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Variation in a population of Theropoda (Dinosauria): *Allosaurus* from the Cleveland-Lloyd Quarry (Upper Jurassic), Utah, USA

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Abstract. Ontogenetic and individual variation in a population of the large theropod *Allosaurus* cf. *A. fragilis* was examined using the Björk superimposition method on the premaxillae, maxillae, lachrymal, postorbital, and jugal. This method allows utilization of incomplete specimens without having to estimate (fabricate) missing data. In addition, it visually shows regions of ontogenetic change and variation. Comparison of these results with other morphometric studies of the same specimens show that most allometric trends are not supported. Instead, ontogenetic change is mostly isometric. In addition, the wide range of individual variation in all the skull elements analyzed makes some autapomorphic characters used to define other theropod taxa suspect.

Key words: *Allosaurus*, ontogeny, superimposition, variation

Introduction

The Cleveland-Lloyd Dinosaur Quarry in central Utah has produced the largest assemblage of a single species of large theropod in the Upper Jurassic Morrison Formation. This theropod has been referred to as *Allosaurus fragilis* by most authors (e.g., Madsen, 1976; Gates, 2005; Loewen, 2009), although Paul (per. com. 2010) questions the assignment of the specimens to the much older *A. fragilis*. Regardless, at least 46 individuals of different size classes are represented (Gates, 2005). These classes are thought to reflect age (Madsen, 1976; Gates, 2005). The occurrence of so many individuals at the Quarry is explained as a predator death trap (Dodson *et al.*, 1980; Bilbey, 1999; Richmond and Morris, 1996; but see Gates, 2005; Hunt *et al.*, 2006), although there is no consensus as to its origin (cf. Richmond and Morris, 1996; Bilbey, 1999; Gates, 2005; Hunt *et al.*, 2006). The geology and taphonomy of the quarry and surrounding area have been variously discussed by Stokes (1985), Dodson *et al.* (1980), Bilbey (1998, 1999), Gates (2005), Suarez (2004a, b).

Regardless as to the cause for so many specimens of *Allosaurus* being accumulated at one spot, the assemblage is important because it represents what is believed to be a single population (e.g., Loewen, 2009; Hunt *et al.*, 2006) and thus, differences in the skeletal parts are thought to be due to individual variation, sexual dimorphism, and allometry (Madsen, 1976). Attempts have been made to quantify these differences (Madsen, 1976), especially the morphometric studies of Smith (1996, 1998, 1999), Smith *et al.* (1999), and Loewen (2004, 2009). These morphometric studies follow the procedures elaborated by Bookstein *et al.* (1985). Other studies of the Cleveland-Lloyd *Allosaurus* specimens include the description of variation in the pneumatic system of the basicranium by Chure and Madsen (1996), the histological study of the limbs by Bybee *et al.* (2006), and paleopathologies by Hanna (2002).

Methods

Molnar (1990) discussed the origins of variation in the fossil record, especially its effects on alpha taxonomy of theropods. He identified individual, sexual, ontogenetic, geographical and chronological, intraspecific, postmortem deformation, and pathological variation. Of these, individual and ontogenetic are the focus of this study. Furthermore, in contrast to many previous studies of variation (e.g., Smith, 1996, 1998, 1999; Smith *et al.*, 1999), I use only specimens from the Cleveland-Lloyd Quarry so as to avoid possible mixing of different species.

