Correspondence

How many species of giraffe are there?

Fred B. Bercovitch[1,2,3,*],
Philip S. M. Berry[4], Anne Dagg[3,5],
Francois Deacon[2,3], John B. Doherty[3,6,7],
Derek E. Lee[3,8], Frédéric Mineur[6,7],
Zoe Muller[3,9,10], Rob Ogden[11],
Russell Seymour[3,6], Bryan Shorrocks[12,13],
and Andy Tutchings[3]

In a recent paper in *Current Biology*, Fennessy and colleagues [1] conclude that there are four species of giraffe and that their numbers are declining in Africa. Giraffes (*Giraffa camelopardalis*) are presently classified as one species, with nine subspecies, which are considered 'Vulnerable' on the IUCN Red List [2]. The present consensus of one species divided into nine subspecies has previously been questioned (Supplemental information), and Fennessy and colleagues [1] provide another viewpoint on giraffe taxonomy. The fundamental reason for different taxonomic interpretations is that they are based upon different datasets that adopt different statistical techniques and follow different criteria for nomenclature.

For example, Fennessy and colleagues [1] claim that "population genetic, phylogenetic, and network analyses of nuclear sequences demonstrate that the giraffe is genetically well structured into four distinct species" [1]. This conclusion rests upon their use of the 'genetic species concept' that is based solely upon genetic data and omits ancillary data on morphology, population distribution, ecology and behavior. Rather than a *fait accompli*, as suggested in [1], their taxonomic model should be viewed as one of a number of ways proposed to revise the presently accepted classification of giraffes.

We highlight seven problems below. First, the authors state: "concordance between maternally inherited mitochondrial and biparentally inherited nuclear markers indicates reproductive isolation for at least four giraffe groups" [1]. However, Figure 2 in their paper indicates inconsistencies, not concordance, between the two data sets. Most notably, Figure 2B shows that South African giraffes are genetically more similar to Masai than to Angolan giraffes, yet Figure 2A combines South African and Angolan giraffes into a single cluster.

Second, Fennessy *et al*. [1] state: "the phylogenetic analysis of mtDNA from all nine giraffe subspecies (Figure 2B) produced a tree that conforms to previous analyses". However, Figure 2B conflicts with a previous analysis [3]. The five Thornicroft's giraffe samples are intermixed into a cluster containing Masai giraffes in Fennessy *et al*. [1], while in [3], the 34 Thornicroft's giraffe samples form a single cluster. In addition, [3] concludes: "morphologically, however, there are skull and pelage differences that do separate [*G. c. thornicrofti*] from *G.c. tippelskirchil*" and that "*G. c. thornicrofti* is a valid and important evolutionary unit and that no changes in subspecific designation be made" unless "additional genetic markers" suggest otherwise. Genomic information, when integrated with other biological traits, provides a more solid foundation for protecting biodiversity and developing conservation management plans than does reliance solely upon sampling from across nuclear and mitochondrial genomes [4]. Thornicroft's giraffe is a reproductively isolated population [5] that has been classified as a separate species (Supplemental information) and should be a candidate for consideration as a conservation unit [4].

Third, Figure 3A in Fennessy *et al*. [1], based upon a STRUCTURE analysis of seven nuclear loci from 105 individuals, reveals that the best cluster is when K = 4 [subgroups], and that "K = 5 or higher shows no further resolution". However, Figure 3 in [6], based upon a STRUCTURE analysis of 14 microsatellites obtained from 381 individuals, indicates that at least six distinctive subgroups of giraffes are present. The contention in Fennessy *et al*. [1] that [6] is based on faulty statistics, while their own "multi-locus coalescent-based analyses on sequence data allow for rigorous statistical testing and did not find support for such a grouping" is an unsatisfactory and unconvincing explanation of the discrepancy.

Fourth, Fennessy *et al*. [1] write that pelage patterns are "variable and taxonomically unreliable morphological traits". Coat color patterns are linked to specific gene complexes with mutations leading to variation subject to natural selection [7]. Phenotypic traits regulate mating patterns and sexual selection that establish a foundation for the 'recognition species concept' [8]. Complex color patterns in subspecies of Australian dragon lizards (Agamidae) probably arose from sexual selection [9], and a similar process might contribute to variation in giraffe pelage patterns [6]. Neutral genetic markers provide only a limited perspective on taxonomy because they reflect genetic drift and gene flow, while excluding phenotypic traits that underlie natural selection and local adaptations that could impact speciation [4,8].

Fifth, Fennessy *et al*. [1] report admixture among species and note that giraffes "can interbreed in captivity… However, the genetic differentiation between the four giraffe groups is strong despite their similar appearance." The two clauses are independent, so the authors have not explained why admixture in the wild, and hybridization in captivity, should be ignored in constructing giraffe taxonomy.

Sixth, Fennessy *et al*. [1] claim: "the conservation implications are obvious, as giraffe population numbers and habitats across Africa continue to dwindle due to human-induced threats". We find the implications obscure because giraffe numbers have declined by 40% over the last few decades in Africa [2] regardless of their taxonomic status. Given that *Giraffa camelopardalis* is regarded as 'Vulnerable' to extinction, we do not understand why subdividing the single species into four species has obvious conservation implications.

