(Summary from my first review): This manuscript describes a new specimen of a centrosaurine ceratopsid from the Judith River Formation (Kennedy Coulee, northern Montana), as the holotype for a new genus and species, Lokiceratops rangiformis. Alongside closely related specimens from the same geographic area, the specimen is proposed to represent a period of exceptional diversity for ceratopsids, which is used to support hypotheses of biogeography.

The specimen is important and should be described. However, many of the points I raised in my previous review were not commented on by the authors, indeed the main review document was not commented upon at all. Only minor line edits were implemented. I do think this paper should be published, but I have outstanding concerns. A good portion of my 2nd review comprises parts that were not even commented on in the first.

I am still put in a difficult position on this manuscript. I don't agree with the paleobiological ideas about biogeography etc. I've complained in the past about some researchers only allowing one hypothesis to be entertained at a time, so I can hardly complain if I disagree with someone else's ideas. I also think these debates are better had out in the open in the literature, not hidden in a review – I loathe reviewers who just block work they disagree with.

There are still lots of things that need fixing, and various things I think need commenting on or clarifying. Below I have reiterated things that were not covered from my previous review, and added more.

I still think there should be more acknowledgement that there are alternative paleobiological interpretations, which in my opinion at least, are more parsimonious with the record. We are not that far from each others thinking in terms of the number of lineages, I just doubt that every time we see a new morphology, that it is evidence of vicariance.

It's the editor's call, but I think that the issues remaining are acceptable with major edits.

WRITING

The writing still has problems. Although the authors have made inroads into correcting typos, basic content errors, reference to the taxon instead of the specimen etc. there are many errors still in the document. I have highlighted a few where I have noticed them, but surely more remain. I urge the many coauthors to read through the manuscript, and help correct these mistakes.

I still think the descriptions are overlong – but maybe this is a matter of style.

FIGURES

I appreciate that there are lots of figures, and that they are nice graphic images. I still would like more (all) views of the frill pieces. These can just go in supp.

THE SPECIMEN

(unanswered from first review)

For example, the left side of the parietal is broken into two main pieces. Do they fit together with a good click, or are they more assumed to fit? The Ep3 looks quite triangular, and it is supposedly incomplete. Similarly the Ep2 has a broken edge (although the inadequacy of the image means this is not possible to tell how broken). Is it possible that "Ep3" is actually the broken edge of Ep2?

(also outstanding from first review)
I would like to see good dorsal and ventral views of the skull bones, with each bone piece given a large figure. This could be in supp if necessary, but I think it is essential in order to assess the specimens and the characters they exhibit. For example, imbrication of the epis is mentioned in the descriptions, but the imbricated edge of the frill is not well figured – I can't observe this. I'd also like to be able to see textural changes more clearly, and the ventral side of the frill is important to see too, as not all ontogenetic changes occur on the upper surface (or at least, not first).

(not addressed from first review)
IS THIS REALLY DIFFERENT FROM MEDUSACERATOPS or ALBERTACERATOPS?

It would be more parsimonious if EMK 0012 was just a specimen of a previously named taxon; either Medusa or (perhaps less likely) Alberta. Although there is a list of autapomorphies (and "differentia" for Medusa and Alberta) many differences with Medusa and Alberta are features that are known to be variable individually, or change through ontogeny. Given that EMK 0012 is probably a very aged individual, the possibility should be taken into more consideration that its unusual features are a result of it being an ontogenetic endmember.

Characters used to diagnose or differentiate the taxon are quite weak, or dubious:

(Diagnoses copied from manuscript).

"Diagnosis— Lokiceratops rangiformis is an albertaceratopsin centrosaurine ceratopsid distinguished from other centrosaurines by the following autapomorphies:

- presence of unadorned nasal;
    - The nasal in EMK 0012 is incomplete medially (so the presence of a nose horn is not fully observable anyway, and it has a thickened dorsal border in the preserved section (can be seen in Figure 8), which could be a thickened low nasal horn-like structure. The nasal horns of Medusa and Alberta are not prominent at all, so it is not like EMK 0012 would be expected to have had a huge nose horn anyway. Moreover, EMK 0012 is a very large and seemingly mature individual, more so than either Medusa or Alberta. Reduction in horns is something seen during ontogeny in other ceratopsids, including many centrosaurs. Furthermore, the figure caption (8 and 9) state "Note that while the nasal appears to have a peaked ornament dorsally, there is no evidence of a narial ornament in this specimen.". What is the "peaked ornament" then, if not some small incipient nose horn?
- elongate, uncurved ep1 epiossification directed in plane of frill along posterior margin of parietosquamosal frill
    - This is indeed different from the other taxa, however I could believe that this was a late ontogeny character. It is at least possible.
- and hypertrophied, lateral curving epiparietal ep2 directed in plane of frill. The hypertrophied ep2 is relatively larger than any other parietal epiossification within Centrosaurinae.
    - But a hypertrophied EP2 is present in Medusaceratops, and let's be honest, the big EP1 in Alberta is propbably homologous to this too – the "lack" of ep1 in Alberta could be overgrowth from the large Ep2, and it's not as if the ep1 in Medusa is very obvious either, it's a tiny bump.
- Both ischia are distinctly kinked distally about two-thirds of the length the shaft at the point where the two ischia contact medially.

    - I’d say this is fairly dubious. I don’t want to sound too skull-obsessed but this seems like a fairly major postcranial character that has no precedent, so a person should be skeptical. Looking at Figure 19, one of the ischia (F, G) is broken and reconstructed in the area of the kink, and it is possible that the other ischium is too (D, E). This is not mentioned in the text. Another reason to have larger figures.
- Postorbital horncore bases are deeply excavated by pneumatic cornual sinuses penetrating distance equivalent to two orbit radii into horncore to an extent unknown in other long horned centrosaurs.
    - Excavation of cornual sinuses progresses through growth, at least where documented in chasmosaurines. I don’t see any good reason to think that this was not the case in centrosaurines that had long brow horns. I know that some chasmosaurines are being defined taxonomically on the presence of cornual sinuses (e.g. Titanoceratops, Bisticeratops), and I find that rather alarming since these are unusually large individuals giving indication of great age. The Lokiceratops holotype is also a large, presumably old, individual, so the possession of relatively well developed cornual sinuses might not be unexpected. It’s just another dubious character.

Medusaceratops lokii differs from the stratigraphically similar Lokiceratops rangiformis in a number of key features including:

- presence of nasal ornamentation;
    - see above
- a lesser extent of postorbital pneumaticity;
    - (see above)
- presence of four episquamosals (three in Lokiceratops);
    - Dubious… see comments above
- presence of multiple, raised undulations on midline ramus of parietal between the parietal fenestrae;
    - In Chasmosaurines, bumps along the midline of the parietal are more prominent in juveniles, and become resorbed thtrough ontogeny. Again, this kind of theing would therefore not be surprising in an especially large centrosaurine, as in Lokiceratops. Anyway, the bumps on the midline parietal surface are only seen in one (referred) Meduaceratops parietal, and they are not especially prominent (Chiba et al, 2017).
- lack of a narrow, medially restricted embayment on the midline of the posterior edge of the parietal;
- a reduced, rather than elongate, posteriorly directed ep1 epiossifications along the posterior margin of the parietosquamosal frill;
- the length of the largest curving epiparietal ep2;
- and the presence of five bilateral epiparietals (seven in Lokiceratops).
    - A variable character in centrosaurines even between left and right sides of the same individual (see EMK 0012).

(not addressed from first review)

PHYLOGENY

The resultant phylogeny is odd. When Jordan Mallon had a chasmosaurine phylogeny come out upside down, with late-occurring taxa coming out basal, and older taxa derived, he said that it didn’t make a lot of sense (I forget the exact phrasing but I mention it in Fowler & Freedman Fowler 2020). Anyway, parts of this phylogeny don’t make a lot of sense, including lokiceratopsins. You can say that all you can do is objectively code the morphology, then the resultant phylogeny is basically whatever it turns out to be, but I think that some thought can go into how characters are coded, and what results that might have.

It's also not all that well supported. For example:

>LINE 1548: “Lokiceratops rangiformis is recovered as the sister taxon to Albertaceratops nesmoi and Medusaceratops lokii, and all three form the clade Albertaceratopsini. This grouping is supported by two synapomorphies;

>character 127, a circular or oval rather than narrow and slit-like frontoparietal fontanelle;

Is this even visible in EMK 0012?

>and character 357, epiparietal 1 oriented in the plane of the frill in lateral view (note that this is a local synapomorphy, found in other clades within Centrosaurinae also);

This is pretty weak. And this also means that the Loki-Medusa-Alberta clade is not united by any of the ornamentation features that would, at first, look pretty obvious – i.e. the large laterally oriented epis (either ep2 or ep1). Even if the topology is what the authors are looking for, it’s not supported by characters at nodes that make much sense.

>The decay index (1) and bootstrap support (<50%) for the relationships within Albertaceratopsini are low, although we note that low branch support is unsurprising—in this analysis: the confidently established clade Centrosaurinae itself has a decay index of only 2 and bootstrap support <50 percent.”

And this is not compelling evidence for any kind of Lokiceratops clade. Coupled with the fact that the stratigraphically young nasutoceratopsins come out basal to this in a polytomy with Xenoceratops… Either Nasutoceratopsins have a long ghost lineage, or (as seems more likely) there are problems with the cladogram from bottom up. That’s ok, not all cladograms make sense, but if you have something like this with inconsistencies it probably is not best to make this the basis of some quite serious claims about biogeography in the discussion.

(partially addressed)
STRATIGRAPHY

The manuscript has had a number of improvements regarding the dates used. I’m still not totally happy, but I do accept that the Ramezani dates are what many people are using, with some justification, even if I think they have issues (outlined in my previous review). I will end up having to revisit the dates myself and cross compare them to illustrate the issues and implications for dinosaur evolution.

