycephalosaurs. One

or more lines of large forms may have swung the head to deliver blows during combat with the bodies in an antiparallel orientation, developed a nasal projection, and evolved into the kritosaurs. Kritosaurs apparently diversified their behavior in several directions not all clear. Some may have evolved an inflatable diverticulum used in both visual and acoustic display, later encasing it in bone and developing into the lambeosaurs. Some (Brachylophosaurus) apparently adopted frontal shoving as a combat mode. Some developed a solid crest likely useful as a horn or to support a display structure, and became the saurolophs. Some may have lost the diverticulum and became the edmontosaurs. The various selective pressures here are not clear.

Another group probably also swinging the head to deliver blows developed first a jugal projection which acted as a horn, and later a nasal horn. These became the psittacosaur. Use of the head in such a fashion led to selection for enlargement of the cervical epaxial musculature and hence of the insertion area of these muscles on the skull. This, together with selection related to the masticatory apparatus, may have initiated the ceratopsian frill. The process whereby the nasal horn replaced the jugal "horn" as a weapon is not clear and needs further work. Use of the nasal horn in frontal clashes led to the development of type I combat and the protoceratopsids. The frill became involved with courtship and combat-related display (as well as with the jaw musculature). Refinement of type I combat led to the development of type III combat among certain ceratopsians of the short-frilled line. The long-frilled line developed brow horns and these replaced the nasal horn as primary weapons in frontal clashes and type II combat was developed. One line adopted the frontal shoving match and led to Pachyrhinosaurus. A transition occurred in the short-frilled line, also leading to the development of brow horns and type II combat in the line leading to Triceratops. This last transition seems conceptually difficult and requires further comment.

Transition from type I combat of the protoceratopsids to type III of the long-frilled ceratopsians can plausibly be ascribed to the development of brow horns functioning in frontal clashes to concentrate the force delivered by contact of the supraorbital portions of the combatants' skulls. Protoceratops already foreshadowed this development (Kurzanov, 1972) suggesting that this transition occurred early in at least one ceratopsian line. But the transition from the elongate nasal horn of ceratopsids such as Monoclonius with small to nonexistent supraorbital horns to the elongate brow horns and small to nonexistent nasal horn of Triceratops is less obvious. There is of course the alternative that it did not in fact occur. While Monoclonius is usually considered ancestral to Triceratops (e.g. Lull, 1933) the evidence is not compelling.

On the other hand one is rarely so fortunate as to be able to successfully resolve a problem by simply denying its existence; and Lull (1933) has pointed out that Agathaumas, unfortunately known only from the postcranium, has features suggesting that it may have been transitional between Monoclonius and Triceratops. It might be that fencing with elongate, single nasal horns led to difficulties in defense, particularly in the parrying of blows. This seems to be the case in rhinos, which reportedly relatively often suffer injury in combat (Goddard, 1973). If the clash were delivered head on (as in rhinos), the skulls of ceratopsians being broader than those of rhinos, any blow not parried would result in contact of the skull roofs, the nasal horns slipping off the snouts. Such a clash might lead either to a shoving match, as in Pachyrhinosaurus, or to the development of horns elsewhere on the dorsum of the skull, as in Triceratops. The brow horns would be expected to develop rapidly while the nasal horn, because it was still used in combat would be lost more slowly as the behavior altered

to make use of the brow horns.

Parallel with artiodactyls

The parallel with the ungulates, especially the artiodactyls, is not such as involves the entire anatomy, locomotor adaptations being among the more obvious differences. Too, forms other than ungulates exhibit analogies to some specific combat and display adaptations of certain ornithischians, e.g. the development of horns in chamaeleons and ceratopsians (cf. Bustard, 1963). The striking parallel is in the sequence of development of these structures, set forth in the introduction and elucidated in the following sections, and in the inferred behaviors resulting in the observed structures.

Presumably both ornithopod and ungulate ancestors at some stage used either the tail solely, or more likely, the tail and teeth in combat. This however is probably the basic condition from which most tetrapods developed and thus cannot be considered as part of the parallel. (In addition, it is somewhat more removed from the ungulates than from the ornithopods.) Both lines early develop canine or caniniform teeth, which were later lost in many (but in both cases, not all) lines. Ungulates clearly (Geist, 1971; Frädrich, 1974), and ornithopods by inference (Hopson, 1975), later adopted lateral displays and combat modes, which were even later replaced by frontal modes. These frontal modes may involve clashes, as in sheep and pachycephalosaurids, shoving matches, as in antelope and Brachylophosaurus and Pachyrhinosaurus, and frontal fencing, as in rhinos and some ceratopsians.

