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# **The Evolution of the Long-Necked Giraffe (*Giraffa camelopardalis* L.) – What Do We Really Know?**

Part 1 of 2006: <http://www.weloennig.de/Giraffe.pdf>

Part 2 of 2007: <http://www.weloennig.de/GiraffaSecondPartEnglish.pdf>

5 October 2008 some language corrections for Part 2 and a brief comment on Brown et al. 2007: "Extensive population genetic structure in the giraffe" on p. 79 and below.

## **Not One but Six Giraffe Species?**

### **Supplement on the Paper of**

**Brown, D.M., Brenneman, R.A., Koepfli, K.-P., Pollinger, J.P., Milá, B., Georgiadis, N.J., Louis, E.E. Jr., Grether, G.F., Jacobs, D.K. and R.K. Wayne (2007): Extensive Population Genetic Structure in the Giraffe. BMC Biol 5: 57-(69?).**

<http://www.biomedcentral.com/content/pdf/1741-7007-5-57.pdf>

Brown et al. (pp. 63/64, if I counted correctly, - the page numbers on the PDF of the paper are “not for citation puposes”) suggest “that the giraffe might represent more than one species” and that their results and arguments “support viewing the giraffe as containing **multiple distinct species** rather than a single polymorphic form. Reciprocal monophyly in mtDNA sequences and nearly absolute partitioning in microsatellite data support **minimally six species**, corresponding to *Giraffa peralta*, *G. rothschildii*, *G. reticulata*, *G. tippelskirchi*, *G. giraffa*, and *G. angolensis*.” Also, “the Masai might constitute more than one species” and “additional taxa might be defined, pending analysis of the subspecies included in taxonomic schemes (Table 1) not sampled in our study design (e. g. *G. c. antiquorum* [10]). Finally **many of these species appear to include multiple distinct population units that are genetically differentiated.**”

However, if *every genetically (molecularly) differentiated population unit* were finally raised to the status of a species of its own, one might ask, among other things: How great, then, would the number of giraffe species eventually be? (The authors already detected “**at least 11 genetically distinct populations**” (p. 57).) Also, would this not mean that many species could be distinguished from each other only after thorough molecular investigations? (In several cases even members of the same phenotype of the giraffe would have to be assigned to different species. To which of these “species” would the giraffes of your nearest zoo belong to?). Moreover, applying the author’s species concept to humans: How many *species* (“genetically

distinct populations”) could be discriminated – in more than one sense of the verb – among present human beings? For some mistakes of the past, see please <http://www.weloennig.de/AesII.Me.html> .

Yet, as we have seen in detail above (p. 55), most probably all the giraffe “species” can mate and produce fertile hybrids. And “forms which, in all characters, follow the Mendelian laws upon reciprocal crossings have to be viewed as varieties of the same species” (De Vries in agreement with almost all classical Mendelian geneticists up to the present; see <http://www.weloennig.de/Artbegriff.html>, 622 pp., especially <http://www.weloennig.de/AesIV3.html>). Thus, there is **only one species, *Giraffa camelopardalis*, with many subspecies** (and, interestingly, even with molecularly defined populations within these subspecies; Richard Goldschmidt would possibly call them “subsubspecies”, see <http://www.weloennig.de/AesIV2.A.3.Ka.html>).

Let me supplement the list of p. 55 by also quoting the hybridizations mentioned by Ingo Krumbiegel 1971, p. 65 (according to Fig. 41; subspecies on the left here not always the female parent):

Southern subspecies *Giraffa camelopardalis tippelskirchi* X *Giraffa camelopardalis reticulata* (Northern subspecies)  
 Southern subspecies *Giraffa camelopardalis tippelskirchi* X *Giraffa camelopardalis camelopardalis* (Northern subsp.)  
 Southern subspecies *Giraffa camelopardalis tippelskirchi* X *Giraffa camelopardalis antiquorum* (Northern subspecies)  
 Southern subspecies *Giraffa camelopardalis tippelskirchi* X *Giraffa camelopardalis peralta* (Northern subspecies)  
 Southern subspecies *Giraffa camelopardalis capensis* X *Giraffa camelopardalis antiquorum* (Northern subspecies)  
 Northern subspecies *Giraffa camelopardalis rothschildi* X *Giraffa camelopardalis peralta* (Northern subspecies)  
 Northern subspecies *Giraffa camelopardalis congolensis* X *Giraffa camelopardalis peralta* (Northern subspecies)  
 Northern subspecies *Giraffa camelopardalis peralta* X *Giraffa camelopardalis reticulata* (Northern subspecies)

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[**Insertion from p. 55:** “All the „species“ of the extant genus *Giraffa* can cross-breed. Gray, in her work *Mammalian Hybrids* (1971, pp. 148/149) lists the following examples:

„Family GIRAFFIDAE [Giraffes]

### **Giraffa** Brisson

478. *Giraffa camelopardalis angolensis* Lydekker [Angola Giraffe]  
 x *Giraffa camelopardalis tippelskirchi* Matschie [Masai or Kilimanjaro Giraffe]  
 A hybrid was born in Berlin Zoo in 1962.  
*International Zoo Yearbook* 1963.
479. *Giraffa camelopardalis antiquorum* Jardine [Kordofan Giraffe]  
 x *Giraffa camelopardalis camelopardalis* Linnaeus [Nubian Giraffe]  
 Hybridization occurred at Fort Worth, U.S.A., in 1962.  
*International Zoo Yearbook* 1963.
480. *Giraffa camelopardalis camelopardalis* Linnaeus [Nubian Giraffe]  
 x *Giraffa camelopardalis antiquorum* Jardine [Kordofan Giraffe]  
 See No. 479. x *Giraffa camelopardalis reticulata* De Winton [Reticulated Giraffe]  
 Hybrids (at least one a female) have been born in zoos in Vienna (Austria) and Honolulu (U.S.A.).  
*International Zoo Yearbook* 1967, 19680, 1970.

