Sex-biased sampling may influence *Homo naledi* tooth size variation

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Abstract

A frequent source of debate in paleoanthropology concerns the taxonomic unity of fossil assemblages, with many hominin samples exhibiting elevated levels of variation that can be interpreted as indicating the presence of multiple species. By contrast, the large assemblage of hominin fossils from the Rising Star cave system, assigned to *Homo naledi*, exhibits a remarkably low degree of variation for most skeletal elements. Many factors can contribute to low sample variation, including genetic drift, strong natural selection, biased sex ratios, and sampling of closely related individuals. In this study, we tested for potential sex-biased sampling in the Rising Star dental sample. We compared coefficients of variation for the *H. naledi* teeth to those for eight extant hominoid samples. We used a resampling procedure that generated samples from the extant taxa that matched the sample size of the fossil sample for each possible Rising Star dental sex ratio. We found that variation at four *H. naledi* tooth positions—I_2, M_1, P^4, M_1—is so low that the possibility that one sex is represented by few or no individuals in the sample cannot be excluded. Additional evidence is needed to corroborate this inference, such as ancient DNA or enamel proteome data, and our study design does not address other potential factors that would account for low sample variation. Nevertheless, our results highlight the importance of considering the taphonomic history of a hominin assemblage and suggest that sex-biased sampling is a plausible explanation for the low level of phenotypic variation found in some aspects of the current *H. naledi* assemblage.

Keywords: Taphonomy; Rising Star cave; Hominin; Sex ratio; Sex bias; Skeletal sampling

1. Introduction

Homo naledi was diagnosed as a novel taxon based on the morphology of approximately 1550 fossils, whole and fragmentary, recovered from the Dinaledi Chamber of the Rising Star cave system (Berger et al., 2015; Dirks et al., 2015). Although the Dinaledi material is noteworthy for its abundant hominin fossils, including articulated remains, there is a dearth of recovered faunal material (Berger et al., 2015, 2023; Dirks et al., 2015; Kivell et al., 2015; Dirks et al., 2016; Val, 2016; Bolter et al., 2018; Elliot et al., 2021). This gives the assemblage a taphonomic signature that is distinct from that of nearby hominin-bearing karst sites, like Sterkfontein and Swartkrans, where faunal remains predominate and hominin fossils are proportionally rare (Dirks et al., 2016). Geochronological and radiometric dates from flowstones that bracket the Dinaledi Chamber's fossil-bearing deposits and electron-spin-resonance dates from a small sample of *H. naledi* teeth suggest that the material entered the chamber between 335 and 241 ka (Dirks et al., 2017; Robbins et al., 2021), but younger dates were noted on some samples (Dirks et al., 2017).

Fossil material attributed to *H. naledi* comes from several spatially distinct localities within the Rising Star cave system. The largest sample comes from the Dinaledi Chamber, where surface collection and a limited excavation produced remains from a minimum of 15 individuals and more than 190 teeth (Berger et al., 2015). A smaller number of fossils come from the Hill Antechamber and locality U.W. 110, which are also part of the Dinaledi subsystem (Elliott et al., 2021). The Hill Antechamber has been the subject of recent excavation (Berger et al., 2023), but the previously described sample from this setting contains three isolated teeth (Berger et al., 2015; Delezene et al., 2023). The U.W. 110 locality has produced cranial remains and teeth from one immature *H. naledi* individual (Brophy et al., 2021). The Lesedi Chamber is outside the

Dinaledi subsystem and distant from it; this locality has yielded fossils from at least three individuals, including an adult partial skeleton with complete dentition, a subadult with mixed dentition and associated postcrania, and a partial adult mandible retaining M_1 and M_2 (Hawks et al., 2017; de Ruiter et al., 2019; Feuerriegel et al., 2019; Cofran et al., 2022). Where focused analyses have compared them, the Lesedi and U.W. 110 fossils have been shown to be morphologically indistinguishable from the Dinaledi Chamber and Hill Antechamber homologs (e.g., Hawks et al., 2017; Davies et al., 2019a, 2019b; Feuerriegel et al., 2019; Brophy et al., 2021). Elliott et al. (2021) reported *H. naledi* fossils from other localities within the Rising Star cave system, and Berger et al. (2023) presented additional material from the Dinaledi Chamber and Hill Antechamber, but these fossils are not yet formally described. Though the tally is sure to grow, the published fossils from the four loci already represent the largest African Middle Pleistocene hominin assemblage recovered to date (e.g., Berger et al., 2017).

Hominin teeth and jaws are numerous in the Rising Star fossil assemblage and represent individuals ranging in age from infant to older adult (Cofran and Walker, 2017; Hawks et al., 2017; Bolter et al., 2018; Bolter and Cameron, 2020; Brophy et al., 2021; Cofran et al., 2022; Delezene et al., 2023). Berger et al. (2015) and Bolter et al. (2018) reported a dental minimum number of individuals (MNI) of 15 for the Dinaledi Chamber and Hill Antechamber material. Adding to that total, the subadult from U.W. 110 and the three individuals from the Lesedi Chamber raise the dental MNI to 19 for the published assemblage.

Despite the large number of recovered individuals, the *H. naledi* dental sample exhibits remarkable morphological homogeneity. Commenting on this feature of the assemblage in the original diagnosis, Berger et al. (2015:24) noted that “almost every aspect of the morphology of the dentition, including the distinctive form of the lower premolars, the distal accessory cuspule of the mandibular canines, and the expression of nonmetric features that normally vary in human populations, is uniform in every specimen from the collection." Subsequent analyses of crown shape (Davies et al., 2019a, 2019b, 2020), root morphology (Kupczik et al., 2019), molar topography (Berthaume et al., 2018), and nonmetric traits (Irish et al., 2018) have all found low intrasample variation, supporting Berger et al.'s (2015) initial conclusion. Another insight into *H. naledi* dental variation comes from Garvin et al. (2017), who assessed coefficients of variation (CVs) for the buccolingual widths (BL) of the mandibular and maxillary M1s and M2s and mesiodistal (MD) and labiolingual (LL) dimensions of the mandibular and maxillary canines for the Dinaledi Chamber and Hill Antechamber samples. They reported CVs of 2.0 (M^1 BL), 3.2 (M_1 BL), and 3.8 (M^2 BL and M_2 BL) for the molars, and 2.8 (C_1 LL), 5.5 (C^1 MD), 6.2 (C_1 MD), and 7.4 (C^1 LL) for the canines. They compared the *H. naledi* CVs to sex-balanced samples of four extant hominoids and found that the *H. naledi* values fall within the lower bounds of expectations, or just below them.

Relative to other hominin fossil assemblages, the *H. naledi* CVs reported in Garvin et al. (2017), especially for molar size, tend to be low. For example, Moggi-Cecchi (2003) analyzed MD, BL, and LL dimensions for all permanent maxillary and mandibular tooth positions in species of *Australopithecus* and *Paranthropus.* They found that *Australopithecus africanus* CVs ranged from 3.9 to 12.5, *Paranthropus robustus* from 4.2 to 8.9, and *Paranthropus boisei* from 3.1 to 15.5. For *A. africanus* and *P. robustus*, only one dimension for each taxon (I^1 LL for *A. africanus* and M^1 MD for *P. robustus*) had a CV less than 5.0. For *P. boisei*, only three dimensions (C^1 MD, M^1 MD, and M_1 MD) had CVs less than 5.0, while 15 were greater than 10.0. Lockwood et al. (2000) reported CVs ranging from 4.5 to 13.6 for MD, BL, and LL dimensions of all permanent maxillary and mandibular teeth except the incisors of

Australopithecus afarensis; only two of the dimensions they considered (M^2 MD and BL) had CVs below 5.0. Thus, the CVs Garvin et al. (2017) reported for *H. naledi*, especially the molars, fall below most point estimates for tooth size variation in other fossil assemblages.

In this study, we expand upon the analysis of Garvin et al. (2017) by including the entire published hypodigm of *H. naledi*, by considering all tooth positions, and by setting up hypothesis testing to consider sex-biased sampling as an explanation for low sample variation. Our goals are to 1) determine if the *H. naledi* sample has unusually low variation in comparison to expectations derived from extant hominoids, 2) generate hypotheses about the Rising Star material that can be tested as the assemblage grows, and 3) facilitate comparisons of variation with other hominin fossil assemblages. These objectives are important because many hominin assemblages, even those small in sample size, exhibit skeletal and dental variation that is perceived to be high in comparison to recent human populations and, in some cases, the most sexually dimorphic extant apes. Sources of high variation in fossil samples have been discussed extensively and include temporal and geographical heterogeneity, phylogenetic polymorphism, population history, sexual dimorphism, ontogeny, pathology, and the pooling of multiple species into a single analytical unit (e.g., Lockwood et al., 2000; Skinner et al., 2006; Harmon, 2009; Royer et al., 2009; Scott et al., 2009; Rightmire et al., 2019; Grine et al., 2021). By contrast, discussions of the meaning of low sample variation are encountered less often owing to the small sizes of most fossil samples. Possible sources of low variation that are informative with regard to a species' biology include low genetic variation resulting from the action of genetic drift or natural selection, or sexual monomorphism related to aspects of socioecology. However, our ability to make such inferences depends on whether we can confidently exclude sampling error and taphonomy as explanations for low variation.

Taphonomic processes that are not random with regard to sex (e.g., predator bias, size-biased preservation, intersexual differences in home range) can influence the composition of fossil assemblages (e.g., Lockwood et al., 2007; Gower et al., 2019), which could yield a sample with lower variation than the population from which it was drawn. Even where the probability of entering the fossil record does not differ between the sexes, a random process, like the chance of fossil recovery, can produce strong sex bias in fossil samples, especially when the number of individuals in the assemblage is relatively small. Here, we investigate the *H. naledi* dental sample, asking whether variation at each tooth position is unusually low and, if so, whether this is consistent with sex bias in the fossil assemblage.

2. Materials and methods

2.1. Fossil data

Homo naledi tooth crown sizes for published specimens from the Dinaledi Chamber, Hill Antechamber, U.W. 110, and the Lesedi Chamber were considered here (Tables 1 and 2). The data for the Dinaledi Chamber fossils are from Delezene et al. (2023); data for the Hill Antechamber and Lesedi Chamber teeth were collected by L.K.D; and those from the U.W. 110 locality are from Brophy et al. (2021). Post-depositional taphonomic damage to the Dinaledi teeth is minimal, but interproximal and occlusal wear are substantial for some specimens (e.g., Figs. 42 and 43 in Delezene et al., 2023). Because interproximal wear has a strong effect on MD dimensions, we restricted analyses to the BL and LL dimensions. In cases where antimeres have been proposed for isolated teeth in the Dinaledi assemblage (Delezene et al., 2023; Table 1), we treated the pair as a single analytical unit by averaging the two measurements.

2.2 Extant comparative samples

When evaluating variation in hominin fossil samples, extant humans and great apes—*Pan*, *Gorilla*, and *Pongo*—are typically viewed as the most appropriate analogs because they represent the immediate phylogenetic context for extinct hominins and therefore share, to varying degrees, important aspects of biology with hominins (e.g., body size, life history, skeletal morphology). Because the *H. naledi* sample may have unusually low variation, we broadened the phylogenetic context to include a species of *Hylobates*, increasing the number of comparative samples drawn from species with low levels of sexual dimorphism. For the same reason, we also included three samples of extant humans: two from living populations and one from an archaeological assemblage.

