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The Evolution of the Long-Necked Giraffe
(*Giraffa camelopardalis* L.)
What do we really know?
Summary of Part 2 and
Appendix on Cameron & du Toit (2007): "Winning by a Neck: Tall Giraffes Avoid Competing With Shorter Browsers"

As for **Part 1**, see http://www.weloennig.de/Giraffe.pdf
And for the Entire **Part 2**, see http://www.weloennig.de/GiraffaSecondPartEnglish.pdf

Some Questions, Facts and Quotations to Supplement Part 1
Repetitio est mater studiorum –Repetition is the best teacher (literally: the mother of studies)

Summary

Introduction: the story which is commonly taught in high schools about the evolution of the long-necked giraffe by natural selection (*feeding-competition*-hypothesis) fails to explain, among other things, the size differences between males and females. Giraffe cows are up to 1.5 meters shorter than the giraffe bulls, not to mention the offspring. The wide migration range of the giraffe and the low heights of the most common plants in their diet likewise argue against the dominant selection hypothesis. Now to the main points: 1) The fossil „links", which according to the theory should appear successively and replace each other, usually exist simultaneously for long periods of time. 2) Evolutionary derivations based on similarities rely on circular reasoning (to refer once more to Kuhn's statement) 3) The giraffe has eight cervical vertebrae. Although the 8th vertebra displays almost all the characteristics of a neck vertebra, as an exception to the rule the first rib pair is attached there. 4) The origin of the long-necked giraffe by a macromutation is, due to the many synorganized structures, extremely improbable. 5) Sexual selection also lacks a mutational basis and, what is more, is frequently in conflict with natural selection („head clubbing" is probably „a consequence of a long neck and not a cause"). 6) In contrast to the thus-far proposed naturalistic hypotheses, the intelligent design theory is basically testable. 7) The long-necked giraffes possibly all belong to the same basic type inasmuch as 8) a gradual evolution from the short-necked to the long-necked giraffe is ruled out by the duplication of a neck vertebra and the loss of a thoracic vertebra. 9) Chance mutations are principally not sufficient to explain the origin of the long-necked giraffe. 10) The intelligent design theory offers an adequate and satisfying solution to the problems and points to numerous „old" and new research projects. 11) Mitchell and Skinner present a good analysis of the selectionist problem; however, their phylogenetic hypotheses presuppose the correctness of the synthetic evolutionary theory, and their claims of „*intermediate forms*" are unproven.

14.   Appendix (27 October 2007, page numbers in text refer to the original paper http://www.weloennig.de/GiraffaSecondPartEnglish.pdf)

A Note on the Paper by **Elissa Z. Cameron and Johan T. du Toit (2007): "Winning by a Neck: Tall Giraffes Avoid Competing with Shorter Browsers."** *The American Naturalist* **169***: 130-135.*

The authors assert in their abstract (p. 130) that their findings provide "the first experimental support for the classic evolutionary hypothesis that vertical elongation of

the giraffe body is an outcome of competition within the browsing ungulate guild."

Accordingly, the paper has been celebrated as the neo-Darwinian solution to the problems of the origin of the giraffe by natural selection in the popular press and elsewhere (for some examples see the links below) – as if all questions have now been answered in agreement with the dictum that "all of biology rests on the foundation of neo-Darwinism, drawing on the principles of population biology and molecular genetics" (G. T. Joyce in *Nature* **346**, p. 806, 1990). However, **the article does not address any of the key problems** discussed at length in our two papers (2006, 2007) on *The Evolution of Long-Necked Giraffe* (*Giraffa camelopardalis*) - *What do we really know?*

First to mention some details (not to criticize the authors Cameron and du Toit on the majority of the following points, but their readers and commentators who, in their enthusiasm for Darwin and natural selection, seem to have overlooked the fact that the writers did not speak about the following topics):

1. The paper by Cameron and du Toit does not address any of the problems presented by the fossil record (see Part 1 and several chapters and notes of Part 2 above, especially pp. 6-10, 23-24, 33-47, 50-51, 54, 58-61)

2. It does not address any of the problems that natural selection has to explain concerning the prominent sexual dimorphism of *Giraffa camelopardalis*, not to mention the special requirements of young animals (see summary and introduction above as well as pp. 20-22, 29-32, 62).

3. It does not address any of the anatomical or physiological questions and problems discussed in detail in our two papers. No word on the number of vertebrae (see pp. 13-18 above), no word on synorganization or coadaptation (Part 1, pp. 4, 8-10, 23-24, Part 2, pp. 18-20, 26, 52-54, 65, 66, 69, 70, 75, 77). No word on the points addressed on p. 26 of this paper (to repeat):

(a) the duplication of a neck vertebra, as well as the many related specific anatomical structures discussed above by Solounias… (b) the especially muscular esophagus (ruminator), (c) the various adaptations of the heart, (d) the muscular arteries, (e) the complicated system of valves, (f) the special structures of the *rete mirabile* (system of blood-storing arteries at the brain base), (g) the „coordinated system of blood pressure controls" (for, among other things, the enormously high blood pressure), … (h) „The capillaries that reach the surface are extremely small, and (i) the red blood cells are about one-third the size of their human counterparts, making capillary passage possible"; (j) the precisely coordinated lengths, strengths and functionality of the skeletal, muscular and nervous systems; (k) the efficient „large lungs" (l) „the thick skin, which is tightly stretched over the body and which functions like the anti-gravity suit worn by pilots of fast aircraft".

4. Moreover, the paper by Cameron and du Toit does not address any of the genetic questions, i.e. random 'macromutations' vs. an almost infinite number of accidental 'micromutations' (pp. 18-20, 25-27).

5. Apart from the missing question of sexual dimorphism, neither does the article address the essential problem of the theory of natural selection for the origin of the giraffes in general: i.e. the behaviour of the giraffe and "the survival of the fittest" *under extreme food shortages,* especially with regard to the young animals again (remember Mitchell and Skinner quoted p. 29 of the present paper):

"While dependence on leguminous browse seems essential, the idea that tallness enables **exploitation of**

food sources that are beyond the reach of competitors such as bovids, **is unlikely to be true**. Pincher (1949) made one of the first objections to this hypothesis. He indicated that a **Darwinian dearth** severe, long-lasting enough, and/or frequent enough for natural selection to operate to produce a long neck, would cause the recurrent wastage of young giraffes, and **would thus lead to extinction of the species rather than its evolution**.”

