




Is Malaysia’s “mystery monkey” a hybrid between *Nasalis larvatus* and *Trachypithecus cristatus*? An assessment of photographs

Stanislav Lhota^{1,2} · Jo Leen Yap^{3,4} · Mark Louis Benedict⁵ · Ken Ching⁶ · Bob Shaw⁷ · Ben Duncan Angkee⁸ · Nicole Lee⁹ · Vendon Lee^{6,10} · Jean-Jay Mao¹¹ · Nadine Ruppert^{3,4} 

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Abstract

Interspecific hybridization in primates is common but hybridization between distantly related sympatric primate species is rarely observed in the wild. We present evidence for a possible hybridization event between *Nasalis larvatus* and *Trachypithecus cristatus* in the Lower Kinabatangan Wildlife Sanctuary, Sabah, through assessment of photographs. We used a set of categorical characters and metric measurements to compare the putative hybrid with the likely parent species. Nonmetric comparison showed that this “mystery monkey” is intermediate in several characters. Measurements of limb proportions on photographs showed that the brachial, humerofemoral, and intermembral indexes are above 100 for *N. larvatus* and below 100 for *T. cristatus* on all photographs, whereas the crural index is higher than 100 in both species and the distributions of this index in the two species overlap. Brachial and intermembral indices of the putative hybrid were similar to those of *N. larvatus*. Crural and humerofemoral indices were closer to the values for *T. cristatus* than those of *N. larvatus*. Multiple observers confirmed the occurrence of mixed-species groups in the area, and interspecific mating has been photographed. The putative hybrid is now an adult female and was last photographed in September 2020 with an infant and swollen breast, suggesting lactation. We propose further noninvasive fecal sampling for genetic analyses to confirm the origins of this “mystery monkey.” This case of hybridization may be related to anthropogenic changes to the landscape, whereby expansion of oil palm plantations confines *N. larvatus* and *T. obscurus* to narrow riverine forest patches along the Kinabatangan. This observation therefore also may have conservation implications, indicating limited mate access and dispersal opportunities for these threatened primates.

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Extended author information available on the last page of the article

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Introduction

Interspecific hybridization in primates has recently attracted the attention of researchers worldwide, as evidenced by a Special Issue of the *International Journal of Primatology* (Cortés-Ortiz, 2019). Several decades ago, primate species were thought to be reproductively isolated. Although hybridization was known to occur in the contact zones of parapatric species (e.g., *Hylobates lar* x *H. pileatus*, Brockelman & Schilling, 1984; *Papio hamadryas* x *P. anubis* and *P. cynocephalus*, Detwiler et al., 2005; *Macaca mulatta* x *M. fascicularis*, Hamada et al., 2006; Bulungsup et al., 2017; *Alouatta palliata* x *A. pigra*, *Alouatta caraya* x *A. guariba alamtans*, Mourthe et al., 2018; Kitchen et al., 2019; *Callithrix jacchus* x *C. penicillata*, Malukiewicz et al., 2015; *Eulemur rufus* x *E. albocollaris*, Wyner et al., 2002), these well-documented hybrid zones were treated as localized phenomena. Only with the advance of molecular genetics did it become evident that cryptic introgression of genes from one species to another along the contact zones and reticulate evolution play important roles in phylogeny (*Hylobates lar* and *H. pileatus*, Matsudaira et al., 2012; *Gorilla* and *G. beringei*, Ackermann & Bishop, 2009; *Eulemur mongoz* and *E. fulvus*, Pastorini et al., 2009, *Papio* spp.; Zinner et al., 2009; colobines, Roos et al., 2011). However, compared with parapatric hybridization, crossbreeding between sympatric primate species that inhabit different ecological niches in the same or overlapping habitat is rarely observed. It has been perhaps best documented in several species of *Cercopithecus* guenons, Detwiler et al., 2005) and in macaques (e.g., *Macaca fascicularis* x *M. nemestrina*, Gilhooly et al., 2021; *M. nemestrina* x *M. leonina*, Malaivijitnond et al., 2007).

Classification of primates as distinct genera is based on consideration of several aspects of phylogeny, including phylogenetic distance and the degree of morphological (and sometimes also behavioral) differentiation. Both of these aspects are supposed to increase the reproductive incompatibility of the taxa. Intergeneric hybridization is therefore expected to be rare compared to interspecific hybridization within genera. Hybridization between currently recognized primate genera is known from captivity (e.g., *Hylobates moloch* x *Symphalangus syndactylus*, Myers & Shafer, 1979, *Theropithecus gelada* x *Papio hamadryas*, Jolly et al., 1997). In the wild, intergeneric hybridization has been reported between *Theropithecus gelada* and *Papio anubis* (3 individuals; Dunbar & Dunbar, 1974), and molecular evidence shows that such incidents also occurred in the past (*Rungwecebus* and *Papio*, Roberts et al., 2010; *Homo*, *Pan* and *Gorilla*, Arnold & Meyer, 2009).

