



Historical contingency in the evolution of primate color vision

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Abstract

Primates are unique among eutherian mammals for possessing three types of retinal cone. Curiously, catarrhines, platyrrhines, and strepsirrhines share this anatomy to different extents, and no hypothesis has hitherto accounted for this variability. Here we propose that the historical biogeography of figs and arborescent palms accounts for the global variation in primate color vision. Specifically, we suggest that primates invaded Paleogene forests characterized by figs and palms, the fruits of which played a keystone function. Primates not only relied on such resources, but also provided high-quality seed dispersal. In turn, figs and palms lost or simply did not evolve conspicuous coloration, as this conferred little advantage for attracting mammals. We suggest that the abundance and coloration of figs and palms offered a selective advantage to foraging groups with mixed capabilities for chromatic distinction. Climatic cooling at the end of the Eocene and into the Neogene resulted in widespread regional extinction or decimation of palms and (probably) figs. In regions where figs and palms became scarce, we suggest primates evolved routine trichromatic vision in order to exploit proteinaceous young leaves as a replacement resource. A survey of the hue and biogeography of extant figs and palms provides some empirical support. Where these resources are infrequent, primates are routinely trichromatic and consume young leaves during seasonal periods of fruit dearth. These results imply a link between the differential evolution of primate color vision and climatic changes during the Eocene–Oligocene transition.

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1. Introduction

The ability of primate visual systems to discriminate color is unique among eutherian mammals (Ahnelt and Kolb, 2000; Arrese et al.,

2002). However, the geographic variation in primate color vision is striking and the evolutionary ecology poorly understood (Dominy et al., 2001). Remarkably, only some primates simultaneously possess three cones maximally sensitive, or tuned, to different regions of the spectrum. To account for this variation we propose an evolutionary (or co-evolutionary) link between the visual systems of

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primates and the color and abundance of keystone fruits, such as figs and arborescent palms.

2. Variation in primate color vision

Among anthropoid primates, trichromatic vision of both sexes is routine only in Old World monkeys, apes, and humans (Jacobs and Deegan, 1999). The genes coding for the short- (S), middle- (M), and long- (L) wavelength pigment opsins are located on chromosome 7 and neighboring sites on the X-chromosome, respectively (Nathans et al., 1986). Apart from humans, M or L cones are seldom missing in catarrhines (Onishi et al., 1999; Jacobs and Williams, 2001). In New World monkeys the nature of color vision is different. Although they share with catarrhines the S-cone specified by an autosomal gene, platyrrhines have only a single X chromosome opsin gene locus. This results in polymorphic variation in the M/L opsin gene, such that all males receive only a single type of M/L pigment. In conjunction with the S-cone, this polymorphism yields dichromatic color vision. Due to X-chromosome inactivation, heterozygous females (approximately 50–60% of females in most platyrrhine species) produce two types of M/L cone and possess trichromatic vision (Mollon et al., 1984; Jacobs and Deegan, 2001). Among platyrrhines, however, there are two exceptions to this general pattern. The night monkeys (*Aotus*) have lost both the functional S-cone pigment and polymorphic variation in the M/L opsin gene (Jacobs et al., 1993). Accordingly, they possess only a single visual pigment, and cannot discriminate color. In contrast, howling monkeys (*Alouatta*) are routinely trichromatic and exhibit a gene duplication of the X-chromosome opsin similar to that in catarrhines, but independently evolved (Jacobs et al., 1996; Boissinot et al., 1998; Kainz et al., 1998; Dulai et al., 1999).

Recently, a genetic analysis of 20 strepsirhine species revealed allelic variation of M/L opsin genes in sifakas (*Propithecus verreauxi*) and ruffed lemurs (*Varecia variegata*) (Tan and Li, 1999), both of which forage diurnally. The presence of an M/L cone opsin polymorphism indicates the presence of trichromatic vision in heterozygous

females. This is confirmed with spectral sensitivity data from both taxa, although it is unclear how acute the capacity might be (Jacobs et al., 2002; Jacobs and Deegan, 2003).

3. Color vision and feeding

Given that one advantage of trichromatic over dichromatic vision is the capacity to discriminate between red and green (Párraga et al., 2002), primate trichromacy has historically been interpreted as an adaptation to detect foods against a background of mature foliage. However, opinions have differed over which foods offer the greater selective advantage. Whereas many have stressed the importance of detecting ripe fruits (Regan et al., 2001), others emphasize the advantages of detecting young leaves (Lucas et al., 1998; Dominy and Lucas, 2001). Indeed, both food items are often distinctive from mature foliage (Sumner and Mollon, 2000a,b).

However, few studies have examined both the nutritional content and color properties of primate foods. Compared to mature, nonconsumed foliage, edible reddish and red-yellowish young leaves are less tough (Lucas et al., 1998), richer in protein (Dominy and Lucas, 2001), and richer in free amino acids (Dominy, 2003). Conversely, fruit color provides no consistent nutritional cue in the 12 most commonly consumed species of Kibale Forest, Uganda (Dominy, 2003). Indeed, a literature survey of 43 primate species grouped into visual categories of dichromats, nonroutine trichromats, and routine trichromats, indicates that, regardless of visual capacity, red and orange fruits combined (17–24% of food species) are consumed less frequently than green fruits (30–65% of food species) (Dominy, 2003). This study and others (e.g. Wheelwright and Janson, 1985) suggest that the evolutionary value attributed to detecting orange and red fruit has been overstated.

However, linking the evolution of trichromacy to diet becomes complicated when considering the diverse feeding behaviors of genera possessing an M/L cone opsin polymorphism. For example, there are large ecological and morphological differences between spider monkeys (*Ateles*), which

are ripe-fruit specialists, and callitrichines, which are characterized by insectivory, gummivory, and frugivory. Moreover, sifakas and ruffed lemurs are highly folivorous and frugivorous, respectively. Accordingly, it would appear tenuous to reason that primate trichromacy is (a) evolutionarily optimized or (b) linked to diet. Nevertheless, we attempt here to provide an adaptive account for the diversity of primate visual systems. We propose a general evolutionary and ecological scenario in which a balanced M/L cone opsin polymorphism could be favored in some primate taxa and not others. Specifically, we suggest a link between primate visual capacities and the hue, abundance, and biogeography of keystone resources.

4. Keystone resources

Some plant taxa consistently provide food during community-wide periods of fruit dearth. Keystone resources thus sustain frugivore populations during crucial periods (Power et al., 1996). Indeed, seldom-consumed but critical food resources may exert a powerful selective pressure on animal adaptation (Grant and Grant, 2002). Terborgh (1986) identified fruits of palms (Arecaceae) and figs (Moraceae: *Ficus*) as keystone resources for primates. He estimated that, despite representing <1% of the plant diversity in Cocha Cashu, Peru, keystone resources sustained approximately 1600 kg km⁻¹ of mammals and birds for 3 months annually. He considered figs to be most important: “subtract figs from the ecosystem and one could expect to see it collapse” (p. 339). In fact, calcium-rich figs are an important food resource to an impressive variety of frugivores throughout the tropics, including virtually all primates (O’Brien et al., 1998; Shanahan et al., 2001). However, due to relatively low densities, Afro-Madagascan figs are not keystone resources to the same extent that they are elsewhere (Goodman and Ganzhorn, 1997; Shanahan et al., 2001).

