

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, the lateral semicircular canal is an inconsistent baseline for comparative studies of craniofacial morphology in dinosaurs.

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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 entirely congruent to the others. When orthodontists use
41 one reference framework, be it Reid's plane or the Frankfurt plane, the system is
42 fortunately relatively stable because anatomical variation at an intra-specific (human)
43 scale is small. However, important inconsistencies arise when extrapolating the use of
44 these anatomical reference systems at larger taxonomic scales.

45 Lebedkin (1924) was the first to suggest that the lateral semicircular canal (LSC) within
46 the inner ear could serve as a proxy to estimate at rest or alert head postures, and de
47 Beer (1947) argued that angular deviations between the LSC and the Earth's horizon in
48 such a stereotyped posture are small enough to support such assumption. This
49 notwithstanding, de Beer also found important inconsistencies for this rule, since the
50 method could not be applied to humans, in which the deviation of the orientation of the
51 LSC and the Earth's horizon at such stereotype postures is nearly 37° (Fig. 1).
52 Subsequently, striking differences in the position of the labyrinths in the skulls of
53 different species of birds led van der Klaauw (1948) to point out the possibility of a
54 functional relationship between the position of the labyrinth and a stereotyped head
55 posture. To test this hypothesis, Duijm (1951) undertook an inter-specific study through
56 direct observations on living birds, and like de Beer previously, demonstrated that the
57 craniofacial anatomy was best compared when skulls were oriented according to the
58 animals' alert posture (Marugán-Lobón and Buscalioni, 2006). Nonetheless, this study
59 also documented inconsistencies between the orientation of the LSC and that of the
60 skull in such a stereotyped posture—the LSC showed a broad rotational spectrum
61 when the skulls were oriented in the alert posture (Figs 1b and 2). This
62 notwithstanding, the author endorsed the use of a horizontal placement of the LSC as
63 an anatomical proxy for the way in which birds hold their heads in such postures. Just
64 as de Beer had reasoned previously, Duijm advocated that the angular deviation of the
65 LSC from a horizontal position (approximately -19° to 30° relative to the horizon while
66 the skull is in the alert position) was smaller than that of any other skull structure and
67 that the mean orientation was close to 0° (Fig. 2).

68 De Beer and Duijm's seminal works were inspiring, and have been widely followed not
69 just in the context of interpretations of how extinct animals held their heads but also as
70 a reference system for descriptive morphology and anatomical comparisons (e.g.,
71 Rogers 1998, Sampson & Witmer 2007, Sereno et al. 2007, Evans 2006, Witmer &
72 Ridgely 2009, Witmer et al. 2008). For instance, using the orientation of the LSC
73 Sereno et al. (2007) estimated the 'alert' head posture of the rebbachisaurid
74 *Nigersaurus*, discussing that this animal's head was bizarre because its face was

75 oriented vertical to the ground. However, the estimation of head posture from the LSC
76 is very imprecise (Duijm 1951) and if this is used as a reference system, it can lead to
77 descriptive inconsistencies, as Taylor, Wedel & Naish (2009) rightfully argued. Take the
78 human head as an example; using the LSC as a reference system (Fig. 1) one would
79 describe the anatomy of the human skull bent forwards and downwards, as if the
80 person looked on to the ground at a point one or two meters away (Girard 1923), yet
81 clearly, the human face is not anatomically sloped downwards. Implicitly, all these
82 comparisons entail that the LSC is oriented differently relative to the components of the
83 human skull, and that such may likely be the case of the sauropod *Nigersaurus*. Thus,
84 if the orientation of the LSC is potentially unpredictable and problematic as an
85 anatomical reference system, is there an alternative approach that can allow
86 anatomical comparisons of the skulls to be standardized? Here we argue that methods
87 of mathematical shape analysis are suitable for that purpose, in particular the
88 Procrustes methods of geometric morphometrics.

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

104 Here, using GM and a case study in saurischian dinosaurs, we assess whether
105 there is any discrepancy between the orientation of skulls according to the LSC and
106 that based on a system of coordinates provided by craniofacial landmark homology. In
107 light of our findings, we argue that landmark homology provides a more consistent and
108 easier to standardize anatomical reference system for depicting and comparatively
109 studying anatomical systems than do classic reference systems such as the orientation
110 of the LSC.

