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## A Reevaluation of Sexual Dimorphism in the Postcranium of the Chasmosaurine Ceratopsid *Chasmosaurus belli* (Dinosauria: Ornithischia)

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The sexual dimorphism attributed to *Chasmosaurus belli* by Sternberg (1927) is revisited and reevaluated. A reexamination of the two specimens originally considered by Sternberg reveals that they are less complete than first suggested, with only a moderate amount of overlapping material between them. Only a few of the postcranial elements (humeri, sternal plates, and presacral vertebrae) show evidence of dimorphism, the significance of which is either doubtful or equivocal. Instead of representing sexual dimorphs, it is likely that the two specimens belong to separate species, *C. belli* and *C. russelli*, as evidenced by their distinct frill morphologies and by their stratigraphic segregation within the Dinosaur Park Formation of Alberta. These findings emphasize the need to remain sceptical about claims advocating sexual dimorphism in the fossil record in the absence of statistical significance or stratigraphic control.

Key Words: *Chasmosaurus*, Ceratopsia, Dinosaur Park Formation, sexual dimorphism, variation, Alberta.

*Chasmosaurus* are modest-sized (~1500 kg) ceratopsid dinosaurs known from the upper Campanian-aged beds (~75 Ma [million years ago]) of western North America. They are characterized by the possession of a premaxillary flange, recurved supraorbital horncores, and a broad parietosquamosal frill with a straplike posterior border (Forster et al. 1993). The type species, *Chasmosaurus belli* (Figure 1), was discovered in the middle strata of the Dinosaur Park Formation in Alberta and was originally named *Monoclonius belli* (Lambe 1902). Two additional species of *Chasmosaurus*, *C. russelli* and *C. irvinensis*, are currently recognized from elsewhere in the formation (Godfrey and Holmes 1995; Holmes et al. 2001; Ryan and Evans 2005). A further species, *C. mariscalensis*, has been described from the Aguja Formation in Texas (Lehman 1989), though it was recently given the new genus name *Agujaceratops* (Lucas et al. 2006) and may prove to be more closely related to *Pentaceratops* than to *Chasmosaurus* (Holmes et al. 2001; Diem and Archibald 2005).

Charles M. Sternberg (1927) reported on two specimens of *Chasmosaurus*, both identified as *C. belli*, on display at the National Museum of Canada (now the Canadian Museum of Nature) in Ottawa (Figure 2).



FIGURE 1. Life restoration of *Chasmosaurus belli*, based on CMN 2245. Illustration by JCM.



FIGURE 2. CMN 2280 (left) and CMN 2245 (right) on display at the National Museum of Canada (circa 1926). (Courtesy of the Canadian Museum of Nature).

As restored, the skeletons measured “approximately the same length but the bones of one... are much lighter in construction than those of the other” (Sternberg 1927: 67). According to Sternberg, the total length of the ‘gracile’ skeleton measured 4.93 m, while that of the ‘robust’ skeleton measured 4.95 m. Unfortunately, their supports have since been disassembled and these original measurements cannot be verified. Sternberg attributed the difference in robustness between the two specimens to sexual dimorphism, stating, “it is thought that they represent male and female as it is common, among reptiles, for the female to be larger than the male” (Sternberg 1927: 67). This assumption has gone largely unchallenged in the literature (e.g., Lull 1933; Carpenter and Currie 1990; Dodson 1996), except for an implication by Godfrey and Holmes (1995) that the reported differences between the specimens do not reflect sexual dimorphism because they pertain to two separate species of *Chasmosaurus*.

The recognition of sexual dimorphism in a fossil species must begin with the establishment that the variation observed within that species does represent dimorphism. With only two reasonably complete skeletons of *Chasmosaurus belli* at his disposal, Sternberg could not have established this with certainty, and indeed, he neither quantified nor qualified the differences he observed between the specimens. It is also important to note that many of the bones were highly reconstructed with plaster and subsequently painted over so that the reconstructed portions cannot be easily identified.

As chronicled by C. H. Sternberg (C. M. Sternberg’s father) regarding the restoration of one of the skulls: “we had colored our plaster to resemble the fossil bone – no small task, by the way, as we had to learn to mix colors as well as do the work of a sculptor – with wax” (Sternberg 1917: 83). As such, the possibility remains that the difference in robustness between the two specimens might in part be attributable to the extensive restoration of certain elements. With these concerns in mind, we set out to identify and describe the variation noted between the skeletons, and conducted a reevaluation of Sternberg’s original attribution of sexual dimorphism to *C. belli*.