So, then, which problems do Cameron and du Toit actually address? We read on p. 130:

“The problem was that no study had been designed to explicitly test whether giraffes achieve a foraging advantage by foraging above the reach of smaller browsers.”

(That is, under normal conditions including dry seasons, yet not extreme “Darwinian dearths”) – What did they do to solve the problem posed for such normal conditions?

“We erected exclosures around individual *Acacia nigrescens* trees in the greater Kruger ecosystem, South Africa. After a complete growing season, we found no differences in leaf biomass per shoot across height zones in excluded trees but significant differences in control trees.”

Their inference:

“We conclude that giraffes preferentially browse at high levels in the canopy to avoid competition with smaller browsers.”

Joe Bowman, staff writer of the *Deseret Morning News* (Salt Lake City), wrote a favourable comment on the work of Cameron and du Toit and published the following photograph (by du Toit) for illustration with the accompanying text as quoted below:
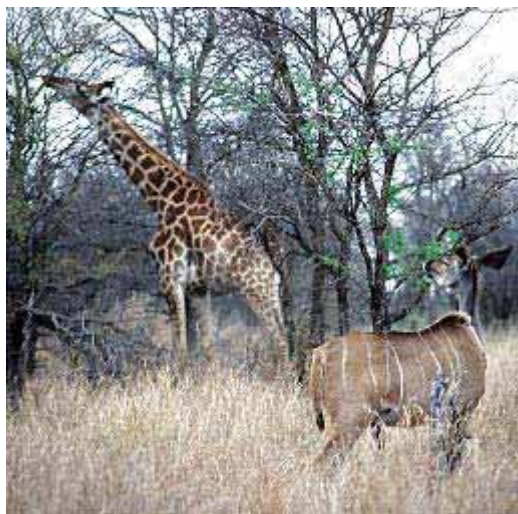
“Giraffes feeding efficiency is reduced at low heights” because of competition with smaller animals such as the kudu, a study finds.
(Johan du Toit)
http://deseretnews.com/dn/view/1,1249,650224911,00.html

For the argument’s sake let’s first assume that the procedures, experiments and inferences of the paper by Cameron and du Toit are correct. Would this *prove* that the long-necked giraffe originated by selection of random mutations in a series of severe, long-lasting (and frequent enough) Darwinian dearths? Would it explain the prominent sexual dimorphism and (an almost preferential) survival of the young ones? Would it throw light on the question how all the complex anatomical and physiological synorganizations (as repeated under point 3.) just happened

accidentally at the time when needed? Would it decide the question, whether an almost infinite number of naturally selected random 'micromutations' were the genetic cause or just one or a few accidental 'macromutations' (not to mention ID in this context)? The intelligent reader will give the correct answers.

Young giraffe getting forage at corresponding height in Cologne Zoo.
Picture by W.-E.L. (9 June 2007, 15.00; young giraffe born 8 March 2007)

Now, as to the dry seasons Simmons and Scheepers had noted (see p. 6 above):

"…we find that during the dry season (when feeding competition should be most intense) giraffes **generally feed from low shrubs**, not tall trees; females spend over 50% of their time feeding with their necks horizontal; both sexes feed faster and most often with their necks bent; and other sympatric browsers show little foraging height partitioning. Each result suggests that long necks did not evolve specifically for feeding at higher levels."

Concerning the Giraffe's behaviour during those dry seasons, see also the long quotation on p. 49 of the present paper, where Simmons and Scheepers mention the following observations (to repeat in abbreviated form):

(1) In the Serengeti "giraffes spend almost all of the dry-season feeding from low Grewia bushes" ("…contrary to the prediction that giraffe should use their feeding height advantage at times of food scarcity.") (2) Concerning *all* browsing, about 50% is below 2 m in the Tsavo National Park "within reach of potential competitors such as gerenuk *Litocranius walleri* and lesser kudu *Tragelaphus imberbis* (Leuthold and Leuthold 1972)." And "during the dry season, 37% of the browse taken by giraffe was below 2 m." (3) "Giraffe were not avoiding interspecific competition by selecting different food plants (the third prediction): considerable (unquantified) overlap was apparent between giraffe and sympatric browsers in Tsavo (Leuthold and Leuthold 1972)."

Interestingly, according to Simmons and Scheepers "it was only in South Africa were giraffe found to allocate 90% of their time to feeding above the average feeding height of browsers such as kudu *Traxelphus strepsiceros* (1,0 m) and impala *Aepyceros melampus* (ca. 0.3 m; du Toit 1990), but lower than their long necks allow (5-6 m)." – *So Cameron's and du Toit's observations appear to be the exception from the rule mentioned by Simmons and Scheepers.* But even in this case the following points have to be considered:

"In each study both sexes frequently fed at or below shoulder height (ca. 3.1 m and 2.8 m for adult males and females; L. Scheepers, unpublished data). For example, female giraffe spent over 50% of the time feeding with their necks at or below shoulder height in both South Africa (du Toit 1990) and Kenya (Young and Isbell 1991), contrary to the second prediction."… "…only dominant bulls regularly fed at 5.0 m or more in both South and Eastern Africa" (see p. 49 of the present paper).