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112 Materials and methods

113 When comparing the position of the labyrinth in the skulls of different birds, one
114 finds striking differences, and Duijm's (1951) experiment aimed at testing if these
115 differences in the orientation of the LSC are related to differences in head posture (Van

116 der Klaauw 1948). The experiment involved three steps: (1) determining a stereotyped
117 head posture in live birds, (2) measuring and describing skull morphologies in the
118 stereotyped posture, and finally (3) testing if such measurements allowed estimation of
119 the stereotyped posture from the orientation of the LSC (i.e., if there is a relationship
120 between LSC orientation and head posture). The first step involved measuring the
121 orientation of the head in several species of birds at the Amsterdam's zoo and in the
122 field. These measurements were performed with binoculars equipped with a graduated
123 arc in the lenses, a plumb-rule (used to test verticality), and a hairline to indicate the
124 horizon. The baseline in the animal's head was the ventral edge of the beak. The
125 second step was to replicate the observed alert head posture of the studied species
126 ($n=32$) in the lab, and it was achieved by reorienting the beaks of their respective skulls
127 to the corresponding degrees measured in the stereotyped alert posture, relative to the
128 horizon. Then, the skulls were dissected through the midline, and the orientations of
129 the cranial floor, the clivus (i.e., the basioccipital bone), the foramen magnum, and the
130 LSC, were all measured and analyzed. The third step focused on discussing the
131 observed variability in orientation of the LSC in the stereotyped alert posture, which
132 was less random (i.e., apparently more normally distributed) than that of the other
133 variables, yet highly variable between extremes (ca. 50°). In the original paper, all of
134 these data are provided as skull sketches of each species with labeled lines denoting
135 the angular orientation of the skull structures in the specific alert posture (Duijm 1951;
136 Figure 3, p. 208). We recovered the angular data and generated Fig. 1b (the stork's
137 head posture in alert), and Fig. 2 (polar histogram). To this end, we scanned that figure
138 with a high-resolution flatbed scanner (at 300ppp) and measured the schemes using
139 the digital protractor utility of TPSdig2 (2.16; Rohlf 2010).

140 We studied a sample of saurischian dinosaurs that embraces a broad range of
141 skull shape disparity (Marcus, Hingst-Zaher & Zaher 2000) and thus, of potential
142 semicircular canal orientations (Duijm 1951). Digital pictures corresponding to 16 taxa
143 of saurischian dinosaurs and one extant crocodile in lateral view were studied in two
144 dimensions (Table 1). CT-scan information on the orientation of the LSC was taken
145 from the literature for only 10 of these skulls (Table 1). Additionally, the orientation of
146 the LSC for the stork, while in alert posture, was taken from Duijm's data. On each
147 specimen in the sample, we digitized the coordinates of 5 homologous landmarks (Fig.
148 3a; see caption for their anatomical description). The landmark configurations
149 homogeneously cover the entire skull (facial skeleton and cranium) to guarantee that
150 additional landmarks will not lead to significant differences in the results
151 (Marugán-Lobón & Buscalioni 2004). Landmarks were selected to be visible across a
152 variety of taxa with disparate cranial anatomy. Ideally, the landmarks should be
153 coplanar in 2D to avoid the effect of foreshortening, and our choice of coordinates is
154 significantly close to this requirement, as it is on most studies of skull geometry that
155 use GM. The only exception is landmark 4, but the variation of this coordinate should
156 not alter the results since it is anatomically medial and sagittal, and therefore restricted

157 to vary only in a single 2D plane, comparable to that of the rest of landmarks (i.e., it will
158 not change coronally).

159 The landmark coordinates were aligned by a Generalized Procrustes Analysis
160 (Gower, 1973) using the program Morphue et al. (Slice 2002). This method is the
161 standard in GM and allows comparison of 2D or 3D configurations of landmarks within
162 a common reference system (Fig. 3b), which is statistically estimated as the mean from
163 the superimposition of the configurations after optimally minimizing the distances
164 between homologous landmarks. This optimal superimposition is performed by
165 translating, scaling and rotating the coordinates without altering the original distances
166 between the landmarks (i.e., the topology of the configuration). The configurations are
167 first brought to a common coordinate system that by consensus is the average
168 configuration (or Grand Mean). The configurations are then rigidly scaled to the same
169 size (i.e., isometric scaling), and they are subsequently rotated over the shared
170 geodesic centroid. The residual mismatch and irreducible distance among homologous
171 landmarks after the Procrustes alignment is due to the geometric differences between
172 the configurations (after translation, rotation and scaling have been filtered out), and is
173 known as Procrustes shape data; such data is suitable for further multivariate analyses.
174 Importantly, these newly obtained data are 'invariant' to (i.e., it does not possess any
175 information about) translation, scale and rotation (i.e., posture) (see also; Slice 2007,
176 Mitteroecker and Gunz, 2009, Viscosi and Cardini 2011, Zelditch et al. 2012).