### Materials

The two *Chasmosaurus belli* skeletons (Figure 3) described by Sternberg (1927) reside in the collections of the Canadian Museum of Nature in Aylmer, Quebec. The “gracile” specimen was designated CMN 2245; the “robust,” CMN 2280. CMN 2245 was collected from quarry Q037, and CMN 2280 from Q010, of the Dinosaur Park Formation (upper Campanian, ~75 Ma) in Dinosaur Provincial Park, Alberta (originally referred to by Sternberg [1927: 67] as the “Belly River series”).

CMN 2245 (Figure 3A) is represented by the posterior half of a skull and mandibles (missing only the prementary), complete presacral series, synsacrum complete to the sixth sacral vertebra, twenty-four caudal vertebrae, most cervical and thoracic ribs, pectoral gir-

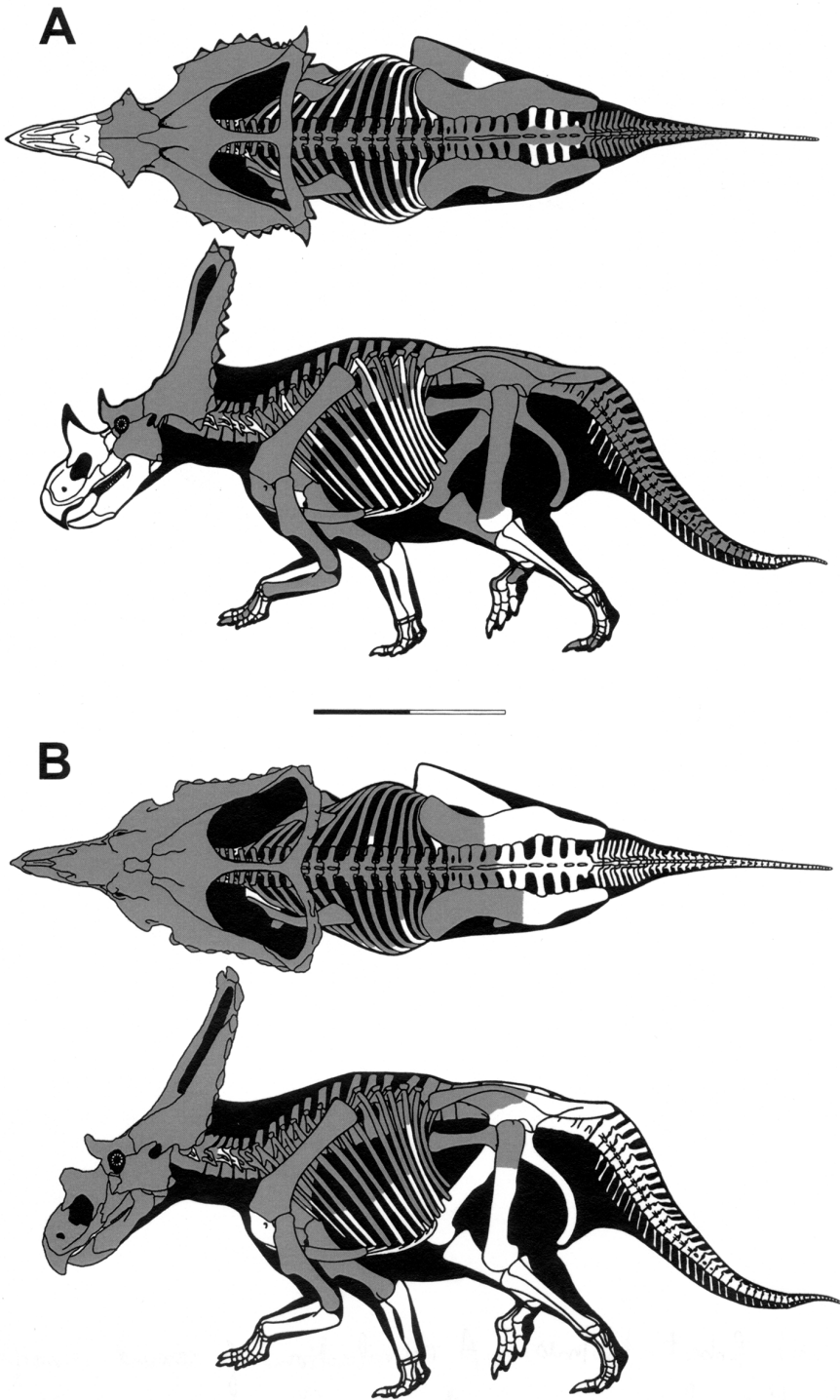


FIGURE 3. Material (in grey) attributed to (A) CMN 2245 and (B) CMN 2280. Scale bar = 1 m. Modified from original skeletal drawing by Gregory S. Paul. Used with permission.

dle (missing only the right coracoid), both humeri, left ulna, pelvic girdle, both femora, right tibia and fibula, and several carpal and tarsal elements.

