

Letter to the editor

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# Importance of genetic data from type specimens: The questionable type locality of southern white-cheeked gibbon, *Nomascus siki* (Delacour, 1951)

## DEAR EDITOR,

Many historical descriptions of new species have included vague or inaccurate information about the type locality. This can lead to confusion in the study of the species and their geographic distributions, thereby hindering conservation efforts. One such example is the southern white-cheeked gibbon (*Nomascus siki* (Delacour, 1951)). The type locality is given as Thua Luu in central Vietnam, which is located within the range of another crested gibbon species (*N. annamensis*) and more than 200 km south of the known range of *N. siki*. To investigate the problematic type locality of *N. siki*, we sequenced the mitochondrial genome of the holotype and compared its cytochrome *b* gene sequence to those of other georeferenced crested gibbon samples. As expected from the phenotype, the *N. siki* holotype clustered with the other *N. siki* specimens, but not with the parapatric or even sympatric samples of gibbons from the region close to its type locality (distance <5 km). This suggests that the type locality may not be the place where the specimen was collected in the wild. Our study highlights the importance of genetic data from name-bearing types, as they represent an important reference for taxonomic and biogeographic research.

Formal descriptions of new species are based on at least one specimen, namely the holotype (Sluys, 2021). Descriptions normally entail physical information about the specimen itself, e.g., sex, age (class), measurements, and external appearance, as well as its geographic provenance, i.e., type locality. However, it is not uncommon to find that information regarding provenance is incorrect or unclear (Steinheimer & Dean, 2007), leading to confusion in subsequent studies of the species and their geographic distributions. Likewise, it is often unclear whether the type

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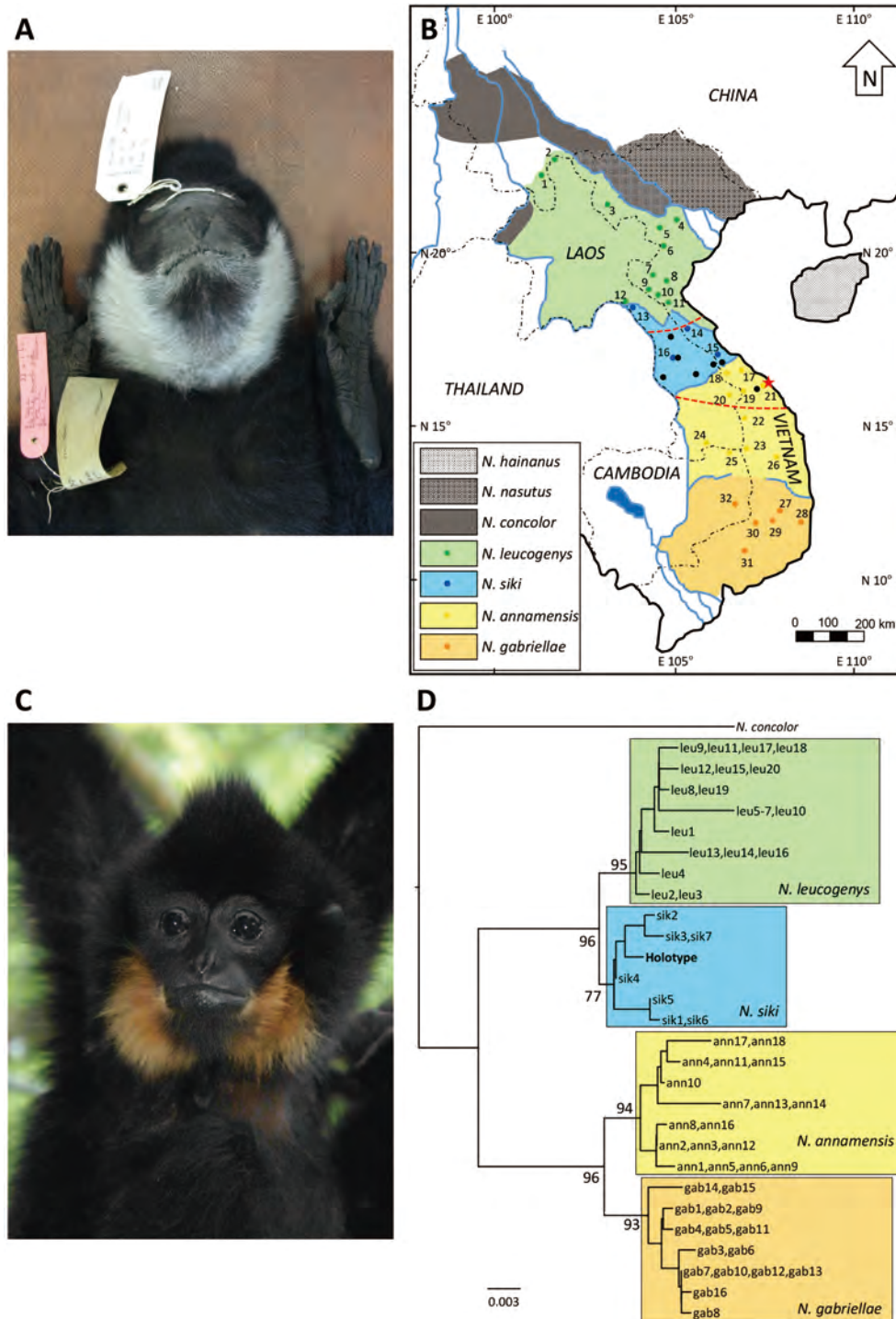
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locality provided is the site of collection in the wild or whether specimens were obtained third-hand at that place, e.g., coastal harbor towns are sometimes mentioned as type localities.

