Finger Ridge-Count Variation among African Rainforest Hunter-Gatherers: Implications for Origins and Diversification

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Abstract

Dermatoglyphic studies of traditional rainforest hunter-gatherers (RHG) have a long history but there has not been an attempt to synthesize the available data to develop a coherent picture of their relationships to each other and to their farmer (AGR) neighbors. This has in part been due to absence of comparable data, a situation that has now been remedied by the late H. Brehme of Freiburg University. Brehme counted ridges and classified patterns on existing prints, mostly collected in the early 20th century. There now exist analyses of dermatoglyphic prints from most African RHG groups done in the same way by the same observer.

The present analysis uses finger ridge-counts to examine the structure of RHG and AGR populations. Eastern RHG and some AGR samples come from the Eastern Democratic Republic of the Congo. Some Eastern AGR samples are from Kenya. Western RHG and AGR samples come from Cameroon and adjacent countries. Statistical procedures include MANOVA, ANOVA, ANCOVA, and canonical variates obtained from the discriminant procedure. The relationship of ridge-counts to adult stature was also examined.

Eastern and Western RHG are clearly differentiated on ridge-counts. Eastern RHG are differentiated from their AGR neighbors by virtue of very low ridge-counts, but Western RHG have higher ridge-counts, more in line with their AGR neighbors. MANOVA reveals significant variation among groups and sexes, and variation among groups in sex dimorphism. Beyond the marked differences between Eastern and Western RHG, the Western AGR show a certain cohesion, but Eastern AGR are highly dispersed. Sex dimorphism variation primarily involves Eastern and Western AGR groups. Ridge-counts are also correlated with stature, suggesting that short stature has prenatal origins.

The general conclusion is that ridge-count variation supports difference between Eastern and Western RHG seen in cranial morphology and genetics. The unanswered question is why Eastern RHG are so differentiated, having the lowest ridge-counts in the world. There is also variation in sex dimorphism, especially among the AGR neighbors implying different responses to prenatal hormones. Ridge-counts demonstrate variation in prenatal development, which is still poorly understood. Genes influencing limb and digit development have been identified, which along with postnatal anthropometric and disease associations provide a basis for future hypothesis development and testing.

Interest in Pygmy populations has a long history, intensifying in recent years as evidenced by the special issue of Human Biology (Endicott 2013). Small statured populations are found in various parts of the world, including South East Asia, Melanesia, as well as Africa. The term Pygmy should refer only to those groups inhabiting the African equatorial forest and following a hunting/gathering subsistence (Ramirez Rozzi 2023). In this paper I will refer to African Pygmies as Rainforest Hunter-gatherers (RHG) and to the non-Pygmy agriculturists as AGR. Recent investigations into African RHG origins and diversity (Migliano et al. 2013; Verdu et al. 2009; Patin et al. 2009; Mendizabal et al. 2012; Ramírez Rozzi and Sardi 2010) have established their common origins and the structure of the populations. Dermatoglyphics of RHG have also been reported, most studies dating to the mid-20th century (Dankmeijer 1947; Geipel 1949; 1950; 1951; 1956; Glanville 1969; Pospišil 1992). Some are descriptive, dealing with individual groups (Glanville 1969; Pospišil 1992), but Geipel carried out comparative studies of Lese-Efe and their mixed offspring (Geipel 1951) and of RHG and SAN (1956). Dankmeijer (1947) conducted an extensive comparison of Western RHG and AGR.

The Lese-Efe mixed offspring result from the well known exchange relationship between the Lese and the Efe (Bailey and DeVore 1989). There is asymmetrical gene flow from Efe into Lese via Lese taking Efe wives. This is not an uncommon practice (Takeuchi, 2014) and will result in Efe-Lese admixed offspring and accumulation of Efe genes in the Lese population. This has the potential to provide insight into ridge-count variation.

Despite these early works and insights they provided into certain specific aspects of RHG dermatoglyphics, no systematic syntheses have been conducted of most of the RHG samples available and into their relationship to AGR Africans of the same region. The early studies were hampered by methodological variation and lack of emphasis on regional syntheses. That

situation has now been remedied through the efforts of the late Heinz Brehme, who counted ridges and classified patterns of many African samples (see Hunt 1989 for a general synthesis of African dermatoglyphics).

Historically, the emphasis on finger ridge-counts has been on their high heritability, in particular because total ridge-count (TRC) usually has a heritability greater than 0.9. However, individual digits are always lower than TRC. Froehlich and Giles (1981) estimate heritability at around 0.7, still relatively high compared to most other quantitative traits (Cheverud 1988). Even that is an overestimate, the heritability dropping to 0.2-0.3 once covariance structure is considered (Ousley 1997). Ridge-counts have also usually been considered selectively neutral and as such useful in assessing population relationships (Meier 1980).

Van Valen (1963) found no evidence of selection in ridge-counts and that proposition has been generally accepted until more recently. Babler (1978) has presented evidence that prenatal selection acts against arch patterns. The question then becomes is there evidence of selection acting postnatally? To do so it would have to act postnatally, either on the patterns directly, which seems unlikely, or on traits that are correlated with prenatally fixed ridge-counts. Blangero (1988) could find no evidence of selection in his Napalese samples. However Loesch and LaFranchi (1990) found correlations of anthropometrics with ridge-counts, most prominently between wrist breadth and thumb ridge-count, interesting because wrist breadth is highly dimorphic and thumb ridge-count is the most dimorphic digit. Recent genome wide studies have identified loci that influence limb and digit development which in turn influence finger pattern development (Li et al. 2022). Genes influencing pattern types are also expressed in certain sub types of cancer (Ho et al. 2016). Kahn et al. (2001) found that the difference between right digit four and five was correlated to the waist/thigh ratio in healthy military

recruits and to survivorship in Bangalore India. The relationship was especially strong in diabetic patients. Specific evidence of selection is still elusive but the weight of evidence is behind the likelihood that prenatally fixed ridge-counts are subject to selection via genes that are linked to the developmental processes of ridge-counts and also resulting in postnatal phenotypes.

