

WETTABILITY AND PHYLOGENETIC DEVELOPMENT OF FEATHER STRUCTURE IN WATER BIRDS

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INTRODUCTION

Many water birds spend a large part of their lives in or under water. It is therefore not surprising to find that extensive physical and behavioural adaptations occur in a wide variety of aquatic birds to deal with the problem of shedding water continuously. Very few birds, if any, allow water to penetrate to the skin, and all feathers invariably exhibit the structural elements required to provide a basis for flotation or to establish a lasting water repellency.

Water birds, and, in particular, ducks, were generally regarded as having attained perfection in water repellency, and this quality was usually attributed to the superior properties of the uropygial gland oil. The gland is largest in aquatic birds but some birds lack the gland altogether. Some experiments in which the gland was extirpated failed to show that the oil is indispensable and no evidence of the oil having any value in waterproofing was found by several workers (Rutschke, 1960). Early investigation into the chemical composition of the oil revealed the presence of an ester of octadecylalcohol and a fatty acid (Elder, 1954) and possibly of cholesterol. The fatty nature of the octadecyl hydrocarbon chain rules out the feasibility of a greatly increased waterproofing, compared with ordinary paraffin waxes, based on elementary physico-chemical principles (Moilliet, 1963). Further support for the conventional nature of gland oil is the finding that when the oil is spread on a *smooth* solid substrate, a contact angle of 90° and 60° is measured for the advancing and receding drop respectively. This is essentially the same as found for any waxy surface (Adam, 1956).† Thus, both chemical and physical evidence suggests that factors other than the properties of the gland oil are responsible for the unusual water-shedding qualities of feathers.

Later studies on the wettability of porous surfaces by Cassie & Baxter (1944) have shown that the water repellency of a surface with air entrapped in the interface is greatly enhanced by some structural parameters peculiar to the surface. These principles are also applicable to feathers. In fact, a microscopic investigation reveals that the substructure of feathers conforms closely to the theoretical requirements of optimal water repellency (Rijke, 1968, 1967). The effective contact angle θ_A , which causes the drop to 'pearl' and roll off, is related to the true contact angle θ by

$$\cos \theta_A = f_s \cos \theta - f_a, \quad (1)$$

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† The contact angle is the angle between the tangent to the curved air-water surface at the point of contact with the solid surface, measured through the water. The extent of water repellency can be conveniently expressed in terms of this contact angle.

where f_s is the area of solid-water interface and f_a that of air-water interface per unit apparent surface area. The true contact angle θ is the contact angle that water drops would establish if the feather surface were smooth and continuous without the formation of air-water interfaces. It is seen from equation (1) that θ_A will always be larger than θ if f_a is positive, i.e. when air-water interfaces are formed. θ_A will be larger if f_a is larger and f_s is smaller.

When drops of water under zero hydrostatic pressure rest on a feather surface, a flat air-water interface will touch the barbs under a contact angle θ , as depicted schematically in Fig. 1. The solid-water interface in this cross-section is given by the arc BC . Elementary calculations on this model show that (Cassie & Baxter, 1944)

$$f_s = (\pi - \theta) r / (r + d) \quad (2a)$$

and

$$f_a = 1 - r \sin \theta / (r + d), \quad (2b)$$

r being the radius of the (cylindrical) barbs with their axes $2(r+d)$ apart. It is seen that the contribution of the feather structure to the values of f_s and f_a is determined not by the absolute value of the radii of the barbs and their distance apart, but by the

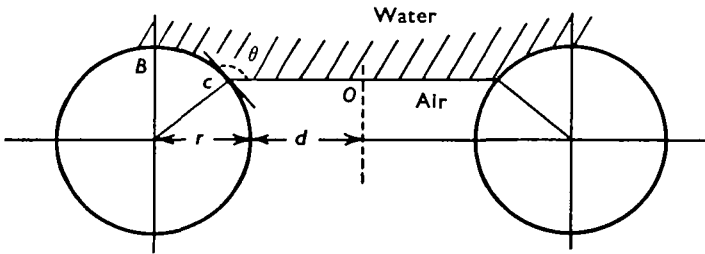


Fig. 1. Schematic of cross-section of two barbs with their axes perpendicular to the plane of the paper (barbules not shown). $f_s = (\text{arc } BC)/(r+d)$ and $f_a = (CO)/(r+d)$.

