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THE AVIAN EGG: MASS AND STRENGTH

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In a series of recent works, attention has been paid to the functional properties of the avian eggshell: water vapor and respiratory gas conductances, water loss, metabolic rate and incubation time—all these major physiological characteristics of eggs may be closely and intimately related to egg mass, which, in turn, is allometrically related to eggshell structural properties such as thickness, porosity, mass, density and surface area (Wangensteen 1972, Ar et al. 1974, Rahn and Ar 1974, Paganelli et al. 1974, Rahn et al. 1974, Ar and Rahn 1978).

These structural and functional relations of bird eggs reveal some variables of importance to the physiology of the embryo, including the gradient in water vapor pressure between egg and nest, the fractional water loss constant, the constancy of gas composition in the air cell, and total oxygen consumption per gram egg during incubation. The ability to hatch successfully is the outcome of a delicate equilibrium among several factors, some of which are inherited in the structure and function of the egg itself, while others are either imposed on the egg by the environment or controlled by the incubating parents.

The eggshell provides the egg with an external "skeletal" support that utilizes the dome principle to obtain strength with economy in building material and without need for internal supporting posts. It must satisfy conflicting demands: On the one hand, it must be strong enough to support the incubating bird's mass plus the egg's own mass and to protect and prevent it from being crushed during incubation. On the other hand, it must not be too strong for the hatchling to break its way out, a problem that may become crucial in bigger eggs where shell thickness increases and the specific metabolic rate of the embryo decreases (Paganelli et al. 1974, Rahn et al. 1974). The ratio of total shell pore area to shell thickness is largely evolved to meet the forthcoming metabolic demands of the growing embryo, which in turn, are a function of mass (Ar et al. 1974). Adding to this the belief that any saving in building material should benefit the laying bird, we hypothesize that eggshell strength should be related to egg mass.

Eggshells have been subjected to numerous strength tests in the past. They have been crushed, cracked, pierced, snapped, compressed, bent and deformed in various ways. Force has been applied inwards and outwards, on whole eggs and on pieces of shells. Various methods and instrumentations have been used (Brooks 1960, Tyler and Geake 1963, 1964, Tyler and Coundon 1965, Tyler and Thomas 1966, Carter 1971, Scott et al. 1971). However, most of these studies were designed to establish practical "quality" criteria as they are understood by the poultry industry (Petersen 1965). As a result, most of the research has been concentrated on domestic hen (*Gallus domesticus*) eggs and little has been published on other species (Romanoff and Romanoff 1949, Brooks 1960, Tyler 1969a, Radcliffe 1970, Peakall et al. 1973). Strength has been correlated with factors such as calcium diet, diet in general, insecticides, shell microstructure, specific gravity, incubation period and shape index (e.g., Sluka et al. 1967, Wells 1967a, b, Vanderstoep and Richards 1969, Connor and Arnold 1972, King and Robinson 1972, Cooke 1973, Carter 1976). However, Tyler (1969b) clearly demonstrated that the main factor affecting strength in hen eggs is shell thickness, where strength is a function of shell thickness squared.

It is our purpose here to describe how egg strength scales with mass. We do not try to explain the relationship, but rather attempt to define the common principles that emerge from this relationship.

MATERIALS AND METHODS

As an overall simplified expression of egg size we have chosen to use the initial egg mass W (Günther 1975). This eliminates the need to treat length, breadth, shape and their variations separately for each species. In other words, for our general comparisons, we consider eggs to have a common general shape. Egg mass, as the most accessible egg variable, has been used often for comparisons.