Coming back to the figure of the Giraffe and the Kudu presented by Bowman/du Toit above, it could be interpreted to be a "dominant bull" feeding at 5.0 m or more. Now add to the picture a female (feeding with its neck at or below shoulder height, like on the left, photo by W.-E.L.) and being anyway 1 to 1.5 m shorter than the bull and projecting also a young one of about 2 m height into the figure (right), you'll get about the following result:
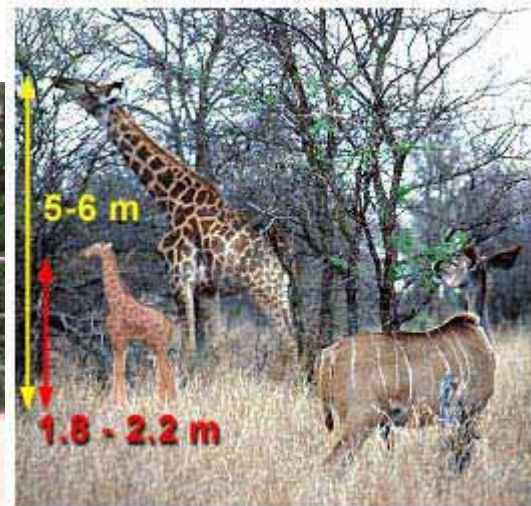
Moreover, the hypothesis of "depletion of higher-quality plant parts by smaller browsers" (Cameron/du Toit, p. 131) appears to be doubtful already from a look at the original figure shown on p. 64 above: Are we really to assume that the entire range of higher-quality plant parts below the giraffe's stretched-out neck and head (of the photograph on the right) has already been depleted by smaller browsers? But if so, why and how do the young ones and female giraffes keep on living? – Yet, if I interpret the photograph correctly, there is enough to browse for the smaller browsers as well as the larger ones and there is hardly any depletion of the lower plant layers, which would drive "giraffes to forage higher in the canopy, thereby supporting the competition hypothesis, paralleling results from the grazing guilt" (also p. 131). And looking at the following photographs (left and middle from South Africa, right from Namibia; see links to sources below) the depletion and competition hypothesis may appear even more unconvincing:

See references for the photographs at the end of the appendix under (1), (2), and (3).

See references for the photographs at the end of the appendix under (4), and (5).

Photographs of Kudus (above) and Giraffes (below) on this page were also taken from South Africa by different photographers (see again sources at the end of the appendix). Of course, one should check whether the plant species shown belong to diet of ca. 70 plant species of giraffes (in South Africa), Kudus and other browsers. Nevertheless, as long as there is a sufficient food supply even under dry conditions, one may doubt the depletion and competition hypothesis. Yet under a series of severe Darwinian dearths the young giraffes would be heavily affected, too.

It may also be worthwhile to remember in this connection the long distance movements of giraffes (for the details see pp. 4 und 5 above).

See references for the photographs at the end of the appendix under (6), (7), and (8).

As to the photographs of the giraffes above one may note that concerning the left one the words of Dagg and Foster for the young animals may apply: "…they supplement the milk with solids at about one month. Perhaps they need relatively little milk because of the high nutritional value of the acacia tips they eat" – see full quotation on p. 3 above). Anyway, the young animals would starve to death if they had to avoid "competition" with Kudus able to browse up to a height of 2.5 m. The photographs in the middle and on the right show examples where the giraffes are larger than the plants surrounding them in KNP (remember that in the Serengeti "giraffes spend almost all of the dry-season feeding from low Grewia bushes").

Let's return to the experiment of Cameron and du Toit. They explain their method as follows (2007, p. 131):

> "Fences excluding smaller browsers were built and maintained for a growing season at a savanna site in South Africa with an intact guild of indigenous browsing ungulates."…

> "We constructed fences around individual *A. nigrescens* trees in November 2001. Nine exclosure plots were created by selecting trees that were taller than 4 m and had branches throughout their height range. We constructed fences 2.2 m in height, l m from the outside canopy branches. Therefore, we excluded all small browsers and partially excluded larger browsers, except giraffes, who could freely forage at heights above 2.2 m. … Each excluded tree was paired with the nearest unfenced (control) tree within 10 m that met the same selection criteria (at least 4 m tall with branches at all potential foraging heights)."

So the authors *excluded not only the smaller browsers from the trees but also the giraffes, the young ones as well as the adult female and male animals, from browsing below 2.2 m*.

For Kruger National Park (KNP), South Africa, du Toit and co-workers report (2006, p. 249) that "Giraffe browsing range was observed to be PH2 and PH3 (*c.* **1.7-5.1 m**)" for *Acacia nigrescens*. And, as can be concluded from Figure 1 of du Toit (1990, p. 58), even in KNP giraffe allocated *more than 10%* of feeding time 'at the height ranges of kudu, impala, and steenbok', that is *below 1.7 m* (or from the ground up to 1.7 m). Moreover, du Toit himself notes (p. 59) that "giraffe are also quite capable of feeding at lower levels though, so even this separation [between giraffe and the other browsers] is not always complete. For example, in Tsavo East National Park, Kenya, giraffe have been found to allocate about 50% of feeding time to browsing below a height of 2 m (Leitholt & Leuthold, 1972)". Similar observations have been made by Ginnett and Demment (1997, 1999) in Mikumi National Park, Tanzania.
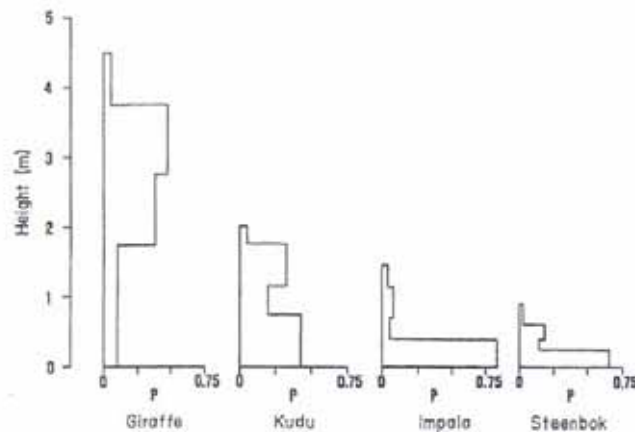

Figure 1 from du Toit for the central region of KNP (1990, p. 58): 'Proportions (P) of feeding time allocated to height classes, which correspond to the four neck angle classes [45°, 90°, 135° and 180° respectively] for each browser species, calculated over the complete seasonal cycle.'

Also, the African savanna biome comprises more then 46 ungulate species. Though a majority of them are grazers and some are both, grazers and browsers, there are many more browsers than the 4 species mentioned above (by the way, the giraffe is grazing a bit, too, for example on the *Tribulus zeyheri*, an annual forb [belonging to the low-growing Zygophyllaceae], "which constitutes a moderately important forage source for giraffe during the wet season (**9% of its diet**)" in northwestern Namibia; Fennessy 2004, p. 207). For a photograph of the plant, see for example http://www.biologis.de/photo/botanik/fenster/art/bild_th/tribulus_zeyheri0040tt.html .

