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White sclera is present in chimpanzees and other mammals

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1. Introduction

Humans can communicate with a subtle glance. This is due, in part, to our eyes having visible white sclera that contrasts with the iris, thereby enabling humans to effectively attend to others' gaze direction (Kobayashi and Kohshima, 1997, 2001; Tomasello et al., 2007; Yorzinski et al., 2021). Both our white sclera and complex social cognition have long been considered unique among mammals, strengthening the hypotheses that these traits are linked—i.e., cooperative eye hypothesis (Tomasello et al., 2007), gaze signaling and gaze camouflage hypotheses (Kobayashi and Kohshima, 2001). However, the last two decades have revealed that our closest ape relatives, especially chimpanzees, exhibit complex perspective-taking abilities (Hare et al., 2001, 2006; Krupenye et al., 2016), and that there may be greater variability in the eye color of apes and other primates than previously thought (Perea-García et al., 2022). Some gorillas exhibit white sclera (Mayhew and Gómez, 2015; Caspar et al., 2021), and many Sumatran orangutans (Perea-García, 2016; Caspar et al., 2021) and bonobos (Perea-García et al., 2019) exhibit light brown sclera. Recent studies have sparked debate over the extent to which the sclera needs to be white to effectively contrast with the iris and enhance the visibility of gaze direction (Perea-García et al., 2019; Caspar et al., 2021; Kano et al., 2021, 2022; Mearing and Koops, 2021; Whitham et al., 2022). A critical piece of information is missing from this debate: studies continue to report chimpanzees, our closest living relatives along with bonobos, as having dark sclera. Early reports of the occasional wild chimpanzee with white sclera have been considered pathologies or anomalies (Goodall, 1986; Boesch and Boesch-Achermann, 2000). More recent studies have not addressed the few cases that diverge from the assumed norm of uniformly dark sclera (e.g., Perea-García et al., 2019; Kano et al., 2022). Is white sclera an anomaly among chimpanzees, or might prior studies have failed to detect variation due to small samples? Here, we examine the prevalence and development of white sclera from photographs in the largest sample of wild chimpanzees studied to date (n = 230 individuals). We then explore the presence of white sclera in 70 zoo mammal species.

2. Methods

The Ngogo chimpanzees live in the center of Kibale National Park, Uganda. Continuous long-term research began in 1995, and regular photographs of chimpanzees have been taken since 2003 by K.C.L. and K.E.L. Our main cross-sectional dataset primarily consists of photographs taken between May 2017 and February 2020 on a Nikon D500 DSLR camera (~85% of dataset), supplemented by photographs taken between November 2003 and June 2019 on Canon DSLR cameras. During this period, there were a total of 332 chimpanzees in the Ngogo population that survived to at least one month of age. Of these, photographs of eyes were available for 230 individuals. We analyzed 1187 photographs of 230 subjects ($\bar{x} = 5 \pm 3$ photographs per subject), ranging in age from 1 month to an estimated 68 years old ($\bar{x} = 17 \pm 15$ years). Birthdates were known to within one day to three months for those born at Ngogo since 1995 and are estimated for older adults based on physical features and parentage relationships (Wood et al., 2017). Non-natal females were estimated to be 13 years old at the time of immigration (Wood et al., 2017). Age classes were defined as: young infant (≤1.5 years), older infant (>1.5 years to ≤5 years), juvenile (>5 years to ≤10 years), adolescent (>10 years to ≤15 years), and adult (>15 years) (Goodall 1986; Bădescu et al., 2017). Some individuals were represented in multiple age classes, resulting in a final dataset of 246 distinct data points.

