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Response to Kellner (2017) 'Rebuttal of Martin-Silverstone, E., J.R.N. Glasier, J.H. Acorn, S. Mohr, and P.J. Currie, 2017'

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Kellner's (2017) rebuttal to our paper (Martin-Silverstone et al., 2017) affords us an opportunity to further develop our position regarding the pterosaur specimen UALVP 24238. Because three of us (Martin-Silverstone, Glasier, and Mohr) were in the final stages of thesis preparation, and Currie was in the field, Acorn was designated to compose our response in a timely fashion. However, all authors have seen, contributed to, and approved the following text.

There are two broad areas of disagreement between our interpretation and that of Kellner, and both go well beyond the study of pterosaurs *per se*. The first has to do with statistics, and the importance of assessing variation among individuals. The second has to do with the interpretation of equivocal evidence. A quick summary of our perspectives on these two points should guide other workers through this debate. Before beginning this summary, however, we freely acknowledge that Kellner is not a splitter in many of his other published works, and that we missed the difference between his rostral value and the rostral index of Martill and Naish (2006). He admits that he misread Bennett (1992) and that UALVP 24238 is likely male, and we admit that the ontogenetic maturity of this specimen at death was likely more advanced than we thought.

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In our original paper (Martin-Silverstone et al., 2017), we note that Bennett (1992) focuses on patterns in the data for *Pteranodon* as a whole, whereas Kellner (2010) focuses on similarities and differences between particular specimens. This difference, between what might be termed statistical and non-statistical approaches, is, in our opinion, the reason behind what Kellner (2017) calls, "the importance of this debate for pterosaur research in general." However, from a statistical perspective, the quantitative techniques involved here are very simple, so it is important to realize that this debate is not about the difference between good statistics and bad, it is about the difference between some statistics and none.

In our paper, we provide novel quantitative details in support of the assignment of UALVP 24238 to *Pteranodon sternbergi*, and these are the data that best support our argument (Martin-Silverstone et al., 2017, figs. 6 and 9 in particular). As well, we provide graphic, qualitative support for the idea that the mandible of UALVP 24238 is not distinct from other specimens of *Pteranodon* (Martin-Silverstone et al., 2017, fig. 7). Most importantly, we show that, whereas UALVP 24238 and KUVP 967 exhibit the shallowest rostral taper of any known *Pteranodon*, the rostrum of CMNFV 41358 possesses an intermediate condition between these specimens and FSHM VP 339 (Martin-Silverstone et al., 2017, fig. 9). Kellner (2017) does not mention these data in his rebuttal. Instead, he focuses on comparisons between only two specimens: UALVP 24238 and FHSM VP 339 (the holotype of *Pteranodon sternbergi*). Kellner maintains that because both are mature males, the differences between them (the shapes of the rostra and cranial crests) are taxonomic, not ontogenetic or the product of intraspecific variation.

We appreciate how tempting it is to look at Kellner's (2017) Figure 1, and conclude that these two specimens represent obviously different taxa. Coincidentally, however, in a recent blog post, that appeared before our paper was published, another pterosaur specialist, Mark Witton (2016) presents a figure almost identical to Kellner's, superimposing outline drawings of the same two skulls plus Kellner's *Geosternbergia maiseysi* holotype. Revealingly, Witton's figure is presented in support of Bennett's position, not Kellner's.

For us, the data that spring most strongly to mind during this discussion are the eleven size-frequency histograms in Bennett (1992). They show, among other things, that some large (likely male) *Pteranodon* were larger than others. If crest size, and the length of the crest base, was positively allometric with skull size, then it does not matter whether UALVP 24238 was a subadult, or an adult. What matters is that there was significant variation within *Pteranodon sternbergi*. Additionally, if the cranial crests of *Pteranodon* were sexually dimorphic (Bennett 1992; Tomkins et al. 2010; Hone et al. 2012; Knell et al. 2013), then they were probably under the influence of sexual selection. In modern animals, sexually selected or "signal" traits are more variable than those of non-signal traits, with respect to their size, shape, colour, and presence/absence (e.g., Alatalo et al. 1988; Wiens 2001; Cuervo and Møller 2009; Tazzyman and Iwasa 2010; Emlen et al. 2012). For this reason, it is both reasonable and parsimonious to expect significant morphological variation in the cranial crests of mature males of a single species of *Pteranodon*.

With respect to how one assesses equivocal evidence (such as poorly preserved fossils), Kellner maintains that our logic, "contains in some parts indications of circular reasoning," but does not elaborate on how he thinks our conclusions are embedded in our premises; the mark of circularity in logic. Later in his text, however, Kellner returns to a critique of our reasoning, and asserts that, with respect to the features he uses to diagnose *Dawndraco*, "the morphological differences *are there*," and that "although recognizing their existence, [we] have dismissed them by arguing postmortem distortion or incomplete preservation." This criticism takes us into the realm of paleontological philosophy, and it deserves a careful response.

Incomplete preservation, by definition, necessitates that at least part of a fossil is, in fact, not there. The missing distal portion of the rostrum of UALVP 24238 is a clear example of a character that simply does not exist, and the putative total length of the rostrum is one of the eight characters used by Kellner to diagnose *Dawndraco kanzai*. Then there are the caudal vertebrae, which Kellner mis-measured. Again, the character does not exist, although a different structure does. Kellner's skull angle character clearly cannot be measured with any precision, for lack of discrete landmarks, and because of postmortem distortion. In this instance, the character is an approximation—a value with an uncertain range of potential error. When one thinks statistically, the existence or non-existence of particular features becomes a matter of probability, not a matter of presence or absence, or directly observable fact. In our paper, we show that four of Kellner's other diagnostic characters each fall within a range of continuous variation that appears to characterize *Pteranodon* specimens as a whole. The existence or non-existence of these characters is not at issue—what is at issue is the existence of broad patterns of variation, which we recognize and find instructive. Finally, the lacrimal process certainly exists on UALVP 24238, but is absent in other specimens because of (we suggest) incomplete preservation. Postmortem distortion and incomplete preservation both exist in UALVP 24238 (although in a different sense than structural characters exist), and in the vast majority of other pterosaur specimens, and should not be rationalized away, no matter how tempting it is to see a different-looking specimen as representing a different taxon.

When evidence is equivocal, and thus difficult to interpret in a straightforward fashion, a scientist should be cautious of perceptual errors. In almost all sciences, the primary safeguard against such errors is the application of quantitative analyses, and the search for objectively demonstrable patterns in nature. This is just as true in paleontology as in other fields, and quantitative studies of *Pteranodon*, beginning with Bennett (1992), are an outstanding example of this approach. In summary, we continue to base our opinion on the fact that the known *Pteranodon* specimens form a bimodal size continuum, probably anagenetic, just as Bennett demonstrated some 25 years ago. Very few skulls possess complete rostra, or complete crests, and we therefore remain open minded regarding the variety of shapes that may have been present over the evolutionary history of the genus, the ontogenetic history of individuals, or among individuals in a population. Although we acknowledge that future research or new discoveries may validate *Dawndraco kanzai* as a distinct taxon, we feel that the characters currently used to distinguish it from *Pteranodon sternbergi* are more parsimoniously interpreted within the framework of individual, ontogenetic and/or sexual variation, and preservational differences between UALVP 24238 and other *Pteranodon* specimens.

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