Thus, the findings of Cameron and du Toit from KNP can neither be generalized for all of parts of Africa where giraffes occur today nor can they be correct for their area of investigation as long as giraffes are fully excluded from browsing below 2.2 m, since usually giraffes may eat a not inconsiderable amount of plant material even below 1.7 m in more than 10% of their feeding time.

A few lines downstream of *Winning by a Neck* (2007, p. 131) Cameron and du Toit define the giraffe browse unit as follows:

> "For sampling forage availability, we used a previously defined giraffe browse unit (GBU). The GBU is equivalent to the average twig pruned or leaf stripped by a giraffe in a single bite, which for *A. nigrescens* is 144 mm long (Woolnough and du Toit 2001). The GBU thus incorporates the smallest bites of steenboks, impalas, and kudus and provides a measure of biomass return per bite, reflecting both foliage depletion and foraging efficiency."

And before this definition the authors write:

> "Experimental and control trees were sampled before fencing and again in the early dry season (July 2003) after two complete growing seasons. We defined three levels for sampling available browse: l m (available to steenboks, impalas, kudus, and giraffes), 2.5 m (available for kudus and giraffes), and 4 m (available only to giraffes). At each height level, we recorded the presence of recent browsing of shoot ends on a presence/absence basis for 10 randomly selected shoots around the canopy. This provided a proportional index of browsing intensity up and down the canopy (du Toit et al. 1990)."

I have to admit that I am not yet fully persuaded to accept the "10 randomly selected shoots around the canopy", for this "random selection" method is not convincingly explained.

> "We calculated the difference in leaf biomass from prefencing to postfencing two growing seasons later. Two experimental trees were excluded from the final analysis because of elephant damage."

So, apart from the difficulties just mentioned, eventually the authors had seven trees ("enclosure plots") for further evaluation – not too strong a basis for sweeping inferences on the origin of species with so many varying random factors all around (which control tree and enclosure plot is visited by how many individuals of which animal species of which gender how many times? – One can hardly assume that all seven cases were simply equal).

Now let's have a closer look at their results (p. 132):

> "Before fencing, our results confirm the findings of previous research. There was a significant difference in forage availability at the different heights, with less browse per GBU low in the tree and more at heights available only to giraffes (ANOVA, $F = 9.20$, df $= 2,51$, $P < .0005$)."

The difference in biomass per GBU was about 1 g (dry mass) less at 1 m in the controls and an inverse ½ g at 2.5 m according to their Figure 1 (however, the authors assert that the unexpected difference of <u>less</u> biomass in the experimental trees in the exclosures at 2.5 m as compared to the controls was statistically insignificant).
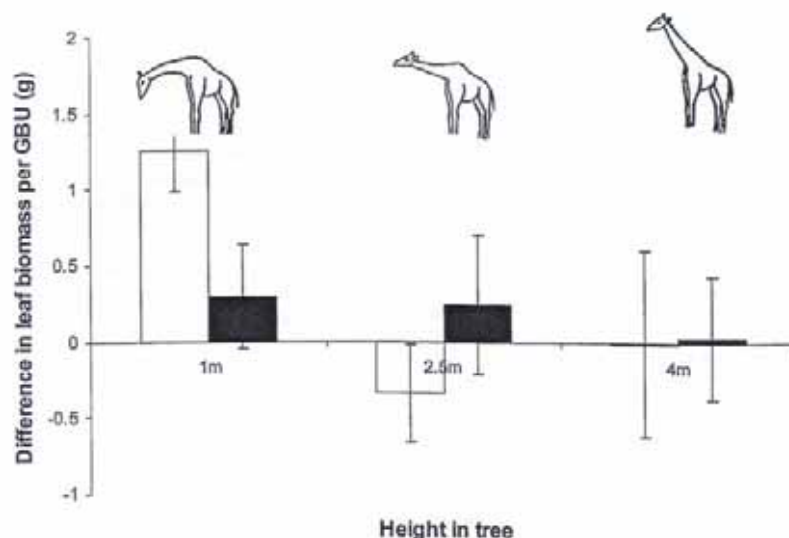

Figure 1 of Cameron and du Toit (2007): "Difference in leaf biomass per giraffe browse unit *(GBU)* between prefencing and two growing seasons after the erection of exclosures around experimental trees. Open bars are excluded trees; filled bars are control trees. Schematic giraffes indicate the posture of an adult female when browsing at each height."

Nevertheless, I have to admit that I have some problems to match their results for 2.5 m as shown in Figure 1 with those of the same height in Figure 2 A:
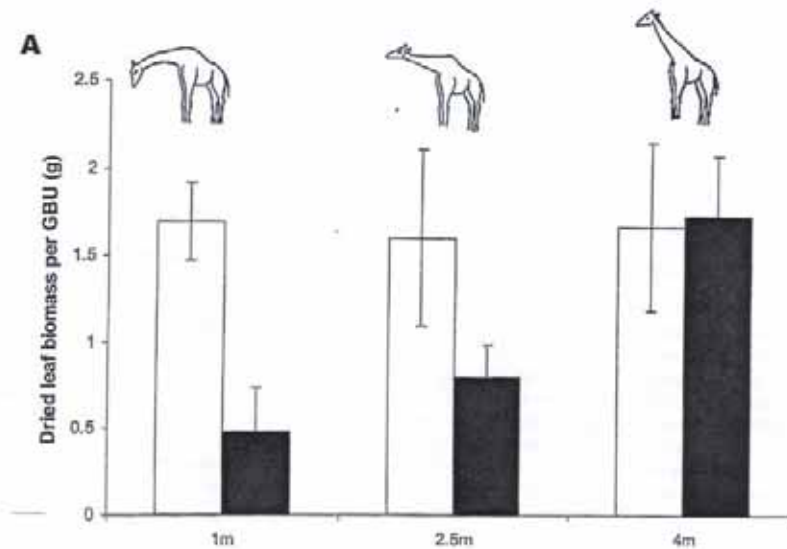

Figure 2A of Cameron and du Toit: Leaf biomass per giraffe browsing unit (GBU). Open bars are again excluded trees; filled bars the control trees and – as in Figure 1 – the "schematic giraffes indicate the posture of an adult female when browsing at each height".