Tooth size data were collected by J.D.I. from two dental hardstone samples taken with consent from living people in Botswana and South Africa who self-identified, respectively, as San[1] and Pedi. These casts are housed in the School of Human Evolution and Social Change at Arizona State University (Haeussler et al., 1989). The third human sample comprises data collected by J.D.I from a Predynastic Egyptian cemetery (ca. 3500–3200 BCE) at Hierakonpolis (HKW) (e.g., Irish, 2006); these remains are stored on site. Sex was recorded for the two southern African samples at the time of casting. The sex of the HKW individuals was determined based on diagnostic skeletal features (Buikstra and Ubelaker, 1994). Extant ape data, collected by L.K.D., are from large samples of *Pan troglodytes troglodytes*, *Gorilla gorilla gorilla*, *Pongo pygmaeus*, and *Hylobates lar carpenteri*. In the case of *Pa. t. troglodytes*, *G. g. gorilla*, and *Hy. lar carpenteri*, the samples represent single subspecies originating from restricted geographical

[1] 'San,' as recorded for the individuals here, is an exonym applied to diverse indigenous peoples of southern Africa that traditionally spoke a non-Bantu language. Its use is not intended to imply more specific reference to a particular ethnolinguistic group (e.g., du Plessis, 2019).

areas (Supplementary Online Material [SOM] Table S1). The *Po. pygmaeus* sample includes specimens from across Borneo (SOM Table S1) that may represent more than one subspecies (e.g., Goossens et al., 2009). We also included *Pan paniscus* metrics from Johanson (1974). Sample sizes for the extant taxa vary by measurement, species, and sex (Tables 3 and 4).

2.3. Hypothesis testing

We quantified size variation using the CV, a measure of relative variation that expresses the sample standard deviation as a percentage of its mean. Sample sizes for *H. naledi* range from $n = 5$ to $n = 10$. All CVs computed in the procedures outlined below were adjusted using the correction for sample size: CV * $(1 + 1/4n)$, where n is the sample size (Sokal and Braumann, 1980). This correction accounts for bias that occurs in the uncorrected CV at small sample sizes (i.e., population variation tends to be underestimated; Haldane, 1955; Sokal and Braumann, 1980).

We compared *H. naledi* to the extant hominoid samples using the bootstrap (i.e., resampling with replacement) in R v. 4.2.1 (R Core Team, 2022). The analysis was conducted using code written by the authors that employs the 'sample' function. Our approach to hypothesis testing differs in two important ways from that used in most previous studies of variation in fossil primate samples (e.g., Cope and Lacy, 1992, 1995; Lockwood et al., 1996, 2000; Lockwood, 1999; Silverman et al., 2001; Schrein, 2006; Royer et al., 2009; Melillo et al., 2021), including Garvin et al.'s (2017) analysis of the Dinaledi sample canines and molars. First, instead of resampling only from the comparative taxon to determine the probability of drawing a sample with the same characteristics as that of the fossil sample, we bootstrapped the fossil sample as well (see also Villmoare, 2005; Gordon et al., 2008; Scott et al., 2009). For each comparison, we used the following procedure: 1) bootstrap the *H. naledi* sample using the available number of *H. naledi* specimens for each tooth and compute the CV; 2) bootstrap each of the extant comparative samples at a sample size that matches the *H. naledi* sample and compute their CVs; 3) calculate the difference between the bootstrapped CVs of *H. naledi* and each of the extant samples; and 4) repeat the first three steps 9999 times. This procedure resulted in distributions of CV differences used to generate confidence intervals for the difference between *H. naledi* and each of the extant comparative samples. The CV for the extant taxon was always subtracted from that of *H. naledi* so that a negative difference indicates a smaller CV for *H. naledi*. The null hypothesis was equal relative variation (equal CVs) for *H. naledi* and the reference sample; thus, if zero (i.e., no difference in the CV between the two samples) was not contained within the confidence interval, then the null hypothesis was rejected. This approach is more conservative and robust than resampling only from the extant taxon because it accounts for sampling error in the fossil sample as well (Villmoare, 2005; Gordon et al., 2008; Scott et al., 2009). All statistical tests were two-tailed using $\alpha = 0.05$; 95% confidence intervals were calculated from the bootstrapped distributions using the percentile method.

The second difference from previous applications is that we examined how assumptions about the sex ratio of the fossil sample influence comparisons with extant taxa. Bootstrap tests are typically conducted using sex-balanced extant samples and resampling occurs without regard to sex. Although many of the bootstrap samples generated in this way will have biased sex ratios, the resulting distribution will reflect the sex-balanced nature of the original sample (Scott and Stroik, 2006). When the goal is to evaluate whether variation in a fossil sample is unusually high, this procedure is appropriate. However, when the question is whether variation in the fossil sample is unusually low, controlling the sex ratio during resampling becomes more critical.

When sexual dimorphism is present, samples in which one sex is overrepresented will provide misleading estimates of intraspecific variation (Plavcan, 1994) and confound statistical comparisons (Scott and Stroik, 2006). The extent to which a given fossil sample is biased toward one sex is difficult to determine with high confidence in most cases. We therefore considered all possible sex ratios for each tooth position in our comparisons between the fossil and extant samples. As an example, given a sample size for *H. naledi* of $n = 5$, six separate bootstrap analyses were performed with the sex ratio fixed for the comparative taxa at each possible sex ratio, given the size of the fossil sample: 5:0, 4:1, 3:2, 2:3, 1:4, and 0:5 (male:female). In other words, six distributions were generated from each of the comparative samples—one distribution for each sex ratio—and each distribution was compared to the fossil distribution. By holding the sex ratio constant for each comparison, but conducting comparisons across multiple sex ratios, we evaluated the plausibility of sex bias as an explanation for low variation in the *H. naledi* samples.

3. Results

Given the large number of statistical tests performed (SOM Tables S2–S17), we focus the reporting of the results on general patterns. The results can be divided into five groups. First, for both the maxillary and mandibular canines, *H. naledi* is statistically indistinguishable from humans and gibbons for most sex ratios, but the fossil sample exhibits significantly lower variation relative to the great apes for all but the most extreme sex ratios (Figs. 1 and 2; SOM Tables S4 and S12). This pattern is expected based on the known differences between hominins and great apes in canine size sexual dimorphism (e.g., Plavcan, 2012). The second group of results includes the CVs for the *H. naledi* I_1 and P_4, which are unremarkable in comparison to the comparative samples (SOM Figs. S1 and S2; SOM Tables S2 and S6). The third group includes the CVs for the *H. naledi* I^1 and P^3, which are consistently lower than those of the comparative samples, but none of the comparisons are statistically significant. The fourth pattern characterizes most of the other tooth positions. In these cases, the observed *H. naledi* CVs are lower than those of the extant hominoid samples and there are significant differences for some sex ratios involving the most dentally dimorphic species (*Po. pygmaeus*: P_3, M_2, M_3, I^2, M^2, and M^3; *G. gorilla*: M^3). However, *H. naledi* is never significantly different from humans, gibbons, or chimpanzees at these positions (SOM Figs. S3–S5, S7, S9 and S10; SOM Tables S5, S8, S9, S11, S16, and S17). The P_3 results for *P. paniscus* deserve further discussion. In this comparison, variation in *H. naledi* is significantly lower regardless of the sex ratio. We suspect that this result reflects differences in measurement technique for this tooth; Johanson (1974:40), the source of the *P. paniscus* data used here, noted "difficulties associated with the measurement of the sectorial premolar are recognized."

The final group of results includes the remaining four teeth—I_2 (Fig. 3; SOM Table S3), M_1 (Fig. 4; SOM Table S7), P^4 (Fig. 5; SOM Table S14), and M^1 (Fig. 6; SOM Table S15). These teeth provide evidence for unusually low variation in *H. naledi*. The I_2 CV of *H. naledi* is significantly lower than those of all extant hominoids, regardless of sex ratio, except for the comparison to *Pa. troglodytes* when the sex ratio is 0M:5F and compared to *Pa. paniscus* when the sex ratio is 5M:0F, 4M:1F, and 3M:2F (for the last sex ratio, the *p*-value is low: $p = 0.0504$; Fig. 3; SOM Table S3). The *H. naledi* P^4 is also significantly less variable in all tests except for the comparison to *G. gorilla* when the sex ratio is 0M:8F ($p = 0.0806$) or in comparison to *Pa. paniscus* at any sex ratio (but note that in six out of nine comparisons with *Pa. paniscus*, the *p*-values for P^4 are low: $0.05 < p < 0.10$; SOM Table S14). The mandibular and maxillary M1s of

H. naledi are significantly less variable than those of extant hominoids, including the human samples, in most comparisons, but with several exceptions where extreme sex ratios are assumed (Figs. 4 and 6; SOM Tables S7 and S15). In the case of M_1, *H. naledi* cannot be statistically distinguished from the human HKW sample when the ratio is approximately sex-balanced or female-biased (Fig. 6; SOM Table S7).

4. Discussion

The low level of variation noted throughout the skeleton of *H. naledi* in previous studies (Berger et al., 2015; Garvin et al., 2017; Irish et al., 2018; Davies et al., 2020) contrasts with the pattern observed in many other large fossil assemblages, where debates often focus on the causes of high variation—i.e., whether an assemblage contains more than one species, a single species with high levels of sexual size dimorphism, or a single lineage characterized by anagenetic trends or random fluctuations in morphology over time (e.g., Lockwood et al., 1996; Kelley and Plavcan, 1998; Lockwood et al., 2000; Silverman et al., 2001; Schrein, 2006; Skinner et al., 2006; Humphrey and Andrews, 2008; Scott et al., 2009). Because most fossil samples are small, low variation is often regarded as random sampling error; however, it can signal something interesting about the evolutionary history of the population from which an assemblage was drawn or the circumstances under which it accumulated. Demonstrating that variation is unusually low is difficult, however, given that few fossil samples are large enough to have sufficient power to detect it. Although the *H. naledi* dental samples are not large by conventional statistical criteria, some of the teeth are represented by samples that are large by paleoanthropological standards. Thus, they provide a rare opportunity to address some of these issues.

4.1. Sex-biased sampling

Our analysis focused on the potential for sex-biased sampling to produce low variation in the *H. naledi* dental assemblage. Previous discussions of variation in fossil assemblages have noted that in cases where sexual dimorphism is present and intrasexual variation is low relative to intersexual variation, disproportionate representation of one sex in a sample can provide downwardly skewed estimates of population variation (Plavcan et al., 2005; Scott and Stroik, 2006). The methods used here differ from those of previous studies in that our resampling procedures considered the full range of sex ratios possible for the Rising Star dental sample. This framework allowed us to directly evaluate whether different assumptions about sex ratio influence tests of the hypothesis of equal relative variation for *H. naledi* and each of the extant comparative samples. We found that, in most cases, it is not necessary to posit biased sex ratios to explain low variation in *H. naledi*, as most of our resampling analyses showed no significant differences between *H. naledi* and the modern comparative samples.

However, according to our analytical framework, four tooth positions are candidates for unusually low variation in *H. naledi*. The M_1, I_2, and P^4 are each significantly different from seven of the eight extant samples for all but the most extreme sex ratios. For example, variation in the *H. naledi* M_1 sample is not significantly different from that in the HKW human sample at nearly balanced or female-biased sex ratios (Fig. 4; SOM Table S7), but the fossil sample has significantly lower variation in comparison to all other extant samples unless we assume that one sex contributed disproportionately to the sample. A fourth tooth, the M^1, has a significantly lower CV than all of the extant taxa except for comparisons involving extreme sex ratios (Fig. 6; SOM Table S15). The M1 results are notable because these teeth are represented by the largest samples (n = 9 for M_1 and n = 10 for M^1). Thus, statistical power to detect differences in the comparisons with the extant taxa is greatest for these two tooth positions[2]. Further, these teeth are the least likely to have highly skewed sex ratios if we assume that males and females have equal probabilities of recovery.

The question of whether each sex had an equal probability of contributing to the sample is an important one. If male and female *H. naledi* individuals had an equal chance of being preserved and recovered, then the binomial probability of drawing a sample where one sex is represented by fewer than two specimens ranges from 0.375 at n = 5 down to 0.021 at n = 10. However, the assumption that males and females had an equal chance of entering the fossil accumulation may be incorrect and the real probabilities of drawing samples with extreme sex ratios could be much higher. For example, Gower et al. (2019) found a widespread male bias in many fossil and museum collections. Sexual skew has been inferred in other hominin samples as well. For example, Lockwood et al. (2007) proposed that the Swartkrans *P. robustus* sample is strongly male-biased, which they attributed to differential predation on young males. The Shanidar sample of Neandertals and the A.L. 333 sample of *A. afarensis* are also thought to be biased in favor of male individuals (Trinkaus, 1980; Plavcan et al., 2005). If the presence,

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[2] Smith (2020: 523) suggests that a general guideline is that power "varies with the square root of sample size (larger sample sizes have greater power) and with the size of the effect (it is easier to detect a larger effect than a smaller one)." Given that guideline, if we hold effect size constant, then it follows from this principle that statistical power should increase quite rapidly initially and then level out as sample sizes become large (that is, the proportional effect of adding one more specimen decreases as overall sample size increases.)