177 In most cases, the landmarks were digitized in lateral view in arbitrary
178 orientations. However, in those specimens for which the LSC orientation within the skull
179 was known, the landmark data were digitized with the LSC set at 0° (i.e., the LSC
180 horizontal, see Table 1). Once the configurations have been aligned with GM any
181 change in the orientation of the latter skulls corresponds to an angular change in the
182 orientation of the LSC and can be measured. To be consistent with Duijm's (1951) data,
183 we maintained the author's notation of positive and negative values above and below
184 the horizon, respectively. Importantly, the Procrustes data is invariant to translation,
185 scale and rotation, and the way to depict the superimposed configurations is arbitrary. A
186 logical orientation thus is often selected to neatly illustrate the results. Here we chose
187 to orient the superimposed data according to the skull of *Crocodylus johnstoni*, digitized
188 as if resting horizontally with its ventral surface on a flat surface (Fig. 2a) (Witmer et al.
189 2008). Given that the body plan of *Crocodylus johnstoni* is characteristically
190 dorsoventrally compressed, there is little doubt about what is dorsal, ventral, anterior or
191 posterior relative to Earth's spatial directions (i.e., the vector of gravity and the horizon).
192 Thus, such selection guarantees that the dinosaur landmarks, once superimposed by
193 the Procrustes method, will nearly share the same spatial coordinates relative to the
194 Earth's axes. Furthermore, in such a posture the orientation of the LSC of *Crocodylus*
195 *johnstoni* is nearly co-planar with the horizon (Witmer et al. 2008). Therefore, any
196 angular differences in the semicircular canal's orientation that may result from the
197 Procrustes superimposition (differences in the orientation of the LSC of each dinosaur

198 taxon with respect to the horizontal one of *Crocodylus*) can be intuitively visualized. It is
199 important to stress, however, that this way of depicting the results is as arbitrary as any
200 other, it does not alter the results, and importantly, it does not have any functional
201 meaning (i.e., postural).

202 In order to compare the geometric similarity between skulls we used a phenetic
203 clustering algorithm (the unweighted pair group method, UPGMA (Rohlf & Sokal 1981))
204 on the shape data, and compared this result with a UPGMA classification of the
205 landmark configurations recovering rotational—postural—information (i.e., using the
206 orientation of the LSC as a reference system in those specimens where this
207 information was available).

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209 Results

210 When the skulls are oriented relative to the Procrustes mean, the average
211 orientation of the LSC with respect to the horizon is approximately -9° (Std.
212 Dev.= 16.96° ; Confidence interval $\pm 95\%=[11.67; 29.31]$; Fig. 3), although this mean
213 value may not be particularly informative given that deviations involve complementary
214 (i.e., positive or negative) orientations (Mardia, 1972). Comparing the extremes (the
215 prototyped skull of the rebbachisaurid *Nigersaurus* and the theropod *Incisivosaurus*),
216 the total range of degrees of deviation relative to the horizon is approximately 55.6°
217 (Range [Maximum= -52° , Minimum= 4.5°]), which is nearly equivalent to the range of
218 LSC orientations documented for living birds when their head is in the alert posture
219 (approximately 50° [2]; compare Figs. 2 and 4). The rebbachisaurid sauropod
220 *Nigersaurus* is an outlier yielding a notable negative skewness to the distribution of
221 LSC in saurischians. Although some skull postures after the Procrustes superposition
222 do not differ much from the postures in which the LSC is horizontal, others differ more
223 notably, and this is obviously due to the fluctuating orientations of their LSCs relative to
224 their craniofacial geometry (Table 1). For instance, the skulls of *Tyrannosaurus* and
225 *Majungasaurus* remain in a nearly identical position (i.e., its LSC remains nearly
226 parallel—less than 1° —to the ground in both instances). In *Allosaurus* and
227 *Camarasaurus* there is also a very slight deviation from their original posture (2.3° and
228 -4.0° , respectively), whereas in the owl and in *Diplodocus* this deviation is definitively
229 higher (-9.3° and -12.5°). In other skulls such as those of *Nanotyrannus* and
230 *Nigersaurus* (both largely reconstructed fossils) the orientation of the canals changes
231 significantly, (-22.3° and -51.0° , respectively). Although there is a tendency in the
232 sampled dinosaurs to pitch up the LSC relative to the horizon, in *Incisivosaurus* the
233 LSC is pitched down 4.5° (Table 1).