I’m trying to figure out a way of explaining why unrecalibrated dates are an issue, and I think I have a way of explaining this.

You probably remember, back in 1992 and 1993 Swisher et al published an Ar/Ar date for the K-T boundary. This date was 65Ma. Everyone said the K-T was 65Ma, and there’s even that new movie called 65 because the date became so ingrained in pop culture. Well, you probably also remember that shortly afterwards this was refined to 65.5Ma, and just as we scientists were getting used to that it changed again to 66.0Ma (and became the K-Pg). The reason for these changes is not because the methods got better -well it is a little- but the vast bulk of that change was because the age of the Ar/Ar dating standards got older.

When you measure Ar/Ar dates, you don't get a direct date result – you basically measure the age of a known "standard" and compare your unknown sample to that.

Standards need to be mineralogically homogenous, abundant, and yield a consistent date.

Back in the 1980's and 1990's there were a number of standards used. The McClure Mountain hornblende (MMhb), the Fish Canyon Sanidine, the Taylor Creek Rhyolite, and a few others. Occasionally, a paper would be published that intercalibrated between the different standards (e.g. Renne et al., 1994).

However all but the Fish Canyon Sanidine (FCT or FCs) have now been rejected for various reasons. Modern Ar/Ar analyses use the FCs only.

Ok, so the key point here is that the known ages of these standards has been refined, getting progressively older. The known age for the Fish Canyon Sanidine started as 27.79Ma (1986) and changed thus:

27.79 Ma (Cebula et al, 1986)
27.84 Ma (Samson & Alexander, 1987)
28.02 Ma (Renne et al., 1998)
28.201 Ma (Kuiper et al., 2008)

So lets go back to the K-Pg date. In 1992/93 the standard used was FCT=27.84Ma. 65/27.84 = 2.33, ie. the K-T sample was 2.33 times the known FCT standard age.

When the K-T date changed to 65.5 it was because the standard had gotten older, to 28.02. Thus, 65.5/28.02 = 2.34.

And when the K-Pg changed again to 66.0 it was because the standard had changed to 28.201. Thus 66.0/28.201 = 2.34

It's the same ratio each time (allowing for slight rounding), because it's the same sample, same date getting recalibrated each time. If you ran new ash samples you'd expect a slightly different result maybe, but something close to Swisher et al's 1993 date.

(NOTE: this is not how I recalibrated the dates in Fowler 2017, this is just a very simple way to illustrate the point)

So my point here is that citing the Goodwin and Deino (1989) dates is like citing 65Ma for the K-Pg boundary. It's not accurate – it's about a million years away from what it should be. I don't think anyone would cite the K-Pg as 65Ma and expect to get it through review, so it should be the same for other dates of that vintage. This didn't stop Rogers et al 2023 citing the Goodwin and Deino dates… as I said in my previous review, I rather suspect Rogers et al did this because the Goodwin and Deino original dates are closer to the Ramezani U-Pb dates than the recalibrated Fowler (2017) dates are. It's still incorrect to do this, but there you go. I guess if you can sneak it past reviewers that's ok right?

Recalibrating Ar/Ar dates was made simple by the EARTHTIME institute that made a recalibration excel spreadsheet and put it online free to download. This is what Fowler (2017) used to recalibrate the dates, and it is what Roberts used too for the Kaiparowits dates in Sampson et al. (2010; not actually stated in the paper) and Roberts et al (2013). The problem with Roberts et al (2013) was that they did not input the correct original standard age for 11 out of the 18 dates. Fowler (2017) re-ran all the dates in Roberts et al. (2013) and replicated their results, so there is no doubt over what numbers they input. Fowler (2017) uses the same method (the EARTHTIME excel sheet) but inputs the correct standards – you have to go sleuthing for these in the literature. Some are obvious, and others are not, and you also have to sometimes use one of the intercalibration papers mentioned above. Fowler (2017) lists everything used for each recalibration. Ad nauseam.

This actually underlines a significant issue with the Ramezani U-Pb dates – they sometimes align with Ar/Ar dates (near perfectly with the Kaiparowits dates), but for a select few other dates, notably those of the Dinosaur Park Fm and surrounding strata, they are off by a million years. Ramezani et al. never note this discrepancy or any other potential issues resulting from these new dates (some explanations, including zircon residence times, would potentially explain this, although may render the DPFm dates as unreliable). One notable problem is that one new date (the only marine date in Ramezani et al 2022– for the Bearpaw Shale above the Dinosaur Park Fm) is dated at 74.289Ma, 1 my younger than the recalibrated Ar/Ar dates. The problem here is that being a marine shale, it inevitably contains ammonites and other marine fauna, so that it now requires that ammonite biostratigraphy across the WIS be revised for this period (since this is based on recalibrated Ar/Ar dates also). I rather suspect that if this was noted explicitly, that there would be pushback from people working on ammonite biostratigraphy, especially since this biostratigraphic framework is quite well resolved for multiple sections across the US (and this has integrated magnetostratigraphy, other ash dates, it will no doubt be a mess). Then there is the weird statement that (in the results): "Our U–Pb age model is unable to accurately constraint [sic] the age of the lower boundary of the Kaiparowits Fm., as bentonites are notoriously absent from its lower unit"… despite there being an Ar/Ar date published by one of the Ramezani et al 2022 coauthors for the lower Kaiparowits (Ash KDR-5, see Roberts et al 2005; 2013, or Zanno et al., 2011, or other papers). Making a statement that there is no date for the lower Kaiparowits is thus bizarre and surely requires explanation.

Anyway, the point being that the new Ramezani U-Pb dates have problems. Using them mixed with recalibrated (Fowler 2017) and unrecalibrated (Goodwin 1989) Ar/Ar dates is like having measurements in inches and cm and treating them as if they are the same. Ironically, the recalibration of the Fish Canyon Sanidine by Kuiper et al (2008) was supposed to improve alignment of Ar/Ar dates with U-Pb (and this has since been further fine-tuned), so if anything, recalibrated Ar/Ar dates should align better with U-Pb dates than previously (and for the most part they do, which is what makes a few of the Ramezani dates so problematic).

I appreciate that I am one of the only people that pays any real attention to taxon ranges, radiometric dates, and cross references this with magstrat, sequence strat, anything I can get my hands on. Most paleontologists might find all this confusing, especially when there are conflicts between methods. I suggest therefore that this manuscript acquire a coauthor who is a stratigrapher, to go through these dates and make some reasonable statements about the choices made on correlations and ranges. The authors have worked with e.g. Federico Fanti before. He would hopefully be able to fix some of these issues. As it stands it's a mess.

TAXON RANGES

The authors suggest that (line 1727), because of the Signor Lipps effect, that we should expect Lokiceratops, Medusaceratops, and Albertaceratops to have longer stratigraphic ranges (although the same is not suggested for other taxa, which is inconsistent). Given the closeness in stratigraphic position of the specimens (as little as 4meters), then this would mean that they would inevitably have overlapping ranges. Overlaps presumably form the basis for stating that these taxa were coeval (Line 1712), then from there the logical leap is made that this represents extraordinary diversity in very small geographic area. Signor Lipps is not always appropriate. If you are sampling an anagenetic lineage, then you would not expect a given morphology to have any time range at all. See for example, the "community groups" concept (and other discussion) in Boucot (2006). I'm not saying everything is anagenesis, but I find the idea that everything is cladogenesis to be limited and likely wrong.

TAXON RANGE ERRORS

I highlighted this before: Spinops is of unknown range – it could be from the uppermost Oldman, or it could be from the Dinosaur Park Fm. The authors show it as in text uppermost Oldman, but the dates include some overlap into the Dino Park. The text should be corrected to say Oldman or Dino Park.

Pachyrhinosaurus lakustai is shown as having a range of about 600ky, yet it is known from a single mass death assemblage bonebed. This is contrasted with Einiosaurus which is also from a bonebed, yet it is shown as effectively a single line. Inconsistent. Should both of these taxa have Signor Lipps extensions, as the authors suggest for Loki, Medusa, and Albertaceratops?

Perhaps the authors need to come up with a way of showing the difference between 1. known range (ie. the position of actual fossil specimens, well constrained by stratigraphy); 2. Signor-Lipps range; 3. Possible range based on either unknown stratigraphic position or uncertain age range of host formation. I tried to do this in Fowler (2017), and included detailed notes on each taxon stipulating why it was plotted where it was. The authors should include this kind of data; a reference is not enough given the importance of stratigraphic range to the paleobiological hypotheses proposed and discussed.

Ramezani 2023 is cited as a source of stratigraphic data (supp table 2), but no citation is list in the references. Is this a pers. comm.?

FIGURES

The schematic diagrams are nicely drawn, and useful, but few individual bones are adequately figured in close up or otherwise. A lot of the time it's impossible to see the morphology described in the text. For example, I found myself squinting at the images of the frill pieces, trying to see if they had broken edges, or trying to see details of the textures. All you can really see in the figures is the shape of the reconstructed skull. The braincase is probably the only adequately imaged bone. All the skull bones could really do with a big image in supp info, in multiple orientations.

I really appreciate that Figure 1 includes both the Rogers et al. (2016) members of the Judith alongside the much more useful Canadian terminology (including subunits). It makes it much easier for people to understand the correlation. Although see comments in MS.

Typos etc in Figures:
Figure 3:"D" is still missing from the caption.
Figure 11 caption, still no J for jugal, no L for lacrimal, and others. I assume that this is intentional since the same problem of missing terms is in figs 12 and 13.

DISCUSSION

Most of the discussion I disagree with strongly. However, I can accept that the authors have a right to put forward their interpretation, but I will insist that there does need to be some acknowledgement that alternative explanations exist, however much the authors might not like them.