CMN 2280 (Figure 3B) consists of a complete skull and mandibles, complete presacral series, synsacrum complete to the fourth sacral vertebra, most cervical and thoracic ribs, pectoral girdle (missing only the left coracoid), both humeri, anterior halves of both ilia, both pubes, and the proximal third of the left femur. A return visit to the quarry has yielded more hindlimb material, but it was in poor condition and not collected (D. H. Tanke, personal communication).

Overlapping material between the two specimens therefore consists of the posterior region of the skull, presacral and anterior sacral vertebrae, most ribs, most of the pectoral girdle, humeri, anterior ilia, pubes, and left proximal femur.

## Methods

In order to facilitate distinction between the original bone and plaster, the brown paint was removed from many of the bones using acetone and a stiff-bristled brush. In some instances, the removal of the paint was not warranted when it was obvious that the element of interest had been created entirely of plaster (in which case a simple tap with the knuckle would confirm suspicion). In this way, the original elements common to CMN 2245 and CMN 2280 could be identified.

Three hundred and fourteen measurements were then taken from the postcranium of each specimen to the nearest millimetre, primarily according to the standards of Chinnery (2001). For those elements not considered by Chinnery, such as those belonging to the axial skeleton, one of us (JCM) devised our own measurement parameters. Measurements below 300 mm were generally taken with Mitutoyo SD type dial callipers and measurements above 300 mm were taken either with simple outside callipers and measuring tape or with large (1.04 m) Helios brand Vernier callipers. Circumferences were measured using a tailor's measuring tape. Angles were measured from photographs using a protractor. All available postcranial elements were measured, but only those bones deemed reliably complete and shared between the two skeletons were considered in this study.

## Comparative Osteology

### Description of Overlapping Material

Although CMN 2245 and CMN 2280 exhibit modest variability in the dimensions of their overlapping elements (Figure 4), much of this appears to be due to the extensive restoration and occasional postmortem deformation of the skeletons. Despite this, the best preserved elements usually differ in size by only a few percent, which is insufficient to produce visually discernable dimorphism, and is probably within the realm of individual variation that might be expected in tetrapods (e.g., Rising and Somers 1989; Zaaf and Van Damme 2001; Kelly et al. 2006). The coracoids of

CMN 2245 and CMN 2280 are noticeably different in shape, although the left and only coracoid preserved in the former specimen has been badly weathered and highly reconstructed as a result, and is therefore of limited use. Only a few bones differ considerably in several dimensions and are described below.

### Humerus

The humerus (Figure 4A) of CMN 2280 is considerably more robust than that of CMN 2245 in most dimensions (Table 1), particularly those of the humeral head, deltopectoral crest, and midshaft circumference. Besides proportional differences in the humerus, the insertional scar for the *latissimus dorsi* muscle on the deltopectoral crest is much less pronounced in CMN 2245.

### Sternal Plate

Although the sternal plate (Figure 4B) is quite similar in size and shape between the two specimens, the process at the posterior end of the element extends 42-55% further laterally in CMN 2280 than in CMN 2245.

### Presacral Vertebrae

The presacral vertebrae (Figure 4C) of these specimens are uniform in most dimensions, with most apparent differences being attributable to the addition of plaster. However, in the region of the withers (anterior thoracics), the vertebrae of CMN 2280 average 21% taller (Figure 5A) and their neural spines 19° more erect (Figure 5B) than in CMN 2245. Similarly, the transverse processes of the cervical and anterior thoracic vertebrae of CMN 2280 average 17° more erect than in CMN 2245 (Figure 5C), although this is difficult to state with confidence given the artificial coalescence of the vertebrae and the incompleteness of many of their spinous processes in CMN 2245. It seems, too, that the transverse widths of the vertebral centra anterior to the sixth thoracic average 10% wider in CMN 2280 (Figure 5D).

## Discussion

### Preservation of CMN 2245 and CMN 2280

While CMN 2245 is the most complete skeleton of *Chasmosaurus* known to date, it is less complete and less well preserved than generally supposed (e.g., Dodson 1996: 107). Some of the elements touted by Sternberg (1927) as being complete, such as the femora and caudal vertebrae, are actually only partially represented by nondescript scraps of bone buried in plaster, causing confusion among later authors (e.g., Lull 1933). Many of the presacral vertebrae have also been artificially "fused" together with plaster, obscuring much of the detail. CMN 2280 is by far the better preserved of the two specimens, although it is less complete. Consequently, there is only a moderate amount of material shared between the two specimens, and additional overlapping material would be desirable to make a convincing case for dimorphism in *C. belli*.