234 The phenetic clustering algorithm (UPGMA) on the Procrustes shape data finds
235 two well defined groups differentiable on the basis of morphology (i.e., the orientation
236 of the rostrum and the location of the nares) (Fig. 5, left column). All sauropods

237 (including the prototyped skull of *Nigersaurus*) group together, and a parallel
238 association happen with the skulls of the two tyrannosaurids in the sample
239 (*Tyrannosaurus* and *Nanotyrannus*, the latter possibly a juvenile *T. rex*), which are also
240 morphologically very similar to each other. However, all these congruent taxonomic
241 groupings made by the UPGMA on the Procrustes shape data are dispersed if skulls
242 are compared by re-setting the orientation of the landmarks so the LSC is at 0°; Fig. 5,
243 right column).

244

245 Discussion

246 Orienting skulls for anatomical comparison using the LSC generally requires
247 both the preservation of the canals, as well as CT scan data of sufficient quality to
248 reliably delineate these structures. These criteria are not easily or often met
249 (particularly for fossils), and thus finding skull orientations for comparative purposes
250 using GM is more practical in the broadest range of cases, when general skull
251 morphology can be restored. On the other hand, the obtained results stress that the
252 orientation of the LSC of saurischian dinosaurs varies greatly relative to the rest of the
253 skull (Fig. 4) and that such variability is independent of skull geometry (i.e., as in other
254 tetrapods, including birds, there is no fixed alignment between the orientation of the
255 LSC and skull morphology; David et al. 2010). When combined with information from
256 living birds (Duijm, 1951), our results also show that a broad spectrum of LSC
257 orientation remained relatively constant for at least the last 200 million years of
258 dinosaur evolutionary history. In light of this, it is unlikely that the LSC serves as a
259 consistent baseline to describe or compare craniofacial morphologies among these
260 animals. Moreover, its use may lead to heterogeneous anatomical descriptions (Fig. 4),
261 hence introducing inconsistencies when scoring character-states in cladistic analyses
262 and inferring paleobiological attributes.

263 Before the establishment in GM of the Procrustes methods based on the Least
264 Squares procedure, one way to register all landmark configurations to a common
265 reference system (i.e., to standardize a set of coordinates for location, orientation, and
266 size for comparative purposes) was to use the Two-point registration method
267 (Bookstein 1991), which establishes a fixed baseline between two landmarks. It was
268 soon realized that truly invariant landmarks are extremely rare in complex forms, which
269 entails that fixing any given two landmark locations to zero variance (i.e., as a baseline)
270 inevitably and randomly transfers their true variation throughout the entire system
271 (Zelditch et al. 2012). This situation even worsens if the selected landmarks are too
272 close, such as the two points that would define the plane of a LSC. A very similar
273 situation takes place when establishing the LSC as a reference system. When a skull is
274 oriented on the basis of aligning the labyrinth to a fixed set of coordinates (i.e., a
275 horizontal LSC), the orientation of the LSC (with all its variability relative to other skull
276 structures) is transferred to the orientation of the entire skull, resulting in an equivocal

277 perception of the skull's geometry (i.e., confounding anatomical spatial directions
278 across taxa). For example, using the LSC as a reference system, Sereno et al. (2007)
279 envisioned the prototyped skull of the rebbachisaurid *Nigersaurus* as a very unusual
280 animal because, among other morphological particularities, its rostrum pointed almost
281 vertically towards the ground (Figs. 4 and 5). However, when the skull of *Nigersaurus* is
282 oriented according to its craniofacial landmark homology with GM, its skull geometry is
283 comparable to that of other sauropods (Fig. 5). Objectively, when viewed from the
284 perspective of GM, it is the orientation of the labyrinth of *Nigersaurus* (not the head
285 posture or its craniofacial geometry) that is unusual among other saurischians.
286 Furthermore, given that the development of the semicircular canals has a strong
287 genetic component (Jeffery & Spoor 2004), it is plausible to assume that the orientation
288 of the LSC is case-specific (Billet et al. 2012), although this needs to be further tested
289 in extant taxa.

290 The use of the LSC as a reference system assumes that the orientation of the
291 semicircular canal matches the coordinate system defined by Earth's gravity (Vinchon
292 et al. 2007), presupposing that every species' stereotyped head posture (at rest or in
293 alert) will be congruent with the vertical axis via the orientation of the LSC (de Beer
294 1947). However, the fact that in every dinosaurian taxon the LSC does not share the
295 same spatial orientation with respect to Procrustes-aligned craniofacial landmarks and
296 to the horizon challenges that assumption. Such an assumption is also inconsistent
297 with physiological evidence related to vestibular control, which indicates that LSC
298 biomechanics sense angular acceleration stimuli and respond to head motion (David et
299 al., 2010; Fitzpatrick, Butler & Day 2006). In effect, there is a documented tendency in
300 tetrapods to misalign the semicircular canals with the Earth's axes, which
301 physiologically helps all canals to receive a component of angular acceleration during
302 horizontal head rotations and thus, to actively participate in producing horizontal
303 compensatory movements during motion (Cohen & Raphan 2004). This vestibular
304 control is jointly guided within the cerebellum through information provided by visual
305 pathways specialized to detect translational visual flow (Wylie, Bischof & Frost 1998;
306 Wylie and Frost 1999; Van de Water 2012). Furthermore, the characteristic physical
307 organization of the labyrinth in three dimensions renders the canals biomechanically
308 insensitive to the direction of gravity (Rabbitt, Damiano & Grant 2004) and that function
309 is restricted to the otolith within the vestibular system.