We used a qualitative assessment to determine the color of the majority of the visible sclera. I.R.C. and K.C.L. independently scored gaze direction, sclera coloration, and patchiness as separate variables. We scored the eye direction for each photograph as ‘direct’ or ‘averted,’ as the sclera may be more visible when a chimpanzee is gazing upward or sideways. Due to limited sample sizes, we were unable to evaluate differences among averted directions (i.e., up vs. left or right), nor exact location and size of patches in our analyses. To assess inter-rater agreement, we calculated Cohen’s kappa scores using the ‘kappa2’ function from the R package ‘irr’ v. 0.84.1 (Gamer et al., 2019), as well as raw percentage agreement scores. Inter-rater agreement across the full dataset for all variables was acceptable: Cohen’s Kappa scores (weighted by ‘squared distance’ of sorted levels when appropriate) for gaze direction was 0.61, for sclera majority coloration was 0.86, and for patchiness was 0.73; raw concordance scores for all three variables were over 85%. The raw codes across variables were combined to produce a single score characterizing degree of depigmentation for each eye in each photo. Additionally, because any presence of depigmentation is of interest and because some subjects had asymmetrical depigmentation patterns (e.g., Fig. 1c, see also *Gorilla* in Caspar et al., 2021), we report the maximum depigmentation level between the two eyes, between raters, and across all photographs of each individual at a given age class. We first determined the minimum depigmentation score between raters for each eye in each photo separately, before compiling across all photos for each individual. Chimpanzees were thus scored as having, in at least one eye, (1) white sclera, (2) brown or tan sclera, which we classified as ‘intermediate,’ (3) dark sclera with some patches of light or white sclera, or (4) dark sclera (Fig. 1).

To quantitatively measure contrast between the iris and sclera and facilitate comparison with previous studies, we adapted Perea-García et al.’s (2019) measure of relative iris luminance, calculated as the darker of the two grayscale values divided by the lighter value. For a subset of 180 high-quality photographs of 148 chimpanzees, we calculated weighted grayscale values of iris and sclera based on RGB pixel values measured using the NIH ImageJ program (1.52q, National Institutes of Health, Bethesda; http://imagej.nih.gov/ij). Both right and left eyes were measured in 1–2 photographs per individual, and we assigned the luminance values to that individual rather than calculating the average across photographs and eyes (Perea-García et al., 2019) to account for individuals exhibiting different patterns or degrees of depigmentation in each eye. We selected points that were representative of the majority of the sclera and iris, respectively, avoiding reflective or shadowed areas. For each individual, we used the minimum relative iris luminance value (i.e., highest contrast) across eyes and photographs in our analysis.

To explore longitudinal changes in scleral pigmentation within individuals, we identified a subset of individuals who have matured into an older age group since February 2020 and compiled an additional set of 137 photographs taken between March 2020 and March 2022. This supplemental set of photos was scored by K.C.L. and focused on a single summary score—maximum level of depigmentation from either eye, across all available photos for a given individual, of both ‘direct’ and ‘averted’ gaze when possible. Combined with the data points from the original cross-sectional dataset, the development-focused dataset included 69 individuals that were represented across two age classes, plus one individual represented across three age classes (SOM Table S1).

To explore whether scleral depigmentation was more common across mammals more broadly, I.R.C. and T.P. photographed 70 species (n = 1–8 individuals/species, 200 individuals total) housed at the Bronx Zoo, Central Park Zoo, and Prospect Park Zoo in New York, USA, from public viewing areas over several days in July and August 2018. T.P. applied the qualitative assessment described above to identify individuals with predominantly white sclera from photographs. I.R.C. scored a subset of this dataset to check for reliability of scores. Cohen's Kappa score (weighted by 'squared distance' of sorted levels) for sclera color was 0.75, while raw concordance between raters was 82%. We report the minimum rating (i.e., darker sclera) in the case of discrepancy between raters (SOM Table S2).

3. Results

In a large population of wild chimpanzees at Ngogo in Kibale National Park, Uganda, we found considerable variation in eye color (Fig. 1). Fifteen percent of chimpanzees exhibited white sclera, representing 34 of 230 individuals. For five of these 34 individuals, white sclera was visible when they looked directly forward (Fig. 2). For the other 29 chimpanzees, white sclera was visible only when not looking directly forward, exposing more sclera at the periphery of the eyes. An additional 95 chimpanzees exhibited other forms of scleral depigmentation, with 37 individuals exhibiting predominantly tan/brown sclera and another 58 individuals exhibiting dark sclera with patches of depigmentation. As with white sclera, these forms of depigmentation were especially apparent when gaze was averted rather than direct (Fig. 2).

