

# The variability of inner ear orientation in saurischian dinosaurs: Testing the use of semicircular canals as a reference system for comparative anatomy

The vestibular system of the inner ear houses three semicircular canals—oriented on three nearly-orthogonal planes—that respond to angular acceleration stimuli. In recent years, the orientation of the lateral semicircular canal (LSC) has been regularly used to determine skull orientations for comparative purposes in studies of non-avian dinosaurs. Such orientations have been inferred based on fixing the LSC to a common set of coordinates (parallel to the Earth's horizon), given that the orientation to gravity of this sensory system is assumed constant among taxa. Under this assumption, the LSC is used as a baseline (a reference system) both to estimate how the animals held their heads and to describe craniofacial variation among dinosaurs. However, the available data in living birds (extant saurischian dinosaurs) suggests that the orientation of the LSC in non-avian saurischian dinosaurs could have been very variable and taxon-specific. If such were the case, using the LSC as a comparative reference system would cause inappropriate visual perceptions of craniofacial organization, leading to significant descriptive inconsistencies among taxa. Here, we used Procrustes methods (Geometric Morphometrics), a suite of analytical tools that compares morphology on the basis of shared landmark homology, to show that the variability of LSC relative to skull landmarks is large (ca. 50°) and likely unpredictable, thus making it an inconsistent reference system for comparing and describing the skulls of saurischian (sauropodomorph and theropod) dinosaurs. In light of our results, we argue that the lateral semicircular canal is an inconsistent baseline for comparative studies of craniofacial morphology and that geometric morphometrics provides a more consistent method for establishing anatomical comparisons among dinosaur taxa.

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29 Introduction

30 Anatomical reference systems determining the spatial context by which different  
31 parts of an animal's body should be compared (horizontal and vertical axes) are  
32 essential for comparative anatomical and phylogenetic studies. In anthropology and  
33 paleoanthropology, multiple reference systems have been devised to that end, such as  
34 Broca's plane (the plane of the optic nerves) and the Frankfurt plane (the orbito-meatal  
35 plane) (Gould, 1981). Anatomical studies in primates also use Reid's baseline, a  
36 standard reference system in anthropometry that is particularly common in  
37 conventional radiography and computer tomography (CT) (Strait & Ross 1999).  
38 Historically, all these morphological reference systems have been established relative  
39 to a stereotyped head posture (when at rest or in alert) and Earth's gravity, yet not  
40 surprisingly, none of them is congruent to each other. In fact, when orthodontists use  
41 one reference framework, be it Reid's plane or the Frankfurt plane, the system is  
42 relatively stable because anatomical variation at an intra-specific (human) scale is  
43 small. However, important inconsistencies arise when extrapolating the use of these  
44 anatomical reference systems at larger taxonomic scales.

45 Lebedkin (1924) was the first to suggest that the lateral semicircular canal  
46 (LSC) within the inner ear could serve as a proxy to estimate at rest or alert head  
47 postures, and de Beer (1947) argued that angular deviations between the LSC and the  
48 Earth's horizon in such a stereotyped posture are small enough to support such  
49 assumption. This notwithstanding, de Beer also found important inconsistencies for this  
50 rule, since the method could not be applied to humans, in which the deviation of the  
51 orientation of the LSC and the Earth's horizon at such stereotype postures is nearly 37°  
52 (Fig. 1). Subsequently, the fact that many bird species show skull modifications similar  
53 to those of primates (Marugán-Lobón and Buscalioni, 2009), led Duijm (1951) to  
54 undertake an inter-specific study through direct observations on living birds. Like de  
55 Beer previously, Duijm's study also demonstrated that the craniofacial anatomy was  
56 best compared when skulls were oriented according to the animals' posture of alert.  
57 Nonetheless, this study also documented inconsistencies between the orientation of  
58 the LSC and that of the skull in such stereotyped posture—the LSC showed a broad  
59 rotational spectrum when the skulls were oriented in the alert posture (Figs 1b and 2).  
60 This notwithstanding, Duijm endorsed the use of a horizontal placement of the LSC as  
61 an anatomical proxy to the way in which birds hold their heads in such postures. Just  
62 as de Beer had reasoned previously, Duijm advocated that the angular deviation of the  
63 LSC from a horizontal position (approximately -19° to 30° relative to the horizon while  
64 the skull is in the alert position) was smaller than that of any other skull structure and  
65 that the mean orientation was close to 0° (Fig. 2).

66 De Beer and Duijm's seminal works were inspiring, and have been widely  
67 followed not just in the context of interpretations of how extinct animals held their heads  
68 but also as the reference for morphological comparisons (e.g., Rogers 1998, Sampson  
69 & Witmer 2007, Sereno et al. 2007, Evans 2006, Witmer & Ridgely 2009, Witmer et al.  
70 2008). Nonetheless, Taylor, Wedel & Naish (2009) rightfully argued that the latter use

71 might lead to descriptive inconsistencies. If the orientation of the LSC is thus potentially  
72 unpredictable and problematic as an anatomical reference system, is there an  
73 alternative approach that can allow anatomical comparisons of the skulls to be  
74 standardized? Here we argue that methods of mathematical shape analysis are  
75 suitable for that purpose, in particular the Procrustes methods.