Colobine monkeys are a distinct lineage of the primate radiation. They feature distinct coloration and loud vocalizations and have been subject to numerous molecular genetic studies as detailed below. These studies have enabled researchers to identify a range of directly observable and cryptic hybridization phenomena that played a role in the evolutionary diversification of this subfamily. For example, morphological (coloration), bioacoustic, and molecular evidence suggest both observable

hybridization and cryptic introgression of genes between ecologically distinct langurs that co-inhabit the mosaic of evergreen and deciduous forest in the south of Indian subcontinent (*Semnopithecus johnii*, *S. priam*, and possibly *S. hypoleucos*) (Hohman, 1988; Ashalakshmi *et al.*, 2015; Nag, 2020). Hybridization between *Semnopithecus priam thersites* and *S. vetulus* in Sri Lanka is supported by behavioral evidence and observation of coat color pattern (Lu *et al.*, 2020). Choudhury identified hybrids between *Trachypithecus geei* and *T. pileatus* in Bhutan based on coat coloration (Choudhury, 2008). A female that appeared to be a hybrid between *Trachypithecus obscurus* and *T. cristatus* was spotted and photographed at Air Hitam Dalam dam, Butterworth Penang in 2017 (YJL, personal observation). There also is molecular genetic evidence of past reticulate evolution of *Trachypithecus cristatus* and *T. auratus* in Sundaland (Rosenblum *et al.*, 1997). At least one of the colobine species, *Trachypithecus crepusculus*, may be of hybrid origin (Roos *et al.*, 2017), and the species *T. geei* and *T. pileatus* may have evolved from hybridization between *Trachypithecus* and *Semnopithecus* (Karanth, 2010). Brandon-Jones proposed treating these two closely related genera as a single genus, *Semnopithecus* (Brandon-Jones *et al.*, 2004, pp. 131–132). Hybridization between *Pygathrix* species also has been reported (*Pygathrix nemaesus* x *P. cinerea*, Rawson & Roos, 2008).

More distantly related colobine taxa are so far reported to hybridize only in semicaptive and captive settings. A hybrid between *Pygathrix nemaesus* and *Trachypithecus hatinhensis* was conceived in a large naturalistic enclosure in the Endangered Primate Rescue Center (EPRC) in Vietnam, where it survived to adulthood (Schempp *et al.*, 2008). A hybrid between *N. larvatus* and *Pygathrix nemaesus* was born in Erfurt Zoo, Germany, where it died before it reached maturity. It was photographed by Karola Walter (Supplement Fig. S1).

Using photographs to describe diversity in primates is becoming a common practice, but it also has been criticized. The kipunji was the first primate to be described (as *Lophocebus kipunji*) based on photographs as a holotype and paratype and in the absence of the dermoplastic specimen or any other biological tissue (Jones *et al.*, 2005). This practice was immediately criticized (Timm *et al.*, 2005). More recently, another species of primate, *Trachypithecus johnaspinalli*, was named based on photographs of monkeys sold in a bird market in Java (Nardelli, 2015). Kipunji proved to be a valid and taxonomically highly distinct species, now considered a monotypic distinct genus, *Rungwecebus kipunji* (Davenport *et al.*, 2006). However, *T. johnaspinalli* turned out to be *T. auratus* bleached for the purpose of selling (Nijman, 2021). Another attempt to identify a new species through photos was a “new mammal” discovered on camera trap pictures in Borneo; it later turned out to be an arboreal flying squirrel, probably *Aeromys thomasi*, photographed in an unusual terrestrial setting (Meijaard *et al.*, 2006). The comparison of various metric and nonmetric parameters across taxa used in that case proved to be a useful tool for identifying species in photographs (Meijaard *et al.*, 2006).

Sightings of a “mystery monkey” along the Kinabatangan River in Sabah, Malaysia, were uploaded to some social media wildlife photography groups in 2017. While these posts did not identify the source of the photos, commenters speculated about an unknown species of primate in Sabah, or a possible hybrid. NR, who saw the first posts in 2017, tried to contact several researchers in the area to identify the

photographers but was not successful in identifying the photographers until 2019 after more anonymously posted pictures of the “mystery monkey” circulated on social media. On bringing all the photographers together to discuss their sightings, a clearer picture and timeline of their observations emerged. It also became evident that mixed-species groups of *T. cristatus* and *N. larvatus* along the Kinabatangan are a common sight for the nature guides and photographers who frequently cruise along this river.

In this study, we used a set of categoric characters and metric measurements to compare the “mystery monkey” from the Kinabatangan with the two likely parent species of this putative hybrid: *N. larvatus* and *T. cristatus*. If the monkey is a hybrid, we predict that the measures will be intermediate between the two putative parent species or will combine characteristics of both parent species. We also include observations of behavior, including interspecific mating and allomothering, reported and documented by the photographers in the same area.

Methods

Ethical statement

This desktop study adhered to USM’s Animal Ethics guidelines, the Wildlife Conservation Enactment (1997) of Sabah, and the IPS Code of Best Practices for Field Primatology.

All photos presented are original photos taken by the authors of this article. We obtained the photographs of the “mystery monkey” and mixed-species groups along the Kinabatangan opportunistically from a safe distance of more than 10 m during leisure river cruises. We collected additional photos for morphometric measurements of the parent species from the internet and present the links to the original sources/authors in the Supplement.

Data availability

The data that support the findings of this study are available in the Supplement and additional information can be obtained from the corresponding author upon reasonable request.

Data collection

The first photograph of the putative hybrid individual, as a juvenile, was published in a public Malaysian Facebook group on 22 June 2017, where a user (not the photographer) shared the images of the “mystery monkey” being groomed by a female *T. cristatus* (Fig. 1A). NR was interested to learn more about the background of this primate, but the photographer was untraceable at that time. In 2019, several new photos of the “mystery monkey,” now a subadult, were shared in a WhatsApp naturalist group of which NR is a member. The origins of these shared images were