Possibly this is simply an artifact of the non-significant statistical results.

The differences per GBU may perhaps be relevant at the brink of starvation (with the unfortunate young ones dying first). But is it really a question of life and death and the survival of the fittest in a normal situation with still enough forage all around? Also, it has to be considered that GBU varies strongly depending on the plant species browsed and that there are differences of bite size between the sexes ("because IWP [average within-patch dry-matter intake rate] is positively related to bite mass, males could increase IWP and thereby shorten feeding times by taking larger bites than females" and there was "significant variation across forage species" – Ginnett and Demment 1997, pp. 297/298 and 295).

Yet probably the more important question continues to be: ***to what extent do the giraffes themselves contribute to the depletion*** found by Cameron and du Toit? The figures of the authors reproduced above clearly show that female giraffes do browse at a height of 1 m.

On p. 131 the authors had stated:

> "Giraffes gain a nutritional advantage by foraging above the height of the other species, as they receive more biomass per bite higher in the canopy (Woolnough and du Toit 2001)."

Prima facie this seems to be obvious. But again: granted that animals are the main cause for the depletion, the author's experiments cannot solve the question as to what extent exactly the giraffes themselves (especially the juvenile and the female ones) are responsible for the reduced biomass *at* the height of other species. *In fact, the experiment has even excluded the solution of this question.*

Yes, as the authors stated, giraffes "could freely forage at heights above 2.2 m",

but hardly below – and this seems to be the decisive weakness of their method concerning feeding competition. *All* animals are excluded: steenboks, impalas, kudus and others, **and giraffes**. In order to forage below 2.2 m, the giraffes would have had to bend their necks down over the fences for food whilst the same high-quality food was just before their mouths and all around their heads without any bending over the fences at all. And, as expected, the animals did not display such a curious behaviour.
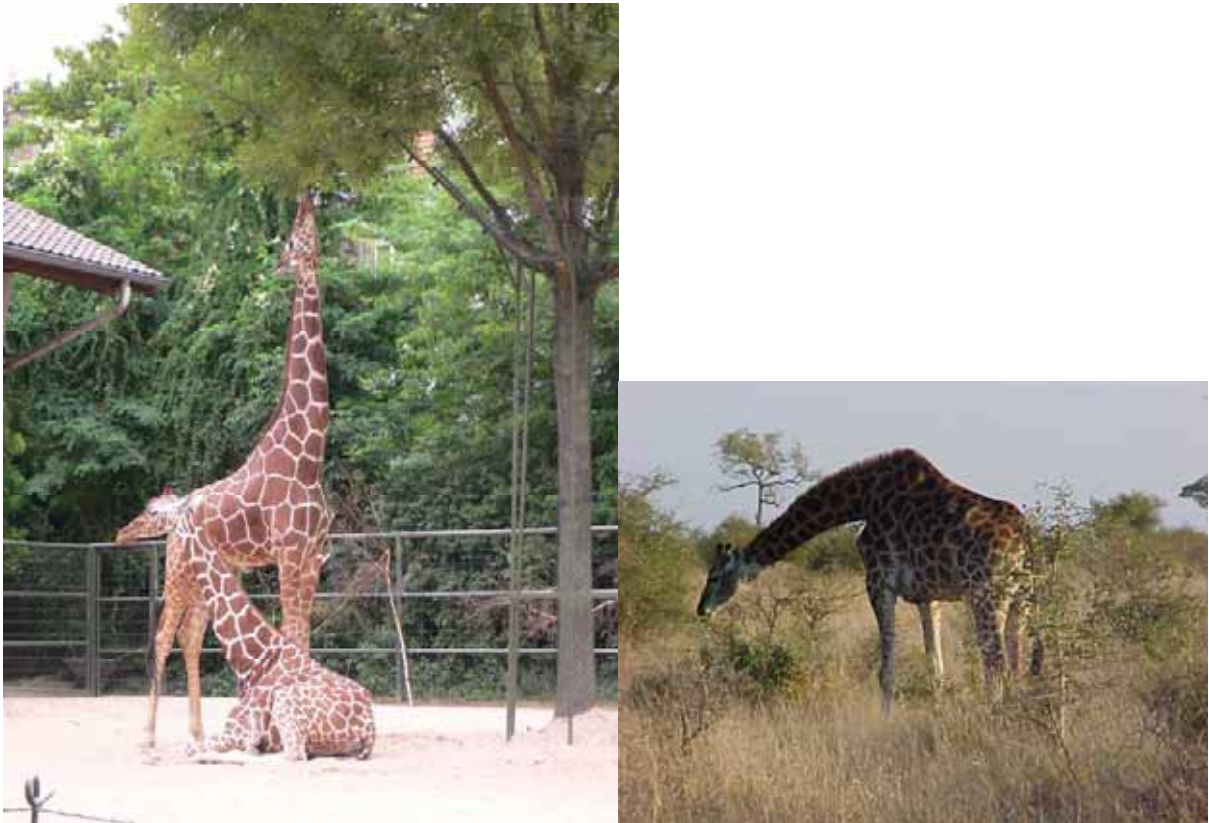
The tree on the right side of the left photograph is fenced around up to a height of ca. 5 m because giraffes also eat 'everything' below (photo by W.-E.L. 9 June 2007 at Cologne Zoo). Giraffe on the right from Kruger National Park according to http://www.satowns.co.za/Photo%20Library/kruger/Giraffe%205.jpg. On 3 October 2007 I asked Prof. Cameron for some photos or links to photos of their enclosures in KNP, South Africa. So far she did not answer.

Cameron and du Toit continue on p. 131:

> "This suggests that the depletion of higher-quality plant parts by smaller browsers drives giraffes to forage higher in the canopy, thereby supporting the competition hypothesis, paralleling results from the grazing guild (Illius and Gordon 1987; Murray and Illius 2000)."