Palm fruits are a similarly important resource for a wide variety of frugivores (Zona and Henderson, 1989). Their importance is supported

not only by a fruiting phenology characterized by year-round availability (Terborgh, 1986; Peres, 1994; Ribeiro et al., 1999), but also by their nutritious content. The flesh of palm fruits consumed by primates is an exceedingly valuable source of lipids and fat (e.g. Rogers et al., 1990; Palacios et al., 1997). Indeed, complex nut-cracking behaviors reported in capuchins (Struhsaker and Leland, 1977; Terborgh, 1983) and tool-assisted nut-hammering by chimpanzees (Yamakoshi, 1998) underscore the value of accessing palms during times of food scarcity. In fact, it is estimated that chimpanzee palm-nut hammering provides an energetic reward (the endosperm) ca. seven times greater than the energy expended (Günther and Boesch, 1993).

5. Hypothesis for the geographic variation in primate color vision

To attract vertebrate seed dispersers, fruits often employ conspicuous chromatic signals, the pantropical frequencies of which differ little at the generic taxonomic level (Fischer and Chapman, 1993). The fruits of figs and palms, however, are often inconspicuously colored and do not contrast chromatically with their background. For detecting such fruits it is plausible that dichromatic vision may be advantageous. Although evidence is scant, reduced “chromatic noise” may improve detection of edges and contours (Regan et al., 2001). A variety of anecdotes and at least one empirical study support the notion that dichromacy is better suited to breaking color camouflage (Morgan et al., 1992). Advantages may be most manifest under low-light conditions (Verhulst and Maes, 1998) or when viewing stimuli reflecting middle wavelengths (500–570 nm) (Jacobs, 1990). Recently, an experiment comparing trichromatic and dichromatic marmosets reported that trichromats tend to be hampered when seeking camouflaged food items, although the finding did not reach statistical significance (Caine, 2002). Collectively, these results tend to suggest a selective advantage enjoyed by primate foraging groups with mixed capabilities for chromatic discrimination. Accordingly, foraging groups may rely on

conspicuous small fruits during times of fruit abundance and large cryptic palms and figs during times of fruit scarcity.

We thus hypothesize that the primate M/L cone opsin polymorphism will be favored in regions characterized by camouflaged keystone fruits, and, concomitantly, that routine trichromacy will be favored in regions where keystone fruits are relatively scarce (and the primary keystone food resource is young leaves instead). We further hypothesize that the physical properties of figs and palm fruits will vary geographically in response to primate visual systems. We evaluate these hypotheses by reviewing the hue and historical biogeography of palms and figs.

6. Methods

To test the hypothesized value of the M/L cone opsin polymorphism for detecting camouflaged keystone resources, we surveyed the available literature for descriptive characteristics of fig fruits (Appendix A) and palm fruits (Appendix B). Following Peres (1994) we considered palms to be keystone resources if they are free-standing and arborescent, i.e. ≥ 10 m. We considered only native species. Stem heights and fruit dimensions are the maximum values reported. With figs, we disregarded height because epiphytic and hemi-epiphytic species are considered equally important resources to tropical frugivores (Shanahan et al., 2001). Classification of fruit hue is based on the qualitative description given in the original source, with further grouping into categories of purple, green, yellow, orange, red, brown, and black. Such basic color terms are virtually universal (Hardin, 1998), and we assume that they are equally salient to tropical botanists. However, it is conceivable that some of the 28 cited individuals have anomalous color vision. If authors described a fruit as bicolored, e.g. orange-red, we classify the fruit by the first hue reported, for example, orange. If an author described a fruit as ‘brownish-red’, we treat the suffix *-ish* to indicate only a “touch or trace of” per Webster’s Dictionary. In this example the fruit would be categorized by its overriding hue, red. Lastly, given that similarities in palm fruit color

may partially reflect phylogeny, we focused sampling units at the generic level in order to prevent speciose taxa from dominating the analyses. Generic color is represented by the modal specific color. If a color is equally represented at the specific level, the genus was counted in each color category.

Because figs and palms (a) frequently do not emerge from the canopy overstory and (b) display their fruits against foliage or the surface of their own bole, we classify dark and chromatically similar hues as camouflaged or ‘cryptic’ to trichromatic primates (i.e. black, dark purple, brown, and green). Although dark or dull coloration does not necessarily reflect crypsis (indeed, it may improve specularly), it is likely chromatically ineffectual for attracting trichromats from distances of 25 m under shaded conditions (Janson and Di Bitetti, 1997). We categorize the remaining hues as ‘conspicuous’ (i.e. yellow, orange, and red).

To test for an evolutionary response of figs and palms to primate visual systems, a chi-square analysis was performed between regions characterized by primate (a) absence (New Caledonia, New Guinea, Northern Queensland, South Pacific), (b) polymorphism of the M/L cone opsin (Central Panama, Madagascar, South America), and (c) routine trichromacy (Africa, Borneo, Peninsular Malaysia).

7. Results

In regions with polymorphic primates, both figs and palm fruits are frequently, generally even predominantly, cryptically colored (Tables 1 and 2). Cryptic fruits, moreover, are larger than conspicuous fruits (Table 3), and their prevalence differs among regions (a–c) (*Ficus*: $n=206$, $\chi^2=43.3$, $df=2$, $P<0.0001$; Arecaceae genera: $n=72$, $\chi^2=6.2$, $df=2$, $P<0.05$; Arecaceae species: $n=206$, $\chi^2=9.9$, $df=2$, $P<0.01$) (Fig. 1). In primate-inhabited regions (b)+(c), palm fruits are more frequently cryptic (genus level: $\chi^2=5.2$, $df=1$, $P<0.05$; species level: $\chi^2=9.0$, $df=1$, $P<0.01$) than where primates are absent (a), whereas no difference was found among figs. Conversely, when

Table 1
Frequency of cryptic and conspicuous fruit hues attributed to ripe *Ficus*

Regions surveyed	Cryptic hues				Conspicuous hues		
	Black	Purple	Green	Brown	Yellow	Orange	Red
(a) No primates							
New Guinea	0	0	7	0	3	8	6
(b) Polymorphic primates							
Madagascar	0	1	3	1	0	2	5
Central Panama	0	0	15	0	0	0	4
South America	0	3	22	2	6	1	11
(c) Trichromatic primates							
Africa	0	2	10	1	12	7	21
Peninsular Malaysia	1	1	0	1	2	1	19
Borneo	0	0	2	2	2	25	12

Table 2
Frequency of cryptic and conspicuous ripe-fruit hues attributed to arborescent genera (and species) in the family Arecaceae