Fig. 1 **A.** Juvenile “mystery monkey” near Kampung Bilit, Kinabatangan, Sabah, groomed by adult female *Trachypithecus cristatus* (likely the mother) (photo by Ken Ching, June 19, 2017). **B.** Subadult “mystery monkey,” alone (photo by Ben Duncan Angkee, November 17, 2018). In this photo, the individual may appear younger, because the phone camera had an automatic softening filter activated. **C.** Subadult “mystery monkey,” alone, feeding (photo by Bob Shaw, November 17, 2018). **D.** Subadult “mystery monkey” with juvenile *T. cristatus* (in color change phase), adult female *T. cristatus*, and another *T. cristatus* individual while grooming (photo by Ken Ching, November 22, 2018). **E.** Adult male *Nasalis larvatus* mating with adult female *T. cristatus* in the same area (photo by Jean-Jay Mao, September 10, 2017). **F.** Adult putative hybrid now clearly identifiable as female with swollen breasts, holding an infant, which appears to be her offspring (photo by Nicole Lee, September 7, 2020)

still not identified but on further investigation, NR was introduced to the photographers by a mutual contact 6 months later. In June 2019, all authors met to discuss their sightings. The “mystery monkey” had been spotted on three different occasions between June 2017 and November 2018 near Kampung Bilit, Kinabatangan, Sabah, by the authors and their associates. The monkey was spotted again in September 2020, during the drafting of the manuscript. The photographers shared their photographs as well relevant anecdotal observations on behaviour of the “mystery monkey” and on mixed species (*N. larvatus* and *T. cristatus*) groups in the same area. Further planned river tours to search for the monkey to obtain more and better-quality pictures for morphometric assessment were disrupted by the strict lockdown in Malaysia due to the ongoing global COVID-19 pandemic.

Data analysis

We assessed all pictures of the “mystery monkey” and as many photographs of both putative parent species as possible from our personal collections and from the internet (Supplement Table S1) for 20 nonmetric comparisons (Table 1). For morphometric assessment, we used PixelStick (<https://plumamazing.com/pixelstick-manual>) to measure the length of limb segments. PixelStick measures the distances between

selected points on screen in pixels. We marked the measuring point with arrows, measured the distances between the first pixels of two arrows, and saved the marked photos for future reference or correction (Supplement Table S1).

We could not exactly apply standard measurements based on the femur and tibia proportions (such as those in Schempp *et al.*, 2008), because it was impossible to identify the bone measurement points in photos of living animals. Instead, we attempted to apply the standard surface measurements used to measure human body (Cameron and Bogin, 2012). However, some of the surface features may be hidden by the hair, such as the ankles in *T. cristatus* and the “mystery monkey.” As a compromise, we defined the following four measurements that are measurable on the photographs of living monkeys:

- 1) Upper arm length measured from the acromion to the olecranon. The acromion was either visible due to the slightly erect hair pattern on the shoulder or estimated from the shape of the shoulder. The olecranon was usually visible; we did not include long protruding hair at the elbow in the measurement.
- 2) Forearm length measured from the olecranon to the styloid. The styloid was often visible on the wrist due to short hair, or we estimated it from the shape of the wrist.
- 3) Thigh length measured from the distal edge of the patella to the inguinal crease. The shape of patella was often visible thanks to the short hair. The inguinal crease was sometimes visible; where it was hidden by long hair (the mane), we estimated the position from the shape of the thigh.
- 4) Calf length measured from the distal edge of the patella to the dorsal side of the metatarsus.

The position of the animals on photographs proved to be crucial for taking valid measurements. Measurements taken from photos of the same putative hybrid individual varied even if the photos were taken in relatively short succession. We therefore looked for photos where the hips, shoulders, and ankles were as close to one plane as possible and as perpendicular to the camera as possible. We used the same criteria to select the comparative photographs of both parent species. The animals could be in sitting or standing position. Because there are many more photos of the parent species than the “mystery monkey,” we based our comparisons on the mean values of the four best-positioned photos of each sex of both parent species. We limited the selection to the few best photos, as increasing the sample size would increase the error due to suboptimal positioning of the animals on photographs.

The “mystery monkey” (a female) was a subadult in the best-positioned photos. Her body position on more recent photographs, when she was fully adult (with her breasts swollen and holding an infant), was suboptimal for taking the measurements. We think that using photographs of her as a nearly grown subadult is a reasonable compromise between choosing the photographs that represent the most appropriate development stage and those that show the most suitable body position. We made separate comparisons of each of the three selected photographs with adults of each sex of each parent species.

From our measurements, we calculated following four indices:

- 1) Brachial index, calculated as $(\text{upper arm} \times 100) / \text{forearm}$, which measures the relative degree of elongation of the distant segment of the arm.
- 2) Crural index, calculated as $(\text{calf} \times 100) / \text{thigh}$, which measures the relative degree of elongation of the distant segment of the leg.
- 3) Humerofemoral index, calculated as $(\text{upper arm} \times 100) / \text{thigh}$, which measures the relative degree of elongation of the proximal segment of the arm compared to the homologous segment of the leg.
- 4) Intermembral index, calculated as $(\text{upper arm} + \text{forearm} \times 100) / (\text{thigh} + \text{calf})$, which measures the relative degree of elongation of the arm compared to the leg.

To assess validity of the measurements taken from photographs, we compared the indices measured for *N. larvatus* and *T. cristatus* with published measurements taken on skeletal material of both species (Schultz, 1942; Washburn, 1944).

To summarize all data, we categorized each of the metric and non-metric characters based on the resemblance of the putative hybrid in a given character to one of the putative parent species. We classified traits that exceeded the value for one of the parent species as resemblance; therefore, there are five categories of this classification: resembling *N. larvatus*, closer to *N. larvatus*, intermediate, closer to *T. cristatus*, and resembling *T. cristatus*.