Seventh, Table 1 in Fennessy *et al*. [1] is misleading. The data are not "from Giraffe Conservation Foundation", but are appropriated from a preliminary draft of a report compiled by the IUCN SSC Giraffe and Okapi Specialist Group. The numbers were early estimates and four of them are inaccurate [2]. The statement that Rothschild's and Thornicroft's giraffes "are now subsumed under *G. c. tippelskirchi* and *G. c. camelopardalis*, respectively" [1] should be considered a suggestion, not a fact. The subsuming of Rothschild's giraffes conflicts with their classification as a separate species (Supplemental information) and is based upon a sample size of nine individuals from Uganda, and none from Kenya [1] out of a population containing 1,671 individuals [2]. The subsuming of Thornicroft's giraffes conflicts with their classification as a

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separate species and is based upon a sample size of five individuals [1] out of a population estimated at 500–600 [2,5]. In summary, Fennessy et al. [1] present a new perspective on giraffe taxonomy, but the conclusions should not be accepted unconditionally.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one table and can be found online at http://dx.doi.org/10.1016/j.cub.2016.12.039.

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[1]Primate Research Institute, Kyoto University, Inuyama, Aichi, Japan. [2]Department of Animal, Wildlife, and Grassland Sciences, University of the Free State, Bloemfontein, South Africa. [3]IUCN, Species Survival Commission, Giraffe and Okapi Specialist Group. [4]P. O. Box 33, Mfuwe, Zambia. [5]Department of Independent Studies, University of Waterloo, Ontario, Canada. [6]Reticulated Giraffe Project, Nairobi, Kenya. [7]School of Biological Sciences, Queen's University Belfast, Belfast, Northern Ireland. [8]Wild Nature Institute, Hanover, NH, USA. [9]Giraffe Research and Conservation Trust, Nairobi, Kenya. [10]School of Biological Sciences, University of Bristol, Bristol, UK. [11]Wildlife Research Center, Kyoto University, Kyoto, Japan. [12]Environment Department, University of York, Heslington, York, UK. [13]Department of Biology, University of Leeds, Leeds, UK.
*E-mail: Bercovitch.fred.2u@kyoto-u.ac.jp

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Correspondence

Response to "How many species of giraffe are there?"

Julian Fennessy[1], Sven Winter[2,3], Friederike Reuss[2], Vikas Kumar[2], Maria A. Nilsson[2], Melita Vamberger[4], Uwe Fritz[4], and Axel Janke[2,3,*]

It is not unexpected that a proposal, such as ours [1], of four new mammalian species stirs up controversy, as evident in the correspondence by Bercovitch et al. [2]. We appreciate that their concerns are unrelated to the quality of the genetic data, the methodological approach or analyses, but are focused on the interpretation. Thus, we provided an analysis of giraffe speciation based on genomic sequence data, and not just "another viewpoint on giraffe taxonomy" [2]. We maintain our perspective that there is not only one but four species of giraffe (Figure 1).

Bercovitch et al.'s [2] concerns focus on the concordance of results, interpretation of data in relation to previous findings, morphological data, and conservation issues. Implicit in their correspondence [2] is an unspecific critique about species delineation and genetics, the latter being an increasingly valuable and objective tool to study speciation. In our analyses, we randomly chose neutrally evolving autosomal loci for sequence variability. The analysis of neutral loci is a prerequisite for coalescent-based methods and allows a conservative approach for species delineation by other methods, because neutral loci require more time to become fixed than loci under selection. Compared to microsatellite data, DNA sequences allow estimating divergence times and, finally, autosomal loci are preferred over uniparental inherited loci (i.e. mitochondrial DNA, mtDNA) for species delineation [3]. The reason is that in species with non-dispersing females (philopatry), mtDNA can show local or regional subdivisions and ancient maternal lineages that may not be consistent with the nuclear gene pool [4]. The fact that mtDNA and multi-locus analyses do not agree in every topological aspect with the nuclear gene tree is therefore not

unexpected. Still, there is concordance for at least four distinct groups of giraffe [1] fulfilling the concordance criterion for species delineation in integrative taxonomy. Notably, mtDNA analysis is also consistent with Thornicroft's giraffe nested within Masai giraffe [5]. Disagreement about the exact grouping can be attributed to limited resolution, limited sampling, misidentified individuals [5] or mitochondrial capture.

We agree with the hypothesis of Bercovitch et al. [2] that sexual selection on pelage pattern may contribute to giraffe speciation and add to species delineation. However, this is not fully supported by data, and pelage pattern is a poor estimator of species delineation. In giraffe, pelage pattern and ossicones were described as unreliable taxonomic characters, because of sexual differences and variations within populations [6]. Thus, other morphological measurements e.g. from skulls were suggested for taxonomic purposes [6] and further research will assess these morphological traits among and between the four species. Interestingly, three giraffe species reproduce at different times according to regional differences in rainfall [7], a factor that could act as a mechanism to isolate the giraffe species in that area.

Bercovitch et al. [2] imply that we suggest the findings of Brown et al. [8] were "based on faulty statistics". Yet, the previous Structure analyses [8] did not calculate additional statistics such as a ΔK, a measure for the fit of the data to the number of assumed clusters. This method was available then to avoid speculating on the number of clusters. The absence of admixture in lower cluster numbers [8], however, complements our findings [1]. Also, three other species delineating methods agreed with four giraffe species: PCA, BPP and Bayesian multi-locus analyses [1].

Furthermore, the claim of Bercovitch et al. [2] that we ignore absence of admixture and hybridization in captivity for taxonomy is based on an out-of-context quote. The corresponding paragraph describes that levels of admixture among the four giraffe clusters are very limited despite the ability to interbreed in captivity. There is strong differentiation between the four groups of giraffe into distinct units despite the lack of a reproductive barrier and being highly vagile animals, which