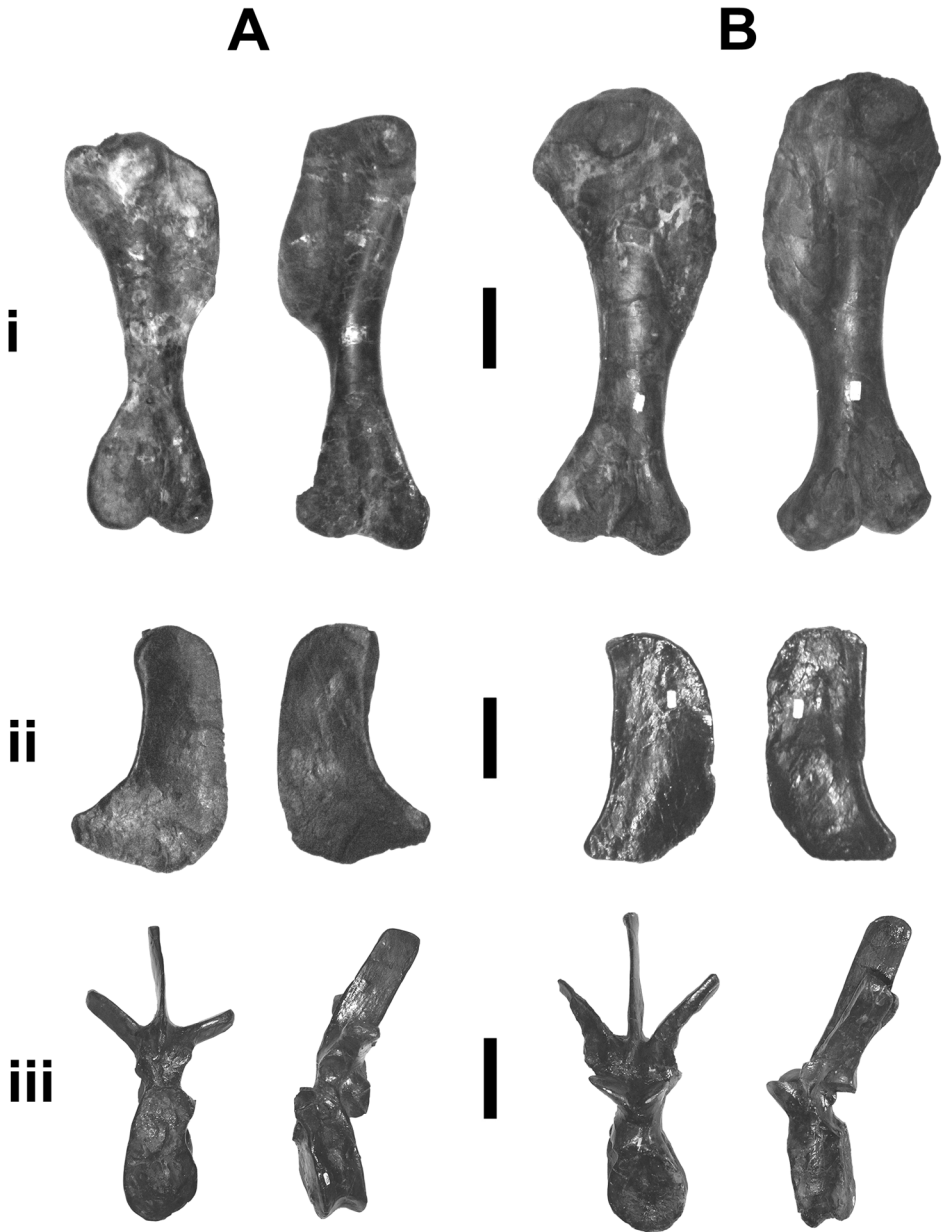


FIGURE 4. Dimorphic overlapping material of (A) CMN 2245 and (B) CMN 2280. **i**, right and left humeri; **ii** right and left sternal plates; **iii** posterior thoracic vertebrae in anterior (left) and left lateral (right) views. Note that, because of the poor preservation of the overlapping vertebrae, the eighth thoracic vertebra is figured for CMN 2245 and the tenth thoracic vertebra is figured for CMN 2280. Scale bar = 10 cm.