Results

Observations by the photographers show that the "mystery monkey" is a member of a group of *T. cristatus* near Kampung Bilit, Kinabatangan, Sabah. When first observed by KC on June 19, 2017, the animal was still a juvenile. It was groomed by an adult female *T. cristatus* and spotted with other langurs (Fig. 1A). On September 10, 2017, JJM took photos of an adult male *N. larvatus* mixing with a group of *T. cristatus* near Kampung Bilit who was mating with one of the adult female langurs (Fig. 1E). On November 17, 2018, BS and BC spotted the "mystery monkey," by then subadult, seemingly alone feeding in the trees on the riverbank near Kampung Bilit and both photographers took photos (Figs. 1B, C). Four days later, KC photographed the individual with an adult female *T. cristatus* with a dependent infant. The small group groomed one another during the observation (Fig. 1D). Subsequent attempts by nature guides, photographers, and researchers in the area to spot the "mystery monkey" in the following years were unsuccessful (to our knowledge) until NL sighted and photographed the "mystery monkey" in the same area on June 8, 2020. The monkey was then an adult female with an infant, which seemed to be her dependent offspring (Fig. 1F). Figure 1 shows a selection of more than 30 photos taken of this primate. We cannot exclude the possibility that the "mystery monkey" observed at different times were different animals, but given the closeness of the locations and the consistent pattern of aging, we conclude that there is only one animal.

Multiple observers confirmed more mixed-species groups with strong affiliative interspecies interactions, including mating and allomothering in the area. Near

Sukau, Kinabatangan in 2011, MLB observed a female *N. larvatus* allomothering a newly born *T. cristatus*, nursing and grooming the infant with other female *N. larvatus* nearby. No group of *T. cristatus* was observed nearby during this observation (Supplement Fig. S3). Photographs also show a male *N. larvatus* mixing with the *T. cristatus* group at Kampung Bilit that contained the “mystery monkey.” VL described three mixed groups in this area, each a group of *T. cristatus* with one adult male *N. larvatus* (personal observation, June 2020).

Nonmetric comparison of putative hybrid with putative parent species

The nonmetric characteristics of the putative hybrid differ from those of adult females of *N. larvatus* and *T. cristatus* (Table 1). The face is more like *N. larvatus* than *T. cristatus*, with a rather pronounced nose, but the facial skin has grey tinge, and the nose is only slightly elongated. There is a wedge-shaped crown on the top of the head and prominent whiskers around the face. The rather long and dense hair resembles *T. cristatus*, but the coloration shows some of the patterns typical for *N. larvatus* and the mane on the sides, typical for *T. cristatus*, is missing. The off-white rump patch typical for *N. larvatus* is absent, and the tail is bicolored, not off-white like in *N. larvatus*. There is only indistinct grizzle on the trunk, but a delicate grizzle on the calves and forearms, as in *N. larvatus*. The hands and feet are dark and nearly black, such as for *T. cristatus*. This comparison should be considered with caution, because it is subjective and may depend on the quality of photos, including light conditions and the body posture.

The values for the putative hybrid for most nonmetric and metric indices were closer to *N. larvatus* than to *T. cristatus* (9) or resemble *N. larvatus* (6) more (Table 2). Two characters were intermediate between the putative parent species. Only four characters resembled *T. cristatus* (4) or were closer to *T. cristatus* than to *N. larvatus* (3).

Morphometric comparison of the putative hybrid with the putative parent species

Metric comparisons of the limb indices between the two likely parent species show that there is no overlap between *N. larvatus* and *T. cristatus* in the values of the brachial, humerofemoral, and intermembral indices (Fig. 5; Supplement Table S2). All of these indices are above 100 for *N. larvatus* and below 100 for *T. cristatus*. There is, however, overlap in the values for the crural index. This index is higher than 100 overlapping in both species. There is a pronounced sexual dimorphism in the index values in *N. larvatus* but much less so in *T. cristatus* (Fig. 2; Supplement Table S2). The values of the indices differ from measurements taken on museum specimens (Schultz, 1942; Washburn, 1944; Fig. 3). For example, the crural index is higher and intermembral index lower in *N. larvatus* when measured from photographs than from museum specimens, while both humerofemoral and intermembral indices are higher in *T. cristatus* when measured from photographs than from museum specimens. However, when we compare pairs of the same indices obtained with the two

Table 1 Nonmetric comparison of photographs of the putative subadult female hybrid (later an adult), photographed near Kampung Bilit, Kinabatangan, Sabah, between June 19, 2017 and June 18, 2020, from a large set of photographs of various *Nasalis larvatus* and *Trachypithecus cristatus* adult females (Supplement Table S1). Darker shaded boxes indicate that the putative hybrid resembles the respective putative parent species; lighter shaded boxes indicate features intermediate between *N. larvatus* and *T. cristatus*

Features	Putative hybrid female (subadult and adult)	<i>Nasalis larvatus</i> (adult female)	<i>Trachypithecus cristatus</i> (adult female)
Eye color (may depend on light/exposure)	Reddish brown to brown.	Light brown to reddish brown or brown.	Reddish brown to brown or greyish brown.
Facial skin	Light with greyish tinge and lighter color eye rings and around mouth.	Uniform light reddish.	Dark (slate grey) with indistinct or near-absent eye rings.
Nose shape	Rather long. Indistinctly protruding.	Long. Distinctly protruding.	Short. Not protruding.
Nostrils	Tube-shaped. Open downward.	Tube-shaped. Open downward or slightly uplifted.	Slit-shaped. Open to sides.
Crown shape	Wedge-shaped with indistinct crown. Without whorl.	Flat with whorl.	Distinct long crest. Without whorl.
Crown color	Distinctly dark brown.	Indistinctly darker reddish.	Without distinct coloration.
Eyebrow rim	Not prominent.	Not prominent.	Long and prominent. Joins with whiskers a part of the parabolic facial rim.
Cheek whiskers	Prominent cheek whiskers hiding base of ear pinnae. Connected under chin.	Cheek whiskers flat but elongated. Hiding base of ear pinnae. Longer hair extends to nape and shoulders.	Distinct long parabolic-shaped whiskers connected under the chin. Anteriorly from ear pinnae that remain visible from the side. Hair texture not extending behind cheeks and throat.
Collar (whiskers and shoulder band)	Orange color pattern extends from whiskers to chest and marginally to nape and shoulder.	Reddish collar. Intermediate tinge between dorsal and ventral color. Cheeks may be darker; extending as a broad band to nape, shoulder, and chest.	Coloration not distinct from the upper side.
Beard	Distinct. Short. Whitish.	Short or indistinct. Light yellow.	Indistinct or absent. Whitish.
Body hair texture	Rather long and dense. Hiding ankles, wrists and tendons.	Short and sparse. Ankles, wrists and some tendons are visible.	Rather long and dense. Covering ankles, wrists and tendons.