310 In most anatomical descriptions of archosaur skulls, the plane of reference used
311 to align skulls for comparison is not specified. Judging by figures in many of these
312 studies, this is most typically done by orienting the maxillary tooth row horizontally
313 (e.g., Sampson et al., 2010; Horner and Goodwin, 2009; Campione and Evans, 2012).
314 In order to be consistent in anatomical descriptions, here we recommend that, (1) the
315 frame of reference for aligning anatomical axes should be stated, and (2) that the axes
316 obtained using the geometric morphometric methods described here are easily
317 standardized and reproducible, either in 2D or 3D. Whereas our results do not address

318 the possibility of estimating how fossil organisms held their heads (i.e., how the head
319 was carried), an issue that needs to be further studied in living organisms, they clearly
320 show that the horizontal alignment of the LSC cannot provide a consistent anatomical
321 reference system for skull comparisons in dinosaurs, and possibly in other tetrapods.
322 Instead, we argue that by analyzing homologous morphological landmarks, Geometric
323 Morphometrics offers a more consistent anatomical reference system, one that is
324 independent of posture and purely based on homologous anatomical variables.

325

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482 Figure Legends

483 Figure 1. Differences in reference systems in skulls. (A) In the human skull there is a
484 30° difference between the Frankfurt plane and that of the LSC, thus yielding
485 substantially different head orientations (from de Beer, 1947). (B) When a stork is in
486 alert its LSC is oriented 19° above the horizon, thus when putting the LSC at 0°
487 (horizontal) head posture differs from its alert posture (from Duijm, 1951).

488

489 Figure 2. Schematic depiction of the semicircular canals and polar histogram of LSC
490 orientations in extant birds, measured in alert posture. The semicircular canals are
491 three interconnected tubes that define three nearly orthogonal planes, and are part of
492 the bony labyrinth of the inner ear. The measurements were obtained relative to the
493 Earth's horizon by Duijm (1951) when the birds were in a stereotyped alert posture at a
494 zoological garden (n=29). Notice that the orientation of the lagena and the cochlear
495 duct in the vestibular apparatus normally varies among species; in our scheme they are
496 steady for simplicity. Although the average orientation was close to zero, LSC angles
497 when birds are in alert approximately ranges from -19° to 30° relative to the horizon.

498

499 Figure 3. Landmarks and Procrustes alignment of dinosaur skulls. (A) Example of the
500 configuration of $p=5$ landmarks in lateral view of the skull of a crocodile (*C. johnstoni*),
501 as it leans on its mandibles over a flat surface. Landmarks are: 1-tip of premaxilla,
502 2-margin of nasal opening closer to tip of premaxilla, 3-margin of nasal opening further
503 from tip of premaxilla, 4-junction between supraoccipital and parietal at cranial roof,
504 5-mandibular articulation of quadrate. In this crocodile the orientation of the LSC
505 relative to the horizon is ~0° (Witmer et al., 2008). (B) Superimposed configurations of
506 landmarks using Geometric Morphometrics (Generalized Procrustes methods, or GPA).
507 The enlarged black landmarks correspond to the Procrustes mean (the consensus
508 reference system). The x-y crosses at each landmark are depicted to illustrate the
509 concomitant correspondence with the spatial directions determined by the
510 morphological plan of the crocodile relative to the Earth's axes. However, note that
511 these skull orientations do not necessarily correspond to head postures in the live
512 specimens.

513

514 Figure 4. Distribution of estimated measurements after Generalized Procrustes
515 Analysis (GPA) of semicircular canal orientations for the studied dinosaur skulls. In the
516 distribution, the maximal range of angular variance spans between the skull of
517 *Nigersaurus* (~-52°) and that of *Incisivosaurus* (~4.5°). The schematic skulls are shown
518 in the posture obtained by the Procrustes alignment, and LSC orientations are
519 measured relative to the horizon and as the difference between 0° and the new GPA
520 orientation. Obtained LSC orientations for all dinosaurs after GPA are listed in Table 1.