ratios $(r+d)/r$ only. Large values for this ratio mean large f_a and small f_s values, increasing the apparent contact angle in the manner described by equation (1). The effect of relatively small values of $(r+d)/r$ on the increase of the contact angle θ_A is very pronounced; for instance, when $(r+d)/r$ is 3, a contact angle of 90° gives an apparent contact angle $\theta_A = 130^\circ$; if $\theta = 60^\circ$, θ_A will be 115° . A similar reasoning applies to the barbules. Assuming that the two sets of parallel barbules intersect each other under an angle ψ , the relative areas of solid-water and air-water interface can be calculated to be

$$f_s \simeq (\pi - \theta) \left[1 - \frac{d_1 d_2 \sin^2 \psi}{(r_1 + d_1 \sin \psi)(r_2 + d_2 \sin \psi)} \right] \quad (3a)$$

and

$$f_a = \left[1 - \frac{r_1 \sin \theta}{r_1 + d_1 \sin \psi} \right] \left[1 - \frac{r_2 \sin \theta}{r_2 + d_2 \sin \psi} \right], \quad (3b)$$

where the subscripts 1 and 2 refer to proximal and the distal set of barbules respectively. The rigorous expression for f_s differs from the right-hand side of equation (3a) by a factor $r_1 r_2 [1 - (\pi - \theta)/\sin \psi]$. For values of ψ observed to range between 60° and 75° this factor equals zero for θ between 130° and 124° . The experimentally

measured value for θ is about 90° , but this difference introduces only a very small error as $r_1 r_2$ is invariably small.

The equations (3) are similar to equations (2) in that, apart from the angle ψ , only the ratios $(r+d)/r$ contribute to the values of f_s and f_a and not the absolute values of r and d . Equation (1) is valid only for finite values of θ , viz. θ larger than about 10° , and indicates that the contact angle—and, herewith, the water-shedding properties—are greatly enhanced by structural features. Contact angles smaller than about 10° are not increased according to equation (1), and surfaces that show all the qualities for optimal water repellency are wetted instantaneously if the contact angle θ is zero. These conclusions have been tested experimentally and found to be correct using paraffinated ($\theta = 114^\circ$) and uncoated ($\theta = 0$) stainless steel wire grids (Rijke, 1965). On the other hand, experiments on ducks without oil glands whose feathers had been de-fatted with ether and alcohol have seemingly failed to support these findings (Rutschke, 1960). Only after several weeks did the ducks start to avoid water when their feathers became rough and brittle and lost their normal coherence. This observation has given rise to the assumption that the gland oil mainly serves as a lubricant, keeping the feathers smooth and flexible, whereas the excellent water repellency would be exclusively due to the feather structure. Equation (1) and the experiments with wire grids have shown that this cannot be correct. Structure alone cannot confer water repellency. The relatively long-lasting water repellency after the feathers had been washed with ether and alcohol is presumably due to the great difficulties to be expected when trying to remove the gland oil completely. Zisman *et al.* (1957) have shown that the removal of fatty monolayers adhering to solid surfaces is, even if possible, extremely tedious, and a single monolayer is sufficient to alter the surface properties drastically. A simple solvent rinse will certainly fall very short of a complete de-fatting. The function of the gland oil necessarily involves, besides lubrication, the basis for a finite contact angle θ , which, in turn, is considerably increased as a result of surface structure. This also explains why the treated ducks did not avoid water until later when the structure, rather than the contact angle θ , began to fail for reasons of roughness and inflexibility.