It is now clear that small body size has evolved independently several times (Migliano et al. 2013; Bergey et al. 2018). In Africa, the split between the ancestors of Eastern and Western RHG occurred ca. 20,000 years ago (Patin et al. 2009), allowing ample time for small body size to evolve in different ways. Although finger patterns were not explored here it is unclear whether finger pattern types and body size are related as far as African RHG are concerned. Eastern RHG have high arch-low whorl frequencies, while Western RHG have lower arch-higher whorl frequencies (Dankmiejer 1947). Eastern RHG are shorter than Western RHG (Cavalli-Sforza 1986). Finger ridge-counts of Eastern and Western RHG differ correspondingly, Lower in Eastern and higher in Western.

Results from genomic analyses can provide a useful framework within which to interpret ridge-count variation. The primary components of this framework are 1) shared ancestry among small bodied hunter-gathers in Africa, including Khoisan speakers of South and East Africa (Tishkoff et al. 2009; Scheinfeldt et al. 2019; Fan et al. 2013), 2) Among the RHG the Eastern and Western are differentiated (Tishkoff et al. 2009) most prominently on mtDNA (Quintana-Murci et al. 2008), 3) Western RHG exhibit high levels of inter-population variation (Tishkoff et al. 2009; Verdu et al. 2009) due in part to admixture with AGR (Lopez et al. 2019).

Also relevant to the present study is research that shows adult height in RHG is programmed early in development, no later than early childhood (Pineau and Ramirez Rozzi 2021). Differences in the pygmy phenotype between Western and Eastern groups appear to result

from different growth patterns. In the former (Biaka) it results from slower growth during infancy while in the latter (Efe and Sua) it results from slower prenatal growth as seen in lower birth weights (Ramirez Rozzi et al. 2015). Childhood programming is also seen in African (Daasanach pastoralists of Northern Kenya) on the opposite end of the height continuum (Swanson et al. 2023).

Considering the above, this paper will conduct a quantitative analysis using finger ridge-counts, in order to address the following questions:

1. How differentiated are Eastern and Western RHG?
2. Is there significant variation within the Eastern and Western populations?
3. Are RHG and AGR within regions differentiated?
4. Are sexes differentiated, and is there variation in sex dimorphism?
5. Do ridge-counts provide insight into height variation?

Materials and Methods

Table 1 shows the RHG and AGR samples, where the data were collected and by whom, and references to previous use of the samples, if available. Missing data were excluded so the samples sizes given in Table 1 apply to all analyses. Except for one of the Efe samples (EFE), the Eastern RHG samples were collected by Martin Gusinde (Gusinde 1948;1949). Dermatoglyphics of the Eastern RHG were analyzed by Geipel (1950). Gusinde collected substantially larger samples, most of which are no longer available because they were destroyed during the Second World War. Western RHG and Efe (EFE) were collected by P. Julien. Although the prints were collected by different investigators, all were counted and classified by the late H. Brehme of Freiburg University. There is therefore no inter-observer variation. It is not now possible to evaluate intra-observer variation but there is good reason to believe it is minimal. Brehme counted ridges and classified patterns of over 50,000 individuals over his career, using the same methodological procedures throughout.

Table 1 here

The Lese were the only AGR group sampled living in close proximity to a RHG group (the Efe) and with whom they have an exchange relationship (Bailey and DeVore 1989). Gusinde was also able to collect a small sample resulting from Lese-Efe marriages (LEM). In addition, Gusinde collected a small sample of Mangbetu, a group also living in the rain forest and practicing agriculture but having no exchange relationship with RHG groups.

Data consist of radial and ulnar ridge-counts for the ten fingers. It has traditionally been the practice to reduce the number of variables from 20 to 10 by using only the larger of the radial and ulnar count (Holt 1968). This has the advantage of eliminating the large number of zeroes associated with ulnar counts and creating a unimodal continuous distribution. It has the disadvantage that it loses information about the orientation of the counts and eliminates one of them in the case of whorl patterns. This can be countered to some degree by taking the sum of the radial and ulnar count for each digit. This also results in ten variables and more symmetrical distributions. I have used both approaches but present results only for the larger counts because they had slightly higher among group variation.

Inter group relationships were analyzed using canonical variates derived from discriminant analysis. Analysis was done using the local groups in Table 1, including both sexes. Significant canonical variates were subjected to further examination using Multivariate Analysis of Variance (MANOVA) with group, sex and their interaction as treatments. For both canonical variate analysis and MANOVA, Wilks lambda and its associated F ratio were used to accept significant variation. These analyses were conducted using NCSS (2021).

In addition to examining ridge-count variation among RHG and AGR groups, the relationship of ridge-counts to stature was examined by matching each group's mean canonical

score with its mean stature as given in Gusinde (1942;1948). For the Eastern RHG, the Lese and the Lese- Efe offspring, stature and ridge-count were obtained from the same individuals. For Western RHG I paired the mean RHG and AGR statures as given in Becker et al. (2011) to the mean CV scores. Gusinde collected dermatoglyphics of Mangbetu but not anthropometrics. Therefore, anthropometrics of three tribes in the Ituri region (Ndaka, Bali, Beyru) that do not have exchange relationships with RHG were paired with Mangbetu. This requires the assumption that these three groups approximate the height of the Mangbetu, who also do not have an exchange relationship with RHG groups.

Results

The canonical variate analysis, shown in Table 2, resulted in four significant canonical variates. Together the first four account for almost 75 % of the among group variation, but the first is considerably more important than the subsequent three. The structure coefficients allowing interpretation of the canonical variates are shown in Table 3. The first CV has similar negative loadings on all variables. It is only approximately equivalent to TRC, which gives equal weight to all digits. On CV1 digits 1 and 5 are more heavily weighted than digits 2-4 , resulting in a correlation with TRC of only -0.74. CV2 contrasts digits 1 and 2 (positive loadings) to digit 3 (negative loadings). CV3 loadings are dominated by digits 4 and 5, with lesser loadings in the same direction on digits 2 and 3. CV4 emphasizes left digit 1 and right digit 3.

