

News and Views

Keeping Asymmetry in Perspective: A Reply to Eckhardt and Henneberg

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Eckhardt and Henneberg's criticism of our analysis of craniofacial asymmetry centers on the lack of one-to-one correspondence between our landmarks and the linear measurements presented in the study by Jacob et al. (2006). This argument is a red herring: the salient topic for debate regards our findings that asymmetry in LB1 is within the normal ranges of asymmetry exhibited by African apes and humans (Baab and McNulty, 2009). These results are not contested by Eckhardt and Henneberg, who instead direct attention to differences between one of our analyses and that of Jacob et al. (2006).

These differences were explicitly acknowledged in our results section (Baab and McNulty, 2009: 617). We also included a table (Baab and McNulty, 2009: Table 3) that compared measurements in both studies, so that informed readers could evaluate differences for themselves. To wit, five of the six landmarks were either identical to points used by Jacob et al. (2006) (infraorbital foramen, alare) or located in the same anatomical region and would likely reflect similar degrees of asymmetry (frontomale temporale, M2-M3 contact, and lingual canine margin). Given our efforts to provide a transparent comparison between the two studies, we do not see the value in Eckhardt and Henneberg (2010) republishing these differences.

Our substitution of porion for "maximum cranial breadth" is specifically criticized, because it is not "a vault measurement" (Eckhardt and Henneberg, 2010). In fact, the maximum breadth in LB1 is across the supramastoid region (Brown et al., 2004), as it is in many fossil hominins and in our sample of extant apes. In modern humans, however, the maximum breadth is across the parietal rather than temporal bones. We chose porion due to its proximity to the supramastoid and its appropriate correspondence across our sample of apes, humans, and fossil hominins. It is reasonable to expect that asymmetry near porion might differ from asymmetry higher up on the cranial vault, which is why we highlighted this difference between the two studies (Baab and McNulty, 2009: Table 3).

Finally, we located the M2-3 contact landmark on the preserved alveolar margin, as explicitly defined in our Table 2 (Baab and McNulty, 2009); the absence of M3 in LB1 has no effect on our ability to locate this point.

Eckhardt and Henneberg (2010) also reference new data on palatal rotation, measured from photographs of 55 recent aboriginal Australian crania published by Milicerowa (1955). Theoretically, this provides a comparative context against which their previously reported measurement of rotation in LB1 (4–5°) can be judged. In evaluating their results, however, two relevant issues should be considered.

1. The angle measured by Eckhardt and Henneberg (2010) will vary according to the specimen's orientation in the photograph. Both Jacob et al. (2006) and Eckhardt and Henneberg (2010) constrain their cranial base line and palatal line to intersect by projecting them into a 2D plane (i.e., the photograph). This projection and, therefore, the angle at which these lines intersect, will change according to the specimen's orientation relative to the camera (see also Falk et al., 2009). In other words, *two lines drawn on photographs of the same cranium will intersect at different angles depending on how the specimen was oriented*. This is demonstrated here in Figure 1, which shows a difference of ~0.8° in the angle of intersection between a staphylion-orale line and an opisthion-basion line drawn on a single chimpanzee cranium rotated within a midsagittal plane. A similar rotation of LB1 (computed using the 2D protocol described below), from Frankfurt Horizontal to a plane defined by right/left poria and staphylion, causes the intersection between these 2D line projections to change by a full degree.