Regions surveyed	Cryptic hues				Conspicuous hues		
	Black	Purple	Green	Brown	Yellow	Orange	Red
(a) No primates							
New Caledonia	3 (8)	3 (5)	0 (0)	2 (2)	0 (0)	2 (2)	8 (11)
Northern Queensland	2 (3)	2 (2)	0 (0)	3 (3)	0 (0)	2 (2)	3 (4)
South Pacific	1 (1)	0 (0)	1 (1)	1 (1)	2 (2)	2 (7)	6 (13)
(b) Polymorphic primates							
South America	0 (2)	2 (10)	1 (5)	9 (20)	2 (6)	3 (10)	1 (3)
Madagascar	0 (2)	2 (4)	1 (4)	6 (10)	0 (2)	3 (9)	2 (5)
(c) Trichromatic primates							
Africa	0 (0)	2 (2)	0 (0)	4 (13)	0 (1)	2 (4)	1 (1)
Thailand and Malaysia	3 (4)	2 (2)	1 (1)	5 (5)	3 (4)	1 (1)	1 (5)

comparing between regions where primate trichromacy differs (b) vs. (c), figs are more frequently cryptic where primates are polymorphic ($\chi^2=40.7$, $df=1$, $P<0.001$), whereas no difference was found among palms.

8. Discussion

Palms were abundant throughout tropical forests from the late Cretaceous to the early Tertiary (Morley, 2000). From the Oligocene onwards, palm diversity and abundance was greatly reduced in continental Africa and to a lesser extent in Southeast Asia due to increased

Table 3
Two-way factorial ANOVA of fruit diameter as a function of color and region and their interaction

Independent variable		s.s.	df	F	P
Color	Areaceae	57.3	1	8.0	<0.01
	<i>Ficus</i>	1138.5	1	11.4	<0.001
Region	Areaceae	392.2	2	27.4	<0.001
	<i>Ficus</i>	167.9	2	0.8	n.s.
Color:region	Areaceae	7.3	2	0.5	n.s.
	<i>Ficus</i>	218.6	2	1.1	n.s.

desiccation (Morley, 2000). Tropical South America and parts of Madagascar escaped desiccation to a greater extent and retained a rich,

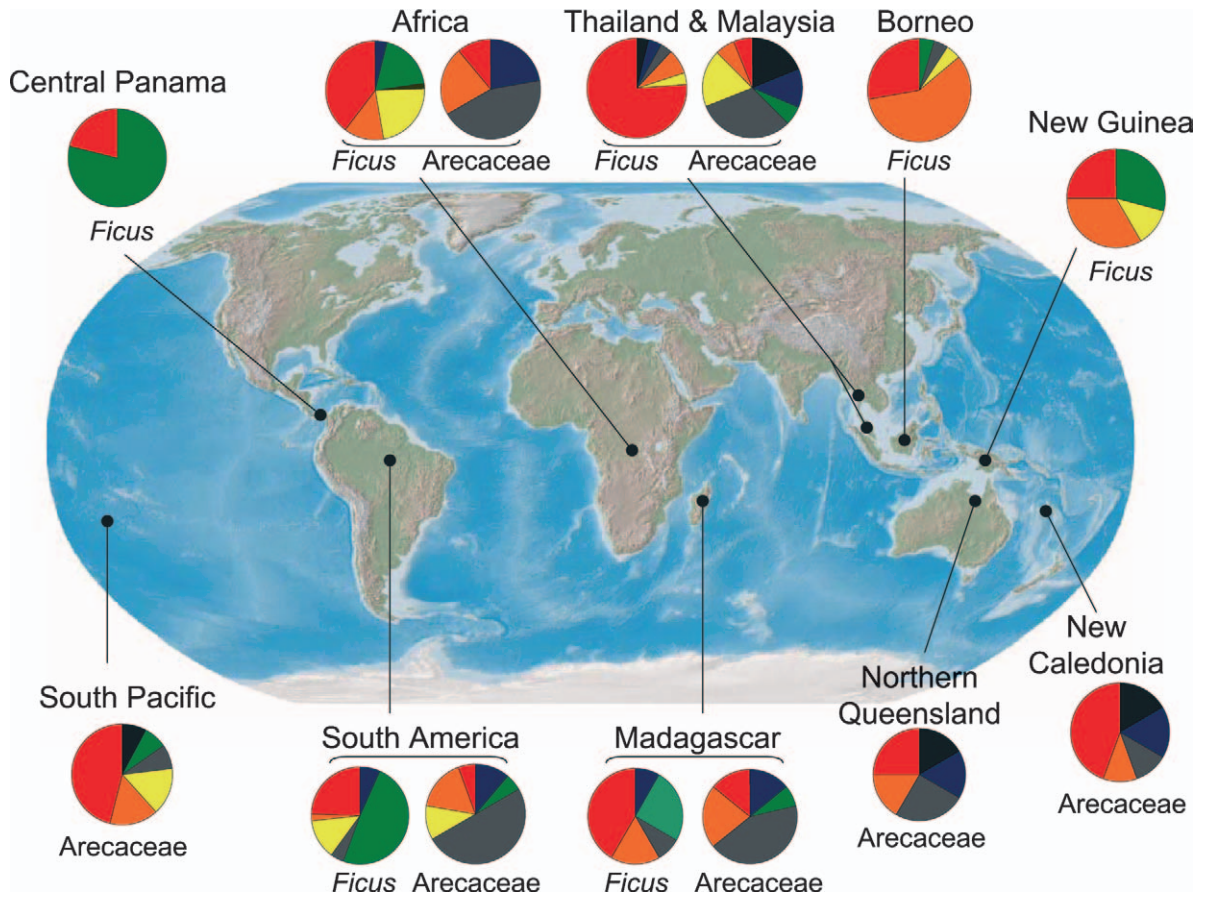


Fig. 1. The global diversity of conspicuous (yellow, orange, and red) and cryptic (black, dark purple, brown, and green) hues attributed to the ripe fruits of figs (*Ficus*) and palms (*Arecaceae*). Note: palm fruit hues are represented at the generic taxonomic level.

abundant palm flora (Dransfield and Beentje, 1995; Morley, 2000). Compared to continental Africa and Asia, arborescent palms today constitute a much more important component of forests in South America and Madagascar, where they are a major canopy element (Gentry, 1988).

The paleogeography and distribution of *Ficus* is more difficult to model, although the genus is known to occur in Middle Eocene deposits (Muller, 1981; Morley, 2000). Today, the greatest diversity of *Ficus* is centered in Australasia (ca. 500 spp.), where the genus presumably originated. Diversity is considerably lower in the neotropics (ca. 150 spp.), Africa and Madagascar (ca. 100 spp.) (Kubitzki et al., 1993).