Table 2 and 3 here

Further insight into patterning of group and sex variation is provided by subjecting the canonical variates to MANOVA, using group, sex and their interaction as treatments. Table 4 shows the results for group, sex and interaction. All treatments are significant, including the interaction, indicating variation in sex dimorphism. Table 5 shows the ANOVA results for the

individual canonical variates. Both CV1 and CV2 have significant group and sex effects, but the interaction is not significant. Group for CV3 is significant, but neither sex nor interaction are significant. The interaction for CV4 is significant, indicating that the interaction in the MANOVA model is due almost entirely to CV4.

Tables 4 and 5 here

Considering these results, the group effects of CV1 and CV2 can be shown graphically by sex. Although group effects for CV3 are significant, they do not appear to be patterned in an intelligible way. Variation in sex dimorphism by groups can be shown using sexes as axes on which to display CV4.

Figures 1a and 1b show the canonical variate plots of intergroup relationships for males and females, respectively. Males present a reasonably structured picture. Eastern RHG have high scores on CV1. Western RHG are clustered with Eastern AGR, except for Bakah which have a high score on CV2.Western AGR, except for Foulbe, form a tight cluster with low scores on CV2. Lese-Efe (LEM) offspring share high scores with Eastern RHG but have the lowest CV2 score. As such, they are far removed from both of their parent populations. Females present a somewhat less structured picture, although are broadly similar to the male results. Western RHG actually have lower scores on CV1 (higher ridge-counts) than most AGR groups. Unlike males, the female Lese-Efe offspring do not have high scores on CV1. Also striking is that the Lese females are differentiated from other Eastern AGR groups on CV2 and are close to their mixed offspring, which, as in males have low scores on CV2. Lese females differ significantly from the other Eastern AGR groups on CV2 ($t=2.88$, $P=0.005$), but Lese males do not differ from other Eastern AGR groups.

Figure 1 here

It is evident from Figure 1 that there is considerable dispersion within each of the RHG groups, particularly on CV2. A post hoc two level ANOVA using group, sex and interaction as treatments was conducted for each of the RHG groups. For the Western RHG group CV2 shows significant variation. Importantly the group-sex interaction for this subset is significant ($F=3.4$, $P=0.03$). Because the interaction is significant the group effect cannot be directly interpreted. One way ANOVA for the sexes separately shows male variation is highly significant ($F=8.3$, $P<0.001$) but females are not significant. Therefore the interaction is mainly due to male variation and specifically the difference between BAK and the other two. CV1 also shows significant variation, the group effect being significant ($F=8.2$, $P<0.001$), but neither sex nor the interaction is significant. BAB have the highest score (lower ridge-counts), BKO the lowest (higher ridge-counts) and BAK are intermediate.

The Eastern RHG show significant intergroup variation on CV2 ($F=4.1$, $P=0.007$), but neither sex nor the interaction is significant. The source of the intergroup variation results from the AKA's differentiation from the other groups.

Table 3 and 4 here

Figure 2 shows the sex specific coordinates on CV4, the male mean on the x axis, the female mean on the y axis. The upper left and lower right quadrants contain points where the sexes have disparate values. The upper left quadrant is occupied by three of the four Eastern AGR groups. The one exception is the Lese in the lower right, along with four of the five Western AGR groups. The Bamilike (BAM) are isolated in the upper right quadrant. Also included in the lower right quadrant are an Eastern RHG (Efe) and marginally a Western RHG (Bakolah). The upper right and lower left quadrants contain groups where the sexes are concordant on the CV4 score. These two quadrants contain most of the RHG groups.

Figure 2 makes clear the source of sex dimorphism variation in CV4. It primarily involves Eastern and Western AGR groups, females in the former having high scores and males low scores, while the opposite is true for the latter. RHG groups overall tend to have concordant scores on CV4. The structure coefficients involve primarily left digit 1 and right digit 3. Closer examination reveals different behavior for the right and left hand. On the left hand digit 1 has the highest loading, after which they generally decline, digit 5 having the lowest loading. On the right hand the loadings begin low on digit 1, then increasing to digit 3 and decreasing again thereafter. CV4 accounts for only 8.3% of among group variation. It is subtle but one that is patterned by sex and geography.

Figure 2 here

The ANCOVA regression of stature onto CV scores resulted in CV1 with a significant relationship. Regression slopes for the sexes do not differ significantly, but the regression of stature onto CV1 is significant ($F=36.9$ $df= 1,15$ $p<0.001$), and sex is also significant ($F=29.5$,$df=1,15$, $p<0.001$). These relationships are shown in Figure 3. It shows that the Eastern RHG are characterized by small stature and high CV1 scores. Groups with low CV1 scores encompass Western RHG and both Eastern and Western AGR. Because CV1 is negatively related to TRC, the meaning in terms of original ridge-counts is that Eastern RHG with small stature have low ridge-counts, while the Western RHG and both Eastern and Western AGR have higher ridge-counts.

Figure 3 here

The Lese and Lese-Efe offspring present interesting patterns. LEM male stature is on the regression line and is intermediate between Efe and Lese, slightly closer to Efe. Female LEM have a CV1 score about the same as Lese, but stature below the CV1 prediction and are closer to

the Lese parent than to Efe. Stature and ridge-counts therefore appear to respond differently to Lese-Efe admixture events. Also notable from Figure 3 is that Lese male stature is about the same as other Eastern AGR, but Lese females are considerably smaller than other AGR groups. Both male and female Western AGR samples are taller than others and consequently depart the most from the regression line, the females falling on the male regression line.

Discussion

Eastern vs Western RHG vs their AGR Neighbors

The question of whether Eastern and Western RHG differ in finger ridge-counts is clearly answered in the affirmative. That is most clearly seen on CV1where Eastern RHG have higher scores (lower ridge-counts) than Western RHG. This is in agreement with earlier work using TRC. The low ridge-counts of the Efe were reported by Glanville (1969), based on essentially the same sample used here, and on a different sample by Pospisil (1992). Pospisil (1992; Geipel 1950;1951;1956; Barrai 1986) have all described the high frequency of arches and low frequency of whorls seen in the Eastern RHG. Dankmeijer (1947), in one of the most extensive of the early works, reached the conclusion that the Western RHG did not share the high arch-low whorl frequency seen in the Eastern groups, and concluded that they were separate populations.