76 Procrustes methods are widely applied in comparative morphology (Adams  
77 Slice & Rohlf, 2004) and more recently, they have been used as a tool to improve the  
78 comparative study of animal behavior by filtering out uninformative body postures  
79 (Fureix et al. 2011). In the field of morphological research, Procrustes methods are  
80 known as Geometric Morphometrics (GMM), and their effectiveness relies on the  
81 comparison of configurations of biologically definable—anatomically homologous—  
82 Cartesian coordinates of points (*a.k.a.* landmarks) involving mathematical operations  
83 rather than concepts rooted in biological intuition or classical morphology, such as the  
84 use of recognizable postures and fixed comparative baselines (Zelditch et al., 2012). To  
85 this end, GMM compares configurations of 2D and 3D biologically homologous  
86 landmarks within a common reference coordinate system (the statistically computed  
87 mean configuration; Chapman 1990, Rohlf & Slice 1990; Bookstein 1991, Adams, Slice  
88 & Rohlf 2004). Such a procedure is accomplished by a least-squares estimation of  
89 translation, rotation (posture), and scaling parameters that help to optimally  
90 superimpose the landmark configurations without altering their original topology.

91 Here, using GMM and a case study in saurischian dinosaurs, we assess  
92 whether there is any discrepancy between the orientation of skulls according to the  
93 LSC and that based on a system of coordinates provided by craniofacial landmark  
94 homology. In light of our findings, we argue that landmark homology provides a more  
95 consistent and easier to standardize anatomical reference system for depicting and  
96 comparatively studying anatomical systems than do classic reference systems such as  
97 the orientation of the LSC.

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## 99 Materials and methods

100 We studied a sample of saurischian dinosaurs that embraces a broad range of  
101 skull shape disparity (Marcus, Hingst-Zaher & Zaher 2000) and thus, of potential  
102 semicircular canal orientations (Duijm 1951). Digital pictures corresponding to 16 taxa  
103 of saurischian dinosaurs and one extant crocodile in lateral view were studied in two  
104 dimensions (Table 1). CT-scan information on the orientation of the LSC was taken  
105 from the literature for only 10 of these skulls (Table 1). Additionally, the orientation of  
106 the LSC for the stork, while in alert posture, was taken from Duijm's data. On each  
107 specimen of the sample, we digitized the coordinates of 5 homologous landmarks (Fig.  
108 3a; see caption for their anatomical description). The landmark configurations  
109 homogeneously cover the entire skull (facial skeleton and cranium) to guarantee that

110 additional landmarks will not lead to significant differences in the results  
111 (Marugán-Lobón & Buscalioni 2004). Landmarks were selected to be visible across a  
112 variety of taxa with disparate cranial anatomy.

113 The landmark coordinates were aligned by a Generalized Procrustes Analysis  
114 (GPA) (Gower, 1973) using the program Morpheus et al. (Slice 2002). This method  
115 compares 2D or 3D configurations of landmarks within a common reference system  
116 (Fig. 3b), which is statistically estimated as the mean from the superimposition of the  
117 configurations after optimally minimizing the distances between homologous  
118 landmarks. This optimal superimposition is performed by translating, scaling and  
119 rotating the coordinates without altering the original distances between the landmark  
120 configurations (i.e., the topology of the configuration). The configurations are first  
121 brought to a common coordinate system that by consensus is the average  
122 configuration (or Grand mean). The configurations are then rigidly scaled to the same  
123 size (i.e., isometric scaling), and they are subsequently rotated over the shared  
124 geodesic centroid. The residual mismatch and irreducible distance among homologous  
125 landmarks after the Procrustes alignment is due to the geometric differences between  
126 the configurations (after translation, rotation and scaling have been filtered out), and is  
127 known as Procrustes shape data; such data is suitable for further multivariate analyses.  
128 Importantly, this newly obtained data is 'invariant' to (i.e., it does not possess any  
129 information about) translation, scale and rotation (i.e., posture) (see also; Slice 2007,  
130 Mitteroecker and Gunz, 2009, Viscosi and Cardini 2011, Zelditch et al. 2012).

131 The raw data of each skull posture was digitized with the LSC set at 0° (LSC  
132 horizontal, in those specimens for whom this information was available, see Table 1).  
133 Once the configurations have been aligned with GMM, any change in the orientation of  
134 the skull corresponds to an angular change in the orientation of the LSC and can be  
135 measured. To be consistent with Duijm's (1951) data, we maintained the author's  
136 notation of positive and negative values above and below the horizon, respectively.  
137 Importantly, the Procrustes data is invariant to translation, scale and rotation, the way  
138 to depict the superimposed configurations is arbitrary, but a logical orientation is often  
139 selected to neatly illustrate the results. Here we chose to orient the superimposed data  
140 according to the skull of *Crocodylus johnstoni*, digitized as if resting horizontally with its  
141 ventral surface on a flat surface (Fig. 2a) (Witmer et al. 2008). Given that the body plan  
142 of *Crocodylus johnstoni* is characteristically dorso-ventrally compressed, there is little  
143 doubt about what is dorsal, ventral, anterior or posterior relative to Earth's spatial  
144 directions (i.e., the vector of gravity and the horizon). Thus, such selection guarantees  
145 that the dinosaur landmarks, once superimposed by the Procrustes method, will  
146 unambiguously share the same spatial coordinates relative to the Earth's axes.  
147 Furthermore, in such a posture the orientation of the LSC of *Crocodylus johnstoni* is  
148 nearly co-planar with the horizon (Witmer et al. 2008). Therefore, any angular  
149 differences in the semicircular canal's orientation that may result from the Procrustes

150 superimposition (differences in the orientation of the LSC of each dinosaur taxa with  
151 respect to the horizontal one of *Crocodylus*) can be easily visualized.