The radii of the barbs and the distance between their axes have been measured for mallards, *Anas platyrhynchos*, and found to be about 46μ and 270μ respectively near the rachis and slightly higher in the middle regions. This corresponds to an $(r+d)/r$ value of 5.9. Inserting this value in equation (2) and using 90° and 60° for the advancing and receding contact angle θ respectively, we calculate an effective contact angle θ_A , according to equation (1), of 150° and 143° , roughly correct according to experimental observations. These high contact angles cause the water to 'pearl' off the duck's back indefinitely, and this excellent characteristic, due to the physical structure of the feathers, is preserved by elaborate and frequent preening by the bird. Similar measurements have been performed on cormorant feathers yielding somewhat lower values for $(r+d)/r$ and the reduced water repellency has been proposed as the proximate cause of the cormorant's characteristic habit of wing-spreading (Rijke, 1968, 1967).

In this paper we report our results of a study on the feathers of a large number of water-bird families which show an evolutionary pattern in terms of waterproofing structure.

EXPERIMENTAL

Breast feathers were measured under a suitable microscope provided with a calibrated scale ocular. Only the structured parts of the feather, which allow for an evaluation in terms of water repellency, were recorded. Other parts that had obviously suffered from damage or abrasive effects were ignored. In a few cases where the presence of large amounts of preening oil was expected to have affected the dimensions the samples were rinsed in a 50/50 alcohol-ether mixture by soaking overnight.

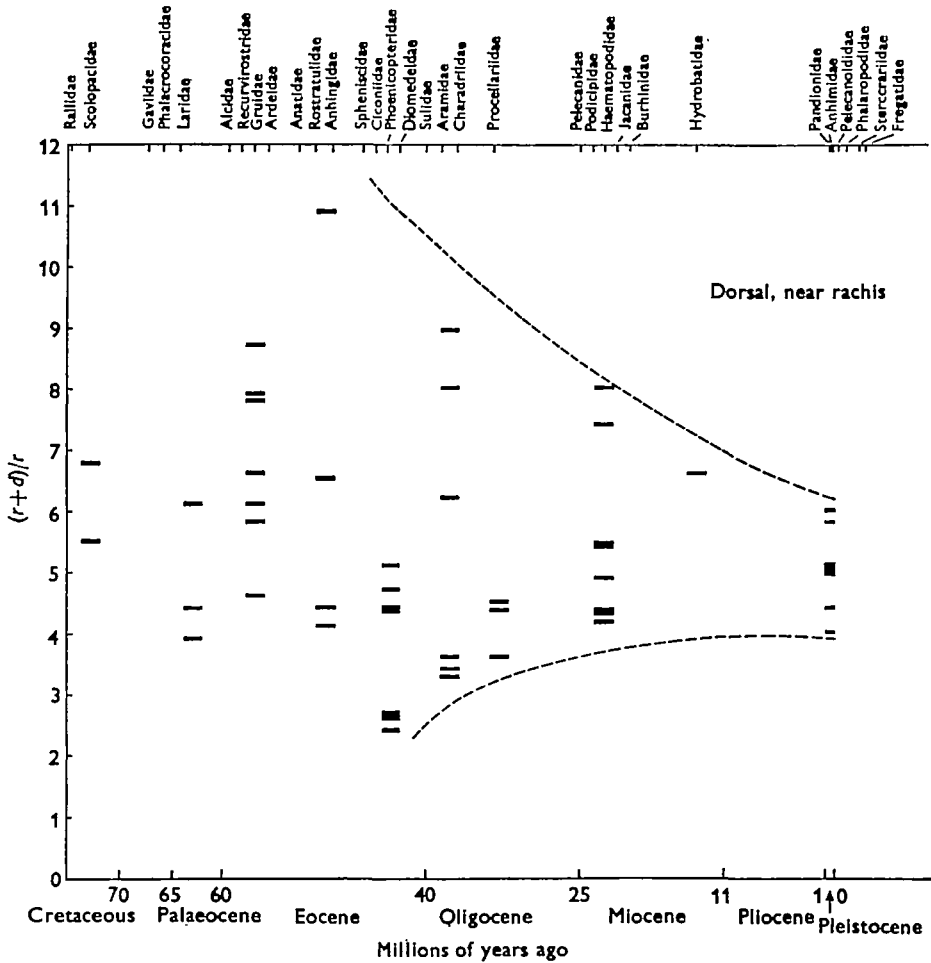


Fig. 2. Values of $(r+d)/r$ for water-bird feathers plotted against geological time interval of earliest fossil record. Values measured for dorsal side near rachis.

