

The Taxonomic History of Giraffe – a Brief Review

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The giraffe has long been considered a single species, albeit highly polymorphic. Its high degree of geographically structured phenotypic variation has led to 27 recorded specific or subspecific taxon names (Grubb, 2005). This article briefly reviews the significant episodes in the complex taxonomic history of the giraffe.

Linnaeus (1758) described the giraffe based on the work of Belon who had seen a captive giraffe in Cairo some two hundred years earlier. With no specimens to work with, Linnaeus classified the giraffe with the American elk and the red deer as *Cervus camelopardalis*. The giraffe was reclassified in 1762 by Brisson as *Giraffa giraffa* and amended in 1848 to the currently used *Giraffa camelopardalis*. Although now considered a monospecific genus, the giraffe was long classified as two species.

In 1761 Dutch explorers sent a skin from the Orange River region of South Africa to Leyden University (Dagg and Foster, 1982). This southern giraffe was formally described by Levaillant in his account of his travels in Southern Africa, published in 1790 (Dagg and Foster, 1982). The French anatomist, St. Hilaire, following his study of Levaillant's specimens at the Paris museum and the living northern giraffe in the collection of King Charles X of France (Allin, 1998), decided that the two represented different species. Richard Owen, the British anatomist and zoologist, maintained two species (Owen, 1841) in discussing the features of the Cape and Nubian giraffes separately. Lesson (1842) also classified the northern and southern forms as different species. However, other contemporary authors, including Ogilby (1836), Sundevall (1842) and Swainson (1835), considered the two types of giraffes to indicate variation in the same species.

de Winton (1897) reviewed the taxonomic status of the giraffe, considering the paucity of available specimens to be "the reason for the nomenclature of the *two species* being left in a very unsettled state" (p. 274, with my italics added), and maintained the separation between northern and southern species. However, the distinction was confused by de Winton's use of a specimen from Somalia, rather than material from the northern type locality. In this specimen the pelage spots were "large, sharply defined, and only separated from each other by narrow pale lines" (Thomas, 1894, p. 135); the pattern now recognised as *G. c. reticulata*; the reticulated giraffe. de Winton (1899) later recognised his error and sought to "correct a statement ... which may cause confusion if not rectified" (p. 211). He realised that the Somali specimen was, in fact, "very distinct from the true *Giraffa camelopardalis* from Senaar (the type locality) and the adjacent countries" and was "a strikingly different animal" that was "well worthy of a separate name" (all quotes de Winton, 1899, p. 212). To this end he redefined this taxon as a subspecies of the northern species; *Giraffa camelopardalis reticulata*.

Thomas (1901) argued that the reticulated giraffe deserved specific recognition due to the lack of intermediate forms between it and any neighbouring forms. He further suggested that the northern form grades, through intermediate populations, into the southern form at best making the southern form a subspecies. Hence, while Thomas (1901) also recognised two species these were different from those previously proposed.

Lydekker (1904) carried out the first major review of giraffe subspecific variation that included a reasonable geographic representation of specimens, although his sample sizes were small for many taxa. He followed Thomas's (1901) arrangement and considered the reticulated (*G. reticulata*) and blotched (*G. camelopardalis*) giraffe to be separate

species because of pelage patterns with the former monotypic and the latter containing ten subspecies. Although Lydekker's geographic ranges (Figure 1) were inadequate by today's standards, and even incorrect in some cases, his classification provides the basis of the contemporary classification. His subspecies descriptions were largely based upon the variation of the pelage patterns, although he stated that "most, if not indeed all, of the subspecies of Giraffe are distinguishable by cranial differences." (p. 202). Lydekker (1911) subsequently named a further blotched giraffe subspecies (*G. c. thornicrofti*) and a subspecies of the reticulated giraffe (effectively creating two subspecies within this species, the nominate subspecies and the newly recognised *G. r. nigrescens*).

Krumbeigel's (1939) work followed Lydekker's (1904 and 1911) classification. Rather than reviewing the validity of Lydekker's subspecies Krumbeigel sought to describe them more adequately using larger sample sizes. His classification recognises a single species with two subspecies. Intrasubspecific groups, previously recognised as subspecies, were recognised by a fourth latinised name. As such Krumbeigel's work is not consistent with the requirements of the ICZN (1999). Krumbeigel's work is noteworthy as he extends Lydekker's subspecies ranges and presents a more realistic range map (figure 2) that has, apparently, remained the basis for contemporary range maps.

Until recently Dagg (1971) was the authority most frequently consulted for the status of giraffe taxonomy. She based her classification on that of Ansell (1968) who provided detailed descriptions of the ranges of each subspecies. Ansell's (1968) classification, in turn, was largely based on Dagg's previous work (Dagg, 1962; 1968) and that of Haltenorth (1962). Ansell (1971, p. 13, in an updated version of his 1968 paper) stated that his list of subspecies "should be regarded as provisional".

