Zoological Journal of the Linnean Society (1997), *121:* 293–337. With 10 figures

Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): taxonomic and behavioral implications

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Received June 1995; accepted for publication August 1996

Centrosaurine ceratopsians are characterized by well developed nasal horncores or bosses, relatively abbreviated supraorbital horncores or bosses, and adorned parietosquamosal frills. Recent study of several paucispecific (low diversity) bonebed assemblages in Alberta and Montana has contributed greatly to our understanding of ontogenetic and taxonomic variation in the skulls of centrosaurines. Relative age determination of centrosaurines is now possible through examination of ontogenetic change in several characters, including the surface bone morphology of specific skeletal elements. The within-group taxonomy of centrosaurines is based almost entirely on characters of the skull roof, relating particularly to horns and frills. Juvenile and sub-adult centrosaurines are characterized by relatively simple, unadorned skulls compared to their adult counterparts. As in numerous living taxa, the cranial ornaments of centrosaurines developed late in ontogeny, as individuals approached or attained adult size. An important implication arising directly from this study is that juvenile and sub-adult centrosaurines are difficult to distinguish taxonomically at the specific level. Two monospecific genera represented only by immature materials, *Brachyceratops montanensis* and *Monoclonius crassus*, cannot be defended and should be considered *nomina dubia.* The late ontogenetic development and diverse taxonomic variation of horn and frill morphologies support the contention that these structures are best interpreted as reproductive characters employed in mate competition.

ADDITIONAL KEY WORDS:—Centrosaurinae – horned dinosaurs – taxonomy – variation – mass death – mate competition – bonebeds.

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INTRODUCTION

The horned dinosaurs, or Ceratopsia, are perhaps the best represented dinosaurian clade, with several genera known from hundreds of skeletal elements, including numerous complete or nearly complete skeletons. For example, *Protoceratops* and *Psittacosaurus* are small-bodied Asian forms each known from dozens of partial and complete skeletons, generally recovered as isolated specimens (Brown & Schlaikjer, 1940a, b; Sereno, 1986; Dodson & Currie, 1990). The clade Ceratopsidae consists of large-bodied, North American forms also represented by numerous partial and complete skeletons (e.g. *Styracosaurus*; Brown & Schlaikjer, 1937). In addition, ceratopsids are commonly found in low diversity (paucispecific) mass death assemblages containing tens, hundreds, and perhaps thousands of individuals, with most assemblages dominated by what appears to be a single species (Currie & Dodson, 1984; Lehman, 1989; Rogers, 1990; Sampson, 1995a, b). This remarkable abundance stands in stark contrast to most dinosaurian groups. Approximately half of all known dinosaur genera are represented by single specimens, and complete skulls and skeletons are known for only about 20% of these taxa (Dodson, 1990a).

Ceratopsia consists of North American and Asian Cretaceous ornithischians, generally divided into Psittacosauridae, Protoceratopsidae, and Ceratopsidae, with the latter two groups placed in Neoceratopsia (Sereno, 1986). While Psittacosauridae and Ceratopsidae are recognized as monophyletic clades, monophyly of Protoceratopsidae has been questioned and appears in doubt (Sereno, 1986). For the purposes of this discussion, we refer to all protoceratopsid 'grade' taxa simply as protoceratopsians. Ceratopsids are confined to the Late Cretaceous and are divided into two monophyletic clades: the short-frilled forms, or Centrosaurinae, and the long-frilled forms, or Chasmosaurinae (Lehman, 1990). Other than isolated specimens found in Alaska (Currie, 1989), all known centrosaurine fossils have been recovered in Alberta, Saskatchewan, and Montana. Recognized genera within Centrosaurinae include *Monoclonius* Cope 1876, *Centrosaurus* Lambe 1904, *Styracosaurus* Lambe 1913, *Brachyceratops* Gilmore 1914, *Pachyrhinosaurus* Sternberg 1950, and *Avaceratops* Dodson 1986. Sampson (1995a) recently erected two additional genera, *Einiosaurus* and *Achelousaurus*, from the late Campanian of Montana.

Vertebrate paleontologists must delimit species strictly on morphological grounds, usually employing a single subset of morphology, fossilized bones. Although clear distinctions between species are sometimes apparent, often they are not, and we are faced with the uncomfortable reality that "a species is a species if a competent specialist says it is" (Raup & Stanley, 1978: 108). The problem is one of compartmentalizing variation into supposedly discrete units. Perhaps the best (if not the only) way to increase the relative degree of objectivity in species determinations is to gain a better understanding of intraspecific variation. Such an understanding is critical to addressing virtually all paleontological questions, from taxonomy and phylogeny to function and behavior (Sampson & Ryan, in press). Therefore, mass death assemblages offer important and unique opportunities to investigate variation within species, particularly when there is confidence that a given bonebed sample is dominated by a single taxon.

We present here the first analysis of the ontogeny of centrosaurine ceratopsians, based largely on several low diversity mass death assemblages. Each of these bonebeds includes remains of individuals from a range of size and age classes. Thus it is now possible to provide at least a preliminary assessment of intraspecific variation relating to ontogeny, individual differences, and potential sexual dimorphism. Ceratopsid taxa are remarkably conservative in their osteology other than the skull roof; braincases, jaws, vertebrae, limb elements, etc. appear to vary as much or more within ceratopsid species as between them (Sampson, 1993, 1995a), although postcrania have received minimal formal study. This investigation focuses on variation in four regions of the centrosaurine skull roof: (1) nasal horncores; (2) supraorbital horncores; (3) frontal fontanelle and supracranial cavities; and (4) parietosquamosal frill. In each case, we address the general features, ontogeny, and taxonomic variation particular to that region.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, New York; ANSP, Philadelphia Academy of Natural Sciences, Philadelphia, Pennsylvania; MOR, Museum of the Rockies, Bozeman, Montana; NMC, Canadian Museum of Nature, Ottawa, Ontario; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UALVP, University of Alberta Laboratory of Vertebrate Palaeontology, Edmonton, Alberta; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.; YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut.

Table 1. Selected measurements of centrosaurine parietals (mm): * = estimate. Taxon Code: A = *Achelousaurus*; Av = *Avaceratops*; B = *Brachyceratops*; C = *Centrosaurus*; E. procurv. = *Einiosaurus procurvicornis*; M = *Monoclonius*; P = *Pachyrhinosaurus*; S = *Styracosaurus*. Age class code: J = juvenile; SA = sub-adult; A = adult; OA = old adult. One-half width: (R) = right; (L) = left; (A) = average of right and left where preserved. SL/W Ratio = Sagittal Length/One-Half Width. Sagittal Thick. = Sagittal Thickness

Specimen#	Designated[1] Taxon	Age Class	Sagittal Length	Total Length	One-Half Width	SL/W Ratio	Sagittal Thick.
NMC 971	*C. apertus*	A	421	620	445 (R)	0.95	66
NMC 348	*C. flexus*	A	537	–	573 (R)	0.94	55
NMC 11839	*C.* sp.	SA	495	570*	355 (R)	1.40	33
NMC 8795	*C. longirostris*	OA	470	688	468 (A)	1.00	54
NMC 8798	*C. dawsoni*	A	460	590	450 (R)	1.02	–
AMNH 5351	*C. nasicornis*	OA	508	679	418 (R)	1.22	56
AMNH 5239	*C. flexus*	A	511	775	477 (L)	1.07	44
AMNH 5429	*C.* sp.	A	545	650	470 (R)	1.16	–
ROM 767	*C. apertus*	A	443	580	388 (A)	1.14	30
UALVP 16248	*C.* sp.	OA	460*	590	–	–	47
UALVP 11735	*C.* sp.	OA	503	656	480 (A)	1.05	38
TMP 86.126.1	*C.* sp.	SA	434	535	499 (A)	0.87	52
NMC 344	*S. albertensis*	A	379	1000*	408 (L)	0.93	60*
MOR 456–8–9–6–1	*E. procurv.*	A	500*	830*	363 (L)	1.38	41
MOR 456 Skull 2	*E. procurv.*	A	474	810*	–	–	44
MOR 485	*A. horneri*	A	535	854	390 (L)	1.37	55
TMP 86.55.157	*P.* sp.	SA	530*	–	–	–	17
AMNH 3998	*M. crassus*	SA	508	541	413 (R)	1.23	24
NMC 8790	*M. lowei*	SA	609	725	477 (L)	1.23	19
AMNH 5442	*M.* sp.	SA	556	595	445 (L)	1.25	26
ROM 1427	*M.* sp.	SA	481	–	382 (R)	1.26	–
TMP 80.54.1	*M.* sp.	SA	530*	575*	449 (R)	1.18	19
TMP 82.16.11	*M.* sp.	J	215*	225*	125 (L)	1.72	13
USNM 7951	*B. montanensis*	J	269	290	–	–	12
USNM 7956	*B. montanensis*	J	286	–	–	–	12
USNM 14765	*B. montanensis*	SA	533	630	382 (R)	1.40	24
ANSP 15800	*Av. lammersi*	J	344	–	224 (A)	1.54	13

[1] Designated taxon refers to the common taxonomic assignment of the specimen and does not necessarily reflect the views of the authors (see Discussion).

MATERIAL AND METHODS

Material

This analysis is based on direct observations and measurements of over 1000 ceratopsid cranial elements housed in various North American institutions. All measurements were recorded to the nearest millimeter, repeated three times, and averaged where necessary. In addition to a large number of partial and complete articulated skulls of various size (and, presumably, age) classes (partial list shown in Table 1), hundreds of isolated cranial elements were examined, recovered primarily from paucispecific ceratopsid bonebeds (in collections of MOR, TMP; not listed here). Most known ceratopsid skulls are of adult size, with the cranial sutures typically obscured due to extensive fusion. Isolated skull bones, often found in abundance in bonebed deposits, have therefore been extremely valuable for determining the limits of elements in the cranium (Sampson, 1993, 1995a).

Figure 1. Map of selected paucispecific centrosaurine bonebed (mass death) localities in Alberta and Montana: 1. Pipestone Creek, Alberta, early Maastrichtian, *Pachyrhinosaurus* sp.; 2. Scabby Butte, Alberta, early Maastricthian, *Pachyrhinosaurus canadensis*; 3. Dinosaur Provincial Park, Alberta, late Campanian, *Centrosaurus apertus*; 4. Dinosaur Provincial Park, Alberta, late Campanian, *Styracosaurus albertensis*; 5. Landslide Butte, Montana, late Campanian, *Einiosaurus procurvicornis*.

Bonebed localities from late Campanian and early Maastrichtian deposits in Alberta and Montana preserve remains of at least five centrosaurine taxa (Fig. 1). Bonebeds may be defined as "thin, laterally-restricted concentrations of disarticulated, commonly abraded and broken vertebrate skeletal remains" (Wood *et al.*, 1988). Remains of *Centrosaurus apertus* and *Styracosaurus albertensis* are separately preserved in several bonebeds from late Campanian deposits of the Dinosaur Park Formation (previously Judith River Formation), Dinosaur Provincial Park, Alberta (Currie, 1981; Currie & Dodson, 1984; Wood *et al.*, 1988). *Einiosaurus procurvicornis* is based on remains from two bonebeds in the late Campanian Two Medicine Formation of northwestern Montana (Sampson, 1995a). *Pachyrhinosaurus* is well represented in two Maastrichtian bonebed assemblages: *P. canadensis* is known from the St. Mary Formation of southern Alberta (Sternberg, 1950; Langston, 1975), and an undescribed species of pachyrhinosaur has been excavated from the Wapiti Formation of west-central Alberta.

An assumption of this study is that each of the mass death assemblages examined herein includes only one centrosaurine taxon. There are several reasons for having confidence in this assumption. (1) At most of the bonebed localities used in this study, geologic indicators are suggestive of relatively short term mortality (in the range of hours to months) rather than time-averaged attritional mortality (Currie & Dodson, 1984; Rogers, 1990). Shorter time spans increase the likelihood that the ceratopsids at each locality represent a single species, perhaps even a single population. (2) The patterns of putative intraspecific variation observed within each bonebed sample are repeated in other samples, which together span a range of environmental and temporal settings. (3) The range of variation observed within the mass death assemblages does not appear to exceed that of extant species of large herbivores (although this has not been tested quantitatively). (4) Many modern examples of species-specific mass mortality events have been documented (Corfield, 1973; Hillman & Hillman, 1977; Haynes, 1987, 1988). (5) In some instances, the fine-grained nature of the entombing sediments suggests that the carcasses underwent minimal transport (Rogers, 1990). Thus, in order to uphold an hypothesis of multiple taxa in these cases, one would have to argue that two or more closely-related species occupied the same habitat, at least at the time of death. (6) Finally, it seems improbable that multiple individuals of two or more closely related taxa would perish together in the same mortality event, to the virtual exclusion of other large herbivore taxa, and that this sequence of events would occur multiple times over millions of years in a variety of taphonomic settings. Exceptions are known; a bonebed in Dinosaur Provincial Park, Alberta, dominated by the remains of *Centrosaurus*, also included the partial skull of a chasmosaurine (Currie & Dodson, 1984). Nonetheless, in the absence of contrary evidence, we argue that the assumption of a single centrosaurine taxon per locality is justified. If this assumption is incorrect, it does not mean that all or even most of our conclusions are necessarily false. Any exceptions to the assumption of monospecificity would have to be examined on a case by case basis.

Methods

With minor exceptions (see Table 1), the study sample was not subjected to quantitative analysis. There are several reasons for this decision. Even in the largest of the bonebed assemblages, there are generally too few examples of a given element for comparative statistical analyses ($n<20$). Although landmark-based quantitative approaches have been applied to mostly complete ceratopsid skulls with some success (Forster, 1990; Dodson, 1993), morphometric analyses of ceratopsid skulls are problematic due to several factors including incompleteness, postmortem crushing, and variation as to limits (with margins often remarkably different even on opposite sides of the same skull). In addition, most of the study sample consists of isolated craniofacial elements. Thus, this study focuses on comparative analysis of qualitative or discrete characters in an attempt to discern the nature of variations (e.g. ontogenetic and individual versus phylogenetic).

An important aspect of this study is the recognition of ontogenetic stages. In extant vertebrates, relative sexual maturity can be ascertained through examination of egg or sperm development in the ovaries or testes, respectively. As this is obviously not possible for extinct species, this study employed two size-independent techniques to estimate relative age: (1) fusion of cranial elements, including accessory or dermal elements, and (2) bone surface texture. No embryonic or hatchling materials are known for Ceratopsidae. Thus, for the purposes of this study, ontogenies are divided into three stages: juvenile, sub-adult and adult. Juveniles are those individuals ranging from hatchling to near full grown. Sub-adults refer to individuals of adult or virtually adult size, with additional characters indicating pre-adult status (see below). The sub-adult category may be viewed as corresponding to a period of 'adolescence', in which sexual maturity may be complete but individuals lack several adult characters. Adults are fully grown individuals with full expression of adult characters, often including fusion of skull elements. A fourth stage, old adult, appears to be recognizable on the basis of several craniofacial features, but cannot be verified independently using either of the above ageing techniques.

Fusion of cranial elements

The relative degree of suture closure or fusion between cranial elements has often been applied as an indicator of relative age, with complete suture closure associated with fully mature individuals. Living 'reptiles' are, and presumably dinosaurs were, constantly growing, so one would not expect complete fusion at all sutural contacts, even if remodelling obscured external evidence of sutures. Moreover, postmortem disarticulation of skulls is almost certainly influenced by a variety of taphonomic factors (aqueous versus non-aqueous environments, oxic versus anoxic environments). This is not to say that suture closure should be avoided as an age indicator, only that it must be used in conjunction with other techniques of age estimation. For the purposes of this initial study, elements of the middle and posterior skull roof of ceratopsids (i.e. palpebrals, frontals, postorbitals, squamosals, parietals) were examined and assigned to one of three general categories: (1) sutures fully visible; (2) sutures partially obscured; (3) sutures fully obscured. Note that the fully obscured condition does not necessarily imply complete fusion of the elements involved, only that the suture is not visible externally due to remodelling.

Ceratopsids possess accessory ossifications terminally on the jugals (epijugals) and along the lateral margin of the frill (epoccipitals). The presence or absence of these accessory elements on ceratopsid crania can be useful indicators of relative age (Lehman, 1989). However, epoccipitals are often missing, even in adults, particularly if the specimen is weathered or has undergone transport. Perhaps more reliable than simple presence or absence is the degree of epoccipital fusion. For example, two supposed sub-adult centrosaurs (ROM 767, TMP 86.126.1) have numerous epoccipitals present with clearly visible lines of fusion whereas two putatively old adult centrosaurs (NMC 8795, AMNH 5351) possess well-fused epoccipitals in which the margins of contact have virtually disappeared. In all of the above specimens, relative age estimations were based on multiple indicators (see below).