CV2, which emphasizes ridge-counts on radial digits one and two in opposition to the other digits, mainly digit three, reveals at least three interesting relationships. First, Western RHG are differentiated from Western AGR and aligned more closely with Eastern AGR, most clearly seen in males.

Second, the Lese-Efe offspring are removed from most other groups by virtue of low scores on CV2. Also noteworthy is that Lese females depart from other Eastern AGR and align

with their admixed offspring. In his anthropometric analysis of the current admixed sample Gusinde (1942) notes that six of eleven (55 %) females are second generation, for males it is11 of 19 (58%). That means that the majority (57%) of admixed offspring are only one quarter Efe. One might expect that would move the admixed offspring closer to the Lese parent group, but that is not the case, and in females it is the Lese parent group that is somehow affected. The male Lese-Efe admixed differ significantly from Lese on CV2, but the female means are virtually identical.

Third, variation within the RHG groups presents a curious picture. Both sexes for Eastern and Western RHG differ significantly on CV2 scores, and the Western group males also show significant variation on CV1. This puts ridge-count variation in broad agreement with genomic data (Verdu, et al. 2009). But again the sexes differ. In males BAK is the outlier with a high score on CV2, in females it is BAB. On CV1 BAB and BAK males have a higher score (lower ridge-counts) than BKO. In the Western group admixture with AGR groups is relatively high, reaching 43% in Bongo (Lopez et al 2019). Y chromosome analysis shows that AGR admixture into Western RHG is of male origin (Anagnostou et al. 2010). It is therefore interesting that ridge-count variation is most strongly expressed in males. There does not appear to be an obvious explanation for BAK to be differentiated from BAB or BKO. The structure coefficients indicate that digits one and two have the highest loadings and are opposed to the other digits, three in particular. Previous work implicates the radial digits as sexually dimorphic and responsive to fetal hormones (Jantz 2021; Polcerová et al. 2023). This could potentially reflect differences in fetal sex steroids that may be mediated by Y chromosomes.

Apart from the Eastern vs Western RHG difference, supported by cranial morphology (Ramírez Rozzi and Sardi 2010) and genomic analyses (Scheinfeldt et al. 2019), the other

patterns of variation do not admit to ready explanations. That sex differences are present may point to chromosomal or hormonal effects. With regard to Lese-Efe relationships the asymmetric gene flow of Efe into Lese via Lese males taking Efe wives is well known (Takeuchi 2014). Takeuchi (2014) reports that between 17 % and 25% of Lese males take Efe wives. The pattern of ethnic intermarriage would result in accumulation of Efe X chromosomes into the Lese population. Jantz and Hunt (1986) showed that sex chromosomes influenced several dermatoglyphic patterns. Both Lese males and females can carry Efe X chromosomes, but males can have only one while some females could have two Efe derived X chromosomes, potentially having the greater effect on females.

It may be unexpected that present results show Eastern RHG differ markedly from their AGR neighbors while the Western RHG, while statistically different from their AGR neighbors, are not markedly so. These results agree to some extent with craniometric distances (Ramírez Rozzi and Sardi 2010). They found, in agreement with present results, that Eastern RHG and AGR are differentiated, that Western RHG and AGR are less differentiated, and that Eastern and Western RHG are differentiated. Also of note is Franklin et al.'s (2010) finding that their Western RHG sample differed markedly from subsaharan Africans generally, mainly by virtue of small cranial size and pronounced prognathism. Destro-Bisol et al. (2000) also found Eastern and Western Pygmies to be differentiated on microsatellites, and, among the latter, Mbenzele were not differentiated from nearby AGR groups, but the Biaka are somewhat differentiated from the Mbenzele AGR group. As a general proposition, it appears that cranial morphometrics, dermatoglyphics and DNA data only partially converge onto patterns of RHG affinities

Variation in sex dimorphism,

My results found significant variation among the samples on CV4, which has the interesting right-left loading differences. However, the variation in dimorphism primarily involved differences between Eastern and Western AGR. RHG dimorphism is mostly concordant, if variable. CV4 accounts for only 8.3 % of among group variation, but it shows how complex interactions among digits can still reveal important variation. How this should be interpreted is far from clear. It may involve variation in fetal hormones. There is some indication that populations of West African derivation have lower second to fourth digits ratios (2d:4d, a marker of prenatal hormones) than East Africans (Manning et al. 2000; Apicella 2016). East Africans also lack the 2d:4d dimorphism seen in most other populations, including West Africans. Finger ridge-counts are also correlated with 2d:4d ratio, implicating prenatal hormones in their formation (Jantz 2021).

What Accounts for RHG Ridge-count Variation?

Addressing the question of why Eastern and Western RHG differ necessarily raises the question of why Eastern RHG differ from their AGR neighbors, but Western RHG do not differ markedly. Part of the explanation likely is that the Western RHG are more admixed with AGR, while Eastern RHG show relatively little admixture with their AGR neighbors (Tishkoff et al. 2009). If one assumes that the Western RHG original ridge-counts/pattern types were similar to those seen in the Eastern RHG, as might be inferred from Destro-Bisol et al. (2004), then by the additive model, Western RHG should exhibit intermediate values, depending on the degree of admixture. Previous work on two admixed populations suggests a different expectation. Robson and Parsons (1967) found that individuals with various degrees of European Australian and Aborigine admixture had ridge-counts closer to their Aborigine ancestors than predicted by the