521

522 Figure 5. UPGMA phenograms grouping dinosaur skulls by geometric similarity.
523 Separate columns illustrate the different skull postures obtained using Procrustes
524 methods (left column) or by aligning the LSC with the horizon (right column). The
525 branching diagram on the right column groups skulls comparing landmark data for
526 which only translation and scale were filtered out, but not rotation (i.e., this data
527 includes skull posture as morphological information, determined by the LSC set to 0°).
528 The large white dots at the nodes are highlighting cases of notable grouping
529 differences, such as considering the skull geometry of *Nigersaurus* as that of either a
530 sauropod (left) or a bizarre dinosaur (right), and that of *Nanotyrannus* (presumably a
531 juvenile *T. rex*; Carr 1999) as different from that of *Tyrannosaurus*. The grouping in the
532 right column indicates that rotation is a main source of morphological difference among
533 skull geometries. The numbered terminal branches denote the taxa listed in Table 1;
534 the 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° 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° above the horizon, thus when putting the LSC at 0° (horizontal) head posture differs from its alert posture (from Duijm, 1951).

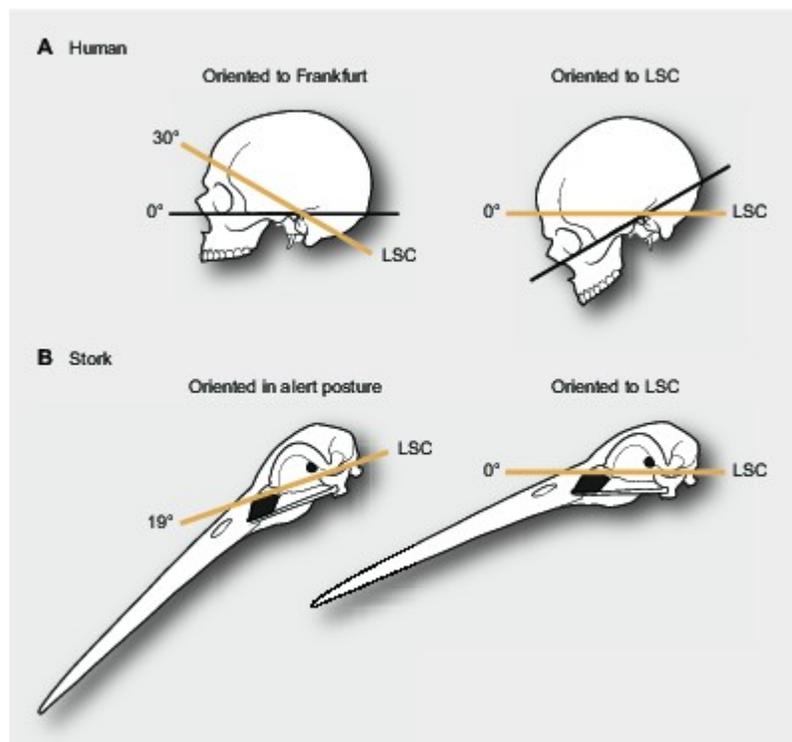


Figure 2

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° to 30° relative to the horizon.

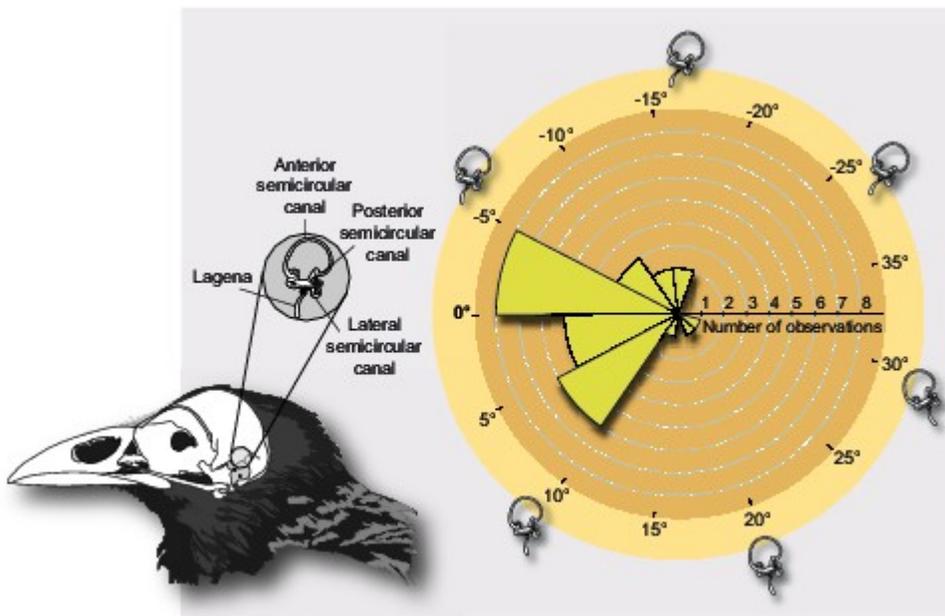


Figure 3

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.