Periosteal ageing

A new, independent technique for assessing relative age, here referred to as periosteal aging, developed directly out of this study. Periosteum is osteogenic soft

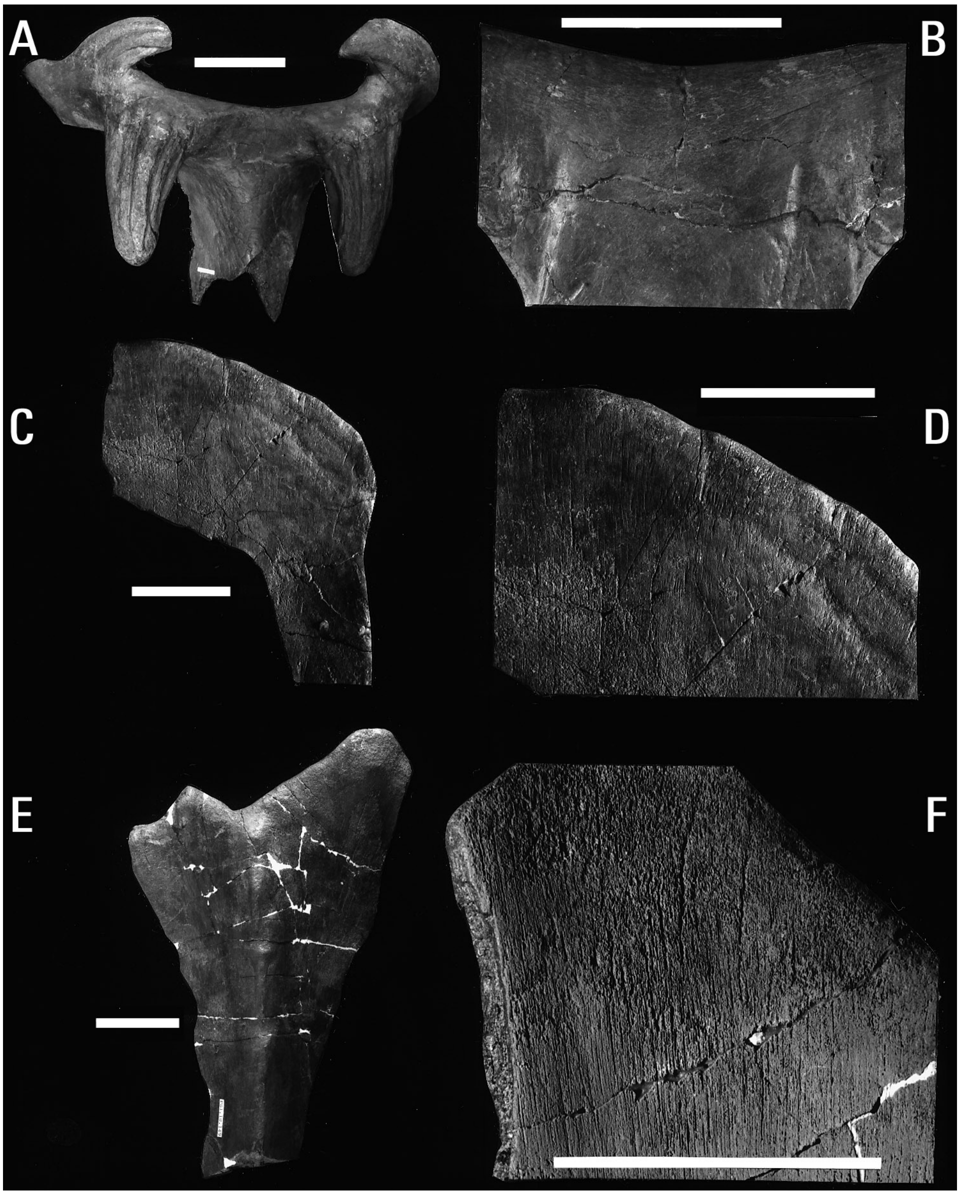

Figure 2. Examples of surface bone texture on three partial parietals from three age classes. All specimens derived from bonebed 43, Dinosaur Provincial Park, Alberta, containing disarticulated remains of *Centrosaurus apertus*: A, B. Adult, TMP 82.18.79, showing non-striated texture; C, D. Sub-adult, TMP 80.18.110, showing mosaic of striated and non-striated texture: E, F. Juvenile, TMP 81.18.149, showing striated texture. A & E = dorsal view; B, C, D, F = ventral view. Scale bars: A & B = 10 cm; C-F = 5 cm.

tissue surrounding bone and as such is generally not preserved in fossils. However, in ceratopsians, the texture of periosteal or surface bone is often a good indicator of relative age (Fig. 2). Juveniles are characterized by striated or long-grained bone texture consisting of extremely thin parallel ridges of bone (Fig. 2E, F). These osseous striations, apparently indicative of rapid growth, tend to be oriented in the direction of bone growth. In juvenile and sub-adult ceratopsians, various cranial and postcranial elements invariably have striated bone surfaces. Relatively flat elements, including those of the ceratopsid frill, are generally best for observing this phenomenon. Adult bone surface texture can exhibit a variety of forms (e.g. rugose, mottled, smooth), depending on the element involved and the age of the individual, but invariably lacks the striations characteristic of juveniles (Fig. 2A, B). Accordingly, sub-adults generally show a mosaic of juvenile and adult bone surface textures with striated bone occurring only in regions that presumably were still undergoing rapid growth at the time of death (Fig. 2C, D).

Numerous examples can be cited in support of an observed correlation between surface features of bone and relative age. The type materials of *Brachyceratops*, long thought to represent young animals (Gilmore, 1914, 1917), are characterized by an abundance of striated texture. Conversely, a large skull of *Centrosaurus longirostris* (NMC 8795) with fully developed nasal, supraorbital, and parietal characters exhibits virtually no evidence of cranial sutures. The bone surface texture of this specimen is of the non-striated, adult type, much of it extremely rugose. An undescribed centrosaurine skull (TMP 86.126.1) illustrates the intermediate, sub-adult condition. The nasal horn is not preserved on this specimen but the supraorbital horns and the parietal indicate a sub-adult status (see below). Mottled surface texture characteristic of adults occurs around the margins of the parietal fenestrae, suggesting cessation of growth, while the bone surface texture along the lateral margins is of the striated, juvenile type, suggesting continued growth.

This simple method of relative age estimation allows gross visual determination of ontogenetic stages from well-preserved (i.e. non-abraded, non-weathered) bone fragments. A preliminary survey of dinosaurian elements in the collections of the Royal Tyrrell Museum, Alberta, and the Museum of the Rockies, Montana, indicates that periosteal aging can be applied not only to ceratopsians, but to a number of other dinosaur taxa, including theropods and ornithopods. Although periosteal aging is relatively coarse, one can, in most instances, minimally distinguish between juveniles, sub-adults and adults. The method can be applied to cranial and postcranial elements, although bone texture pattern is best revealed on elements with flat surfaces such as scapulae, ilia, and (in the case of ceratopsids) the parietosquamosal frill.

Interestingly, Bennett (1993) independently arrived at similar conclusions regarding ontogenetic changes in the bone surface morphology of limb elements of the pterosaur, *Pteranodon*. He describes the bone grain of sub-adult ('immature') limb specimens as more porous, with abundant vascular canals considered to be indicative of rapid bone growth. This contrasts with the less porous, generally smooth condition observed in adult ('mature') individuals. Without further comparative study, it is unclear whether the patterns of periosteal ontogeny described here for centrosaurines are homologous, or simply analogous, with those described by Bennett (1993) for *Pteranodon*. The general applicability of this method for determining the relative age of archosaur specimens will be considered in detail elsewhere.

There is an obvious danger of circularity in assessment of relative age. That is, a given character (e.g. striated bone surface texture) is first associated with a particular age class and then used to define that age class. In every instance, we attempted to guard against such circularity by supporting all age diagnoses with multiple independent criteria (e.g. bone texture, relative size, degree of suture closure). Our confidence in age determination is strengthened by patterns witnessed repeatedly in isolated specimens and bonebed samples. For example, specimens covered with striated, juvenile type bone texture are typically characterized by some other feature indicative of juvenile status (e.g. small size, sutures fully visible, relatively unadorned skull). The bonebeds appear to preserve a spectrum of developmental stages from single species, and perhaps single populations. Suture closure and bone surface texture both correspond well to expected changes in size and to age-related modifications in reproductive characters, described below.

NASAL HORNCORES

General features

Centrosaurine nasals are broad, deep, horn-bearing elements constituting a large portion of the facial region. Sutural contacts include the premaxillae anteriorly and ventrally, the lacrimals and prefrontals (and occasionally the frontals) posteriorly, and the maxillae ventrally. A posterodorsally directed process of the premaxilla contacts the lacrimal in some specimens, thereby preventing contact between the nasal and maxilla. The nasal forms the dorsal and posterior surfaces of the external nares and contributes (along with the premaxillae) to finger-like processes that protrude into the narial opening from the posterior margin. The latter is a synapomorphic character of Centrosaurinae. While centrosaurines are characterized by well developed nasal horncores or bosses and diminutive supraorbital horncores, the reverse generally applies to chasmosaurines.

The development of nasal horncores in ceratopsian dinosaurs has been the subject of considerable debate. While it is now accepted that the nasal horncores were formed at least partially from outgrowths of the nasal bones, there has been disagreement as to the existence of a separate terminal nasal element, sometimes called the ‘epinasal’ (Lambe, 1915). Ceratopsids possess a number of ‘accessory’ elements including epijugals, which attach to the ventrolateral surface of each jugal, and epoccipitals, which fuse to processes on the lateral margin of the parietosquamosal frill. A separate epinasal element has been confirmed on numerous chasmosaurine skulls and is likely a synapomorphy of the group (Forster, 1990). Gilmore (1914, 1917) noted what he thought to be a distinct ossicle on the tip of the left nasal horncore in *Brachyceratops montanensis* (Fig. 3). He argued that this ossicle “may represent the incipient horn of later ceratopsians where it is known to be developed from a center of ossification distinct from the nasal bones” (1914: 4). It is now apparent that the ‘later ceratopsians’ referred to by Gilmore (e.g. *Triceratops*) are chasmosaurines, while specimens assigned to *Brachyceratops* are Centrosaurinae. Close examination of USNM 7951 suggests that the apparently separate terminal element on the nasal is in reality the broken tip of the horncore. No other juvenile or sub-adult centrosaurine nasals examined during the course of this study show any indication of a distinct terminal ossification.

Ontogeny

In neoceratopsians, the nasal horncore arises as a direct outgrowth of the nasal bones. *Brachyceratops montanensis* has been regarded as a pivotal taxon, intermediate

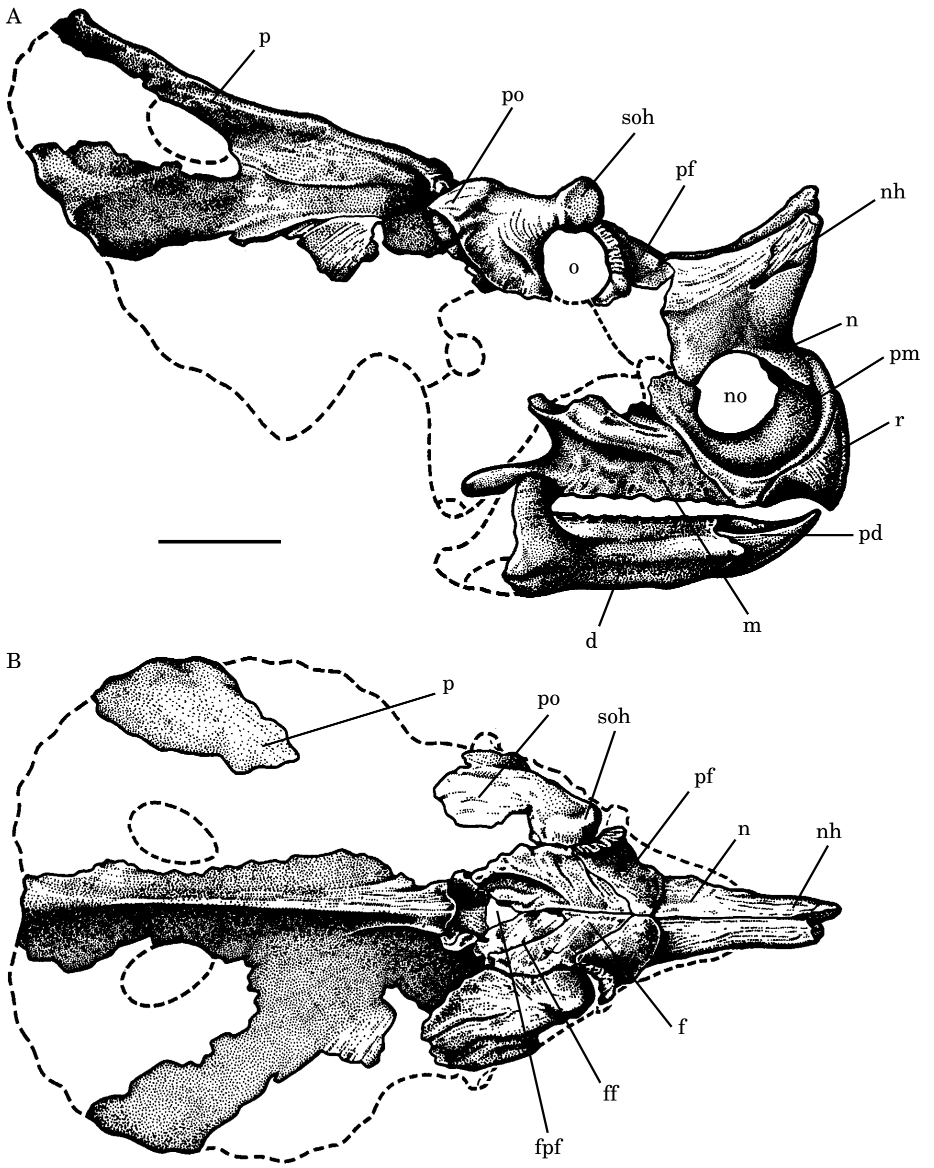

Figure 3. *Brachyceratops montanensis*, USNM 7951 (holotype), skull in (A) right lateral and (B) dorsal views. Abbreviations: d = dentary; f = frontal; ff = frontal fontanelle; fpf = fronto-parietal foramen; m = maxilla; n = nasal; nh = nasal horncore; no = narial opening; o = orbit; p = parietal; pd = predentary; pf = prefrontal; pm = premaxilla; po = postorbital; r = rostral; soh = supraorbital horncore. Scale bar = 10 cm. Modified from Gilmore (1917).

in a number of characters relative to other ceratopsians (Brown & Schlaikjer, 1940a; Sternberg, 1949). Gilmore (1914) pointed out in his original description of *Brachyceratops* that the type collection consists of elements from several immature individuals. The holotype skull (USNM 7951), which will be referred to extensively below, includes a well-preserved nasal horncore that is laterally compressed, slightly recurved and divided sagittally (Fig. 3). Although Gilmore considered these characters

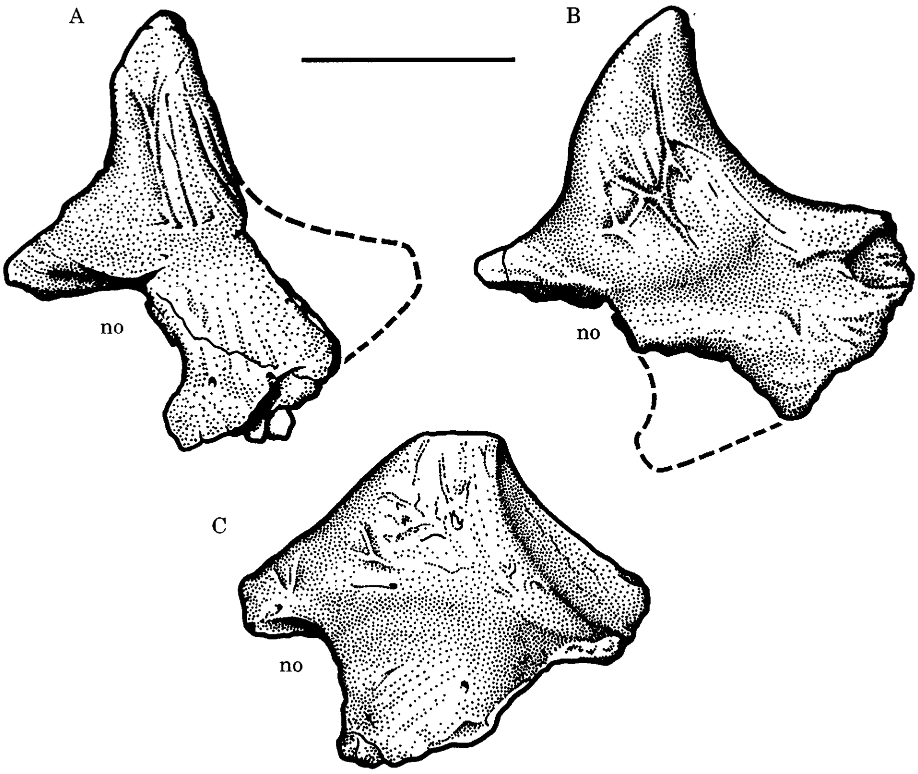

Figure 4. Sub-adult centrosaurine nasal horncores in left lateral view: A, *Centrosaurus apertus*, TMP 79.11.83; B, *Einiosaurus procurvicornis*, MOR 373 7-15-6-16; C, *Pachyrhinosaurus* sp., TMP 88.55.80. Abbreviations: no = narial opening. Scale bar = 10 cm.

to be generically and specifically diagnostic for *Brachyceratops*, he recognized that other ceratopsians might show an equivalent stage of nasal horn ontogeny. "It appears quite probable there are some of the described Belly River species that will show a similar mode of nasal horn development when juvenile specimens are found" (Gilmore, 1914: 3). In retrospect, Gilmore's statement is prescient, as numerous immature centrosaurine specimens, including many examples from bonebeds, display exactly this type of nasal horn morphology.