additive model. Jantz et al. (1982) showed that South African Coloured were more similar to Europeans (Germans) and South Asians (South African Indians) than to any African sample. South African Coloured admixture proportions are almost 60 % African (San and non-San) and only about 25 % European, the remainder consisting of South and Southeast Asians (Daya et al. 2013). Despite having a majority of African genes, South African Coloured exhibit no tendency toward an intermediate position. As was the case with Robson and Parsons (1967) Australian study, the admixed individuals have ridge-counts favoring the higher count ancestral population. Singh (1979) attributed higher ridge-counts to dominance or over dominance. Thus prior work suggests that admixed populations may assume the ridge-count of the higher ridge-count ancestral group, in this case their AGR neighbors. These results conflict with the classical additive models (Holt 1968), although subsequent analyses have identified dominance toward higher ridge-counts (Martin et al.1982). Alternative explanations might involve sensitivity to growth hormone or related hormones (Merimee et al. 1972). That ridge-counts behave in this manner could also involve their likely response to steroid hormones. Polani and Polani (1979) argued for a hormone response in androgen insensitivity syndrome. Several other studies also point to hormonal involvement in dermatoglyphic traits (Hall 2000; Jantz and Hunt 1986; Jamison et al. 1993). A more direct line of evidence is the relationship between ridge-counts and 2d:4d. Manning (2002) found a significant regression of right digit 4 ridge-count on 2d:4d of the right hand, lower ridge-counts being associated with lower 2d:4d, and vice versa. This relationship was supported and extended (Jantz 2021).

What remains puzzling is the exceedingly low ridge-counts of Eastern RHG. It is mainly a consequence of high arch frequencies but Eastern RHG loops and whorls also have fewer ridges than Western RHG. In the present sample the Eastern RHG have an arch frequency of

16.6% vs 7.0 % for Western RHG. An interesting observation is the arch frequency Babler (1978) found in spontaneous vs elective abortions, 17.7 % and 6.4% respectively. Eastern RHG are more closely aligned with fetuses that did not make it to term while Western RHG are comparable to normal fetuses. Babler (1991) has shown that arch patterns are associated with late ridge formation, but there are also relationships to shape of the terminal phalanx. Whorl patterns are associated with wider phalanges, arches with narrower phalanges. Could this suggest that Eastern RHG have later ridge formation and narrower phalanges than populations with normal arch frequencies. Extrapolating from Babler's American sample to Eastern RHG may be invalid and the process of arch formation in Eastern RHG may be different.

Do Ridge-Counts Provide Insight into Height Variation

On a worldwide basis, there appears to be no correlation between ridge-counts and height. Small statured groups in New Guinea typically have large ridge-counts, while relatively tall groups in East Africa have lower counts. Even in the RHG in the present study, we see that Western RHG assume ridge-count values more in line with their AGR neighbors while their stature remains below AGR. Efe gene flow into Lese does not appear to have aligned Lese more closely to Efe. But it can be noted that Lese have the lowest statures of all of the AGR groups reported by Gusinde (1942), presumably because of Efe genetic contribution.

Recent work has shown that variation in human body size results from processes already in place in early development (Pineau and Ramirez Rozzi 2021). In the case of Eastern and Western RHG short statures apparently result from different processes (Ramirez Rozzi et al. 2015). They show the Western RHG have the same birth weights as AGR but Eastern RHG are smaller at birth. That indicates that Western RHG achieve their short stature by slower postnatal growth while in Eastern RHG the small body size has prenatal origins. Does the prenatal origin

reach as far back into fetal life as ridge formation? It well could. Some alleles having higher frequencies in RHG populations are involved in bone formation and remodeling (Mendizabal et al. 2012; Lopez et al. 2019) that could influence height, a process that could begin during fetal life. Babler (1991) has shown that pattern type and ossification of bones in the fetal hand are related, whorl patterns being associated with less ossification. The timing of ridge development relative to bone formation resulting in this association is not clear, so it is presently not possible to formulate any specific hypotheses about how these two processes may have interacted to produce the reduced ridge-count in Eastern RHG.

Because the relationship observed in the present analysis was obtained from the mean values of stature and ridge-counts, it might be argued that it does not imply an underlying relationship. Eastern Pygmies are shorter than western Pygmies and have lower ridge-counts and this may result from biologically unrelated processes. But almost all groups fall close to the regression line in Figure 3, including offspring of Lese-Efe marriages, which may imply a common underlying cause. It is noteworthy that Lese appear to have experienced secular change in height. Lese in the present analysis were measured by Gusinde (1948) in 1934/1935, and Dietz et al. (1989) present data from Lese measured in 1980. Both sexes appear to have experienced some secular increase in height. Lese males are taller in 1980 by 1.35 cm but Lese females are taller by 5.7 cm, a rather remarkable increase in the approximately two generations separating the two studies. We do not know whether ridge-counts have changed over that time period.

Conclusions

African RHG ridge-counts provide additional insight into their specific features. Eastern RHG in particular have some of the lowest ridge-counts in the world. Reasons for this remain unclear, highlighting the need to better understand the variation in ridge-counts in general

(Hauther 2023). Ridge-counts do not behave as ordinary additive quantitative traits. To some degree ridge-counts are similar to genomic results, such as the difference between Eastern and Western RHG. But in other respects they differ, such as minimal differences of Western RHG from their AGR neighbors. In addition there are sex differences lacking a ready explanation. It is important that all variation observed has prenatal origins. The extent to which this variation has postnatal ramifications, such as intriguingly, stature, remains to be elucidated.

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Captions for Figures

Figure 1. Canonical variates scores for males (a) and females(b). Individual samples are coded by broad regional groups and as RHG, AGR. Offspring of Lese-Efe marriages are coded separately as LEM.

Figure 2.Scores on canonical variate four using sexes as axes to show variation in sex dimorphism.

Figure 3. Regression of stature on CV1. A fitted linear regression line for each sex is shown. Regressions lines were obtained from the ANCOVA analysis assuming equal slopes for the sexes. Solid line males, dashed line females

Table 1. Dermatoglyphics samples, samples sizes, investigator, location, and reference to original paper, if known. NM and NF are samples sizes for males and females respectively.