Estimating statistical power for the bootstrapping tests like those performed here is more complex than a typical power analysis for differences between means. It is probably the case that the true CVs vary among the teeth as a result of differences in within- and between-sex standard deviations, within- and between-sex means (i.e., sexual dimorphism in size), and sample size.

preservation, and/or recovery process for a given fossil assemblage is sex-biased, then skewed sex ratios are much more probable and would not require an unusual sampling event. If we assume that the processes that led to the formation of the Rising Star hominin assemblage were biased toward one sex with a 7:3 ratio, then the binomial probabilities of drawing samples of size $n = 9$ and $n = 10$ that contain fewer than two individuals of one sex are 0.196 and 0.149, respectively (Fig. 7).

Given the low levels of dimorphism generally observed for primate molar, premolar, and incisor size, and the fact that many of the teeth in this study are isolated or not definitively associated with skeletal material that may provide a clue as to the sex of the individuals, it is not possible to speculate about which sex may be overrepresented in the assemblage using tooth size variation alone. Possible ways of ruling out sex bias include the successful extraction of ancient DNA or enamel proteins (e.g., Welker et al., 2020; Madupe et al., 2023). As some of the peptide-coding alleles are sex-linked, methods have been developed to infer sex in archaeological and paleontological collections from proteomic analyses (e.g., Stewart et al., 2017; Welker, 2018; Ziganshin et al., 2020; Demeter et al., 2022; Palesa et al., 2023). Current work on *H. naledi* enamel proteins may help to contextualize the patterns of tooth size variation observed here. In any case, our results are consistent with two interpretations: 1) at least some of the *H. naledi* dental samples are characterized by strong sex bias or 2) the low variation seen at some tooth positions is a real feature of the population from which the fossils were drawn.

4.2. Other aspects of the Rising Star assemblage

Both the time across which a sample accumulated and the possible genealogical relatedness of individuals within the sample are relevant to interpreting its variation. In contrast to the gradual accumulation of individuals by random processes over a long period of time, we would not necessarily expect an assemblage produced by geologically rapid processes to preserve the same level of variation as seen across a large population or species with substantial temporal depth. The amount of time represented by the *H. naledi* sample is unknown. Geochronological assessment of the Dinaledi Chamber sample constrains it to a 94,000-year span, between 335 and 241 ka (Dirks et al. 2017; Robbins et al. 2021), but the other *H. naledi* localities have no geochronological age estimates. The occurrence of *H. naledi* fossils within the remote areas of the cave system has been interpreted as being inconsistent with passive transport from outside the system, which may indicate behavioral use of the caves (Dirks et al., 2015, Elliott et al., 2021), perhaps including mortuary activity (Randolph-Quinney 2015; Berger et al., 2023; but see Val, 2016; Egeland et al., 2018; Nel et al., 2021, Martinón-Torres et al., 2023).

A geologically rapid accumulation (i.e., years to centuries) could yield a sample with low variation. To address this possibility, we included a *H. sapiens* cemetery sample (HKW) that contains individuals interred over the span of approximately 300 years (Irish, 2006). The San and Pedi human samples that we included represent shorter temporal intervals than the HKW sample, but it is likely that they contain individuals who are more distantly related to each other than is the case for HKW. The *H. naledi* sample differs from the HKW sample in the same way that it does from the other two human samples: the magnitudes and directions of the CV differences between *H. naledi* and each of the human samples are similar, indicating that the HKW teeth are not appreciably less variable than the contemporary human samples. The one result where the comparison to the HKW sample stands out is the M_1. For that tooth, *H. naledi* has significantly lower variation than the Pedi and San samples for most sex ratios, but it cannot be statistically distinguished from the HKW sample in the resampling analysis that assumed nearly balanced sex ratios or those that are biased towards females. The Sima de los Huesos assemblage of Middle Pleistocene *Homo* has also been proposed to have arisen from intentional deposition and may serve as a useful taphonomic comparison for the Rising Star *H. naledi* sample. Bermúdez de Castro et al. (2001) found that, for some dimensions, the Sima de los Huesos tooth sizes are significantly more variable than in extant human groups. The Sima de los Huesos and HKW samples indicate that single-site assemblages that accumulate quickly need not be low in variation.

Individuals from all four published *H. naledi* loci are considered here, but most of the teeth are from the Dinaledi subsystem (i.e., Dinaledi Chamber, Hill Antechamber, and U.W. 110). Thus, our current view of variation in *H. naledi* is shaped mainly by this subset of fossils. The only tooth position for which individuals from all four collection areas are represented is the M^1, but several positions contain at least one individual from three collection areas. The C^1, P^3 and M_1 are represented by specimens from all loci except U.W. 110, and the I^1, I^2 and P^4 are represented by specimens from all loci except the Hill Antechamber. It is possible that the individuals from the Dinaledi Subsystem represent an unusual sampling event, but note that the M^1, which has at least one representative from all four loci, has significantly lower variation than all comparative samples except when extreme sex ratios are assumed. The P^4 and M_1 also exhibit low variation and they are both represented by at least one individual from three of the loci.

Finally, it is also worth noting that the results for each tooth do not provide independent snapshots of *H. naledi* tooth size variation, but instead capture a sample of individuals with similarly sized teeth. Some individuals in this study are represented by complete or nearly complete dentitions. For example, every maxillary and mandibular tooth position is available for Dinaledi Hominin 1, the holotype of *H. naledi*, and LES1 from the Lesedi Chamber (de Ruiter et al., 2019). Other individuals have nearly complete mandibular dentitions (e.g., Association 2; Delezene et al., 2023). In some cases, Delezene et al. (2023) were unable to link teeth in the upper and lower arcades, or anterior and posterior teeth in the same arcade, so it is possible that many individuals have teeth represented in both the maxillary and mandibular samples considered here. In other words, the results for each tooth position are not statistically independent tests of the hypothesis of equal relative variation. Previous studies have shown that homologous dimensions of primate postcanine teeth have strong phenotypic and genetic correlations (e.g., Hlusko and Mahaney, 2009; Hlusko et al., 2011; Delezene, 2015; Stojanowski et al., 2017; Delezene and Roseman, 2019). Covariation among postcanine tooth size may, therefore, partially explain why the M^1, M_1, and P^4 all indicate low variation. However, phenotypic and genetic correlations between incisor and postcanine size are not strong within species (e.g., Hlusko and Mahaney, 2009; Hlusko et al., 2011; Delezene, 2015). Thus, the low CV observed for *H. naledi* I_2 size is less likely to be explained by covariation with the postcanine teeth.

Identifying the taphonomic processes that led to the burial and preservation (e.g., Behrensmeyer et al., 2000; Behrensmeyer, 2008) of the Rising Star hominin assemblage is an ongoing focus of investigation. Current evidence about the depositional history of the assemblage does not clearly test whether the individuals lived across a very short time or whether they were close genetic relatives. Either of these scenarios might contribute to the observation of low morphological variation, and neither of these factors is mutually exclusive. Future research may establish that each has played a role.

4.3. The taxonomic unity of the Homo naledi *assemblage*

Variation in the tooth samples is low and low enough in a few cases to raise questions about whether two sexes are present in the sample for a given tooth. Sample size alone cannot explain the pattern observed here since our resampling procedures account for sample size and small samples are not necessarily less variable than the populations from which they are drawn (SOM S1; SOM Fig. S11). In no case does the *H. naledi* dental assemblage exceed variation expected based on the reference samples (see also Garvin et al., 2017). Combined with studies that show a consistent anatomical pattern within and among the various collection loci and across the skeleton (e.g., Feuerriegel et al., 2019; Walker et al., 2019; Davies et al., 2020; Cofran et al., 2022), it would be remarkable if more than one species is mixed in the assemblage. From a dental perspective, these species would have to be astonishingly similar in tooth size, relative tooth size, and nonmetric morphology (Irish et al., 2018; Irish and Grabowski, 2021).

The pattern seen in *H. naledi* contrasts with that found in nearly contemporaneous hominin assemblages. An age of 335–241 ka (Dirks et al., 2017) places the Dinaledi fossils within the late Middle Pleistocene, a period noted for the existence of multiple differentiated hominin lineages (e.g., Hublin et al., 2017; Bermúdez de Castro et al., 2022). The Dinaledi assemblage was deposited slightly before the oldest fossils firmly attributed to *H. sapiens* (Robbins et al., 2021; Vidal et al., 2022). A recent study by Grine et al. (2021; see also Grine, 2023) suggested that Middle and Late Pleistocene populations of *H. sapiens* across Africa exhibit a range of variation in craniodental form that exceeds that of extant human groups. They referred to this pattern as “persistent Pleistocene variation” (Grine et al., 2021:15). Although the geographic and temporal ranges of the *H. sapiens* fossils are much greater than is the case for the currently available *H. naledi* sample, it is notable that single sites with relatively small samples of early *H. sapiens* remains—i.e., Omo and Klasies River—also express a high level of variation relative to extant human groups (Royer et al., 2009; Grine et al., 2021). In the case of Klasies River, Grine et al. (2021) found that variation in a small sample of teeth that accumulated over no more than 18,000 years exceeded that in extant human samples. The contrast between *H. naledi* and early *H. sapiens* raises interesting questions about the population dynamics of the two species. However, given that we cannot confidently rule out a biased sampling process as one driver of variation in the current *H. naledi* sample—as opposed to a general feature of the species' biology—we do not think it is justified to speculate on how the evolutionary histories of *H. naledi* and early *H. sapiens* may have differed.

5. Conclusions

Variation in tooth size in the current hypodigm of *H. naledi* mostly fits expectations for a single species using extant hominoids as models. Some teeth provide evidence for unusually low variation. The most notable of these is the M^1, but M_1, I^2 and P^4 exhibit low size variation as well. Our findings match descriptions of other aspects of phenotypic variation in *H. naledi*, such as body size and brain size. At least two interpretations are consistent with our results. First, low population- or species-level variation may have been a biological feature of *H. naledi*, a pattern that contrasts with other Middle Pleistocene hominins. Second, one sex may be disproportionately represented in the *H. naledi* assemblage, resulting in downwardly biased estimates of variation. In the case of M^1, extreme sex ratios (9:1 or 10:0) must be assumed for sample variation in *H. naledi* to be consistent with expectations derived from any of the extant hominoid samples. Other factors related to the formation of the *H. naledi* assemblage may also have contributed to low variation in the samples (e.g., geologically rapid accumulation of closely related individuals) but this must apply across the four published loci in which *H. naledi* remains have been described within the Rising Star cave system. Such hypotheses can be tested as the fossil sample expands and our understanding of the geology and taphonomy of the Rising Star cave system improves. Most promising would be studies of molecular aspects of *H. naledi* (ancient DNA and enamel proteomic analysis) that could provide insight into the sex ratio of the individuals recovered from the cave system to date.

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References

Berger, L.R., Hawks, J., de Ruiter, D.J., Churchill, S.E., Schmid, P., Delezene, L.K., Kivell, T.L., Garvin, H.M., Williams, S.A., DeSilva, J.M., Skinner, M.M., Musiba, C.M., Cameron, N., Holliday, T.W., Harcourt-Smith, W., Ackermann, R.R., Bastir, M., Bogin, B., Bolter, D., Brophy, J., Cofran, Z.D., Congdon, K.A., Deane, A.S., Dembo, M., Drapeau, M., Elliott, M.C., Feuerriegel, E.M., Garcia-Martinez, D., Green, D.J., Gurtov, A., Irish, J.D., Kruger, A., Laird, M.F., Marchi, D., Meyer, M.R., Nalla, S., Negash, E.W., Orr, C.M., Radovcic, D., Schroeder, L., Scott, J.E., Throckmorton, Z., Tocheri, M.W., VanSickle, C., Walker, C.S., Wei, P., Zipfel, B., 2015. *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. Elife 4, e09560.