All juvenile and sub-adult centrosaurines apparently possessed a nasal horncore broadly triangular in lateral aspect, laterally compressed, divided longitudinally by a median suture, and either erect or slightly recurved (Fig. 4). Only after the attainment of adult size were adult morphologies characteristic of the various genera fully expressed, including anteriorly-curved horns and nasal bosses. Nasal horncores fused from the tip down, a pattern unknown in other vertebrates as far as we are aware. Several *Centrosaurus* and *Einiosaurus* nasals consist of only one side of the nasal horn with the tip of the other side fused or, conversely, with the tip missing (indicating that it had fused and, when broken, remained with the opposite side). Some sub-adult skulls (e.g. MOR 591, *Achelousaurus*) preserve a relatively small, complete nasal horncore with the longitudinal suture visible, except at the tip, indicating that fusion had commenced by the time of death. In support of this pattern, *Montanoceratops* *cerorhynchus* has the largest nasal horncore of any known protoceratopsian and, although the two sides are divided along the midline, fusion has occurred at the apex (Brown & Schlaikjer, 1942).

In juvenile centrosaurines, the nasal horncore overlies most of the narial opening while in adults the horn overlies only the posterior margin of the opening. Juvenile and sub-adult nasal horncores, though not as rugose in texture on the external surface as in adults, show a variable pattern of deep vascular grooves that tend to originate posteroventrally and converge dorsally (Fig. 4). The medial contact surface, clearly seen in the split nasals, is typically flat and smooth. Sub-adult individuals of *Centrosaurus* and *Einiosaurus* share a common nasal horncore morphology, although in the latter the horn is often longer based, a distinction useful in distinguishing these taxa (Fig. 4A, B). *Pachyrhinosaurus* juveniles also have long-based nasal horncores that differ only in lacking a pointed dorsal tip, possessing instead a broad, flattened appearance as viewed laterally (Fig. 4C). It appears that the nasal horncore halves fused completely prior to the development of the adult condition (horncore or boss). An ontogenetic nasal series for an undescribed pachyrhinosaur from Alberta shows progressive development from a small, sagittally divided horncore in juveniles to a full-fledged pachyostotic boss in adults. The highly rugose, convoluted texture of the boss indicates rapid deposition of bone in conjunction with the attainment of adult body size.

Taxonomic variation

In adult centrosaurines (Fig. 5), there is a wide diversity of nasal horncore morphologies, even within a single species. The rugose, well vascularized horncores range between 200 mm and 500 mm in height (basal skull length in adult centrosaurines varies between about 650 mm and 875 mm, with the exception of the larger-bodied *Pachyrhinosaurus canadensis*; Sampson, 1995a). *Centrosaurus* has a relatively short-based nasal horncore that varies in orientation from erect to somewhat recurved to strongly procurved (Fig. 5A). A large *Centrosaurus* bonebed in Dinosaur Provincial Park (Quarry 143), which may represent part of a single population, preserves examples of all of these horn varieties. The nasal horncores of adult *Styracosaurus* are also variable and similar to those of *Centrosaurus* (Fig. 5C), although no procurved styracosaur nasals are known. *Einiosaurus*, though represented by fewer nasal specimens, apparently had a broad range of variability in adults. Two individuals have short, erect nasal horncores while five specimens are extreme with nasal horncores so highly curved anteriorly as to be reminiscent of can-openers (Fig. 5E).

Several specimens of *Centrosaurus* and *Einiosaurus* possess a groove on the dorsal or posterior surface of the nasal horncore, particularly in specimens with procurved horns. In the type specimen of *Centrosaurus longirostris* (NMC 8795), this groove is a long, deeply excavated posterodorsal cavity with a smooth surface (Sternberg, 1940). Several other features on this skull (mature bone surface texture; fused sutures; fully developed parietosquamosal processes with fused epoccipitals; large basal skull length; eroded supraorbital horns) indicate an advanced age for this individual. The function of these dorsal nasal grooves is unknown but they appear to be an ontogenetic feature, present only in mature individuals.

Achelousaurus closely resembles *Pachyrhinosaurus* in the possession of well developed nasal bosses (Fig. 5G, H). The rugose, highly pitted nasal boss of *Achelousaurus*

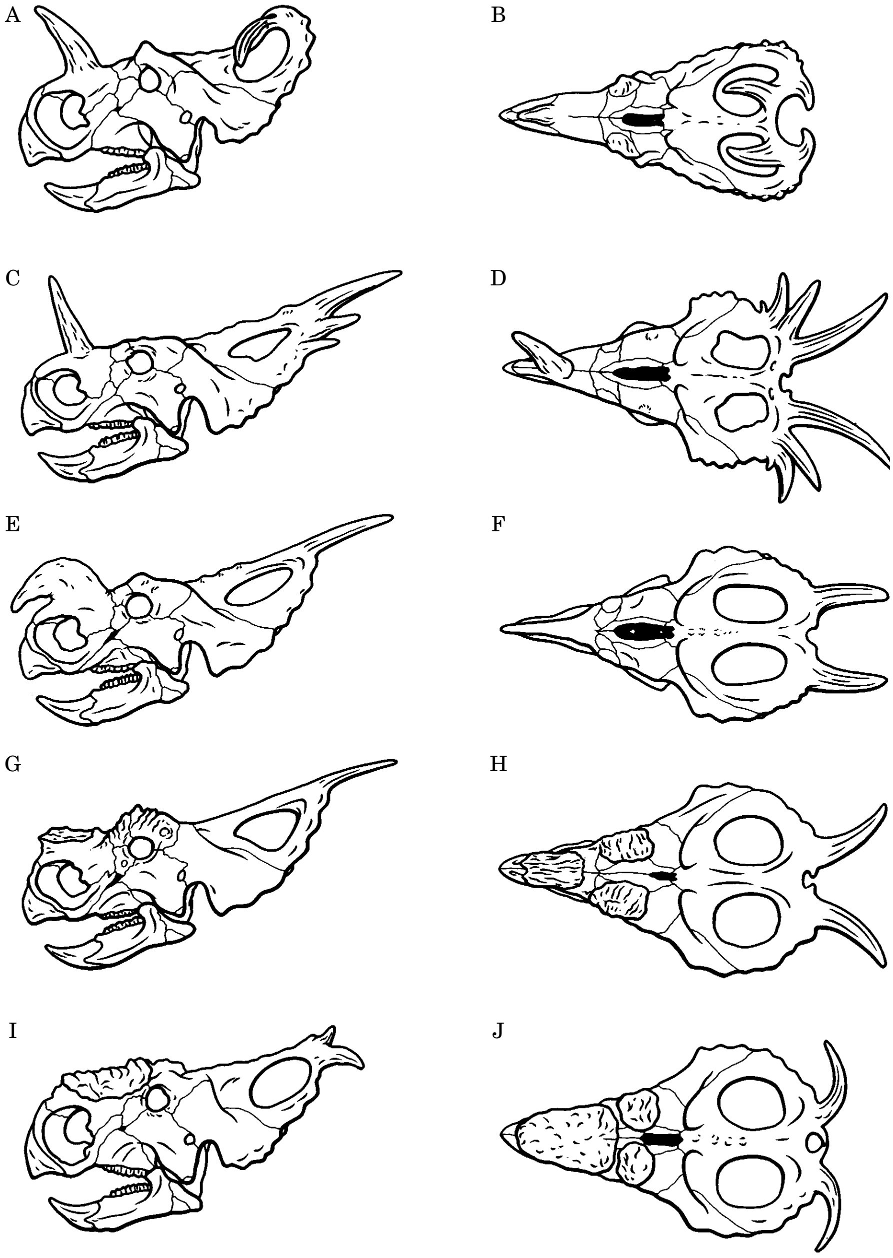

Figure 5. Representative centrosaurine skulls in left lateral and dorsal views: A & B, *Centrosaurus apertus*; C & D, *Styracosaurus albertensis*; E & F, *Einiosaurus procurvicornis*; G & H, *Achelousaurus horneri*; I & J, *Pachyrhinosaurus canadensis*. After Brown (1914), Lambe (1913), Langston (1975), and Sampson (1995a).

developed from the juvenile, conventional style split nasal horncore. An anterior extension of the boss may indicate that it developed from a procurved horn similar to that of *Einiosaurus*, as suggested by Horner *et al.* (1992). However, given the ontogenetic pattern known for at least one species of *Pachyrhinosaurus* (see below), it is perhaps more likely that the boss developed from a simple, erect horncore and subsequently extended anteriorly to contact the premaxilla. The nasal boss of *Achelousaurus* was likely covered in a tough, keratinous sheath.

The last known centrosaurine, *Pachyrhinosaurus*, is also the most derived in several characters, including the nasal (Fig. 5I, J). Adults resemble *Achelousaurus* in displaying a broad, rugose mass of bone over the nasal region, but in *Pachyrhinosaurus* the boss hypertrophies to include most of the skull roof exclusive of the frill, from the dorsal extensions of the premaxillae posterior to (and often including) the prefrontals and frontals. In at least one population of *P. canadensis*, this boss achieved thicknesses in excess of 200 mm (Sternberg, 1950). Viewed dorsally, the nasofrontal boss is generally elliptical, though significantly broader posteriorly. In an undescribed species of *Pachyrhinosaurus*, the nasofrontal boss occurs in two distinct morphs, one generally flat or slightly convex ($n = 8$) and the other gently concave ($n = 8$). Sexual dimorphism may be cautiously inferred from this dimorphic boss morphology (see Discussion). The nasal region was undoubtedly covered in life by some form of horny sheath. This 'freakish development' (Sternberg, 1950:109) may have supported a non-osseous, epidermal horn (Currie, 1989), but we consider this unlikely. Why evolve two independent solutions to the same problem of developing a nasal horn? And why would sub-adults lose a nasal horn only to develop an epidermal version as an adult? Furthermore, the occurrence of supraorbital bosses rather than horns (see below) suggests that the dramatic exostosis in *Pachyrhinosaurus* was a means of creating an osseous platform on the anterior skull roof, perhaps employed in intraspecific competition as a head-butting platform (Farlow & Dodson, 1975).

Summary

Centrosaurine nasal horncores developed as direct outgrowths of the nasal bones and fused from the tip down relatively late in ontogeny (sub-adult), yet prior to expression of the adult horncore condition. Sub-adult nasal horncores are similar in that they are transversely compressed, sagittally divided and broadly triangular in lateral aspect. In some instances, taxa can be differentiated based on the detailed shape of sub-adult horncores. Intraspecific variation in adults can be considerable, given the diversity of horncore orientations derived from one *Centrosaurus* bonebed in Dinosaur Provincial Park, Alberta. Yet adult nasals are usually species-specific, characterized either by a horncore or a boss of particular shape and/or orientation.

SUPRAORBITAL HORNCORES

General features

Unlike their chasmosaurine counterparts, which developed supraorbital horncores up to one meter in length, centrosaurines had comparatively small supraorbital horncores, typically less than 150 mm in length (Dodson & Currie, 1990). The supraorbital horncore of ceratopsids arises primarily as an outgrowth of the postorbital bone, apparently involving only a single center of ossification, as argued by Hatcher *et al.* (1907) and Brown & Schlaikjer (1940a). In *Protoceratops*, a rugose process develops from the postorbital in much the same fashion as in later-occurring ceratopsids (Brown & Schlaikjer, 1940b). Confusion as to whether or not ceratopsid horns represent secondary centres of ossification is caused by a number of well-preserved centrosaurines that possess shallow depressions or pits on or in place of the supraorbital horncores (e.g. NMC 344, *Styracosaurus*). These specimens are discussed below. The subcircular palpebral (supraorbital of some authors) contacts the anterior margin of the postorbital and generally makes some contribution to the horncore itself, particularly in sub-adults where it can comprise greater than one-third (e.g. MOR 591, *Achelousaurus*).

Ontogeny

As discussed above for nasal horns, all juvenile centrosaurines possessed approximately the same form of supraorbital horncore and expressed adult horncore morphology only after the attainment of adult body size. In juveniles the supraorbital horncore consists of a long, low rounded process (Fig. 6). Laterally, it tends to be flush with the external surface of the face, whereas the medial surface slopes steeply toward the midline. The surface texture of juvenile supraorbital horncores and surrounding bone is generally smooth or finely pitted. Sub-adult supraorbital horncores are also closely similar across taxa, although by the time the skull has reached adult size, there are often characters that can be used to differentiate between taxa (see Taxonomic Variation below).