152 In order to compare the geometric similarity between skulls we used a phenetic  
153 clustering algorithm (the unweighted pair group method, UPGMA (Rohlf & Sokal 1981))  
154 on the shape data, and compared this result with a UPGMA classification of the  
155 landmark configurations using the orientation of the LSC as a reference system (i.e.,  
156 recovering rotational—postural—information).

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## 158 Results

159 When the skulls are oriented relative to the Procrustes mean, the average  
160 orientation of the LSC with respect to the horizon is approximately  $-9^\circ$  (Std.  
161 Dev.= $16.96^\circ$ ; Confidence interval  $\pm 95\%=[11.67; 29.31]$ ; Fig. 3), although this mean  
162 value may not be particularly informative given that deviations involve complementary  
163 (i.e., positive or negative) orientations (Mardia, 1972). Comparing the extremes (the  
164 prototyped skull of the rebbachisaurid *Nigersaurus* and the theropod *Incisivosaurus*),  
165 the total range of degrees of deviation relative to the horizon is approximately  $55.6^\circ$   
166 (Range [Maximum= $-52^\circ$ , Minimum= $4.5^\circ$ ]), which is nearly equivalent to the range of  
167 LSC orientations documented for living birds when their head is in the alert posture  
168 (approximately  $50^\circ$  [2]; compare Figs. 2 and 4). The rebbachisaurid sauropod  
169 *Nigersaurus* is an outlier yielding a notable negative skewness to the distribution of  
170 LSC in saurischians.

171 While after the Procrustes superposition some skull postures do not differ much  
172 from the postures in which the LSC is horizontal, others differ more notably, and this is  
173 obviously due to the fluctuating orientations of their LSCs relative to their craniofacial  
174 geometry (Table 1). For instance, the skulls of *Tyrannosaurus* and *Majungasaurus*  
175 remain in a nearly identical position (i.e., its LSC remains nearly parallel—less than  $1^\circ$   
176 —to the ground in both instances). In *Allosaurus* and *Camarasaurus* there is also a  
177 very slight deviation from their original posture ( $2.3^\circ$  and  $-4.0^\circ$ , respectively), whereas in  
178 the owl and in *Diplodocus* this deviation is definitively higher ( $-9.3^\circ$  and  $-12.5^\circ$ ). In other  
179 skulls such as those of *Nanotyrannus* and *Nigersaurus* (both largely reconstructed  
180 fossils) the orientation of the canals changes significantly, ( $-22.3^\circ$  and  $-51.0^\circ$ ,  
181 respectively). Although there is a tendency in the sampled dinosaurs to pitch up the  
182 LSC relative to the horizon, in *Incisivosaurus* the LSC is pitched down  $4.5^\circ$  (Table 1).

183 The phenetic clustering algorithm (UPGMA) on the Procrustes shape data finds  
184 two well defined groups differentiable on the basis of morphology, i.e., the orientation of  
185 the rostrum and the location of the nares (Fig. 5, left column). All sauropods (including  
186 the prototyped skull of *Nigersaurus*) group together, and a parallel association happens  
187 with the skulls of the two tyrannosaurids in the sample (*Tyrannosaurus* and  
188 *Nanotyrannus*, the latter possibly a juvenile *T. rex*), which are also morphologically very

189 similar to each other. However, all these congruent taxonomic groupings made by the  
190 UPGMA on the Procrustes shape data are dispersed if skulls are compared by  
191 re-setting the orientation of the landmarks so the LSC is at 0°; Fig. 5, right column).

192

193 Discussion

194         Orienting skulls for anatomical comparison using the LSC generally requires  
195 both the preservation of the canals, as well as CT scan data of sufficient quality to  
196 reliably delineate these structures. These criteria are not easily or often met  
197 (particularly for fossils), and thus finding skull orientations for comparative purposes  
198 using Procrustes methods are more practical in the broadest range of cases. On the  
199 other hand, the obtained results stress that the orientation of the LSC of saurischian  
200 dinosaurs varies greatly relative to the rest of the skull (Fig. 4) and that such variability  
201 is independent of skull geometry (i.e., as in other tetrapods, including birds, there is no  
202 fixed alignment between the orientation of the LSC and skull morphology; David et al.  
203 2010). When combined with information from living birds (Duijm, 1951), our results also  
204 show that a broad spectrum of LSC orientation remained relatively constant for at least  
205 the last 200 million years of dinosaur evolutionary history. In light of this, it is unlikely  
206 that the LSC serves as a consistent baseline to describe or compare craniofacial  
207 morphologies among these animals. Moreover, its use may lead to heterogeneous  
208 anatomical descriptions (Fig. 4), hence introducing inconsistencies when scoring  
209 character-states in cladistic analyses and inferring paleobiological attributes.