As Adams *et al.*, (2004, p. 10, 13) have noted, homolo-

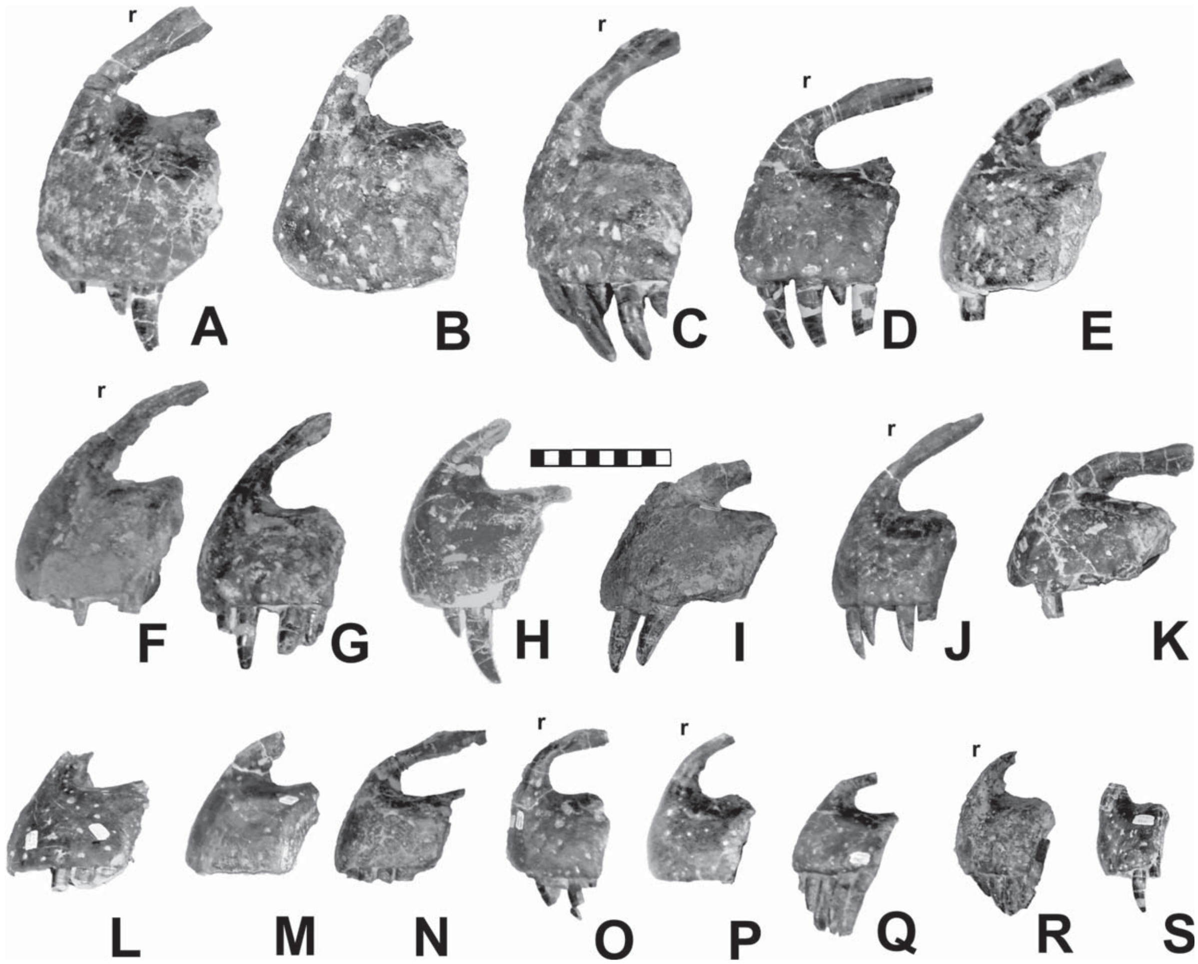

Figure 1. Premaxillae of *Allosaurus* cf. *A. fragilis* from the Cleveland Lloyd Dinosaur Quarry, Utah, arranged by size, which presumably forms an ontogenetic series. Scale in cm. **A.** UMNH 9248; **B.** UMNH 9252; **C.** UMNH 9160; **D.** UMNH 1251; **E.** UMNH 8258; **F.** UMNH 9231; **G.** UMNH 6504; **H.** UMNH 1852; **I.** UMNH 9263; **J.** UMNH 6052; **K.** UMNH 9264; **L.** UMNH 9270; **M.** UMNH 9262; **N.** UMNH 6500; **O.** UMNH 10393; **P.** UMNH 9241; **Q.** UMNH 9265; **R.** UMNH 6505; **S.** UMNH 9261. Abbreviation: r—reversed image.

gous landmarks are not necessarily identical landmarks owing to the vagaries of biological structures. Because these structures are not stamped out mechanically and thus would be exactly identical, differences result that can be difficult to quantify by morphometrics. For example, in Figure 1 an obvious landmark is the notch at the anterior of the external nares, where the base of the nasal, or ascending, process joins the main body of the premaxilla. However, differences in the shape of the notch among the various specimens makes it difficult to place a point in exactly the same spot: Note that the anterior most position of the notch in Figure 1E is located higher on the nasal process than in Figure 1F or 1I. The morphometric studies of Smith and his colleagues have not been concerned with that level of detail, using homologous rather than exact points. However, this lack of congruence, which highlights variability, is what is addressed here.

The numerical order of variation presented below do not imply ordered ranking of importance, but are simply to separate categories of variations. Variation caused by obvious postmortem deformation and pathologies are not included.

The cranial elements presented below represent the most abundant specimens currently available. These represent only a portion of the specimens originally collected because some specimens were incorporated into reconstructed skulls. Nevertheless, what remains should represent a random sampling of the specimens originally collected. All of the specimens are at the Utah Museum of Natural History (UMNH). The processes of many specimens are incomplete, which limits the usefulness of measurements. For this reason, superimposition overlays images of specimens were used so that homologous landmarks match closely as possible (Rohlf and Marcus, 1993). These results are compared with the morphometric analysis of Loewen (2009) on many of the same premaxillae, maxillae, lachrymals, and jugals. To aid com-

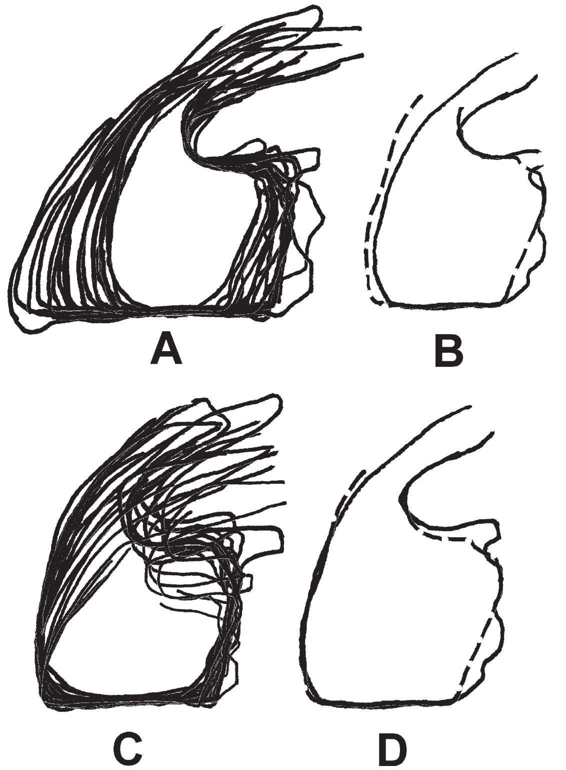

Figure 2. Björk method of superimposition of the premaxillae of Figure 1. All are to the same scale. **A.** scaled to same premaxillary body height. **B.** Smallest (dashed) and largest (solid line) specimens superimposed. **C.** scaled to same premaxillary body length. **D.** Smallest (dashed) and largest (solid line) specimens superimposed.

parisons, all specimens are shown as if from the left side, meaning bones from the right side were reversed.