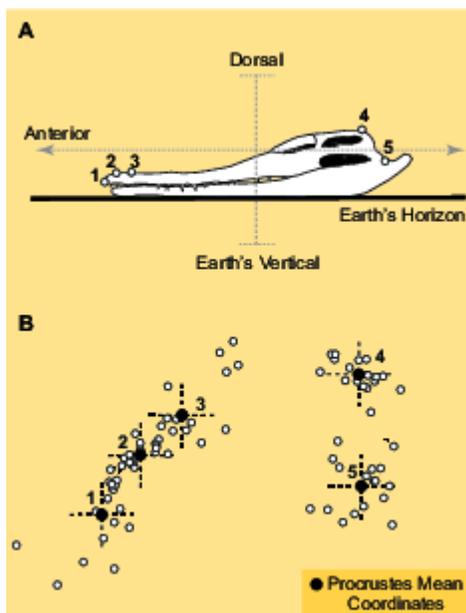


Figure 4

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° and the new GPA orientation. Obtained LSC orientations for all dinosaurs after GPA are listed in Table 1.

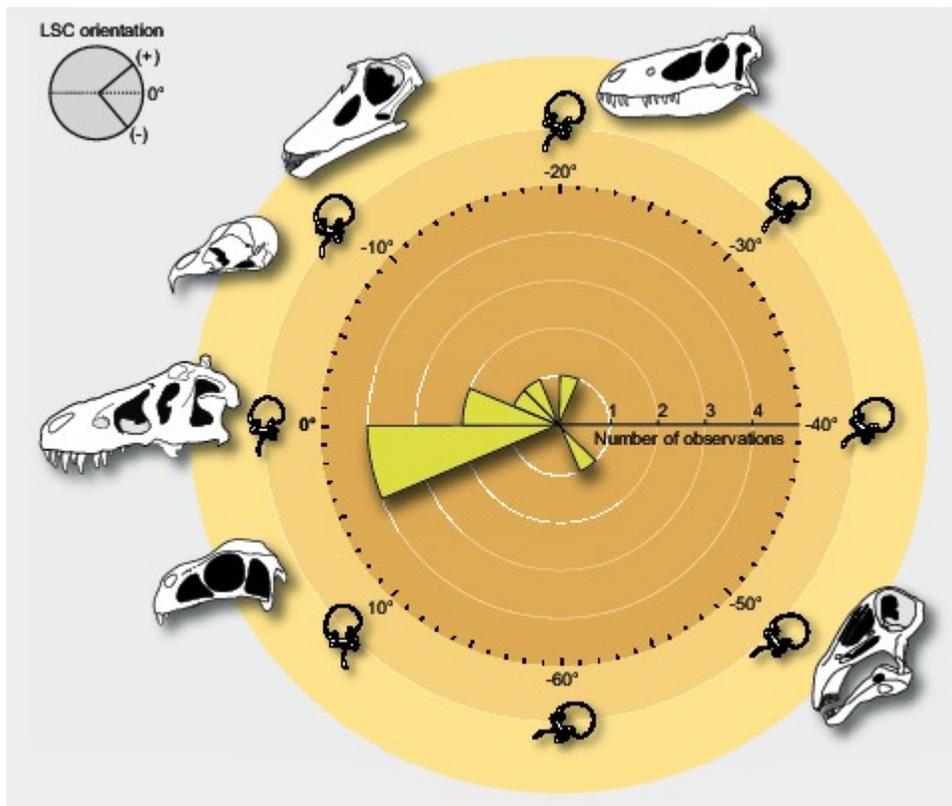


Figure 5

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.