210         Before the establishment of the Procrustes methods, one way to register all  
211 landmark configurations to a common reference system (i.e., to standardize a set of  
212 coordinates for location, orientation, and size for comparative purposes) was to use the  
213 Two-point registration method (Bookstein 1991), which establishes a fixed baseline  
214 between two landmarks. It was soon realized that truly invariant landmarks are  
215 extremely rare in complex forms, which entails that fixing any given two landmark  
216 locations to zero variance (i.e., as a baseline) inevitably transfers randomly their true  
217 variation throughout the entire system. This situation even worsens if the selected  
218 landmarks are too close, such as the two points that would define the plane of a LSC. A  
219 very similar situation takes place when establishing the LSC as a reference system.  
220 When a skull is oriented on the basis of aligning the labyrinth to a fixed set of  
221 coordinates (i.e., a horizontal LSC), the orientation of the LSC (with all its variability  
222 relative to other skull structures) is transferred to the orientation of the entire skull,  
223 resulting in an equivocal perception of the skull's geometry (i.e., confounding  
224 anatomical spatial directions across taxa). For example, using the LSC as a reference  
225 system, Sereno et al. (2007) envisioned the prototyped skull of the rebbachisaurid  
226 *Nigersaurus* as a very unusual animal because, among other morphological  
227 particularities, its rostrum pointed almost vertically towards the ground (Figs. 4 and 5).  
228 However, when the skull of *Nigersaurus* is oriented according to its craniofacial

229 landmark homology with Procrustes methods, its skull geometry is comparable to that  
230 of other sauropods (Fig. 5). Objectively, when viewed from the perspective of  
231 comparative homology, it is the orientation of the labyrinth of *Nigersaurus* (not the head  
232 posture or its craniofacial structure) that is unusual among other saurischians.  
233 Furthermore, given that the development of the semicircular canals has a strong  
234 genetic component (Jeffery & Spoor 2004), it is plausible to assume that the orientation  
235 of the LSC is case-specific, although this needs to be further tested in extant taxa.

236         The use of the LSC as a reference system assumes that the orientation of the  
237 semicircular canal matches the coordinate system defined by Earth's gravity (Vinchon  
238 et al. 2007), presupposing that every species' stereotyped head posture (at rest or in  
239 alert) will be congruent with the vertical axis via the orientation of the LSC (de Beer  
240 1947). However, the fact that in every dinosaurian taxon the LSC does not share the  
241 same spatial orientation with respect to Procrustes-aligned craniofacial landmarks and  
242 to the horizon challenges that assumption. Such an assumption is also inconsistent  
243 with physiological evidence related to vestibular control, which indicates that LSC  
244 biomechanics sense angular acceleration stimuli and respond to head motion (David et  
245 al., 2010; Fitzpatrick, Butler & Day 2006). In effect, there is a documented tendency in  
246 tetrapods to misalign the semicircular canals with the Earth's axes, which  
247 physiologically helps all canals to receive a component of angular acceleration during  
248 horizontal head rotations and thus, to actively participate in producing horizontal  
249 compensatory movements during motion (Cohen & Raphan 2004). Furthermore, the  
250 characteristic physical organization of the labyrinth in three dimensions renders the  
251 canals biomechanically insensitive to the direction of gravity (Rabbitt, Damiano & Grant  
252 2004) and that function is restricted to the otolith within the vestibular system.

253         In most anatomical descriptions of archosaur skulls, the plane of reference used  
254 to align skulls for comparison is not specified. Judging by figures in many of these  
255 studies, this is most typically done by orienting the maxillary tooth row horizontally  
256 (e.g., Sampson et al., 2010; Horner and Goodwin, 2009; Campione and Evans, 2012).  
257 In order to be consistent in anatomical descriptions, here we thereby recommend that,  
258 (1) the frame of reference for aligning anatomical axes should be stated, and (2) that  
259 the axes obtained using the geometric morphometric methods described here are  
260 easily standardized and reproducible, either in 2D or 3D. Whereas our results do not  
261 challenge the possibility of estimating how fossil organisms held their heads, an issue  
262 that needs to be further studied in living organisms, they clearly show that the  
263 horizontal alignment of the LSC cannot provide a consistent anatomical reference  
264 system for skull comparisons in dinosaurs, and possibly in other tetrapods. Instead, we  
265 argue that by analysing homologous morphological landmarks, Geometric  
266 Morphometrics offers a more consistent anatomical reference system, one that is  
267 independent of posture and purely based on homologous anatomical variables.

268

269 Acknowledgements

270 We thank C. Mehling (American Museum of Natural History, New York) and D. Unwin  
271 (Museum für Naturkunde, Berlin) for specimen access and A. Balanoff for the CTs  
272 scans of *Incisivosaurus*. We are also grateful to S. Abramowicz and W. Evans for  
273 creating the art work and editing the manuscript, respectively. J. Lobón-Cerviá, A.  
274 Buscalioni, and N. Martínez-Abadías provided helpful comments to the manuscript and  
275 L. Witmer and M. D’Emic reviewed an earlier version of the paper—all these  
276 discussions strengthened our study.  
277

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401 Figure Legends

402 Figure 1. Differences in reference systems in skulls. (A) In the human skull there is a  
403  $30^\circ$  difference between the Frankfurt plane and that of the LSC, thus yielding  
404 substantially different head orientations (from de Beer, 1947). (B) When a stork is in  
405 alert its LSC is oriented  $19^\circ$  above the horizon, thus when putting the LSC at  $0^\circ$   
406 (horizontal) head posture differs from its alert posture (from Duijm, 1951).