Herein, we present the southern white-cheeked gibbon (*N. siki*) as one such example. According to the original description (Delacour, 1951), the *N. siki* holotype (Figure 1A) was collected by Jean Delacour and Pierre Jabouille on 4 February 1931 in “Thua-luu, au sud de Huê, Centre-Annam” (Delacour, 1951:122) (=Thua Luu, South of Hue, central Annam=Thua Luu, Thua Thien-Hue Province, central Vietnam; N16°16', E108°00'; Figure 1B) and later described as a new taxon (*Hylobates concolor siki* Delacour, 1951). Based on this and other specimens obtained in Hue (Thua Thien-Hue Province, Vietnam), Tourane (=Da Nang, Vietnam), Lao Bao (Quang Tri Province, Vietnam), Tchépone (=Xepon, Savannakhet Province, Laos), Napé (=Ban Nape, Bolikhamxai Province, Laos), and Nakai (Khammouane Province, Laos), Delacour (1951) concluded that the taxon occurs in central Annam (Vietnam) and neighboring Laos (Figure 1B).

*Nomascus siki* is one of seven species belonging to the clade known as “crested gibbons” (genus *Nomascus*) (Beauséjour et al., 2021; Mittermeier et al., 2013; Roos et al., 2014). Crested gibbons exhibit sexual dimorphism in fur coloration. Adult males are usually black, with the four southern species possessing white (*N. leucogenys*, *N. siki*) or yellow (*N. annamensis*, *N. gabriellae*) cheeks, hence collectively known as the light-cheeked gibbons. In contrast, adult females are yellowish or cream in body color, with a blackish crown patch or streak (Geissmann, 1995, 2007; Geissmann et al., 2000; Groves, 2001; Mootnick, 2006; Mootnick & Fan, 2011). Thus, in addition to genetics (mitochondrial DNA sequence data) and vocalization (Geissmann et al., 2000; Konrad & Geissmann, 2006; Monda et al., 2007; Roos et al., 2007; Ruppell, 2010; Takacs et al., 2005; Tinh et al., 2010a, 2010b, 2011; Zhang, 1997), pelage color pattern, particularly in males, is an important

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**Figure 1** Photographs of *N. siki* and *N. annamensis*, distribution map of crested gibbons, and phylogeny of "light-cheeked" gibbons

A: Skin of *N. siki* holotype (subadult male; NHMUK ZD.1933.4.1.6(a)) from the Natural History Museum, London, United Kingdom (NHMUK). Photo by Anna Barros. B: Distribution map of crested gibbons, genus *Nomascus* (modified from Thinh et al. (2010b)). Black and blue lines refer to country borders and major rivers, respectively. Area between red lines is approximate distribution of *N. siki* according to Delacour (1951) and the red star indicates the type locality of *N. siki*. Colored circles indicate sampling sites for comparative cytochrome *b* gene sequences (for further details and locality IDs see Supplementary Table S1). Black circles indicate sites where Delacour obtained additional *N. siki* specimens (adapted from Figure 1 in Delacour (1951)). C: Subadult male of *N. annamensis* from the Endangered Primate Rescue Center, Vietnam. Photo by Tilo Nadler. D: Maximum-likelihood tree showing phylogenetic relationships among "light-cheeked" gibbons based on mitochondrial cytochrome *b* gene sequences. Numbers at nodes refer to bootstrap values and bar below indicates substitutions per site. Sequence of *N. siki* holotype is in bold.

distinguishing characteristic of crested gibbon species (Geissmann, 1995, 2007; Geissmann et al., 2000; Groves, 2001; Mootnick, 2006; Mootnick & Fan, 2011).