I will say that the suggestion that the manuscript's claim that mountains offer no barrier to dispersal is quite a claim since it runs against long established basic principles of biogeography. Also note that in Fowler and Freedman Fowler (2020) we propose a hypothesis (based on previously unutilized high stratigraphic resolution paleomaps) where high sea levels repeatedly separated north and south(ish) regions of Laramidia during the early Campanian, potentially generating the multiple lineages of ceratopsids that we see in middle to upper Campanian rocks (I think that we're broadly in agreement about the different lineages, I just wouldn't split them up as much as the current authors do). Anyway, even if you don't like this hypothesis it is current, reasonable, supported by data, and should be cited.

We deleted 'lower' as a qualifier to the McLelland Ferry member in response to the reviewer's arguments. However, the correlation between the MFM and the lower formations of the Belly River Group are solidly supported by new CA-TIMS dates, and further discussed by Rogers et al. (in press, GSA Bulletin). We are therefore choosing to maintain the general regional correlations laid out in this paragraph.

Since these taxa are predominantly known from singleton specimens like Lokiceratops, or from bonebeds with a limited extent, there is no statistical reason to expect stratigraphic overlap between them. Using this lack of statistical power to evaluate stratigraphic ranges as possible evidence of anagenesis is misguided. Nevertheless, as noted farther below, Lokiceratops and Wendiceratops occur at the same stratigraphic level proving they were sympatric species and cannot be regarded as an ancestor-descendant

The Loki Quarry sits 922 meters above sea level and 12 meters above the top of the Marker A Coal (MAC) seam. The Marker A Coal seam is equivalent to the top of the Taber Coal Zone (*sensu* Goodwin & Deino, 1989) based on multiple sections measured in the Kennedy Coulee and at the *Probrachylophosaurus* (Freedman et al., 2015) locality (MOR locality JR-

82 518). The Mansfield Bonebed producing *Medusaceratops* occurs ~10 meters above the Marker A
83 Coal. All of these quarries occur near the top of a 10–15 meter thick interval of interbedded
84 organic-rich mudstones with discontinuous carbonaceous seams, siltstone, and sandstones (Fig.
85 1).

So, what sediment is the Loki quarry in, as compared with the Wendiceratops quarry? If I recall correctly, the Herronton Sandstone (base of the lower Oldman Fm) is thicker in Kennedy Coulee than it is in southern Alberta.

Wendi was excavated from a mudstone in a mudstone dominated succession ~15m above the Taber Coal Zone (Scott et al, 2022)

Medusa

The strat section for Kennedy coulee… does not have a very thick Herronton Sandstone. Indeed this is not marked.

There is only 300ky between the two Ar/Ar ash dates. So this amount of error is not very good really.

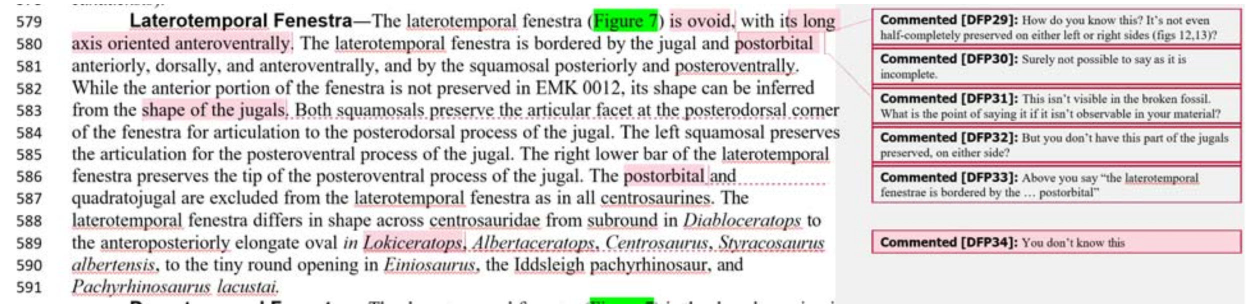
but that doesn't take into account the associated uncertainties, which the Bayesian model does. The use of Bayesian models to bound ages allows for better accommodation of changes in sedimentation and also more honest (i.e. asymmetric) evaluation of uncertainties.

440 Albertaceratops nesmoi differs from the stratigraphically similar, but possibly slightly
441 younger Lokiceratops rangiformis, in key features including: presence of nasal ornamentation;
442 presence of four episquamosals (three in Lokiceratops); presence of multiple raised undulations on
443 midline ramus of parietal between the parietal fenestrae; reduced, rather than elongate posteriorly
444 directed, ep1 epiossifications along the posterior margin of the parietosquamosal frill; the length of
445 the largest curving epiparietal ep2; and presence of five bilateral epiparietals (vs. six or seven in
446 Lokiceratops).

Figure 21 shows the largest epi being ep1 not ep2. Thus the long epis of medusaceratops (ep2) and Albertaceratops (ep1) are not homologous. Either that or change your figure.

we changed this to 'ep 1' in repsonse to the reviewer's comment

This still means that the long wide epis of Lokiceratopsini are not homologous between Alberta and Loki-Medusa. Surely it is more parsimonious for Alberta simply to have lost (or not yet developed) ep1, and for the large flat epi on the posteriormost position of the parietal to be ep2, same as in Loki and Medusa? I comment about this in the phylogeny section above too.



Laterotemporal Fenestra—The laterotemporal fenestra (Figure 7) is ovoid, with its long axis oriented anteroventrally. The laterotemporal fenestra is bordered by the jugal and postorbital anteriorly, dorsally, and anteroventrally, and by the squamosal posteriorly and posteroventrally. While the anterior portion of the fenestra is not preserved in EMK 0012, its shape can be inferred from the shape of the jugals. Both squamosals preserve the articular facet at the posterodorsal corner of the fenestra for articulation to the posterodorsal process of the jugal. The left squamosal preserves the articulation for the posteroventral process of the jugal. The right lower bar of the laterotemporal fenestra preserves the tip of the posteroventral process of the jugal. The postorbital and quadratojugal are excluded from the laterotemporal fenestra as in all centrosaurines. The laterotemporal fenestra differs in shape across centrosauridae from subround in *Diabloceratops* to the anteroposteriorly elongate oval *in Lokiceratops*, *Albertaceratops*, *Centrosaurus*, *Styracosaurus albertensis*, to the tiny round opening in *Einiosaurus*, the Iddsleigh pachyrhinosaur, and *Pachyrhinosaurus lacustai.*

Commented [DFP29]: How do you know this? It's not even half-completely preserved on either left or right sides (figs 12,13)?

Commented [DFP30]: Surely not possible to say as it is incomplete.

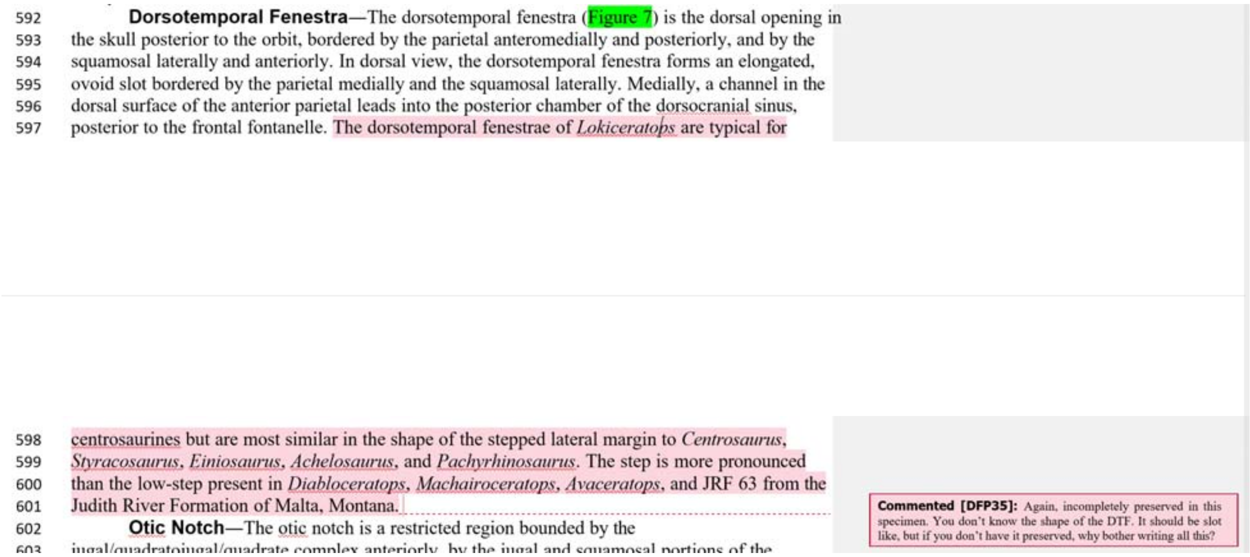
Commented [DFP31]: This isn't visible in the broken fossil. What is the point of saying it if it isn't observable in your material?

Commented [DFP32]: But you don't have this part of the jugals preserved, on either side?