Berger, L.R., Hawks, J., Dirks, P.H.G.M., Elliott, M., Roberts, E.M., 2017. *Homo naledi* and Pleistocene hominin evolution in subequatorial Africa. Elife 6, e24234.

Berger, L.R., Makhubela, T., Molopyane, K., Kruger, A., Randolph-Quinney, P., Elliott, M., Peixotto, B., Fuentes, A., Tafforeau, P., Beyrand, V. Dollman, K., Jinnah, Z., Gillham, A.B., Broad, K., Brophy, J., Chinamatira, G., Dirks, P.H.M., Feuerriegel, E., Gurtov, A., Hlophe, N., Hunter, L., Hunter, R., Jakata, K., Jaskolski, C., Morris, H., Pryor, E., Ramaphela, M., Roberts, E., Smilg, J.S., Tsikoane, M., Tucker, S., van Rooyen, D., Warren, K., Wren, C.D., Kissel, M., Spikins, P., Hawks, J., 2023. Evidence for deliberate burial of the dead by *Homo naledi*. eLife 12, RP89106.

Behrensmeyer, A.K., 2008. Paleoenvironmental context of the Pliocene A.L. 333 ‘First Family’ hominin locality, Hadar Formation, Ethiopia.” In: Quade, J., Wynn, J.G., (Eds.), The Geology of Early Humans in the Horn of Africa. Geol. Soc. Amer. Spec. 446, 203–214.

Behrensmeyer, A.K., Kidwell, S.M., Gastaldo, R.A., 2000. Taphonomy and paleobiology. Paleobiology 26, 103–147.

Bermúdez de Castro, J.M.B., Sarmiento, S., Cunha, E., Rosas, A. Bastir, M., 2001. Dental size variation in the Atapuerca-SH Middle Pleistocene hominids. J. Hum. Evol. 41, 195–209.

Bermúdez de Castro, J.M.B., Martinón-Torres, M., 2022. The origin of the *Homo sapiens* lineage: When and where? Quat. Int. 634, 1–13.

Berthaume, M.A., Delezene, L.K., Kupczik, K., 2018. Dental topography and the diet of *Homo naledi*. J. Hum. Evol. 118, 14–26.

Bolter, D.R., Hawks, J., Bogin, B., Cameron, N., 2018. Palaeodemographics of individuals in Dinaledi Chamber using dental remains. S. Afr. J. Sci. 114, 1–6.

Bolter, D.R., Cameron, N., 2020. Utilizing auxology to understand ontogeny of extinct hominins: A case study on *Homo naledi*. Am. J. Phys. Anthropol. 173, 368–380.

Brophy, J.K., Elliott, M.C., De Ruiter, D.J., Bolter, D.R., Churchill, S.E., Walker, C.S., Hawks, J., Berger, L.R., 2021. Immature hominin craniodental remains from a new locality in the Rising Star Cave System, South Africa. PaleoAnthropology 1, 1–14.

Buikstra, J.E., Ubelaker, D.H., 1994. Standards for data collection from human skeletal remains. Fayetteville, AR: Arkansas Archeological Survey Research Series No. 44.

Cofran, Z., Walker, C. S., 2017. Dental development in *Homo naledi*. Biol. Lett. 13, 20170339.

Cofran, Z., VanSickle, C., Valenzuela, R., García- Martínez, D., Walker, C.S., Hawks, J., Zipfel, B., Williams, S.A., Berger, L.R., 2022. The immature *Homo naledi* ilium from the Lesedi Chamber, Rising Star Cave, South Africa. Am. J. Biol. Anthropol. 179, 3–17.

Cope, D.A., Lacy, M.G., 1992. Falsification of a single species hypothesis using the coefficient of variation: a simulation approach. Am. J. Phys. Anthropol. 89, 359–378.

Cope, D.A., Lacy, M.G., 1995. Comparative application of the coefficient of variation and range-based statistics for assessing the taxonomic composition of fossil samples. J. Hum. Evol. 29, 549–575.

Davies, T.W., Delezene, L.K., Gunz, P., Hublin, J.-J., Skinner, M.M., 2019a. Endostructural morphology in hominoid mandibular third premolars: Geometric morphometric analysis of dentine crown shape. J. Hum. Evol. 133, 198–213.

Davies, T.W., Delezene, L.K., Gunz, P., Hublin, J.-J., Skinner, M.M., 2019b. Endostructural morphology in hominoid mandibular third premolars: Discrete traits at the enamel-dentine junction. J. Hum. Evol. 136, 102670.

Davies, T.W., Delezene, L.K., Gunz, P., Hublin, J.-J., Berger, L.R., Gidna, A., Skinner, M.M., 2020. Distinct mandibular premolar crown morphology in *Homo naledi* and its implications for the evolution of *Homo* species in southern Africa. Sci. Rep. 10, 13196.

Delezene, L.K., 2015. Modularity of the anthropoid dentition: Implications for the evolution of the hominin canine honing complex. J. Hum. Evol. 86, 1–12.

Delezene, L.K., Skinner, M.M., Bailey, S., Brophy, J.K., Moggi-Cecchi, J., Irish, J.D., Hawks, J., Berger, L.R., 2023. Descriptive catalog of *Homo naledi* dental remains from the 2013–2015 excavations of the Dinaledi Chamber, Site U.W. 101, within the Rising Star cave system, South Africa. J. Hum. Evol. 180, 103372.

Demeter, F., Zanolli, C., Westaway, K.E., Joannes-Boyau, R., Duringer, P., Morley, M.W., Welker, F., Rüther, P.L., Skinner, M.M., McColl, H., Gaunitz, C., 2022. A Middle Pleistocene Denisovan molar from the Annamite chain of northern Laos. Nat. Commun. 13, 2557.

de Ruiter, D. J., Laird, M. F., Elliott, M., Schmid, P., Brophy, J., Hawks, J., Berger, L. R., 2019. *Homo naledi* cranial remains from the Lesedi Chamber of the Rising Star cave system, South Africa. J. Hum. Evol. 132, 1–14.

Dirks, P.H., Berger, L.R., Roberts, E.M., Kramers, J.D., Hawks, J., Randolph-Quinney, P.S., Elliott, M., Musiba, C.M., Churchill, S.E., de Ruiter, D.J., Schmid, P., 2015. Geological and taphonomic context for the new hominin species *Homo naledi* from the Dinaledi Chamber, South Africa. Elife 4, e09561.

Dirks, P. H., Berger, L.R., Hawks, J., Randolph-Quinney, P.S., Backwell, L.R., Roberts, E.M., 2016. Deliberate body disposal by hominins in the Dinaledi Chamber, Cradle of Humankind, South Africa? J. Hum. Evol. 96, 1–5.

Dirks, P.H., Roberts, E.M., Hilbert-Wolf, H., Kramers, J.D., Hawks, J., Dosseto, A., Duval, M., Elliott, M., Evans, M., Grün, R., Hellstrom, J., 2017. The age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa. Elife 6, e24231.

du Plessis, M., 2019. The Khoisan languages of southern Africa: Facts, theories and confusions. Crit. Arts 33, 33–54.

Egeland, C.P., Domínguez-Rodrigo, M., Pickering, T.R., Heaton, J.L., 2018. Hominin skeletal part abundances and claims of deliberate disposal of corpses in the Middle Pleistocene. Proc. Natl. Acad. Sci. USA 115, 4601–4606.

Elliott M., Makhubela, T., Brophy, J., Churchill, S., Peixotto, B., Feuerriegel, E., Morris, H., Van Rooyen, D., Ramalepa, M., Tsikoane, M., Kruger, A., 2021. Expanded explorations of the Dinaledi subsystem, Rising Star cave system, South Africa. PaleoAnthropology 1, 15–22.

Feuerriegel, E.M., Voisin, J-L., Churchill, S., Haeusler, M., Mathews, S., Schmid, P., Hawks, J., Berger, L.R., 2019. Upper limb fossils of *Homo naledi* from the Lesedi Chamber, Rising Star System, South Africa. PaleoAnthropology 311–349.

Garvin, H.M., Elliott, M.C., Delezene, L.K., Hawks, J., Churchill, S.E., Berger, L.R., Holliday, T.W., 2017. Body size, brain size, and sexual dimorphism in *Homo naledi* from the Dinaledi Chamber. J. Hum. Evol. 111, 119–138.

Goossens, B., Chikhi, L., Jalil, M.F., James, S., Ancrenaz, M., Lackman-Ancrenaz, I., Bruford, M.W., 2009. Taxonomy, geographic variation and population genetics of Bornean and Sumatran orangutans. In: Wich, S.A., Atmoko, S.S.U., Tatang, M.S., van Schaik, C.P. (Eds.), Orangutans: Geographic Variation in Behavioral Ecology and Conservation., Oxford University Press, New York, pp. 215–224.

Gordon, A.D., Green, D.J., Richmond, B.G., 2008. Strong postcranial size dimorphism in *Australopithecus afarensis*: Results from two new resampling methods for multivariate data sets with missing data. Am. J. Phys. Anthropol. 135, 311–328.

Gower, G., Fenderson, L.E., Salis, A.T., Helgen, K.M., van Loenen, A.L., Heiniger, H., Hofman-Kamińska, E., Kowalczyk, R., Mitchell, K.J., Llamas, B., Cooper, A., 2019. Widespread male sex bias in mammal fossil and museum collections. Proc. Natl. Acad. Sci. USA 116, 19019–19024.

Grine, F. E., 2023. Introduction: The fossil record of *Homo sapiens* in Africa–morphological fariability in the Late Quaternary and the significance of the Hofmeyr skull. In: Grine F.E. (Ed.), Hofmeyr: A Late Pleistocene Human Skull from South Africa. Springer Cham, Switzerland, pp. 1–5.

Grine, F.E., Gonzalvo, E., Rossouw, L., Holt, S., Black, W., Braga, J., 2021. Variation in Middle Stone Age mandibular molar enamel-dentine junction topography at Klasies River Main Site assessed by diffeomorphic surface matching. J. Hum. Evol. 161, 103079.

Haeussler, A.M., Irish, J.D., Morris, D.H., Turner, C.G., 1989. Morphological and metrical comparison of San and Central Sotho dentitions from southern Africa. Am. J. Phys. Anthropol. 78, 115–122.

Haldane, J.B.S., 1955. The measurement of variation. Evolution 9, 484.

Harmon, E., 2009. Size and shape variation in the proximal femur of *Australopithecus africanus*. J. Hum. Evol. 56, 551–559.

Hawks, J., Elliott, M., Schmid, P., Churchill, S.E., de Ruiter, D.J., Roberts, E.M., Hilbert-Wolf, H., Garvin, H.M., Williams, S.A., Delezene, L.K., Feuerriegel, E.M., Randolph-Quinney, P., Kivell, T.L., Laird, M.F., Tawane, G., DeSilva, J.M., Bailey, S.E., Brophy, J.K., Meyer, M.R., Skinner, M.M., Tocheri, M.W., VanSickle, C., Walker, C.S., Campbell, T.L., Kuhn, B., Kruger, A., Tucker, S., Gurtov, A., Hlophe, N., Hunter, R., Morris, H., Peixotto, B., Ramalepa, M., van Rooyen, D., Tsikoane, M., Boshoff, P., Dirks, P.H.G.M., Berger, L.R., 2017. New fossil remains of *Homo naledi* from the Lesedi Chamber, South Africa. Elife 6, e24232.

Hlusko L.J., Mahaney, M.C. 2009. Quantitative genetics, pleiotropy, and morphological integration in the dentition of *Papio hamadryas*. Evol. Biol. 36, 5–18.

Hlusko, L.J., Sage, R.D., Mahaney, M.C., 2011. Modularity in the mammalian dentition: mice and monkeys share a common dental genetic architecture. J. Exp. Zool. B Mol. Dev. Evol. 316, 21–49.

Hublin J-J., Ben-Ncer, A., Bailey, S.E., Freidline, S.E., Neubauer, S., Skinner, M.M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., Gunz, P., 2017. New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. Nature 546, 289–92.

Humphrey, L., Andrews, P., 2008. Metric variation in the postcanine teeth from Paşalar, Turkey. J. Hum. Evol. 54, 503–517.