RESULTS AND DISCUSSION

Feathers of at least one species of every available aquatic family were investigated and the results were compared with those of another specimen or species of the same family in order to ascertain that the observed $(r+d)/r$ values are representative of the

family. $(r+d)/r$ values are nearly always larger in the middle region of the vexillum and frequently immeasurable at the edges, due to extensive fraying. The results are summarized in Figs. 2 and 3, where the $(r+d)/r$ values of the barbs are given for 45 species of 32 different families of water birds for the dorsal and ventral side respectively. It is seen from the figures that the values cover a wide range from about 2 for

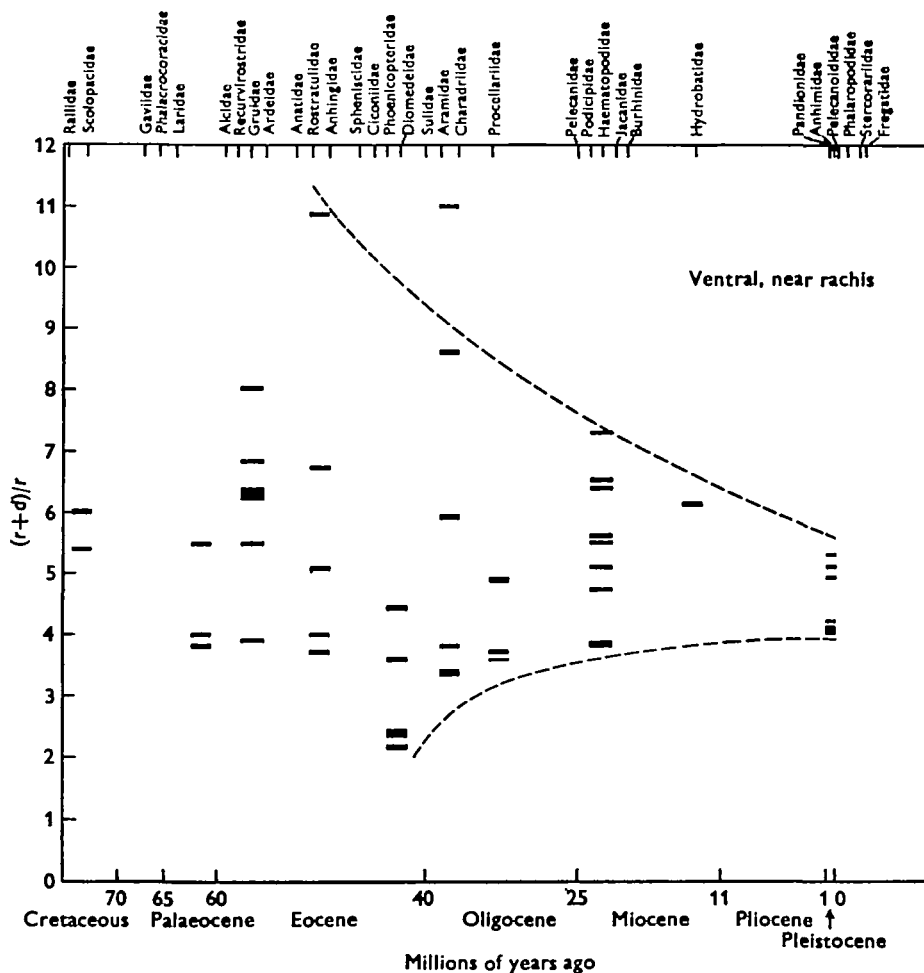


Fig. 3. Same as under Fig. 2 for values of $(r+d)/r$ measured for the ventral side near rachis.

penguins (Spheniscidae) to about 11 for darters (Anhingidae*) but for a large number $(r+d)/r$ values lie between 4 and 6.5. Values for the ventral side are generally somewhat smaller, as a comparison between Figs. 2 and 3 illustrates. This means, therefore, that the ventral side is somewhat less water repellent than the dorsal side, a feature that becomes readily evident when a duck's feather is dipped into water and then withdrawn. The difference between the contact angles at the dorsal and ventral side is easily seen and gives an excellent demonstration of the importance of surface