Commented [DFP33]: Above you say "the laterotemporal fenestrae is bordered by the … postorbital"

Commented [DFP34]: You don't know this

This was not commented on

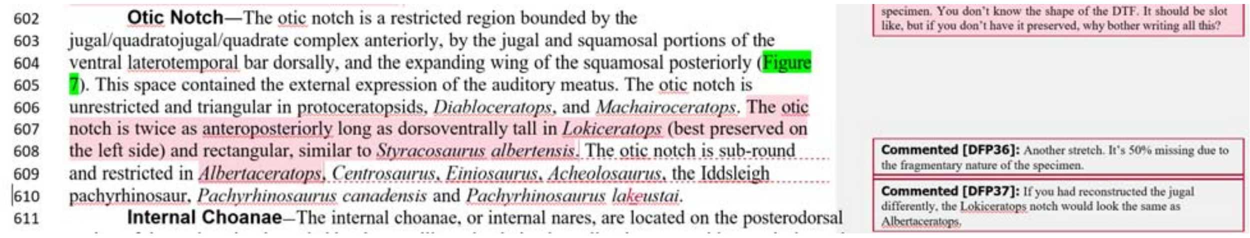


Dorsotemporal Fenestra—The dorsotemporal fenestra (Figure 7) is the dorsal opening in the skull posterior to the orbit, bordered by the parietal anteromedially and posteriorly, and by the squamosal laterally and anteriorly. In dorsal view, the dorsotemporal fenestra forms an elongated, ovoid slot bordered by the parietal medially and the squamosal laterally. Medially, a channel in the dorsal surface of the anterior parietal leads into the posterior chamber of the dorsocranial sinus, posterior to the frontal fontanelle. The dorsotemporal fenestrae of *Lokiceratops* are typical for centrosaurines but are most similar in the shape of the stepped lateral margin to *Centrosaurus*, *Styracosaurus*, *Einiosaurus*, *Achelosaurus*, and *Pachyrhinosaurus*. The step is more pronounced than the low-step present in *Diabloceratops*, *Machairoceratops*, *Avaceratops*, and JRF 63 from the Judith River Formation of Malta, Montana.

Otic Notch—The otic notch is a restricted region bounded by the

Commented [DFP35]: Again, incompletely preserved in this specimen. You don't know the shape of the DTF. It should be slot like, but if you don't have it preserved, why bother writing all this?

Also not addressed



specimen. You don't know the shape of the DTF. It should be slot like, but if you don't have it preserved, why bother writing all this?

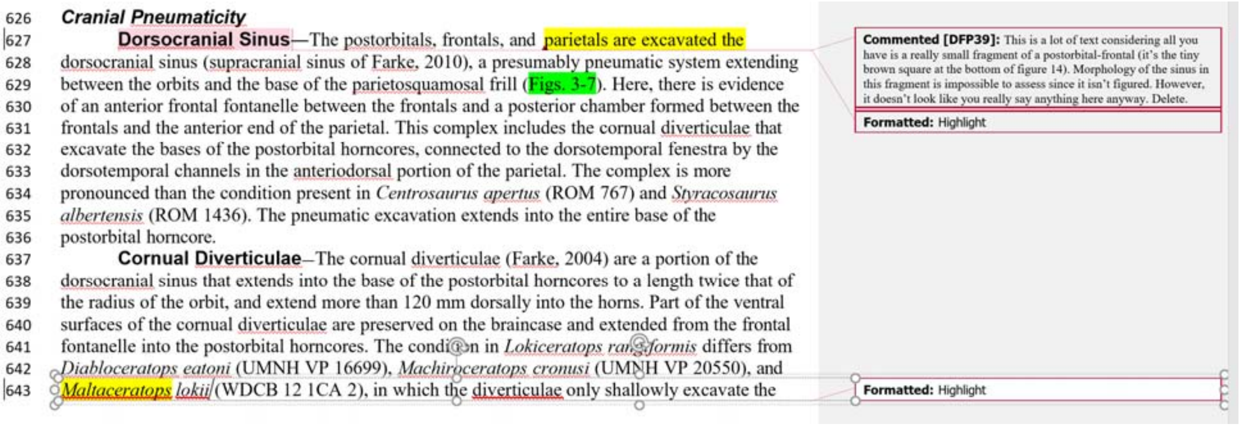
Otic Notch—The otic notch is a restricted region bounded by the jugal/quadratojugal/quadrate complex anteriorly, by the jugal and squamosal portions of the ventral laterotemporal bar dorsally, and the expanding wing of the squamosal posteriorly (Figure 7). This space contained the external expression of the auditory meatus. The otic notch is unrestricted and triangular in protoceratopsids, *Diabloceratops*, and *Machairoceratops*. The otic notch is twice as anteroposteriorly long as dorsoventrally tall in *Lokiceratops* (best preserved on the left side) and rectangular, similar to *Styracosaurus albertensis*. The otic notch is sub-round and restricted in *Albertaceratops*, *Centrosaurus*, *Einiosaurus*, *Acheolosaurus*, the Iddsleigh pachyrhinosaur, *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus lakeustai*.

Internal Choanae—The internal choanae, or internal nares, are located on the posterodorsal

Commented [DFP36]: Another stretch. It's 50% missing due to the fragmentary nature of the specimen.

Commented [DFP37]: If you had reconstructed the jugal differently, the Lokiceratops notch would look the same as Albertaceratops.

Not addressed



Cranial Pneumaticity

Dorsocranial Sinus—The postorbitals, frontals, and parietals are excavated the dorsocranial sinus (supracranial sinus of Farke, 2010), a presumably pneumatic system extending between the orbits and the base of the parietosquamosal frill (Figs. 3-7). Here, there is evidence of an anterior frontal fontanelle between the frontals and a posterior chamber formed between the frontals and the anterior end of the parietal. This complex includes the cornual diverticulae that excavate the bases of the postorbital horncores, connected to the dorsotemporal fenestra by the dorsotemporal channels in the anteriodorsal portion of the parietal. The complex is more pronounced than the condition present in *Centrosaurus apertus* (ROM 767) and *Styracosaurus albertensis* (ROM 1436). The pneumatic excavation extends into the entire base of the postorbital horncore.

Cornual Diverticulae–The cornual diverticulae (Farke, 2004) are a portion of the dorsocranial sinus that extends into the base of the postorbital horncores to a length twice that of the radius of the orbit, and extend more than 120 mm dorsally into the horns. Part of the ventral surfaces of the cornual diverticulae are preserved on the braincase and extended from the frontal fontanelle into the postorbital horncores. The condition in *Lokiceratops rangiformis* differs from *Diabloceratops eatoni* (UMNH VP 16699), *Machiroceratops cronusi* (UMNH VP 20550), and *Maltaceratops lokii* (WDCB 12 1CA 2), in which the diverticulae only shallowly excavate the

Commented [DFP39]: This is a lot of text considering all you have is a really small fragment of a postorbital-frontal (it's the tiny brown square at the bottom of figure 14). Morphology of the sinus in this fragment is impossible to assess since it isn't figured. However, it doesn't look like you really say anything here anyway. Delete.

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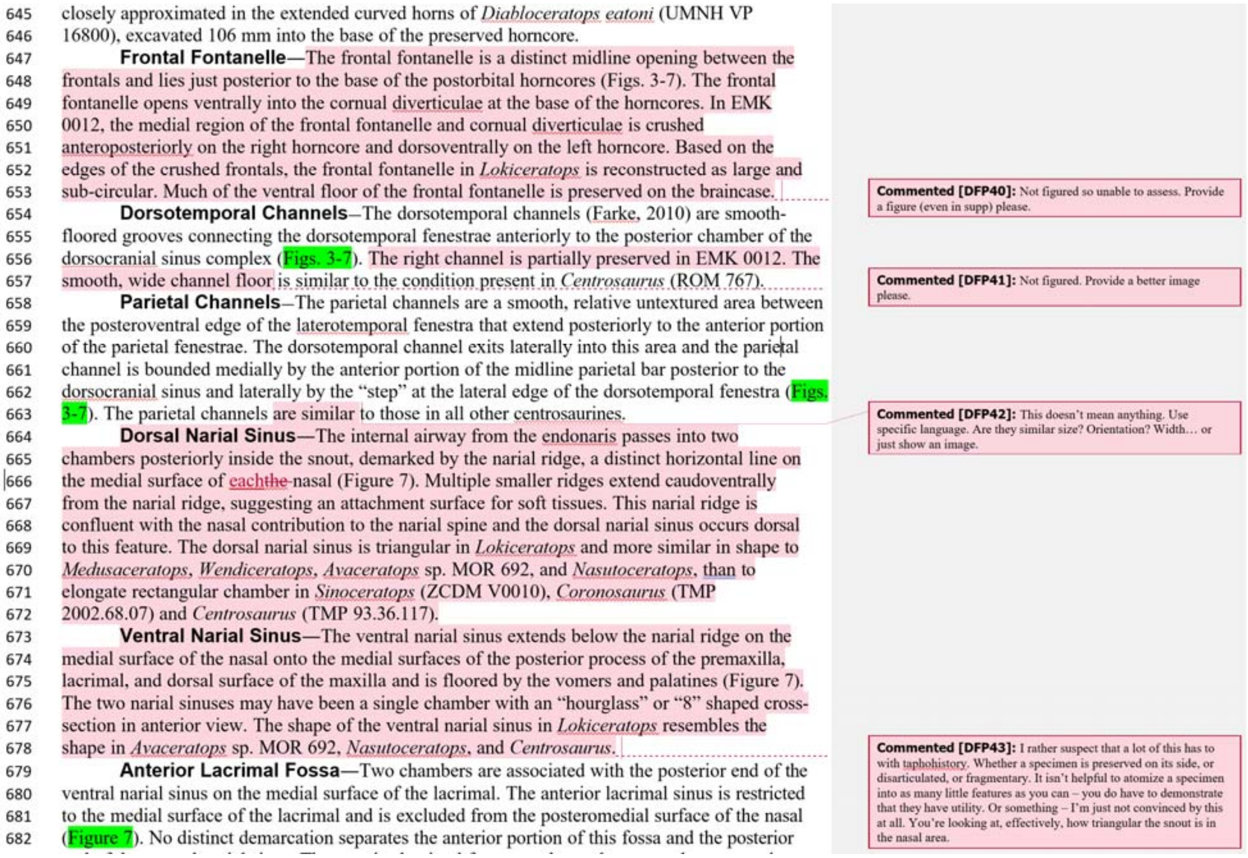
Not addressed



closely approximated in the extended curved horns of *Diabloceratops eatoni* (UMNH VP 16800), excavated 106 mm into the base of the preserved horncore.