Irish, J.D., 2006. Who were the ancient Egyptians? Dental affinities among Neolithic through postdynastic peoples. Am. J. Phys. Anthropol. 129, 529–543.

Irish, J.D., Bailey, S.B., Guatelli-Steinberg, D., Delezene, L.K., Berger, L.R., 2018. Ancient teeth, phenetic affinities, and African hominins: Another look at where *Homo naledi* fits in. J. Hum. Evol. 122, 108–123.

Irish, J. D., Grabowski, M., 2021. Relative tooth size, Bayesian inference, and *Homo naledi*. Am. J. Phys. Anthropol. 176, 262–282.

Johanson, D.C., 1974. Some metric aspects of the permanent and deciduous dentition of the pygmy chimpanzee (*Pan paniscus*). Am. J. Phys. Anthropol. 41, 39–48.

Kelley, J., Plavcan, J.M., 1998. A simulation test of hominoid species number at Lufeng, China: Implications for the use of the coefficient of variation in paleotaxonomy. J. Hum. Evol. 35, 577–596.

Kivell, T.L., Deane, A.S., Tocheri, M.W., Orr, C.M., Schmid, P., Hawks, J., Berger, L.R., Churchill, S.E., 2015. The hand of *Homo naledi*. Nat. Commun. 6, 8431.

Kupczik, K., Delezene, L.K., Skinner, M.M., 2019. Mandibular molar root and pulp cavity morphology in *Homo naledi* and other Plio-Pleistocene hominins. J. Hum. Evol. 130, 83–95.

Lockwood, C.A., 1999. Sexual dimorphism in the face of *Australopithecus africanus*. Am. J. Phys. Anthropol. 108, 97–127.

Lockwood C.A., Richmond, B.G., Jungers, W.L., Kimbel, W.H., 1996. Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. J. Hum. Evol. 31, 537–548.

Lockwood, C.A., Kimbel, W.H., Johanson, D.C., 2000. Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. J. Hum. Evol. 39, 23–55.

Lockwood, C.A., Menter, C.G., Moggi-Cecchi, J., Keyser, A.W., 2007. Extended male growth in a fossil hominin species. Science 318, 1443–1446.

Martinón-Torres, M., Garate, D., Herries, A.I., Petraglia, M.D., 2023. No scientific evidence that *Homo naledi* buried their dead and produced rock art. J. Hum. Evol., 103464.

Melillo, S.M., Gibert, L., Saylor, B.Z., Deino, A., Alene, M., Ryan, T.M., Haile-Selassie, Y., 2021. New Pliocene hominin remains from the Leado Dido’a area of Woranso-Mille, Ethiopia. J. Hum. Evol. 153, 102956.

Moggi-Cecchi, J., 2003. The elusive 'second species' in Sterkfontein Member 4: The dental metrical evidence. S. Afr. J. Sci. 99, 268–270.

Nel, C., Bradfield, J., Lombard, M., Val, A., 2021. Taphonomic study of a modern baboon sleeping site at Misgrot, South Africa: Implications for large-bodied primate taphonomy in karstic deposits. J. Paleolit. Archaeol. 4, 4.

Palesa P. M., Koenig, C., Patramanis, I., Rüther, P.L., Hlazo, N., Mackie, M., Tawane, M., Krueger, J., Taurozzi, A.J., Troché, G., Kibii, J., Pickering, R., Dickinson, M., Sahle, Y., Kgotleng, D., Musiba, C., Manthi, F., Bell, L., DuPlessis, M., Gilbert, C., Zipfel, B., Kuderna, L.F.K., Lizano, E., Welker, F., Kyriakidou, P., Cox, J., Mollereau, C., Tokarski, C., Blackburn, J., Ramos-Madrigal, J., Marques-Bonet, T., Penkman, K., Zanolli, C., Schroeder, L., Racimo, F., Olsen, J.V., Ackermann, R.R., Cappellini, E., 2023. Enamel proteins reveal biological sex and genetic variability within southern African *Paranthropus*. bioRxiv 2023.07.03.547326

Plavcan, J.M., 1994. Comparison of four simple methods for estimating sexual dimorphism in fossils. Am. J. Phys. Anthropol. 94, 465–476.

Plavcan, J.M., 2012. Sexual size dimorphism, canine dimorphism, and male-male competition in primates: Where do humans fit in? Hum. Nat. 23, 45–67.

Plavcan, J.M., Lockwood, C.A., Kimbel, W.H., Lague, M.R., Harmon, E.H., 2005. Sexual dimorphism in *Australopithecus afarensis* revisited: How strong is the case of a human-like pattern of dimorphism? J. Hum. Evol. 48, 313–320.

Randolph-Quinney, P.S., 2015. The mournful ape: Conflating expression and meaning in the mortuary behaviour of *Homo naledi*. S. Afr. J. Sci. 111, 1–5.

Rightmire, G.P., Margvelashvili, A., Lordkipanidze, D., 2019. Variation among the Dmanisi hominins: Multiple taxa or one species? Am. J. Phys. Anthropol. 168, 481–495.

Robbins, J.L., Dirks, P.H., Roberts, E.M., Kramers, J.D., Makhubela, T.V., Hilbert-Wolf, H.L., Elliott, M., Wiersma, J.P., Placzek, C.J., Evans, M., Berger, L.R., 2021. Providing context to the *Homo naledi* fossils: Constraints from flowstones on the age of sediment deposits in Rising Star Cave, South Africa. Chem. Geol. 567, 120108.

Roseman, C.C., Delezene, L.K., 2019. The inhibitory cascade model is not a good predictor of molar size covariation. Evol. Biol. 46, 229–238.

Royer, D. F., Lockwood, C. A., Scott, J. E., Grine, F. E., 2009. Size variation in early human mandibles and molars from Klasies River, South Africa: Comparison with other Middle and Late Pleistocene assemblages and with modern humans. Am. J. Phys. Anthropol. 140, 312–323.

Schrein, C.M., 2006. Metric variation and sexual dimorphism in the dentition *of Ouranopithecus macedoniensis*. J. Hum. Evol. 50, 460–468.

Scott, J.E., Stroik, L.K, 2006. Bootstrap tests of significance and the case for humanlike skeletal-size dimorphism in *Australopithecus afarensis*. J. Hum. Evol. 51, 422–428.

Scott, J.E., Schrein, C.M., Kelley, J., 2009. Beyond *Gorilla* and *Pongo*: Alternative models for evaluating variation and sexual dimorphism in fossil hominoid samples. Am. J. Phys. Anthropol. 140, 253–264.

Silverman, N., Richmond, B., Wood, B., 2001. Testing the taxonomic integrity of *Paranthropus boisei sensu stricto*. Am. J. Phys. Anthropol. 115, 167–178.

Skinner, M. M., Gordon, A. D., Collard, N. J., 2006. Mandibular size and shape variation in the hominins at Dmanisi, Republic of Georgia. J. Hum. Evol. 51, 36–49.Smith, R. J., 2020. P>. 05: The incorrect interpretation of “not significant” results is a significant problem. Am. J. Phys. Anthropol. 172, 521–527.

Sokal, R.R., Braumann, C.A., 1980. Significance tests for coefficients of variation and variability profiles. Syst. Zool. 29, 50–66.

Stewart, N.A., Gerlach, R.F., Gowland, R.L., Gron, K.J., Montgomery, J., 2017. Sex determination of human remains from peptides in tooth enamel. Proc. Natl. Acad. Sci. USA 114, 13649–13654.

Stojanowski, C.M., Paul, K.S., Seidel, A.C., Duncan, W.N. and Guatelli- Steinberg, D., 2017. Heritability and genetic integration of tooth size in the South Carolina Gullah. Am. J. Phys. Anthropol. 164, 505–521.

Trinkaus, E., 1980. Sexual differences in Neanderthal limb bones. J. Hum. Evol. 9, 377–397.

Val, A., 2016. Deliberate body disposal by hominins in the Dinaledi Chamber, Cradle of Humankind, South Africa? J. Hum. Evol. 96, 145–148.

Vidal, C.M., Lane, C.S., Asrat, A., Barfod, D.N., Mark, D.F., Tomlinson, E.L., Tadesse, A.Z., Yirgu, G., Deino, A., Hutchison, W., Mounier, A., 2022. Age of the oldest known *Homo sapiens* from eastern Africa. Nature 601, 579–583.

Villmoare, B., 2005. Metric and non-metric randomization methods, geographic variation, and the single-species hypothesis for Asian and African *Homo erectus*. J. Hum. Evol. 49, 680–701.

Walker, C.S., Cofran, Z.D., Grabowski, M., Marchi, D., Cook, R.W., Churchill, S.E., Tommy, K.A., Throckmorton, Z., Ross, A.H., Hawks, J., Yapuncich, G.S., 2019. Morphology of the *Homo naledi* femora from Lesedi. Am. J. Phys. Anthropol. 170, 5–23.

Welker, F., 2018. Palaeoproteomics for human evolution studies. Quat. Sci. Rev. 190, 137–147.

Welker, F., Ramos-Madrigal, J., Gutenbrunner, P., Mackie, M., Tiwary, S., Jersie-Christensen, S.R., Chiva, S., Dickinson, M.R., Kuhlwilm, M., de Manuel, M., Gelabert, P., 2020. The dental proteome of *Homo antecessor*. Nature 580, 235–238.

Ziganshin, R.H., Berezina, N.Y., Alexandrov, P.L., Ryabinin, V.V., Buzhilova, A.P., 2020. Optimization of method for human sex determination using peptidome analysis of teeth enamel from teeth of different biological generation, archeological age, and degrees of taphonomic preservation. Biochemistry 85, 614–622.

Figure Legends

Figure 1. Resampling results for the C^1. The 95% confidence intervals are indicated by the horizontal lines; the dot is the mean of the resampled distribution.

Figure 2. Resampling results for the C_1. The 95% confidence intervals are indicated by the horizontal lines; the dot is the mean of the resampled distribution.

Figure 3. Resampling results for the I_2. The 95% confidence intervals are indicated by the horizontal lines; the dot is the mean of the resampled distribution.

Figure 4. Resampling results for the M_1. The 95% confidence intervals are indicated by the horizontal lines; the dot is the mean of the resampled distribution.