Group(Abbrev.)		NM	NF	Investigator	Location	References
Aka (AKA)	ERHG	102	90	M. Gusinde	NE Zaire (DRC)	Geipel 1949;1956
Babongo (BAB)	WRHG	90	83	Julien	Gabon	Dankmeijer 1947
Bakah (BAK)	WRHG	74	61	Julien	Cameroon	Dankmeijer 1947*
Basua (BAS)	ERHG	22	94	M. Gusinde	NE Zaire (DRC)	Geipel 1949;1956
Bakolah (BKO)	WRHG	104	92	P. Julien	Cameroon	Dankmeijer 1947
Efe (EFE)	ERHG	45	102	P. Julien	Andudu & Mbasa	Glanville 1969, Dankmeijer 1947.
Efe (EFE2)	EERHG	74	31	M. Gusinde	Mabili, Matangba, Zaire(DRC)	Geipel 1950
Lese (LES)	EAGR	53	30	M. Gusinde	NE Zaire (DRC)	Geipel 1950
Bamileke (BAM)	WAGR	38	25	J. LeGrand	Cameroon	Glanville, 1968
Boran (BOR)	EAGR	95	56	P. Rosa	Marsabit, Kenya	Rosa 1983
Foulbe (FOU)	WAGR	70	32	Huizinga	Basheo, N Cameroon	None located
Kirdi (KIR)	WAGR	52	25	P. Julien	N. Cameroon	None located
Mangbetu (MAN)	EAGR	20	8	M. Gusinde	NE Zaire (DRC)	None located
Nandi (NDI)	EAGR	51	50	Rosa	Nandi District, Kenya	Rosa 1983
Sara (SAA)	WNP	87	45	Mason Detourbet	Tchad	None located
Samo Du Sud (SAS)	WAGR	105	95	Huizinga	Burkino - Faso	None located
Lese-Efe (LEM)	LEM	20	8	M. Gusinde	Zaire (DRC)	Geipel 1950

* How this sample was collected is unclear. Dankmeijer (1947) explicitly states that Julien was unable to secure prints, but Brehme's notes identify Julien as the collector and the location of the prints as Leiden University, where the other Julien samples are located.

Table 2. Eigenvalues and associated statistics for $W^{-1}B$ matrix of 10 ridge-counts.

Fn	Inv(W)B Eigenvalue	Ind'l Pcnt	Total Pcnt	Canon Corr	F Value	Numer DF	Denom DF	Prob Level	Wilks' Lambda
1	0.161	43.1	43.1	0.372	2.2	330.0	19160.4	0.0000	0.699
2	0.047	12.6	55.7	0.212	1.5	288.0	17353.9	0.0000	0.811
3	0.040	10.7	66.3	0.196	1.3	248.0	15523.3	0.0004	0.849
4	0.031	8.3	74.7	0.174	1.2	210.0	13667.7	0.0288	0.883
5	0.025	6.8	81.4	0.157	1.1	174.0	11786.4	0.2080	0.911
6	0.023	6.2	87.7	0.151	1.0	140.0	9878.9	0.5198	0.934
7	0.019	5.1	92.8	0.137	0.9	108.0	7945.5	0.8616	0.955
8	0.014	3.8	96.6	0.118	0.7	78.0	5987.2	0.9834	0.974
9	0.007	1.9	98.5	0.084	0.5	50.0	4006.0	0.9983	0.987
10	0.006	1.5	100.0	0.076	0.5	24.0	2004.0	0.9841	0.994

Table 3. Structure coefficients for first four canonical variates.

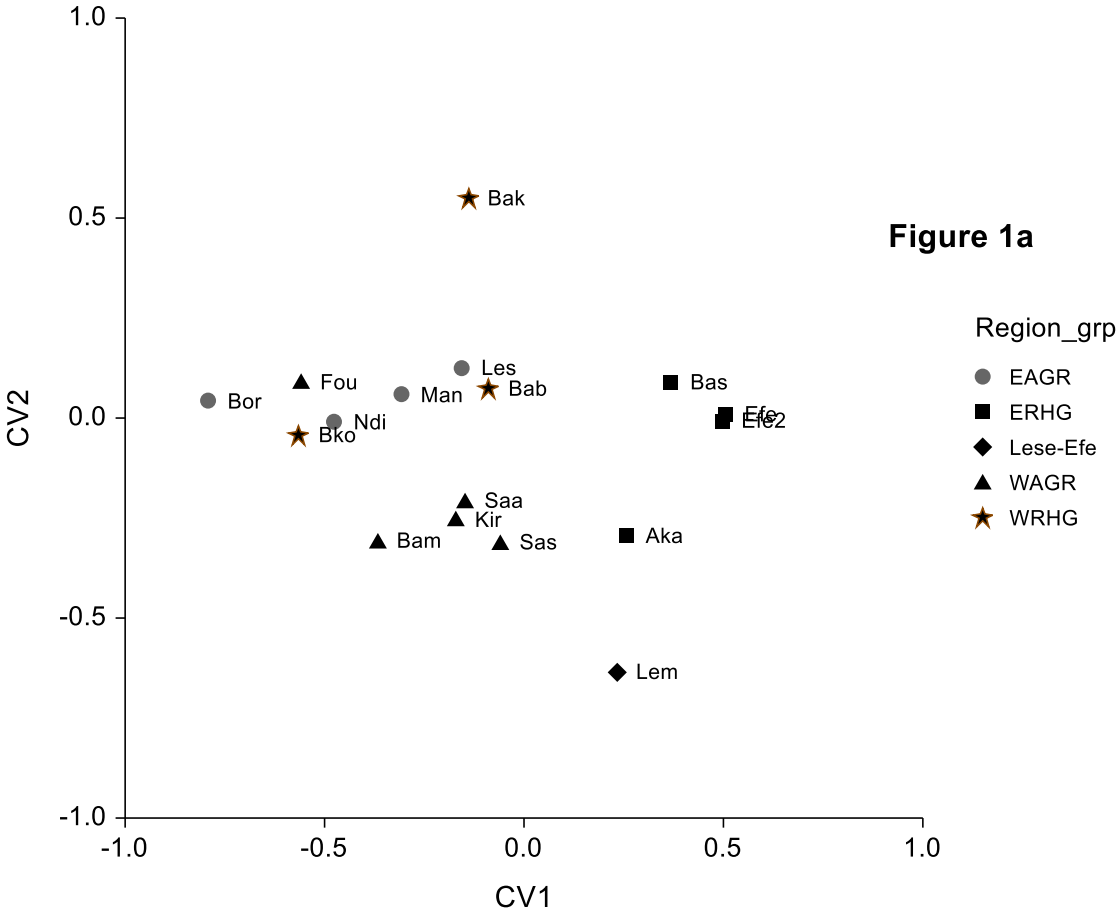
Digit	CV1	CV2	CV3	CV4
Left 1	-0.68	0.37	-0.1	-0.5
Left 2	-0.49	0.21	-0.28	-0.19
Left 3	-0.55	-0.25	-0.21	-0.27
Left 4	-0.63	-0.15	-0.55	0.04
Left 5	-0.84	-0.12	-0.41	0.02
Right 1	-0.63	0.28	0.02	-0.11
Right 2	-0.49	0.36	-0.21	-0.14
Right 3	-0.45	-0.21	-0.27	-0.42
Right 4	-0.43	-0.06	-0.78	-0.11
Right 5	-0.6	-0.04	-0.47	-0.06