The prevalence of scleral depigmentation was significantly associated with age (chi-square test: $\chi^2 = 84.30$, df = 12, $p < 0.0001$; SOM S1; SOM Fig. S1). Young infants accounted for the greatest proportion of individuals with white sclera, with 58.6% (17/29) of infants under 1.5 years of age exhibiting white sclera, and an additional 20.7% (6/29) exhibiting brown or tan sclera. The prevalence of white sclera decreased sharply among older infants, with only 13.8%

(4/29) of 1.5- to 5-year-olds exhibiting white sclera, which more closely resembled the prevalence in older age-classes (Fig. 2). The longitudinal findings corroborate those of our cross-sectional dataset: prevalence of scleral depigmentation significantly differed as individuals matured (chi-square test: $\chi^2 = 62.98$, df = 9, $p < 0.0001$; SOM Fig. S2), driven by increased pigmentation with age (SOM Table S1). Most young infants (26 of 31, 84%) with white or tan sclera developed substantial pigmentation as older infants (Fig. 3; SOM Fig. S3). Similar but less dramatic patterns were observed in the older age classes, in part due to fewer individuals of older age classes having depigmented sclera to begin with. Only four of 70 individuals were scored as becoming more depigmented. Two of these cases were likely due to failure to observe small patches of depigmentation that were not visible with the gaze directions represented in earlier photos. There were no cases of individuals developing white sclera as they matured.

Of the chimpanzees at Ngogo with dark sclera, 75% had relatively lighter irises, which was readily apparent even when chimpanzees were looking directly forward. The contrast between iris and sclera was especially noticeable for chimpanzees with orange- and red-hued irises (Fig. 3). We found no quantitative difference in relative iris luminance between chimpanzees with darker vs. lighter sclera (SOM Fig. S4). Mean values across individuals were 0.50 ± 0.19, based on luminance values of sclera ($\bar{x} = 33.94 \pm 29.48$) and iris ($\bar{x} = 41.23 \pm 19$).

Our analysis of scleral depigmentation in 70 zoo animal species revealed that 19 species had at least one individual with white sclera (SOM Table S2). This included *Gorilla gorilla gorilla* (1/7 individuals), callitrichine monkey species (2/4 *Saguinus geoffroyi*, 1/1 *Leontopithecus rosalia*, 6/7 *Callithrix geoffroyi*), *Theropithecus gelada* (1/4), *Papio hamadryas* (1/3), *Callicebus donacophilus* (1/2), *Trachypithecus auratus* (1/3), *Trachypithecus cristatus* (1/8), and *Eulemur collaris* (2/3). We also found white sclera in some carnivores including

Helogale parvula (3/5), *Panthera pardus* (1/1), *Canis lupus dingo* (1/1), *Zalophus californianus* (2/2), as well as domesticated artiodactyls, *Sus domesticus* (1/1) and *Capra hircus* (3/5); Fig. 4; SOM Table S2).

4. Discussion and conclusions

White sclera is often considered a uniquely human trait in the scholarly literature and popular media. Our study confirms that this is not the case. Almost 1 in 6 chimpanzees at Ngogo had full or partial white sclera in at least one eye, which tended to be more visible when gaze was averted rather than direct. Even a small amount of white or light sclera may make gaze direction more apparent (e.g., Fig. 1d–f) and is thus relevant for hypotheses about gaze signaling and social cognition. White sclera was especially prevalent among young infants (17 of 29 infants ≤1.5 years), and sclera appears to darken with age for many but not all chimpanzees. We suspect that white sclera is more salient in this population because it is over three times larger than other chimpanzee populations. We additionally propose that white sclera may be more common across mammals generally. Recognizing and understanding this variation in eye color is key for formulating hypotheses about the role of eyes in animal communication and the evolution of social cognition, as well as more recent investigation into ecological factors underlying variation in eye morphology.

Our findings on developmental variation suggest that the sclera, like the skin (Post et al., 1975), becomes pigmented with age for many but not all chimpanzees. This provides longitudinal evidence in support of Perea-García et al.'s (2019) suggestion that chimpanzee sclera darkens with age, based on cross-sectional comparisons of age groups. The human sclera also darkens somewhat with age (Russell et al., 2014).