* An earlier study (Rijke, 1968) showed $(r+d)/r = 4.5$ for a quill feather of *Anhinga rufa*.

structure for water repellency. The large effective advancing and receding contact angles shown by feathers have much significance for the movement of water drops on these surfaces. The drops move much as drops of mercury move on glass surfaces and an excellent water resistance will be maintained provided that water drops do not penetrate the feathers on impact and that the weight of the bird does not force water between the barbs and barbules. This latter will be prevented if the distance between the barbs ($2d$) is sufficiently small. The combination of large $(r+d)/r$ and small d values can only be realized if r is very small. In actual practice, however, the barb diameters ($2r$) are rarely smaller than $30\ \mu$. This sets a natural upper limit to $(r+d)/r$ if the feather is to act as a functional water-resistant structure. Above this limit small water drops (about $450\ \mu$) can pass unobstructed, and only a slight pressure will be enough for the water to penetrate. Virtually all water-bird feathers show barb diameters between $30\ \mu$ and $80\ \mu$, and the upper limit for effective water-resisting properties consequently varies with family. Thus, the range of $(r+d)/r$ values that is associated with outstanding waterproofing qualities is restricted; small $(r+d)/r$ values will insufficiently increase the effective contact angle θ_A , whereas too large values will be associated with poor resistance to water penetration and the passage of small drops.

The pressure required to force water between the parallel barbs can be regarded as that necessary to produce the curved air-water interface at the moment of penetration. This pressure is

$$P = \gamma/R, \quad (4)$$

where γ represents the surface tension of water (72 dynes/cm.) and R is the principal radius of curvature (Adam, 1956). It can be shown that R will have its minimum value when the centre of curvature is located in the plane of the barb axes at a distance $r+d$ from these axes (dotted line in Fig. 1). We have then

$$R = r \left[\cos \theta + \sqrt{\left(\frac{r+d}{r}\right)^2 - \sin^2 \theta} \right]. \quad (5)$$

Inserting $\theta = 90^\circ$ for the advancing contact angle we can then calculate the pressure required to force water through the barbs. The results are shown in Fig. 4, where the pressure in g./cm.² is plotted against the parameter $(r+d)/r$ for a range of r values which corresponds to those measured on the water-bird feathers. It is seen from the figure that the effect of the thickness of the barbs is very pronounced, particularly in the high $(r+d)/r$ range. For example, in order to establish a $(r+d)/r$ value of, say, 6, so as to obtain good water repellency, the radius of the barbs should be less than $30\ \mu$ to ensure that a water pressure of 4 g./cm.² does not force water to pass between the barbs. Or, alternatively, if the radius of the barbs is $30\ \mu$, $(r+d)/r$ values larger than 6 will allow the water to penetrate into the feathers unless the pressure that the birds exert on the water is less than 4 g./cm.². This pressure is closely related to the weight of the bird, the surface of contact with the water and the bird's particular habits in the water. Fig. 5 provides a number of examples. Here the pressure in g./cm.² is plotted against $(r+d)/r$, according to equations (4) and (5) (thick lines) for four water birds of different families. The upper shaded regions correspond to the maximum weight for no water penetration between the barbs, using values for $(r+d)/r$ measured near the rachis (upper limit) and in the middle region of the vexillum (lower limit). The lower shaded regions correspond to the range of weights for the birds, expressed in

weight per unit area of surface contact with water. The area of contact with water was assumed to be elliptical allowing a simple calculation of the surface area. The weight ranges as shown in Fig. 5 are probably too wide because the recorded maximum and minimum weights were divided by a contact area measured on a single specimen only, whereas it is likely that the size of the bird would vary with weight. Nevertheless, the results show quite clearly the effects of the various $(r+d)/r$ values in relation to penetration pressure and weight. Feathers of *Larus fuscus* give values between 6.2 and