Table 1 (continued)

Grizzle on trunk and limbs	Indistinct. Reddish rather than grey or white.	Indistinct. Greyish.	Distinct greyish white almost all over the body.
Hand and foot color	Darker (nearly black). The color does not extend far to forearms.	Distinctly grizzled greyish. The color extends to forearms above the elbow.	Darker (nearly black). The color does not extend far to forearms.
Flanks color	Grey hair posteriorly.	Lighter hair posteriorly.	Unicolored (grizzled dark grey). Coloration not distinct from the upper side.
Tail color	Bicolored. Greyish brown with distinct grey hair bellow.	Off-white. Maybe lighter below.	Grizzled dark grey as the upper side with more white hair bellow and near the base.
Rump color	Same color as the back.	Distinct white patch.	Same color as the back.
Upper side coloration	Greyish brown.	Reddish brown.	Grizzled dark grey.
Underside coloration	Reddish on chest. Probably whitish on belly.	Light yellowish. Darker on chest.	Indistinctly lighter grey on belly.
Grizzle on calves and forearms	Delicate grizzle, indistinct on subadult pictures but becomes distinct on calves and possibly forearms in the adult pictures; differs from the coloration of the upperparts.	Delicate grizzle that contrasts with the coloration of the shoulders, back and sides of the trunk; starts appearing indistinctly in juveniles and becomes distinct in some but not all adult females.	Non-delicate grizzle, which does not differ from the coloration of the upper side, starts appearing before the color change phase of ca. 4 months of age when the infant starts changing its color from bright yellow to dark grey.
Mane between upper sides and under sides	Indistinct.	Indistinct.	Distinctly longer. Lighter-colored hair along the midline of chest and belly.

methods, between species (for each sex) or between the sexes (for each species), the differences are in the same direction in all but one comparison (total $n = 11$ comparisons). All values are higher for *N. larvatus* than *T. cristatus*; brachial and crural indices are higher for males than for females in *N. larvatus*; sexual dimorphism is higher in *N. larvatus*; and the humerofemoral index in *T. cristatus* (the only sexually dimorphic index for that species) is higher for females. In other words, the values of indices are different, most likely due to the deviation of the position of limb segments from the medial plane in the photographs, but this does not alter the pattern of differences between the two species or the two sexes.

Comparison of metric proportions of the best three photos of the putative hybrid from Kinabatangan with the four best-positioned photos of each sex of

Table 2 Nonmetric and metric indices based on the resemblance of the putative hybrid to the putative parent species

Character	Resembling <i>Nasalis larvatus</i>	Closer to <i>Nasalis larvatus</i>	Intermediate	Closer to <i>Trachypithecus cristatus</i>	Resembling <i>Trachypithecus cristatus</i>
(1)	Eye color	Facial skin	Crown shape	Tail color	Body hair texture
(2)	Nostrils	Collar	Upper side coloration	Crural index	Hand and foot color
(3)	Eyebrow rim	Beard		Cheek whiskers	Rump color
(4)	Mane	Grizzle on trunk and limbs			Humero femoral index
(5)	Brachial index	Flanks color			
(6)	Intermembral index	Underside coloration			
(7)		Grizzle on calves and forearms			
(8)		Nose shape			
(9)		Crown color			

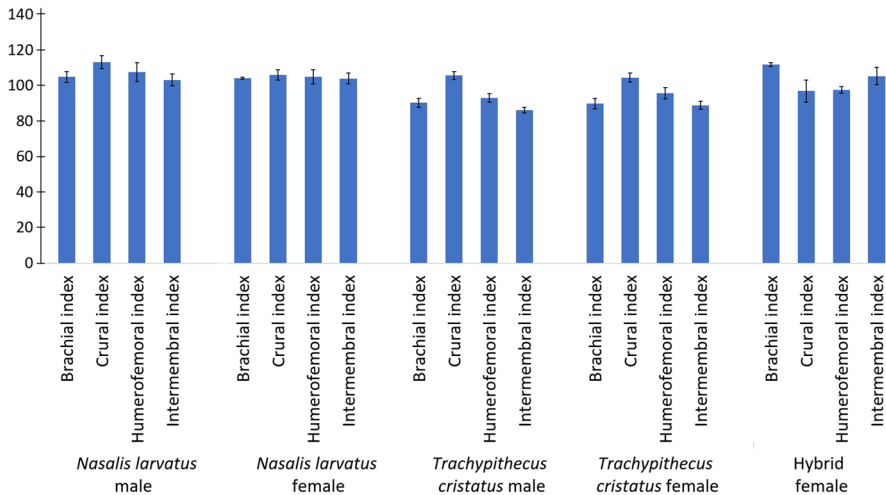


Fig. 2 Morphometric indices (means with standard errors) of limb measurements derived from photographs of both sexes of the putative parent species (*Trachypithecus cristatus* and *Nasalis larvatus*; $n=4$) and the putative hybrid female ($n=3$) near Kampung Bilit, Sabah, 2020 (photo sources in Supplement Table S1)