Frontal Fontanelle—The frontal fontanelle is a distinct midline opening between the frontals and lies just posterior to the base of the postorbital horncores (Figs. 3-7). The frontal fontanelle opens ventrally into the cornual diverticulae at the base of the horncores. In EMK 0012, the medial region of the frontal fontanelle and cornual diverticulae is crushed anteroposteriorly on the right horncore and dorsoventrally on the left horncore. Based on the edges of the crushed frontals, the frontal fontanelle in *Lokiceratops* is reconstructed as large and sub-circular. Much of the ventral floor of the frontal fontanelle is preserved on the braincase.

Dorsotemporal Channels–The dorsotemporal channels (Farke, 2010) are smooth-floored grooves connecting the dorsotemporal fenestrae anteriorly to the posterior chamber of the dorsocranial sinus complex (Figs. 3-7). The right channel is partially preserved in EMK 0012. The smooth, wide channel floor is similar to the condition present in *Centrosaurus* (ROM 767).

Parietal Channels–The parietal channels are a smooth, relative untextured area between the posteroventral edge of the laterotemporal fenestra that extend posteriorly to the anterior portion of the parietal fenestrae. The dorsotemporal channel exits laterally into this area and the parietal channel is bounded medially by the anterior portion of the midline parietal bar posterior to the dorsocranial sinus and laterally by the "step" at the lateral edge of the dorsotemporal fenestra (Figs. 3-7). The parietal channels are similar to those in all other centrosaurines.

Dorsal Narial Sinus—The internal airway from the endonaris passes into two chambers posteriorly inside the snout, demarked by the narial ridge, a distinct horizontal line on the medial surface of each~~the~~ nasal (Figure 7). Multiple smaller ridges extend caudoventrally from the narial ridge, suggesting an attachment surface for soft tissues. This narial ridge is confluent with the nasal contribution to the narial spine and the dorsal narial sinus occurs dorsal to this feature. The dorsal narial sinus is triangular in *Lokiceratops* and more similar in shape to *Medusaceratops*, *Wendiceratops*, *Avaceratops* sp. MOR 692, and *Nasutoceratops*, than to elongate rectangular chamber in *Sinoceratops* (ZCDM V0010), *Coronosaurus* (TMP 2002.68.07) and *Centrosaurus* (TMP 93.36.117).

Ventral Narial Sinus—The ventral narial sinus extends below the narial ridge on the medial surface of the nasal onto the medial surfaces of the posterior process of the premaxilla, lacrimal, and dorsal surface of the maxilla and is floored by the vomers and palatines (Figure 7). The two narial sinuses may have been a single chamber with an "hourglass" or "8" shaped cross-section in anterior view. The shape of the ventral narial sinus in *Lokiceratops* resembles the shape in *Avaceratops* sp. MOR 692, *Nasutoceratops*, and *Centrosaurus*.

Anterior Lacrimal Fossa—Two chambers are associated with the posterior end of the ventral narial sinus on the medial surface of the lacrimal. The anterior lacrimal sinus is restricted to the medial surface of the lacrimal and is excluded from the posteromedial surface of the nasal (Figure 7). No distinct demarcation separates the anterior portion of this fossa and the posterior

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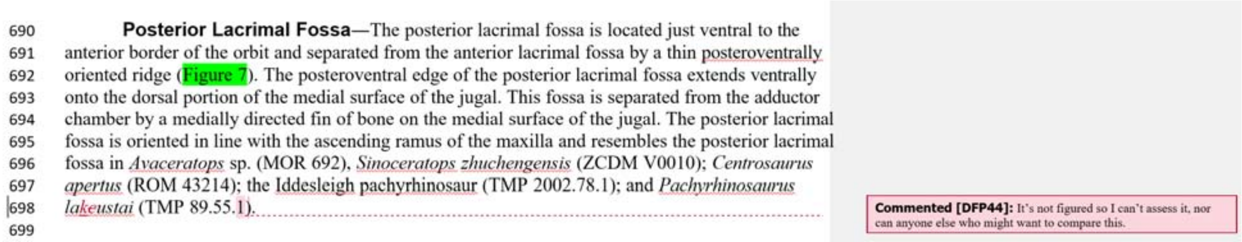
Commented [DFP41]: Not figured. Provide a better image please.

Commented [DFP42]: This doesn't mean anything. Use specific language. Are they similar size? Orientation? Width… or just show an image.

Commented [DFP43]: I rather suspect that a lot of this has to with taphohistory. Whether a specimen is preserved on its side, or disarticulated, or fragmentary. It isn't helpful to atomize a specimen into as many little features as you can – you do have to demonstrate that they have utility. Or something – I'm just not convinced by this at all. You're looking at, effectively, how triangular the snout is in the nasal area.

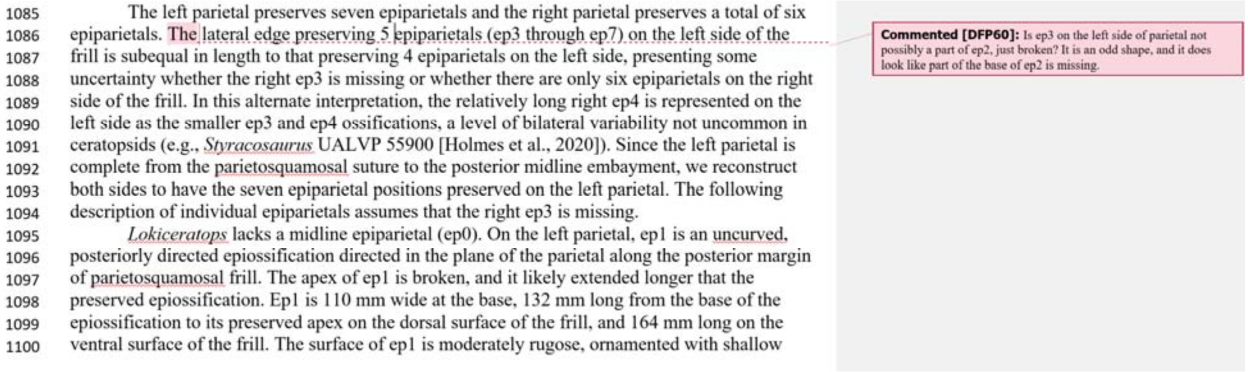
Not addressed



Posterior Lacrimal Fossa—The posterior lacrimal fossa is located just ventral to the anterior border of the orbit and separated from the anterior lacrimal fossa by a thin posteroventrally oriented ridge (Figure 7). The posteroventral edge of the posterior lacrimal fossa extends ventrally onto the dorsal portion of the medial surface of the jugal. This fossa is separated from the adductor chamber by a medially directed fin of bone on the medial surface of the jugal. The posterior lacrimal fossa is oriented in line with the ascending ramus of the maxilla and resembles the posterior lacrimal fossa in *Avaceratops* sp. (MOR 692), *Sinoceratops zhuchengensis* (ZCDM V0010); *Centrosaurus apertus* (ROM 43214); the Iddesleigh pachyrhinosaur (TMP 2002.78.1); and *Pachyrhinosaurus lakeustai* (TMP 89.55.1).

Commented [DFP44]: It's not figured so I can't assess it, nor can anyone else who might want to compare this.

Not addressed.



The left parietal preserves seven epiparietals and the right parietal preserves a total of six epiparietals. The lateral edge preserving 5 epiparietals (ep3 through ep7) on the left side of the frill is subequal in length to that preserving 4 epiparietals on the left side, presenting some uncertainty whether the right ep3 is missing or whether there are only six epiparietals on the right side of the frill. In this alternate interpretation, the relatively long right ep4 is represented on the left side as the smaller ep3 and ep4 ossifications, a level of bilateral variability not uncommon in ceratopsids (e.g., *Styracosaurus* UALVP 55900 [Holmes et al., 2020]). Since the left parietal is complete from the parietosquamosal suture to the posterior midline embayment, we reconstruct both sides to have the seven epiparietal positions preserved on the left parietal. The following description of individual epiparietals assumes that the right ep3 is missing.

Lokiceratops lacks a midline epiparietal (ep0). On the left parietal, ep1 is an uncurved, posteriorly directed epiossification directed in the plane of the parietal along the posterior margin of parietosquamosal frill. The apex of ep1 is broken, and it likely extended longer that the preserved epiossification. Ep1 is 110 mm wide at the base, 132 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill, and 164 mm long on the ventral surface of the frill. The surface of ep1 is moderately rugose, ornamented with shallow

Commented [DFP60]: Is ep3 on the left side of parietal not possibly a part of ep2, just broken? It is an odd shape, and it does look like part of the base of ep2 is missing.

Not addressed

GENERAL:

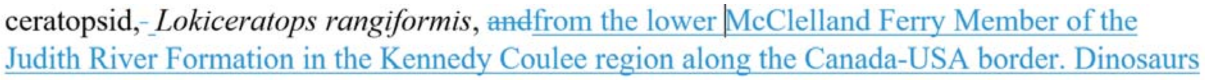
Need to check definitions and correlations of Judith River Fm and Belly River Gp with the new paper by Eberth 2024, which has some differences from Rogers et al. 2016/2023.

I'm also just going to preface this review by saying that I've spent a number of field seasons at Kennedy Coulee, have measured full sections there, discovered new sites and collected from various bonebeds. My wife worked there for over a decade. I am very familiar with its geology. I've also spent the past 7 years collecting in the Judith River along the Canada-Montana border, and a part of this is taking more sections and trying to find stratigraphically informative fossils and stratigraphy.