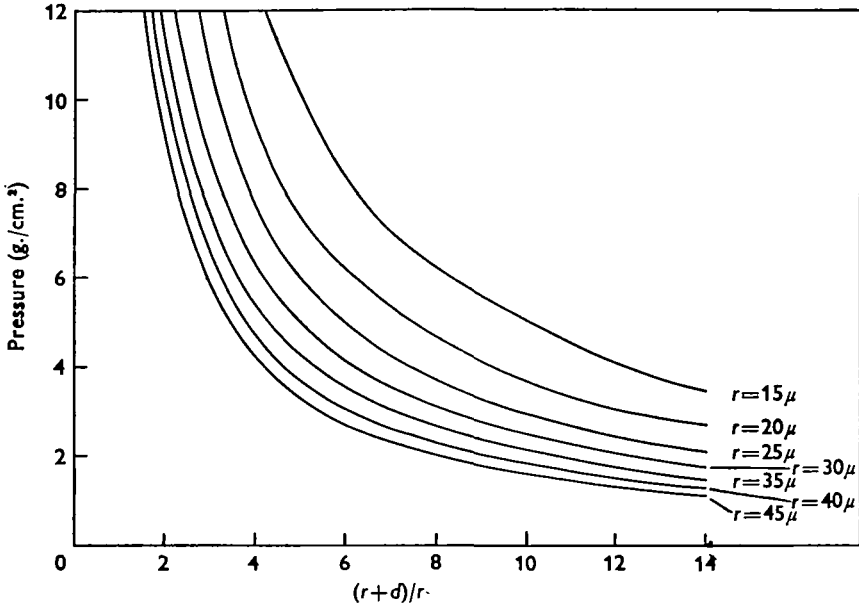


Fig. 4. Plot of pressure in g./cm.² versus $(r+d)/r$, according to equations (4) and (5).

7.2 for $(r+d)/r$, which indicates excellent water-repelling qualities. The weight of this particular specimen was only 654 g., corresponding to a pressure of 2.67 g./cm.². As a result, the pressure that the weight of *Larus fuscus* exerts on the water when swimming remains well below that required to force water between the barbs. In fact, as can be read from the graph, a $(r+d)/r$ of about 10 for $r = 25 \mu$ could be tolerated without the risk of water penetration. Excellent water repellency is also experienced by Anatidae with $(r+d)/r$ between 5 and 6. The weight range for *Alopochen aegyptiacus* is, however, not very much lower than the maximum weight for no penetration. The same result was found for *Anas undulata*. The conditions for Ardeidae, on the other hand, are less favourable. Values for $(r+d)/r$ range between 6 and 8, indicating that water drops will readily 'pearl' and roll off, but the ranges for weights and pressures to cause penetration overlap completely. This implies that a swimming *Ardea cinerea* will suffer from water penetration between barbs, and provides possibly one of the reasons why Ardeidae prefer shallow lakes and river banks where they can wade rather than depend on their buoyancy.

A somewhat unusual set of results is found for Spheniscidae. Values for $(r+d)/r$ are exceptionally small, between 2 and 3, which explains their familiar 'wet' appear-

ance. The whole body is very densely beset with small feathers with wide, flat rachis. The barbs are relatively thick, $r = 38 \mu$, and lengthy barbules densely cover the intermediate spaces and extend beyond the neighbouring barbs. The range of maximum weight for no penetration is very wide, since the low $(r+d)/r$ values coincide with the