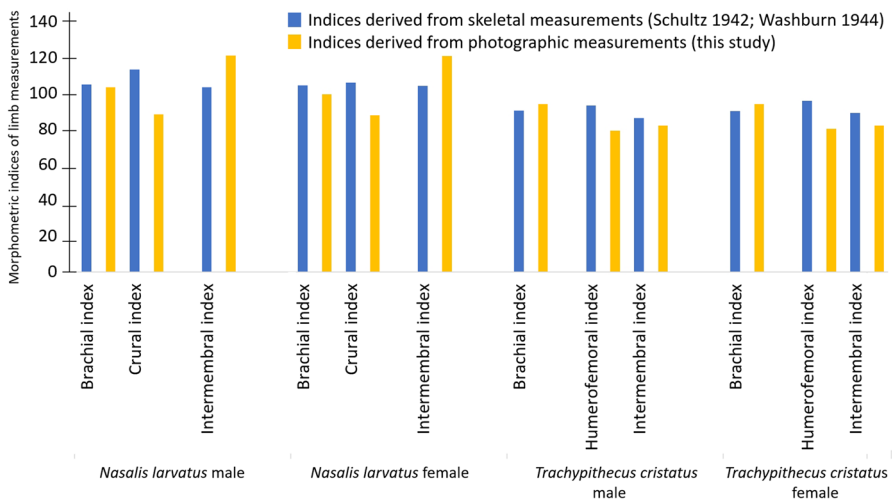


Fig. 3 Comparison of mean morphometric indexes (no standard errors published) between species and sexes derived from skeletal measurements (*Nasalis larvatus*, Schultz, 1942; *Trachypithecus cristatus*, Washburn, 1944; Supplement Table S2) and from photographs in this study (Kampung Bilit, Sabah, 2020)

both putative parent species (Fig. 4) shows that the brachial index of the putative hybrid is consistently high, exceeding values for male *N. larvatus* in all three comparisons. However, this may be influenced by the position of the upper arm, which is slightly extended towards the camera on some of the photographs. The

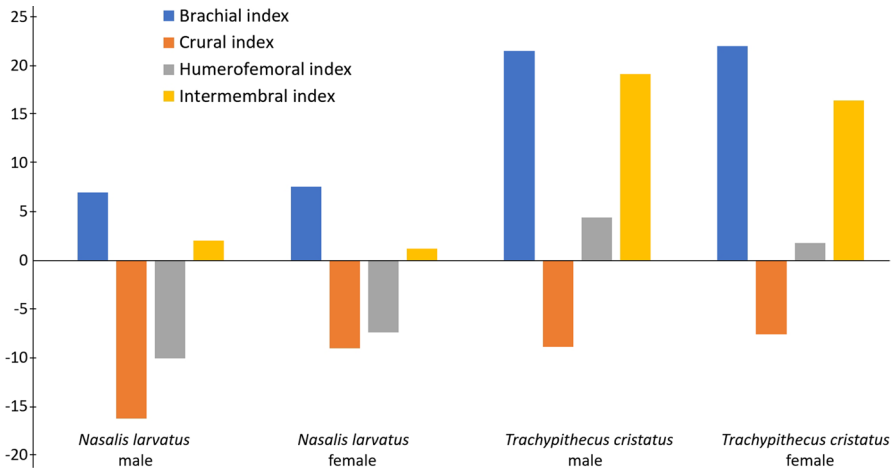


Fig. 4 Differences in mean values of morphometric indices of the putative hybrid from Kampung Bilit, Sabah (2020) compared with the two assumed parent species (*Nasalis larvatus* and *Trachypithecus cristatus*, data in Supplement Table S2)

crural index is rather low, and closer to the values for *T. cristatus* than for *N. larvatus*, and the values measured from different photographs tend to differ. The humero femoral index is intermediate between values for female *N. larvatus* and male *T. cristatus* in two of three comparisons; in the third comparison, it is most similar to male *T. cristatus*. The intermembral index is rather high, its values are higher than for *T. cristatus* and overlapping with those for *N. larvatus*. It is most similar to female *N. larvatus* (two comparisons) or female *T. cristatus* (one comparison; Supplement Table S2). A comparison of the mean morphometric indices with standard errors obtained from the photographs of the putative hybrid and the females of both putative parent species shows that the brachial and intermembral indices approach *N. larvatus* more, while crural and humero femoral indices approach *T. cristatus* more (Fig. 5).

Discussion

Morphometric and observational evidence suggests that the "mystery monkey" of the Lower Kinabatangan is a hybrid between *N. larvatus* and *T. cristatus*. To our knowledge, this is the first reported case of hybridization between colobine genera in the wild and the second reported case of intergeneric hybridization in wild primates. The lineages that lead to *N. larvatus* and *T. cristatus* diverged in the late Miocene, approximately 9.21 mya (Liedigk *et al.*, 2012), earlier than in any other primate genera known to currently hybridize in the wild (*Theropithecus* and *Papio* diverged in Pliocene, approximately 4.07 mya; Liedigk *et al.*, 2012). The primate genera that hybridized in captivity diverged later or at the same time as *Nasalis* and *Trachypithecus*, i.e., *Symphalangus* and *Hylobates* diverged approximately 7 mya