Numerous centrosaurine specimens do not possess true supraorbital horncores but instead have low, rounded masses of bone, simple raised ridges, or true concavities (Fig. 7). The holotype of *Styracosaurus albertensis* (NMC 344) possesses shallow pits in place of both supraorbital horncores (Lambe, 1913). In over 100 postorbitals examined, approximately 25% display some morphology other than a ‘normal’ horn. These variations have been interpreted as possible evidence of separate ossification of the supraorbital horn, at least in some forms (Huene, 1911; Lambe, 1913, 1915; Dodson & Currie, 1990). However, this view is unlikely for at least three reasons. First, juvenile and sub-adult specimens from various taxa indicate that the horncore is formed by outgrowths of the postorbital and palpebral, with no indication whatsoever of the putative sutural surface for a separate ossification. Juvenile postorbitals from *Triceratops* indicate that this statement holds true for chasmosaurines as well (Brown & Schlaikjer, 1940a). If there is a separate centre of ossification, it must have co-ossified completely with the horncores at a very early stage because no suture is visible in available juvenile specimens (e.g. USNM 7591, *Brachyceratops*). Second, all specimens that lack this horncore appear to be mature adults. Third, several centrosaurine postorbitals are morphological intermediates, possessing well-developed, although pitted, horncores. These specimens suggest that once fully developed, the horn was partially resorbed prior to death. Some specimens possess a peculiar morphology in which much of the dorsal surface of the postorbital/frontal/palpebral complex is covered in a low, pitted mass of bone. One *Einiosaurus* skull (MOR 456-8-9-6-1) shows this morphology on the left side (Fig. 7B) and a deep pit (85 mm × 64 mm) in place of the horncore on the right side (Fig. 7C; Sampson, 1995a). Nonetheless, it is worth noting that bovid horns are epiphyseal in nature, developing from a secondary (epidermal) ossification called the *os cornu* that generally fuses to the skull shortly after birth (Dove, 1935; Bubenik, 1990). If

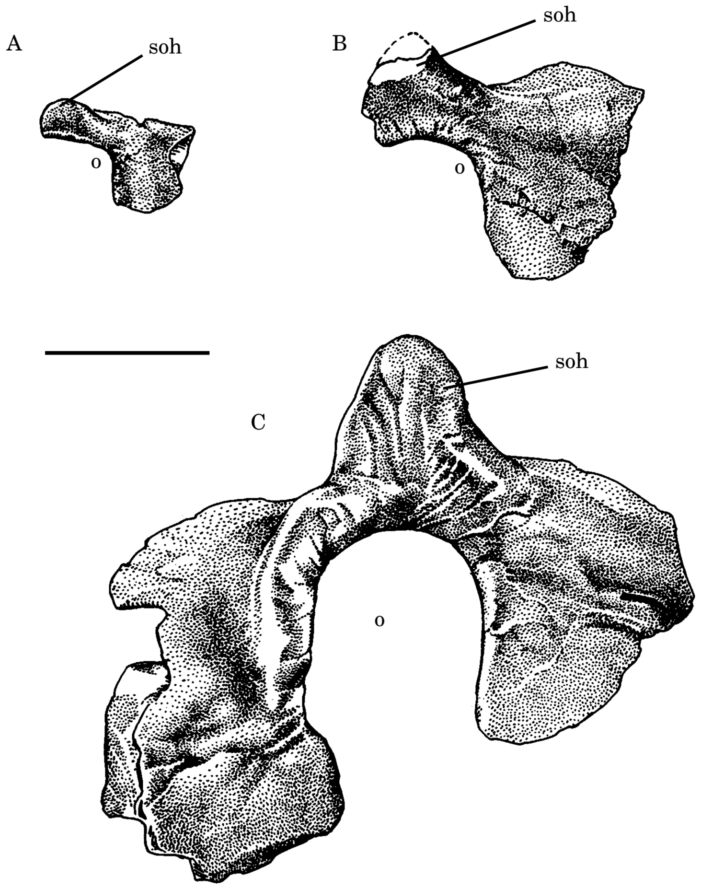

Figure 6. Ontogenetic series of supraorbital horncores of *Centrosaurus apertus* in left lateral view. A. TMP 79.11.157, juvenile postorbital; B. TMP 82.18.139, sub-adult postorbital; C. TMP 79.11.81, adult postorbital, prefrontal, palpebral, and lacrimal. Abbreviations: o = orbit; soh = supraorbital horncore. All specimens derived from bonebed 43, Dinosaur Provincial Park, Alberta. Scale bar = 10 cm.

a similar pattern occurred in ceratopsids, the available evidence shows no indication of it.

Four possible ways to account for the peculiar adult variants that lack supraorbital horncores are: (1) periodic resorption followed by regrowth; (2) age-related resorption; (3) periodic loss due to a seasonal antler-style of replacement; and (4) pathology, related either to disease or trauma. Resorption of horncores might occur due to calcium requirements, perhaps related to egg-laying in females. If the latter is true, we would expect to see a pattern of sexual dimorphism in the presence or absence of supraorbital horns. Such a pattern cannot be determined at this time. It is also possible that these horns were lost in both sexes in aged individuals, perhaps as a result of lack of use. Yet numerous centrosaurine skulls appear to be fully mature and possess well-developed supraorbital horns. Thus we hesitate to claim that all mature centrosaurines eventually lost these horns. A primary problem with the concept of genetically-related resorption is in conceiving a mechanism that would

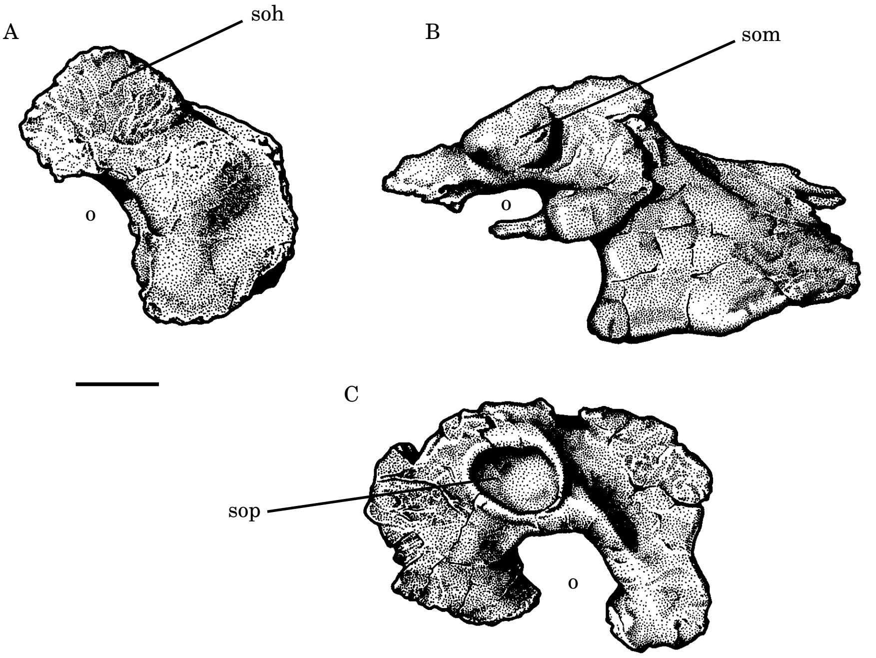

Figure 7. Adult supraorbital variations in *Einiosaurus procurvicornis*. A. MOR 373 8-20-6-11, left postorbital in lateral view, showing long, rounded horncore morph; B. MOR 456 8-9-6-1, left frontal, prefrontal, palpebral, postorbital and squamosal in dorsolateral view, showing supraorbital mass; C. MOR 456 8-9-6-1, right frontal, prefrontal, palpebral, lacrimal, and postorbital in dorsolateral view, showing supraorbital pit. Abbreviations: o = orbit; soh = supraorbital horncore; som = supraorbital mass; sop = supraorbital pit. Scale bar = 10 cm.

lead to such a localized uptake of bone. A further possibility is that the horncores were replaced on a periodic basis, akin to cervid antlers, experiencing rapid seasonal growth followed by partial loss or resorption of the horncore. Langston (1975) suggested that these excavations might be a pathological phenomenon without genetic basis, perhaps resulting from some fungal corrosion. However, postorbitals lacking horns are common and occur in several genera spanning the late Campanian and the early Maastrichtian. Pathology related to agonistic encounters is another possibility. Complete or partial loss of supraorbital horns could feasibly have resulted from head to head intraspecific encounters involving competition for mates or hierarchical disputes. However, several specimens (e.g. NMC 344, *Styracosaurus*) possess symmetrical pits in place of the supraorbital horncores, an unlikely pattern if pathology is the cause. Histological examination of postorbitals may provide clues toward solving this matter.

Taxonomic variation

In adult centrosaurines, the horncore often becomes rugose together with the remaining dorsal surface of the postorbital. In some cases, genera can be distinguished by a distinct adult morph of supraorbital horn (Fig. 5). *Centrosaurus* typically developed a comparatively high, narrow-based and often pointed supraorbital horncore in which the palpebral makes a minor contribution. Sub-adult centrosaurs can be distinguished by the possession of supraorbital horns with a pyramidal shape. To date there are no specimens preserving the morphology of the postorbital in young adult styracosaurs. *Einiosaurus* retained the long, low, rounded morph seen in juveniles and sub-adults. In *Achelousaurus* and *Pachyrhinosaurus*, the horncore was transformed into a well-developed boss possessing the same heavily rugose texture found in the nasofrontal boss. The supraorbital bosses of *Achelousaurus* adults, present in only a single specimen (MOR 485), are more developed than in *Pachyrhinosaurus*, possessing high ridges several millimeters thick at the base and thinning dorsally. The supraorbital bosses of *Pachyrhinosaurus* range in shape from slightly convex to concave, and this variation apparently is not correlated with the shape of the nasofrontal boss. A shallow sulcus often separates the pachyostotic supraorbital boss from the underlying bone (Langston, 1975). Sub-adults of *Achelousaurus* and *Pachyrhinosaurus* are characterized by an *Einiosaurus*-type supraorbital horncore (long, low and rounded) except for a series of deep, transversely-directed grooves on a concave medial surface that likely represent the initial stages of boss formation (Sampson, 1993, 1995a).

An important consequence of the ontogenetic pattern described above is that it is difficult to separate centrosaurine taxa based on the gross morphology of supraorbital horncores. Juveniles from all genera appear essentially equivalent, with a long, low horn lacking any pitting. Once pitting has occurred, adults of *Centrosaurus*, *Styracosaurus* and *Einiosaurus* are often indistinguishable. Only adult-sized specimens show the ‘high’ versus ‘low’ condition of the supraorbital horn in *Centrosaurus* and *Einiosaurus*, respectively. This stage is probably representative of sub-adults and young adults. The same pattern may apply to *Styracosaurus*, but at this time there are no specimens that show the non-eroded supraorbital horncore condition likely to characterize young adults of this genus. Finally, given the variable nature of ceratopsid horncores, it is likely that *Achelousaurus* and *Pachyrhinosaurus* will be difficult to distinguish on the basis of supraorbital morphology.

Summary

Centrosaurine supraorbital horncores developed as outgrowths of the postorbitals, with some contribution from the palpebrals. The ontogenetic pattern parallels that seen in nasals, with juveniles and most sub-adults possessing low, rounded horncores. Following the attainment of adult size, supraorbital horncores were modified into either an adult horncore or pachyostotic boss. Some taxa can be distinguished based on the adult condition of this character (e.g. higher, pointed horncore of *Centrosaurus* versus lower, rounded horncore of *Einiosaurus*). A large proportion of all adult postorbitals, however, are difficult to distinguish taxonomically because the horncores were partially or completely eroded premortem, in some instances leaving a true pit in place of the horncore. This so called ‘erosion’ of supraorbital horncores is invariably associated with advanced maturity (full adult status) and therefore does not appear to be related to early stages of ontogeny. The process underlying these horncore variants is unknown.

FRONTAL FONTANELLE AND SUPRACRANIAL CAVITIES

General features

The morphology the of dermal skull roof in ceratopsids is highly derived and has been debated virtually since the first specimens of horned dinosaurs were found (Lambe, 1913; Gilmore, 1914, 1917; Sternberg, 1927; Lehman, 1990). It is now generally agreed that the frontals, postorbitals, and fused parietals meet to form a variably developed system of supracranial cavities that open dorsally via a large median aperture. This opening has variously been called the pineal foramen (Marsh, 1891), the postfrontal fontanelle (Lambe, 1913) or, more accurately, the frontal fontanelle (Sternberg, 1927). Confusion over the architecture of the ceratopsid skull roof has emerged because most reference specimens to date have been adult, often with partially or completely obliterated sutural contacts.

The only major exception to this paucity of non-adult materials has been USNM 7951, referred to *Brachyceratops montanensis* (Gilmore, 1917). *Brachyceratops* has often been put forth as a relatively primitive ceratopsid because USNM 7951 is a juvenile specimen that closely resembles *Protoceratops* in many features of the cranium, particularly the skull roof and parietosquamosal frill. This specimen has a shallow depression in place of the frontal fontanelle and supracranial cavities, but the surrounding bones remain differentiated (Fig. 3B). The paired elements surrounding the dorsal depression were originally interpreted by Gilmore (1917) to be postfrontals, but were later correctly reinterpreted by Sternberg (1927) as the frontals. The frontals form about two-thirds of the incipient supracranial space in USNM 7951, with the parietal forming the posterior one-third. The postorbitals do not reach the midline due to the intervening frontals.

Examination of ceratopsid specimens derived from mass death assemblages, including partial skulls and isolated elements, provides further insights into the complex morphology of this region. Dozens of isolated postorbitals, centrosaurine and chasmosaurine, show a medial suture surface for contact with the frontal (Sampson, 1995a). In all ceratopsids (and protoceratopsians), the postorbitals are excluded from the midline by the frontals which extend posteriorly to contact the parietals (Figs 3, 5). Thus, the configuration of elements seen in USNM 7951 applies to all adult members of Neoceratopsia. The skull roof is composed of postorbitals bordered medially by frontals, anteriorly by the prefrontals, and posteriorly by the fused parietals. The frontal fontanelle occurs mostly within the frontals, with the parietal forming only the posterior one quarter to one third (e.g. MOR 591, *Achelousaurus*; NMC 344, *Styracosaurus*). Only the magnitude of the fontanelle and supracranial cavities vary, *Protoceratops* having a faint frontal depression while adult ceratopsids show a true fontanelle opening into a system of supracranial cavities.

The supracranial cavities invade the frontals anteriorly, postorbitals laterally, and parietal posteriorly. The supraoccipital and exoccipital, which provide support for the parietal, may also contribute to the posteroventral portion of this supracranial space, although it is difficult to determine the full extent of these elements. The bone lining these cavities is generally smooth with no indication of sutural contacts. If USNM 7951 (*Brachyceratops*) is an accurate guide, however, the floor of the supracranial cavities, at least incipiently, is formed mostly by the frontals, with a substantial posterior contribution from the parietal. Presumably, the postorbitals formed the lateral floor of this space following lateral expansion of the cavities (see below). Most well-preserved ceratopsids possess a bony transverse buttress medial to the orbits and within the supracranial space. The buttress, apparently derived from the frontals, divides the supracranial space into a shallower anterior chamber and a deeper, more extensive posterior chamber. Forster (1990, 1996) independently reached similar conclusions regarding the morphology of the skull roof in *Triceratops* and other chasmosaurine ceratopsids.

A thin (<10 mm), sagittal crest is present anteriorly in the supracranial cavities of most centrosaurines preserving this region. This crest extends from the anterior margin of the frontal fontanelle posteroventrally to contact the transverse buttresses, creating a division of the anterior chamber into left and right compartments. Laterally placed accessory chambers are common, particularly within the postorbitals, and excavations of the supraorbital horn/boss occur in some taxa (see below), in a manner analogous to the cornual sinuses of bovids. In the bovid condition, cornual sinuses are confluent with frontal sinuses which in turn receive an air supply via the nasal passages. To date there has been no demonstration of an air source for the ceratopsid supracranial cavities.

At the junction of the frontals and parietal in USNM 7951 (*Brachyceratops*; Fig. 3) is a median aperture termed by Gilmore (1917) the 'postfrontal foramen'. Gilmore (1917) notes a similar opening in NMC 344, the holotype of *Styracosaurus albertensis*, and also in USNM 5740, a sagittally sectioned specimen of *Triceratops* (Gilmore, 1919). Our observations confirm the presence of this structure in virtually all centrosaurines, and its occurrence in some chasmosaurine specimens suggests that it may well be shared by all members of Ceratopsidae. This large opening (averaging about 30 mm × 23 mm in adult centrosaurines) is located in a shallow depression within the posterior chamber and provides communication between the endocranial and supracranial cavities. In adult centrosaurines, the foramen is oval, with the long axis oriented transversely. Due to its apparent location at the junction of the frontals and fused parietal, we refer to this opening as the fronto-parietal foramen.

This fronto-parietal foramen occurs in the general location of the pineal foramen seen in other reptiles, and has been referred to as such (Gilmore, 1919; Lehman, 1989). However, it seems unlikely that this opening housed a photo-receptive organ homologous with the pineal or parietal eye. First, there is no strong evidence of a pineal foramen in any of the archosaur ancestors of Ceratopsidae (Quay, 1979). Second, as described below, some ceratopsids developed a complete double roof in this region, which would have prevented ambient light from reaching the region of the fronto-parietal foramen. Thus, the function of this cranial foramen is unknown.

Ontogeny

The shape of the frontal fontanelle and supracranial cavities underwent radical alterations during growth. In juveniles (e.g. *Brachyceratops*, USNM 7951) there is only a shallow frontal depression and no sinus system. A similar fossa is seen in adult *Protoceratops* (Brown & Schlaikjer, 1940b). Among sub-adult individuals (e.g. *Achelousaurus*, MOR 591) the fontanelle is fully developed but the system of cavities is simple, composed of relatively narrow and shallow concavities. A transverse buttress is generally present in sub-adults (e.g. MOR 591), but the cavities are restricted laterally and include little, if any, of the postorbitals. The chambers deepen and broaden with maturity, developing complex morphologies in adults, including numerous accessory recesses laterally, and sinus-like excavations of the postorbital horncore (or boss) in some taxa.