Analysis of specimens

Premaxillae.—The eight right and eleven left premaxillae (Figure 1) show a wide range of variability. Two methods of standardization were used. The first scaled the premaxillae to the same body depth (Figure 2A, B), and the other to approximately the same body length (Figure 2C, D).

1. The most obvious variation is size, which is presumably ontogenetic, with the smallest specimens belonging to younger individuals and the larger ones to older individuals.

2. The relative length: height of the premaxillary body (exclusive of the nasal process) forms a continuum from being equal (Figure 1A, S) to being longer than tall (Figure 1D, N) as may be seen in Figure 2A. Loewen (2009) concluded from his morphometric analysis that there was an ontogenetic increase in height relative to its length, as well as an increase in the height of the nasal process. However, the results here and number 7 below suggest this trend is not as clear as Loewen stated because individual variation is far greater than he recognized.

3. The shape of the anterior edge ranges from nearly straight (Figure 1B, D, I, K, O, S) to arcuate (e.g., Figure 1A, C, E-H, P, R), or a combination of both (Figure 1D, J, L-N, Q).

4. Of the straight edged premaxillae in the preceding, the anterior edge may be vertical (Figure 1S), slightly angled (Figure 1P), or angled (Figure 1B, D, I, K). No clear trend is apparent.

5. The maxillary articular surface, along the posterior edge, may be vertical or nearly so (Figure 1O, S), but is usually angled (all other specimens).

6. The shape of the anterior rim of the external narial notch ranges from almost squared (Figure 1D, E, N, O) to rounded (Figure 1B, C, G, H, J, L, M, P-R); although one specimen has a pointed, angled rim (Figure 1F).

7. Related to the shape of the narial notch is the angle of the nasal process. It may be subparallel to the premaxillary body (Figure 1D, N, O, Q) or angled (Figure 1A-C, E-H, J, P, R). Again, there is a near continuum (Figure 2C), although most are angled.

Maxillae.—There are ten left and eight right maxillae (Figure 3). Scaling the maxillae to a standard size is difficult because there is so much variation and because so many specimens are incomplete. Depth of the maxillary body from the ascending or nasal process was the most consistent among the specimens (Figure 4A).

1. As with the premaxillae, ontogentic variation is expressed by size (Figure 3). There is over 350% difference between the length of the smallest maxilla (Figure 3R) and largest (Figure 3A) taking the damaged portions into account.

2. Other variation includes the relative depth of the maxillary body anterior to the ascending process (Figure 4A). This variation forms a continuum from proportionally deep (Figure 3B) to proportionally shallow (Figure 3L, O, P). Loewen (2009) noted that this deepening was allometric during ontogeny.

3. The anterior portion of the maxilla may be proportionally short relative to its height (Figure 3A, C, E, F, H, I) or proportionally long (Figure 3B, N, P). This difference does not appear to be ontogenetic.

4. The angle of the ascending process may be steep (Figure 3C, E), moderately inclined (3I) or almost horizontal (Figure 3B, F). The two extremes are seen in Figure 4B. Contrary to Loewen (2009), the relative height of the inflection point compared to maxillary length does not appear to increase ontogenetically.

5. Related to the angle of the ascending process is the anterior rim of the antorbital fossa, which is formed by the posterior edge of the ascending process. This rim may be sharp, almost V-shaped (Figure 3B, D), but is more typically U- or broadly U-shaped (Figure 3C, E, G, H, J, L. M, N, O, Q).