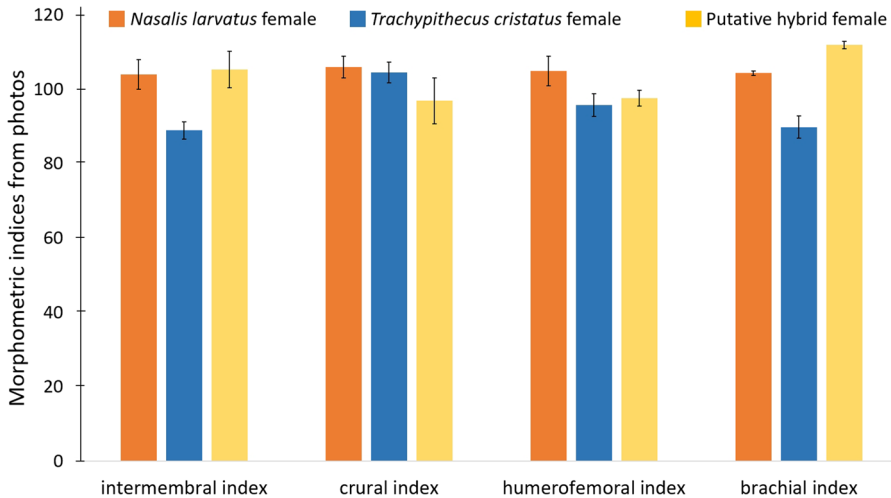


Fig. 5 Comparison of morphometric indices (means with standard errors) obtained from photographs of the putative hybrid (adolescent female; $n=3$) and adult females of both assumed parent species ($n=4$)

(Matsudaira & Ishida, 2010), while *Pygathrix* and *Trachypithecus* diverged at the same time as *Nasalis* and *Trachypithecus* (Liedigk *et al.*, 2012).

The coloration of the “mystery monkey” can be described as intermediate between *N. larvatus* and *T. cristatus*. Intermediate coloration is also described for several other hybrid primates (e.g., *Hylobates lar* x *H. pileatus*, Brockelman & Schilling, 1984; *Semnopithecus johnii* x *S. priam*, Hohman, 1988; *Semnopithecus priam thersites* x *S. vetulus*, Lu *et al.*, 2020; *Trachypithecus geei* x *T. pileatus*, Choudhury, 2008; *Pygathrix nemaus* x *Trachypithecus hatinhensis*, Schempp *et al.*, 2008). However, there are some similarities between the coloration of the putative hybrid and the coloration of a *T. cristatus* infant during the color change phase, namely the pattern of the dark cap and forearms combined with orange shoulders and upper arms. Therefore, it could be argued that the “mystery monkey” represents a color morph of *T. cristatus*, which neotenually retains some pattern of its natal coat. Several aspects of its coloration however differ from any of the developmental phases in *T. cristatus*. Furthermore, while numerous color morphs of *T. cristatus* are observed across its distribution, including near Kampung Bilit, none resembles the “mystery monkey” (V. Lee, personal observation; Supplement Fig. S2). The *T. cristatus* color morphs observed in the wild are of two types, either reduction of melanin, which results in orange or beige coloration of the whole body (Harding, 2011) or a localized loss of pigments, resulting in irregular off-white patches on various part of the body (P. Zoubek, personal communication). None of the observed color morphs features an entirely new symmetric coloration pattern like the “mystery monkey.” Moreover, no striking color morphs have been reported in the other putative parent species (*N. larvatus*) anywhere across its distribution. We therefore think that the “mystery monkey” is not a color morph of *T. cristatus*.

Metric comparison of the photos of *N. larvatus* and *T. cristatus* showed that the brachial, humerofemoral and intermembral indices are above 100 for *N. larvatus* and below 100 for *T. cristatus* on all photographs. This means that *N. larvatus*, in comparison to *T. cristatus*, have relatively longer forelimbs compared to hindlimbs, and longer forearms relative to the upper arms. This corresponds to the frequent use of arm swinging in *N. larvatus* but not in *T. cristatus* (SL, personal observation). The crural index is higher than 100 in both species and the species overlap, which corresponds to a similar basic locomotor pattern of climbing and leaping in the two species. The limb proportions differ less between the two sexes of each species than between species. Males of both species showed a higher brachial and crural index, and a lower intermembral index than females. The humerofemoral index was higher in *N. larvatus* males (compared with females), but lower in *T. cristatus* males (compared with females).

The within-species differences were smaller than the interspecies differences and therefore may be more influenced by the body position on the photographs. The limbs of a naturally positioned animal on a photograph are usually not in a perfect plane; thus, measurements from photographs vary more than measurements taken directly on dead or sedated animals. Although the photographs of *N. larvatus* and *T. cristatus* are plentiful, increasing the sample size by measuring more photos might increase rather than decrease the error, as it would necessitate including more photographs taken in suboptimal positions. Aware of these possible limitations, we argue that the comparison of the two parental species based on the photographs showed the expected results for at least three of the four indices, referring to the available information on museum specimens. Therefore, we believe that the proportions measured on the photographs can be compared meaningfully even between these two species and the putative hybrid, for which no other morphometric evidence is currently available.

There was high variation in the indices for the "mystery monkey," likely due to the limited number of photographs, which did not allow us to select those in a perfect lateral position. The limited selection of photographs led us to the decision to base our measurements on photographs when the female was still a subadult. Even with this limitation, the measurements for the "mystery monkey" fall between values for *N. larvatus* and *T. cristatus*, supporting the hypothesis that it is a hybrid. The values for individual indices are however not central between the two species. The "mystery monkey" resembles *N. larvatus* in having more elongated forearms, which are longer than the upper arms, while the opposite occurs in *T. cristatus*. Furthermore, the "mystery monkey" also is like *N. larvatus* in having relatively longer forelimbs compared to the hindlimbs. In contrast, the crural index (the proportion of hind leg segments) is more like *T. cristatus* than *N. larvatus*. This finding however needs to be considered with caution due to the lack of a distinct difference between the parent species and high variation in the measurements of this index taken from different photographs.