Sternberg (1927) postulated that the supracranial cavities in *Triceratops* formed by folding of the frontals to create a double skull roof. This view arose at least partially from observation of USNM 7951, which has a shallow frontal depression that can be interpreted as the first stages of frontal folding. Gilmore (1919) suggested that the supracranial cavities might be pneumatic structures. A potentially analogous system in bovids involves pneumatic frontal sinuses originating and developing wholly within the frontal bones; pneumatic epithelium invades these elements, dividing them into dorsal and ventral tables supported by bony struts (Schaffer & Reed, 1972; Jaslow, 1987). Particularly given the variable lateral expansion of the supracranial cavities in ceratopsids, the latter mode of growth appears most probable. Thus, ceratopsid frontals likely did not fold over on themselves but rather were excavated from within to form a large system of chambers that, in some taxa, spread laterally to include the postorbitals (Forster, 1990).

However, if the supracranial cavities in ceratopsids are indeed pneumatic structures, the air source for this system has yet to be demonstrated. Frontal sinuses in bovids are supplied via paranasal diverticula. The only openings currently established into the ceratopsid frontal chambers are the frontal fontanelle dorsally and the fronto-parietal foramen ventrally, neither of which is a likely pneumatic pathway. Alternatives to the pneumatic hypothesis could potentially involve non-pneumatic soft tissue structures such as muscle (Sternberg, 1940), vascular tissue, or neural tissue (L. Witmer, pers. comm.). The morphology of this derived and enigmatic region clearly requires further investigation.

An additional character evidently related to advanced age is closing or roofing over of the frontal fontanelle, effectively forming a true double skull roof. This phenomenon is seen only in supposed old adults and occurs from the anterior margin posteriorly. In young animals, the fontanelle extends forward to at least the anterior margin of supraorbital horncores. With age the fontals accrete bone anteriorly, gradually creating an enclosed space or complete double skull roof. An example is MOR 485, *Achelousaurus*, in which the dorsal opening of the frontal fontanelle is 84 mm in length, versus an estimated 185 mm in MOR 591, an absolutely smaller specimen. Secondary roofing of the frontal fontanelle occurs in old *Centrosaurus* individuals as well (e.g. NMC 8795, *C. longirostris*; UALVP 11735, *Centrosaurus* sp.), in at least one instance completely obliterating the fontanelle (AMNH 5351, *C. nasicornis*). This ontogenetic phenomenon also appears to be present in chasmosaurines, as suggested by Hatcher *et al.* (1907) for *Triceratops*.

Taxonomic variation

The frontal fontanelle varies considerably among centrosaurine specimens, as described above, but to date we have not discerned any taxonomic significance. This finding contrasts with Forster's (1990) work on Chasmosaurinae which showed taxon-specific conditions for the shape of the fontanelle. Conversely, the supracranial sinuses do show taxon-specific variation within Centrosaurinae (Sampson, 1995a). In *Centrosaurus* and *Styracosaurus*, the sinus chambers are relatively narrow and, while complex, do not underlie the supraorbital horncores. In *Einiosaurus*, *Achelousaurus* and *Pachyrhinosaurus*, the sinus systems are laterally expanded, underlying and often excavating the supraorbital horncore or boss in a manner analogous to the cornual sinuses of bovids. In the latter group, the cornual cavities are also an extension of a frontal sinus system. Sinus-like cavities are also present in the supraorbital horncores of chasmosaurines, with the condition most developed in the largest horned forms (e.g. *Triceratops*; Forster, 1990).

Summary

Two related features unique to ceratopsids, the frontal fontanelle and supracranial cavities, are associated with the skull roof medial to the orbits. The frontal fontanelle is a large aperture located on the dorsal midline, which opens into a complex system of spaces here termed the supracranial space or supracranial cavities. The fontanelle is composed of parietal and (primarily) paired frontal elements, while the cavities are walled by frontals, parietals, postorbitals (in some taxa), and perhaps supraoccipitals and exoccipitals. A large foramen pierces the floor of the supracranial space, resulting in a communication between this space and the endocranial cavity. Juveniles possess only a shallow fossa in place of these complex structures. Subadults exhibit a fully formed fontanelle and partial development of the supracranial cavities (e.g. including division of this space into anterior and posterior chambers by a transverse buttress). Adults show great variation in the detailed morphology of the cavity system, with some taxon-specific variation (i.e. narrow supracranial cavities in *Centrosaurus* and *Styracosaurus* versus laterally expanded cavities in *Einiosaurus*, *Achelousaurus*, and *Pachyrhinosaurus*). The frontal fontanelle apparently closes with advanced maturity, fusing over to form a true double skull roof in some specimens.

PARIETOSQUAMOSAL FRILL

General features

Although there has been considerable controversy over identification of the major median element of the frill in ceratopsian dinosaurs, it is now generally agreed to be comprised of the fused parietals (Dodson & Currie, 1990). Thus, coalesced parietals, together with paired squamosals, form the frill in ceratopsian dinosaurs. These elements are variably developed in members of Ceratopsia, forming a short shelf in psittacosaurs, and a true frill in neoceratopsians. Maximum expression of this feature is seen in *Torosaurus latus*, with a squamosal 1.43 m in length and a total skull length of 2.4 m (Colbert & Bump, 1947), the longest known for any terrestrial vertebrate (Dodson & Currie, 1990). The elements of the frill, particularly the fused parietals, are of critical importance in ceratopsian taxonomy.

The parietosquamosal complex in adult centrosaurines forms a large posterior shelf or frill, somewhat shorter than the basal skull length (occipital condyle to snout) and covering much of the neck region. The parietals comprise approximately two-thirds of the centrosaurine frill; the remaining third is made up of the anterolaterally placed squamosals. Fusion of the parietals (henceforth referred to as the parietal) must have occurred at an early ontogenetic stage since even juvenile specimens

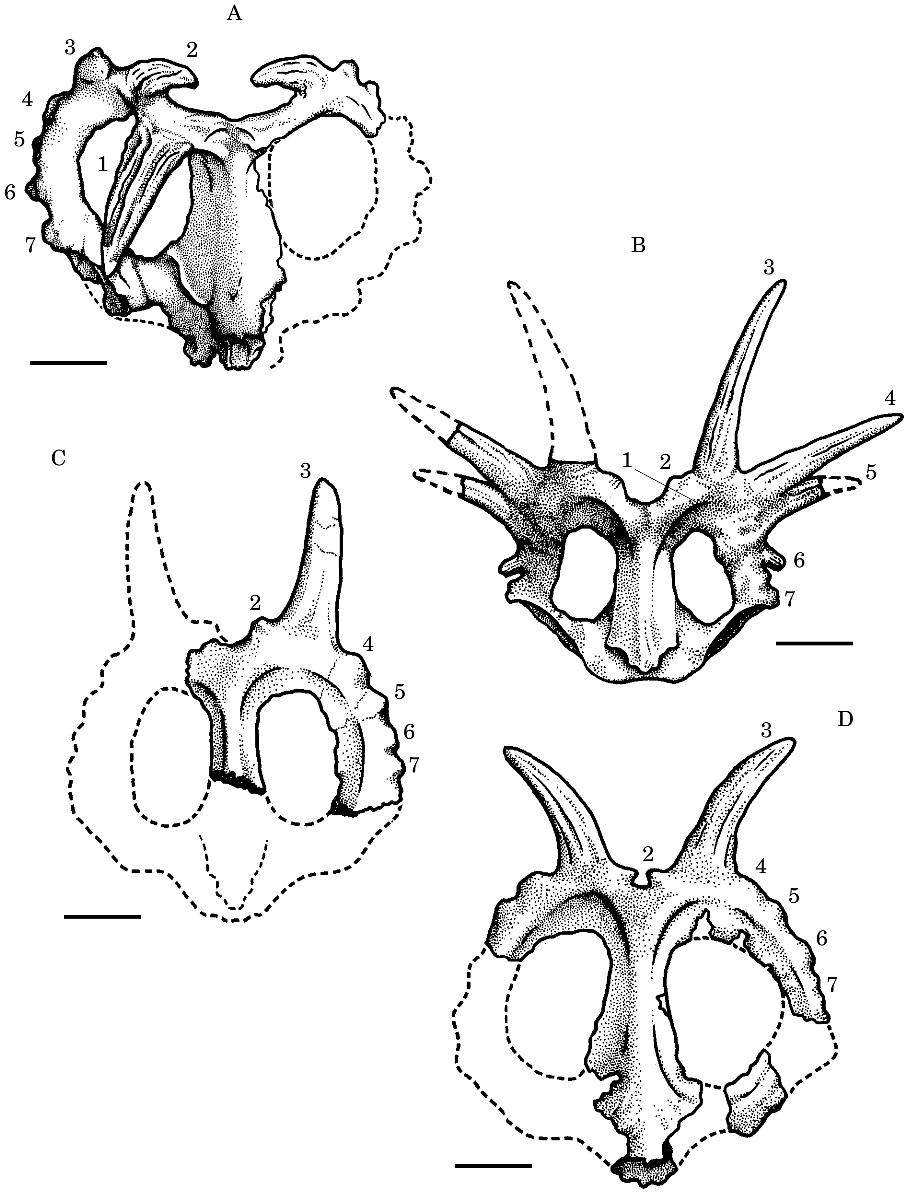

Figure 8. Centrosaurine parietals in dorsal view: A, *Centrosaurus apertus*, NMC 971, adult (holotype); B, *Styracosaurus albertensis*, NMC 344, adult (holotype); C, *Einiosaurus procurvicornis*, MOR 456 8-9-6-1, adult (holotype); D, *Achelousaurus horneri*, MOR 485, adult (holotype); (facing page) E, *Pachyrhinosaurus* sp., TMP 87.55.141, adult; F, *Monoclonius crassus*, NMC 3998, sub-adult (holotype); G, *Brachyceratops montanensis*, USNM 14765, sub-adult; H, *Avaceratops lammersi*, ANSP 15800, juvenile (holotype); I. c.f. *Monoclonius*(?), TMP 82.16.11, juvenile. 1–7 = marginal processes, numbered from medial to lateral (see text). Scale bars = 10 cm.

show no indication of a sutural contact (Dodson & Currie, 1988). The frill is generally saddle-shaped, the dorsal surface being convex transversely and gently concave anteroposteriorly. Variably developed, paired but often asymmetrical fen-

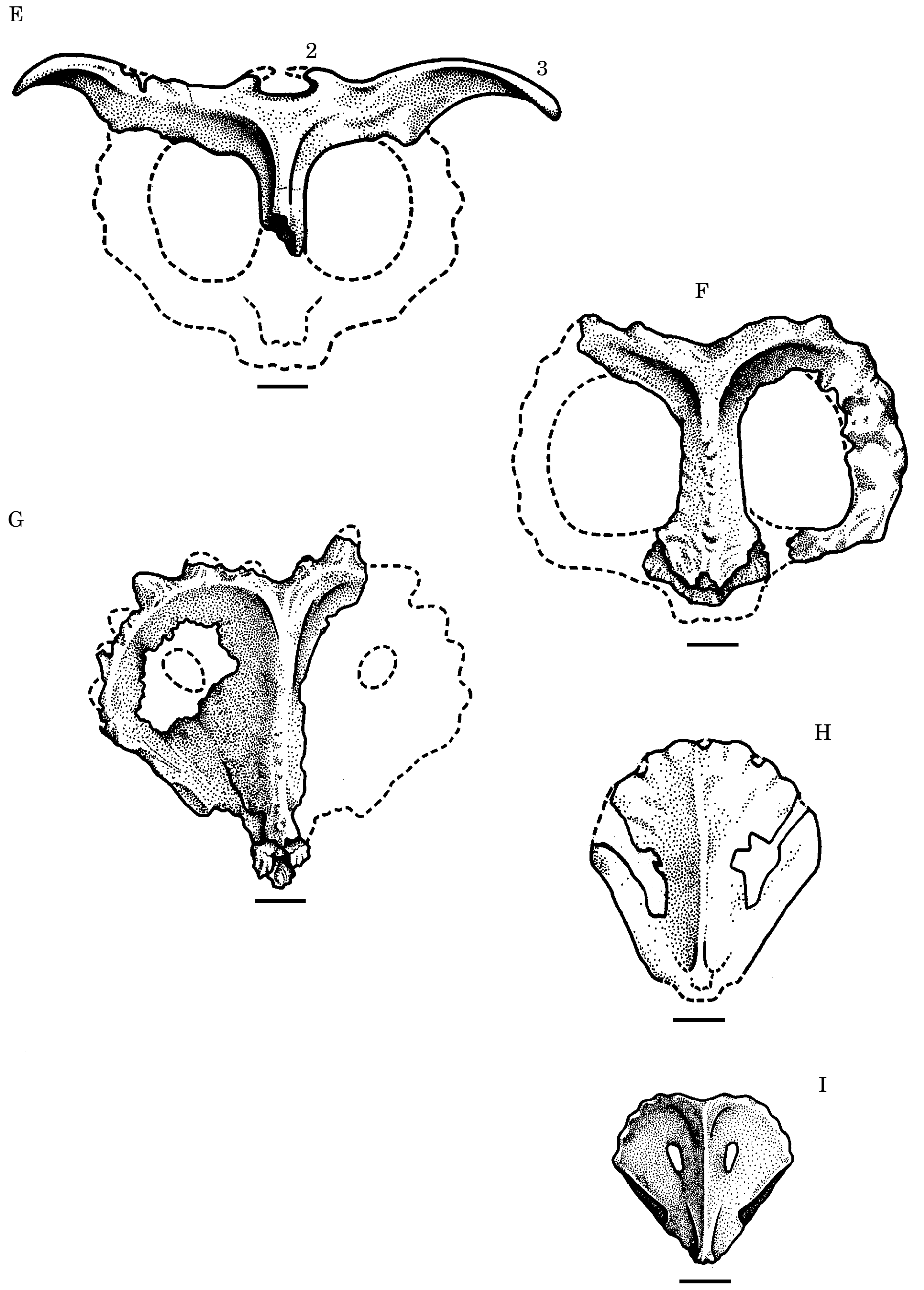

Figure 8. *contd*

estrae, one on either side of the midline, occur wholly within the boundary of the parietal. These fenestrae occur in all centrosaurines, with the possible exception of *Avaceratops lammersi*, known from a single juvenile specimen of uncertain affinity from the Judith River Formation of Montana (Dodson, 1986).

The parietal can be subdivided into three primary components: (1) a robust, longitudinal midline bar, (2) a posterior transverse ramus, forming a 'T' with the parietal bar and possessing a variety of hooks, spikes and/or horns, and (3) lateral rami with scalloped margins bearing variably developed accessory elements or 'epoccipitals'. The median bar is typically robust, convex dorsally and concave ventrally, with a deep ventral groove. Dorsal undulations on the parietal median bar are common to virtually all centrosaurines, juvenile through adult. The undulations range from two to six with four or five being typical. Development of these midline processes varies from low rugosities (AMNH 5351, *Centrosaurus nasicornis*) to prominent bumps (AMNH 3998, *Monoclonius crassus*) to well-developed spikes and hooks in some adult pachyrhinosaurs (TMP 86.55.211, *Pachyrhinosaurus* sp.). Near the anterior end of the median bar, there is a transverse constriction or neck which broadens further anteriorly into a well-developed sutural complex for the frontals, and a deep depression, the posterior portion of the frontal fontanelle complex (Sternberg, 1927). In adults, the posterior transverse ramus of the parietal forms a generally thick, well developed margin with a complex variety of taxonomically-specific processes. The anteriorly-directed lateral rami round out the frill, enclose the parietal fenestrae, and include contact surfaces for the squamosals. A U-shaped midline notch on the posterior border is often present with much variation within species. Some specimens possess a deep emargination in this region while others have virtually a horizontal border and lack this feature.

Parietal processes—whether hooks, horns, spikes, or simple outgrowths—number between five and seven per side, varying between and within taxa and even on opposite sides of the same parietal (NMC 8795, *Centrosaurus longirostris*). For the purposes of discussion, we present here a system of numbering parietal processes from medial to lateral (Fig. 8), with the assumption that equivalently numbered processes are homologous. Thus, the anteriorly directed hooks of *Centrosaurus* are referred to as process 1 and the large, medially directed horns become process 2. Processes further lateral are numbered sequentially. Three genera—*Einiosaurus*, *Achelousaurus* and *Pachyrhinosaurus*—apparently lack parietal outgrowths homologous to process 1 in *Centrosaurus* and *Styracosaurus*. Thus, the most medial process on the periphery of the parietal in the former group is designated process 2.

