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Shell Mass, Thickness and Density of Avian Eggs Derived from the Tables of Schönwetter

Hermann Rahn and **Charles V. Paganelli**

In this study we examine how shell mass and shell thickness vary as a function of egg mass in Passeriformes and non-Passeriformes based on the values described in SCHÖNWETTER's Handbuch der Oologie (1960–83) and discuss the variation of these two dimensions as well as shell density. As reported previously, the length, breadth, shell thickness, shell mass, and egg mass for 7146 species and subspecies were entered into a computer which allowed us to describe the frequency distribution for egg mass (RAHN & PAGANELLI 1988a) and the length, breadth, and elongation of avian eggs (RAHN & PAGANELLI 1988b).

The authors are greatly indebted to LINDA CURRAN-EVERETT for her skillful handling of the computer program.

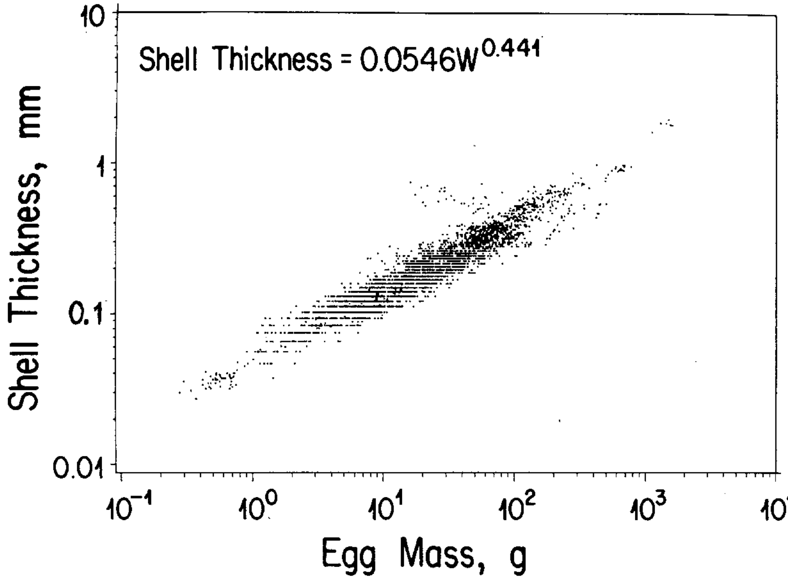

Fig. 1. Log-log regression of shell thickness on egg mass for 3217 extant non-passerine species and subspecies.

Results

Shell thickness.

The log-log regression of individual values of shell thickness (range 0.029 to 2.10 mm) on egg mass (range 0.3 to 1600 g) for extant non-Passeriformes (n = 3217) representing 26 orders recognized by SCHÖNWETTER is described by the following relationship (fig. 1):

Shell thickness (mm) = $0.0546\ W^{0.441\ \pm 0.003}$, $r^2 = 0.89$, X̣SEE = 1.21 (1)

where W = egg mass, g; r = correlation coefficient, and X̣ SEE = the antilog of the standard deviation from regression by which a mean value is multiplied or divided.

The regression for Passeriformes (n = 3929) is similar:

Shell thickness (mm) = $0.0553\ W^{0.358\ \pm 0.003}$, $r^2 = 0.81$, X̣ SEE = 1.13 (2)

Shell mass.

The regression of shell mass (range 0.014 to 290 g) on egg mass for non-passerine species is shown in figure 2 and is described by the following equation:

Shell mass (g) = $0.0524\ W^{1.113\ \pm 0.003}$, $r^2 = 0.98$, X̣SEE = 1.21 (3)

and for passerine eggs

shell mass (g) = $0.0547\ W^{1.024\ \pm 0.003}$, $r^2 = 0.97$, X̣SEE = 1.13 (4)

Discussion

While the standard error of the slopes of the 4 equations is very small, the standard deviation from regression is very large, 1.21, particularly when we compare this value