Among chimpanzees, white sclera is unlikely to be unique to those at Ngogo. First, some of the Ngogo chimpanzees with white sclera were immigrant females (n = at least 3 individuals; SOM File S1) indicating that white sclera also occurs in other communities in Kibale National Park. Second, white sclera occurs occasionally in smaller chimpanzee communities in other populations, but only one or two out of 30–50 chimpanzees might exhibit white sclera, prompting observers to dismiss the trait as anomalous (Goodall, 1986; Boesch and Boesch-Achermann, 2000). Ngogo has over 200 chimpanzees. The presence of several chimps with human-like white sclera and others with subtler forms of depigmentation prompts us to consider this variation biologically meaningful rather than anomalous or pathological.

The fact that white sclera is present in chimpanzees but has largely been ignored raises the possibility that white sclera is more common across mammals than previously thought. In a preliminary, broader comparison across species, we found that in 19 of 70 mammal species, at least one individual exhibited white sclera (SOM Table S2). Contrary to the findings of Kobayashi and Kohshima (2001) that of 88 primate species, only humans exhibited white rather than pigmented 'brown' sclera, we found that several primate species exhibited white sclera, including callitrichine monkeys, *Plecturocebus donacophilus*, *Theropithecus gelada*, *Papio hamadryas*, *Trachypithecus sp.*, and *Eulemur collaris* (Fig. 4), which is further supported by two recent studies (Kano, 2022; Perea-García et al., 2022). The discrepancy in presence of white sclera in these species by Kobayashi and Kohshima and our study may be attributed to random sampling error due to small samples sizes. We additionally found white sclera in some non-primate mammals including *Helogale parvula*, *Panthera pardus*, *Canis lupus dingo*, and some domesticated animals (Fig. 4). The presence of white sclera in canids and domesticated animals raises intriguing ideas about its evolution. Dogs are attuned to human gaze and social cues (Hare et al., 2002; Riedel et al., 2008), and the eyes of wolves may also facilitate gaze communication (Ueda et al., 2014). To what extent does white sclera or other aspects of eye morphology facilitate gaze detection?

Although more prevalent across species than previously reported, the sclera is minimally exposed in many of these species (e.g., *Eulemur collaris*, see Fig. 4f). Whether white sclera makes gaze direction more apparent remains unclear. The iris may be conspicuous against dark as well as white sclera (Pereia-García et al., 2019, Caspar et al., 2021), but uniformly white sclera may enhance gaze detection, particularly at greater distances and low light (Kano et al., 2021, 2022; Yorzinski et al., 2021). Additional comparative studies of eye coloration across species are key for assessing hypotheses about the evolutionary processes influencing sclera and iris pigmentation and contrast (Emery, 2000; Kobayashi and Kohshima, 2001; Tomasello et al., 2007). Additional studies of gaze signaling, including the influence of eye color and morphology (Yorzinski et al., 2021) and whether conspecifics or other species vary in their ability to perceive gaze (Whitham et al., 2022), will enable testing these hypotheses.

Humans may be distinctive in exhibiting uniformly white sclera, with relatively little within-species variation compared to other mammals (Kano, 2022). From a phylogenetic perspective, the fact that white sclera occurs at small but non-trivial numbers in *Pan troglodytes*, as we have found, and in *Gorilla gorilla* (Mayhew and Gómez, 2015), and that tan or brown sclera is frequent in *Pan* spp. (Perea-García et al., 2019), and *Pongo pygmaeus* (Perea-García, 2016; Caspar et al., 2021), suggests a source of standing variation in the last common ancestor of great apes. This, in turn, could have provided the raw material that selection subsequently acted on in humans. Furthermore, our data suggest that most chimpanzees are born with white or light sclera that tends to quickly darken as they mature, which may explain the phenomenon of fixed white sclera in humans from an ontogenetic perspective.