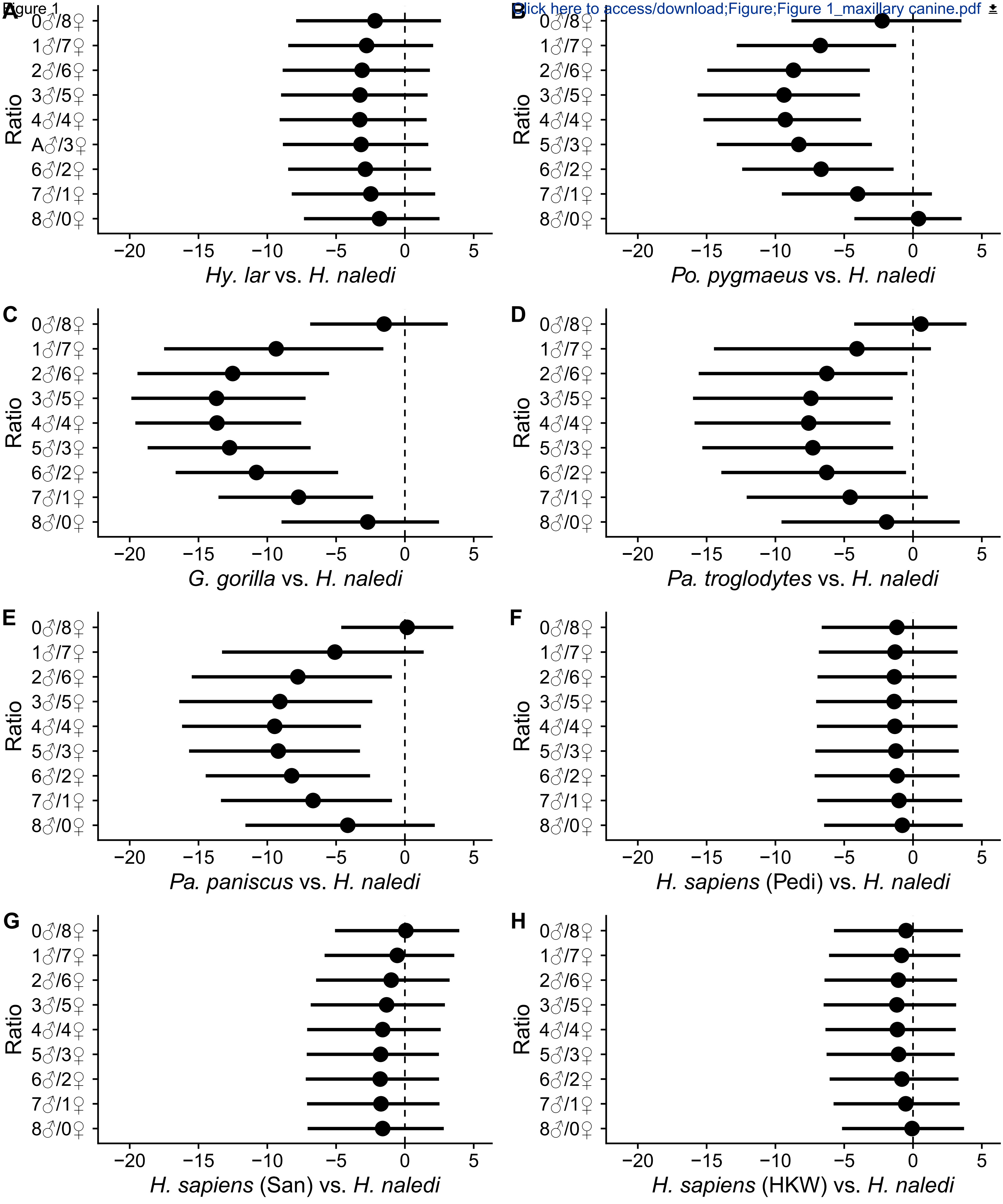
Figure 5. Resampling results for the P^4. The 95% confidence intervals are indicated by the horizontal lines; the dot is the mean of the resampled distribution.

Figure 6. Resampling results for the M^1. The 95% confidence intervals are indicated by the horizontal lines; the dot is the mean of the resampled distribution.

Figure 7. Binomial probability of sampling fewer than two individuals of one sex at a given sample size when preservation and recovery are unbiased (blue) and biased (red, gray) with regard to sex. The blue circles show the probabilities when the relative frequencies of each sex in the fossil record are equal ($p = q = 0.5$); the red circles show the probabilities when the relative

frequencies are p = 0.6 for one sex and q = 0.4 for the other; and the gray circles show the probabilities when the relative frequencies are p = 0.7 and q = 0.3.

Figure 1
Click here to access/download;Figure;Figure 1_maxillary canine.pdf



95% Confidence intervals for C¹ bootstrapped CV differences

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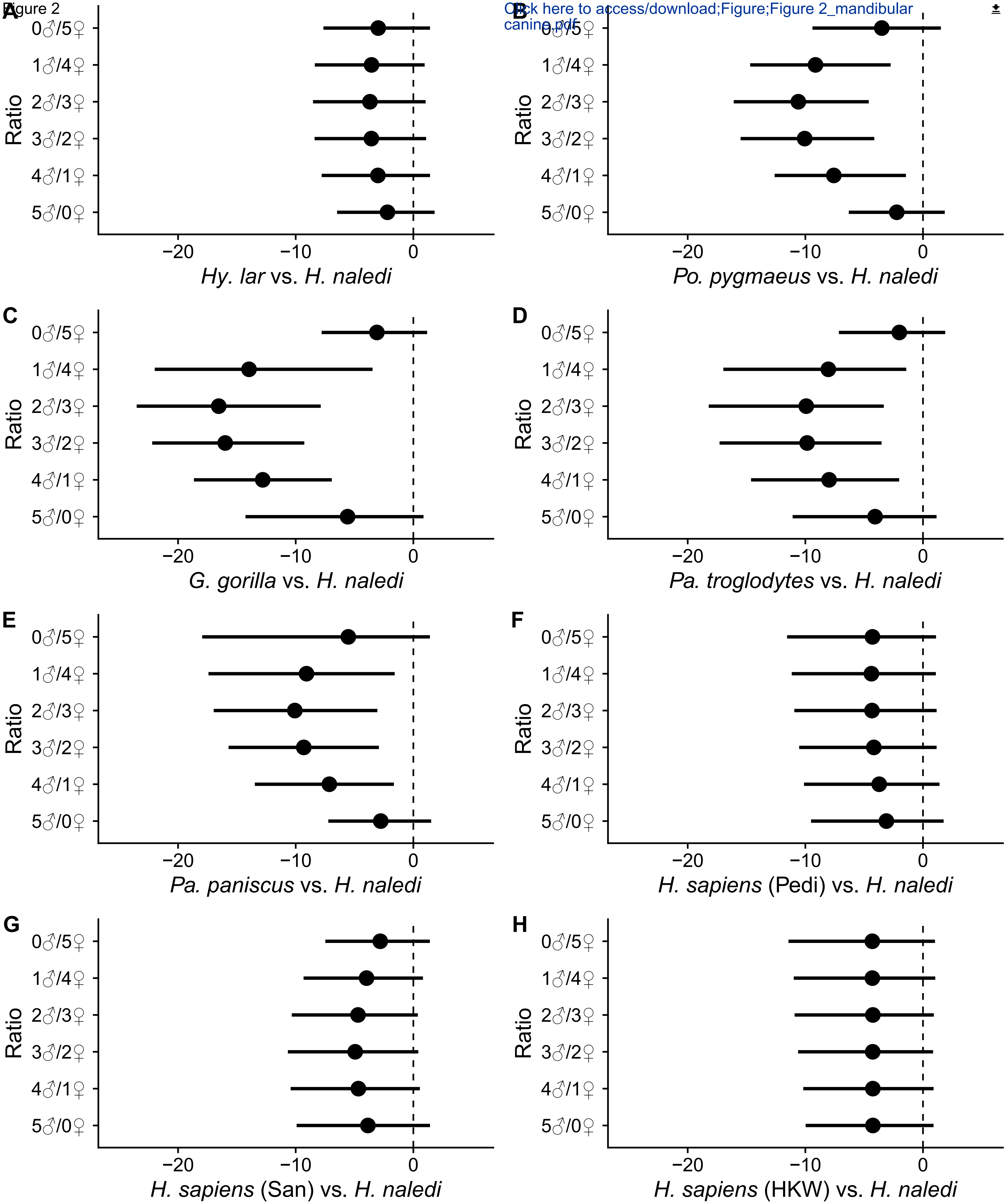