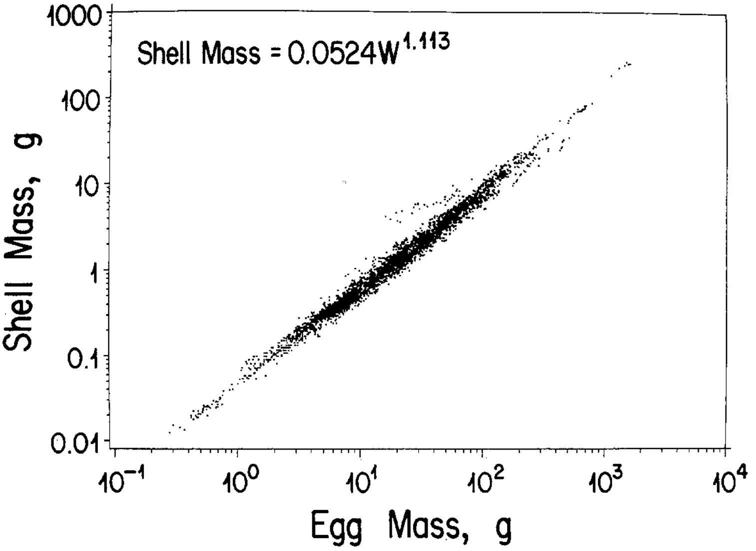

Fig. 2. Log-log regression of shell mass on egg mass for all extant non-passerine species.

with the standard error of egg length (1.06) and particularly egg breadth (1.03; RAHN & PAGANELLI 1988b). While great constraints are placed on the shape of the egg, expressed as length and breadth, the shell thickness and shell mass show a scatter around the mean which is 3.5 to 7.0 times larger, reflecting various adaptations to the environment. Furthermore, it is of interest to note that the exponent of equation 3 is greater than 1.00, indicating that shell mass increases faster than egg mass. Thus, shell mass increases 13 times (antilog of exponent) for every 10-fold increase in egg mass. Also, in the egg mass range from ca 10 to 100 g there are many species which fall conspicuously outside the normal distribution (figures 1 and 2). These exceptions belong to various members of the order Galliformes and in one case to the order Anseriformes; they are discussed below.

The exceptions.

These are of interest because they reveal special adaptions which fall outside the general pattern. For example, figure 3 shows the regression ±2 SEE (stippled area) of shell thickness on egg mass for 338 species or subspecies of the order Galliformes. The individual values for 3 genera of the family Phasianidae are shown on the left graph. Members of the genus *Francolinus* are split between those with normal shell thickness, averaging ca 0.25 mm, and those with an average shell thickness of ca 0.65 mm, but with no members in between. As SCHÖNWETTER noted, this difference cannot be ex-

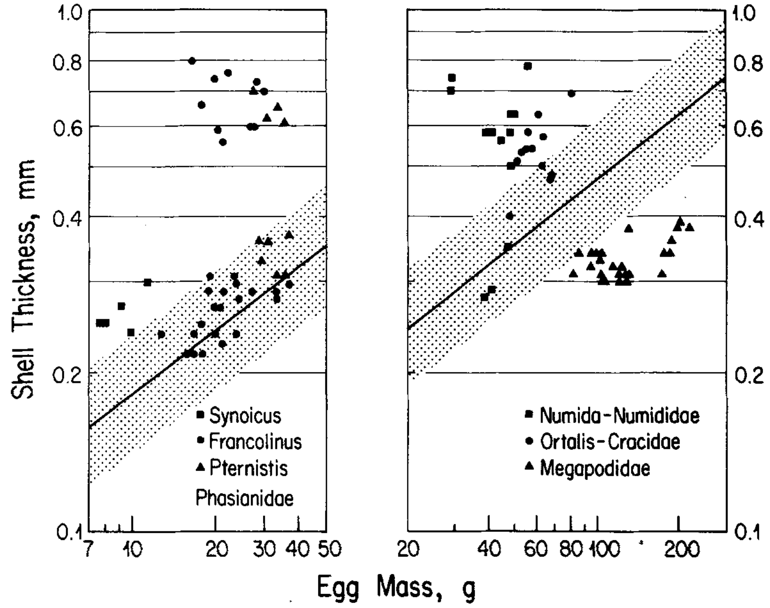

Fig. 3. Log-log regression of shell thickness on egg mass in the order Galliformes where the shaded area represents ±2 SEE for 338 species and subspecies of this order. Symbols identify individual species or subspecies of various genera and their families which have unusually thick or thin shells.