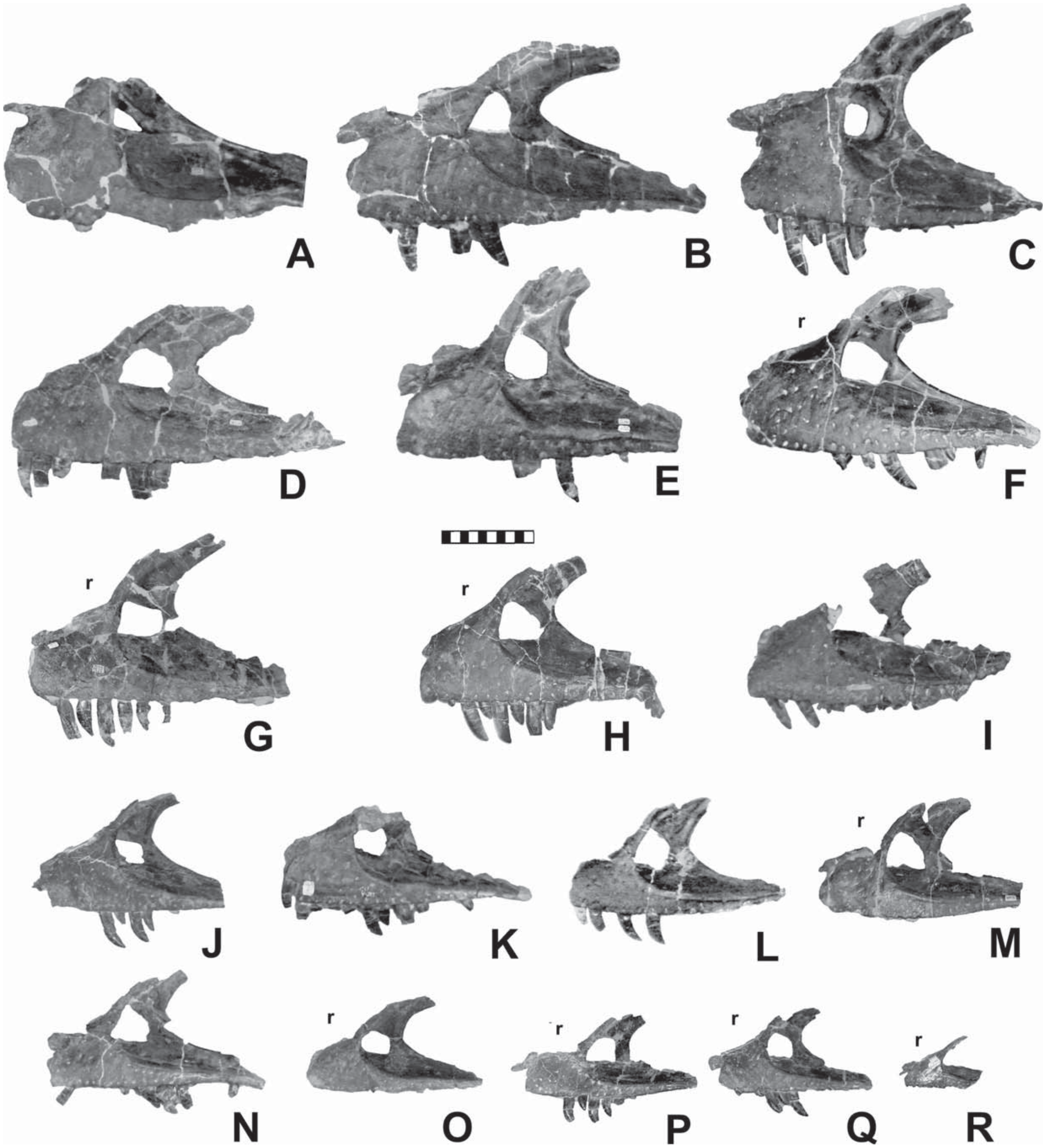

Figure 3. Maxillae of *Allosaurus* cf. *A. fragilis* from the Cleveland Lloyd Dinosaur Quarry, Utah, arranged by size, which presumably forms an ontogenetic series. Scale in cm. **A.** UMNH 9210; **B.** UMNH 9169; **C.** UMNH 16659; **D.** UMNH 9218; **E.** UMNH 5393; **F.** UMNH 9229; **G.** UMNH 9275; **H.** UMNH 9201; **I.** UMNH 9215; **J.** UMNH CLQ-03-34; **K.** UMNH 9169; **L.** UMNH 9211; **M.** UMNH 9272; **N.** UMNH 5316; **O.** UMNH 9274; **P.** UMNH 9273; **Q.** UMNH 9275; **R.** UMNH 6363. Abbreviation: r—reversed image.

6. The anterior edge of the ascending process is also variable, being sloped (Figure 3J, K, O, Q) or abruptly angled (Figure 3C, E, G, L, M). Thus, the posterodorsal inflection of this process is not a reliable taxonomic character.

7. The maxillary fenestra at the base of the ascending process is variable in shape, from almost a right triangle (Figure 3A, H), asymmetrical triangle (Figure 3B, D, E, M, N), to subrectangular (Figure 3C, O). The range of shapes is almost a continuum triangular to subrectangular (Figure 4A).

8. Besides shape, the relative size of the maxillary fenestra varies from proportionally small relative to the maxilla (Figure 3A) to large (Figure 3L). It does appear to be propor-

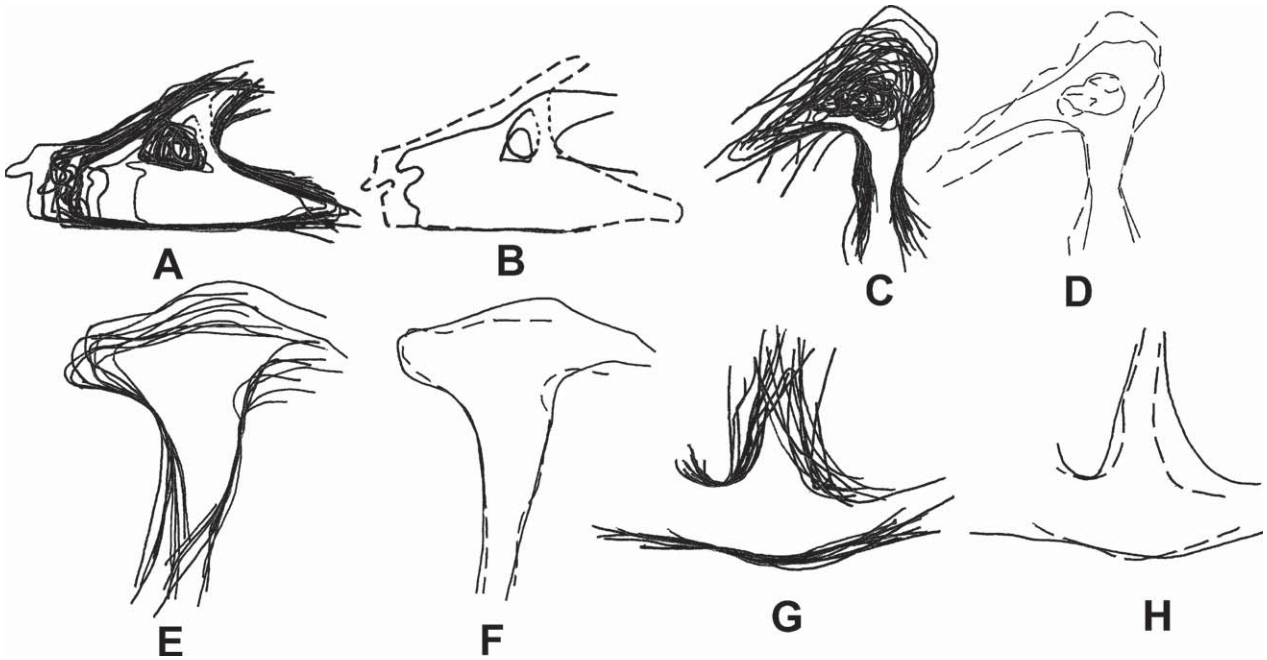

Figure 4. Björk method of superimposition: **A.** maxillae to same maxillary body height; **B.** smallest maxilla (dashed line) and largest (solid line); **C.** lachrymals to same minimum width of descending process below horizontal process; **D.** smallest lachrymal (dashed line) and largest (solid line); **E.** postorbitals to same descending process width below the horizontal process; **F.** smallest postorbital (dashed line) and largest (solid line); **G.** jugals to same body size; **H.** smallest jugal (dashed) and largest (solid line).