The centrosaurine squamosal is roughly rectangular in outline and short in comparison to that of chasmosaurines in which the squamosal is triangular and much longer, often reaching the posterior frill margin. The posterolateral portion of the centrosaurine squamosal forms part of the scalloped lateral margin of the frill. Processes number between three and six with four or five being typical. There is much intraspecific variation in the number of these outgrowths; a sample of six squamosals from an *Einiosaurus* bonebed shows variation between three and five epoccipitals per specimen. A single individual may vary in the number of scallops on opposite squamosals (AMNH 5239, *Centrosaurus flexus*).

The ventral (internal) surface of the squamosal shows several characteristic ridges and grooves, the sutural contacts for the quadrate and exoccipital. The exoccipital slots into a deep groove with a heavy osseous lateral ridge. The quadrate is wedged behind the anteromedial border of the exoccipital groove. The squamosal contacts the posterolateral surface of the parietal with a simple butt suture that is variably grooved on the contact surface but generally concave. In most forms, the posteromedial margin of the squamosal 'steps down' and the medial contact with the parietal is an overlapping, or scarf, suture. This stepped down portion of the squamosal forms part of the anterior margin of the dorsotemporal fenestra, with the parietal forming the rest of this fenestral border. Other contacts include the postorbital and jugal anteromedially. The laterotemporal fenestra is formed primarily by the jugal, with the quadrate process of the squamosal making up the posterior margin.

Ontogeny

All centrosaurine juveniles possess similar frill morphologies, so similar in fact that juveniles of different taxa usually are difficult, if not impossible, to distinguish. The parietal is a thin, fragile element in juvenile and sub-adult centrosaurines, bearing a simple scalloped margin which may or may not show evidence of epoccipitals. Only with adult size came the development of hooks and spikes employed today as generic and specific taxonomic characters (Figs 5, 8). Juveniles often possess a well-defined dorsal sagittal ridge on the parietal midline (USNM 7951, *Brachyceratops*; TMP 82.16.11, ?*Monoclonius*) that decreases in prominence during ontogeny until in the adult the profile is generally low, broad and rounded. The posterior portion of the parietal bar thickened substantially with age, often developing a midline dorsal depression in conjunction with development of large processes on the posterior transverse ramus (NMC 971, holotype of *Centrosaurus apertus*). The posterior ramus is comparatively thin and unadorned in juveniles and sub-adults, with a simple scalloped margin similar to that of the lateral rami (USNM 7951, *Brachyceratops*; ANSP 15800, *Avaceratops*). Due to their fragile nature, complete specimens of juvenile and sub-adult parietals are rare, although fragments are common in paucispecific bonebeds.

The epoccipitals (inappropriately named as they occur only on parietals and squamosals and never on the occiput) are an important ontogenetic feature of the frill. They are accessory elements or osteoderms that fuse to the frill margin during ontogeny. While possession of epoccipitals has been assumed for virtually all chasmosaurines (Lehman, 1989), their occurrence in centrosaurines has been problematic. Gilmore (1914, 1917) suggested that *Brachyceratops* was unique in its lack of these extra marginal ossifications whereas Lambe (1915) claimed that neither *Brachyceratops* nor *Styracosaurus* bore these elements while *Centrosaurus* did. Hatcher *et al.* (1907) stated that *Monoclonius* did not possess epoccipitals and Sternberg (1940) concurred with this view. The bonebed evidence indicates that while most juveniles and sub-adults generally lack epoccipital ossifications, they occur in adults of all centrosaurine taxa. The epoccipitals fuse to the frill margin from the posterior portion of the frill anteriorly. Many specimens clearly display lines of fusion on anterior epoccipitals while bone remodelling has removed all traces of separate ossifications posteriorly. Similarly, posterior undulations on the frill margin often show these extra ossifications while they are absent on the anterior parietal and the squamosal. Unfused, isolated epoccipitals have been recovered from several centrosaurine bonebeds.

Epoccipitals generally fuse directly to the radiating scallops of the squamosal and parietal. However, at the bilateral loci marked by the parietal-squamosal contact, epoccipitals are often present despite the lack of a raised process, suggesting that this is the general condition for centrosaurines. Thus, any count of processes on the

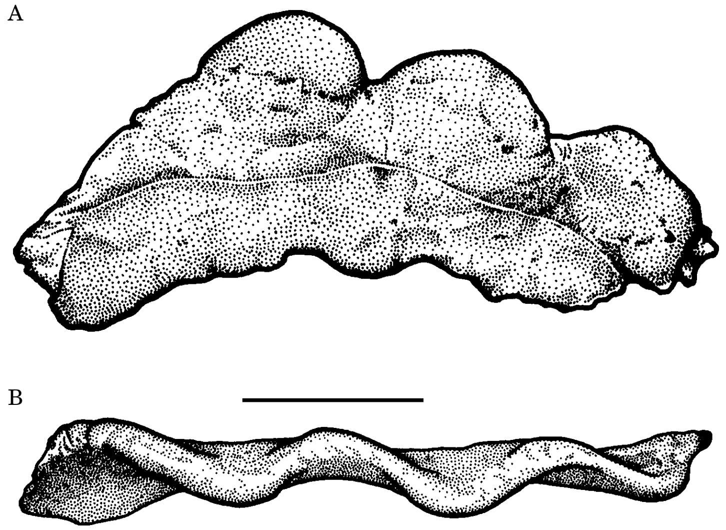

Figure 9. Partial parietal of *Pachyrhinosaurus* sp., TMP 89.55.1030, showing lateral ramus with imbrication effect (see discussion in text): A, dorsal view; B, lateral view. Scale bar = 10 cm.

periphery of the frill must take into consideration the presence or absence of epoccipitals, particularly at the lateral margin of the parietal-squamosal contact. Whether the two or three most medial processes on both sides of the posterior transverse ramus (referred to here as processes 1–3) developed from separate ossifications or are simply outgrowths of the parietal is uncertain. On the basis of currently available evidence it appears that they are outgrowths. No specimen, from juvenile to adult, shows any sign of fusion of separate elements to the parietal processes at these posterior loci.

A peculiar phenomenon associated with mature centrosaurines is the development of an imbrication effect along the lateral margin of the parietal (Fig. 9). In juveniles and sub-adults, the lateral margin is thin and relatively flat. With maturity, however, the scallops or bosses with their fused epoccipitals take on a sine wave-like pattern with the anterior border of each process depressed relative to the posterior border. The effect is one of imbrication because the processes appear crowded along the lateral frill margin. As with the fusion of epoccipitals, this development occurs from the posterior margin forward. Although most conspicuous in adult specimens, this morphology is present on a small, juvenile-sized squamosal of *Pachyrhinosaurus* (TMP 87.55.177). This effect may have been a means of further accentuating the lateral frill margin and increasing the apparent size of the animal by highlighting each process independently. Nonetheless, the lateral rami of the parietal are similar among centrosaurine taxa and differences between specimens apparently are due to ontogenetic and individual variations rather than to taxonomic distinctiveness.

Although there is much variation in the relative and absolute magnitude of parietal fenestrae, there seems to be a general trend toward increasing size of the fenestrae through ontogeny. The only centrosaurine for which an unfenestrated frill seems likely is the single individual of *Avaceratops lammersi* (Fig. 8H; Dodson, 1986), although the requisite regions of this specimen (ANSP 15800) are not fully preserved. The fragmentary juvenile holotype of *Brachyceratops montanensis* (USNM 7951; Fig. 3) preserves relatively small parietal fenestrae, but the edges are broken and Dodson (1990b) has argued that this taxon also had a solid frill. The smallest centrosaurine parietal known, TMP 82.16.11 (Dodson & Currie, 1988), has relatively small, well-preserved fenestrae, less than 20% of the total sagittal length of the parietal (Fig. 8I). Conversely, lengths of parietal fenestrae in adult centrosaurines are typically greater than 50% of the total sagittal parietal length. A feature often associated with well-preserved parietal fenestrae, particularly in mature individuals, are small, flattened osseous processes that project into the fenestrae from their borders (NMC 8798, *Centrosaurus dawsoni*; UALVP 11735, *Centrosaurus* sp.). Perhaps the best examples occur in the parietal fenestrae of NMC 8795, *Centrosaurus longirostris* (Sternberg, 1940), in which some of these processes are more than 10 mm long.

There is a relative increase in parietal width during ontogeny. Comparing parietal sagittal length to parietal width (half widths were used, and an average of both sides calculated where both are preserved), it is clear that the parietal broadens relative to its length with age (Table 1). The ratio of sagittal length to one half width in juveniles yields values of 1.5 and 1.7 ($n=2$), whereas adult values cluster around 1.0 ($n=12$) and putative sub-adults have intermediate values ($n=9$). Interestingly, the two most anomalous parietal specimens are those of *Einiosaurus procurvicornis* and *Achelousaurus horneri*, both of which cluster in the sub-adult range although the presence of well developed processes and non-striated surface bone texture show both to be adults. Despite the small sample sizes and overlap in values between sub-adults and adults, the evidence suggests an ontogenetic trend toward increasing breadth of the parietal. This trend is also indicated by a decrease in the angle of the squamosal suture on the parietal. That is, the posteromedial border of the squamosal shifts relatively anteriorly during ontogeny as it is displaced by the broadening parietal (Fig. 8).

The squamosal undergoes little shape change during ontogeny although alterations in form do occur. There is the fusion of epoccipitals described above. As with the parietal, epoccipital elements tend to fuse from the posterior margin forward and the most anterior epoccipital on the squamosal is generally the smallest (ROM 767, *Centrosaurus*). Juvenile squamosals are generally flat while adult squamosals are often concave posterolaterally and convex anteromedially, as viewed dorsally. The distinction between these two regions occurs slightly posterior to the exoccipital groove. With adult size, the lateral processes curve anterodorsally, once again proceeding from the posterior process forward.

The squamosal is of minimal use in distinguishing centrosaurine taxa. With one exception, there are no discrete characters on the squamosal of any centrosaurine genus or species useful in diagnosing taxa within the clade. The single exception is *Avaceratops lammersi* (ANSP 15800) in which the squamosal has a straight posterior border lacking the stepped effect characteristic of other centrosaurines (Dodson, 1986). This specimen is also unique in its greater relative thickness, despite the small size and immaturity of the individual.

Taxonomic variation

Centrosaurus (Figs 5A, B, 8A)

A good ontogenetic series of parietals is known for *Centrosaurus*, with many specimens derived from the Quarry 143 bonebed in Dinosaur Provincial Park, Alberta (Ryan, 1992). As individuals approach adult size, the simple, scalloped posterior margin blossoms into a robust bar with a variety of processes. The most medial processes on either side of the posterior midline (process 1) develop into anteroventrally-directed hooks extending over the parietal fenestrae, although there is some variation (including asymmetry) in this development. The holotype specimen of *C. apertus* (NMC 971) is a parietal with a long hook on the right side and no evidence of any such hook on the left. In some adults these hooks achieved great lengths, exceeding 300 mm and reaching the anterior margin of the parietal fenestrae (YPM 2015). Lateral to these hooks, the next most medial processes on each side (process 2) develop into medially-directed horns that grew in behind the process 1 hooks. Lateral to process 2 the parietal processes in centrosaurs display variable development, becoming small spikes in some individuals (TMP 86.126.1) and remaining simple bosses in others (NMC 8795). Both process 1 and process 2 tend to be rugose with deep longitudinal grooves or vascular channels, akin to the horns of modern bovids.

This pattern of parietal development would be unclear were it not for a number of specimens showing intermediate development of parietal processes. A sub-adult centrosaurine skull (TMP 86.126.1) possesses a parietal in which process 1 had begun to hook forward and process 2 had started to develop medially. Another *Centrosaurus* parietal (TMP 80.18.110), recovered from Quarry 143, Dinosaur Provincial Park, shows a similar stage of development. These putative sub-adults show the predicted mosaic condition of bone surface texture, further supporting the sub-adult designation. It is important to note that the skull achieved adult size before these processes developed, likely over a short period.

Styracosaurus (Figs 5C, 5D, 8B)

On all *Styracosaurus* parietals known, including 10 specimens from a styracosaur bonebed in Dinosaur Provincial Park (BB42), process 1 grew into a small anteriorly-directed protuberance, an abbreviated version of the forward-hooking process 1 of *Centrosaurus* (e.g. TMP 81.19.60; TMP 66.10.4; ROM 1436). The holotype of *S. albertensis* (NMC 344; Fig. 8B) preserves what appears to be the remnant of this abbreviated hook on the left side, not noted in Lambe's original (1913) description of this specimen. Much of the right side of the frill on this specimen, including the locus of the putative process 1, has been reconstructed to match the better preserved left side. This reconstruction, as well as the numerous subsequent portrayals of this animal, are probably too perfectly balanced as posterior parietal processes are generally asymmetrical.

The second most medial parietal processes (process 2) in *Styracosaurus albertensis* are also abbreviated versions of the same process in *Centrosaurus*, medially-directed horns of variable but generally small size (<50 mm). An exception is an undescribed partial parietal of *S. albertensis* (ROM 1436), with a large, although incomplete, medially directed spike on the right side. The equivalent process on the left side is missing but the base indicates a much smaller growth. Process 3 forms the largest spikes in *S. albertensis*, the left spike being 570 mm long on the holotype (NMC 344). Further marginal processes in this species are variable in size, but process 4 and process 5 are consistently long spikes, 500 mm and 360 mm respectively on the left side of NMC 344. Isolated parietal fragments from a styracosaur bonebed (e.g. TMP 66.10.3), and elsewhere within Dinosaur Provincial Park, support the premise that processes 3 to 5 are well-developed spikes in *S. albertensis*.

Einiosaurus and *Achelousaurus* (Figs 5E–H, 8C, D)

Einiosaurus is similar to, yet distinct from, *Centrosaurus* and *Styracosaurus*. The parietal of *Einiosaurus* develops in similar fashion to *Centrosaurus*, remaining thin and simply scalloped until individuals approach or attain adult size, at which time the characteristic spikes appear. Process 1 is not present in *Einiosaurus* while process 2 forms abbreviated horns directed medially and process 3 forms large spikes averaging about 300 mm in length. Processes 4 and 5 are variable but do not show the same development as in *S. albertensis*. In all specimens recovered from the two *Einiosaurus* bonebeds, the processes lateral and anterior to process 2 (the large spike) are comparatively small and most form simple scallops. It seems that *Centrosaurus* developed the medial processes, process 1 and process 2, whereas *Styracosaurus*, *Einiosaurus*, *Achelousaurus* and (to a lesser extent) *Pachyrhinosaurus* de-emphasized these locations and instead developed the more lateral processes into large spikes and horns. As with the nasal horncore, the posterior parietal processes were likely covered in life by a sheath of keratinized epidermis similar to that in bovid horns.

Achelousaurus differs from *Einiosaurus* in the form of nasal and supraorbital horncores, the former having distinctive supraorbital and nasal bosses. However, the two taxa are virtually identical in parietal morphology; *Achelousaurus* lacks an anteriorly directed process 1, possesses an abbreviated process 2, a large spike at the process 3 locus, and simple outgrowths further lateral. The only significant difference in parietal morphology between these two taxa is that the frill of *Achelousaurus* is significantly more robust than that of *Einiosaurus*. The *Achelousaurus* skull appears closely similar to that of *Pachyrhinosaurus* and the two might be considered congeneric were it not for the shared parietal morphology between *Achelousaurus* and *Einiosaurus* (Sampson, 1995a).

Pachyrhinosaurus (Figs 5I, J, 8E)

Pachyrhinosaurus possesses the most derived parietal among centrosaurines and indeed among all ceratopsians. It resembles *Einiosaurus*, lacking a forward-hooking process 1 and possessing a medially-curving process 2. Process 3, a relatively straight spike in *Styracosaurus*, *Einiosaurus* and *Achelousaurus*, curves strongly laterally in *Pachyrhinosaurus*, becoming a large horn. An extensive, undescribed sample of pachyrhinosaur parietals from the Wapiti Formation locality demonstrates dramatic intraspecific variation, although within well-defined parameters. The parietal is rarely symmetrical, a characteristic apparently common to all short-frilled ceratopsians. Some pathologies are present on the parietal specimens, indicating that horns were occasionally injured during growth.

Langston (1975, fig. 13) illustrated an intriguing partial parietal from a *Pachyrhinosaurus canadensis* bonebed at Scabby Butte, Alberta. This specimen (NMC 9602) has a moderately large and straight spike at (what appears to be) the process 3 locus, similar to equivalently placed processes on the frills *Einiosaurus* and *Achelousaurus*. If Langston's reconstruction is correct, the spike is angled posterolaterally in a conformation intermediate between the *Einiosaurus-Achelousaurus* condition and that of other pachyrhinosaurs. C. M. Sternberg found another large, isolated spike-like process at this locality that may be further evidence of well-developed, straight parietal spikes in *P. canadensis* (Langston, 1975, fig. 14).