Eggshell strength was measured in over 200 individual eggs which covered a wide range of egg weights (more than three orders of magnitude). We tested eggs of 47 species from 26 families and 11 orders of birds. Most eggs were either collected in the field or obtained from the Canadian Center for Ecological Zoology of the Tel Aviv University during several breeding seasons. Fresh eggs were weighed and then subjected to a strength test using a specially constructed duralumin apparatus, modelled after Romanoff (1929). Breaking strength was measured by applying force or contact stress to both ends of an egg mounted vertically between two polished parallel metal plates. (Brooks 1960, Tung et al. 1969). One of the plates was fixed in position and the other mounted under the end of a light counterbalanced lever. A 300 g carriage was string-driven along the 1,000 mm lever scale at a constant rate of about 4 cm/s. The carriage could be loaded with various weights up to 14 kg. A special arrangement jammed the string when not pulled, allowing a pointer fixed on the carriage to rest within ±1 mm of the pulling end point. The egg was considered broken when first signs of either pole flattening were observed. The force F applied at this yield point was recorded. Flattening was generally accompanied by a cracking noise, and a pattern of either concentric or radial cracks could be seen on the damaged end. A limiter prevented the full crushing of the egg. For the ostrich eggs, a special seesaw-like device was built and force was applied by pouring water into a large plastic container placed above the egg. We are aware that eggs are not generally brooded in a vertical position; however, shape factors are believed to exert minimal influence in this position. Preliminary tests on hen eggs show no significant difference in mean values of F between the vertical and the horizontal positions, but the variance was significantly higher in the horizontal position.

Eggshell thickness was measured on shells that had been washed and dried in room air; the measurement included the dried shell membranes. A micrometer caliper with a small steel ball attached to one jaw to accommodate the inside curvature of the shell was employed. The micrometer measurements were accurate to ± 2 μm. Each eggshell was measured at six points: four spaced around the equator of the egg and one near each pole. Differences ranged up to ±7% on the average and the mean of all six measurements, rounded to the nearest micrometer, was taken as eggshell thickness L.

In addition to our measurements, we have extended the list of 367 values of shell thicknesses plotted by Ar et al. (1974) to include 3,434 species. Data have been gathered mainly from Schönwetter (1960–1972).

The analytical approach follows basically the principles reviewed by Gould (1966). Log-log plots were used to derive regression equations where yield-point F and shell thickness L are expressed as a function of egg mass W in the common form of $\log Y = \log a + b \cdot \log X$ or $Y = aX^b$. We also calculated a regression of log F as a function of log L. With such an approach, mean egg masses and mean shell thicknesses within a given species are considered to be independent variables, and their usually small biological variation is neglected. The least-squares method used to derive the regression lines tends to underestimate the slope value in such cases (Riggs 1978). This was not judged to significantly bias the results of the analysis. Thus the standard error of estimate (SEE) of the regression expresses the scatter of log Y values around the regression line.

For convenience, force implied was expressed in weight rather than force units.

RESULTS

Fresh egg mass values W (g), yield-point values F (g) and mean shell thickness L (μm) are presented for 47 species in Table 1. Measurements obtained from more than one egg in a species are presented as a mean ± standard error with the number of eggs measured noted. Species are arranged in order of increasing egg mass. A relation between F and W was derived from a linear least-squares analysis of log F on log W in the form:

$$\log F\,(g) = 1.706 + 0.915 \log W\,(g) \pm 0.2178\,\mathrm{SEE}$$

or

$$F = 50.86\, W^{0.915}. \quad (1)$$

The correlation coefficient is high and significant ($r = 0.9447$; $P \ll 0.001$) and the residual variation is negligible compared with the variation explained by the regression ($F_{1,45} = 373.5$).

Using the same procedure, thickness is expressed as:

$$\log L\,(\mu m) = 1.753 + 0.458 \log W\,(g) \pm 0.0715\,\mathrm{SEE}$$

or

$$L = 56.65 W^{0.458} \quad (2)$$

($r = 0.9751$; $P \ll 0.001$; $F_{1,45} = 869.7$).

Both relationships are expressed graphically in Figures 1 and 2.

The overall equation for the eggshell thicknesses of 3,434 species gathered from the literature is:

$$\log L\,(\mu m) = 1.733\,(\pm 0.003) + 0.448\,(\pm 0.002) \times \log W\,(g) \pm 0.083\,\mathrm{SEE}$$

or

$$L = 54.06 W^{0.448} \quad (3)$$

($r = 0.9572$; $P \ll 0.001$).