Table 4. MANOVA results for sex, group and interaction

Treatment	Wilks	df	F	P
Sex	0.987	4,2001	6.49	<0.0001
Group	0.839	64,7836	5.60	<0.00001
Sex*Group	0.958	64,7836	1.35	0.035

Table 5. ANOVA results for sex, group and interaction for the individual Canonical variates

	Sex		Group		Interaction	
	F	P	F	P	F	P
CV1	19.76	<0.0001	13.50	<0.001	1.16	0.291
CV2	3.69	0.055	3.63	<0.001	1.43	0.119
CV3	2.55	0.111	3.90	<0.001	0.86	0.620
CV4	0.01	0.908	1.75	0.032	1.95	0.013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0.0
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CV2
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Region_grp
EAGR
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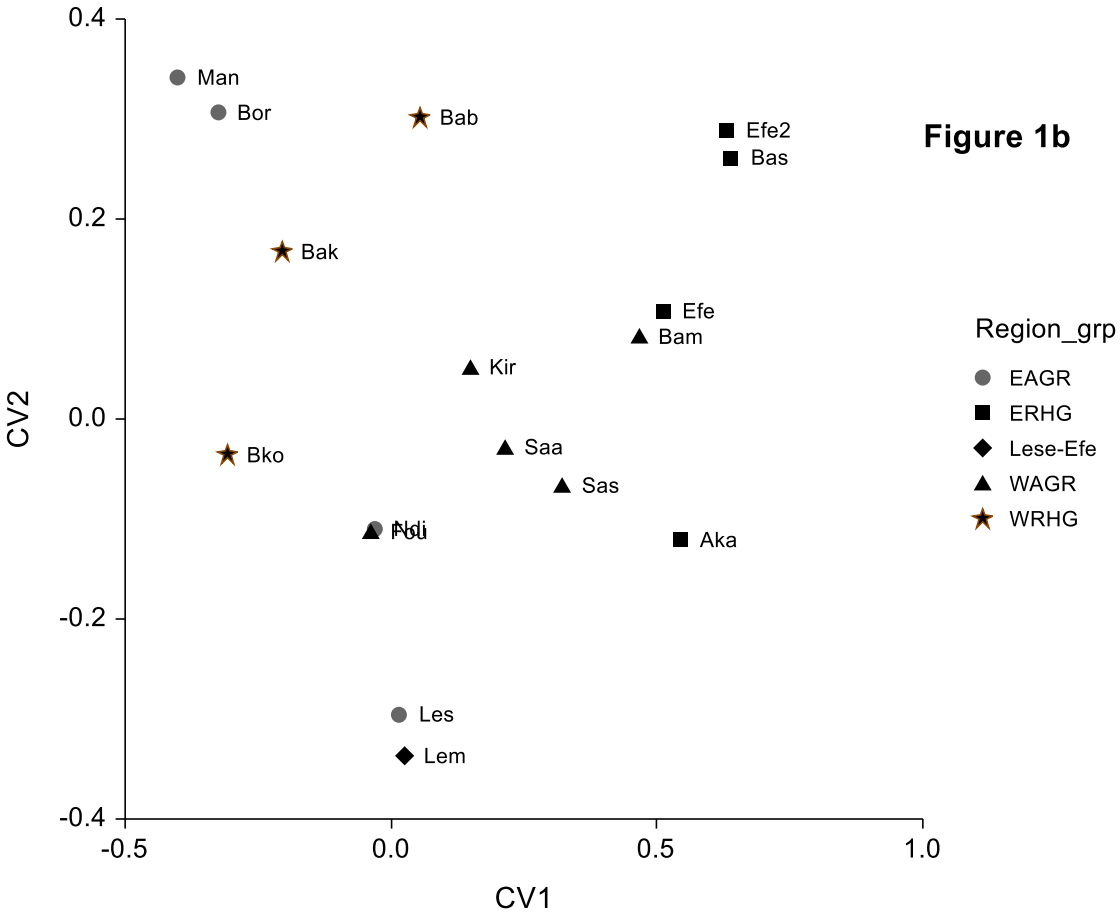
Lese-Efe
WAGR
WRHG