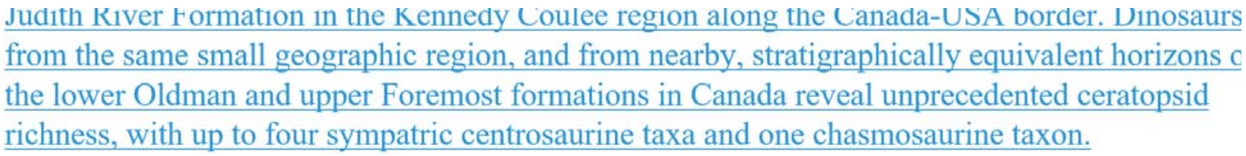
NEW MANUSCRIPT

It is worth noting here that there is sometimes a 1-3m series of fine siltstones and mudstones above the Marker A coal. Sometimes this unit is cut out by downcutting of the Herronton Sandstone. As a fine unit, I consider these mudstones & siltstones to be the uppermost part of the Foremost Fm and the final part of its depositional sequences.

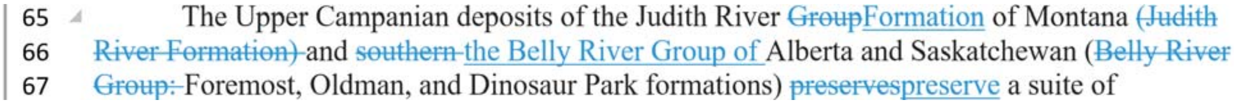
ABSTRACT


ceratopsid,~~-~~ *Lokiceratops rangiformis*, ~~and~~from the lower McClelland Ferry Member of the Judith River Formation in the Kennedy Coulee region along the Canada-USA border. Dinosaurs

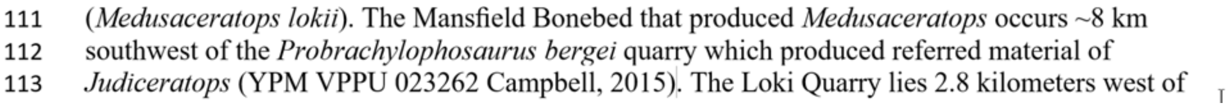
There is no formal or informal lower McClelland Ferry Mbr. You don’t really know that it is form the lower half either, since the thickness of the foremost-equivalent may mean that it comes from relatively higher in section.


Judith River Formation in the Kennedy Coulee region along the Canada-USA border. Dinosaurs from the same small geographic region, and from nearby, stratigraphically equivalent horizons c the lower Oldman and upper Foremost formations in Canada reveal unprecedented ceratopsid richness, with up to four sympatric centrosaurine taxa and one chasmosaurine taxon.

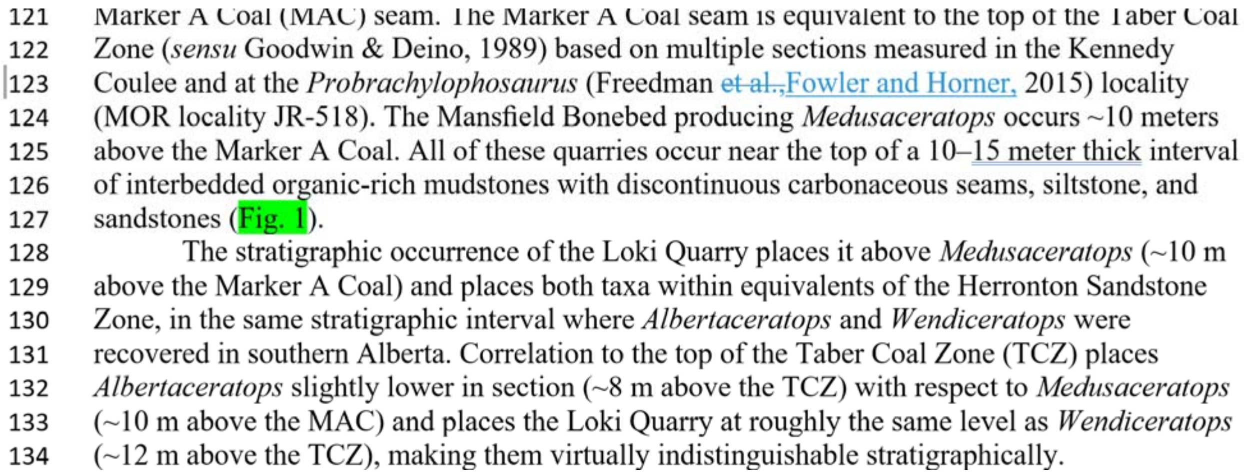
The lower Oldman (which is an informal subdivision) and upper Foremost Fm (which is NOT an informal subdivision) are not stratigraphically equivalent.


The Upper Campanian deposits of the Judith River ~~Group~~Formation of Montana ~~(Judith River Formation)~~ and ~~southern~~ the Belly River Group of Alberta and Saskatchewan (~~Belly River Group:~~ Foremost, Oldman, and Dinosaur Park formations) ~~preserves~~preserve a suite of

These formations are Middle to Upper Campanian. Whichever dates you use, only the Dinosaur Park Fm includes any Upper Campanian.


(*Medusaceratops lokii*). The Mansfield Bonebed that produced *Medusaceratops* occurs ~8 km southwest of the *Probrachylophosaurus bergei* quarry which produced referred material of *Judiceratops* (YPM VPPU 023262 Campbell, 2015). The Loki Quarry lies 2.8 kilometers west of

Perhaps the authors have some information that we do not, but to my knowledge (and my wife, who I asked about this since she excavated there) the Probrachy holotype quarry did not produce the YPM 023262 specimen. Campbell (2015) states that the precise collection location is unknown. If you have information on this, please provide as a pers. comm.



Marker A Coal (MAC) seam. The Marker A Coal seam is equivalent to the top of the Taber Coal Zone (*sensu* Goodwin & Deino, 1989) based on multiple sections measured in the Kennedy Coulee and at the *Probrachylophosaurus* (Freedman ~~et al.,~~Fowler and Horner, 2015) locality (MOR locality JR-518). The Mansfield Bonebed producing *Medusaceratops* occurs ~10 meters above the Marker A Coal. All of these quarries occur near the top of a 10–15 meter thick interval of interbedded organic-rich mudstones with discontinuous carbonaceous seams, siltstone, and sandstones (Fig. 1).

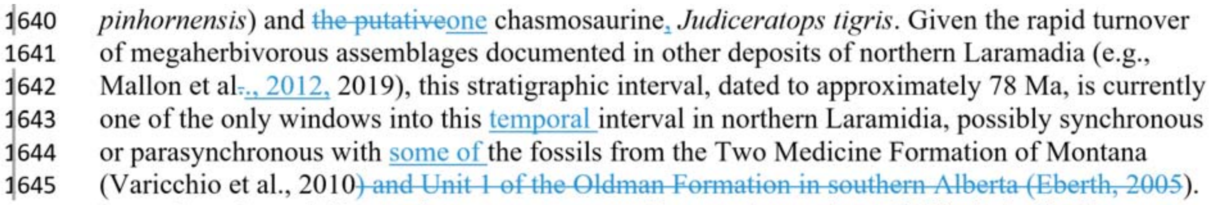
The stratigraphic occurrence of the Loki Quarry places it above *Medusaceratops* (~10 m above the Marker A Coal) and places both taxa within equivalents of the Herronton Sandstone Zone, in the same stratigraphic interval where *Albertaceratops* and *Wendiceratops* were recovered in southern Alberta. Correlation to the top of the Taber Coal Zone (TCZ) places *Albertaceratops* slightly lower in section (~8 m above the TCZ) with respect to *Medusaceratops* (~10 m above the MAC) and places the Loki Quarry at roughly the same level as *Wendiceratops* (~12 m above the TCZ), making them virtually indistinguishable stratigraphically.

The important thing here is whether there is a Herronton sandstone equivalent in the measured section. The Herronton is very thick (up to 12m) in the southeastern part of Kennedy Coulee, near the Redding farmhouse, but it varies significantly in thickness through this area (as you might expect). If the Herronton is taken to be an amalgamated channel deposit then

FIGURE1
Note that it's "Taber" not "Tabor"

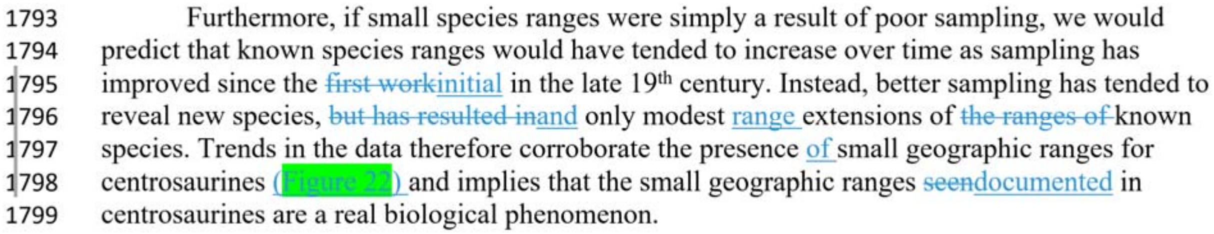
Fig 20: spelling – procurvicornis

1297-1315 – spelling. Multiple cases of prezygapophyses misspelled.
1377,1387,1395, 1441, 1451: EMK0012 or "holotype of" not just "Lokiceratops" -please check through the document for more examples.
1391: the holotypes of Nasuto…