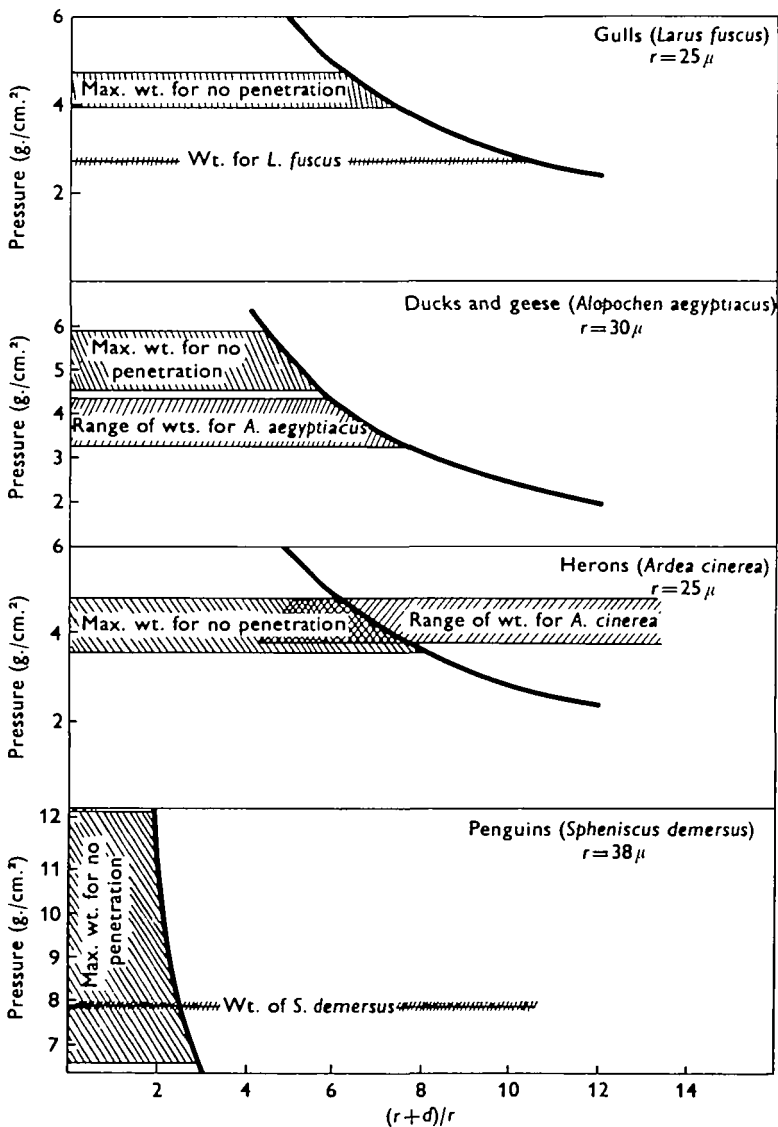


Fig. 5. Plot of pressure in g./cm.² against $(r+d)/r$ for four species of different families, showing regions for maximum weight for no penetration and weight ranges of the species.

steep part of the curve. The weight of *Spheniscus demersus* lies within the lower part of this range, so that a certain extent of water penetration is likely to occur. The rich growth of barbules, on the other hand, could very well assist in resisting extensive water penetration. Apart from serving as a highly sophisticated water-repelling

structure, feathers perform many other—aerodynamical, hydrodynamical and heat-preserving—functions. Several structural requirements may therefore have evolved by sacrificing perfection for versatility. This is most likely to occur when adaptations to extreme conditions need to be made. The relatively poor waterproofing of Spheniscidae should possibly be viewed in this light.

A number of other families, where data were available, have been investigated for their water resistance. The results indicate the Podicipedidae and Burhinidae are comparable to *Larus fuscus*. Sulidae are very similar to Anatidae.

In Figs. 2 and 3 the values for the parameter $(r+d)/r$ of the different families are placed in the geological time interval that corresponds to the earliest fossil finding of the family (Brodkorb, 1967; Harland, 1967). It is seen that the widest range of the structural parameter occurs in the middle and upper Eocene when many birds existed whose anatomical characteristics were closely related to those of their present-day descendants. Fossil records from more recent periods involve families with more narrowly spaced $(r+d)/r$ values, which ultimately narrow down to the range of about 4 to 6 for families of Pleistocenic origin. The few early records from upper Cretaceous and Palaeocenic times also show a limited range, but this is probably coincidental since the fossil information from these ancient periods is inevitably scarce.