Figure 1a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Efe
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Region_grp
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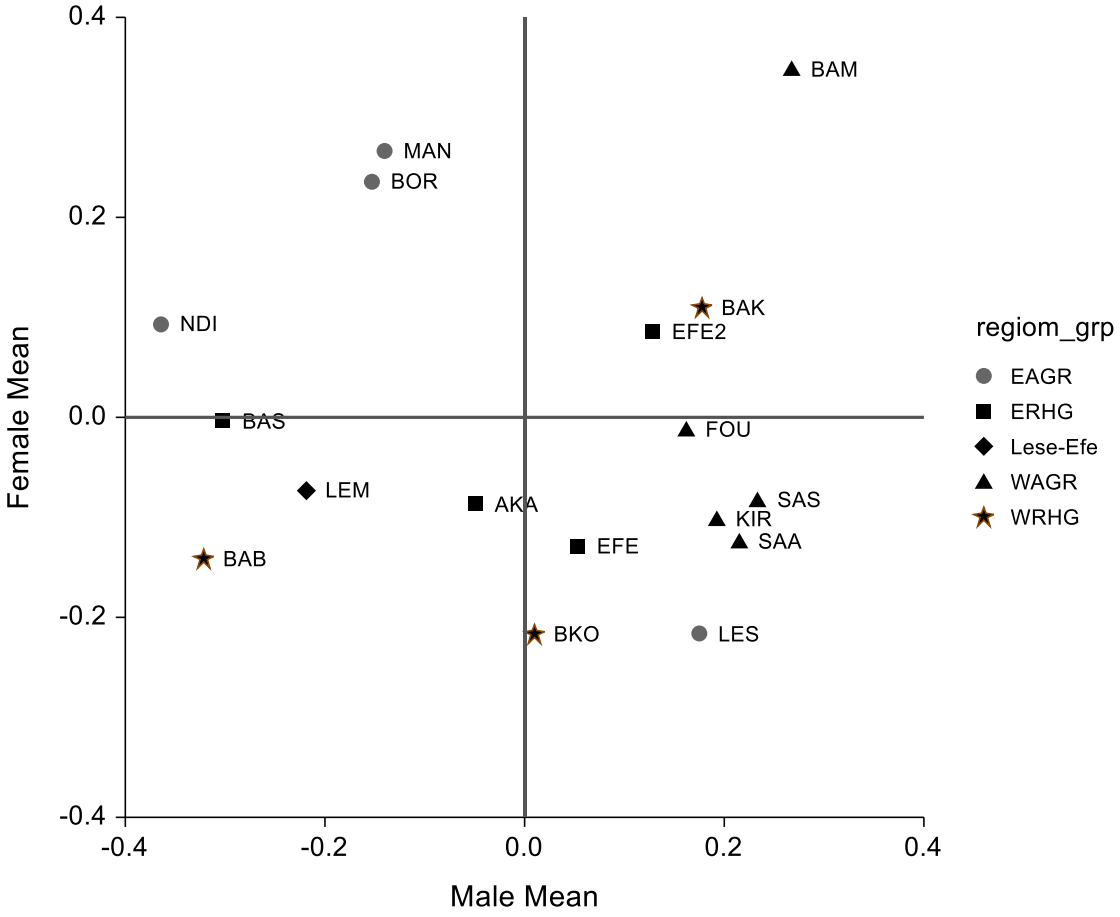
ERHG
Lese-Efe
WAGR
WRHG

Figure 1b


0.4
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Female Mean
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BAM
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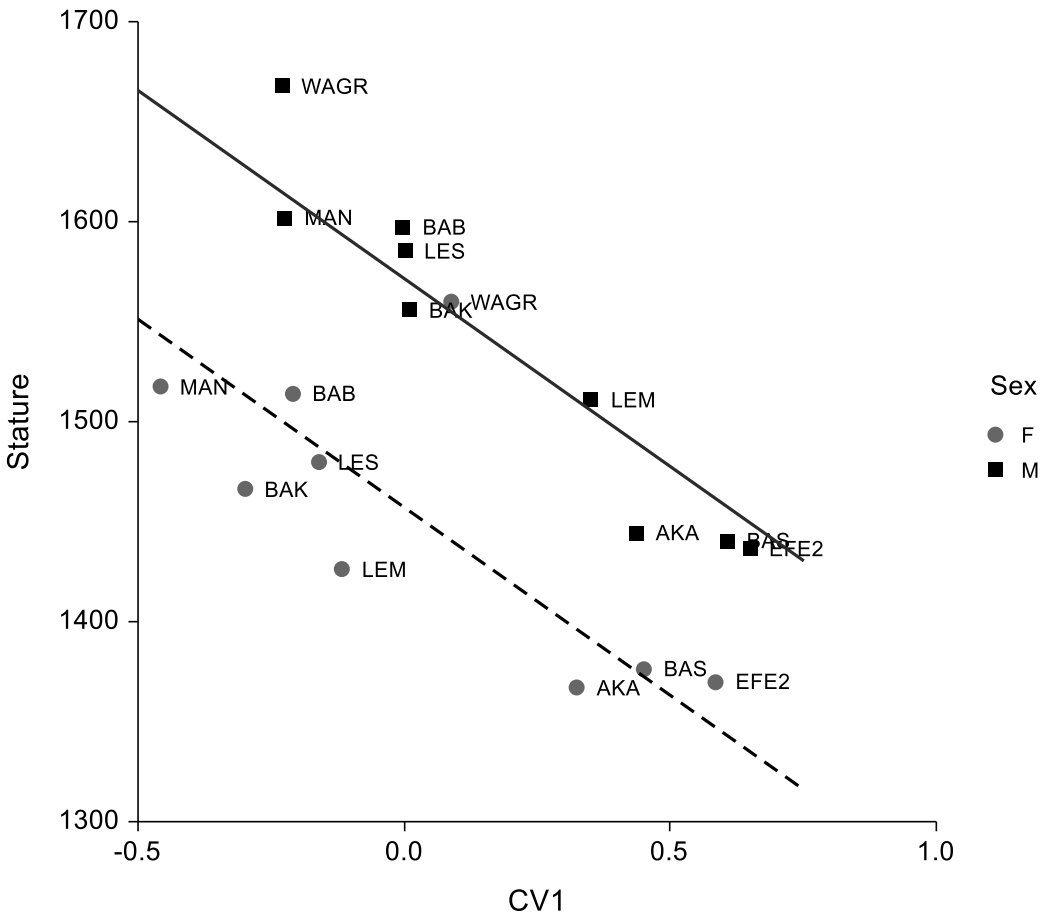
WAGR
WRHG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