The type locality of *N. siki* (Thua Luu) is close (<5 km) to Bach Ma National Park (N16°05–15', E107°43–53'; Figure 1B, locality ID 21). Indeed, the holotype may have come from this park, as another museum specimen (NRM 8747) collected by Bertil Björkegren in March 1939 and stored in the Swedish Museum of Natural History, Stockholm, is labelled with the locality information “Bach Ma, Thua Luu” (Geissmann et al., 2000). However, the cheeks of this specimen are yellow rather than white, as found in *N. siki* (Geissmann et al., 2000).

In recent decades, it has been shown that gibbons from Bach Ma National Park and surrounding areas differ from typical *N. siki* specimens in phenotype (e.g., yellow instead of white cheek patches) and vocalization (Geissmann, 1995, 2007; Geissmann et al., 2000; Konrad & Geissmann, 2006; Ruppell, 2010). Consequently, the validity of Thua Luu as the type locality of *N. siki* has been questioned (Duckworth, 2008; Geissmann et al., 2000; Konrad & Geissmann, 2006). Furthermore, during range-wide genetic and acoustic analyses of crested gibbons (Thinh et al., 2010b, 2010c, 2011) and a subsequent taxonomic revision of the genus, the gibbons of central Vietnam and neighboring areas in Laos, including the population of Bach Ma National Park, were identified as a new species *N. annamensis* Thinh et al., 2010c (Figure 1C). As a result of this extensive research and classification, the putative type locality of *N. siki* fell deep within the range of *N. annamensis* and ca. 200 km south of its southernmost known geographic limit (Thinh et al., 2010c). Delacour collected gibbons not only at the type locality but also at several other sites (see Figure 1 in Delacour (1951)). Except for the holotype and a specimen from the Danang vicinity and probably another one from Hue vicinity (if not the holotype), all other specimens mentioned by Delacour from Vietnam (Lao Bao) and Laos (Xepon, Ban Nape, and Nakai) are in the known range of *N. siki* (Figure 1B).

In the absence of novel archival or historical information and to help elucidate the type locality of *N. siki*, we sequenced the complete mitochondrial genome (mitogenome) of the holotype using next-generation sequencing methods and phylogenetically related the obtained sequence with a large set of available cytochrome *b* gene sequences of known, georeferenced crested gibbon samples (Thinh et al., 2010b, 2010c). We collected a small piece of skin (ca. 5 mm×5 mm) of the *N. siki* holotype (NHMUK ZD.1933.4.1.6(a); Figure 1A) stored at the Natural History Museum, London, United Kingdom (NHMUK). DNA was extracted in the ancient DNA laboratory of the German Primate Center using a column-based method specifically designed to recover degraded DNA fragments (Dabney et al., 2013; Rohland et al., 2004). After extraction, DNA concentration was measured with a Qubit 4.0 fluorometer (ThermoFisher Scientific, USA), and DNA quality and degradation were checked using a Bioanalyzer 2100 (Agilent Technologies, USA). Genomic DNA (50 ng) was then used to construct a shotgun sequencing library with the NEBNext Ultra II DNA Library Prep Kit (New England Biolabs, USA) following standard protocols of the supplier (DNA fragmentation before library preparation was omitted). After