As long as the giraffes themselves are debarred, this suggests hardly anything. Moreover, one could as well argue that the depletion of higher-quality plant parts also *drives the smaller browsers to forage perpetually higher and higher in the canopy transforming them into giraffe-like animals in the long run*.

One of the basic problems with natural selection, however, is that – to illustrate – it only acts like a sieve which selects (screens) tea leaves from a certain size onwards

but, of course, *sieves never create the tea leaves* themselves (for a detailed discussion on the limits of natural selection, see http://www.weloennig.de/NaturalSelection.html.). Hence, it is necessary to clearly distinguish between selection and the rich but limited genetic potential for phenotypic variations of any species (the range of 'tea leaves', so to speak, that it can offer for survival to the sieve of natural selection). So for the smaller browsers this definitely means that phenotypic variation is limited too. Moreover, whatever 'selection pressure' may exist, one may safely predict it will never transform them into 6 m tall animals at all. And naturally this was true for the past as well.

Let's return to the authors' results (p. 132). After stating the initial condition as follows:

> "There was no significant difference between control and treatment trees at any height. The patterns for recent foraging were more ambiguous, with no significant difference in foraging with tree height and no difference between control and treatment trees."

– Cameron and du Toit continue to report:

> "There was a significant difference from pre- to post-fencing between control and excluded trees at l m (paired *t*-test, $t = 2.62$, $P = .03$). At 2.5 m, the pattern looked similar (fig. 2) but was not significant (paired *t*-test, $t = 1.30$, $P = .24$), and there was no difference at 4 m (paired *t*-test, $t = 0.07$, $P = .95$; fig. 1). In addition, there was a significant difference in forage availability at l m between excluded and control trees $(t = 3.60, P < .005)$ but not at 2.5 m $(t = 1.48, P = .16)$ or 4 m $(t = 0.10, P = .92)$. After fencing, there was still a significant difference in forage availability by height for the control (unfenced) trees, with less forage available at l and 2.5 m and significantly more at 4 m (ANOVA, F = 5.54, df = 2,22, P < .01; fig. 2). However, there was no significant difference in forage availability for the excluded trees (ANOVA, $F = 0.01$, df = 2,22, P = .98)."

Thus, the result of their investigations was (not unexpected):

> "Our recently browsed shoot data confirmed that we had successfully excluded foragers at low foraging heights; no shoots were foraged on excluded trees at l m (fig. 2). Because fences were 2.2 m high, we reduced but did not eliminate foraging at 2.5 m."

So what does this prove concerning the evolution of the giraffe in the authors' view? First, they maintain:

> "Our study confirms that there are differences in browsing intensity with foraging height in an intact browsing guild…"

This seems to be almost self-evident and I tend to accept it. Yet apart from the many weak points already mentioned above, for this generalization the authors seem to have overlooked that they have investigated *just 7 individuals (of thousands) of only 1 plant species out of about 100 different ones*, which are eaten by giraffes under different ecological and environmental conditions (see pp. 4 and 5 of the present paper and the further links below on South Africa). Moreover, in agreement with Ginnet and Demment quoted above, Woolnough and du Toit have shown in 2001 that the results can vary strongly for different plant species (p. 588):

> "For *A. nigrescens* we found that browsing intensity (% shoot ends freshly browsed) increased significantly across browsing heights as a function of leaf dry mass/GBU (P<0.005), although there was no significant relationship between browsing intensity and leaf biomass within any browsing height (Fig. 1). **No similar trends were found for B. [Boscia] albitrunca, however, probably because giraffes tend to leaf-strip the non-spinescent B. albitrunca shoots more frequently than they prune them.**"

And on p. 589 we read:

"The generality of this pattern [browsing intensity increases with height] could vary depending on the composition of the browsing guild and the browse resources available. For example, **Ginnett and Demment (1997, 1999) found no significant variation in intake rate (g/min) across the 0- to 3-m feeding-height range for giraffes in Tanzania, but these were feeding mainly on trees that did not include *Acacia* species.**"

Moreover (p. 586):

"From a pilot study of twigs recently browsed by giraffes, the mean GBU was **144 mm ... for *A. nigrescens* and 89.5 mm ... for *B. albitrunca*,** reflecting the different leaf and twig morphologies of the two species."

These observations corroborate the conclusion that one ***cannot*** simply generalize the results from *Acacia nigrescens* – important as it is – to all plant species eaten by the giraffes. Yet this is what the authors continually do.

Cameron and du Toit continue (2007, p. 132):

"…and that browsing pressure across feeding heights is associated with the available leaf biomass per bite for browsers (Woolnough and du Toit 2001)."

One may doubt whether there is any "browsing *pressure*" at all as long as there is enough forage for all the browsers. Incidentally, in the late dry season in *A. nigrescens* as well as in *B. albitrunca* the lowest percentages of browsed shoot ends were found at a height of 0.5 m as compared to 1.5 and 2.5 m; Woolnough & du Toit 2001, table 2, p. 588 (an important point not mentioned in the paper of 2007). Thus, according to the feeding competition hypothesis, severe depletion could be completed first in one of the higher levels eventually resulting in competition for the rest of the forage at 0.5 m and below with perhaps correspondingly unexpected evolutionary consequences for giraffes and other browsers. – Only under extremely sore environmental conditions and food shortages (Darwin's series of severe dearths not addressed by the authors), one may postulate such a thing as "browsing pressure across feeding heights" (perhaps nothing left below 2.5 m – still available for Kudus – yet also leading to the starvation of the young giraffes, at least if all the giraffes stayed in that area; see, however, home range areas pp. 4 and 5). And obviously the giraffes themselves do not display much respect for this hypothesis either. Remember the key observations by Simmons and Scheepers from p. 65 above, "that during the dry season ... giraffes generally feed from low shrubs, not tall trees" etc. and that each result of their investigations "suggests that long necks did not evolve specifically for feeding at higher levels."

Besides, the ***mean feeding height of giraffe is ca. 2.7 m*** (du Toit 1990, p. 58). And Young and Isbell (1991) found "that giraffe feeding rates were greatest for both sexes at intermediate heights" (Ginnett and Demment 1999, p. 103). One would perhaps expect a higher figure of 4 m or even more from the feeding competition and selection hypothesis.