*A Reevaluation of Sexual Dimorphism in Chasmosaurus belli*

Recognizing sexual dimorphism in a fossil species is rarely a straightforward task, especially given small sample sizes where subtle but statistically significant dimorphic characters are difficult to resolve (Padian

et al. 2005). Chinnery (2001, 2004) attempted to discern morphological variation, including sexual dimorphism, in the appendicular skeleton of the Ceratopsia, but could find none. The dimorphism originally ascribed by Sternberg (1927) to CMN 2245 and CMN 2280 was presumably based on variation in the postcranial skele-

TABLE 1. Selected measurements (after Chinnery 2001) for left humeri of CMN 2245 and CMN 2280, showing the large differences between their dimensions. Dimensions in square brackets are estimated.

Measurement parameter	Dimensions (mm)		Disparity (%)
	CMN 2245	CMN 2280	
Width of deltopectoral crest	95	72	24
Deltopectoral crest length, from external tuberosity to distal end of deltoid muscle scar	225	272	17.3
Cranio-lateral view; proximal width	44	76	42
Head height	[56]	78	28
Head width	55	86	36
Circumference about midshaft*	216	275	21.5

\* = parameter not used in Chinnery (2001).

ton, although distinct differences in frill morphology are also present (see below). These differences cannot be attributed to either allometry or ontogeny since both specimens are of comparable size. Nor are they likely due to geographic variation since both specimens were found less than nine kilometres from one another. Post-mortem distortion cannot account for the differences either, as most of the elements are relatively uncrushed.

A review of the overlapping material reveals that the most striking differences between CMN 2245 and CMN 2280 lie with the humerus. The disparity in the robustness of the humerus and in the size of the insertional scar for the *latissimus dorsi* muscle seems to follow the prediction made by Chapman et al. (1997) that sexual dimorphism in ceratopsians would be expressed in the limb bones. It is also reminiscent of the condition seen in the humerus of many pachypleurosaurid sauropterygians (e.g., Sander 1989; Cheng et al. 2004) and of the sauropod *Camarasaurus* (Ikejiri 2005). However, if these humeral characters alone separate male from female, then other specimens of *Chasmosaurus belli* should exhibit the same disparity in humeral robustness as well. A bivariate plot derived from a Principle Components Analysis by Chinnery (2001: 134) revealed that the humerus of CMN 2245 plots as an outlier from the other eleven *Chasmosaurus humeri* included in the study. As the deviation lies along the y-axis, the differences are likely due to shape rather than size. Thus, while the shape differences between the humeri of CMN 2245 and CMN 2280 are real, the highly asymmetrical sex ratio implied is very unlikely. The inability of Lehman (1990) to identify dimorphism in the humeri from a population of *C. mariscalensis*, and M. J. Ryan's (personal communication) failure to find the same in several populations of *Centrosaurus apertus*, further supports this position. Sternberg (1927) specifically states that "[t]here have been no bones of other individuals used in the mounts", so the differences cannot be ascribed to the incorporation of material from a smaller individual into the mount. It seems that the humeri of CMN 2245 are simply unusually small and gracile, although the reason for this is unclear.

The reasons for the disparity in the dimensions of the

sternal plates and of the presacral vertebrae are likewise uncertain in the absence of more material. The apparently longer and more erect neural spines and transverse processes of CMN 2280 coincide with observations made by Tereshchenko (2001) of protoceratopsids, in which the spinous processes of the vertebrae were reputedly shown to be longer and more erect in males than in females. If this apparent dimorphism is sexual, however, it would imply the "robust" specimen (CMN 2280) was male rather than female (*contra* Sternberg 1927). This type of "normal" sexual dimorphism, in which the male is more massive than the female, is typical of most reptiles (Fitch 1981; Shine 1989; Brochu 2002).

Thus, undoubted differences (albeit fewer than originally implied by Sternberg) between the two specimens do exist. The marked difference in the size and shape of the humerus may simply be anomalous, unless we accept the unlikely hypothesis that of the twelve *Chasmosaurus humeri* measured by Chinnery (2001), eleven are of one sex and only one is of the other. Other differences, such as the specific shape of the sternal plates and the relative size and orientation of the spinous processes of the presacral vertebrae, might represent sexual dimorphism or intraspecific variation. It is also possible that all of the postcranial discrepancies noted here are functionally related, reflecting a developmental compensation of the extrinsic muscles of the forelimb in response to the atrophied humeri of CMN 2245. However, in the absence of a statistically significant sample, it is impossible to resolve this question. Whatever the significance of the variation, there seems little choice but to reject the hypothesis of sexual dimorphism.