end repair, adapter ligation, and ligation cleanup without size selection, the library was indexed with multiplex oligos and then cleaned with purification beads from the kit. Library concentration and size distribution were determined via Qubit and Bioanalyzer measurement, respectively, and molarity was quantified by quantitative polymerase chain reaction (qPCR) using the NEBNext Library Quant Kit (New England Biolabs, USA). Sequencing, together with 23 other libraries, was conducted on one lane of an Illumina HiSeq 4000 sequencer (100 bp single-end read) by the core unit of NGS Integrative Genomics (NIG) at the University Medical Center Goettingen, Germany. Raw sequencing reads were demultiplexed with Illumina software. The subsequent bioinformatic analyses were performed with the Geneious Prime 2021.2.2 package (<https://www.geneious.com/>). First, we trimmed and quality-filtered reads with BBDuk v38.84 in the BBTools package (<https://jgi.doe.gov/data-and-tools/bbtools/>) and then removed duplicate reads with Dedupe v38.84 (BBTools package), both with default settings. We then mapped reads onto the *N. siki* reference mitogenome (GenBank accession No. NC\_014051) using the Geneious Assembler with default settings (maximum five iterations). After trimming, quality-filtering, and duplicate removal, 19 636 050 of the original 22 368 573 sequence reads remained, 17 784 of which were mapped onto the *N. siki* reference mitogenome, resulting in a complete mitogenome of the *N. siki* holotype, with a high average sequence depth of 94.6× and total length of 16 476 bp. The newly produced mitogenome was manually checked, annotated with Geneious, and submitted to GenBank (accession No. OM287160). Alignment was conducted using Muscle v3.8.31 (Edgar, 2010) in AliView v1.18 (Larsson, 2014) with the cytochrome *b* gene sequences (1 140 bp) of the *N. siki* holotype and 61 other light-cheeked crested gibbons (*N. leucogenys*: *n*=20, *N. siki*: *n*=7, *N. annamensis*: *n*=18, *N. gabriellae*: *n*=16; for details see Supplementary Table S1 and Thinh et al. (2010b)). *Nomascus concolor* was used as the outgroup. A maximum-likelihood tree was reconstructed with IQ-TREE v2.1.3 (Minh et al., 2020) with 1 000 ultrafast bootstrap replicates (Hoang et al., 2018) and the best-fit substitution model (TN+F+I) was automatically calculated with ModelFinder (Kalyaanamoorthy et al., 2017) in IQ-TREE according to Bayesian information criterion.

We obtained strong nodal support for all major clades (>70%) and found that light-cheeked gibbons initially diverged into white-cheeked (*N. leucogenys*, *N. siki*) and yellow-cheeked (*N. annamensis*, *N. gabriellae*) forms, with further division into corresponding northern and southern species (Figure 1D), consistent with earlier studies (Thinh et al., 2010b, 2010c). Corresponding to its phenotype (white cheeks), the *N. siki* holotype was nested within the *N. siki* clade and did not cluster with the para-/sympatric samples from Bach Ma National Park (samples ann5-7), which were clearly nested within the *N. annamensis* clade. The gibbons from Bach Ma National Park also exhibit the typical song repertoires and phenotypic traits of yellow-cheeked *N. annamensis*, rather than white-cheeked *N. siki* (Geissmann, 1995, 2007; Geissmann et al., 2000; Konrad & Geissmann, 2006; Ruppell, 2010; Thinh et al., 2010b, 2010c, 2011). Nevertheless, we were unable to locate the source population

of the *N. siki* holotype. Although mitochondrial sequence data can allow the taxonomic diagnosis of crested gibbon species, information on geographic structure cannot be determined as haplotypes are often shared among different local populations. This is likely because, in contrast to many other primate species, female gibbons are not philopatric (Brockelman et al., 1998; Matsudaira et al., 2018), thus contributing to the geographic mixing of matrilineally inherited mitochondrial haplotypes.

From our analysis, it is evident that the type locality of *N. siki* is problematic. Unfortunately, there is no information available on how Jean Delacour and Pierre Jabouille obtained the holotype specimen. Furthermore, the corresponding field notes are not traceable, either in NHMUK or any other natural history museum where Delacour's field notes may exist. One explanation for the incorrect type locality may be that Delacour and Jabouille, like other collectors, received or purchased the specimen from local people who had kept the animal as a pet or for trade. Thua Luu is close to the Vietnamese coast and Vietnam's Highway No. 1, which has been the country's major trading route for centuries (Logan, 2002). Hence, the specimen may have arrived by trade from a wild origin other than Thua Luu. However, if the specimen was indeed collected at Thua Luu, various explanations are possible. First, the specimen may have been a previously released or escaped pet. Second, a small enclave population of *N. siki* may have existed historically (but not currently) near Thua Luu, surrounded by a larger population of *N. annamensis*. Third, the historical geographic distribution of the two species may have differed substantially from current distributions, with *N. annamensis* replacing a viable *N. siki* population at Thua Luu/Bach Ma National Park in recent decades. However, the latter two explanations are unlikely as a yellow-cheeked specimen (NRM 8747) was collected at the same (or nearly the same) site as the type specimen ("Bach Ma, Thua Luu") only eight years after Delacour and Jabouille, indicating that a yellow-cheeked phenotype (*N. annamensis*) already existed at that time. Fourth, Thua Luu/Bach Ma National Park may be a natural hybridization zone between *N. siki* and *N. annamensis*. However, this also seems unlikely as the distribution ranges of *N. siki* and *N. annamensis* are separated by large river barriers, as with most crested gibbon species. Hence, hybridization between *N. siki* and *N. annamensis* could only occur along the narrower upper river reaches, not 200 km away from such a barrier. Consequently, if the given type locality is correct, the specimen was most likely a released or escaped former pet or was obtained at the site from local people.