In addition to the nasofrontal boss, supraorbital bosses and posterior frill projections, an undescribed species of *Pachyrhinosaurus* in the Wapiti Formation bonebed of west-central Alberta possesses from one to three spikes on the parietal midline bar. Not surprisingly, there is much variation in this character. As described above, virtually all Campanian centrosaurines exhibit a series of small midline processes that are likely homologous precursors to the larger spikes seen in this later-occurring species of *Pachyrhinosaurus*.

Summary

The parietosquamosal frill is a large posterior shelf present in the skull of all ceratopsids (and neoceratopsians generally). It is formed from fused parietals medially and posteriorly and paired squamosals anterolaterally. Following the pattern established for other regions of the skull roof, centrosaurine juveniles are closely similar in parietosquamosal morphology, possessing a thin, unadorned frill. This relatively undifferentiated stage extends into sub-adulthood, and it is only after the attainment of adult size that the variety of species-specific appendages develop, including a diverse array of hooks, horns, and spikes on both the outer frill margin and the median parietal bar. Much of the taxonomic variation in frill morphology is reflected in differential emphasis on the various marginal processes. For example, *Centrosaurus* emphasized the two most medial parietal processes while ornamentation in *Styracosaurus* focused on more lateral loci. Other ontogenetic trends affecting the parietal include an increase in relative breadth and overall thickness, and a relative increase in the size of the paired parietal fenestrae. While the parietal is perhaps the single most diagnostic element in the ceratopsid skull, the squamosal is of little taxonomic value.

DISCUSSION

The ontogenetic evidence presented here on the centrosaurine skull has several important implications, ranging from intraspecific growth patterns and correlated behavioral consequences to taxonomy. Dodson & Currie (1988: 929), in their description of the smallest known juvenile centrosaurine parietal, stated, “It is possible that strong positive allometry of the parietal during growth could result in the production of a thickened caudal bar and parietal horns. However, this must remain a matter of conjecture until additional specimens are found.” The bonebed materials described here provide the ‘additional specimens’ to support the above hypothesis. Despite differing considerably in adult appearance, centrosaurine ceratopsids passed through very similar stages with regard to the ontogeny of horns and frills. The frill begins as a simple, relatively unadorned parietosquamosal shelf and remains simple until individuals near adult size, at which time it develops into a species-specific variety of horns, hooks, and spikes. Similarly, the supraorbital horns of juveniles appear to have shared a common morphology, being low and rounded. Sub-adults begin to show the adult form, which is then fully expressed only in adult individuals. Older adults commonly experienced secondary loss of supraorbital horncores, leaving a pitted horn, rugose mass, or true concavity in its place. In parallel fashion, the nasals of all centrosaurines developed as outgrowths of the nasal elements, fusing from the distal tip proximally. Only after this fusion of opposing nasals did the horncore blossom into its mature species-specific form, either a horncore of variable shape and orientation or a pachyostotic boss. The overall picture is one of morphological conservatism throughout most of the development followed by a veritable explosion of cranial appendages following the attainment of adult size.

Taxonomic and phylogenetic implications

The most obvious taxonomic implication of this study is that juveniles and subadults are morphologically similar and thus difficult to distinguish taxonomically. In addition, determination of species in ceratopsids is a complex matter because of the high degree of individual and ontogenetic variation, as well as the possibility of sexual dimorphism (see below). Palaeontologists are faced with the difficult task of attempting to discriminate species using the same characters that are likely to show the greatest intraspecific variation, namely horns and frills. Conversely, reproductive characters are also used by the animals themselves to recognize and select conspecifics, and thus these same characters are likely to have phylogenetic significance. "We should expect to detect speciations with greatest reliability in the fossil record when the fossils in question represent biparental organisms that bear characters of importance in the fertilization system of the species, such as the genitalia of insects, horncores of the Bovidae, antlers of the Cervidae or cranial ornaments in dinosaurs" (Turner & Paterson, 1991: 766).

The phylogeny of the Ceratopsidae is currently in flux and most researchers agree that too many species and genera are in use. Recent attempts have been made to codify the group (Ostrom & Wellnhoffer, 1986; Dodson, 1990b; Forster, 1990; Lehman, 1990; Sampson, 1995a). The species-level systematics of centrosaurines have traditionally been confounded by small sample sizes. In this regard, paucispecific bonebeds are a welcome addition, providing information on numerous individuals from single species. It is now possible to define minimum parameters of qualitative variation for centrosaurine species.

Given these findings regarding the ontogeny of centrosaurines, what conclusions can now be drawn regarding the systematics of the group? Clearly, before a reliable species-level taxonomy can be approached it is necessary to gain an understanding of intraspecific variation. Dodson (1975) examined variation in several genera of lambeosaurine hadrosaurs from the Campanian of Alberta, and concluded that of the three genera and twelve species in use at the time, only two genera and three species are valid. He argued that the genus *Procheneosaurus*, rather than being a small adult hadrosaur, represents juveniles of *Corythosaurus* and *Lambeosaurus*. The results of this study suggest that analogous conclusions should be made for Centrosaurinae.

Avaceratops (Fig. 8H)

Avaceratops lammersi is based on the remains of a single juvenile individual (ANSP 15800; Dodson, 1986). This specimen has a relatively small skull with a thin, unadorned parietal lacking epoccipitals. Unfortunately, the nasal and supraorbital horncores are not preserved. The centra of the first three cervical vertebrae, which generally fuse completely in adult ceratopsids, retain their separate identities (Dodson, 1986). The bone surface texture on most of the cranial elements is clearly of the striated juvenile-type, further supporting the contention of juvenile (and not sub-adult) status. The unguals of ANSP 15800, as well as its enigmatic squamosal described above, indicate that this animal may be distinct from other centrosaurines (Dodson, 1986). However, more centrosaurine fossils are needed from the Judith River Formation of Montana before *Avaceratops* can be placed confidently with respect to other members of Centrosaurinae. In particular, this study demonstrates the necessity of having adult materials in order to place a ceratopsid taxon within a cladistic framework. Consequently, *Avaceratops* will not be considered further in this discussion.

Brachyceratops

Gilmore (1914, 1917) established *Brachyceratops* on materials from several individuals that he recognized to be juvenile or sub-adult (Fig. 3). It is now evident that many of his generic and specific characters are common to all centrosaurine juveniles: small size, abbreviated facial portion, small supraorbital horncores, nasal horncore outgrowth of nasals and divided longitudinally, border of frill scalloped. Gilmore discovered *Brachyceratops* in the upper Two Medicine Formation in northwestern Montana, the same strata and field area that has yielded *Einiosaurus* and *Achelousaurus* (Sampson, 1995a). Subsequently, and in the same area, Gilmore (1939) found a larger centrosaurine (USNM 14765), including a parietal, orbital region, and partial nasal horncore, which he also assigned to *Brachyceratops*. This specimen is much larger than the holotype materials, the latter falling into approximately the same size class as *Avaceratops*.

In his review of centrosaurine taxa, Dodson (1990b) maintains that *Brachyceratops montanensis* is a valid taxon distinct from related forms. His claim is based primarily on characters present in the larger referred specimen, USNM 14765. Dodson notes that the frill of this individual is relatively long and may have been unfenestrated. The skull is fragmentary but, according to Dodson, Gilmore's reconstruction (1939, fig. 11) indicates a basal skull length shorter than the sagittal length of the frill, a conformation otherwise unknown in centrosaurines. Dodson further notes that the jaw associated with USNM 14765 is small and possesses a reduced number of alveoli (approximately 20) compared to adult centrosaurines from the Campanian (about 25–31 alveoli). The holotypic collection of *B. montanensis* includes a maxilla with an estimated 20 alveoli. From this, Dodson concludes that there was no ontogenetic increase in alveoli in this genus.

Several characters strongly indicate that USNM 14765 is a sub-adult: longitudinally divided nasal horncore; low, rounded, non-pitted supraorbital horncore; relatively thin, unadorned parietal with no epoccipitals; mosaic surface bone morphology including striated and mottled textures. The frill may or may not have been fenestrated as this area is missing on the specimen (Fig. 8G). Certainly the preserved bone in the fenestral region was extremely thin. Interestingly, there is a broken process at the process 3 locus on the left side suggestive of an incipient spike as occurs in *Einiosaurus* and *Achelousaurus*. Aside from the fact that basal skull length is estimated on a reconstruction of a fragmentary skull, by our estimation the basal length is equal to or somewhat greater than the length of the frill, as is typical of centrosaurines. The jaw and number of alveoli fall into the sub-adult size class associated with the *Einiosaurus* bonebed collection. It seems highly improbable that *Brachyceratops* would be unique among ceratopsids (and perhaps ornithischians generally) in lacking any ontogenetic increase in alveolar number.

Unfortunately, detailed stratigraphic and geographic information is unavailable for most specimens assigned to *B. montanensis*. Only the locality yielding the holotype material has been re-discovered. It occurs approximately 15 m below the level of the *Einiosaurus* bonebeds and about 40 m below the *Achelousaurus* localities. Given the morphological and taxonomic variation that occurs stratigraphically in the upper Two Medicine Formation (Sampson, 1995a), any specimens removed from stratigraphic context and without definitive characters must be regarded with caution. *Brachyceratops* may represent a juvenile *Einiosaurus*, *Achelousaurus*, or some other taxon but more fossils are needed to resolve this problem. Until such time, the genus *Brachyceratops* should be regarded as a *nomen dubium* because it has no well-established characters and is founded on juvenile and sub-adult materials.

Monoclonius

Undoubtedly the most problematic centrosaurine has been *Monoclonius* Cope. Discovered in the Judith River Formation (Campanian) of Montana, *Monoclonius* was the first named centrosaurine (Cope, 1876), and has had a rather dubious history recently reviewed by Dodson (1990b). The type material of *M. crassus* is a composite collection of at least two individuals, and many of the included elements are not diagnostic at the generic or species levels. There has also been considerable confusion over the generic identities of *Monoclonius* and *Centrosaurus* (Hatcher *et al.*, 1907; Lambe, 1910, 1915; Brown, 1914, 1917; Sternberg, 1938, 1940; Dodson, 1990b). Nine species of *Monoclonius* and six of *Centrosaurus* have been named, most of them early in this century. Dodson (1990b) proposes that *Monoclonius* and *Centrosaurus* are distinct, valid, monospecific genera. He designates a relatively unadorned partial parietal, originally described by Cope (AMNH 3998; Cope, 1889), as the neotype of *M. crassus* (Fig. 8F). Another parietal (NMC 971), this one more robust and possessing well-developed caudal processes, is the holotype of *C. apertus* (Lambe, 1904, 1910; Fig. 8A). This controversy is partially the result of previously inadequate sample sizes. Of the specimens referred to *Monoclonius*, there is one complete skull (NMC 8790, *M. lowei*; Sternberg, 1938, 1940), and four partial skulls, three of which are undescribed. *Centrosaurus* is represented by 17 skulls, bonebed materials, and isolated finds of juveniles and sub-adults (Dodson & Currie, 1990; Currie, pers. comm., 1994). Much of this material has not been included in taxonomic assessments of these genera.

Upon first examination, *Monoclonius* appears to be a relatively unadorned adult centrosaurine; either a primitive form which never developed the diverse horn and frill characters of its kin, or an example of paedomorphosis in which the derived characteristics experienced phylogenetic loss. *M. lowei* (NMC 8790) is characterized by: a short, recurved nasal horn longitudinally divided; low, rounded, non-pitted supraorbital horns; and a thin, unadorned parietal lacking epoccipitals (Sternberg, 1940). The generic neotype designated by Dodson (AMNH 3998) is a well-preserved parietal, once again thin and lacking epoccipitals or any significant degree of development of the marginal processes. In fact, *Monoclonius* specimens are generally defined on the presence of a thin, scalloped parietal and on the absence of hooks, spikes and horns seen on the posterior transverse ramus of other genera (Dodson, 1990b).

However, a number of characters indicate that *Monoclonius* has been established on sub-adult materials, perhaps representing better established genera. It is significant that the only nasal horncore known for *Monoclonius*, preserved on *M. lowei* (NMC 8790), is laterally compressed, divided longitudinally and slightly recurved in a manner closely similar to *Brachyceratops*, as well as sub-adult specimens of *Centrosaurus*, *Styracosaurus* and *Einiosaurus*. In his original description of this skull, Sternberg (1938: 285) stated that, “This longitudinal division is not regarded as of specific importance and only shows that the animal was immature”. The supraorbital horncores of *M. lowei*, although relatively nondescript, are typical of sub-adults as well, being long, low, rounded and non-pitted. The external surface of the parietal of this specimen, although not definitive, does appear to show the predicted sub-adult condition, with a mosaic of striated and non-striated bone texture.

Some skulls attributed to *Monoclonius* are of large size; indeed the frill of NMC 8790 is slightly longer than that of any other Campanian centrosaurine (Table 1). Yet several indicators strongly support the contention of sub-adult status for all of these specimens. One such indicator is surface bone texture which, in most cases, shows a predictable mixture of juvenile and adult surface bone texture, the expected condition for sub-adults. For example, the parietal of AMNH 3998 exhibits striated juvenile-type periosteum dorsolaterally, whereas the bone texture surrounding the parietal fenestrae is mottled, suggesting a cessation of growth in this region. Only the left side of the parietal is preserved in this specimen. Process 1, the most medial process, is not directed posteriorly but rather anterodorsally, suggesting that it had begun to hook forward at the time of death. Were the individual to have lived longer, this parietal process would probably have developed into the procurved hook of a styracosaur or centrosaur. An undescribed partial skull attributed to *Monoclonius* (ROM 1427) is similar, with a thin, unadorned frill and a medial parietal process directed somewhat anteriorly.

Dodson (1990b) posits the validity of *Monoclonius* on biometric grounds. However, with the exception of parietal length, all the biometric distinctions between *Monoclonius* and *Centrosaurus* could be attributed to ontogenetic variation, with *Monoclonius* representing the sub-adult and *Centrosaurus* the adult condition. The problem of parietal sagittal (midline) length is an interesting one. According to our measurements (Table 1), which differ somewhat from those of Dodson, the parietal of *M. lowei* (NMC 8790) is approximately 6 cm longer than the longest *Centrosaurus* parietal (AMNH 5429). It is difficult to determine if this difference is taxonomically significant, particularly given the small sample size and the known variability of ceratopsid frills. Interestingly, the parietal of another *Monoclonius* specimen (ROM 1427) fits well within the range of variation of *Centrosaurus* and other Campanian centrosaurines (Table 1).

Perhaps the most convincing evidence against the validity of *Monoclonius* are the parietals found in paucispecific centrosaurine bonebeds. A number of parietals recovered from *Centrosaurus*, *Einiosaurus* and *Pachyrhinosaurus* bonebeds in Alberta and Montana are of the typical *Monoclonius* type: adult-sized and relatively thin with simple margins lacking horns, hooks and spikes. Were these elements found isolated, they would almost certainly be assigned to *Monoclonius*. It might be suggested that *Monoclonius* individuals were preserved alongside other centrosaurine taxa. Taxonomic mixing does occur; a *Centrosaurus* bonebed in Dinosaur Provincial Park (Quarry 143) has produced one partial chasmosaurine skull in addition to a vast collection of centrosaur material (Currie & Dodson, 1984). However, it seems highly improbable that *Monoclonius* individuals were mixed with remains of three genera in separate bonebeds covering independent events over a large time period spanning the late Campanian and early Maastrichtian. In addition, specimens with parietal morphologies transitional between *Monoclonius* and *Centrosaurus* (e.g. TMP 86.126.1) make more feasible the conclusion that *Monoclonius* specimens represent sub-adult individuals of better established Campanian taxa.

Finally, most centrosaurine taxa have been found in low diversity bonebeds. There is a ceratopsid mass death locality in Dinosaur Provincial Park, Alberta (BB 30), which has long been designated a *Monoclonius* bonebed, though no excavations have been undertaken. During the summer of 1990, the authors visited this site and surface collected numerous specimens. Included in this collection were several thin and simply scalloped, *Monoclonius*-like frill fragments. However, a number of other specimens—postorbitals with well-developed horncores and parietal fragments with well-developed processes—strongly indicate that the animal preserved at this site is *Centrosaurus*, with the assortment of juveniles, sub-adults, and adults characteristic of a paucispecific centrosaurine bonebed. Specimens assigned to *Monoclonius* are known from the late Campanian of Alberta and Montana. If it is indeed represented by sub-adult individuals, as postulated here, the genus *Monoclonius* may consist of immature *Styracosaurus*, *Centrosaurus, Einiosaurus*, and/or *Achelousaurus*.