tionally smaller relative to the size of the maxillary body in the large vs. smaller specimens. Loewen (2009) indeed did note the overall size has negative allometry with size.

9. Finally, the relative depth of the posterior process, which contacts the jugal, varies from being relatively deep (Figure 3C, E, R) or shallow (Figure 3F, K, L, O, P, Q). The extremes may be seen in Figure 4A, B.

Lachrymal.—There are twelve left and eight right lachrymals (Figure 5) and these show an extreme range of variation.

1. Ontogeny best explains the size differences because they can easily be arranged in a size continuum (Figure 5).

2. The lachrymal "horn", the dorsally projecting portion, ranges from barely projecting (Figure 5S, L), to extremely pronounced (Figure 5A, G, K, N, Q, T), but most fall between these extremes. The "horn" development is not ontogenetic because the smallest specimen (Figure 5T) has an extremely well developed structure, whereas the second smallest lachrymal (Figure 5S) has the smallest structure.

3. The "horn" may be tapering (Figure 5F, G, K, Q, T), rounded (D, I, L, O, R, S), or truncated (Figure 5E, J, M, P). One horn is pathologically truncated (Figure 5H) leaving a opening wound into the pneumatic cavity; this specimen is not counted among forms of variation.

4. The shape of the pneumatic fenestra ranges from nearly circular (Figure 5Q) to triangular (Figure 5A, F, G, L, O), but most are polygonal. Some are horizontally elongate (Figure 5C, R, S), but most are taller than wide.

5. The number of pneumatic fenestra is variable, from one (Figure 5A, C, D, L), two (Figure 5I, N, P, Q, T), three (Figure 5J), or a partial division in two (Figure 5B, E). Paired fenestra may by separated by a thin septum (Figure 5N), a thick septum (Figure 5P, Q, T) or be widely separated (Figure 5I, J).

6. The relative size of the pneumatic fenestra to the size of the lachrymal may range from large (Figure 5A, B, C, J, K, L, O, R, S) to small (Figure 5I, H, M, N, T). In multiple fenestra, one may be larger than the other (Figure 5D, I, J, Q), or they may be nearly equal in size (Figure 5N). See also Figure 4C.

7. The angle between the anterior or nasal process and vertical or descending process may be very tight (Figure 5D, E) or almost at right angles (Figure 5L, P), but are typically more open (Figure 5A, B, C, H, I, N). Surprisingly, there is a gradation in the two extremes (Figure 4C) making it difficult to dismiss the tight angled lachrymals as pathological. It seems likely that there were short-faced individuals. It is unfortunate that these lachrymals cannot be matched with any maxilla, thus it is unknown if these tight lachrymals (Figure 5D, E) belong to the short bodied maxilla (Figure 3A, C, E, F, H, I).

8. The anterior edge of the descending (maxillary) process, where it forms the posterior edge of the antorbital fenestra,