Thus, Eckhardt and Henneberg's claim (2010) that they "measured palatal deviation...in exactly the same way as in the study by Kaifu et al. (2009) and Jacob et al. (2006)" is unlikely, given that neither study published the orientations used in their photographs. Without details on how the specimen and camera were oriented, the different measurements are not comparable. Variation in photographic protocol may well explain the published differences in palatal rotation for LB1 (Jacob et al., 2006: 4–5°; Kaifu et al., 2009: 6°). More importantly, this issue calls into question the compatibility of the angle measured by Jacob et al. (2006) with those measured from photographs by Milicerowa (1955), who also did not describe specimen orientations. Even small variations

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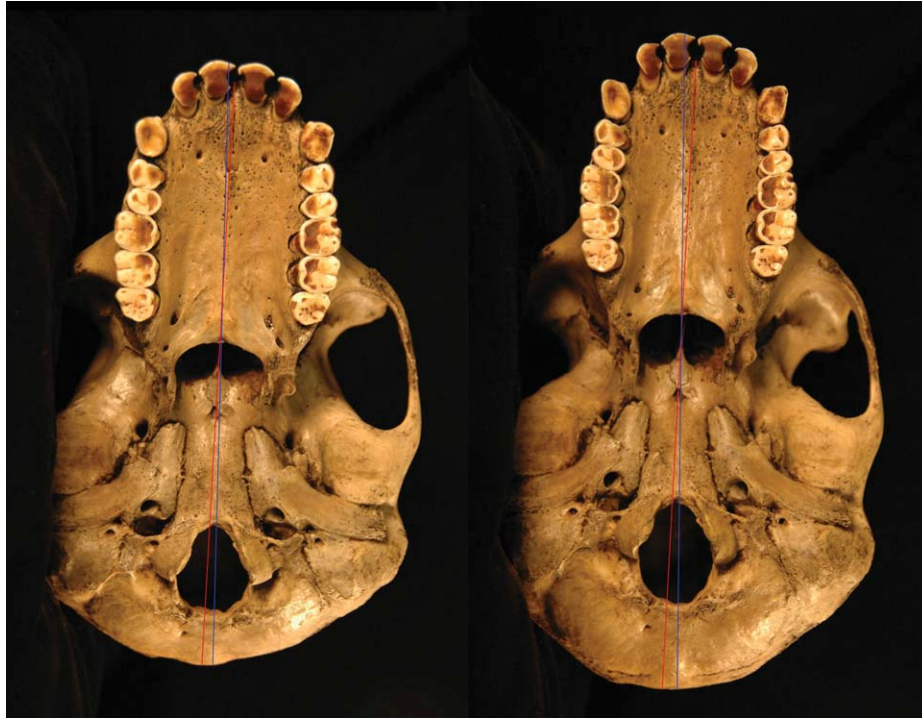


Fig. 1. Two photographs of a single chimpanzee skull taken at different orientations. The specimen was placed at the center of a turntable and oriented in approximately the Frankfurt Horizontal plane relative to a camera mounted 105.2 cm away. Between photographs, the turntable was adjusted by 20°, rotating the specimen in the midsagittal plane (with the axis of rotation approximately bipterionic). Lines passing through orale-staphylion (red) and opisthion-basion (blue) are drawn on both images, and their angles of intersection were measured using tpsDIG (Rohlf, 2008) (see online publication for color images). Left: when the specimen is oriented in the Frankfurt Horizontal plane, the lines intersect at 1.62°. Right: When the specimen is rotated 20° away from Frankfurt Horizontal, the same lines intersect at 2.41°.

in orientation could affect whether LB1 falls within or beyond the range of variation exhibited by Eckhardt and Henneberg's (2010) small sample of recent humans.

- The second point to consider is Eckhardt and Henneberg's (2010) persistence in only comparing the ~18,000-year-old LB1 cranium (Roberts et al., 2009) to those of recent modern humans. We previously raised the issue that recent humans may not provide an appropriate benchmark for judging the magnitude of nonpathological asymmetry expected in ancient humans (Baab and McNulty, 2009: 613; see also, Eckhardt and Henneberg, 2010). Although skulls of aboriginal Australians might provide more reasonable comparators than the clinical standards referenced by Jacob et al. (2006: references 54–57), they still represent a population of modern humans who were likely impacted by cultural advances in nutrition and healthcare.