407

408 Figure 2. Schematic depiction of the semicircular canals and polar histogram of LSC  
409 orientations in extant birds, measured in alert posture. The semicircular canals are  
410 three interconnected tubes that define three nearly-orthogonal planes, and are part of  
411 the bony labyrinth of the inner ear. The measurements were obtained relative to the  
412 Earth's horizon by Duijm (1951) when the birds were in a stereotyped alert posture at a  
413 zoological garden ( $n=29$ ). Notice that the orientation of the lagena and the cochlear  
414 duct in the vestibular apparatus normally varies among species; in our scheme they are  
415 steady for simplicity. Although the average orientation was close to zero, LSC angles  
416 when birds are in alert approximately ranges from  $-19^\circ$  to  $30^\circ$  relative to the horizon.

417

418 Figure 3. Landmarks and Procrustes alignment of dinosaur skulls. (A) Example of the  
419 configuration of  $p=5$  landmarks in lateral view of the skull of a crocodile (*C. johnstoni*),  
420 as it leans on its mandibles over a flat surface. Landmarks are: 1-tip of premaxilla,  
421 2-margin of nasal opening closer to tip of premaxilla, 3-margin of nasal opening further  
422 from tip of premaxilla, 4-junction between supraoccipital and parietal at cranial roof,  
423 5-mandibular articulation of quadrate. In this crocodile the orientation of the LSC  
424 relative to the horizon is  $\sim 0^\circ$  (Witmer et al., 2008). (B) Superimposed configurations of  
425 landmarks using Geometric Morphometrics (Generalized Procrustes methods, or GPA).  
426 The enlarged black landmarks correspond to the Procrustes mean (the consensus  
427 reference system). The x-y crosses at each landmark are depicted to illustrate the  
428 concomitant correspondence with the spatial directions determined by the  
429 morphological plan of the crocodile relative to the Earth's axes.

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431 Figure 4. Distribution of estimated measurements after Generalized Procrustes  
432 Analysis (GPA) of semicircular canal orientations for the studied dinosaur skulls. In the  
433 distribution, the maximal range of angular variance spans between the skull of  
434 *Nigersaurus* ( $\sim -52^\circ$ ) and that of *Incisivosaurus* ( $\sim -4.5^\circ$ ). The schematic skulls are shown  
435 in the posture obtained by the Procrustes alignment, and LSC orientations are

436 measured relative to the horizon and as the difference between  $0^\circ$  and the new GPA  
437 orientation. Obtained LSC orientations for all dinosaurs after GPA are listed in Table 1.

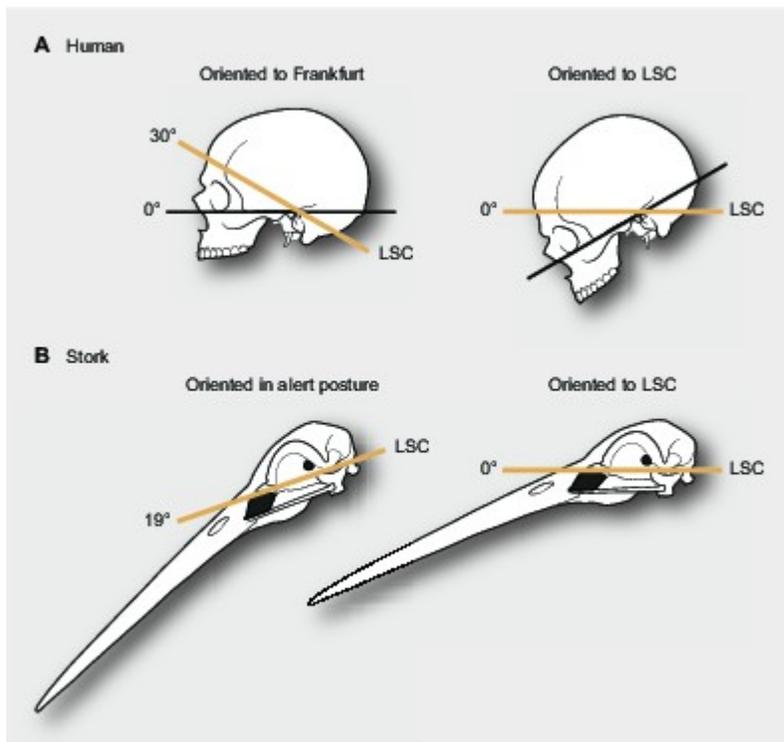
438

439 Figure 5. UPGMA phenograms grouping dinosaur skulls by geometric similarity.  
440 Separate columns illustrate the different skull postures obtained using Procrustes  
441 methods (left column) or by aligning the LSC with the horizon (right column). The  
442 branching diagram on the right column groups skulls comparing landmark data for  
443 which only translation and scale were filtered out, but not rotation (i.e., this data  
444 includes skull posture as morphological information, determined by the LSC set to  $0^\circ$ ).  
445 The large white dots at the nodes are highlighting cases of notable grouping  
446 differences, such as considering the skull geometry of *Nigersaurus* as that of either a  
447 sauropod (left) or a bizarre dinosaur (right), and that of *Nanotyrannus* (presumably a  
448 juvenile *T. rex*) as different from that of *Tyrannosaurus*. The grouping in the right  
449 column indicates that rotation is a main source of morphological difference among skull  
450 geometries. The numbered terminal branches denote the taxa listed in Table 1; the  
451 LSC orientation is known for those with an asterisk.