Several points require further attention. First, a survey of the known fossil forms reveals that the record is not continuous. Gaps of many millions of years exist and many families are missing altogether (Brodkorb, 1967). Only 32 out of the 45 families studied are reported on here by reason of the incompleteness of the record. Second, the earliest fossil findings do not necessarily indicate the periods in which the birds evolved into their present forms. It is quite possible that they were already well established before then, and future discoveries may well bear evidence upon this point. This means that we have at most an estimate of the minimum duration of the family history. Thus, the true positions of the points in Fig. 2 and 3 may well lie more to the left. Third, there is no *a priori* reason to assume that the structural characteristics of the feathers evolved simultaneously with the anatomical features that classify the families. Studies on the actual fossil records could provide a fair argument for the validity of this point, but, although possible in principle, it is doubtful whether many records allow a reliable evaluation. As a result of this uncertainty the points in the figures may deviate vertically from their present positions, or, alternatively, fossil records of a later date than those indicated would be more representative. In spite of this there is clearly a phylogenetic tendency toward increasingly enhanced water repellency and resistance to water penetration with the course of time, as indicated by the lower and upper dotted lines in the figures. The lines converge to a $(r+d)/r$ range of about 4 to 6, which corresponds to structures of optimal waterproofing properties. The specific optimal $(r+d)/r$ value for each family varies within this range, depending on barb radius, r , weight and size characteristic of the family as outlined above.

It is tempting to speculate on how certain behavioural patterns may have evolved under the selective pressure of poor water repellency or poor resistance to water penetration. The underwater feeding habits of Anhingidae are probably assisted by extensive penetration, where too much buoyancy would prove to be a disadvantage. Their characteristic habit of wing-spreading, on the other hand, probably serves to

dry the feathers after a period in the water (Rijke, 1968, 1967). Feathers of the brown pelican, *Pelecanus occidentalis*, have much smaller barb diameters and slightly higher $(r+d)/r$ values than those of Ethiopian pelicans. The resulting increased waterproofing qualities may well be an adaptation to their habit of diving for food from the air, a different behaviour from that exhibited by other pelicans. Many waders and shore birds with their high $(r+d)/r$ values appear to be well equipped to shed water drops continuously, but, in general, are less suited for swimming. The opposite appears to be true for the fully aquatic families such as Gaviidae, Phalacrocoracidae, Alcidae, and Spheniscidae which show low $(r+d)/r$ values, combining relatively poor water repellency with a good resistance to water penetration. They spend long periods lying deep in the water. Procellariidae also show small $(r+d)/r$ values but the closely related Hydrobatidae show 6.3. Such a high value suggests a relatively poor resistance to water penetration, possibly a reason why Hydrobatidae feed from the water surface without alighting; but on the rare occasions that they do alight, they float buoyantly high on the surface (Austin, 1963) as a direct consequence of the greatly increased contact angle θ_A .

As a comparison a number of non-aquatic families have been investigated as well. Caprimulgidae, Psittacidae, Apodidae, Cuculidae and Columbidae yield $(r+d)/r$ values ranging between 6 and 11, which suggest that they have evolved in their terrestrial habitat under the pressure of water repellency only, without the necessity to prevent water penetration.

It is to be expected that several other examples will corroborate the conclusion that water repellency and resistance to water penetration are determinative for specific behavioural patterns. It should be borne in mind, however, that the principles which govern waterproofing properties are not limited to parameters expressed in terms of barb distance and diameter only. For instance, a similar role in effecting waterproofing is played by the barbules which will add additional potential waterproofing qualities to the feathers by virtue of their small size. Moreover, the manner in which the feathers are packed together will add another dimension to the functional structure. However, these contributions are operative on the basis of the same principles that underlie water repellency and resistance to water penetration as outlined above for the barbs.

SUMMARY

1. The water repellency of feathers is determined mainly, but not exclusively, by a structural parameter which can be expressed in terms of diameter and spacing of the barbs and barbules.
2. Effective waterproofing properties result from the optimal balance of structural parameter and resistance to water penetration.
3. Comparison of the structural parameters for water birds with the geological time interval of their earliest fossil record shows a phylogenetic tendency toward optimizing waterproofing properties with the course of time.
4. Several behavioural patterns are discussed which may have evolved under the selective pressure of the quality of water repellency and resistance to water penetration.

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