Our findings do not support or refute prior hypotheses for the function of white sclera in humans (Tomasello et al., 2007; Hare, 2017; Kano, et al., 2021, 2022). However, until recently, such hypotheses have relied on a false premise: that white sclera is unique to humans. This is not the case. Our findings suggest that white sclera is not an anomalous trait in chimpanzees, and likely persists in chimpanzee populations, albeit rarely. White sclera is also likely more prevalent than previously thought in a range of mammalian species, including some other primates (Mayhew and Gómez, 2015; Caspar et al., 2021; Kano, 2022; Perea-García et al., 2022). Better documentation of this variability will spur novel hypotheses and enable comparative analyses to test existing hypotheses concerning variation in sclera color, such as the gaze signaling and cooperative eye hypotheses (Tomasello et al., 2007; Kano 2022), gaze camouflage hypothesis (Kobayashi and Kohshima, 2001), self-domestication hypothesis (Hare, 2017; Mearing et al., 2022), and alternative ecological explanations (Perea-García et al., 2021, 2022). Given that evolution by natural selection acts on variation, it is not surprising that our closest living relatives provide compelling glimpses into our unusual eyes.

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Figure captions

Figure 1. Examples of eye pigmentation in 12 Ngogo chimpanzees: a–c) majority white sclera; b–f) majority white sclera only when gaze is averted; g–i) intermediate sclera; j–l) majority dark sclera (with dark iris, depigmented patches on sclera, and light iris, respectively. a) Pincer, 33 years; b) Gatsby, 0.7; c) Baez, 16.7; d) Fiona, 21.5; e) Hester, 18; f) Dexter, 34.7; g) Khutulun, 17; h) Dorothy, 1.8; i) Gus, 11.4; j) Billy Bragg, 13.5; k) Buckner, 19.7; l) Wilson, 18.5.

Figure 2. Proportion of Ngogo chimpanzees with different levels of scleral pigmentation, grouped by age class and gaze direction (direct vs. averted). Sample sizes for each age/gaze direction class were as follows: newborn/direct = 23 individuals; newborn/averted = 27; infant/direct = 25; infant/averted = 27; juvenile/direct = 32; juvenile/averted = 35; adolescent/direct = 30; adolescent/averted = 34; adult/direct = 95; adult/averted = 113.

Figure 3. Examples of developmental change in scleral pigmentation, from light to dark: a–b) Kofi at 3 months and 3 years, c–d) Malaika at 7 months and 2.7 years, and from light to intermediate: e–f) RBG at 1 month and 2 years. Example of an infant retaining depigmentation with age: g–h) Dorothy at 5 months and 1.9 year.

Figure 4. Examples of white sclera in 12 animal species at Wildlife Conservation Society zoos: a) *Gorilla gorilla gorilla* ; b) *Papio hamadryas*; c) *Theropithecus gelada*; d) *Trachypithecus auratus*; e) *Saguinus oedipus*; f) *Eulemur collaris*; g) *Helogale parvula*; h) *Panthera pardus*; i) *Sus domesticus*; j) *Zalophus californianus*; k) *Bos taurus indicus*; l) *Capra hircus*. Photos by T.P.