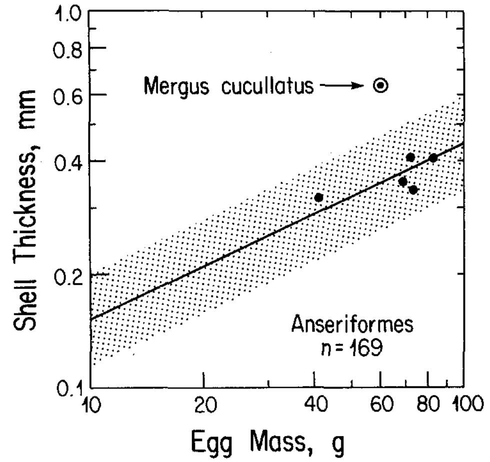

Fig. 4. Log-log regression of shell thickness on egg mass in the order Anseriformes, where the shaded area represents ±2 SEE for 169 species or subspecies of this order. The points identify 6 species of the genus Mergus (Mergansers).

plained by their geographic distribution. A similar split is seen among the members of the genus *Pternistis*. On the right graph are shown the thick-shelled eggs of the genera *Numida* and *Ortalis*, while the eggs of the Megapodidae have significantly thinner shells. Figure 4 shows the shell thickness of *Mergus cucullatus* (Hooded Merganser) in contrast to 5 other species of the same genus which fall within a ±2 SEE range of the regression for 169 species or subspecies of the Anseriformes. The unusual shell thickness in all these species presumably reflects the need for special protection in their nests; this is not required by the Megapodidae whose eggs are buried in artifical mounds or volcanic sand and once deposited are not moved or disturbed.

Among the family Icteridae the parasitic species (n = 14) have on average for comparable egg mass a 40 % thicker and 30 % heavier shell than non-parasitic species (n = 106; Rahn et al. 1988); and, as discussed below, a 40 % increase in shell thickness would double the force required to break the shell (Ar et al. 1979).

Relative shell mass among various orders.

How does the relative shell mass (expressed as per cent of egg mass) vary with egg mass? The log-log regression for non-Passerines provides the following relationship:

$$(\text{shell mass}/\text{egg mass}) \times 100 = 5.24\ W^{0.113\ +0.003},\ r^2 = 0.36,\ \overset{\cdot}{\underset{\cdot}{X}}\text{SEE} = 1.21 \quad (5)$$

The antilog of the exponent indicates that relative shell mass increases on average 1.3-fold for every 10-fold increase in egg mass. For example, in a 1 g egg the relative shell mass = 5.2 %; in a 1000 g egg, 11.4 %.

How does relative shell mass vary among various taxa? This requires a comparison at the same egg mass. For this analysis we chose an egg mass of 30 g, representing the largest number of orders whose eggs include this value. For each order the regression equation of relative shell mass vs egg mass was established to predict the relative shell mass (% of egg mass) of a 30 g egg. These are shown for 17 orders in Table 1, ranging from 9.7 % in Galliformes to 5.7 % in Caprimulgiformes. While this compilation does

Table 1. Comparison of shell mass of 30 g eggs (% of egg mass) of 17 orders, arranged by decreasing values.

Galliformes	9.7	Tinamiformes	6.8
Podicipediformes	9.5	Ciconiiformes	6.8
Pelecaniformes	9.3	Procellariiformes	6.4
Anseriformes	8.0	Falconiformes	6.4
Psittaciformes	8.0	Charadriiformes	6.4
Gruiformes	7.8	Columbiformes	6.4
Cuculiformes	7.8	Passeriformes	5.9
Strigiformes	7.6	Caprimulgiformes	5.7
Coraciiformes	7.2		

not reveal the many exceptions that can be found among various families within one order, these ordinal differences show no specific relationship to either hatchling maturity or type of nest, as noted previously by SCHÖNWETTER (1986—87) using other examples.