# Figure 1

Figure 1

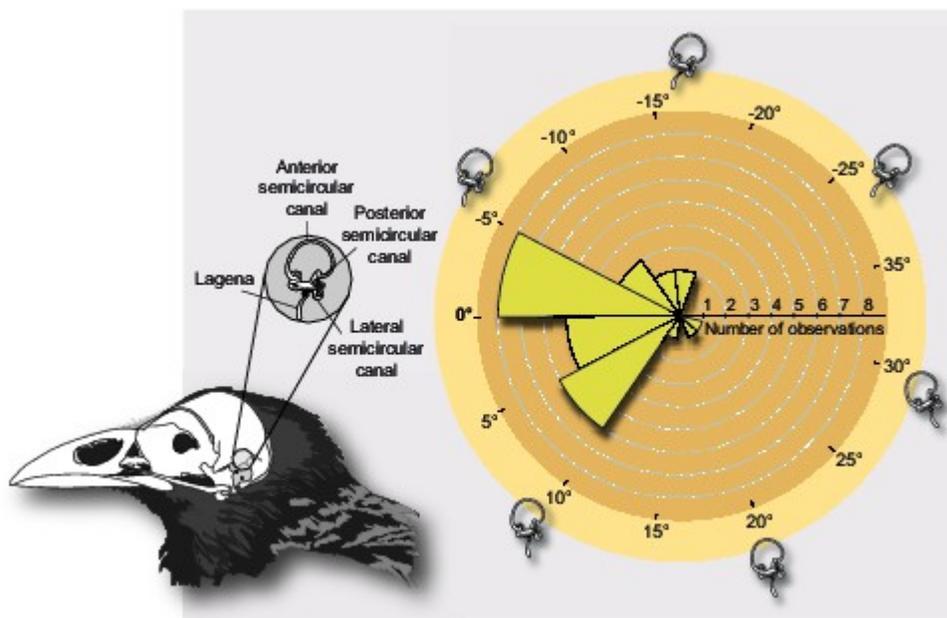
Differences in reference systems in skulls. (A) In the human skull there is a  $30^\circ$  difference between the Frankfurt plane and that of the LSC, thus yielding substantially different head orientations (from de Beer, 1947). (B) When a stork is in alert its LSC is oriented  $19^\circ$  above the horizon, thus when putting the LSC at  $0^\circ$  (horizontal) head posture differs from its alert posture (from Duijm, 1951).



## Figure 2

Figure 2

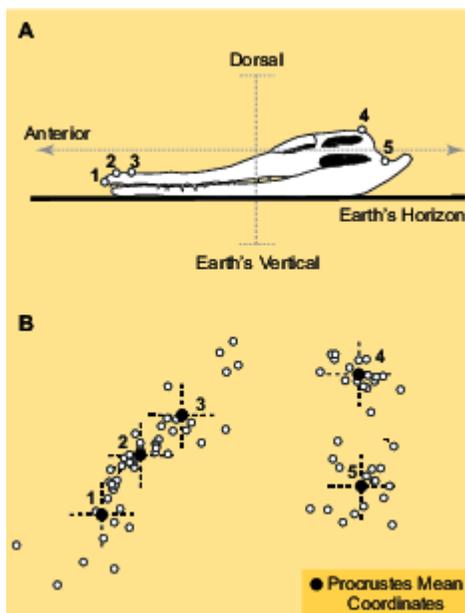
Schematic depiction of the semicircular canals and polar histogram of LSC orientations in extant birds, measured in alert posture. The semicircular canals are three interconnected tubes that define three nearly-orthogonal planes, and are part of the bony labyrinth of the inner ear. The measurements were obtained relative to the Earth's horizon by Duijm (1951) when the birds were in a stereotyped alert posture at a zoological garden ( $n=29$ ). Notice that the orientation of the lagena and the cochlear duct in the vestibular apparatus normally varies among species; in our scheme they are steady for simplicity. Although the average orientation was close to zero, LSC angles when birds are in alert approximately ranges from  $-19^\circ$  to  $30^\circ$  relative to the horizon.