95% Confidence intervals for C_1 bootstrapped CV differences

Figure 3 Click here to access/download;Figure;Figure 3_LowerI2summary.pdf

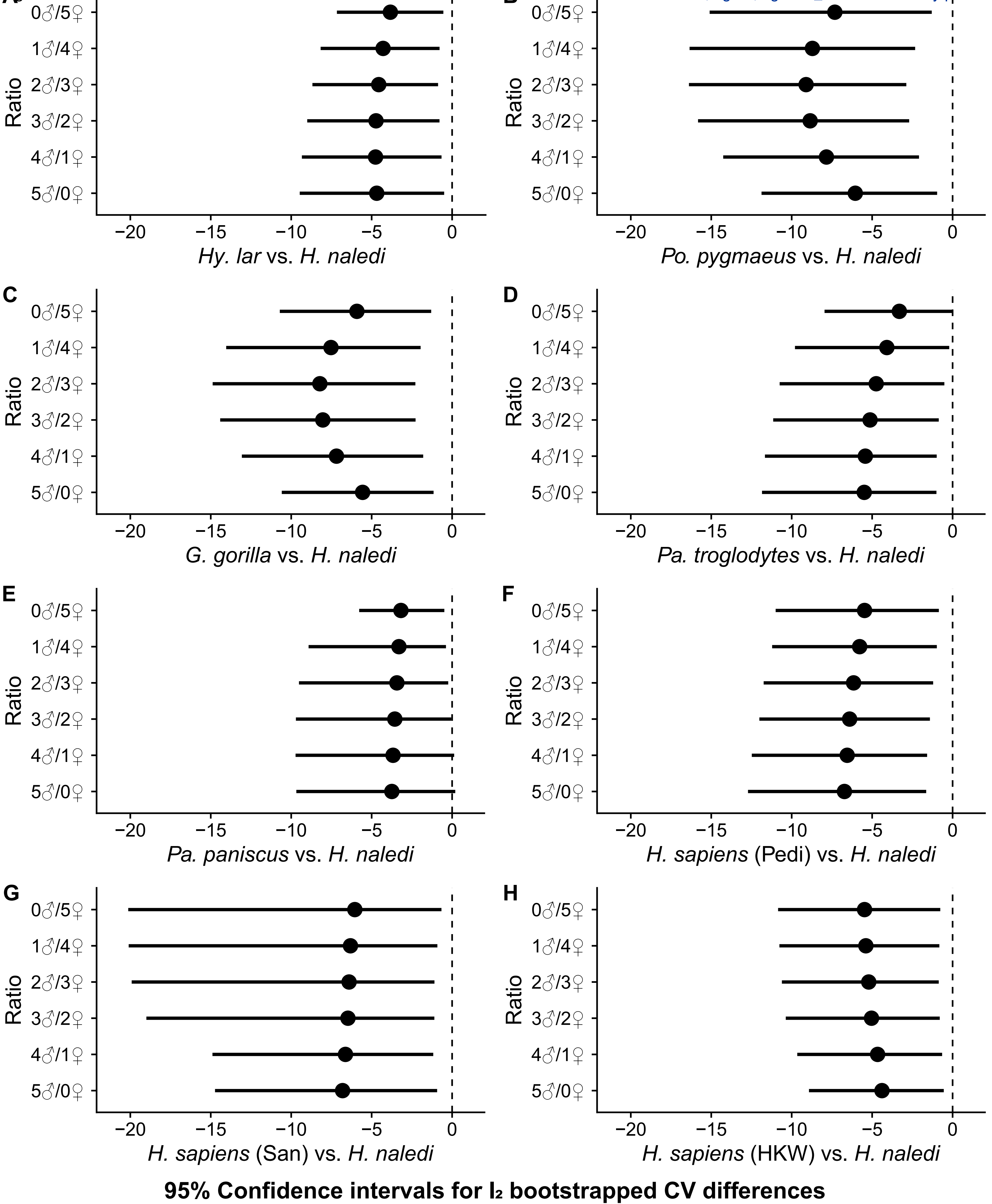

Figure 4

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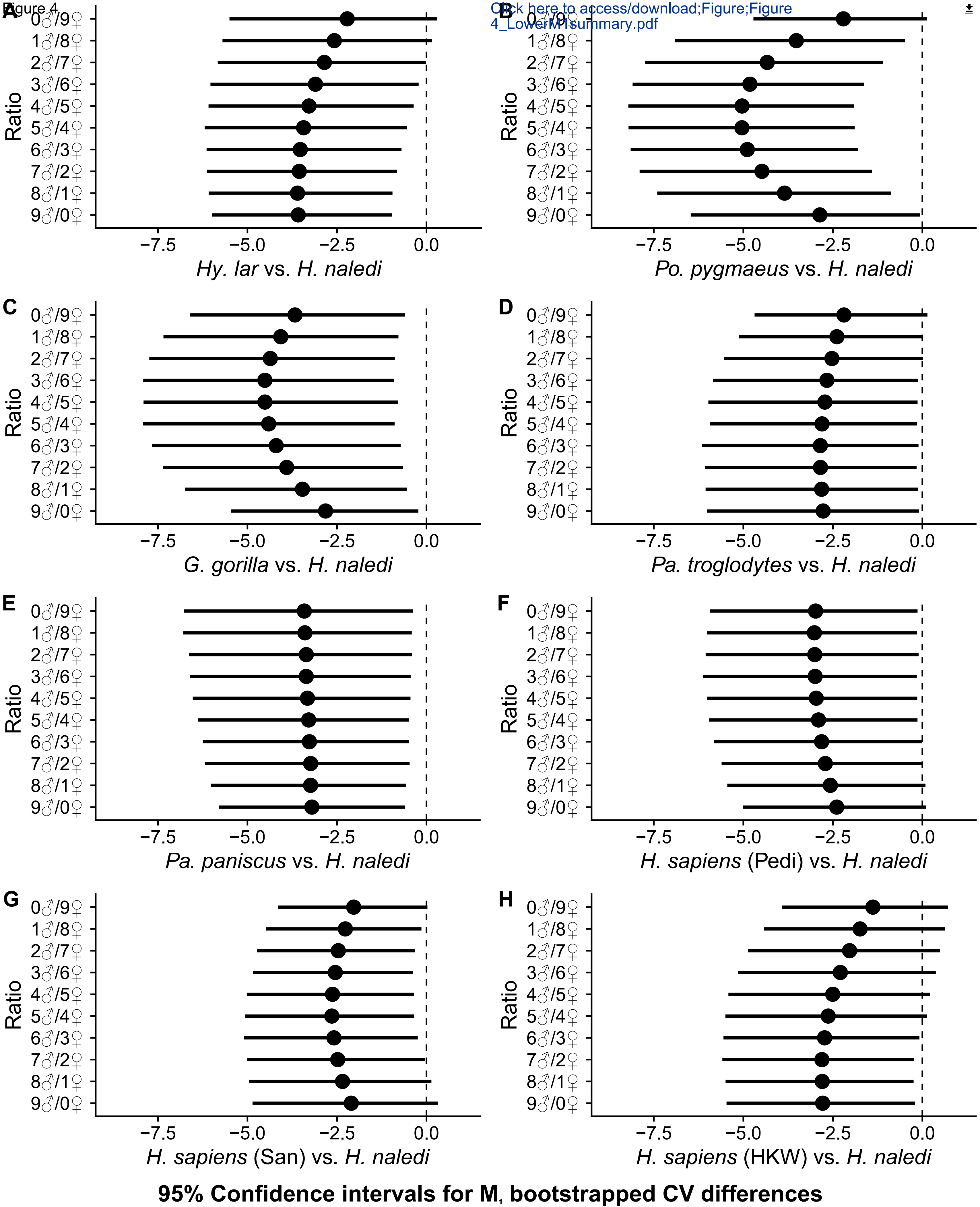

Figure 5
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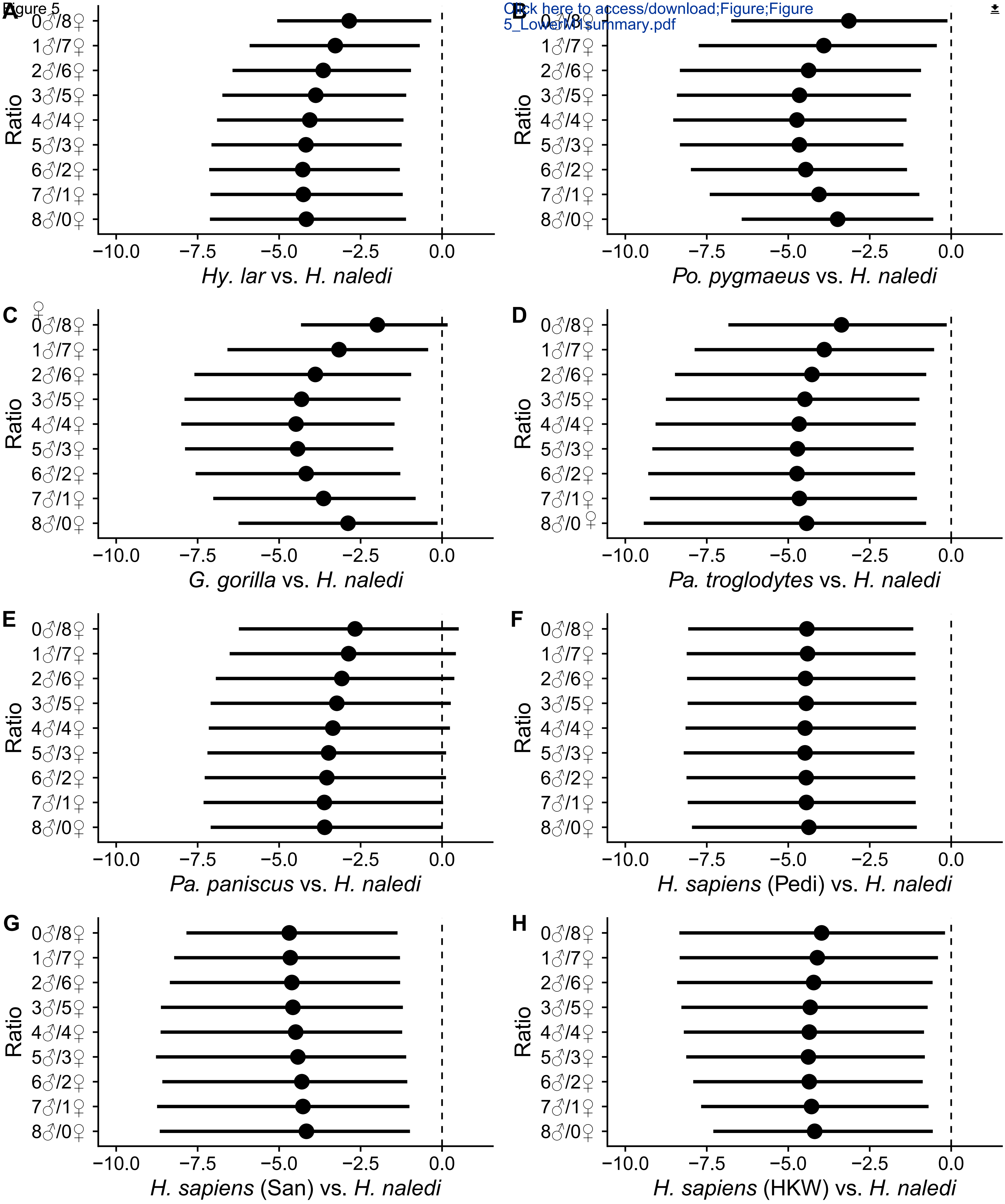
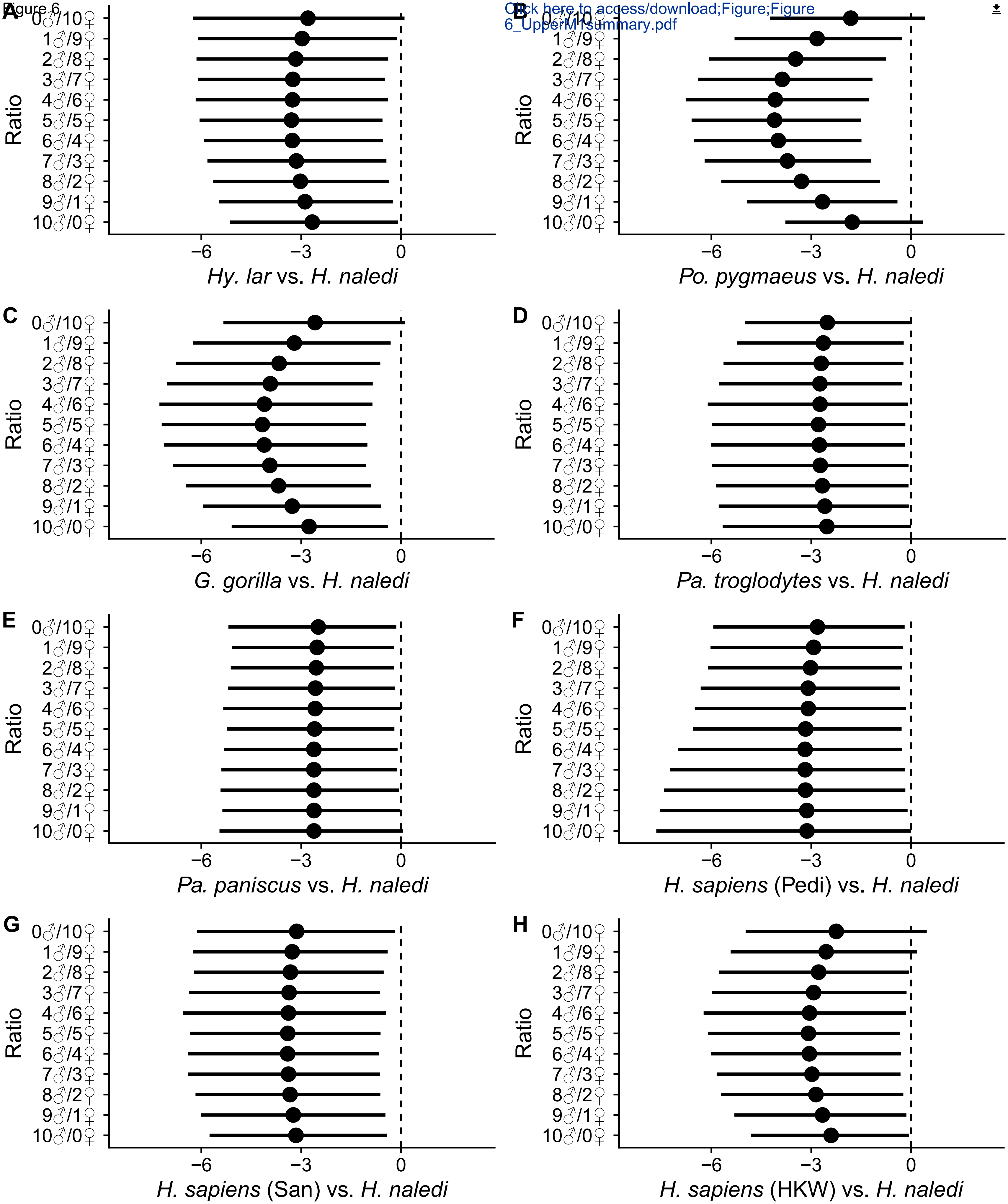


95% Confidence Intervals for M_1 Bootstrapped CV Differences

Figure 6
Click here to access/download;Figure;Figure 6_UpperM1summary.pdf



95% Confidence intervals for M¹ bootstrapped CV differences

Figure 7

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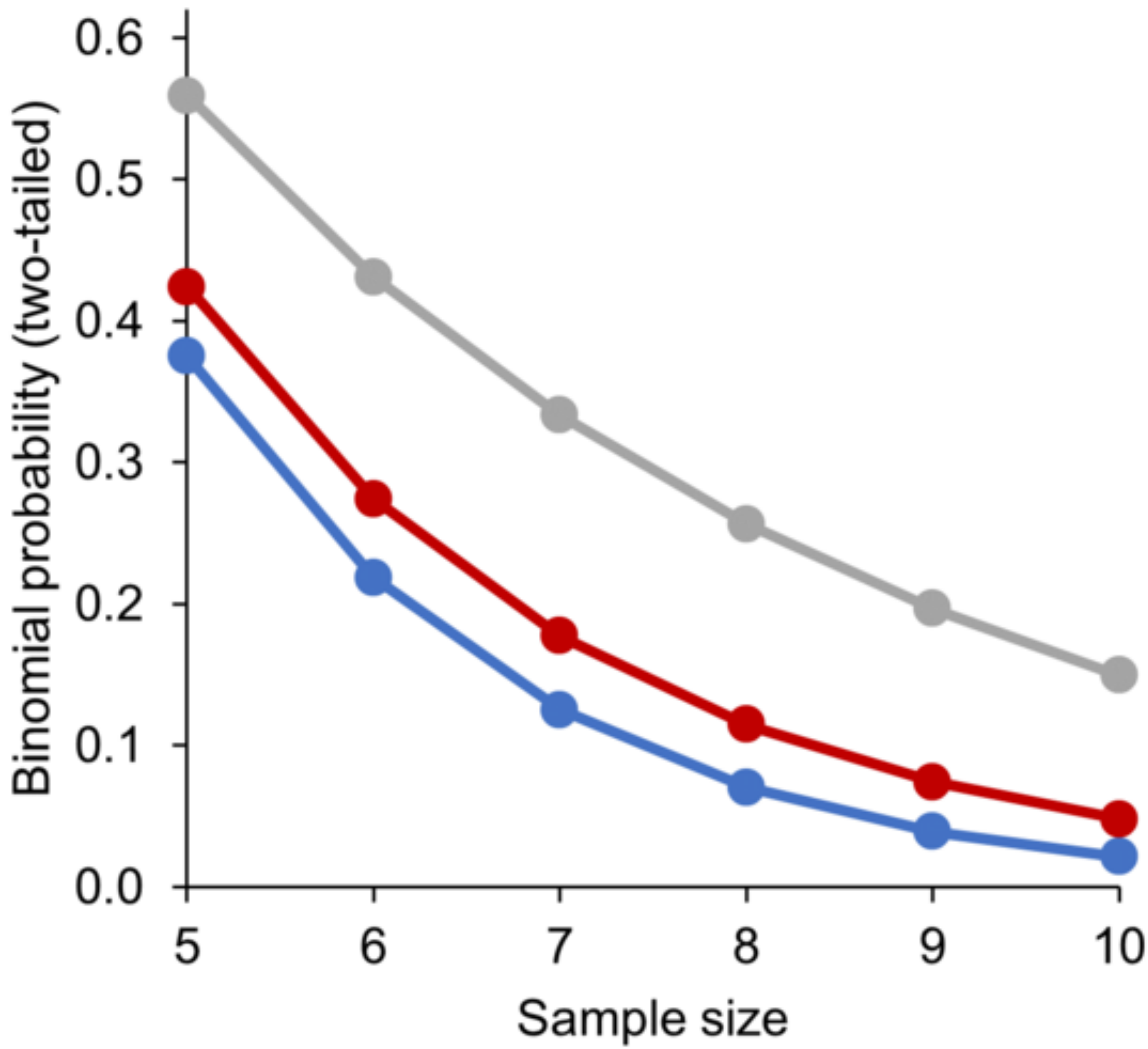