DISCUSSION

RELATIONSHIP BETWEEN STRENGTH, THICKNESS AND MASS

It would be simple to assume a linear correlation between shell strength and egg mass, where the bigger the egg, the stronger it is. Romanoff and Romanoff (1949) wrote: "The breaking strength . . . of the eggs of different species of birds is correlated with the size of the egg." The fact that the power in equation (1) relating force applied to egg mass ($b = 0.915$) is close to unity, suggested the possibility of a linear relationship between F and W (or with the third power of the linear dimensions of the egg). We have found that the equation obtained from the linear regression of F on W is an unreliable model for predicting the yield points of small and medium-sized eggs although the correlation is good ($r^2 = 0.9874$). One pos-

TABLE 1. Initial egg mass (g) (in increasing order), yield point values (g) and shell thicknesses (μm) for various avian species. S.E. = standard error, n = number of eggs.

Species	Egg mass			Yield point			Shell thickness		
	mean	±S.E.	n	mean	±S.E.	n	mean	±S.E.	n
Nectarinia osea	0.86	.01	2	37	—	1	52	1	2
Prinia gracilis	1.12	.02	6	86	—	1	69	2	6
Carduelis carduelis	1.23	.04	5	80	9	3	70	1	5
Passer moabiticus	1.50	.06	17	132	9	16	88	1	26
Muscicapa striata	1.85	.03	3	75	4	3	76	2	3
Carduelis chloris	1.94	.07	3	73	—	1	68	2	5
Melopsittacus undulatus	2.25	.06	6	185	11	7	116	1	7
Erythropygia galactotes	2.30	.02	3	93	1	2	80	0	3
Lanius nubicus	2.46	—	1	220	—	1	95	—	1
Passer domesticus	2.76	.06	9	252	26	3	102	2	11
Galerida cristata	2.93	.05	12	149	9	12	95	1	28
Pycnonotus capensis	3.05	.14	4	105	13	7	83	1	11
Turdus merula	6.36	.31	4	254	39	4	122	2	12
Streptopelia senegalensis	6.63	.19	7	194	21	5	120	2	9
Streptopelia decaocto	7.45	.13	3	194	9	3	132	3	3
Streptopelia risoria†	8.03	.06	111	207	4	74	119	1	75
Streptopelia turtur	8.30	—	*	221	22	4	137	6	4
Glareola pratincola	8.42	.23	17	359	20	13	151	1	20
Falco naumanni	10.84	.71	2	729	—	1	194	8	2
Athene noctua	14	—	*	384	83	5	187	9	7
Chlidonias leucoptera	14.04	.67	4	323	—	1	148	6	2
Gallinula chloropus	14.29	.64	4**	1,217	232	4	229	5	4
Corvus corone	14.99	.55	12**	387	41	8	177	2	12
Falco tinnunculus	18.09	.37	9**	989	40	7	242	3	9
Alectoris graeca	18.23	.62	7	1,671	162	16	278	4	19
Himantopus himantopus	18.51	.93	2	590	37	2	185	1	2
Tyto alba	18.71	.44	20	740	50	14	241	3	24
Sterna hirundo	19.50	.21	2	281	—	1	171	3	3
Nycticorax nycticorax	20.75	2.20	5	697	103	5	205	3	5
Bubulcus ibis	23.22	.54	5**	645	140	4	204	4	5
Egretta garzetta	28.52	1.54	3	533	33	2	218	1	4
Phasianus colchicus	29.22	.44	4	3,495	233	4	308	7	4
Burhinus oedicnemus	33.51	.53	2	654	65	2	266	10	2
Gallus domesticus	35.88	.21	2	2,552	12	2	295	24	2
Strix aluco	36.14	.28	5	1,134	127	6	268	4	8
Larus ridibundus	37.50	—	*	622	68	5	231	5	5
Ardea cinerea	49.60	.66	2	1,044	446	2	242	12	4
Geronticus eremita	50.16	1.21	5**	1,797	431	3	394	9	5
Gallus domesticus	52.85	.42	12	2,607	514	6	359	7	12
Anas platyrhynchos	54	—	*	2,294	162	3	315	19	6
Buteo rufinus	60.72	—	1	1,846	—	1	371	—	1
Bubo bubo	69.30	1.18	3	2,826	192	3	349	12	5
Ciconia ciconia	78.78	2.76	5	3,912	222	5	502	11	5
Aquila rapax	92.83	.09	2	3,207	543	2	520	8	2
Anser anser	173.01	2.77	2	11,330	283	13	741	16	14
Gyps fulvus	243.88	—	1	5,500	—	1	676	—	1
Struthio camelus	1,460.85	50.07	4***	75,750	1,974	4	2,245	75	4
Streptopelia risoria† (DDE-fed)	7.02	.30	9	152	11	8	107	2	9

