[A translation of H. Hemmer, 1971, "Intraspezifische Unterschiede der relativen Hirngrösse beim Löwen (*Panthera leo* L.)", *Experientia* 27(12): 1500-1501. Where I'm not sure of the proper translation of a word or phrase, I provided the original in square brackets afterward. Translation ©2006 Krister T. Smith.]

## COMMENT

## Intraspecific differences in relative brain size in the lion (Panthera leo L.)

In the structure of the skull, lions (*Panthera leo* L.) from the range of the species in sub-Saharan Africa differ from Indian lions primarily in the "relatively shorter palatal, broader facial, and more constricted cranial proportions"<sup>1</sup> of the latter and in the lesser width of the postorbital constriction<sup>2</sup> of the Indian (as well as Berber) lion (Figure 1) and the stronger development of the crista sagittalis and of the bony postorbital crest that attaches anteriorly in the Asiatic lion<sup>3</sup>. On the basis of his findings regarding the breadth of the mastoid Todd<sup>1</sup> posed the question of possible differences in cranial capacity between the African and Indian forms. The increased development of a crista on the cranium of the latter suggested a likewise smaller capacity.

Measurements of the cranial capacity on the skulls of one Indian and two Persian lions in the Muséum d'Histoire naturelle Paris<sup>4</sup>, values for two Indian lion skulls from the American Museum of Natural History<sup>5</sup>, and comparative measurements of a series (n = 17) of African lion skulls (in the museums of Bonn, Frankfurt am Main, Stuttgart, Paleontological Institute of the University of Mainz<sup>4</sup>) confirm this supposition (Figure 2). Compared to African lions, whose capacity/basal length ratios are distributed on the bivariate plot according to an allometric line with an exponent of 0.23 (for my own series of measurements =  $0.26 \pm 0.04$ , for Röhrs'<sup>6</sup> = 0.19), the Asiatic lion possesses for the same absolute basal length (as a measurement of body size) a significantly smaller brain size.

The very low position of the point for one Persian lion (male), compared to the points of the other Asiatic skulls, corresponds (for the level of the Asiatic lion) to the mean  $\sim 15\%$  difference in cranial capacity between wild lions and old, zoo-raised individuals with pathologic alterations to the brain, as described for African lions<sup>7,8</sup>. The especially great relative zygomatic breadth of this skull suggests the conclusion of long care in the zoo, consistent with the situation in the skulls of zoo lions already referred to<sup>7</sup>.

As Röhrs<sup>6</sup> already determined, a parallel transposition of the allometric relation between lion and leopard (allometric exponent for the latter 0.25, according to Röhrs, but according to my own measurements (n = 32)  $0.26 \pm 0.03$ ) exists in the allometry  $\sqrt[3]{CC}/BL$  [CC = cranial capacity, BL = basal length]. From Figure 2 it emerges that the lengthening of the leopard line results from the range of the Asiatic lion. The latter can thus be regarded as lying at the lower brain size level (compared to African lions) of the leopard, the smallest species, in respect of body size, of the subgenus *Panthera* [Letztere können also auf der gegenüber afrikanischen Löwen unteren Hirngrößerstufe des Leoparden liegend angesehen werden, der bezüglich der Körpergröße kleinsten Art des Subgenus Panthera].

*Vis-à-vis* leopards and Asiatic lions this means: interspecifically identical allometric relations and identical relative brain sizes corresponding to the intraspecific allometry of the smaller species, despite great differences in absolute basal length. With that the general conclusion of Röhrs—"Different intraspecific and interspecific principles of order are present, which regulate the increase in cranial capacity with increase in basal length"—is confuted.

On the other hand the comparison between Asiatic and African lions shows that within one species different levels of brain size for the same body size can exist. A third such level in the lion can be assumed for the late Pleistocene North American form *Panthera leo atrox*<sup>10</sup>. In the relative breadth of the postorbital constriction, which correlates beautifully with the cranial capacity (correlation coefficient in the leopard and African lion between 0.5 and 0.6) and in the Asiatic and African lions differs in parallel from the difference in brain size (Figure 1), these American lions significantly depart from the African lions in having even higher values (Figure 1). In addition, volumes published by Merriam and Stock<sup>11</sup> of two endocranial casts speak directly for a greater encephalization level, with a distance to that of the African lion similar to that between the latter and the Asiatic form (cf. Figure 2).

The situation found here in the lion intraspecifically fulfills the definition of phylogenetic changes to encephalization, as Röhrs gave it: "The phylogeny is characterized by the absolute increase in brain size independent of body size. Phylogenetic development is therefore marked by the 'breaking' of allometries." The assertion (Röhrs<sup>6</sup>), that such transpositional differences of allometries between different large, closely related species, as we have before us here in the comparison of leopard and African lion, "can certainly not be valued as an expression of a different phylogenetic grade/level [Ranghöhe]", is therefore invalid. The emergence of a socalled "interspecific" allometry of brain size to body size (allometric exponent of 0.5–0.6) in the view of Herre and Röhres<sup>6,12,13</sup> is understandable only as a secondary consequence of evolution, when lower encephalization levels disappear in larger-bodied species through selection processes (cf. "intraspecific" allometry between leopard and Asiatic lion, "interspecific" allometry between leopard and African lion). As an expression of the encephalization level of a form, therefore, only the intercepts [Integrationskonstante] b of the so-called "intraspecific" allometry of brain size to body size (allometric exponents generally varying around 0.23) can be used, but not the intercepts of the fictional "interspecific" allometry, in the sense of an inevitable consequence of between-species changes in body size [zwischenartlicher Körpergrößenveränderungen], which Herre and Röhrs<sup>13</sup> represent as an expression of different organizational levels of systematic entities.

[English summary]

H. Hemmer

Fig. 1. Allometric graph of postorbital breadth to basal length (log-log scale [*doppelt-logarithmische Auftragung*]. (open circle), *Panthera leo*, East Africa; (solid circle), *P. leo persica*, India (values after Todd<sup>1,5</sup>); (half-solid circle), *P. leo atrox*, late Pleistocene of North America (values after Merriam and Stock<sup>11</sup>); (cross), *P. pardus*, all parts of the range. Allometric line drawn in for the lion series, with correlation significant at the 0.1% level.

Fig. 2. Allometric graph of  $\sqrt[3]{CC/BL}$  (log-log scale). (open circle), *Panthera leo*, sub-Saharan Africa; (solid circle), *P. leo persica*, Persia and India (two values from Anderson, written comm.<sup>5</sup>); (half-solid circle), *P. leo atrox*, late Pleistocene of North America (values from Merriam and Stock<sup>11</sup>); (cross), *P. pardus*, all parts of the range. Allometric lines drawn in for African lions and leopards as well as their elongation (dashed line) in the range of the Asiatic lion.