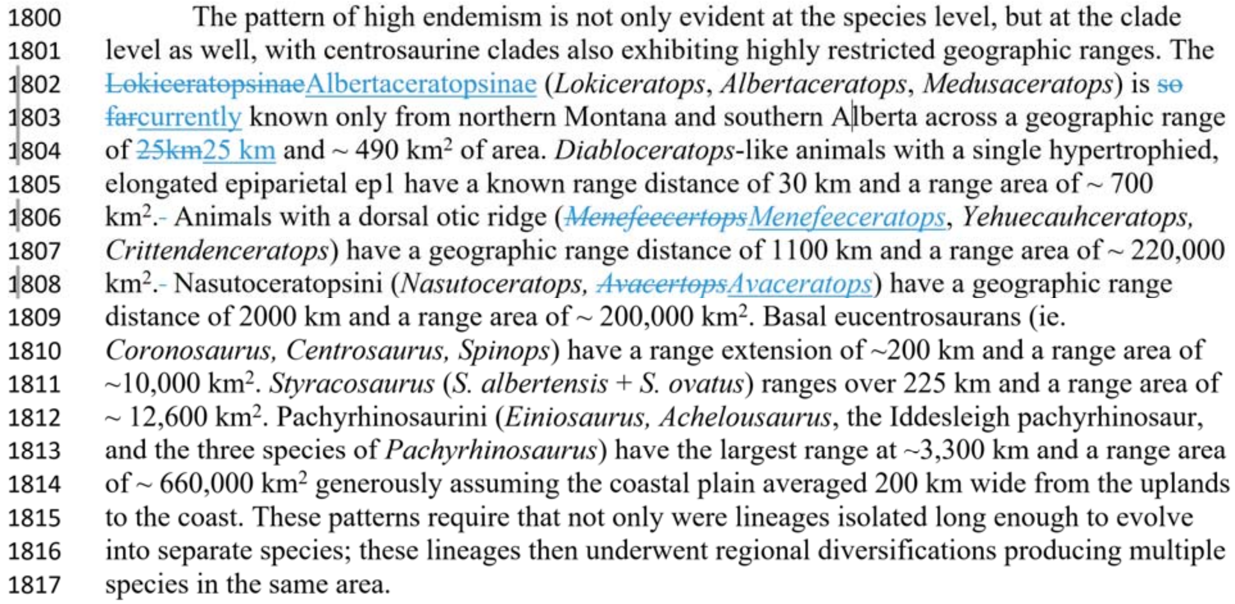
pinhornensis) and ~~the putative~~one chasmosaurine, *Judiceratops tigris*. Given the rapid turnover of megaherbivorous assemblages documented in other deposits of northern Laramadia (e.g., Mallon et al~~.~~., 2012, 2019), this stratigraphic interval, dated to approximately 78 Ma, is currently one of the only windows into this temporal interval in northern Laramidia, possibly synchronous or parasynchronous with some of the fossils from the Two Medicine Formation of Montana (Varicchio et al., 2010~~) and Unit 1 of the Oldman Formation in southern Alberta (Eberth, 2005~~).

Why is the reference to Unit1 of the Oldman deleted? Kennedy Coulee is Unit1 of the Oldman.



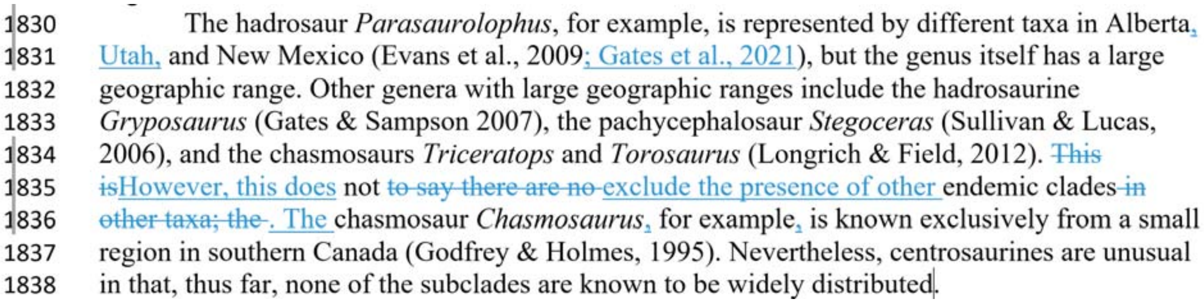
Furthermore, if small species ranges were simply a result of poor sampling, we would predict that known species ranges would have tended to increase over time as sampling has improved since the ~~first work~~initial in the late 19th century. Instead, better sampling has tended to reveal new species, ~~but has resulted in~~and only modest range extensions of ~~the ranges of~~ known species. Trends in the data therefore corroborate the presence of small geographic ranges for centrosaurines (Figure 22) and implies that the small geographic ranges ~~seen~~documented in centrosaurines are a real biological phenomenon.

It is also possible that these taxa are evolving rapidly, such that you only stand a chance of sampling the same taxon if you sample the same short (maybe 100-200ky) morphospecies range. If they are constantly evolving (as suggested by sexual selection) then you might not expect to see anything much in terms of stratigraphic range.



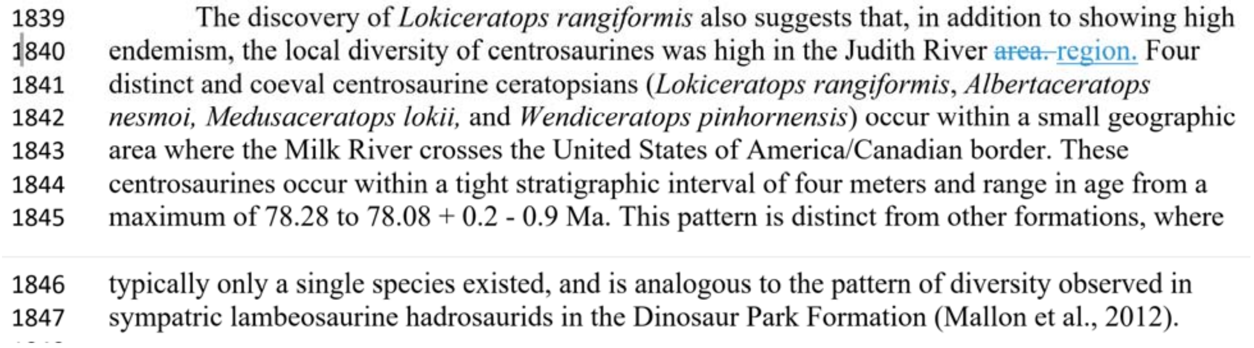
The pattern of high endemism is not only evident at the species level, but at the clade level as well, with centrosaurine clades also exhibiting highly restricted geographic ranges. The ~~Lokiceratopsinae~~Albertaceratopsinae (*Lokiceratops*, *Albertaceratops*, *Medusaceratops*) is ~~so far~~currently known only from northern Montana and southern Alberta across a geographic range of ~~25km~~25 km and ~ 490 km^2 of area. *Diabloceratops*-like animals with a single hypertrophied, elongated epiparietal ep1 have a known range distance of 30 km and a range area of ~ 700 km^2. Animals with a dorsal otic ridge (~~*Menefeecertops*~~*Menefeeceratops*, *Yehuecauhceratops, Crittendenceratops*) have a geographic range distance of 1100 km and a range area of ~ 220,000 km^2. Nasutoceratopsini (*Nasutoceratops,* ~~*Avacertops*~~*Avaceratops*) have a geographic range distance of 2000 km and a range area of ~ 200,000 km^2. Basal eucentrosaurans (ie. *Coronosaurus, Centrosaurus, Spinops*) have a range extension of ~200 km and a range area of ~10,000 km^2. *Styracosaurus* (*S. albertensis* + *S. ovatus*) ranges over 225 km and a range area of ~ 12,600 km^2. Pachyrhinosaurini (*Einiosaurus, Achelousaurus*, the Iddesleigh pachyrhinosaur, and the three species of *Pachyrhinosaurus*) have the largest range at ~3,300 km and a range area of ~ 660,000 km^2 generously assuming the coastal plain averaged 200 km wide from the uplands to the coast. These patterns require that not only were lineages isolated long enough to evolve into separate species; these lineages then underwent regional diversifications producing multiple species in the same area.

If two formations overlap in time, but do not share taxa, then the authors may be right. The question is however, are there many formations that overlap in time where we might expect to see shared taxa, but do not? There are some, but it should be no surprise that many of these clades have very small geographic ranges – there is also the question of outcrop availability – how much outcrop of the right age is there for e.g. Diabloceratops? I doubt there is anywhere else you could find that taxon. See also next:



The hadrosaur *Parasaurolophus*, for example, is represented by different taxa in Alberta, Utah, and New Mexico (Evans et al., 2009; Gates et al., 2021), but the genus itself has a large geographic range. Other genera with large geographic ranges include the hadrosaurine *Gryposaurus* (Gates & Sampson 2007), the pachycephalosaur *Stegoceras* (Sullivan & Lucas, 2006), and the chasmosaurs *Triceratops* and *Torosaurus* (Longrich & Field, 2012). ~~This is~~However, this does not ~~to say there are no~~ exclude the presence of other endemic clades ~~in other taxa; the~~. The chasmosaur *Chasmosaurus*, for example, is known exclusively from a small region in southern Canada (Godfrey & Holmes, 1995). Nevertheless, centrosaurines are unusual in that, thus far, none of the subclades are known to be widely distributed.

Pachyrhinosaurus clade is widely distributed – it’s a clade where there are multiple sites of similar age in Canada where you might expect to find the same clade, and you do.

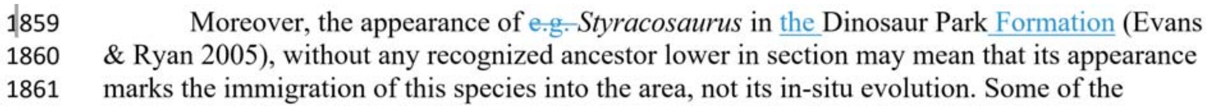


The discovery of *Lokiceratops rangiformis* also suggests that, in addition to showing high endemism, the local diversity of centrosaurines was high in the Judith River ~~area.~~ region. Four distinct and coeval centrosaurine ceratopsians (*Lokiceratops rangiformis*, *Albertaceratops nesmoi, Medusaceratops lokii,* and *Wendiceratops pinhornensis*) occur within a small geographic area where the Milk River crosses the United States of America/Canadian border. These centrosaurines occur within a tight stratigraphic interval of four meters and range in age from a maximum of 78.28 to 78.08 + 0.2 - 0.9 Ma. This pattern is distinct from other formations, where typically only a single species existed, and is analogous to the pattern of diversity observed in sympatric lambeosaurine hadrosaurids in the Dinosaur Park Formation (Mallon et al., 2012).