Thus, the validity of the *Monoclonius crassus* must be questioned for several reasons. First, all the putatively diagnostic characters of this taxon are present in sub-adults of other centrosaurines. Second, suture closure (NMC 8790) and surface bone texture (e.g AMNH 3998), in addition to the immature development of reproductive characters, support the assignment of *Monoclonius* specimens to the rank of sub-adult. Third, *Monoclonius*-type cranial elements, particularly parietals, have been found in bonebed deposits preserving large assemblages of other centrosaurine taxa, suggesting that all centrosaurines passed through a '*Monoclonius* stage' prior to reaching maturity. Therefore, as argued above for *Brachyceratops montanensis*, the taxon *Monoclonius crassus* should be considered *nomen dubium*.

Centrosaurine phylogeny

Sampson (1995a) conducted a phylogenetic analysis of centrosaurine taxa based on seventeen cranial characters. *Avaceratops lammersi* was not included because adult specimens with full expression of horn and frill morphologies are required to place centrosaurine taxa within a phylogenetic context. A single tree was recovered (CI: O.909), with two clades; one with *Styracosaurus* and *Centrosaurus* and the other with *Einiosaurus*, *Achelousaurus*, and *Pachyrhinosaurus* (Fig. 10). Unambiguous character support for each stem is limited to one or two characters. For example, the clade containing *Centrosaurus* and *Styracosaurus* is united by a single unambiguous apomorphy, presence of prefrontal-prefrontal contact. Thus, it would not be surprising if future analyses based on larger samples necessitated a re-arrangement of taxa.

Significantly, virtually all characters useful in diagnosing taxa within Centrosaurinae occur on the skull roof in association with the nasal horn, supraorbital horns, and parietosquamosal frill. All other elements of the skull (basicranium, dentition, jaws, etc.) are phylogenetically conservative as is the postcrania. This result suggests that the horns and frills may have played a critical role in the phylogenetic diversification of centrosaurines, and perhaps also in their daily lives.

Horns and frills as secondary sexual characters

Ceratopsid horns and frills have often been regarded as weapons for predator defence. Yet several authors have argued that these structures are best considered

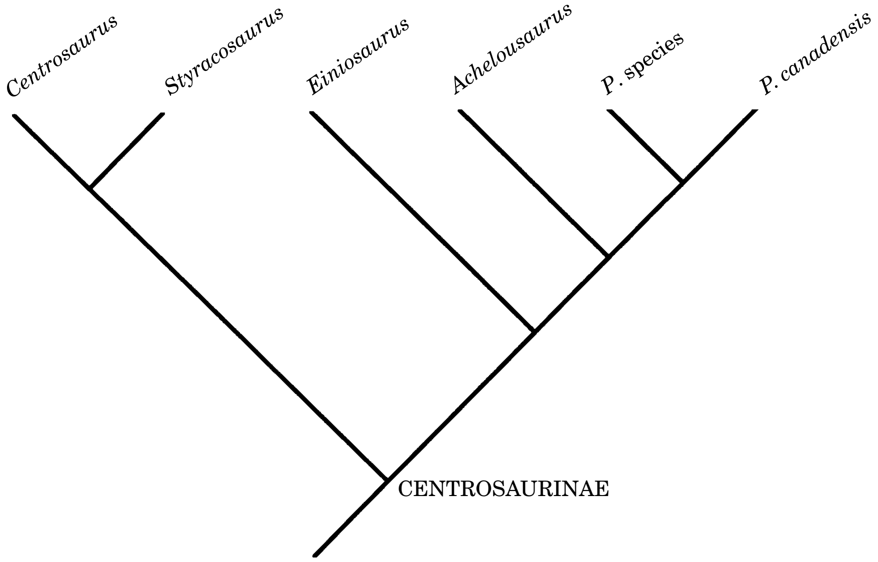

Figure 10. Cladogram of centrosaurine relationships from the analysis of Sampson (1995a). Outgroups: Chasmosaurinae and *Protoceratops*; number of characters: 17; number of trees: 1; number of steps: 24; CI: 0.91. Abbreviation: P. = *Pachyrhinosaurus*.

adaptations for intraspecific display and combat, that is, mate competition (Davitashvili, 1961; Farlow & Dodson, 1975; Spassov, 1979; Sampson, 1993, 1995b). The dramatic variation documented here, both within and between species, strongly supports the latter view. Similarly, in a morphometric study of the protoceratopsian *Protoceratops*, Dodson (1976) recognized considerable variation in frill morphology. If interspecific combat were the primary function of cranial ornamentations, one would expect morphological conservatism in contrast to the extreme variation observed. Delayed growth of horns and frills also does not make sense in a context of predator defence. If defence were the principal function of these structures, it would clearly be advantageous for them to reach full development as early in ontogeny as possible.

The most convincing point in support of the mate competition hypothesis is the fact that horns and other cranial ornamentations in extant animals, from beetles to bovids, are highly variable, often subject to delayed growth, and almost invariably employed first and foremost in mate competition (e.g. Geist, 1966; Gans, 1967; Farlow & Dodson, 1975; Jarman, 1983). Clearly, it is parsimonious to assume that the horns and frills of ceratopsids are adaptations for reproductive success, although they may have been 'exapted' for secondary functions including predator defence in some instances. Thus, the classic head-to-head confrontation between *Triceratops* and *Tyrannosaurus*, a perennial favorite of artists, may well have been a rare event. If ceratopsids were highly social, gregarious animals, as the bonebed evidence suggests, group defence may have occurred. It seems likely that Cretaceous predators, like their extant counterparts (Schaller, 1973), would have sought the easiest prey possible, preferentially hunting the young, the old, the sick and the wounded.

Delayed onset of adult morphologies in the horncores, particularly in males, may indicate that full development coincided with entry into the breeding population.

Many large-bodied mammalian herbivore males enter the rut and breed several years after reaching sexual maturity. This prolonged period of adolescence culminates with the full development of cranial appendages (Jarman, 1983). Retarded growth of cranial appendages appears to be associated with the maintenance of a dominance hierarchy in which sub-adult males are easily differentiated from adult males based on size and weaponry; such an ontogenetic pattern decreases the chance of dangerous encounters between conspecifics (Geist, 1968; Jarman, 1983). Thus, dominance hierarchies and ritualized combat may well have been typical of ceratopsids generally, as they are in many horned ungulates today (Geist, 1966, 1971; Walther, 1984).

Although the frill probably had a role as an attachment area for adductor muscles inserting on the lower jaw (Ostrom, 1964, 1966), numerous ceratopsid skulls (AMNH 5239; ROM 767) possess a pronounced ridge of bone on the posterior margin of the dorsotemporal fenestrae which would have effectively limited the rearward extension of the muscle onto the parietal. Indeed, it is likely that the adductor musculature made this ridge. There is also a noticeable difference in adult surface bone texture between these areas, with the fenestral border being smooth and the posterior frill more rugose. The smooth posterior border of the upper temporal fenestra is likely associated with muscle attachment while the more rugose texture on the frill generally includes numerous well-defined vascular traces suggesting extensive blood flow. Indeed it is difficult to envision attachment of the adductor muscle any further posterior than the anterior margin of the parietal fenestrae, despite claims to the contrary (Lull, 1908; Russell, 1935; Haas, 1955; Ostrom, 1964, 1966).

Finally, sexual dimorphism has been postulated for several neoceratopsian dinosaurs. Dodson (1976), building on the work of Brown & Schlaikjer (1940b) and Kurzanov (1972), applied allometric techniques to analyse the ontogeny and sexual dimorphism of the skull of *Protoceratops*. Dodson found one of the most reliable indicators of sex to be the angle of the parietal. With regard to ceratopsids, Lehman (1990) has argued for the presence of sexual dimorphism in several chasmosaurine taxa, based primarily on differing size and orientation of supraorbital horn cores. The undescribed *Pachyrhinosaurus* collection from the Wapiti Formation includes nasal bosses in which two adult morphs are present, concave and convex, perhaps further evidence of sexual dimorphism.

Dodson (1990b) postulated, on the basis of several isolated skulls, that *Centrosaurus* can be divided into male and female morphs, but evidence is slight, and is contradicted by the patterns of ontogenetic and individual variation present in bonebed samples. For example, Dodson posits that one variant of *Centrosaurus* (*C. nasicornis*) represents the female of *Styracosaurus albertensis*. The two taxa are linked on the basis of morphometric similarities such as thickness of the parietal midline and height of the nasal horncore. However, this contention is based on comparison of only two specimens and again is unsupported by the bonebed data. Large, paucispecific bonebeds containing either *Styracosaurus* or *Centrosaurus* have yet to produce specimens attributable to the other taxon. In addition, the linking of *C. nasicornis* and *S. albertensis* at the specific level is unlikely on evolutionary grounds. If Dodson's claim is correct, the female morph (*C. nasicornis*) possesses elaborate secondary sexual features (e.g. large hooks) that are abbreviated or absent in the male morph (*S. albertensis*). That is, both males and females of this putative species developed elaborate, sexually independent ornaments. In contrast, visual mating signals in extant animals typically exhibit either monomorphism (parallel development of ornaments in males and females; = homeomorphism of Jarman [1983]) or dimorphism (one sex more elaborate than the other). Given that conspecifics often recognize one another on the basis of secondary sexual features, it seems prudent for palaeontologists to consider unique display morphologies as taxonomically significant. While *Styracosaurus* and *Centrosaurus* are close relatives and might better be considered congeneric (Dodson, 1990b), it is conservative to conclude that the taxa are distinct at the specific level until contrary evidence comes to light. Thus, in the absence of larger, statistically significant samples, it is difficult to distinguish between individual and sexual variation, even in cases where only two morphs are present. Although sex-specific morphologies may well be present in ceratopsid horns and frills, we see no persuasive evidence at this time of sexual dimorphism in either centrosaurine or chasmosaurine dinosaurs.

However, a lack of sexual dimorphism in no way detracts from the hypothesis that horns and frills are secondary sexual characters. Sexual dimorphism (in horns, body size, etc.) among extant ungulates tends to be least in small-bodied forms, greatest in medium sized forms and reduced in large-bodied gregarious forms inhabiting open environments (Walther, 1966; Estes, 1974; Geist, 1974, 1977). For example, among bovids, the sexes of small species (less than 20 kg) look alike, the sexes of medium to large species (over 80 kg) often show great dimorphism, and in species where males weigh over 300 kg both sexes tend to have horns and there is minimal sexual dimorphism, particularly in gregarious forms (Jarman, 1983). Sexual dimorphism in the largest bodied forms tends to be focused on reproductive characters, particularly horns. The relative lack of dimorphism in large bodied mammals may relate to several factors, including predation and social competition (Treisman, 1975; Kiltie, 1985). Ceratopsids certainly qualify as large-bodied herbivores, and the abundance of paucispecific bonebeds is suggestive of gregarious behaviour. Thus, although the analogy compares distantly related taxa and undoubtedly variant ecological conditions, it is possible that a similar pattern of dimorphism occurred among ceratopsids.

Moreover, it must be remembered that dimorphism is often associated with non-osseous tissues preserved rarely if at all in the fossil record (e.g. horn sheaths, colour, skin flaps, inflatable sacs). In bovids, keratinous sheaths covering the horns may be sexually dimorphic, with males possessing more complex patterns of ridges to aid in grappling with an opponent. Ceratopsid horn sheaths may well have been equally complex and dimorphic. Colour may have been used to great advantage by males to increase the apparent size and ornateness of the frill, as speculated by some artists. Bright and/or contrasting colours are often found in gregarious open-country birds and mammals (Geist, 1977).

SUMMARY

A recent influx of data from paucispecific ceratopsian bonebeds has permitted study of ontogeny in centrosaurine skulls. The horns and frills achieved their adult morphologies late in ontogeny, after individuals approached or attained adult body size. Immature centrosaurines of various taxa exhibit remarkable similarity in the morphology of horncores. All juveniles and sub-adults have transversely-compressed, sagittally-divided nasal horncores that co-ossified late in ontogeny. Only subsequent

to the fusion of opposing nasals did the characteristic horncore or boss morphology of adults develop. Supraorbital horns followed a parallel developmental sequence. All juveniles and sub-adults had relatively small supraorbital horncores with minor differences between some genera. With full maturity came the various horns, bosses and pitted features present only in adults.

An equivalent pattern holds true for the ontogeny of parietal frills in centrosaurines but not for squamosals, which exhibit evidence of only minor shape changes during growth. Juvenile parietals are invariably thin and fragile, with small to nonexistent parietal fenestrae, a simple, scalloped margin lacking epoccipitals, a pronounced sagittal ridge on the median bar, and a predominance of striated or long-grained surface bone texture. Sub-adult parietals are large, often adult-sized, with well-developed parietal fenestrae, but otherwise resemble juveniles in being relatively thin and unadorned. Additional sub-adult characters include: variable fusion of epoccipitals, when present; a predictable mixture of surface bone morphology, including striated juvenile texture and mottled or rugose adult texture; and variable evidence of the transition to adult parietal processes, particularly those placed most medial and posterior on the parietal, which may show the initial stages of anterodorsally directed growth (*Centrosaurus* and *Styracosaurus*). The parietal thickens with age, particularly on the posterior transverse ramus, and epoccipitals are often present on the marginal processes of adults, fusing from the posterior anteriorly. The median bar of adults is low and rounded dorsally with several variably developed processes that are usually small but attained large size in at least one undescribed species of *Pachyrhinosaurus*. Mature surface bone texture is variable but lacks the striations indicative of relatively rapid growth.

Thus, substantial positive allometry resulted in adult centrosaurine skulls with taxonomically distinct complexes of horns, hooks, spikes and bosses. An important consequence of this ontogenetic pattern is that juveniles and sub-adults are remarkably similar across genera and species, a pattern observable in many bovid taxa. Because of previously unrecognized ontogenetic stages, some genera established on immature elements are probably members of better known taxa and caution is required when establishing taxa on anything but adult materials. *Brachyceratops montanensis* and *Monoclonius crassus* should be considered *nomina dubia* as both are based on immature, non-diagnostic materials.

The dramatic variation in ceratopsid horns and frills strongly indicates that these structures are best interpreted as reproductive characters employed in mate competition. Delayed or prolonged growth of secondary sexual characters has been documented in numerous extant vertebrates, typically in association with gregariousness and dominance hierarchies. The bonebed evidence supports the hypothesis of gregariousness in ceratopsids, and the delayed growth of horns and frills suggests the presence of complex social structures including dominance hierarchies. Despite abundant bonebed data, the evidence for sexual dimorphism in ceratopsids is meager and still hampered by small sample sizes. However, analogies with extant vertebrates suggests that sexual dimorphism in ceratopsid body size may turn out to be minimal. Horns and frills are most likely to be the targets of dimorphism, and preliminary evidence supports this pattern.

ACKNOWLEDGEMENTS

We would like to express gratitude to the following people for insightful discussions and helpful criticism on earlier drafts of this paper: Braxton Alfred, Charles (Rufus)

Churcher, Philip Currie, Peter Dodson, David Eberth, Greg Erickson, Catherine Forster, Gina Gould, John Horner, Thomas Lehman, Pat Leiggi, Chris McGowan, Robert Reisz, Anthony Russell, Matt Smith, Hans-Dieter Sues, David Varricchio, David Weishampel, Jim Wilson, and Larry Witmer. Expert editorial assistance was provided by Charles Churcher and Larry Witmer. Special thanks go to Edward Heck and Donna Sloan for the specimen illustrations, and to the staff and volunteers of the Royal Tyrell Museum of Palaeontology. Access to specimens was kindly provided by Eugene Gaffney (AMNH), Peter Dodson and Ted Daeschler (ANSP), Jack Horner and Pat Leiggi (MOR), Dale Russell and Kieran Shepherd (NMC), Chris McGowan and Kevin Seymour (ROM), Philip Currie and Andy Neuman (TMP), Richard Fox and Alan Lindoe (UALVP), and Michael Brett-Surman (USNM). Funding was provided, in part, by grants to SDS from the Natural Sciences and Engineering Research Council of Canada and from the Geological Society of America. Additional funds were provided through grants to Charles Churcher and to A. P. Russell from the Natural Sciences and Engineering Research Council of Canada.

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