Eggs which exhibit an unusually large relative shell mass are the same species with exceptionally thick shells (figure 3). These are shown in figure 5 where the relative shell mass is plotted on linear coordinates. The various thick-shelled members of the Galliformes are identified by symbols. Circle (1) represents the genus *Struthio* and Circle (2) identifies the large eggs of the extinct orders Dinornithiformes and Aepyornithiformes. As SCHÖNWETTER pointed out, most remarkable are some but not all

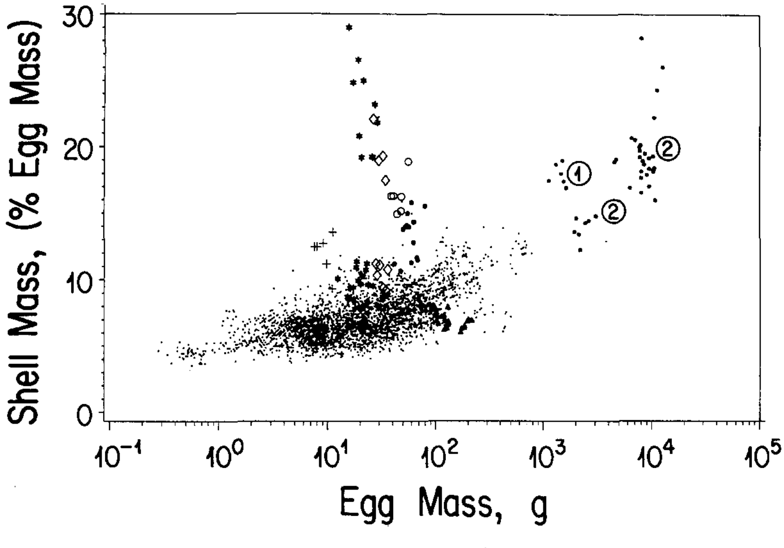

Fig. 5. Semilog regression of relative shell mass on egg mass for all extant non-passerine species as well as representatives of the extinct orders Dinornithiformes and Aepyornithiformes identified by circle (2). Struthioniformes, circle (1). Various genera of the Galliformes are identified by the following symbols: * *Francolinus*, ○ *Numida*, ● *Ortalis*, ◇ *Pternistis*, + *Synoicus*, and ▲ family Megapodidae.

members of the genus *Francolinus* where the relative shell mass constitutes 20 to 28 % of the egg mass.

Eggshell density.

ROMANOFF & ROMANOFF (1949) cite shell densities (g/cm^3) ranging from 2.55 in *Struthio* to 1.50 in some passerine species. More recently TYLER (1964, 1965, 1966) measured in many species the shell mass/cm^2 as well as the shell thickness, from which he derived the apparent shell density. Among 69 species of Anatidae (waterfowl) shell density varies between 2.3 and 2.4 g/cm^3, in 10 species of Spheniscidae (penguins) from 2.15 to 2.22 g/cm^3, and in 25 species of the Falconiformes (raptors) from 1.86 to 2.18 g/cm^3. SCHÖNWETTER (1985—86) at the time of his writing was unaware of these results and discussed (Vol. 4) at length his calculations of specific weight, providing a table listing such values for 81 species or families which ranged from 2.54 to 1.85 and suggested a general overall value of 2.05. The term specific weight or specific gravity is a dimensionless ratio of the density of a substance to that of water. We prefer here the term shell density, defined as shell mass/shell volume with the dimension of g/cm^3.

We used an approach similar to that of SCHÖNWETTER for estimating shell density by dividing the shell mass of each species by the product of its shell thickness and shell surface area. Surface area was calculated from the allometric equation A (cm^2) = 4.835

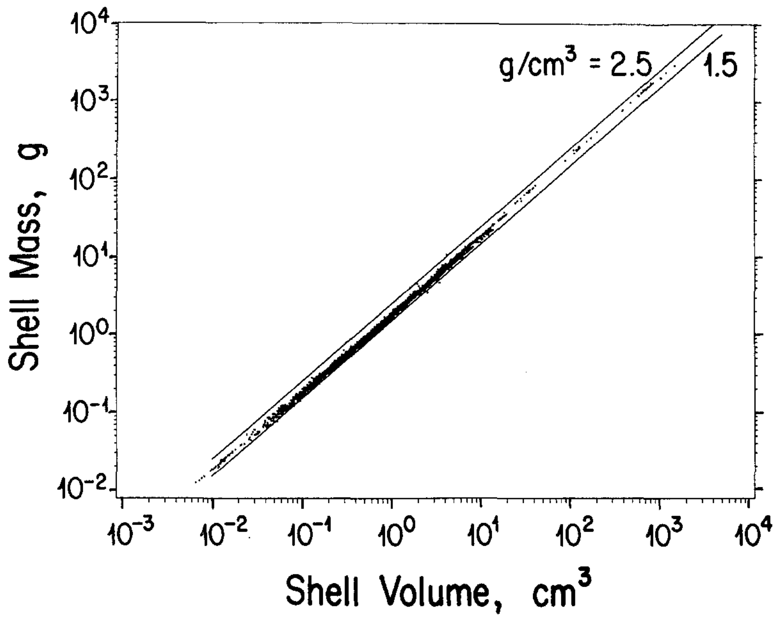

Fig. 6. Log-log regression of shell mass on shell volume for non-passerine eggs including 2 extinct orders (n = 3317). For discussion see text.