Cameron and du Toit go on as follows:

"Consequently, giraffes gain a foraging advantage by browsing above the reach of smaller browsers."

Yet obviously they don't care too much for the ½ to 1 g difference per GBU found for the 7 trees of *A. nigrescens* – otherwise also their young ones and females would

perpetually practice it as far as possible. But even if they did, this would also be fully compatible with the ID-hypothesis on the origin of the giraffe (see pp. 22 and 25-28). And it would prove nothing concerning evolution by the postulated random mutations and natural selection. – Incidentally, the hypothesis of an intelligent origin of species/families would, of course, not expect the design of an animal almost 6 m high with forage options on all levels just to limit its foraging say to 1 m above the ground. Rather, it would postulate and predict multiple options of behaviour and organismal reasons as well as ecological factors contributing to the welfare of our 'tall blondes' as constitutive elements of the synorganization of the entire ecological system of plants and animals. "Foraging in large herbivores can be viewed as a hierarchical process (Johnson 1980; Senft et al. 1987)" – Ginnett and Demment 1997, p. 292. Besides, there may be no necessary foraging advantage *in competition* with smaller browsers. Cameron and du Toit continue:

> "We additionally show that variation in leaf biomass per shoot across browsing heights diminishes significantly if the smaller browsers are experimentally excluded."

Once again: the authors have excluded ***not only the smaller browsers but the giraffes as well*** – possibly the weakest point in the entire experimental scheme.

> "Consequently, the pattern of variation in leaf biomass per GBU across feeding heights must be due to depletion of leaf biomass by selective browsing at low canopy levels,…"

There is neither a "consequently" nor a "must be". They have excluded the giraffes (especially the young and the female animals) from the outset of their experiment and *they simply postulate* that only the smaller browsers are responsible for the depletion found.

Also, the question may be raised *whether* and if so to what extent the trees themselves compensate for only being browsed at higher levels by perhaps producing more leaf biomass per GBU at the lower levels excluded from browsing ("...increased tolerance and resistance in heavily browsed trees is associated with important changes in tree branching, prickle spacing, shoot growth rates, shoot diameter and shoot number" - Fornara 2005, p. 80; "The higher number of shoots produced by heavily browsed trees suggests that the removal of apical dominance stimulates the growth of secondary shoot meristems" and "Our evidence is that browsing lawns increase the feeding efficieny of browsers through increased production of shoot mass all around the distinctly hedged canopies of browsed trees. This makes more food available to ungulate browsers such as giraffes, kudus, and impala, which often remove shoot ends and, hence, have a pruning effect (Pellew 1983, du Toit 1990). Leaf mass did also increase in regrowth shoots" – Fornara and du Toit 2007, pp. 204 and 207).

Moreover, some browsers – including the juvernile and female **giraffes** – being barred from forage below 2.2 m on the excluded trees, may turn to the next control tree to combat their appetite all the more there.

> "…supporting the hypothesis that giraffe feeding efficiency is reduced at low heights as an outcome of competition with smaller guild members."

At present, this inference is as doubtful as the presuppositions. Moreover, it is in conflict with the observations by Simmons and Scheepers as quoted above as well as Ginnett and Demment (1997, 1999).

My impression is that Cameron and du Toit are trying to force the state of being of the giraffe and other browsers into the Procrustean bed of perpetual Darwinian evolution by natural selection, taking for granted that mutations have produced the genetic variation necessary to evolve all the animals now found; and du Toit has

consistently tried to interpret his observations in terms of selection theory. Just to give another example (du Toit 1990, p. 60):

> "In East Africa too, giraffe bulls usually feed at full neck stretch while cows prefer feeding at body or knee height (Sinclair & Nortan-Griffiths, 1979; Pellew, 1983). Pellew (1984b), who used this difference in feeding posture as a means of sexing giraffe from a distance, proposed that it reduces competition between the sexes. In contrast, I suggest that it could in fact indicate the existence of such competition."

As far as I know there is no evidence for competition between the sexes (see also Ginnett and Demment 1999). Rather, 'the resources are well shared: species survival by cooperation rather than brutal selection' (see p. 5 of the present paper).

Moreover, "vertical zonation of browse quality in tree canopies" – as correct as the investigations and results concerning *A. nigrescens* may be ("giraffe feeding efficiency increases with height up the canopy", but not inevitably in other genera as well, see p. 70 and 72/73 above) – is simply *translated* into the language of competition, selection, and evolution without sufficient scientific evidence for adequate positive mutations and natural selection (see for example Behe 1996, 2007, Lönnig 2001, 2006, 2007). Instead, Darwinism is implicitly assumed to be true and the facts are interpreted according to this presupposition.

Thus, concerning evolution, Cameron & du Toit conclude their paper as follows (p. 134 last paragraph subdivided into several parts for the following discussion):

> "Despite popular acceptance that giraffes have long necks because of foraging competition during their evolution, no previous studies have experimentally investigated foraging competition between giraffes and smaller browsers."

Although the authors maintain that they have done this, *they failed to experimentally investigate foraging competition between giraffes and smaller browsers* by excluding not only the smaller browsers but also the giraffes from the outset for the lower forage levels.

> "Simmons and Scheepers (1996) argued that there was little evidence that giraffes forage high in the canopy because of competition and suggested sexual selection as an alternate hypothesis."

Simmons and Scheepers showed *evidence* to the contrary of competition.

> "However, Woolnough and du Toit (2001) showed that giraffes achieve a bite-size advantage by feeding higher in the tree,..."

– Which especially the young and female giraffes often cannot or do not care for or appreciate too much.

> "…and now we show that this is explained by the avoidance of competition with smaller browsers."

This is exactly what Cameron and du Toit fail to prove. However, their conclusion reads as follows:

> "While not resolving the controversy, our study provides the first experimental evidence that the giraffe's extremely elongated body form is naturally selected in response to competition from smaller browsing species."

So far the experimental evidence is deeply flawed. The title of the paper "Winning by a Neck: Tall Giraffes Avoid Competing with Shorter Browsers" is incorrect. It could perhaps be a truism like "Winning by a Neck? Tall Giraffes Cannot Display Any

Competition with Smaller Browsers *when Forage is Excluded for All Browsers at Least Up to a Height of 2.2 m*." Moreover, to date it is doubtful whether there is any severe competition at all between various species of browsers at different tree heights.