#### *Two-Species Hypothesis*

It is possible that the few differences documented here within the postcranial skeletons of CMN 2245 and CMN 2280 may simply reflect that these two specimens represent separate species. In a review of the systematics of the genus *Chasmosaurus* (Godfrey and Holmes 1995), two species were diagnosed based on differences in parietosquamosal frill structure. *C. belli* was defined as possessing a "parietal frill with nearly straight transverse posterior bars, each bearing one large

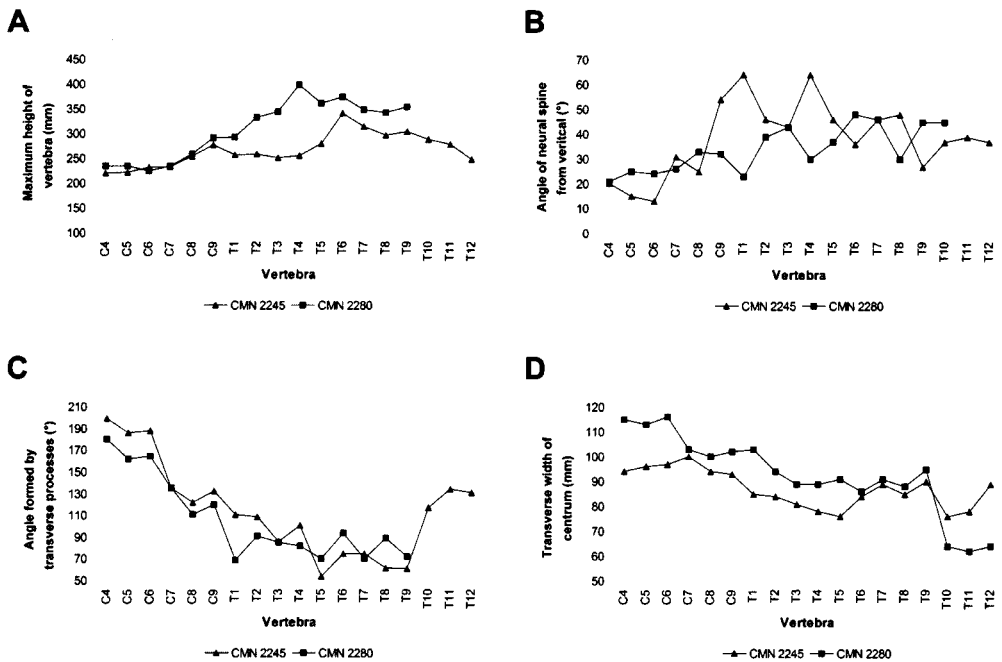


FIGURE 5. Graphical depictions of vertebral disparity between CMN 2245 and CMN 2280. **A**, Differences between maximum heights of vertebrae. The anterior thoracic vertebrae of CMN 2280 are consistently taller than those of CMN 2245. **B**, Differences between angles of neural spines. In the anterior thoracic region, the neural spines of CMN 2245 are angled further posteriorly than in CMN 2280. **C**, Differences between angles formed by transverse processes. The transverse processes of the cervical and anterior thoracic vertebrae of CMN 2280 are more erect than those of CMN 2245. **D**, Differences between transverse widths of centra. The cervical and anterior thoracic centra of CMN 2280 are consistently wider transversely than those of CMN 2245. Abbreviations: C, cervical vertebra; T, thoracic vertebra.

triangular epoccipital on its posterolateral corner; other parietal epoccipitals variable in number and degree of coossification with the parietal, but always much smaller. The lateral bar of the parietal completely encloses the parietal fenestra." *C. russelli* was characterized as having a frill in which the posterior margin is "broadly arched on either side of [the] median emargination. Each side bears three low triangular, roughly equal-sized epoccipitals. The lateral ramus of the parietal is reduced and does not completely encircle the fenestra in all but one specimen, permitting the squamosal to form a part of its lateral border." Under these amended diagnoses, CMN 2245 was retained within the hypodigm of *C. belli*, but CMN 2280 was reassigned to *C. russelli*. This distinction was challenged by Lehman (1998), who argued that the discrete characters used to distinguish *C. belli* from *C. russelli* actually represent end-members of a gradational spectrum of frill morphologies. In support of his argument, Lehman (1998: figure 9) figured seven skulls attributed to *C. belli* and *C. russelli*, illustrating the range of frill morphologies he observed. However, the lateral parietal bars of

AMNH 5402 used by Lehman are not illustrated as being complete as they are in the original specimen, which creates the false impression that the frills exhibit graded variation. Correcting for this splits the series into two discrete groupings of frill morphologies (Figure 6), the contents of which agree with the original hypodigms of Godfrey and Holmes (1995).