$W^{0.662}$ (PAGANELLI et al. 1974) where W = egg mass, g. Figure 6 plots the shell mass against shell volume (shell thickness x surface area) for all non-passerine species including the 2 extinct orders, Dinornithiformes and Aepyornithiformes. Shell mass range extends over 6 decades from 14 mg (Trochilidae) to 3346 g (Aepyornithiformes), and the two lines represent the isopleths of shell density for 2.5 and 1.5 g/cm^3. It will be noted that all values fall between these limits and that there is a general tendency of shell density to increase as shell mass (and egg size) becomes larger. The frequency distribution of shell density for all extant non-passerines is shown in figure 7. The mean value is 2.02 g/cm^3, SD 0.12, n = 3281. For Passeriformes (n = 3928) the mean value is 2.05 g/cm^3, SD 0.12. Both values agree with the overall value of 2.05 suggested by SCHÖNWETTER.

Table 2 lists the mean shell density for 27 orders, ranging from 2.3 g/cm^3 in Rheiformes to 1.85 in Psittaciformes, as well as the number of species or subspecies and the coefficient of variation expressed as percent.

Table 2. Mean values of shell density and coefficient of variation of various orders, arranged in decreasing order. Also shown are the number of species or subspecies for each order.

Shell Density	Orders	n	Shell Density	C.V. %
2.3	Rheiformes	6	2.39	1
	Casuariiformes	12	2.37	2
2.2	Struthioniformes	6	2.26	3
	Apterygiformes	4	2.20	1
	Sphenisciformes	19	2.20	3
	Gaviiformes	5	2.20	2
2.1	Tinamiformes	59	2.13	4
	Podicipediformes	23	2.12	2
	Anseriformes	169	2.10	4
	Galliformes	339	2.10	4
	Cuculiformes	140	2.10	5
2.0	Caprimulgiformes	103	2.08	3
	Ciconiiformes	131	2.07	4
	Passeriformes	3931	2.05	6
	Procellariiformes	93	2.04	4
	Coliiformes	11	2.03	5
	Pelecaniformes	87	2.02	3
	Gruiformes	241	2.02	5
	Piciformes	254	2.02	4
	Apodiformes	115	2.02	5
	Columbiformes	283	2.01	3
	Trogoniformes	24	2.01	5
	Coraciiformes	178	2.00	5
1.9	Charadriiformes	370	1.96	4
	Falconiformes	316	1.95	6
	Strigiformes	127	1.93	3
1.8	Psittaciformes	164	1.85	4

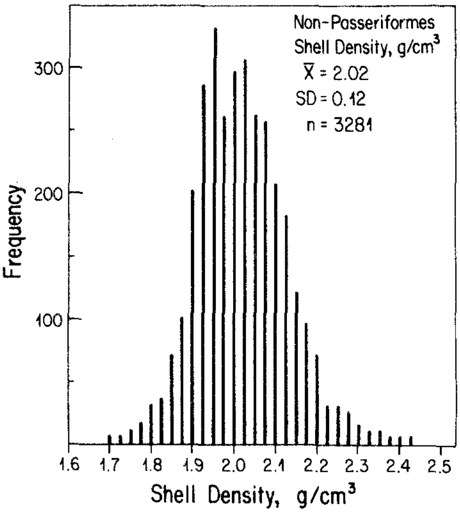

Fig. 7. Frequency distribution of calculated eggshell density for all non-passerine eggs.

Finally, it should be noted that all our values as well as those presented by Schönwetter (1985—86) are at best estimations of actual shell density because shell thickness, egg mass, and surface area values were not measured directly for each species but were derived from general equations. On the other hand, the density values reported by Tyler were done by direct measurements of mass, area, and thickness for each species; yet even he was cautious enough to refer to his measurements as apparent density.