## Figure 3

Figure 3

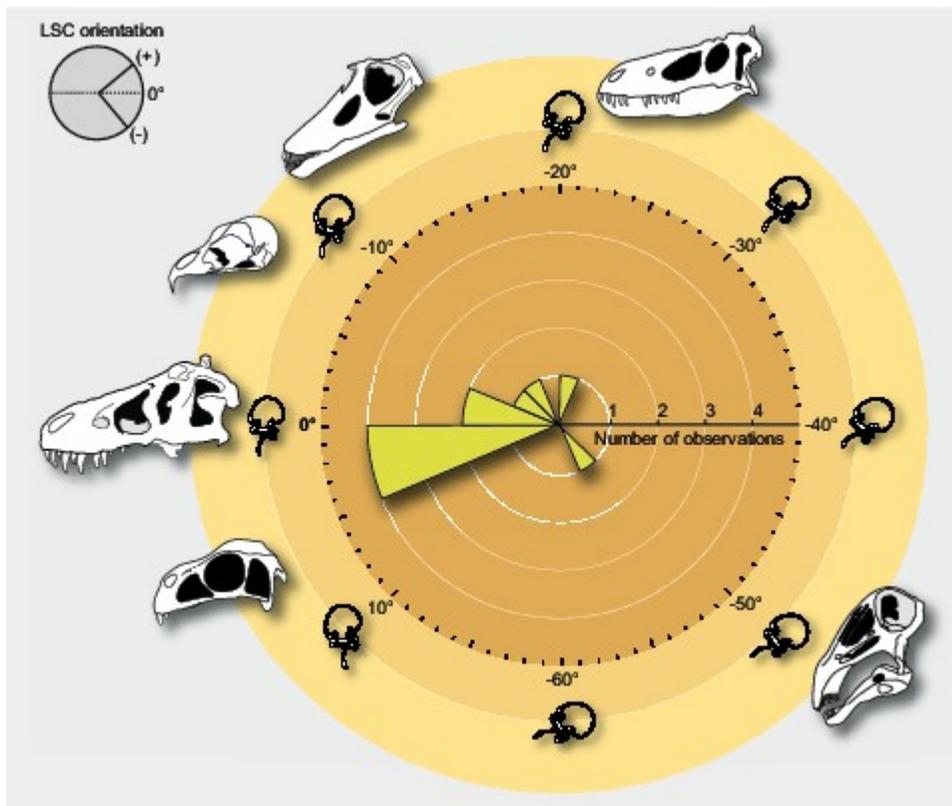
Landmarks and Procrustes alignment of dinosaur skulls. (A) Example of the configuration of  $p=5$  landmarks in lateral view of the skull of a crocodile (*C. johnstoni*), as it leans on its mandibles over a flat surface. Landmarks are: 1-tip of premaxilla, 2-margin of nasal opening closer to tip of premaxilla, 3-margin of nasal opening further from tip of premaxilla, 4-junction between supraoccipital and parietal at cranial roof, 5-mandibular articulation of quadrate. In this crocodile the orientation of the LSC relative to the horizon is  $\sim 0^\circ$  (Witmer et al., 2008). (B) Superimposed configurations of landmarks using Geometric Morphometrics (Generalized Procrustes methods, or GPA). The enlarged black landmarks correspond to the Procrustes mean (the consensus reference system). The x-y crosses at each landmark are depicted to illustrate the concomitant correspondence with the spatial directions determined by the morphological plan of the crocodile relative to the Earth's axes.



## Figure 4

Figure 4

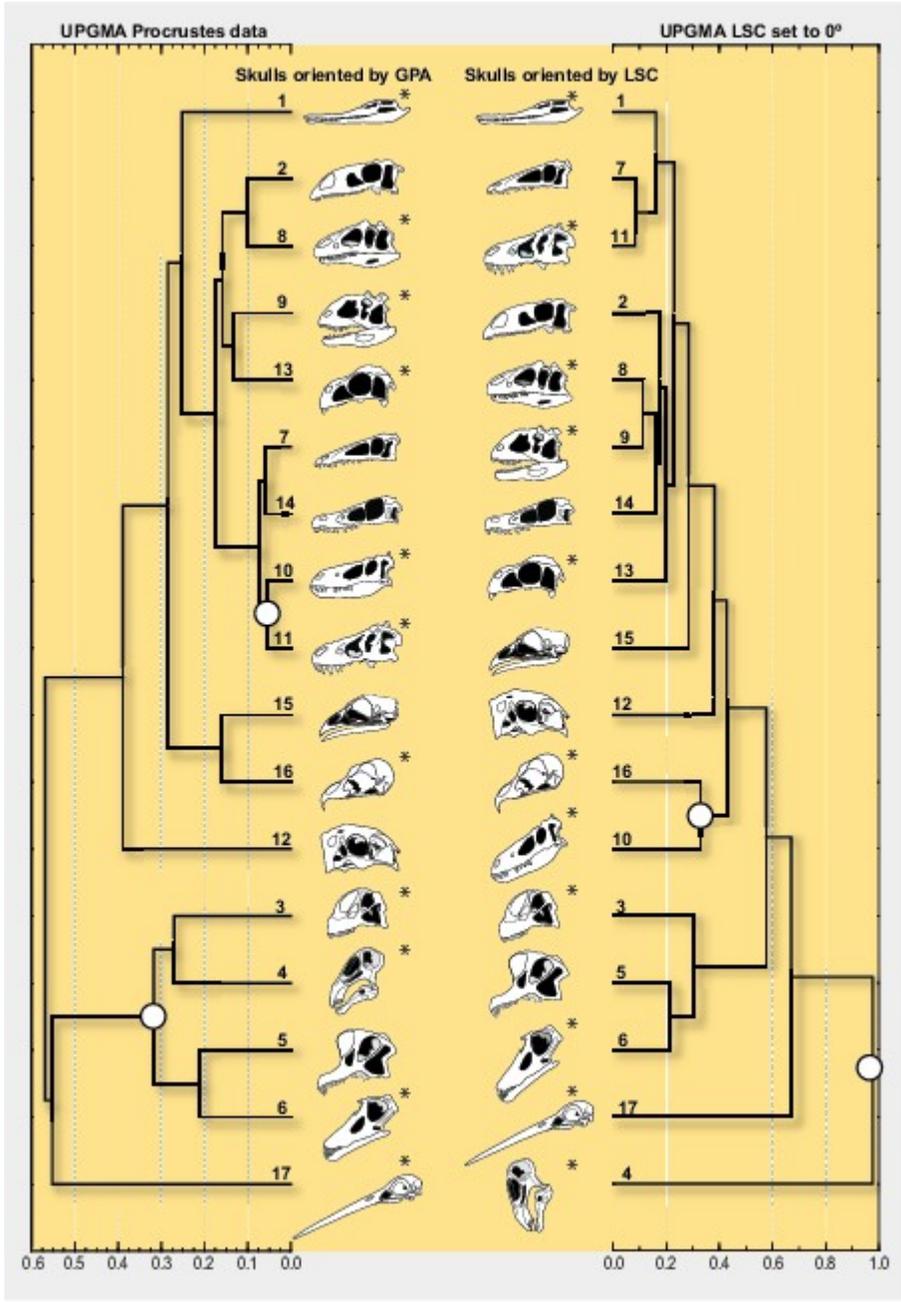
Distribution of estimated measurements after Generalized Procrustes Analysis (GPA) of semicircular canal orientations for the studied dinosaur skulls. In the distribution, the maximal range of angular variance spans between the skull of *Nigersaurus* ( $\sim -52^\circ$ ) and that of *Incisivosaurus* ( $\sim 4.5^\circ$ ). The schematic skulls are shown in the posture obtained by the Procrustes alignment, and LSC orientations are measured relative to the horizon and as the difference between  $0^\circ$  and the new GPA orientation. Obtained LSC orientations for all dinosaurs after GPA are listed in Table 1.