* Data from Schönwetter (1960–72).
** Eggs were not entirely fresh.
*** Estimated from volume.
† Experimental birds were orally administered daily 6.25 mg p,p′ DDE per kg body mass. Data and control data from Ar and Maslaton (unpubl. data).

sible explanation for the high r value is the high coordinate values of the Ostrich (*Struthio camelus*) which cause their separation from the bulk of the other results on linear scales. Without the Ostrich values the linear correlation was lower ($r^2 = 0.7133$). Moreover, a *t*-test showed that the slope on the log-log scales (Fig. 1) is significantly smaller than 1.0 ($P < 0.05$; one-tailed *t*-test), indicating a deviation from simple linear regression. The calculated slope on log-log scales for the few species presented by Romanoff and Romanoff (1949), is also lower than 1.0 ($b = 0.836$). Thus, using Equation (1), a thousand-fold increase in mass between 1- and 1,000-g typical eggs is accompanied by only a 556-fold increase in shell strength.

The shell-to-egg mass ratio is relatively low in small eggs. Eggshell density seems to increase slightly with egg mass (Roman-

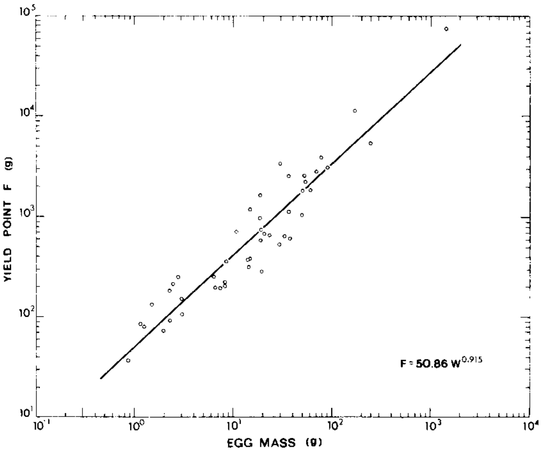

FIGURE 1. Regression of yield point force F on the initial egg mass W (log-log scale). Points represent mean values of the bird species listed in Table 1.

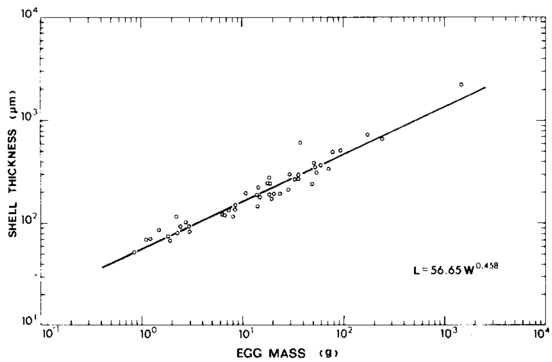

FIGURE 2. Regression of shell thickness L on the initial egg mass W (log-log scale). Points represent mean values of the bird species listed in Table 1.

off and Romanoff 1949, Paganelli et al. 1974). This increase may be related to a decrease in the ratio of organic to inorganic material in the shell, with increasing egg mass. Varying proportions of organic materials in the shells of eggs may influence the brittleness and the strength of the shell's composite material. Porosity (the total effective pore area), increases more than in proportion to egg mass (Ar et al. 1974, Ar and Rahn 1978), and such an increase in perforation may well influence the eggshell strength (Tyler 1955). These counteracting factors as well as special adaptations may influence the final observed relationship between strength and egg mass.

Equation (2) expresses the correlation (shown in Fig. 2) between shell thickness and mass of the above eggs. It is not appreciably different from either the equation of Ar et al. (1974) or the new equation we have derived for 3,434 species (Eq. 3). It shows that, relative to their mass, small eggs have thick shells in spite of the fact that eggshell volume and mass increase more than in proportion to egg mass (Paganelli et al. 1974). However, if linear dimensions are considered (length and breadth), small eggs have relatively thin shells. Thus, for a thousand-fold decrease in egg mass accompanied by a ten-fold decrease in size or in linear dimension, shell thickness is decreased 22.4 times. The Ostrich egg equals 30 hen eggs in mass and 3 hen eggs in length and its shell is 6 times thicker.