Further support for the distinction between *C. belli* and *C. russelli* stems from their stratigraphic segregation within the Dinosaur Park Formation (Figure 7). This observation was made previously by Godfrey and Holmes (1995) and Holmes et al. (2001), and more recent quarry data support this claim, with *C. russelli* confined to the lower part of the formation and *C. belli* located much higher in the section (Ryan and Evans 2005). These independent lines of evidence strongly suggest that the variation between CMN 2245 and CMN 2280 is interspecific in nature, negating Sternberg's case for sexual dimorphism. Stratigraphic separation has also been noted recently among the supposedly sexually dimorphic lambeosaurine hadrosaurids of the Dinosaur Park Formation (Evans et al. 2006),

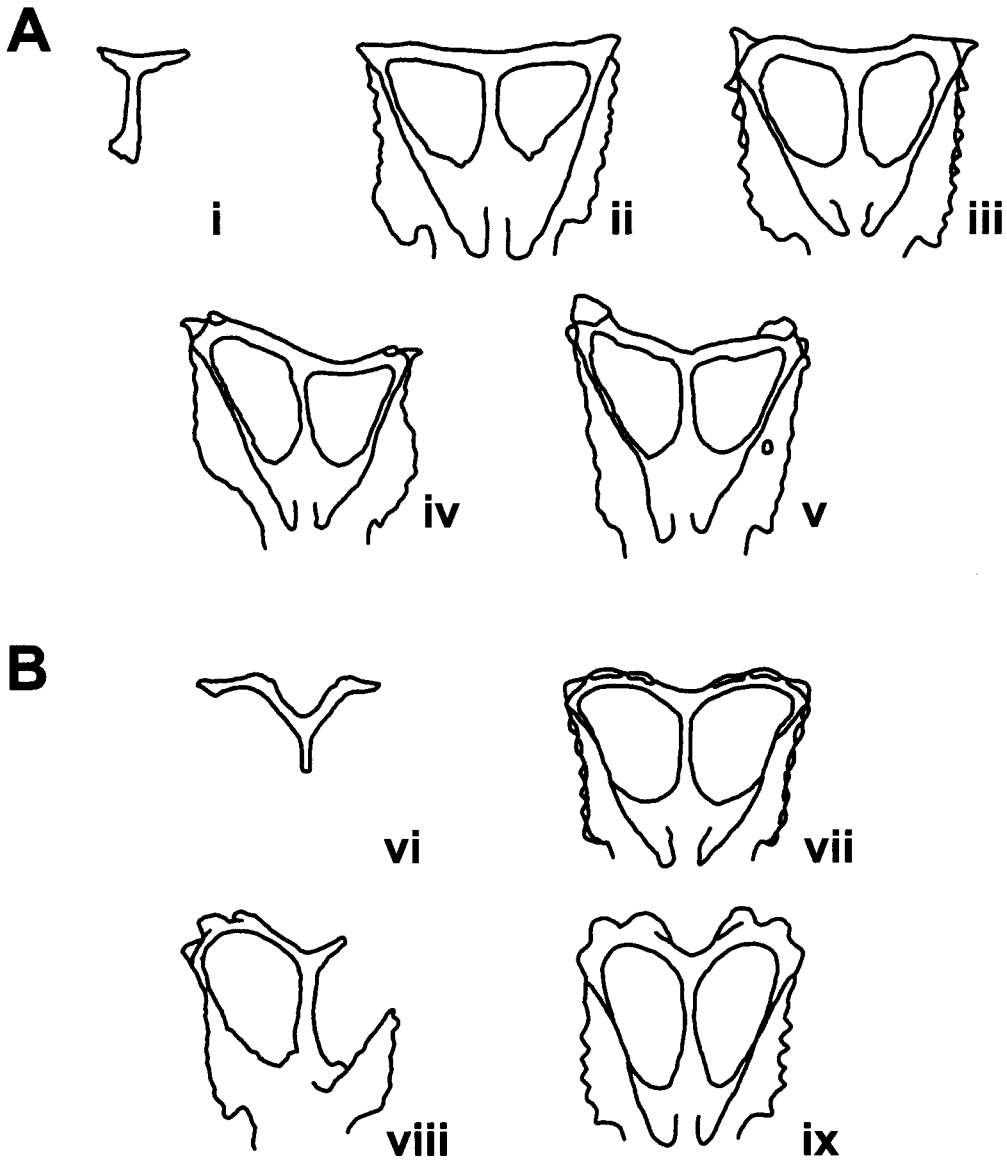


FIGURE 6. Parietosquamosal frills of (A) *Chasmosaurus belli* and (B) *C. russelli* in dorsal view. i, CMN 491 (holotype of *C. belli*); ii, YPM 2016; iii, CMN 2245 (paratype of *C. belli*); iv, AMNH 5402; v, ROM 843; vi, CMN 8803 (paratype of *C. russelli*); vii, CMN 2280; viii, RTMP 83.25.1; ix, AMNH 5656. Frills not to scale.

suggesting a need for more critical consideration of sexual dimorphism in the fossil record.