## Figure 5

Figure 5

UPGMA phenograms grouping dinosaur skulls by geometric similarity. Separate columns illustrate the different skull postures obtained using Procrustes methods (left column) or by aligning the LSC with the horizon (right column). The branching diagram on the right column groups skulls comparing landmark data for which only translation and scale were filtered out, but not rotation (i.e., this data includes skull posture as morphological information, determined by the LSC set to 0°). The large white dots at the nodes are highlighting cases of notable grouping differences, such as considering the skull geometry of *Nigersaurus* as that of either a sauropod (left) or a bizarre dinosaur (right), and that of *Nanotyrannus* (presumably a juvenile *T. rex*) as different from that of *Tyrannosaurus*. The grouping in the right column indicates that rotation is a main source of morphological difference among skull geometries. The numbered terminal branches denote the taxa listed in Table 1; the LSC orientation is known for those with an asterisk.



## **Table 1** (on next page)

Table 1

Studied specimens, source and GPA LSC orientations.

**Table 1.** Studied specimens, source and GPA LSC orientations

Specimen	ID/Source	LSC
1 <i>Crocodylus johnstoni</i>	OUVC 10425 <sup>[15]</sup>	0°
2 <i>Plateosaurus longiceps</i>	MB.R.1937	-
3 <i>Camarasaurus lentus</i>	CM 11338 <sup>[15]</sup>	-4°
4 <i>Nigersaurus taqueti</i>	MNN GAD512 <sup>[12]</sup>	-51.1°
5 <i>Giraffatitan brancaii</i>	HMB t1 ( S-II)	-
6 <i>Diplodocus longus</i>	CM 11161 <sup>[15]</sup>	-12.5°
7 <i>Coelophysis bauri</i>	AMNH 480	-
8 <i>Allosaurus fragilis</i>	UMNH VP 18050 <sup>[14]</sup>	2.3°
9 <i>Majungasaurus crenatissimus</i>	FMNH PR2100 <sup>[11]</sup>	0.2°
10 Juvenile <i>T. rex</i> ( <i>Nannotyrannus lancensis</i> )	CMNH 7541 <sup>[14]</sup>	-22.3
11 <i>Tyrannosaurus rex</i>	AMNH 5117 <sup>[14]</sup>	-1.1°
12 <i>Citipati osmolskae</i>	IGM 100/978	-
13 <i>Incisivosaurus gauthieri</i>	IVPP V 13326	4.6
14 <i>Velociraptor mongoliensis</i>	AMNH FR6516	-
15 <i>Gallus sp</i>	ZMB 77	-
16 <i>Bubo virginianus</i>	OUVC 10220 <sup>[15]</sup>	-9.3°
17 <i>Ciconia ciconia</i>	ZMB 253 <sup>[2]</sup>	3.0°

Institutional abbreviations: AMNH; American Museum of Natural History; HMB, MBR and ZMB, Humboldt Museum für Naturkunde; CM=Carnegie Museum; IVPP=Institute of Vertebrate Paleontology and Paleoanthropology; MNN, Musée National du Niger; FMNH, Field Museum of Natural History; OUVC, Ohio University Vertebrate Collections; IGM, Mongolian Institute of Geology; CMNH, Cleveland Museum of Natural History.