Our results show that cryptic coloration is frequent in figs and palm fruits in regions where primates express an M/L cone polymorphism and that cryptic fruits are larger than conspicuous fruits. Further, our results also show that cryptic figs are most frequent where primates express an M/L cone polymorphism and that cryptic palms are least frequent where primates are absent. These data confirm our hypothesis regarding the optimality of opsin polymorphisms in palm- and fig-rich forests and suggest a possible evolutionary link between keystone fruits and primate color vision. We suggest that Paleogene primates relied on palms and figs and, in turn, provided high quality seed dispersal. On the basis of character

optimization, these primates were most likely routinely dichromatic or possessed an M/L cone opsin polymorphism (Heesy and Ross, 2001). Thus palms and figs likely lost or simply did not evolve conspicuous fruit colors, as this was of little value for attracting dichromatic primates.

The Eocene–Oligocene interval (~40–30 Ma) was characterized by considerable cooling and drying as Antarctica became isolated from South America and Australia (resulting in the continuous circum-Antarctic ocean current). Increased seasonal fluctuations in Africa and Asia dramatically reduced palms (and possibly figs) in these regions by 35 Ma, with further attrition of the palm flora occurring during the latter part of the Tertiary (Morley, 2000). Increased seasonality coupled with attendant periods of fruit scarcity thus coincided with a reduction in keystone resources in Africa. In fact, Africa is still highly seasonal, with a phenology characterized by alternating periods of fruiting and leafing (Terborgh and van Schaik, 1987; van Schaik and Pfannes, in press). Young leaves are an abundant source of protein and they almost certainly represented fallback resources for the earliest catarrhines, particularly as leafing generally occurs when insect abundance is lowest (Wright and van Schaik, 1994). Indeed, young leaves still represent an important seasonal resource for even the most frugivorous catarrhines (e.g. Doran, 1997; and see Jablonski et al., 2000 on the importance of leaves during the Pleistocene). The preponderance of red young leaves in paleotropical floras (Dominy et al., 2002) and the link between leaf color and nutritional quality thus favored the evolution of routine trichromatic vision in catarrhines (Lucas et al., 1998; Dominy and Lucas, 2001; Dominy, 2003). Compellingly, both molecular and osteological evidence are consistent with this scenario. Although Middle Eocene primates ranged in size from above 1 kg (e.g. *Amphipithecus*, *Protoadapis*, and *Notharctus*) to well below 1 kg (e.g. *Pseudoloris* and *Washakius*), there is no evidence for even secondary folivory in any anthropoid prior to the early Oligocene (Kay and Simons, 1980; Kirk and Simons, 2001). However, the dentition of the earliest known catarrhines (e.g. *Catopithecus* and *Propliopithecus* spp.) clearly indicates substantial leaf consumption by

33–34 Ma (Kirk and Simons, 2001). The gene duplication rendering catarrhines routinely trichromatic is estimated at ca. 35 Ma (Yokoyama and Yokoyama, 1989).

The earliest known platyrrhine, *Branisella boliviana*, dates from the late Oligocene (~26 Ma) and weighed ca. 760 g (Kay et al., 2002). In fact, if platyrrhines rafted to the New World, it is estimated that they could have been no larger than 1 kg (Houle, 1999). Given these body masses and an inferred catarrhine–platyrrhine divergence of 35–40 Ma (Goodman et al., 1998), or possibly 70–80 Ma (Arnason et al., 1998, 2001), it would appear the platyrrhine lineage has long-consumed a preponderance of insects and fruits (Fleagle, 1999). Accordingly, palms and figs likely represented reliable fallback resources during critical periods of fruit scarcity. In fact, palms remain important resources for even the smallest platyrrhines (Mamede-Costa and Godoi, 1998). We thus suggest that the abundance of cryptically colored keystone resources in the Neotropics and Madagascar never favored the evolution of routine trichromacy because young leaves never became critical fallback foods. The exceptional evolution of routine trichromacy in *Alouatta* is telling. Howling monkeys are not only well known to favor young leaves, but evince also a variety of behavioral, dental, and digestive adaptations for this purpose (Milton, 1998).

Although evolutionary rates of gene duplications are still being resolved, they appear relatively high in mammals (Lynch and Conery, 2001). Opsins, moreover, appear plastic. In fish, they evolve rapidly in response to environmental changes (Bridges and Yoshikami, 1970), and, in mammals, they are lost during key transitions, e.g. from diurnality to nocturnality (Jacobs et al., 1993) or from land to sea (Peichl et al., 2001). Once duplicated, however, the expression mechanisms yielding differential cone types are facile (Wang et al., 1999; Smallwood et al., 2002). We thus doubt that the M/L cone opsin polymorphism represents a mildly sub-optimal trichromacy adapted to detect ripe, conspicuous fruits. Instead, we submit that the polymorphism represents a balance between dichromatic advantages for detecting cryptic keystone fruits, such as figs and

arborescent palms, and the occasional reliance on heterozygous females to detect conspicuous fruits (Mollon, 1989; Caine and Mundy, 2000; Surridge and Mundy, 2002). Recent field experiments with wild tamarins, however, do not reveal any sex-differences with respect to detecting ripe bananas (Dominy et al., in press). We further suggest that routine trichromacy offered catarrhines a selective advantage during the Eocene–Oligocene transition and onwards, when a scarcity of keystone fruit resources forced them to resort to a seasonal diet of young leaves. In fact, at least one gene duplication facilitating folivory in primates is well established (Zhang et al., 2002), indicating that adaptations to leaf consumption play an important role in primate evolution.

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Appendix A. Descriptive properties of figs

<i>Ficus</i> spp. and geographic origin	Fig length (mm)	Fig diameter (mm)	Mature fruit hue
(a) No primates			
Papua New Guinea			
<i>adenosperma</i>	9	10	green G
<i>benamina</i>	10	9	red-purple R
<i>botryocarpa</i>	n.d.	35	yellow-green Y
cf. <i>caulocarpa</i>	16	16	n.d.
<i>congesta</i>	25	26	yellow Y
<i>copiosa</i>	28	29	yellow Y
<i>drupacea</i>	17	20	orange-red O
<i>glandifera</i>	14	23	n.d.
<i>gul</i>	n.d.	7	orange O
<i>hesperidiiformis</i>	n.d.	35	n.d.
cf. <i>hispidioides</i>	25	35	green-brown G
<i>itoana</i>	32	34	yellow-green G
<i>melinocarpa</i>	8	8	orange-red O
<i>microdictya</i>	9	10	red R
<i>mollior</i>	16	16	green G
<i>nodosa</i>	26	28	green G
<i>pachystemon</i>	n.d.	n.d.	n.d.
<i>papuana</i>	n.d.	25	n.d.
<i>polyantha</i>	n.d.	24	n.d.
<i>porphyrochaete</i>	n.d.	9	n.d.
<i>prasinicarpa</i>	n.d.	7	red R
<i>septica</i>	21	30	green G
<i>sterrocarpa</i>	90	45	n.d.
<i>subulata</i>	9	8	orange O
<i>tinctoria</i>	n.d.	14	orange-red O