The debatable geographic record of the type locality has resulted in uncertainty regarding the number of extant crested gibbon species and their distribution ranges, thus hindering conservation for these (critically) endangered small apes. Notably, the geographic range of *N. siki* was believed to be much larger, but the taxonomic revision of crested gibbons by Thinh et al. (2010c) reassigned several populations previously thought to be *N. siki* to *N. leucogenys* or *N. annamensis*, significantly reducing the number of *N. siki* populations (Nguyen et al., 2020).

Our study verified that genetic data from type specimens

can help address long-standing taxonomic and biogeographic questions. In our example, a precise but likely incorrect type locality was provided with the original description of a new small ape species. In historical species descriptions, type locality information can be ambiguous or inaccurate, e.g., providing only the name of the country where the specimen was collected or the harbor/trading town where the specimen was purchased (Roos et al., 2021). In such cases, genetic data can be an important tool for reassessing or rejecting the geographic origin of such specimens, or at least integrating them into valid taxa if comparable genetic information from conspecifics and congenics is available. Even given accurate and correct type localities, genetic data can still be helpful, e.g., when the type locality is close to a biogeographic barrier, such as a river, and the side from which the specimen was collected is unclear and needs to be more precisely determined (Boubli et al., 2021). Overall, genetic information from name-bearing types provides an important resource for taxonomic and biogeographic research and can inform conservation efforts.

#### SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

#### COMPETING INTERESTS

The authors declare that they have no competing interests.

#### AUTHORS' CONTRIBUTIONS

C.R., T.N., and V.N.T. conceived and designed the study. R.P.M. provided the holotype sample. C.R. analyzed the data. C.R. and D.Z. wrote the paper. All authors discussed the data and read and approved the final version of the manuscript.