East (1999, p. 94) has suggested that "considerable uncertainty surrounds the validity and geographical limits of most of the described subspecies of the giraffe" due to the lack of geographical barriers between supposed subspecies. He suggests instead six "subspecies/subspecies groups" (not given taxonomic trinomials), but states that these groupings are "arbitrary, like other treatments of giraffe subspecies". Grubb (2005) also recognises six subspecies. However, these two authors differ in the demarcation of the ranges of the nominate subspecies; while Grubb (2005) groups the western giraffe (*G. c. peralta*) in *G. c. camelopardalis*, East includes the Rothschild's giraffe with the nominate subspecies. Recently Brown *et al* (2007) have suggested the existence of six full species of giraffe in Africa. Their mitochondrial DNA sequence analyses demonstrate between five and seven geographically defined clades. Reticulated giraffe haplotypes are paraphyletic with respect to a monophyletic sister group pairing of Rothschild's and Western giraffe haplotypes. Reticulated giraffe also demonstrate some female mediated introgression with a Masai haplotype occurring within the clade. The South African giraffe haplotypes are embedded within the Masai clade. Analyses of nuclear data (microsatellite allele frequencies) demonstrate six population groups, with the South African giraffe discrete from the Masai. While this study demonstrates that there is strong genetic structure among giraffe populations, indicating reproductive separation over evolutionary time, and Brown *et al* assert that these population level subdivisions represent species level differentiation, such distinction depends wholly on the species concept used. Interestingly, although also invoking six taxa Brown *et al*'s (2007) conclusions differ from those of both East (1999) and Grubb (2005). At about the same time Hassanin *et al* (2007) published a study of mitochondrial DNA variability in Western and Central African giraffe. They suggest, based on sequence data, that the geographic distributions of the western African giraffe should be adjusted, but they maintain the trinomial nomenclature of the subspecies.

From a taxonomic perspective none of these recent studies do anything to further the classification of giraffe populations as they contain no diagnoses or descriptions of the purported taxa nor any of the required taxonomic discussion. The recent review of ungulate taxonomy by Groves and Grubb (2011) includes eight full species of giraffe, grouped into northern and southern groups (Northern: *G. camelopardalis*, *G. reticulata*, *G. antiquorum* and *G. peralta*).

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Southern: *G. tippelskirchi*, *G. thornicrofti*, *G. giraffa* and *G. angolensis*) though not all of the taxa have full diagnoses and descriptions. Their review does include examination of specimens, though their sample sizes are small for certain taxa, and they find significant overlap in their analyses. Their recognition of eight taxa is somewhat based on novel analyses of morphology and pelage characters, but is largely based on the genetic results of Brown *et al* (2007) and Hassanin *et al* (2007). Their decision to elevate all taxa to species level reflects a philosophical switch, not accepted by all taxonomists, or biologists, to adopt a phylogenetic species concept. Even this treatment, while a welcome addition to the discussion, does not adequately review giraffe taxonomy.

For a century the most complete assessment of giraffe taxonomy remained that of Lydekker (1904), although common use has led to the general acceptance of a single giraffe species containing nine subspecies, following Dagg (1971). However, as this review shows, the giraffe has had a complex taxonomic history. Hence, a re-evaluation of subspecific variation in the giraffe was clearly warranted. My own research (Seymour 2001 and reported in *Giraffa*, Seymour 2007) presented the results of analyses of geographic structure in three complementary data-sets from pelage patterns, morphological data and genetic sequence data from museum specimens gathered all across sub-Saharan Africa, including many areas no longer populated by giraffe. It concluded the probable existence of two species containing six definitive subspecies between them.

Authority	Species	Subspecies
Lydekker, 1904 and Lydekker 1911	<i>G. reticulata</i> <i>G. camelopardalis</i>	<i>G. r. reticulata</i> <i>G. r. nigrescens</i> <i>G. c. camelopardalis</i> * <i>G. c. angolensis</i> <i>G. c. antiquorum</i> <i>G. c. capensis</i> <i>G. c. congoensis</i> <i>G. c. cottoni</i> <i>G. c. peralta</i> <i>G. c. rothschildi</i> <i>G. c. thornicrofti</i> <i>G. c. tippelskirchi</i> <i>G. c. wardi</i>
Dagg, 1971	<i>G. camelopardalis</i>	<i>G. c. camelopardalis</i> <i>G. c. angolensis</i> <i>G. c. antiquorum</i> <i>G. c. cottoni</i> <i>G. c. peralta</i> <i>G. c. reticulata</i> <i>G. c. rothschildi</i> <i>G. c. thornicrofti</i> <i>G. c. tippelskirchi</i>
Seymour, 2001	<i>G. camelopardalis</i> <i>G. giraffa</i>	<i>G. c. camelopardalis</i> <i>G. c. reticulata</i> <i>G. c. rothschildi</i> <i>G. g. giraffa</i> <i>G. c. thornicrofti</i> <i>G. c. tippelskirchi</i>
Brown <i>et al</i> , 2007	<i>G. angolensis</i> <i>G. peralta</i> <i>G. reticulata</i> <i>G. rothschildi</i> <i>G. tippelskirchi</i>	
Groves and Grubb 2011	<i>G. camelopardalis</i> <i>G. angolensis</i> <i>G. antiquorum</i>	

	<i>G. giraffa</i> <i>G. peralta</i> <i>G. reticulata</i> <i>G. thornicrofti</i> <i>G. tippelskirchi</i>	
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Summary of the classifications by five authors. Note that Seymour (2001) did not explicitly name these taxa and maintained *G. c. angolensis*, *G. c. peralta* and *G. c. antiquorum* as provisional subspecies pending examination of further material. Brown *et al's* (2007) classification was based on genetic evidence. They sampled the six taxa shown; other populations were not sampled. * Lydekker's actually used the subspecific name *G. c. typica*. However, current convention repeats the species name for the nominate subspecies.

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Legends for Figures:

Figure 1: Giraffe subspecies ranges according to Lydekker (1904) (Redrawn from Lydekker 1904, text figure 23).

Figure 2: Giraffe subspecies ranges according to Krumbeigel (1939) (Redrawn from Krumbeigel 1939, figure 49. Note that the 'open' ranges of *G. c angolensis* and *G. c reticulata* are as drawn by Krumbeigel).

Figure 3: Giraffe subspecies ranges according to Dagg (1971) (Redrawn from Dagg 1971, figure 3).