<i>Ficus</i> spp. and geographic origin	Fig length (mm)	Fig diameter (mm)	Mature fruit hue
<i>trachypison</i>	7	7	orange-red O
<i>variegata</i>	25	27	green/dark red G,R
<i>virens</i>	9	10	orange-red O
<i>virgata</i>	8	8	orange-red O
<i>wassa</i>	11	11	pink R
<i>xylosicia</i>	26	13	red R
(b) Polymorphic primates			
Madagascar			
<i>cocculifolia</i>	5		green G
<i>lutea</i>	5		red R
<i>pyrifolia</i>		6	yellowish/orange O
<i>soroceoides</i>	5		red R
<i>tiliifolia</i>			red R
sp. 'Amontana'		10	reddish R
sp. 'Grand Voara'	63	48	green G
sp. 'Voara Famakilela'		9	red R
sp. 'Voara Rano'	30	20	purplish P
sp. 'Voara #1'	25	18	orange O
sp. 'Voara #2'	33	28	green/brown G,B
Central Panama			
<i>bullenei</i>		17	green, purplish hairs G
<i>citrifolia</i>		11	green, some purplish G
<i>colubrinii</i>		7	red R
<i>costaricana</i>		13	red R
<i>dugandii</i>		14	bright green G
<i>glabrata</i>			green with white spots G
<i>insipida</i>		40	green with white spots G
<i>maxima</i>		25	green, some reddish G
<i>nymphifolia</i>		22	bright green G
<i>obtusifolia</i>		23	dark green G
<i>paraensis</i>		14	green with red stripes G
<i>perforata</i>		7	dark red R
<i>pertusa</i>		14	green, some purplish G
<i>popenoei</i>	25	15	green, purplish hairs G
<i>tonduzii</i>		30	green with white spots G
<i>trigonata</i>		23	green with red dots G
nr. <i>trigonata</i>			green G
<i>yoponensis</i>		18	green with white spots G
South America			
<i>albert-smithii</i>		6	pink, brown lanate R,B
cf. <i>amazonica</i>			n.d.
<i>broadwayi</i>		22	red R
<i>caballina</i>		7	red or yellow R,Y
<i>calyptroceras</i>	30	30	green G
cf. <i>casapiensis</i>		20	red-purple R

<i>Ficus</i> spp. and geographic origin	Fig length (mm)	Fig diameter (mm)	Mature fruit hue
<i>catappifolia</i>	15	15	green G
<i>citrifolia</i>		11	orange or purple-red O,P
<i>dendrocida</i>	6	6	green G
<i>enormis</i>	10	10	green G
<i>erythrosticta</i>		15	yellow and red Y,R
cf. <i>expansa</i>		10	green G
<i>gardneriana</i>	3	4	green G
<i>gomelleira</i>			green G
<i>guaranitica</i>			green G
<i>guianensis</i>			red R
<i>insipida</i>		30	green-brown G
<i>killipii</i>		10	red R
<i>malacocarpa</i>	10	12	yellow Y
<i>maroniensis</i>		10	yellowish-green G
<i>mathewsii</i>		5	yellow-orange Y
<i>maxima</i>		25	green G
<i>nymphaeifolia</i>	23	22	greenish, reddish, or purplish mottled G,R,P
<i>paludica</i>		10	yellowish, mottled pale green G
<i>paraensis</i>	25	20	yellow and purple Y,P
<i>perforata</i>		5	red R
<i>pertusa</i>		15	yellow and red Y,R
<i>pulchella</i>		35	green G
cf. <i>regularis</i>		25	green G
cf. <i>sanguinosa</i>		30	brown B
<i>schumacheri</i>		5	green with mottling G
<i>trigona</i>		9	(olive) green G
<i>ypsilophlebia</i>		30	green G
sp. 1		25	green G
sp. 1			red R
sp. 2			green G
sp. 3			green G
sp. 4			green G

(c) Trichromatic primates

Africa

<i>abutifolia</i>	n.d.	red R
<i>amadiensis</i>	17	red R
<i>asperifolia</i>	10	yellow or red Y,R
<i>bizanae</i>	n.d.	yellow Y
<i>bubu</i>	3	brownish B
<i>burti-davyi</i>	n.d.	green G
<i>bussei</i>	14	green with whitish warts G
<i>capreifolia</i>	18	green or pale yellow G,Y
<i>chirindensis</i>	23	green to pale yellow Y
<i>congensis</i>	25	reddish R
<i>cordata</i>	8	green to red R
<i>craterostoma</i>	8	yellow or red Y,R

<i>Ficus</i> spp. and geographic origin	Fig length (mm)	Fig diameter (mm)	Mature fruit hue
<i>exasperata</i>		9	red R
<i>faulkneriana</i>		8	yellow or red Y,R
<i>glumosa</i>		9	orange or red O,R
<i>ilicina</i>		n.d.	red R
<i>ingens</i>		9	pink, red or purple R,P
<i>lingua</i>		5	yellow or red Y,R
<i>lutea</i>		15	yellow or orange Y,O
<i>mucoso</i>		40	orange O
<i>natalensis</i>		13	yellow to red R
<i>nigropunctata</i>		8	green to reddish R
<i>ottoniaefolia</i>		15	green to pale orange O
<i>ovata</i>		20	green G
<i>polita</i>		19	green with yellow specks to purplish G
<i>populifolia</i>		9	green with red spots or yellowish G
<i>sansibarica</i>		23	green or purplish G
<i>saussureana</i>		23	yellow or orange Y,O
<i>scassellatii</i>		16	pale green G
<i>stuhlmannii</i>		13	red R
<i>sur</i>		19	orange or red O,R
<i>sycomorus</i>		26	yellow or reddish Y
<i>tettensis</i>		n.d.	red R
<i>thonningii</i>		11	yellow or red Y
<i>tremula</i>		15	green G
<i>trichopoda</i>		n.d.	red R
<i>urceolaris</i>		7	orange or red O,R
<i>vallis-choudae</i>		33	yellow or reddish Y,R
<i>vasta</i>		13	green with white spots G
<i>verruculosa</i>		8	red or purple R,P
Peninsular Malaysia			
<i>annulata</i>	29	22	brownish B
<i>aurantiacea</i>	70	68	black Bl
<i>benjamina</i>	9	8	pink/purple R
<i>binnendykii</i>	9	8	pink/purple R
<i>bracteata</i>	19	22	red R
<i>caulocarpa</i>	5	6	pink/pale yellow R
<i>consociata</i>	14	18	red/deep red R
<i>crassiramea</i>	20	18	red/deep red R
<i>cucurbitina</i>	31	20	deep red/black R
<i>delosyce</i>	10	11	pink/yellow-green R
<i>drupacea</i>	36	28	deep red/purple R
<i>dubia</i>	29	28	deep red/purple R
<i>kerkhovenii</i>	13	12	orange-red/red O
<i>obscura</i>	7	8	red/deep red R
<i>parietalis</i>	15	15	red R
<i>pellucido-punctata</i>	18	12	purple P
<i>pisocarpa</i>	12	12	yellow-orange Y