Such analogies are likely controlled by the initial adoption of an herbivorous diet and later of the use of the head to strike blows in combat in both cases. That such a general pattern is not simply set by the adoption of the role of large terrestrial herbivore is demonstrated by the macropodids which although superficially more resembling the ornithopods than do the artiodactyls have adopted use of the fore and hind limbs in intraspecific (and interspecific) combat. Thus they show a very different sequence of evolution of combat and display modes.

Specialization of the dentition

Geist has suggested that first development of the canine teeth and later shift to frontal contact in combat allowed increasing specialization of the cheek teeth of ungulates. Although not explicitly stated, the situation would seem to be that development of canine (or caniniform) teeth relaxes the selection pressures related to display on the postcanine dentition. With the development of canines, selection for combat function on the postcanines would be relaxed, allowing evolution of more efficient food preparation in an herbivorous form, where selection for combat function would presumably conflict with selection for more efficient grinding of vegetable food. Shift of combat (or display) function to frontal structures would further reduce conflicting pressures on the dentition allowing the loss of the canine teeth and specialization of the entire dentition for feeding.

Geist has shown that this specialization of the dentition occurs in artiodactyles, and it might be expected among the ornithopods as well. Certainly the heterodontosaurs exhibit an herbivorous dentition specialized over that of their presumed ancestors among the thecodonts (such as Euparkeria; cf. Bonaparte, 1975). And such dental specialization was further refined in such later groups as the hadrosaurs with the grinding tooth batteries (Kripp, 1933; Ostrom, 1961)

and the ceratopsians with their shearing dentition (Ostrom, 1964).

Use of the tail in reptilian combat

One aspect of this general scheme which may be criticised is the assumption that the tail was widely used in intraspecific combat among primitive reptiles. This indeed may have been the case, in any event use of the tail in combat is widely known among modern reptiles (Holland, 1915; Carpenter, 1961; Harris, 1964; Bellairs, 1966; Pooley and Gans, 1976) and it is sometimes used in combat-related display (Milstead, 1970).

Neill (1971) has recently claimed that observations of the use of the tail in combat by crocodylians are "a myth", but in fact presents very little evidence in support of his contention. He reports that Ditmars perpetrates this myth, but does not point out (as Guggisberg does, 1972) that Ditmars (1933) reported this as a first-hand observation. Others have also reported such usage (Cott, 1961; and others cited by Guggisberg, 1972). I have made no observations on crocodylian behavior myself, but do not accept that the absence of a behavior in nature can be reliably inferred from its absence under artificial conditions, which is basically what Neill does. Indeed Neill also claims as mythical other behaviors of the crocodile more recently verified in the field (cf. Graham, 1973; Pooley and Gans, 1976). In the absence of compelling evidence that Neill is correct, and in view of reported observations of the use by crocodylians of the tail to deliver blows, I shall tentatively assume the observations to be accurate.

Even though use of the tail is widespread, found in lizards and crocodylians, (and eliminating from consideration both turtles in which the tail is reduced and snakes which have no other appendages save the head) this does nothing to demonstrate whether or not the tail was used by primitive reptiles. Such usage may have independently evolved in both lizards and crocodylians. It would seem most likely that both tail and teeth were used by primitive reptiles, which, when standing firmly on all four legs have no other appendages to fight with. Use of the limbs might not be expected as they were relatively short in most primitive reptiles and would be needed to provide stable support. If this were the case, then the shift was not from tail to head, but rather a decrease in emphasis on the tail and an increase in emphasis on the head which was already being used. The argument presented previously in regard to the decreased mobility of the tail and its relation to the use of the caniniform teeth would still be applicable.

Conclusions

The behavior of extinct organisms cannot be observed but only (at best) inferred. Such inference can be taken to be likely if the structure under consideration can plausibly perform the inferred action (Rudwick, 1964). Several suggested intraspecific social functions of cranial structures of ornithomorphs, pachycephalosaurs and ceratopsians have been presented or culled from the literature. These include use in intraspecific combat or display of the caniniform teeth of heterodontosaurs, the jugal projections of psittacosaurids, the horns and frills of ceratopsians, and the use in combat and combat-related display as well as in courtship display of the crests of hadrosaurs and Ouranosaurus. By and large the structures of these organs match the expectations deduced from their suggested social functions. The match is less convincing for certain

hadrosaurs.

The general sequence of evolution of the display and combat modes seems basically similar for the ornithopods and their derivatives the pachycephalosaurs and the ceratopsians as for the artiodactyls. This sequence was probably controlled by the adoption of herbivory by the carnivorous (or insectivorous) ancestors and of the use of the head to deliver blows in combat. Large terrestrial herbivores that used other appendages to strike blows, such as the macropods, did not follow this sequence.

I would like to thank Valerius Geist, James Grier, Bonnie Dalzell, and an anonymous reviewer for their criticism and comments, and James O. Farlow and Peter Dodson, James A. Hopson and Philippe Taquet for making available at the time unpublished manuscripts and information.

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