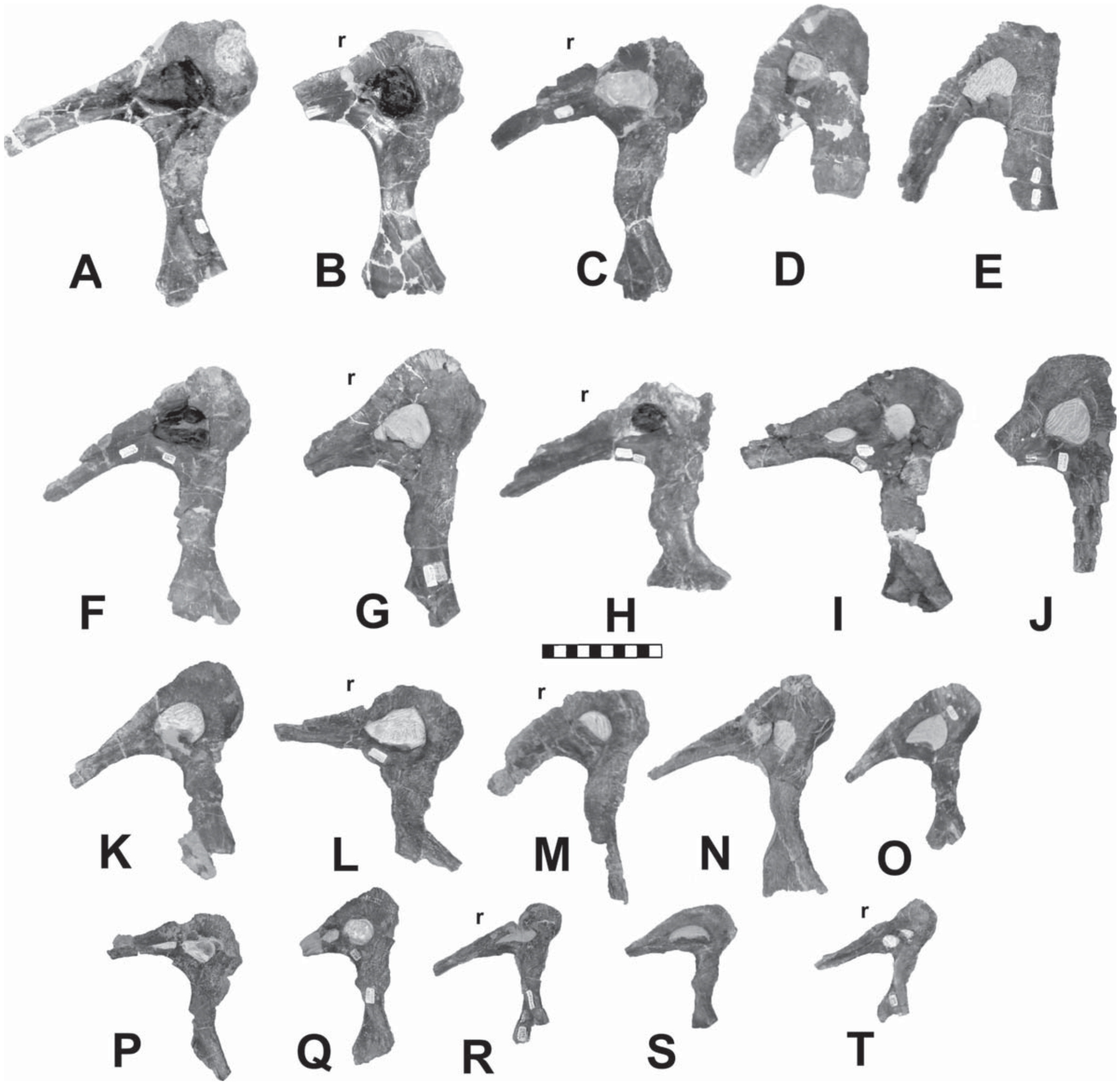

Figure 5. Lachrymals of *Allosaurus* cf. *A. fragilis* from the Cleveland Lloyd Dinosaur Quarry, Utah, arranged by size, which presumably forms an ontogenetic series. Scale in cm. **A.** UMNH 16664; **B.** UMNH 9473; **C.** UMNH 9474; **D.** UMNH 9476; **E.** UMNH 9224; **F.** UMNH 9475; **G.** UMNH 9469; **H.** UMNH 9472; **I.** UMNH 16665; **J.** UMNH 9479; **K.** UMNH 9478; **L.** UMNH 9471; **M.** UMNH 12005; **N.** UMNH 12176; **O.** UMNH 11531; **P.** UMNH 8098; **Q.** UMNH 8971; **R.** UMNH 7786; **S.** UMNH 1765; **T.** UMNH 7785. Abbreviation: r—reversed image.

may be smooth (Figure 5B, J, R, T), or have a projection that is either prominent (Figure 5C, E, G, H) or slightly developed (Figure 5A, F, G, I, M, N, Q, S).

Postorbital.—There are 5 left and 4 right postorbitals currently available and most of these are approximately the same size. There are no small, hence juvenile specimens available. The squamosal processes are incomplete among most of the specimens. Loewen (2009) claims the postorbital body shows positive allometry with age, but I cannot substantiate this claim.

1. Lacking an ontogenetic series, one of the most obvious difference is the relative height of the dorsal protuberance (Figure 4E, F; 6). It may be little developed (Figure 6B, E, G), but it is more commonly well developed and prominent (Figure 6C, D, F, G, H).

2. The dorsally place anterior process may be relatively short (Figure 6B, E) or relatively long (Figure 6F, G, H), but this is related to the relative width of the descending or jugal process (Figure 4E).

3. The descending jugal process may be relatively wide (Figure 6E) or relatively slender (Figure 6F, G, H, I). The width is closely linked to the development of dorsoposterior rim of the orbit below the horizontal process and the dorsoanterior rim of the lateral temporal fossa below the squamosal