<i>Ficus</i> spp. and geographic origin	Fig length (mm)	Fig diameter (mm)	Mature fruit hue
<i>sagittata</i>	12	12	red/deep red R
<i>stricta</i>	16	16	red R
<i>stupenda</i>	32	27	red/deep red R
<i>subcordata</i>	46	35	red R
<i>sumatrana</i>	6	8	dull pink/ochre R
<i>sundaica</i>	14	17	red/deep red R
<i>trichocarpa</i>	16	18	deep red R
<i>virens</i>	7	8	greenish/ochre Y
Borneo (Sarawak)			
<i>acamptophylla</i>	11	12	orange-red O
<i>annulata</i>	33	28	yellow-green Y
<i>aurantiacea</i>	52	52	red R
<i>aurata</i>	11	11	orange-red O
<i>benjamina</i>	10	10	orange-red O
<i>brunneo-aurata</i>	13	13	orange-red O
<i>callicarpides</i>	4	4	red R
<i>callophylla</i>	11	11	orange-red O
<i>cereicarpa</i>	42	43	brown-yellow B
<i>condensa</i>	19	20	green-yellow G
<i>consociata</i>	11	12	orange-red O
<i>cucurbitina</i>	35	17	orange-red O
<i>deltoidea</i>	10	9	red R
<i>dubia</i>	28	21	red-purple R
<i>fulva</i>	16	18	orange-red O
<i>geocharis</i>	17	20	red R
<i>grossivenis</i>	12	11	orange-red O
<i>kerkhovenii</i>	11	10	orange-red O
<i>lanata</i>	4	3	orange-red O
<i>megaleia</i>	14	17	red R
<i>obscura</i>	7	7	orange-red O
<i>pellucido-punctata</i>	12	9	orange-red O
<i>pisocarpa</i>	12	12	orange-red O
<i>punctata</i>	48	49	red R
<i>retusa</i>	7	7	red R
<i>rubrocupidata</i>	5	5	orange-red O
<i>sarawakensis</i>	22	21	red-purple R
<i>schwarzii</i>	24	24	yellow-green Y
<i>sinuata</i>	5	5	orange O
<i>stolonifera</i>	14	13	red R
<i>stricta</i>	24	21	orange-red O
<i>stupenda</i>	36	29	orange-red O
<i>subcordata</i>	46	31	red-purple R
<i>subgelderi</i>	14	11	orange O
<i>subulata</i>	9	8	orange-red O
<i>sumatrana</i>	16	16	orange O
<i>sundaica</i>	13	13	orange-red O

<i>Ficus</i> spp. and geographic origin	Fig length (mm)	Fig diameter (mm)	Mature fruit hue
<i>treubii</i>	15	14	pale brown B
<i>uncinata</i>	20	22	dark red R
nr. <i>uncinata</i>	18	25	white-green G
<i>uniglandulosa</i>	8	8	orange O
<i>urnigera</i>	7	7	orange O
<i>xylophylla</i>	33	25	orange-red O

Note: Letters in bold denote the hue used for analysis; B=brown, BL=black, P=purple, G=green, Y=yellow, O=orange, R=red.

Sources: Madagascar (Dew and Wright, 1998; Birkinshaw, 2001), Panama (Croat, 1978; Kalko et al., 1996), South America (Terborgh, 1983; van Roosmalen, 1985; Defler and Defler, 1996; Lorenzi, 1998, 2000), Africa (Hamilton, 1991; Beentje, 1994), Peninsular Malaysia (Lambert, 1990), Borneo (Sarawak) (Shanahan, 2000), and Papua New Guinea (Shanahan, 2000).

Appendix B. Descriptive properties of arborescent palms

Species and geographic origin	Height (m)	Fruit length (cm)	Fruit diameter (cm)	Mature fruit hue
(a) No primates				
New Caledonia				
<i>Alloschmidia glabrata</i>	15	1.2	0.5	black BI
<i>Basselinia favieri</i>	12	0.8	1	black BI
<i>B. humboldtiana</i>	10	0.8	1	brownish/black BI
<i>B. pancheri</i>	15	0.8	0.9	black BI
<i>B. sordida</i>	12	1	1	black BI
<i>B. tomentosa</i>	20	1	1	black BI
<i>B. velutina</i>	15	1.1	0.9	black BI
<i>Burretio kentia dumasii</i>	12	1.3	1.1	purplish P
<i>B. grandiflora</i>	12	n.d.	n.d.	n.d.
<i>B. hapala</i>	15	1.6	0.9	reddish R
<i>B. koghiensis</i>	18	1.6	1.1	dark purple P
<i>B. viellardii</i>	18	2.2	1.4	purplish red R
<i>Campecarpus fulcitus</i>	15	2.8	1.4	dull brownish red R
<i>Chambeyronia lepidota</i>	15	3.4	2.3	red R
<i>C. macrocarpa</i>	20	6	3.5	red R
<i>Clinosperma bracteale</i>	15	1.6	1.6	black BI
<i>Cyphokentia macrostachya</i>	15	1.5	1.1	red R
<i>Cyphophoenix elegans</i>	15	2	1.4	orange/reddish brown O,B
<i>C. nucele</i>	15	2	1.2	red R
<i>Cyphosperma balansae</i>	15	1.2	1.1	red R
<i>Kentiopsis magnifica</i>	25	2.2	1.2	red R
<i>K. oliviformis</i>	30	1.7	0.9	red R
<i>K. piersoniorum</i>	15	2.3	1	purplish P
<i>K. pyriformis</i>	18	1.7	0.7	purplish pink P
<i>Lavoixia macrocarpa</i>	15	3.8	3.2	dark purplish P
<i>Moratia cerifera</i>	20	1.3	1.4	dull orange to reddish O