This isn't true. Loki, Alberta, and Medusa are from different stratigraphic levels. The authors infer artificially extended stratigraphic ranges using Signor Lipps, but there is no actual evidence that this is a valid approach. Even if it was, the way this is phrased makes it sound like fact whereas it's inference.

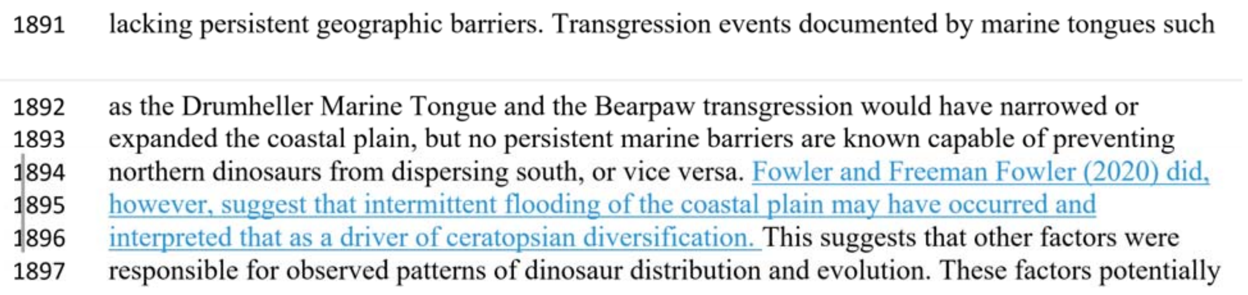
It is at least plausible, if not more parsimonious, that Loki, Alberta, and Medusa represent variation within a single evolving population.

I'm fine with Wendi being a different clade/lineage – it doesn't look like it is closely related to the Loki-clade or the Centro-clade.



Moreover, the appearance of ~~e.g.~~ *Styracosaurus* in the Dinosaur Park Formation (Evans & Ryan 2005), without any recognized ancestor lower in section may mean that its appearance marks the immigration of this species into the area, not its in-situ evolution. Some of the

Wilson et al. (description of Stellasaurus) suggest that there is a non-overlapping anagenetic lineage from Corona-Centro-Styraco-Stella-Einio-Achelou-Pachy. I gather the new cladogram does not support that hypothesis, but anagenesis is more consistent with the fossil record than the inferred ghost ranges of this new cladogram. At the least, Wilson's paper should be cited here as an alternative interpretation.



lacking persistent geographic barriers. Transgression events documented by marine tongues such as the Drumheller Marine Tongue and the Bearpaw transgression would have narrowed or expanded the coastal plain, but no persistent marine barriers are known capable of preventing northern dinosaurs from dispersing south, or vice versa. Fowler and Freeman Fowler (2020) did, however, suggest that intermittent flooding of the coastal plain may have occurred and interpreted that as a driver of ceratopsian diversification. This suggests that other factors were responsible for observed patterns of dinosaur distribution and evolution. These factors potentially

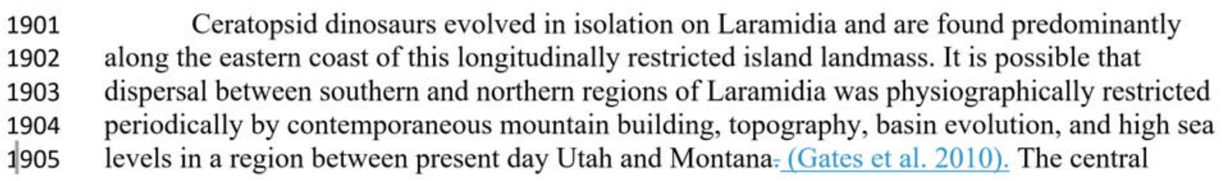
> The key word here is 'persistent'. While there may have been flooding up to the foothills of the proto-Rockies as indicated in the Ostresh and Lillegraven maps cited in Fowler and Freedman Fowler (2020), that A) assumes that the foothills were in their present day location, and B) that the dinosaurs were reluctant to enter highlands. Neither of these assumptions is very solid. However, in recognition of the debate surrounding this issue, we have added a sentence to recognize the diversity of views on this topic.

Persistent is not needed. If the authors are correct, and speciation is occurring in 200ky or less, then you don't need a barrier formed for long for it to have an effect.

On A: The Lillegraven and Ostresh maps show the modern thrust front not foothills. At the times we highlight, the paleoshoreline actually overlaps with the position of the modern day thrust front – clearly this would be impossible in the past as the sealevel cannot rise over the mountains. This therefore suggests the position of the thrust front was more western. The point is not that this represents an impossible scenario, but that sealevel was so high during

On B: Ceratopsids, on which this paper is firmly centered, have been hypothesized basically to be coastal plain specialists, not venturing into upland or inland areas. This is based on the lack or rarity of ceratopsids in inland or. Brinkman et al. (1998) should be cited here. The authors do not have to agree with Brinkman et al, but they would then have to provide some suggestion as to why ceratopsids are not found in inland/upland environments (where we do get basal ceratopsians like Leptoceratopsids etc.).

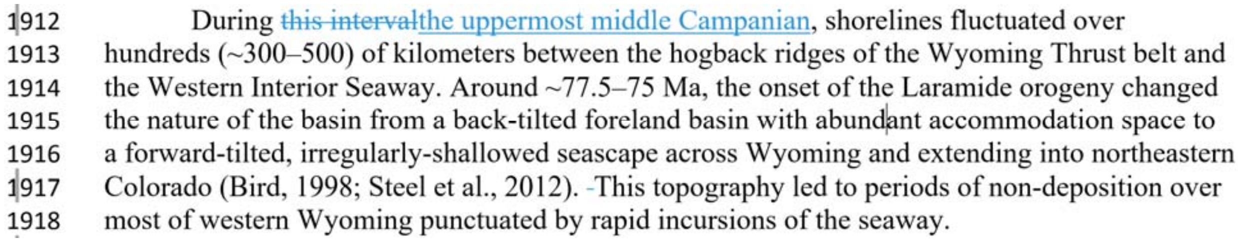
Comment on Fowler and Freedman Fowler.
This sells us short. We came up with the only viable hypothesis for north-south physiographic barriers. It was based on data that had been ignored or was simply not known about by previous workers. We don't make any new geographic data, we take the paleogeographic maps of Lillegraven and Ostresh (which mapped the paleoshoreline at the highest resolution available – individual ammonite zones) and simply noted that the geographic areas where there is overlap of the shoreline and current thrust front match where we expect a physiographic barrier to dispersal, and also when. We note how this works in terms of the sea lapping at the feet of the mountains, and give modern examples where this happens. This isn't something that Gates, Sampson, Lehman, etc. came up with.



Ceratopsid dinosaurs evolved in isolation on Laramidia and are found predominantly along the eastern coast of this longitudinally restricted island landmass. It is possible that dispersal between southern and northern regions of Laramidia was physiographically restricted periodically by contemporaneous mountain building, topography, basin evolution, and high sea levels in a region between present day Utah and Montana~~.~~ (Gates et al. 2010). The central

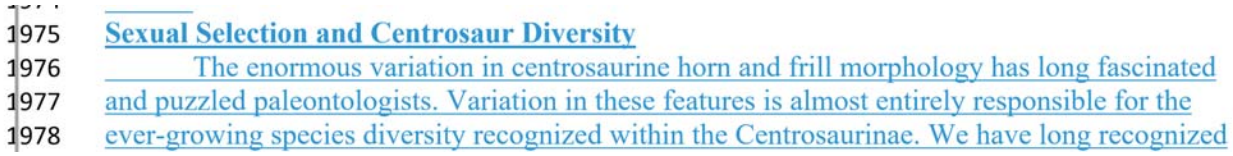
I appreciate that the authors have added a citation in here, but it is the wrong citation. Gates et al. 2010 is not the originator of any of those hypotheses. Indeed, I just did a text search, there is no mention of sea level or transgression anywhere in the Gates et al. 2010 paper. This paper states that (abstract): “ Lacking evidence of any physiographic barrier to north–south dispersal, climatic variation within the WIB is regarded as the most likely explanation for the overarching biogeographic patterns observed for late Campanian vertebrate taxa”

Mountain-building was in the Gates et al. 2012 paper. The inference of sea level cutting off northern and southern faunas was from Fowler and Freedman Fowler 2020. Horner et al. 1992 talk about sea level, but for them it was not a barrier, rather it restricted the areal extent of the floodplain, inducing population stress and prompting evolution (a hypothesis that I don’t think is consistent with data anymore).



During ~~this interval~~the uppermost middle Campanian, shorelines fluctuated over hundreds (~300–500) of kilometers between the hogback ridges of the Wyoming Thrust belt and the Western Interior Seaway. Around ~77.5–75 Ma, the onset of the Laramide orogeny changed the nature of the basin from a back-tilted foreland basin with abundant accommodation space to a forward-tilted, irregularly-shallowed seascape across Wyoming and extending into northeastern Colorado (Bird, 1998; Steel et al., 2012). This topography led to periods of non-deposition over most of western Wyoming punctuated by rapid incursions of the seaway.

This needs citations.



Sexual Selection and Centrosaur Diversity

The enormous variation in centrosaurine horn and frill morphology has long fascinated and puzzled paleontologists. Variation in these features is almost entirely responsible for the ever-growing species diversity recognized within the Centrosaurinae. We have long recognized

Nitpicky, but when you use the term variation in a paper on evolution, you really should not use it in the general differences-among-specimens way. Variation specifically refers to differences among individuals within a species. Differences between species are disparity, not variation. I dare say, the second sentence I very much agree with, but I do not think these authors do so.