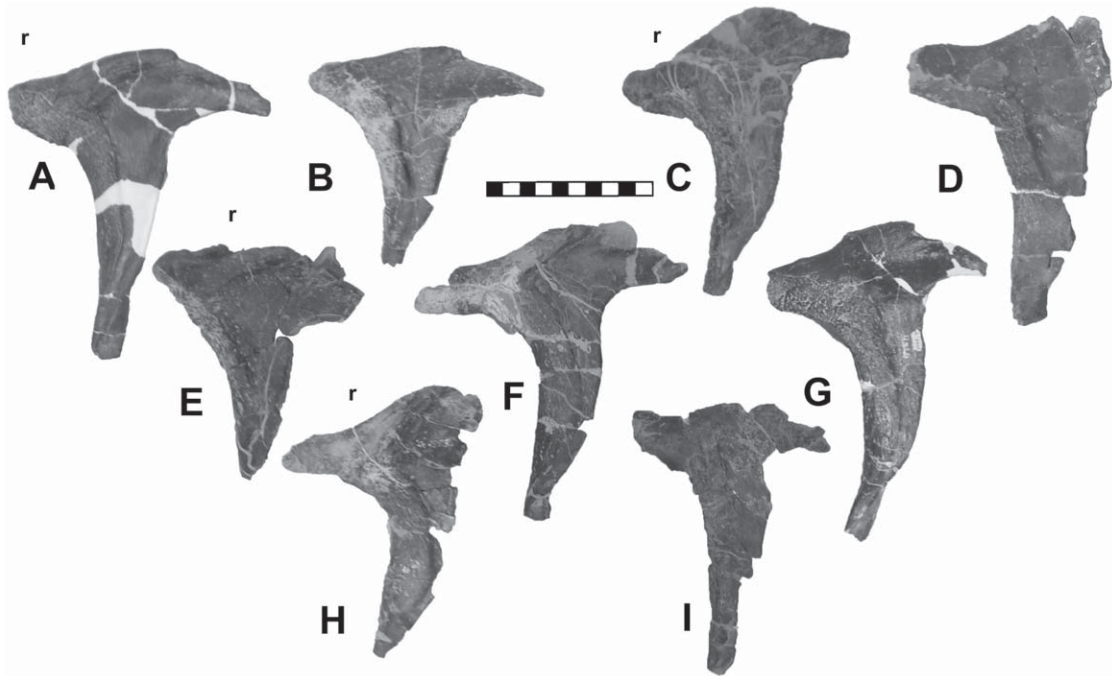

Figure 6. Postorbitals of *Allosaurus* cf. *A. fragilis* from the Cleveland Lloyd Dinosaur Quarry, Utah. Unlike the other skull bones in the collection, most are the same size. Scale in cm. **A.** UMNH 9103; **B.** UMNH 9097; **C.** UMNH 9108; **D.** UMNH 9090; **E.** UMNH 9112; **F.** UMNH 9096; **G.** UMNH 9100; **H.** UMNH 9106; **I.** UMNH 9099. Abbreviation: r—reversed image.

process.

4. The posterodorsal rim of the orbit below the horizontal process may be gently rounded (Figure 6B, E) or may be deeply embayed or notched (Figure 6C, H, I).

5. The anterodorsal rim of the lateral temporal fossa below the squamosal may notched (Figure 6A, F, G, I) or not (Figure 6B, C, E).

Jugal.—There are four right jugals and eight left jugals.

1. There is some size difference, but none seems to have been from very small individuals as in the premaxillae. The smallest jugal is about half the size of the largest (Figure 7L, 7A)

2. The lower orbital rim varies from V-shaped (Figure 7G) to broadly U-shaped (Figure 7A, B, C, K). See also Figure 7G, H.

3. The postorbital (ascending) process may be vertical (Figure 7B, C, E, F, I, J), angled slightly anteriorly (Figure 7B, D, G) or slightly posteriorly (Figure 7H); see also Figure 4G.

4. The base of the postorbital (ascending) process may be narrow (Figure 7A, L) or broad (Figure 7B, F, G, I), but most are intermediate (Figure 7C, D, E, H, J, K); see also Figure 4G, H.

5. Most of the postorbital processes are incomplete, but enough remain to show that they were either relatively tall (Figure 7A, D, E, F, H, J) or short (Figure 7C, I).

6. The sutural surface with the postorbital may be high (Figure 7B, D, E) or low (Figure 7C, L) on the ascending (postorbital) process.

7. The ventral margin of the jugal may be prominent (Figure 7A, B, D, E, H, I) or slightly developed (Figure 7C, F, G, L); see also Figure 4G. Loewen (2009) refers to this ventral prominence as the "ventral deflection" and states that it shows positive allometry. However, the deflection is variously developed in the specimens, and does not follow a linear increase with size.

Discussion

The visual comparisons of the *Allosaurus* cranial material from Cleveland-Lloyd Dinosaur Quarry can be compared with the numerical or morphometric analyses of Smith (1996, 1998, 1999), Smith *et al.* (1999), and Loewen (2004). In cases where the landmarks are missing on specimens, the specimens or the landmarks and associated data may be eliminated from the analysis (Adams *et al.*, 2004). Alternatively, the missing data can be estimated (Adams *et al.*, (2004), but such an approach is tantamount to fabricating data, even if well intended. Alternatively, Loewen (2009) used proxies, such as maxillary tooth row length, rather than maximum length of the maxillae in his analysis of incomplete *Allosaurus* elements. Another shortcoming of multivariate