Eggshell strength is generally agreed to be some function of shell thickness (Romanoff 1929, Tyler and Geake 1963, Tyler and Thomas 1966, Robinson and King 1970, Carter 1971, King and Robinson 1972) but the correlations are not particularly good (Brooks 1960). Brooks (1960) and Carter (1970, 1976) showed that strength in hen eggs may be correlated both with thickness and with thickness squared. Tyler (1969b) concluded that the correlation with thickness squared is better. However, since most studies were made using eggs within one species, the range of both strength and thickness tested was much limited and both natural and experimental variation ranges were not wide enough to enable clear-cut conclusions (Carter 1976).

From Eqs. (1) and (2) in our results it can be seen that the egg mass power in Eq. (1) of 0.915 is almost exactly twice that of Eq. (2) ($2 \times 0.458 = 0.916$). Eq. (2) squared, where L is expressed in cm, yields

$$L^2 = 3.21 \times 10^{-5}\ W^{0.916}. \qquad (4)$$

In comparing Eq. (1) to Eq. (4), the egg mass factor is cancelled out, and F in kg becomes:

$$F = 1{,}585\ L^2. \qquad (5)$$

The calculated regression of log F against log L yields, not surprisingly, a similar result:

$$F = 1{,}718\ L^{2.022}$$
$$(r = 0.9816,\quad F_{1,45} = 1190.4,\ \text{SEE of log } F = 0.1254). \qquad (6)$$

Since the standard error of the power is 0.06, the value in the equation is not significantly different from L^2. Thus, it becomes clear that there is a highly significant correlation between egg strength, as expressed by its yield point, and the square of shell thickness, among species.

EGGSHELL SPECIFIC STRENGTH

Another way of expressing these results is to look at the eggshell strength per unit of thickness (F/L): this value, which might be called the specific strength of an egg, is proportional to the eggshell thickness. This idea was briefly mentioned by Tyler and Geake (1963), who used, as a measure of eggshell strength, the strength estimate per standardized thickness (Carter 1971). The value F/L may be predicted either from Eq. (6) if thickness is known (F/L = 1,718 L kg/cm), or directly from Eqs. (1) and (2) if egg mass is known ($F/L = 8.98\ W^{0.458}$ kg/cm). The results we present for the Ringed Turtle Dove (*Streptopelia risoria*; Table 1) show that DDE-treated females lay eggs whose shells are 90% the thickness of the control, and their strength drops to 74% of the control value. The question that may arise is whether this weakening may be explained by the thinning alone, or whether there are additional structural influences involved. The calculated specific eggshell strength according to either Equations (1) and (2) or Equation (6) is reduced by 6–10% in the treated birds, which may lead to a conclusion that eggshell thinning alone was responsible for reduction in strength. However, the measured F/L ratio is actually 18% lower in eggs of DDE-treated females, as compared to the controls, indicating that shell quality has been affected as well (King and Robinson 1972).

THE STRESS COEFFICIENT AND EGGSHELL YIELD POINT

While, within species, the force per unit of thickness (F/L) is a valuable tool for tests of eggshell quality, it is not suitable for interspecific comparisons, since it varies with eggshell thickness. For interspecific comparisons we propose the following:

In the Strength of Materials Theory, the maximal stress in a thin-walled sphere or cylinder is defined as being directly proportional to the radius of the object r, to the pressure applied P, and inversely proportional to the wall thickness L. Thus, for an egg assuming a mean radius $\bar{r}$ and a constant maximal stress σ_m: $\sigma_m \propto (P \cdot \bar{r})/L$.

P is, of course, force per unit of eggshell area, when this force is distributed equally over the surface of the egg. In our case, the force was applied to the poles of the eggs. We assume that the area in question is proportional to the cross-sectional area of the shell—namely, $2\pi\bar{r}L$. This area is the same for every cross-section plane in a thin-walled sphere; hence the egg may be regarded as a pole or hollow cylinder subjected to buckling load. With such an assumption, the above expression becomes $\sigma_m \propto (F \cdot \bar{r})/(L \cdot L \cdot \bar{r})$, and $\bar{r}$ is cancelled out to give:

$$\sigma_m \propto F/L^2. \quad (7)$$

As may be seen from Eq. (6), the ratio F/L^2 has the numerical value of 1,718 kg/cm^2 or atmospheres. Thus, we consider it to be an estimate of eggshell yield point stress of the avian egg, irrespective of mass and shell thickness, and a predictor of strength values. The egg of the extinct *Aepyornis*, which had an average shell thickness of 0.38 cm (Schönwetter 1960–72), would have had a yield-point of 248 kg, assuming it was a "normal" egg, where the bird is estimated to gross about 440 kg (Amadon 1947), so that she would certainly have had to incubate carefully.