Species and geographic origin	Height (m)	Fruit length (cm)	Fruit diameter (cm)	Mature fruit hue
<i>Pritchardiopsis jeanneneyi</i>	12	4	4	purplish P
<i>Veillonina alba</i>	15	1.6	1.3	brownish B
Northern Queensland				
<i>Archontophoenix</i> sp. aff. <i>alexandrae</i>	20	2	1.5	bright red R
<i>Arenga australasica</i>	10	2	2	dull reddish/purple/brown P,B
<i>Cayota rumphiana</i> var. <i>australasica</i>	15	2	2	dull reddish purple/nearly black P,BI
<i>Corypha elata</i>	25	3	3	dull greenish-brown B
<i>Gulubia costata</i>	25	0.9	n.d.	bluish-grey Blue
<i>Hydriastele wendlandiana</i>	15	0.9	n.d.	red R
<i>Licuala</i> sp. aff. <i>ramsayi</i>	15	1	1	bright orange-red O
<i>Livistona benthamii</i>	25	1.5	1.5	blackish/brown B
<i>L. muelleri</i>	20	1	1	black with bluish waxy bloom BI
<i>L.</i> sp.	30	1	1	dull black BI
<i>Ptychosperma elegans</i>	15	1.5	0.8	deep red R
<i>P. macarthurii</i>	10	1.7	0.8	bright red R
<i>Wodyetia bifurcata</i>	15	5.7	3.7	orange-red O
South Pacific				
<i>Balaka microcarpa</i>	13	1.6	0.8	orange/red O
<i>Carpoxydon macrospermum</i>	18	6	3.5	red R
<i>Clinostigma exorrhizum</i>	20	0.6	0.4	translucent red R
<i>C. harlandii</i>	15	0.6	0.6	black BI
<i>Gulubia cylindrocarpa</i>	27	1.5	0.6	dull yellow Y
<i>G. microcarpa</i>	25	1	0.3	whitish
<i>Hedyscepe canterburyana</i>	10	5	4	dull red R
<i>Howea belmoreana</i>	12	4	2	brownish/red R
<i>H. forsteriana</i>	25	5	2	red R
<i>Metroxylon salomonense</i>	12	9	6.5	green/straw-colored G
<i>M. vitiense</i>	15	7	5	yellowish brown B
<i>Neoveitchia storckii</i>	12	5	2.2	reddish/yellow Y
<i>Pritchardia thurstonii</i>	15	0.7	0.7	deep red R
<i>Rhopalostylis baueri</i>	15	1.6	1.35	bright red/brick red R
<i>R. sapida</i>	10	1.2	0.8	brick red R
<i>Veitchia arecina</i>	18	4	2	bright red R
<i>V. joannis</i>	32	6	3	red/crimson R
<i>V. macdanielsii</i>	25	3	1.7	bright red R
<i>V. metiti</i>	n.d.	4.5	2	orange/red O
<i>V. montgomeryana</i>	30	4.5	2.4	bright red R
<i>V. pedionoma</i>	10	1.4	0.7	bright orange/red O
<i>V. petiolata</i>	35	2.2	1.1	orange/red O
<i>V. sessilifolia</i>	10	2.2	1.2	orange/red O
<i>V. spiralis</i>	20	4	3	orange/red O

Species and geographic origin	Height (m)	Fruit length (cm)	Fruit diameter (cm)	Mature fruit hue
<i>V. vitiensis</i>	16	2.2	0.8	orange/red O
<i>V. winin</i>	20	1.8	0.9	bright red R
(b) Polymorphic primates				
Amazon				
<i>Acrocomia aculeata</i>	12	3.5	3.5	yellowish, yellowish-green G
<i>Aphandra natalia</i>	11	12	11	in woody head (brown) B
<i>Astrocaryum aculeatum</i>	20	6	4.2	yellow-orange, orange-green Y,O
<i>A. chambira</i>	22	6	4.5	yellowish-green, whitish-brown scurfy G,B
<i>A. jauari</i>	13	3.5	2.5	yellowish-green, orange G,O
<i>A. murumuru</i>	15	9	4.5	brown B
<i>A. vulgare</i>	10	5	3.7	orange O
<i>Attalea butyracea</i>	20	8.5	4.5	pinkish-brown, orange-yellow, reddish, yellowish-brown O,B
<i>A. dahlgreniana</i>	15	9	4	brownish B
<i>A. maripa</i>	20	6	3	yellowish-brown B
<i>A. septuagenata</i>	12	10	5	brown, silvery-brown B
<i>A. speciosa</i>	15	10.7	7	brown B
<i>A. tessmannii</i>	19	13	7	brownish B
<i>Bactris gasipaes</i>	18	5	3	yellow, orange, red Y,O,R
<i>B. macana</i>	12	2.3	1.8	orange O
<i>B. major</i>	10	4.5	3.5	purple-black P
<i>B. riparia</i>	10	2	2	orange-red, green O,G
<i>B. setulosa</i>	10	2	1.8	orange-yellow, orange-red O
<i>Chelyocarpus chuco</i>	12	2	2	dark brown B
<i>Dictyocaryum ptarianum</i>	15	3.5	3	yellowish-brown B
<i>Euterpe caatinga</i>	16	1	1	purple-black, black P, Bl
<i>E. longibracteata</i>	15	1.2	1.2	purple-black P
<i>E. oleracea</i>	20	2	2	purple-black, black, green P,Bl,G
<i>E. precatoria</i>	20	1.3	1.3	purple-black P
<i>Iriarteia deltoidea</i>	25	2.8	2.8	greenish-yellow Y
<i>Iriartella setigera</i>	12	1.7	1	scarlet, orange, brown R,O,B
<i>Manicaria saccifera</i>	10	6	6	brownish B
<i>Mauritia carana</i>	15	5	5	dark-red, reddish-brown R,B
<i>M. flexuosa</i>	25	5.3	5.2	brown, reddish-brown B
<i>Oenocarpus bacaba</i>	22	1.5	1.5	purple-black P
<i>O. balickii</i>	14	1.8	1.5	purple-black P
<i>O. bataua</i>	26	4.5	2.5	purple-black P

Species and geographic origin	Height (m)	Fruit length (cm)	Fruit diameter (cm)	Mature fruit hue
<i>O. distichus</i>	10	2	1.7	purple-black P
<i>O. mapora</i>	15	3	2.5	purple-black P
<i>Socratea exorrhiza</i>	20	3.5	2	yellowish Y
<i>S. salazarii</i>	16	3.5	2.5	yellowish Y
<i>Syagrus inajai</i>	15	4.5	3	greenish-brown B
<i>S. orinocensis</i>	12	4	3	brownish B
<i>S. sancona</i>	20	3.2	2.3	yellowish, orangish Y,O
<i>S. smithii</i>	15	8	4	greenish-brown, yellowish B
<i>S. stratincola</i>	14	4.5	4	n.d.
<i>Wettinia augusta</i>	12	3	1.5	brownish B
<i>W. maynensis</i>	19	2.5	2	brown B
Madagascar				
<i>Beccariophoenix madagascariensis</i>	12	3.5	2.5	purple-brown P
<i>Bismarckia nobilis</i>	20	4.8	3.5	dark brown B
<i>Borassus madagascariensis</i>	16	18	n.d.	dull orange/brown O,B (= <i>B. aethiopum</i>)
<i>B. sambiranensis</i>	18	13	11	dull orange/brown O,B (= <i>B. aethiopum</i>)
<i>Dypsis amapasindavae</i>	15	1.3	0.8	n.d.
<i>D. ankaizinensis</i>	15	1.7	1.2	n.d.
<i>D. bejofo</i>	25	2.5	2.1	n.d.
<i>D. canaliculata</i>	15	3	2.1	n.d.
<i>D. ceracea</i>	15	2	1.25	n.d.
<i>D. crinata</i>	15	2.4	1.8	purple-black P
<i>D. decipiens</i>	20	2.5	2.2	n.d.
<i>D. heteromorpha</i>	12	2.3	2.2	n.d.
<i>D. hovomantsina</i>	15	n.d.	n.d.	n.d.
<i>D. ifanadianae</i>	24	0.8	1	n.d.
<i>D. intermedia</i>	10	n.d.	n.d.	n.d.
<i>D. lastelliana</i>	15	2.4	1.7	n.d.
<i>D. leptocheilos</i>	10	1.2	1.2	dark brown B
<i>D. madagascariensis</i>	18	1.6	1	purplish with waxy bloom P
<i>D. malcomberi</i>	25	1	0.7	pale orange O
<i>D. mananjarensis</i>	25	0.6	0.6	n.d.
<i>D. nauseosa</i>	15	n.d.	n.d.	n.d.
<i>D. nodifera</i>	10	1	0.8	green (always?) G
<i>D. nossibensis</i>	10	n.d.	n.d.	n.d.
<i>D. onilahensis</i>	10	1.8	1.5	yellow, waxy? Y
<i>D. oropedionis</i>	20	n.d.	n.d.	n.d.
<i>D. ovobontsira</i>	10	1.7	1.5	green G
<i>D. pilulifera</i>	30	0.7	0.7	n.d.
<i>D. pinnatifrons</i>	12	1.4	6.5	brownish B
<i>D. prestoniana</i>	12	1.5	0.8	orange O
<i>D. saintelucei</i>	10	n.d.	n.d.	n.d.