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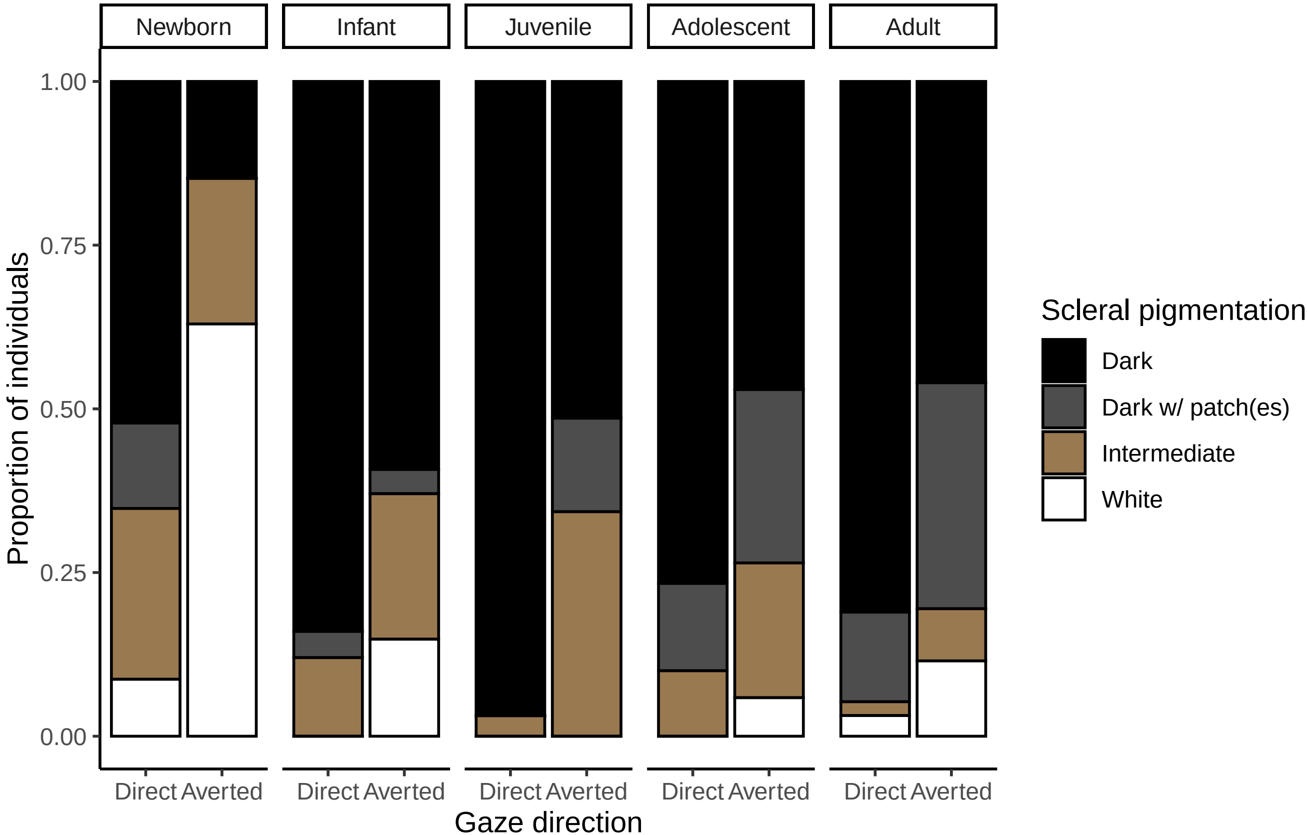
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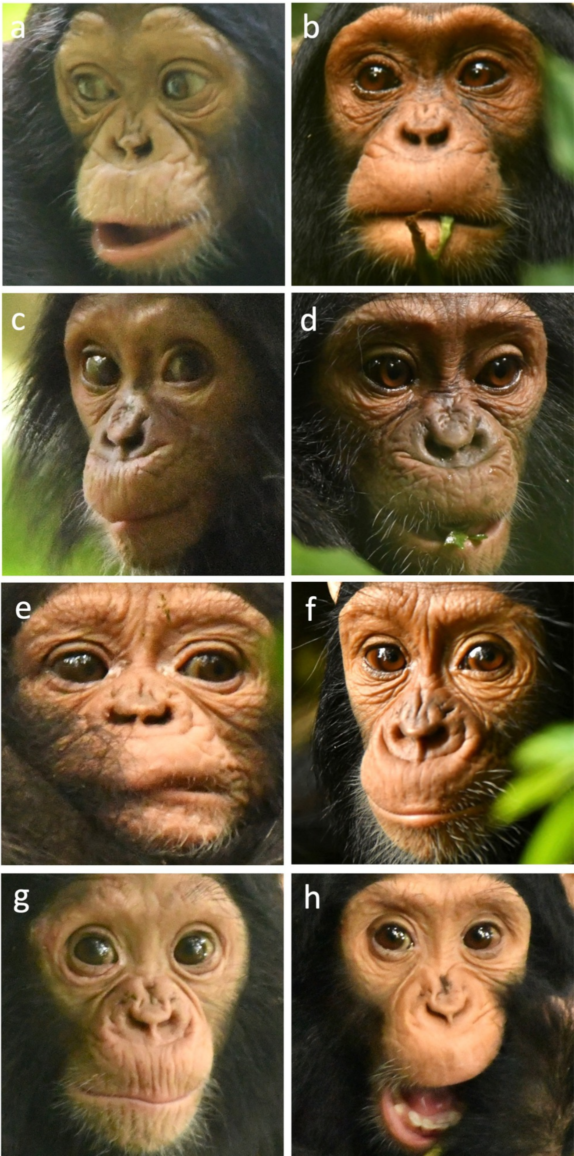
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