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## REFERENCES

- Beauséjour S, Rylands AB, Mittermeier RA. 2021. All Asian Primates. Barcelona: Lynx Edicions.
- Boubli JP, Janiak MC, Porter LM, de la Torre S, Cortés-Ortiz L, da Silva MNF, et al. 2021. Ancient DNA of the pygmy marmoset type specimen *Cebuella pygmaea* (Spix, 1823) resolves a taxonomic conundrum. *Zoological Research*, **42**(6): 761–771.
- Brockelman WY, Reichard U, Treesucon U, Raemaekers JJ. 1998. Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology*, **42**(5): 329–339.
- Dabney J, Knapp M, Glocke I, Gansauge MT, Weihmann A, Nickel B, et al. 2013. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proceedings of the National Academy of Sciences of the United States of America*, **110**(39): 15758–15763.
- Delacour J. 1951. La systematique des gibbons Indochinois. *Mammalia*, **15**(4): 118–123.
- Duckworth JW. 2008. Preliminary Gibbon Status Review for Lao PDR 2008. Vientiane: Fauna & Flora International Indochina Programme.
- Edgar RC. 2010. Quality measures for protein alignment benchmarks. *Nucleic Acids Research*, **38**(7): 2145–2153.
- Geissmann T. 1995. Gibbon systematics and species identification. *International Zoo News*, **42**(8): 467–501.
- Geissmann T. 2007. Status reassessment of the gibbons: Results of the Asian Primate Red List Workshop 2006. *Gibbon Journal*, **3**: 5–15.
- Geissmann T, Dang NX, Lormé N, Mombert F. 2000. Vietnam Primate Conservation Status Review 2000: Part 1 - Gibbons. Hanoi: Fauna and Flora International Indochina Programme.
- Groves CP. 2001. Primate Taxonomy. Washington: Smithsonian Institution Press.
- Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, **35**(2): 518–522.
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, **14**(6): 587–589.
- Konrad R, Geissmann T. 2006. Vocal diversity and taxonomy of *Nomascus* in Cambodia. *International Journal of Primatology*, **27**(3): 713–745.
- Larsson A. 2014. AliView: a fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics*, **30**(22): 3276–3278.
- Logan WS. 2002. Vietnam's Highway No. 1: Corridor of power and patrimony. *Historic Environment*, **16**(2): 23–26.
- Matsudaira K, Ishida T, Malaivijitnond S, Reichard UH. 2018. Short dispersal distance of males in a wild white-handed gibbon (*Hylobates lar*) population. *American Journal of Physical Anthropology*, **167**(1): 61–71.
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, et al. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, **37**(5): 1530–1534.
- Mittermeier RA, Rylands AB, Wilson DE. 2013. Handbook of the Mammals of the World. Volume 3. Primates. Barcelona: Lynx Edicions.
- Monda K, Simmons RE, Kressler P, Su B, Woodruff DS. 2007. Mitochondrial DNA hypervariable region-1 sequence variation and phylogeny of the concolor gibbons. *Nomascus*. *American Journal of Primatology*, **69**(11): 1285–1306.
- Mootnick AR. 2006. Gibbon (Hylobatidae) species identification recommended for rescue or breeding centers. *Primate Conservation*, **2006**(21): 103–138.
- Mootnick AR, Fan PF. 2011. A comparative study of crested gibbons (*Nomascus*). *American Journal of Primatology*, **73**(2): 135–154.
- Nguyen MH, Coudrat CNZ, Roos C, Rawson BM, Duckworth JW. 2020[2022-03-15]. *Nomascus siki*. The IUCN Red List of Threatened Species 2020: e. T39896A17968765. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T39896A17968765.en>.
- Rohland N, Siedel H, Hofreiter M. 2004. Nondestructive DNA extraction method for mitochondrial DNA analyses of museum specimens. *BioTechniques*, **36**(5): 814–821.
- Roos C, Boonratana R, Supriatna J, Fellowes JR, Groves CP, Nash SD, et al. 2014. An updated taxonomy and conservation status review of Asian primates. *Asian Primates Journal*, **4**(1): 2–38.
- Roos C, Miguez RP, Sabin R, Louis EE Jr, Hofreiter M, Zinner D. 2021. Mitogenomes of historical type specimens unravel the taxonomy of sportive lemurs (*Lepilemur* spp. ) in Northwest Madagascar. *Zoological Research*, **42**(4): 428–432.
- Roos C, Thanh VN, Walter L, Nadler T. 2007. Molecular systematics of Indochinese primates. *Vietnamese Journal of Primatology*, **1**(1): 41–53.
- Ruppell JC. 2010. Vocal diversity and taxonomy of *Nomascus* in Central Vietnam and southern Laos. *International Journal of Primatology*, **31**(1): 73–94.
- Sluys R. 2021. Attaching names to biological species: the use and value of type specimens in systematic zoology and natural history collections. *Biological Theory*, **16**(1): 49–61.
- Steinheimer FD, Dean WRJ. 2007. Avian type specimens and their type localities from Otto Schütt's and Friedrich von Mechow's Angolan collections in the Museum für Naturkunde of the Humboldt-University of Berlin. *Zootaxa*, **1387**(1): 1–25.
- Takacs Z, Morales JC, Geissmann T, Melnick DJ. 2005. A complete species-level phylogeny of the Hylobatidae based on mitochondrial *ND3–ND4* gene sequences. *Molecular Phylogenetics and Evolution*, **36**(3): 456–467.
- Thinh VN, Hallam C, Roos C, Hammerschmidt K. 2011. Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology*, **11**: 36.
- Thinh VN, Mootnick AR, Geissmann T, Li M, Ziegler T, Agil M, et al. 2010a. Mitochondrial evidence for multiple radiations in the evolutionary history of small apes. *BMC Evolutionary Biology*, **10**: 74.
- Thinh VN, Mootnick AR, Thanh VN, Nadler T, Roos C. 2010c. A new species of crested gibbon, from the central Annamite mountain range. *Vietnamese Journal of Primatology*, **1**(4): 1–12.
- Thinh VN, Rawson B, Hallam C, Kenyon M, Nadler T, Walter L, et al. 2010b. Phylogeny and distribution of crested gibbons (genus *Nomascus*) based on mitochondrial cytochrome b gene sequence data. *American Journal of Primatology*, **72**(12): 1047–1054.
- Zhang YP. 1997. Mitochondrial DNA sequence evolution and phylogenetic relationships of gibbons. *Acta Genetica Sinica*, **24**(3): 231–237. (in Chinese)