The "mystery monkey" has been observed since she was a juvenile. No adult female or male shows signs of hybridism in the same or other groups observed in the area. This suggests that she is most likely a first-generation hybrid rather than a backcross. Her intermediate coloration and body proportions of the suggest that the

species-specific morphological characteristics of the parental species are determined by polygenetic complexes. Their effect is however not simply additive. Although values for the putative hybrid are between her parent taxa for most characters, her values are not midway between those of the putative parent species. Instead, she resembles one of the parent species more than the other in most characters. This parallels the finding that the temporal pattern of syllables in loud calls of hybrid gibbons reflects a multiplicative rather than additive effect of a polygenetic system (Brockelman & Schilling, 1984). However, interpretation of the genetic basis of the characters observed in a single hybrid monkey, without knowledge of the pedigree, is highly speculative.

In contrast to a study of the morphology of *Theropithecus gelada* x *Papio hamadryas* hybrids in captivity (Jolly *et al.*, 1997), we did not observe different expression of characters that relate to ecologically adaptive traits (body proportions, fur texture) and external epigamic traits (color and ornaments). In *Theropithecus* x *Papio* hybrids, the ecologically adaptive characters tend to be intermediate, while the external epigamic characters were usually present in their plesiomorphic, less derived state, in the hybrids. In the putative *Nasalis* x *Trachypithecus* hybrid, the external epigamic characters were expressed like the ecologically adaptive ones across the gradient of resemblance to one or the other species. While some of the derived traits were indeed absent in the putative hybrid (i.e., the white rump patch, typical for *Nasalis larvatus* and *Pygathrix* spp.), other derived traits of *Nasalis larvatus* were at least partly expressed in the putative hybrid (i.e., patterns of nose shape or ventral coloration). In fact, the general resemblance of the “mystery monkey” to *Nasalis larvatus* appears to be largely because *Nasalis larvatus* evolved more apomorphic (derived) external epigenetic characters that are partly expressed in the putative hybrid. This difference from the *Theropithecus* x *Papio* hybrids may be due to the longer divergence time between *Nasalis* and *Trachypithecus*, which might have resulted in more complex genetic determination of the external epigenetic characters. However, the set of characters under study also differ. Some of the external epigamic characters studied in the *Theropithecus* x *Papio* hybrids were female sexual ornaments, which are absent in colobine females.

It seems that this female “mystery monkey” is a fertile hybrid. She was last photographed in September 2020 with an infant, and her swollen breasts suggest lactation instead of allomothering. As the father of the infant must have been one of the parent species (presumably *T. cristatus*), it seems likely that retrogressive hybridization occurred. The second-generation hybrid is therefore likely to resemble one of the parent species more than the “mystery monkey.” While the “mystery monkey” is highly distinct, her descendants may not be observably different from her parent species. Yet, the genes of the other grandparent species will remain in the gene pool of her offspring. To ascertain whether the case described in Kinabatangan is unique, or whether it has happened in the phylogenetic past, we should look for possible cryptic introgression of the *N. larvatus* genes in the sympatric population of *T. cristatus* and vice versa. Due to the ongoing COVID-19 lockdowns and travel restrictions in Malaysia since March 2020, we have not yet been able to collect fecal materials for genetic analyses.

Some cases of hybridization in primates may be related to anthropogenic change in the landscape or primate translocations, which may have conservation implications (Detwiler *et al.*, 2005). The "mystery monkey" lives in a highly fragmented habitat due to conversion of the forests along the Kinabatangan River into oil palm plantations. Both parent species are now confined to a strip of seasonally flooded forest of varying width, with very limited possibility of dispersal to other forest patches. In species with sex-biased distribution, one sex may tend to leave patches of suboptimal habitat (either finding a better patch, or vanishing), while the other sex is more likely to stay. In *Trachypithecus*, with a unimale-multifemale social structure and male-biased dispersal (Koenig and Borris, 2012), this may result in groups without males in suboptimal habitat patches. These groups may be visited or taken over by male *N. larvatus*, who may find limited mating opportunities in the fragmented habitat. The larger body size of adult *N. larvatus* also may allow them to permanently displace resident adult *T. cristatus* from their groups. This, together with the persisting competition for narrowing ecological niches and resources, may lead to local extinction of one of the two species in the long-term, although some of its genes may be assimilated into the genetic pool of the more successful species.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest.


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Authors and Affiliations

Stanislav Lhota^{1,2} · **Jo Leen Yap**^{3,4} · **Mark Louis Benedict**⁵ · **Ken Ching**⁶ · **Bob Shaw**⁷ · **Ben Duncan Angkee**⁸ · **Nicole Lee**⁹ · **Vendon Lee**^{6,10} · **Jean-Jay Mao**¹¹ · **Nadine Ruppert**^{3,4} 

✉ Nadine Ruppert
n.ruppert@usm.my

- ¹ Department of Animal Science and Food Processing, Faculty of Tropical AgriSciences, Czech University of Life Sciences, Prague, Czech Republic
- ² Ústí Nad Labem Zoo, Ústí nad Labem, Czech Republic
- ³ School of Biological Sciences, Universiti Sains Malaysia, Penang, Malaysia
- ⁴ Malaysian Primatological Society, Kulim, Kedah, Malaysia
- ⁵ APE Malaysia Sdn. Bhd, Petaling Jaya, Selangor, Malaysia
- ⁶ Eco-Education & Resources Centre, Wan Chai, Hong Kong
- ⁷ Aspiration Images, Kiama, NSW, Australia
- ⁸ Kota Kinabalu, Sabah, Malaysia
- ⁹ Marvelous Vacation, Sandakan, Sabah, Malaysia
- ¹⁰ Sepilok Tropical Wildlife Adventure, Sabah, Malaysia
- ¹¹ Department of Forestry and Natural Resources, National Ilan University, Ilan, Taiwan