THE RELATIONSHIP BETWEEN EGGSHELL STRENGTH AND MASS OF THE INCUBATING BIRD

Rahn et al. (1975) have gathered data which show that, in spite of differences amongst orders, and between altricial and precocial birds, a general relationship may be drawn between bird body mass B and egg mass W in the form of $W = 0.277\ B^{0.770}$. They have graphically shown that percent egg mass as a function of body mass declines from some 20% in the smallest birds to about 2% in the largest birds (over the entire range of body size in birds). Combining the above equation from Rahn et al. with ours (Eq. [1]), and solving for F = B, we have calculated that the largest egg which can withstand the entire mass of an incubating parent is an egg of 363 g. If we take into account the variability of both equations, the above estimate of egg mass more or less covers the range between 100 and 1,000 g. (It does not, however, by any means imply that the entire weight of the incubating bird is always pressing on the individual eggs in the nest.) Thus it seems that in large birds, strength may be a greater limiting factor in survival than in small birds, which may have eggs with a strength exceeding their body mass several times. Bird species with large eggs would be relatively more liable to egg breakage (caused by accidental stepping-on) than birds with small eggs. A quantitative measure of the resistance to accidental breakage in the nest (S) may be described in the form of:

$$S = (F/B) - 1 \text{ (dimensionless).}$$

S describes a safety factor component of the egg strength countering the risk of accidental breakage in the nest. Amongst species, the smallest one we tested, the 8 g Palestine Sunbird (*Nectarinia osea*), has a safety factor of S = 3.6, while a median-size Ostrich, of 84 kg (G. A. Clark Jr., pers. comm.), has an S value of −0.1.

Thus, under the influence of insecticides, when shell strength and thickness decrease, the eggs of large species of birds would, in general, be more susceptible to breakage. Unfortunately, we were not able to find references to paired measurements of F and B that would allow the calculation of the safety factor changes in control and experimental conditions. From the work of Peakall et al. (1973), however, we were able to estimate roughly (although a different egg-crushing method was used) that control eggs of domestic ducks (*Anas platyrhynchos*) had S = 1.3 while DDE-treated duck eggs had S = 0.75, only.

For the Ringed Turtle Dove values cited in Table 1, where B averages 150 g, S of the control was 0.46, whereas the S of the DDE-treated dove eggs was 0.02, which indeed corresponded to a high incidence of egg breakage in the nests of the latter doves.

SUMMARY

Paired values of yield point force F (defined as the load required to initiate egg crushing when applied to both egg poles), and eggshell thickness L of 47 species of birds ranging in mass between approximately 1 g to 1,500 g, are reported. An equation describing F (g) as a function of egg mass W (g) was obtained: $F = 50.86\ W^{0.915}$. L (μm) for the same eggs was formulated as $L = 56.65\ W^{0.458}$, not significantly different from the general equation obtained for 3,434 eggshell thickness values gathered from the literature: $L = 54.06\ W^{0.448}$.

We conclude that egg strength as measured by yield point force is correlated with thickness squared. Thus, F/L, force per unit thickness, is proportional to shell thickness among species. This ratio may be used in resolving influences of treatments within a species: DDE-treated Ringed Turtle Doves lay eggs which are weaker because their shells are not only thinner but also of lesser quality.

The calculated constant of $F/L^2 = 1{,}718$ kg/cm^2, estimates the yield point stress of the typical avian egg and is employed to predict F from eggshell fragments. Given a bird mass B, a safety factor against egg breakage in the nest may be designated as S = (F/B) − 1. Its dimensionless value in different species tends to decrease with increasing egg and bird mass, indicating that large bird eggs are more susceptible to accidental breakage in the nest and would be more influenced by environmental contaminants.

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