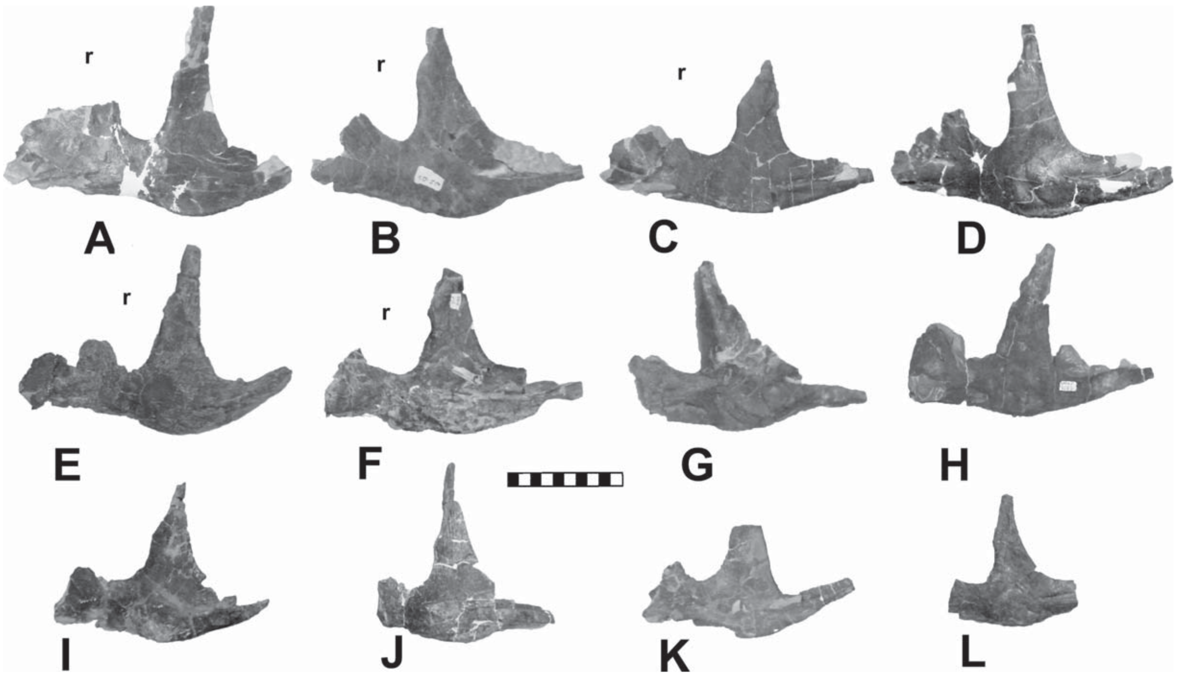

Figure 7. Jugals of *Allosaurus* cf. *A. fragilis* from the Cleveland Lloyd Dinosaur Quarry, Utah, arranged by size, which presumably forms an ontogenetic series. Scale in cm. **A.** UMNH 9085; **B.** UMNH 9083; **C.** UMNH 9086; **D.** UMNH 8972; **E.** UMNH 12000; **F.** UMNH 8976; **G.** UMNH 9084; **H.** UMNH 9087; **I.** UMNH 8475; **J.** UMNH 8974; **K.** UMNH 89088; **L.** UMNH 8973. Abbreviation: r—reversed image.

morphometrics is that the original shape of the object cannot be recreated from the data matrix, thus raising the question whether the shape is really "captured" (Adams *et al.*, 2004). The problem is, as Slice (2005, p. 10) noted, because "some anatomical structures… do not lend themselves to characterization by well-defined, discrete landmarks. They are, instead, partial or complete boundaries of another structure or traces of local maximum surface curvature that are continuous, one dimensional features". Although morphometrics may be the preferable method of analysis because numerical values are used, visual overlays have advantages as well, especially when bones are incomplete or when landmarks are not clear (Adams *et al.*, 2004; Slice 2005). This technique allows use of all specimens, does not require estimation of missing data, and shows the true shape of the object, rather than a series of individual points: "It is the entire underlying *continuous* structure that is to be compared across specimens and not the individual points used to characterize the outline" (Slice, 2005, p. 10, emphasis added).

You and Hägg (1999) investigated the reliability of three superimposition methods, but concluded that there was no statistical difference among them. Two of these, the Björk and Ricketts methods, use overlapping homologous points to note shifting position of other structures, whereas the Pancherz method quantifies the distance of the shifting positions relative to a reference plane. The Björk method overlaps natural structures (landmarks), whereas the Ricketts method uses a reference plane or line, as does the Pancherz method (see You and Hägg, 1999, for details on the methods). The Björk method was used here because the incomplete processes made it difficult to identify a shared reference plane, except for the alveolar margin of the premaxillae and maxillae.

Comparing the results of the superimposition above shows differences from the morphometric analyses of Smith (1998, 1999), Smith *et al.* (1999), and Loewen (2009). The lachrymals do not form a gradational series in horn development, thus the allometry seen by Loewen (2009) for the lachrymals from the Cleveland-Lloyd Quarry is not apparent here. Part of Loewen's problem stems from the incompleteness of the processes, thus requiring him to estimate the missing data. Smith (1998) included the lachrymals from Cleveland-Lloyd, but concluded little other than a wide scatter in an ontogenetic series. Smith (1999) included premaxillae, maxillae, lachrymals, and postorbitals, among other bones, and concluded that cranial bones showed the most variation in shape. Smith *et al.* (1999) presented the bivariate plot for the postorbitals, but besides showing a scatter and possible ontogenetic trend, no interpretation was given.

Most of the morphometric studies have sought to identify the number of species. Smith (1996, 1998, 1999) and Smith *et al.* (1999) concluded that only two species, *Al-*

losaurus fragilis and *Allosaurus maximus* were present, although this conclusion was not based on the bivariate plots. *Allosaurus maximus* was referred to *Saurophagus maximus* by Chure (1995). Smith's analyses failed to detect a probable third taxon from low in the Salt Wash Member of the Morrison Formation described by Chure (2000) in his unpublished dissertation. Loewen (2009) structured his analysis of *Allosaurus* to detect this other taxon, but was able to do so only after Chure (2000) had defined this taxon as having little ventral deflection of the jugal. The utility of this character is equivocal because some of the jugals from Cleveland-Lloyd Quarry have a slight ventral arc and fall within the range of variation for this character in the sample of this new character as identified by Loewen (2009).

Conclusion

Superimposition of bone silhouettes does have a role in variation studies in which various processes are damaged or missing, and measurements are either unattainable or must be estimated; it is not meant to supersede numerical methods. Applied to select *Allosaurus* cranial bones (premaxillae, maxillae, lachrymals, postorbitals, and jugals), ontogenetic changes appear to be mostly isometric, with only a slight allometric trend in some of the bones; these results only partially support the conclusions reported by Loewen (2009). For example, the maxillary body does become proportionally deeper and shorter ontogenetically, but only a little (Figure 4B). One surprising discovery is the proportionally short, deep adult maxilla (Figure 3C) and three steeply angled lachrymals (Figure 5D, E, M) that do not otherwise appear pathological. These suggest the presence of at least two relatively short-faced individuals of *Allosaurus* cf. *A. fragilis*. I view these as extreme variation rather than distinct taxon.

The variation seen in the cranial bones as documented above suggests that greater caution is warranted in selecting autapomorphies based on single specimen taxa of theropods. Certain characters, such as relative size or shape of the lachrymal horn or fenestra, should probably not be used. A similar study such as this one is needed on another large population sample, that of the Ghost Ranch *Coelophysis*. Between the two studies, a better understanding of variation in theropods will be attainable.

Acknowledgments

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