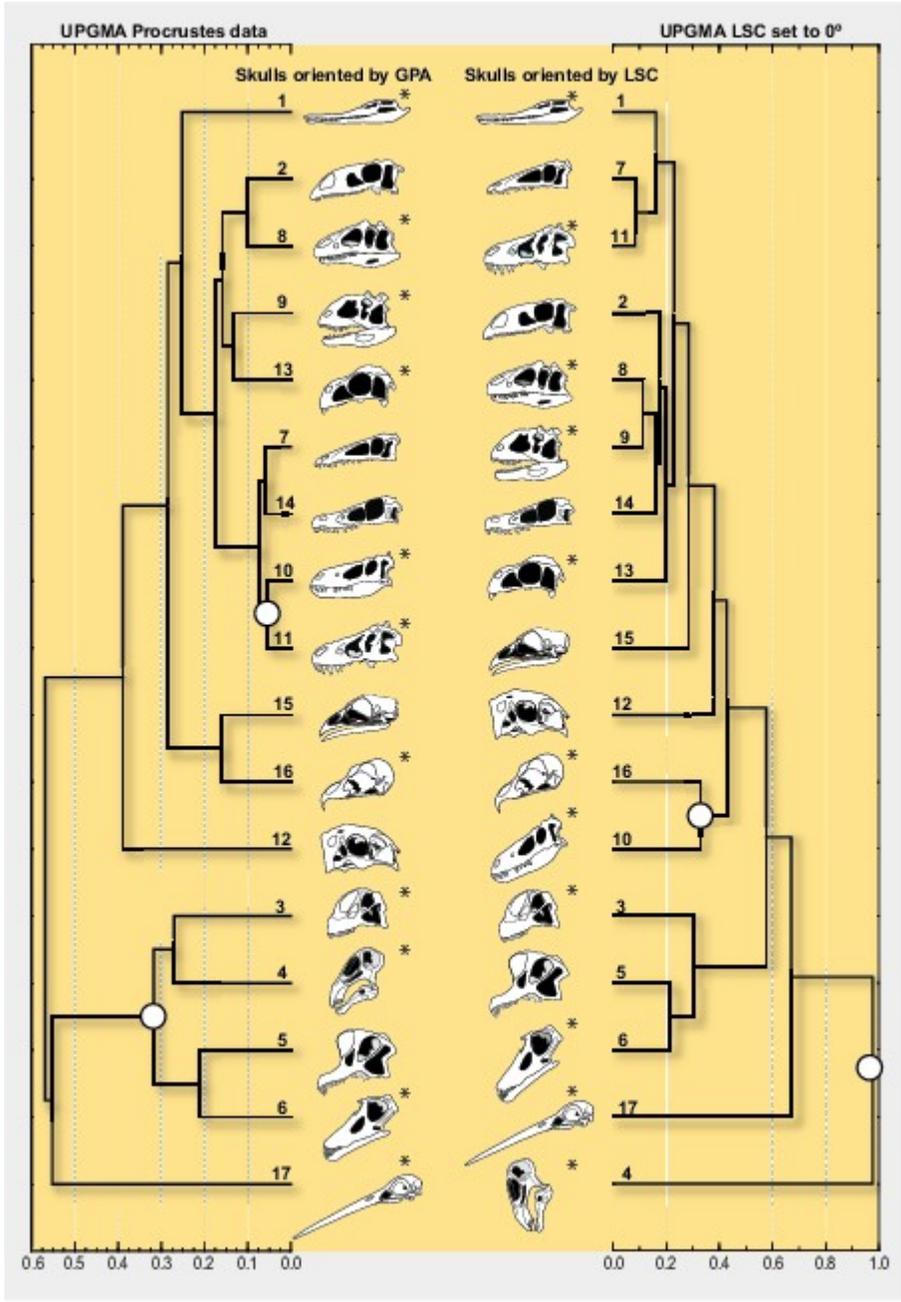


Table 1 (on next page)

Table 1

Studied specimens, collection numbers, and LSC orientations derived from the Generalized Procrustes Analysis.

Table 1. Studied specimens, collection numbers, and LSC orientations derived from the Generalized Procrustes Analysis.

Specimen	Collection #	LSC
1 <i>Crocodylus johnstoni</i>	OUVC 10425 ^[15]	0°
2 <i>Plateosaurus longiceps</i>	MB.R.1937	-
3 <i>Camarasaurus lentus</i>	CM 11338 ^[15]	-4°
4 <i>Nigersaurus taqueti</i>	MNN GAD512 ^[12]	-51.1°
5 <i>Giraffatitan brancaii</i>	HMB t1 (S-II)	-
6 <i>Diplodocus longus</i>	CM 11161 ^[15]	-12.5°
7 <i>Coelophysis bauri</i>	AMNH 480	-
8 <i>Allosaurus fragilis</i>	UMNH VP 18050 ^[14]	2.3°
9 <i>Majungasaurus crenatissimus</i>	FMNH PR2100 ^[11]	0.2°
10 <i>Nannotyrannus lancensis</i>	CMNH 7541 ^[14]	-22.3
11 <i>Tyrannosaurus rex</i>	AMNH 5117 ^[14]	-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 ^[15]	-9.3°
17 <i>Ciconia ciconia</i>	ZMB 253 ^[2]	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.