To address this bias, we compared palatal rotation in LB1 with that seen in extant African apes and humans. We first measured rotation using a 2D approach that corresponded generally to that used by Jacob et al. (2006) and Eckhardt and Henneberg (2010). 3D landmark data (Baab and McNulty, 2009) were projected into a single plane and then the angle between the opisthion-basion and staphylion-incisivion line projections was computed. This analysis does not correspond exactly to previous studies (e.g., Jacob et al., 2006; Kaifu et al.,

2009; Eckhardt and Henneberg, 2010) because: 1) we have substituted incisivion for Jacob et al.'s (2006) orale to accommodate our extant landmark set; and 2) we do not know the cranial orientations used in others' photographs and have therefore oriented our specimens in the Frankfurt Horizontal plane. Nevertheless, our measures are consistent across our samples, providing a robust comparison of palatal deviation in LB1 to a large sample of hominines.

We also measured palatal rotation in three dimensions, where results are unaffected by differences in specimen orientation. Because lines in real (3D) space

TABLE 1. Measures of palatal rotation in LB1 and in extant African apes and humans

	<i>N</i>	\bar{x}	<i>R</i>	SD
Angles measured in 2D projection				
LB1	1	2.91	–	–
<i>Gorilla gorilla</i>	85	1.57°	0.07°–4.37°	1.18°
<i>Homo sapiens</i>	243	1.59°	0.03°–4.65°	1.14°
<i>Pan paniscus</i>	45	1.26°	0.03°–3.32°	0.84°
<i>Pan troglodytes</i>	110	1.48°	0.00°–4.56°	1.13°
Angles measure in 3D				
LB1	1	4.75°	–	–
<i>Gorilla gorilla</i>	85	1.79°	0.02°–5.89°	1.64°
<i>Homo sapiens</i>	243	2.06°	0.01°–5.32°	1.38°
<i>Pan paniscus</i>	45	1.41°	0.01°–4.07°	1.08°
<i>Pan troglodytes</i>	110	1.42°	0.02°–5.03°	1.23°

N, sample size; \bar{x} , mean; *R*, range; SD, standard deviation.

only intersect when they are coplanar, we measured rotation as the angle at which the incisivion-staphylion line intersects a midsagittal plane defined by opisthion-basion-hormion. For both sets of measurements, we report the absolute values of these angles as a measure of fluctuating (nondirectional) asymmetry.

Results of both analyses are shown in Table 1. Again, for angles measured in 2D, the differences in orientation preclude comparison of our measure of palatal rotation in LB1 (2.91°) with other reports (Jacob et al., 2006; Kaifu et al., 2009). Compared with apes and humans measured here, it is clear that the magnitude of palatal rotation is within the normal variation exhibited by all four extant species. Looking at the angle measured in 3D, LB1's palatal rotation is again within the range of all extant samples except *Pan paniscus*. These results conform to our previous conclusion (Baab and McNulty, 2009) that the magnitude of asymmetry in LB1 is relatively high but typically within observed variation of modern hominines.

Unlike most studies, which have addressed the magnitude of asymmetry in LB1, Kaifu et al. (2009) provided a morphological assessment of the pattern of asymmetry. Their results (published shortly after ours) offer more compelling evidence of pathological asymmetry but do not implicate severe developmental abnormalities such as those that might result in microcephaly (see also Falk et al., 2010). It is also not clear that taphonomic deformation is "now disproved" (Eckhardt and Henneberg, 2010). On the contrary, it is apparent that taphonomic factors affected the LB1 cranium (e.g., right coronal suture and zygomatic arch; Falk et al., 2010). These studies, as well as our own, suggest that the only known cranium from Liang Bua corroborates the postcranial evidence for a new type of hominin from the Late Pleistocene of Flores. Ultimately, we concur with Kaifu et al. (2009: 184) that "evidence of cranial deformation itself should not be cited as an independent indicator of severe pathology," and suggest that suppositions of extremely rare developmental abnormalities be supported by convincing evidence.

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