481. *Giraffa camelopardalis cottoni* Lydekker [Cotton's Giraffe]  
 x *Giraffa camelopardalis reticulata* De Winton [Reticulated Giraffe]  
 A hybrid was born at Whipsnade Park (Great Britain) in 1961.  
*International Zoo Yearbook* 1962; Matthews, L. H. 1961, 1963.
482. *Giraffa camelopardalis reticulata* De Winton [Reticulated Giraffe]  
 x *Giraffa camelopardalis camelopardalis* Linnaeus [Nubian Giraffe]  
 See No. 480.  
 x *Giraffa camelopardalis cottoni* Lydekker [Cotton's Giraffe]  
 See No. 481.  
 x *Giraffa camelopardalis rothschildi* Lydekker [Baringo Giraffe]  
 A stillborn hybrid was produced in San Diego Zoological Garden in the 1940's.  
 Dolan, J. M. 1971.  
 x *Giraffa camelopardalis tippelskirchi* Matschie [Masai or Kilimanjaro Giraffe]  
 Male hybrids were born at Dudley (Great Britain) in 1967 and 1969, and also at  
 Sacramento (U.S.A.) in 1968.  
*International Zoo Yearbook* 1969, 1970, 1971.
483. *Giraffa camelopardalis rothschildi* Lydekker [Baringo Giraffe]  
 x *Giraffa camelopardalis reticulata* De Winton [Reticulated Giraffe] See No. 482.
484. *Giraffa camelopardalis tippelskirchi* Matschie [Masai or Kilimanjaro Giraffe]  
 x *Giraffa camelopardalis angolensis* Lydekker [Angola Giraffe]  
 See No. 478.  
 x *Giraffa camelopardalis reticulata* De Winton [Reticulated Giraffe] See No. 482.”

“Hybrids of the giraffe also occur between different subspecies in the wild in border areas and hybrids [of subspecies] are also known among other cloven-hooved animals (R u x t on [and] S c h w a r z [1929])“ – See Krumbiegel p. 64, who continues with a list of examples, too. However, in contrast to these authors, Brown et al. (2007) suggest that there are at least 6 *Giraffa* species (if not many more): see my objections in the brief note in the references p. 79 [and below].”

– **End of insertion from p. 55.**]

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The main reason of the Brown et al. to split *Giraffa camelopardalis* into several species is the rather strong reproductive isolation which they seem to have found in the giraffe populations *in the wild*: “...our results indicate that neighbouring subspecies as well as those that are geographically separated are essentially reproductively isolated, suggesting that some might represent distinct species rather than a single polytypic form” (p. 64).

The authors have to admit, however, that “hybridization in the wild has been reported for some subspecies (e.g., Masai and reticulated giraffes [2]” (p. 61) and that there are suggestions “that hybridization occurs frequently among giraffe subspecies” (p. 63), yet their data so far detected show only that such events seem to be quite rare (according to their microsatellite data in 3 of 381 sampled individuals).

Dagg and Foster write (1976/1982, p. 156 and p. 158): “The reticulated giraffe was

regarded as a separate species until recently, although **many transitional individuals** between the reticulated and blotched giraffe have been recorded **both in captivity and in the wild** (see Krumbiegel, 1951).”...”The range of *G. c. rothschildi* is uncertain, as it is bounded on most sides by ranges of **neighboring races which intergrade with it**, and it has decreased greatly in recent years.”

On the basis of such records, the question may be raised whether the molecular basis and sample collection of Brown et al. were sufficient and specific enough to substantiate their far-reaching taxonomic inferences, even if only for a doubtful evolutionary species concept (these points could constitute the topic of a discussion of its own). Incidentally, I think that the authors should better speak of “**micro**evolutionary significant units” instead of “evolutionary significant units” (pertaining to the genetically differentiated populations).

Especially interesting in this connection are their calculations for the divergence times (p. 60):

“Divergence times between the seven clades obtained from coalescence analysis [19] ranged from 0.13–0.37 million years (MY) between Masai and South African clades, to **0.54–1.62 MY** between the southern clade (Masai, Angolan and South African giraffes) and the northern clade (West African, Rothschild's and reticulated giraffes) (Table 2). Values for the northern giraffe grouping were intermediate, with West African and Rothschild's giraffes diverging about 0.16–0.46 MY ago, and the two splitting from reticulated giraffes about 0.18–0.54 MY ago. These dates argue for a mid to late Pleistocene radiation of giraffes.”

Now, let us extrapolate from the values of up to 1.62 million years, as found for the microevolutionary divergence on the morphological, anatomical and physiological levels between the southern and the northern clade, to the time necessary for the evolution of the enormous differences between the long-necked and short-necked giraffes or even to all the (mega-)differences within the entire giraffe family. As a first educated guess I would say that we could possibly approach the Cambrian period some 544 million years ago. Of course, I am most certainly not the first author who thus concludes that there must be a **fundamental difference between micro- and macroevolution** (see, for example, the authors quoted by Junker 2006 [http://www.genesisnet.info/pdfs/Mikroevolution\\_Makroevolution.pdf](http://www.genesisnet.info/pdfs/Mikroevolution_Makroevolution.pdf), and 2008 <http://www.genesisnet.info/pdfs/Evo-Devo.pdf> as well as Lönnig et al. 2007 <http://www.weloennig.de/Dollo-1a.pdf>).

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