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How many species of giraffe are there?

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

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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

Figure 1. The differences in coat pattern are consistent with four giraffe species.
From left to right: northern giraffe (*Giraffa camelopardalis*), reticulated giraffe (*G. reticulata*), Masai giraffe (*G. tippelskirchi*), southern giraffe (*G. giraffa*). Images: Masai giraffe: B. Dodson. Other three: J. Fennessy Giraffe Conservation Foundation.

strengthens our conclusions for four species [1]. Numerous species that are unambiguously regarded as distinct, such as polar and brown bears or tiger and lion, interbreed in captivity and even in the wild.

Conservation is predominantly undertaken at the species level and sadly often used as a political tool, e.g., the species debate over forest versus savanna elephants [9]. Concerning the species status of the Thornicroft's giraffe, Bercovitch *et al*. [2] ignore that there is little or no genetic difference between them and Masai giraffe [1]. Implying that sampling 1% of Thornicroft's giraffe population (5/500 individuals) is a limited approach [2], overlooks that Thornicroft's giraffe is genetically depauperate, and thus more individuals would not increase the resolution. It is interesting that Bercovitch *et al*. [2] quote [8] in favour of six giraffe species when [8] vaguely suggested a minimum of "six potential giraffe species". Suggesting that [10] had evidence for eight giraffe species Bercovitch *et al*. [2] refer to a non-reviewed book chapter that provides limited analyses and data partially obtained from unknown locations. Some of the proposed species [10] are at odds with the lack of genetic differentiation [1].

Many of the latest numbers of giraffe for the IUCN assessment are based on the data from GCF Country Profiles, which is thus a valid reference. A change in giraffe taxonomy will in the short term not change their conservation status, but the conservation efforts of the endangered species will benefit in the future. Recently, giraffe as a single species was uplisted to 'Vulnerable' on the IUCN Red List. Division into four giraffe species would likely propose to classify three of these species in higher categories of threat. Yet, with the population increase over the last three decades of both Rothschild's and West African giraffe, it is possible that these currently listed 'Endangered' taxa could be downlisted. However, whether or not four giraffe species are suitable management units is independent from their species status.

Our multi-locus analyses objectively demonstrated the presence of four distinct giraffe species with limited gene flow among them [1]. Four giraffe species also appear to be consistent with giraffe coat patterns (Figure 1) and other genetic analyses [8]. Our recent and subsequent studies will hopefully garner African and international interest to implement increased conservation measures for preserving these species for future generations. The first multi-locus analyses of giraffe [1] have brought the threat of giraffe to the attention of the public and create a basis for future taxonomy discussions and conservation efforts.

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Supplemental information

How many species of giraffe are there?

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TABLE S1. Taxonomy of the genus *Giraffa*

[S1]	[S2, S3]	[S4]	[S5]	[S6]	[S7]	[S8]
G. c. camelopardalis	*G. c. camelopardalis*	*G. c. camelopardalis*			*G. camelopardalis*	*G. c. camelopardalis*
G. g. angolensis	*G. c. angolensis*		*G. angolensis*	*G. c. angolensis*	*G. angolensis*	*G. c. angolensis*
G. c. antiquorum	*G. c. antiquorum*			*G. c. antiquorum*	*G. antiquorum*	*G. c. antiquorum*
G. g. giraffa	*G. c. giraffa*	*G. g. giraffa*	*G. giraffa*	*G. c. giraffa*	*G. giraffa*	*G. c. giraffa*
G. c. peralta	*G. c. peralta*		*G. peralta*	*G. c. peralta*	*G. peralta*	*G. c. peralta*
G. reticulata	*G. c. reticulata*	*G. c. reticulata*	*G. reticulata*	*G. c. reticulata*	*G. reticulata*	*G. c. reticulata*
G. c. camelopardalis	*G. c. rothschildi*	*G. c. rothschildi*	*G. rothschildi*	*G. c. rothschildi*	*G. camelopardalis*	*G. c. rothschildi*
G. tippelskirchi	*G. c. thornicrofti*	*G. g. thornicrofti*			*G. thornicrofti*	*G. c. thornicrofti*
G. tippelskirchi	*G. c. tippelskirchi*	*G. g. tippelskirchi*	*G. tippelskirchi*	*G. c. tippelskirchi*	*G. tippelskirchi*	*G. c. tippelskirchi*

The Table includes only recent taxonomic divisions of *Giraffa*. Blank cells indicate that the authors had no data for those types of giraffes. The subspecies with “*c*” are “*camelopardalis*”, while those with “*g*” are “*giraffa*”. The first row lists the Supplemental reference source for each column.

Author contributions

The study was conceived, and the first draft was written, by F.B.B. Comments, ideas, and revisions were provided by P.S.M.B., A.D., F.D., J.B.D., D. L., F.M., Z.M., R.O., R.S., B.S., and A.T. All authors contributed to, and approved, the final manuscript.

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