### Conclusion

After a careful review of CMN 2245 and CMN 2280, it seems that the postcranium of neither specimen is quite as complete or as well preserved as originally described by Sternberg (1927). Consequently, the case for dimorphism (sexual or otherwise) is weaker than previously thought. Most of the variation exhibited by

the shared elements is attributable either to poor reconstruction, postmortem distortion, or individual variation. Exceptional cases involve the humeri, sternal plates, and presacral vertebrae.

While the disparity in the shape of the humerus is indeed genuine, the same dimorphism is not seen in other specimens of *Chasmosaurus*, so this feature is likely anomalous rather than dimorphic. The sternal plates of CMN 2245 and CMN 2280 differ in the lengths of their posterolateral processes, and the presacral ver-



tebrae differ in the lengths and orientations of their spinous processes. However, analysis of additional *Chasmosaurus* material – preferably derived from some yet undiscovered monodominant bonebed (Eberth and Getty 2005) – would be necessary to determine the significance of this variation with regards to sexual dimorphism. The results presented here are therefore only preliminary, pending further investigation of individual variation in the ceratopsian postcranial skeleton.

Finally, previous detailed reviews of the frill morphology of either specimen seem to suggest that CMN 2245 and CMN 2280 may, in fact, belong to separate species (*C. belli* and *C. russelli*, respectively), as first put forth by Godfrey and Holmes (1995). This view is further supported by the stratigraphic segregation of the two specimens within the Dinosaur Park Formation of Alberta. Whether the postcranial differences identified here represent interspecific distinctions remains to be demonstrated. Therefore, although there do seem to be a few legitimate differences between the two specimens, the weight of the evidence so far accumulated does not support sexual dimorphism as Sternberg (1927) first suggested it, and there remains little choice but to reject this hypothesis. In the future, sexual dimorphism should be attributed to fossil species only when statistical significance and stratigraphic control have been demonstrated. Claims made in the absence of such evidence should be regarded with scepticism.

### Acknowledgments

We would like to thank Gilles Danis, Margaret Feuerstack and Kieran Shepherd for offering access to specimens in their care. Philip Currie and Hans Larsson provided valuable resources and discussion. Andrew Farke, Michael Ryan, and two anonymous reviewers provided constructive criticism on earlier versions of this manuscript. This research stems from a B.Sc. Honours thesis written by JCM under the supervision of RH.

### Institutional Abbreviations

AMNH, American Museum of Natural History, New York, New York; CMN, Canadian Museum of Nature, Ottawa, Ontario; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; YPM, Yale Peabody Museum, New Haven, Connecticut.

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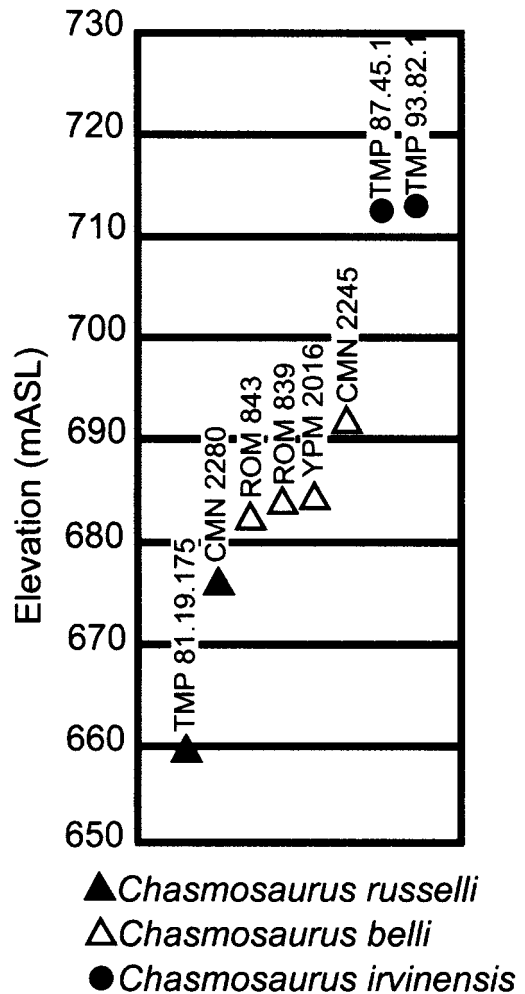


FIGURE 7. Stratigraphic distribution of *Chasmosaurus* from the Dinosaur Park Formation of Alberta (modified from Ryan 2003). Data from Currie and Koppelhus (2005\*).

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