Grazing giraffe. See references for the photographs at the end of the appendix under (9).

The only inference on which one may fully agree with the authors is that they have not resolved the controversy, the rest of their interpretations is hardly more than neo-Darwinian guesswork and story-telling.

As for the ID-hypothesis one may suggest the following scenario (also still in the beginning and to be extended and tested in detail, – as pointed out above and in clear contrast to the neo-Darwinian viewpoint, I think that on the scientific level further options like ID should be carefully investigated as well): Giraffes were 'designed' (front-loaded or otherwise) – according to their respective developmental stages and gender in correlation with different and varying environmental parameters and conditions – to browse from lower layers of vegetation upwards to about 6 m in height with a mean feeding height of about 2.7 m. For a lush vegetation with many different plant species on the menu of the giraffe, "depletion of higher-quality plant parts by smaller browsers" will hardly be a serious competition factor determining the behaviour of this 'altogether exceptional, novel, and specialised' animal (to apply Lancestor's words to the whole animal). And even in the dry seasons giraffes often do not behave as expected. Yet especially the bulls may take some advantage from 'the tendency of trees to allocate more leaf biomass to shoots high in the canopy' without any obligatory competition with other animals.*

The paper of Cameron and du Toit clearly *does not provide* what the authors promise in the abstract of their paper (2007, p. 130), namely "the first experimental support for the classic evolutionary hypothesis that vertical elongation of the giraffe body is an outcome of competition within the browsing ungulate guild." Further options like the intelligent origin of the giraffe should be carefully considered.

*(By modification of a sentence of Cameron and du Toit 2007, p. 131, which reads: "However, it is also possible that the tendency of trees to allocate less leaf biomass to shoots low in the canopy may explain this variation even in the absence of competition (Woolnough & du Toit 2001").

References for the popular press etc. and the photographs:

http://deseretnews.com/dn/view/1,1249,650224911,00.html
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http://www.sciencedaily.com/releases/2006/12/061223092600.htm
(1) http://www.jostimages.com/bilder/preview/000000016280/_(000000016280).jpg
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(8) http://www.fyvie.net/photos/Travel/South%20Africa%20July%202004/slides/IMG_3413.JPG
(9) http://www.miamimetrozoo.com/assets/conservation/giraffe.jpg

"Up to 100 species of plants recorded for the giraffe's diet": http://spot.colorado.edu/~humphrey/fact%20sheets/giraffe/giraffe.htm
70 plant species in KNP: http://www.krugerpark.co.za/Kruger_National_Park_Wildlife-travel/images-of-kruger-the-antelope.html

Brief comments on some objections

As to the two papers on the origin of the long-necked giraffe, sometimes there seem to be some misunderstandings, which I will briefly address here (the basic problem causing these misconceptions probably is that nowadays there are many bloggers and commentators who are *writing much more than they read* – careful study appears to be hard for some people): (1) One blogger thought that I had "a low threshold for jumping to design". This person possibly did not read or understand the last paragraph of p. 48 above: "In this connection it should be clear that *on the scientific level* the two present articles on the evolution of the long-necked giraffe **are only a beginning** (even if one, on a personal level, may consider the basic questions to be completely solved)… " – Neither did he reflect the research projects necessary to corroborate or deny the ID-hypothesis for the giraffe on that scientific level as discussed on pp. 25-28.

(2) "Homeotic shifts" are assumed by other authors to explain, for instance, the number and specific architecture of the neck vertebrae of the giraffe. However, this does not explain why such a functionally favourable homeotic shift should have occurred almost exclusively in the long-necked giraffe out of thousands of other mammal species (see p. 16 above). And, of course, neither would it account for all the other synorganized giraffe features enumerated on p. 25 and repeated on p. 63 of the present paper. It would not even clear up the enormous length of the giraffe's neck vertebrae (for an elongation is not an inevitable by-product of a homeotic shift). At present, the assumption of an accidental homeotic mutation is nothing but a simplistic *ad hoc* explanation with hardly any contents at all. Perhaps I should add that I myself have experimentally worked on homeotic shifts for some twenty years now: regularly there are strong negative pleiotropic side effects so that the organisms thus affected have no chance at all for further evolution. In all the homeotic shifts I have experimentally gained and investigated so far, there was not even one case of which I could say that it was simply positive. To obtain a long-necked giraffe from an okapi-like animal, if only for the number and architecture of the neck vertebrae, much more is necessary than just a random homeotic shift.

So, what do we really know about "the evolution of the long-necked giraffe"? We know that there is an enormous morphological, anatomical and physiological distance between *Giraffa camelopardalis* and its nearest relative, the okapi. Also, a continuous series of connecting links between short-necked and long-necked giraffes is unknown so far. We also know that *Giraffa* "represents not a mere collection of individual traits

but a package of interrelated adaptations" (Davis and Kenyon, see Part 1, p. 10) and that all these intricate parts are perfectly fine-tuned to each other and are integrated into an enormously complex "single pattern" of an impressive and beautiful animal species 'altogether exceptional, novel, and specialized'. – Further research should focus on the question, among others, whether *systems of irreducible and specified complexity* are involved in the origin of the long-necked giraffe (see again the research projects above). If so, then ID is *scientifically* the most likely explanation in this case, too. On the other hand, "the standard [neo-Darwinian] story, in fact, is both fatuous and unsupported" (Gould).

After some remarks on the origin of phyla, subphyla and classes, Michael J. Behe (2007, p. 199) answers the question whether design extends "even further into life, into the orders or even families of vertebrate classes? To such creatures as bats, whales, and giraffes?" as follows: "Because 'all of the structural characters of the edifice, from its overall form to minute aspects that determine its local functionalities…must be specified in the architect's blueprints' [Davidson], I would guess the answer is almost certainly yes. But at this point our reliable molecular data run out, so a reasonably firm answer will have to await further research. Given the pace of modern science, we shouldn't have to wait too long."

15. References for the Present Note as well as Part 1 and Part 2 see

http://www.weloennig.de/GiraffaSecondPartEnglish.pdf