Table 1

Homo naledi specimens considered for analysis. Antimeres are listed together in parentheses.

	Mandibular	Maxillary
I1	(U.W. 101-039, U.W. 101-601), (U.W. 101-1005A, U.W. 101-1005B), U.W. 101-1261, (U.W. 101-1132, U.W. 101-1133), U.W. 102a-240	U.W. 101-038, U.W. 101-591, (U.W. 101-931, U.W. 101-1012), U.W. 101-1277, U.W. 101-1558, U.W. 102a-089, U.W. 110-14
I2	U.W. 101-335, (U.W. 101-998, U.W. 101-1005C), (U.W. 101-1075, U.W. 101-1131), U.W. 101-1261, U.W. 102a-240	(U.W. 101-073, U.W. 101-1588), U.W. 101-417, (U.W. 101-709, U.W. 101-932), U.W. 101-952, U.W. 101-1277, U.W. 101-1684, U.W. 102a-089, U.W. 110-15
C	(U.W. 101-339, U.W. 101-985), (U.W. 101-886, U.W. 101-1126), (U.W. 101-1076, U.W. 101-1014), U.W. 101-1261, U.W. 102a-240	U.W. 101-337, U.W 101-347, (U.W. 101-412, U.W. 101-908), U.W. 101-501, (U.W. 101-706, U.W. 101-816), U.W. 101-1277, U.W. 101-1556, U.W. 102a-089
P3	U.W. 101-010, (U.W. 101-144, U.W. 101-506), (U.W. 101-298, U.W. 101-1565), (U.W. 101-377, U.W. 101-889), U.W. 101-800, U.W. 101-850, U.W. 101-1261, U.W. 102a-240	U.W. 101-037, U.W. 101-182, U.W. 101-729, (U.W. 101-786, U.W. 101-1004), U.W. 101-1107, U.W. 101-1277, (U.W. 101-1402, U.W. 101-1560), U.W. 102a-089
P4	U.W. 101-001, (U.W. 101-184, U.W. 101-383), (U.W. 101-377, U.W. 101-887), U.W. 101-1261, U.W. 102a-240	U.W. 101-277, (U.W. 101-333, U.W. 101-334), (U.W. 101-455, U.W. 101-808), U.W. 101-1277, (U.W. 101-1401, U.W. 101-1561), U.W. 102a-089, U.W. 102b-016, U.W. 110-2
M1	(U.W. 101-285, U.W. 101-582), (U.W. 101-297, U.W. 101-905), (U.W. 101-377, U.W. 101-809), U.W. 101-814, U.W. 101-1261, U.W. 101-1287B, (U.W. 101-1400, U.W. 101-1689), U.W. 102a-240, U.W. 102c-001	U.W. 101-020, U.W. 101-344, (U.W. 101-445, U.W. 101-583), (U.W. 101-525, U.W. 101-1676), (U.W. 101-708, U.W. 101-999), (U.W. 101-1277, U.W. 101-1463), (U.W. 101-1305, U.W. 101-1688), U.W. 101-1396, U.W. 102a-089, U.W. 110-5

M2	U.W. 101-001, (U.W. 101-145, U.W. 101-507), U.W. 101-284, (U.W. 101-377, U.W. 101-789), U.W. 101-1142, U.W. 101-1261, U.W. 102a-240, U.W. 102c-001	(U.W. 101-505, U.W. 101-593), U.W. 101-867, (U.W. 101-1006, U.W. 101-1015), U.W. 101-1277, U.W. 101-1522, U.W. 102a-089
M3	(U.W. 101-001, U.W. 101-516), U.W. 101-361, U.W. 101-1142, U.W. 101-1261, U.W. 102a-240	(U.W. 101-418C, U.W. 101-594), U.W. 101-527, U.W. 101-1269, (U.W. 101-1398A, U.W. 101-1471), U.W. 102a-089

Table 2

Summary statistics for *Homo naledi* bucco(labio)lingual dimensions. Sample size (*n*) refers to the number of individuals, as values for proposed antimeres are averaged.

	I^1	I^2	C^1	P^3	P^4	M^1	M^2	M^3
n	7	8	8	8	8	10	6	5
min.	6.4	5.9	8.2	9.9	10.7	11.3	12.4	12.2
max.	7.1	6.9	9.7	10.9	11.3	12.4	13.6	13.2
$\bar{X}$	6.6	6.4	8.7	10.6	11.1	11.8	12.9	12.7
s	0.28	0.35	0.57	0.45	0.25	0.30	0.46	0.43
	I_1	I_2	C_1	P_3	P_4	M_1	M_2	M_3
n	5	5	5	8	5	9	8	5
min.	5.4	5.9	7.0	8.5	8.7	10.5	11.0	11.7
max.	6.3	6.1	7.6	9.7	10.2	11.4	12.1	12.7
$\bar{X}$	5.7	6.0	7.2	9.0	9.2	10.8	11.4	12.0
s	0.40	0.09	0.26	0.52	0.59	0.27	0.39	0.39

Table 3

Sample sizes for bucco(labio)lingual dimensions of the maxillary dentition for extant comparative samples.

	Pedi	San	HKW	*Pa. paniscus*	*Pa. troglodytes*	*G. gorilla*	*Po. pygmaeus*	*Hy. lar*
Male								
I^1	91	43	24	17	38	40	12	28
I^2	84	44	24	15	42	44	15	36
C	89	45	28	21	42	57	19	31
P^3	91	47	32	24	50	74	34	45
P^4	91	44	33	21	44	73	39	44
M^1	90	46	26	36	50	72	38	41
M^2	85	43	35	23	51	70	42	45
M^3	6	26	29	18	38	60	24	37
Female								
I^1	86	34	39	17	51	36	10	27
I^2	83	34	38	15	53	40	20	29
C	84	37	46	21	55	52	23	29
P^3	86	35	43	24	57	56	30	35
P^4	86	34	44	21	56	52	34	40
M^1	86	35	41	36	59	54	39	45
M^2	79	34	46	23	57	56	39	42

M^3	13	27	38	18	49	47	24	34

Table 4

Sample sizes for bucco(labio)lingual dimensions of the mandibular dentition for extant comparative samples.

	Pedi	San	HKW	*Pa. paniscus*	*Pa. troglodytes*	*G. gorilla*	*Po. pygmaeus*	*Hy. lar*
Male								
I_1	75	26	17	15	38	44	23	43
I_2	87	33	19	18	41	53	23	43
C	89	33	27	23	41	63	17	43
P_3	90	44	31	21	45	65	35	40
P_4	89	43	29	23	44	68	34	38
M_1	91	44	27	38	49	64	37	31
M_2	87	44	33	23	46	68	36	42
M_3	11	24	23	18	39	60	23	36
Female								
I_1	86	34	32	15	52	46	27	43
I_2	82	27	36	18	54	53	32	45
C	84	42	39	23	52	50	25	41
P_3	85	33	43	21	56	55	27	35
P_4	85	33	48	11	53	52	32	40
M_1	84	31	46	38	54	47	29	36
M_2	78	30	50	23	54	54	36	42
M_3	14	27	44	18	49	46	26	29

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Homo naledi specimens considered for analysis. Antimeres are listed together in parentheses.

	Mandibular	Maxillary
I1	(U.W. 101-039, U.W. 101-601), (U.W. 101-1005A, U.W. 101-1005B), U.W. 101-1261, (U.W. 101-1132, U.W. 101-1133), U.W. 102a-240	U.W. 101-038, U.W. 101-591, (U.W. 101-931, U.W. 101-1012), U.W. 101-1277, U.W. 101-1558, U.W. 102a-089, U.W. 110-14
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C	(U.W. 101-339, U.W. 101-985), (U.W. 101-886, U.W. 101-1126), (U.W. 101-1076, U.W. 101-1014), U.W. 101-1261, U.W. 102a-240	U.W. 101-337, U.W 101-347, (U.W. 101-412, U.W. 101-908), U.W. 101-501, (U.W. 101-706, U.W. 101-816), U.W. 101-1277, U.W. 101-1556, U.W. 102a-089
P3	U.W. 101-010, (U.W. 101-144, U.W. 101-506), (U.W. 101-298, U.W. 101-1565), (U.W. 101-377, U.W. 101-889), U.W. 101-800, U.W. 101-850, U.W. 101-1261, U.W. 102a-240	U.W. 101-037, U.W. 101-182, U.W. 101-729, (U.W. 101-786, U.W. 101-1004), U.W. 101-1107, U.W. 101-1277, (U.W. 101-1402, U.W. 101-1560), U.W. 102a-089
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n	7	8	8	8	8	10	6	5
min.	6.4	5.9	8.2	9.9	10.7	11.3	12.4	12.2
max.	7.1	6.9	9.7	10.9	11.3	12.4	13.6	13.2
$\bar{X}$	6.6	6.4	8.7	10.6	11.1	11.8	12.9	12.7
s	0.28	0.35	0.57	0.45	0.25	0.30	0.46	0.43
	I_1	I_2	C_1	P_3	P_4	M_1	M_2	M_3
n	5	5	5	8	5	9	8	5
min.	5.4	5.9	7.0	8.5	8.7	10.5	11.0	11.7
max.	6.3	6.1	7.6	9.7	10.2	11.4	12.1	12.7
$\bar{X}$	5.7	6.0	7.2	9.0	9.2	10.8	11.4	12.0
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Sample sizes for bucco(labio)lingual dimensions of the maxillary dentition for extant comparative samples.

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P^4	91	44	33	21	44	73	39	44
M^1	90	46	26	36	50	72	38	41
M^2	85	43	35	23	51	70	42	45
M^3	6	26	29	18	38	60	24	37
Female								
I^1	86	34	39	17	51	36	10	27
I^2	83	34	38	15	53	40	20	29
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P^3	86	35	43	24	57	56	30	35
P^4	86	34	44	21	56	52	34	40
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P_3	90	44	31	21	45	65	35	40
P_4	89	43	29	23	44	68	34	38
M_1	91	44	27	38	49	64	37	31
M_2	87	44	33	23	46	68	36	42
M_3	11	24	23	18	39	60	23	36
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I_2	82	27	36	18	54	53	32	45
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P_3	85	33	43	21	56	55	27	35
P_4	85	33	48	11	53	52	32	40
M_1	84	31	46	38	54	47	29	36
M_2	78	30	50	23	54	54	36	42
M_3	14	27	44	18	49	46	26	29

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