Breaking strength of eggs.

This was measured by Ar et al. (1979) in 47 species (egg mass range 0.86 to 1461 g) by application of a force F (kg) which yielded the first gross sign of shell deformation.

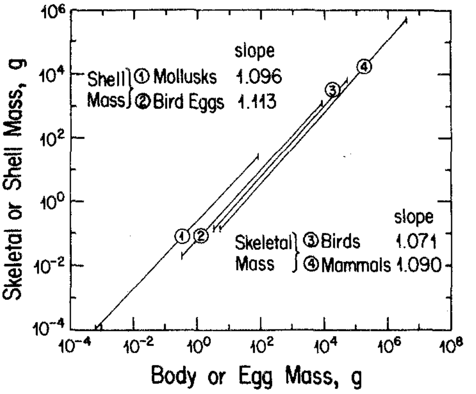

Fig. 8. Log-log regression of shell or skeletal mass on egg or body mass in mollusks, bird eggs, birds and mammals. Replotted from the data of Anderson, Rahn & Prange (1979).

They also showed that this force was directly proportional to the square of shell thickness, or F (kg) = 17.5 L^2, where L = shell thickness, mm. Thus breaking strength for any egg mass can be estimated if the shell thickness is known. For example, the average 48 g egg has a shell thickness of 0.3 mm (equation 1) and F = 17.5 x 0.3^2 = 1.6 kg. On the other hand, the average body mass of a non-passerine bird producing a 48 g egg is 0.8 kg (RAHN et al. 1985, equation 6), thus providing the egg with a safety factor of 2.0.

The shell as an exoskeleton.

About 97 % of the avian eggshell is calcium carbonate and has a density similar to that of bone of birds and mammals (BLITZ et al. 1969). As noted in equation (3) shell mass is proportional to egg mass raised to the 1.11 power, and increases 13-fold for every 10-fold increase in egg mass. How does this rate compare with the supporting structure of other organisms, the exoskeleton of mollusks, or the endoskeleton of birds and mammals. This was reported by ANDERSON et al. (1979) who showed that when these supporting structures were regressed against body mass, the exponents for body mass were essentially the same, ranging from 1.07 to 1.10. In figure 6 these regressions are plotted, including equation 3. The common slope for all these organisms whose body mass extends over 10 decades suggests a general bioengineering principle for supporting structures; evidently avian eggshells are no exception. Furthermore, the regression of the avian endoskeleton shows that it is, notwithstanding frequent statements to the contrary, at least as heavy as that of land mammals.

Summary

Presented are regression equations of shell thickness and shell mass as a function of egg mass for non-passerine (n = 3217) and passerine species (n = 3929) taken from the tables of SCHÖNWETTER. These regressions reveal many species of the order Galliformes that exhibit unusually thick shells and have a relative shell mass which can exceed 20 % of their egg mass. Shell density (g/cm^3) was calculated for all eggs and their frequency distribution plotted. Mean values for non-passerine and passerine eggs are 2.02 and 2.05 g/cm^3, respectively. The breaking strength of eggs as related to shell thickness is discussed. The regressions of exoskeletal, endoskeletal, and eggshell mass on body or egg mass are all shown to have the same slope.

Zusammenfassung

Auf der Grundlage der Tabellen von SCHÖNWETTER werden Gleichungen abgeleitet, die Schalendicke und Schalenmasse als Funktion der Eimasse bei Nicht-Singvögeln (n = 3217) und Singvögeln (n = 3929) beschreiben. Dadurch wird ersichtlich, daß z. B. viele Arten der Galliformes eine auffallend dicke Eischale aufweisen und eine relative Schalenmasse, die jene des Eiinhalts bis um 20 % übertreffen kann. Die Schalendichte ergibt im Mittel für Nicht-Singvögel 2,02 und für Singvögel 2,05 g/cm^3. Die Bruchfestigkeit der Eischalen als Folge ihrer Dicke wird diskutiert. Die Regression der Masse von Außen- und Innenskelett bei Mollusken, Vögeln und Säugetieren im Vergleich zur Körpermasse und jene der Schalenmasse im Vergleich zum Ei zeigt den gleichen Anstieg.

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Anschrift der Verfasser: Dept. of Physiology — Sherman Hall, State University of New York at Buffalo, Buffalo, New York 14214 USA.