Species and geographic origin	Height (m)	Fruit length (cm)	Fruit diameter (cm)	Mature fruit hue
<i>D. tokoravina</i>	20	2	1.3	n.d.
<i>D. tsaravoasira</i>	25	n.d.	n.d.	n.d.
<i>D. utilis</i>	17	2.8	2	purplish brown or black B,BI
<i>Elaeis guineensis</i>	20	3	2	bright orange, sometimes dusky violet in exposed parts O
<i>Lemurophoenix halleuxii</i>	20	5	5	chestnut brown B
<i>Marojejya darianii</i>	15	2.5	2.2	red R
<i>Masoala madagascariensis</i>	10	2.5	1.9	yellowish-brown B
<i>Orania longisquama</i>	20	5.5	4.5	green G
<i>O. ravaka</i>	15	6	6	yellow or pale brown Y,B
<i>O. trispatha</i>	22	5.5	8	green G
<i>Raphia farinifera</i>	10	6	4.5	chestnut-brown B
<i>Ravenea julietiae</i>	10	2.7	2	n.d.
<i>R. krociana</i>	30	3	2.8	orange O
<i>R. lakatra</i>	14	2	2.1	blackish BI
<i>R. latisecta</i>	10	1	0.7	red R
<i>R. madagascariensis</i>	12	1	1	orange O
<i>R. rivularis</i>	22	0.9	0.85	brigt red R
<i>R. robustior</i>	30	1.8	1.5	orange O
<i>R. sambiranensis</i>	30	1.2	1	orange to coral-red O,R
<i>Satranala decussilvae</i>	15	5.6	5	purple-black P
<i>Voaniola gerardii</i>	20	8	5	red-brown R
(c) Trichromatic primates				
Africa				
<i>Borassus aethiopum</i>	30+	18	18	dull orange/brown O,B
<i>Chrysalidocarpus pemeanus</i>	20	1.5	0.7	bright red R
<i>Elaeis guineensis</i>	30+	4	n.d.	orange/yellow to purple O,P
<i>Hyphaene compressa</i>	20	12	9	orange-brown chestnut/golden brown O,B
<i>H. guineensis</i>	≥10	n.d.	n.d.	n.d.
<i>H. petersiana</i>	25	7	7	reddish/brown B
<i>H. thebaica</i>	30	6	5	orange/brown O,B
<i>Livistona carinensis</i>	20	2	n.d.	n.d.
<i>Medemia argun</i>	12	6	4	brownish/violet P
<i>Phoenix djalonenis</i>	10+		n.d.	brown/reddish B
<i>Raphia africana</i>	10+	10	5	light brown/ivory-yellowish B
<i>R. australis</i>	10	9	5	yellowish/dark brown B
<i>R. farinera</i>	10	n.d.	n.d.	glossy reddish-brown B
<i>R. hookeri</i>	15+	12	6	yellow and brown Y,B
<i>R. rostrata</i>	n.d.	9	4	polished, dark reddish-brown B

Species and geographic origin	Height (m)	Fruit length (cm)	Fruit diameter (cm)	Mature fruit hue
<i>R. ruwenzorica</i>	10	13	6.5	dark brown B
<i>R. taedigera</i>	12	8	4.5	yellowish/tan to orange/brown B
<i>R. textilis</i>	10	7	4.5	dark reddish brown B
Malaysia and Thailand				
<i>Areca catechu</i>	30	8	6	orange O
<i>Arenga obtusifolia</i>	15	6	4	yellowish Y
<i>A. pinnata</i>	20	7	6	blackish BL
<i>A. westerhoutii</i>	20	7	7	blackish BL
<i>Borassodendron machadonis</i>	20	10	12	purplish P
<i>Borassus flabellifer</i>	25	20	20	dark brown to black B, BL
<i>Caryota bacsonensis</i>	20	1.7	2.5	yellow to bright red Y,R
<i>C. gigas</i>	40	2.9	3.5	reddish R
<i>C. kiriwingensis</i>	35	2.6	3.3	reddish R
<i>C. maxima</i>	30	2	2.5	reddish R
<i>C. obtusa</i> var. <i>aequatorialis</i>	10+	6.4	6.4	dull red R
<i>Corypha elata</i>	18+	2.3	2.3	olive G
<i>C. lecomtei</i>	15	8	6	brownish B
<i>C. utan</i>	30	3	3	yellowish Y
<i>Livistona jenkinsiana</i>	25	1.5	2.5	blue
<i>L. kingiana</i>	'tall'	5.1	5.1	brown B
<i>L. saribus</i>	30	2.2	1.5	blue
<i>L. speciosa</i>	25	3	2.5	blue
<i>Oncosperma horridum</i>	20	1.7	1.7	purplish black BL
<i>O. tigillarum</i>	30	1	1	dark purple P
<i>Orania sylvicola</i>	20	4	4	greenish yellow to yellow Y
<i>Pholidocarpus macrocarpus</i>	30	13	10	dull brown B
<i>Trachycarpus oreophilus</i>	12	1.2	0.7	yellowish to brown Y,B

Note: Letters in bold denote the hue used for analysis; B=brown, BL=black, P=purple, G=green, Y=yellow, O=orange, R=red.

Sources: Amazon (Henderson et al., 1995), Madagascar (Dransfield and Beentje, 1995), Africa (Tuley, 1995; Steyn, 1996), Malaysia and Thailand (Whitmore, 1979; Hodel and Vatcharakorn, 1998), New Caledonia (Hodel and Pintaud, 1998), the South Pacific (Dowe, 1989), and Northern Queensland, Australia (Tucker, 1988).

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