duced in the ratios given in Table 1 would constitute a considerable portion of the external hazard of fallout, particularly at times greater than 1 yr.

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7 July 1958

Ontogeny of Hemoglobin in the Skate Raja binoculata

In all sufficiently studied mammals, the fetus has a hemoglobin that is biochemically distinct from that of the adult (1). Ontogenetic changes in the hemoglobin are found also in the chicken (2),



Fig. 1. Oxygen dissociation curves of hemoglobin solutions prepared from blood of adult (approximately 100 kg), fetal (9 g), and embryonic (1.5 g) skates. Conditions: 1.5 percent hemoglobin in potassium phosphate buffer; final ionic strength, 0.267; pH, 6.50 to 6.58; temperature, 10°C. Crosses represent a solution of adult hemoglobin subjected to a second analysis 48 hours after the original determination of the oxygen equilibrium.

the terrapin (3), the bullfrog (4), and the teleost fish Scorpaenichthys (5). The possibility that a developmental sequence of at least two hemoglobins is characteristic of the vertebrates appears to be contradicted by McCutcheon's failure to find any difference between the hemoglobin of adult and fetal viviparous rays (3). However, McCutcheon states: "The lack of early stages in the collections leaves open the possibility of an early developmental Hb [hemoglobin] with a higher affinity [for oxygen] than fetal and adult Hb." Because a few egg-cases of the barn-door skate Raja binoculata were collected during otter-trawling, it was possible to study the oxygen equilibrium of hemoglobin solutions and erythrocyte suspensions (equivalent to blood) of this oviparous elasmobranch in individuals of various ages (6).

A comparison of oxygen dissociation curves of adult, fetal, and embryonic hemoglobin is shown in Fig. 1. From such data one can calculate (7) the two constants of the Hill approximation: p_{50} is the oxygen tension at which there are equal quantities of oxygenated and deoxygenated hemoglobin; and n is a measure of the heme-heme interactions. The parameter n determines the shape of the oxygen dissociation curve, and p_{50} determines the position of the curve. Figure 2 shows the variation of these two constants as functions of pH for skate hemoglobin inside and outside the erythrocyte. From the information presented in these figures it can be concluded that fetuses (wet weight 9 to 27 g) and adults (to 100 kg) have hemoglobin with the same oxygen equilibrium.

This finding parallels the studies of McCutcheon on viviparous rays (3). However, the hemoglobin of three embryos (wet weight 1 to 1.6 g) possessed a slightly higher oxygen affinity in both erythrocyte suspensions and hemoglobin solutions; furthermore, for this possible "embryonic hemoglobin," heme-heme interaction was almost completely removed by hemolysis and subsequent dilution, whereas the same treatment did not alter "fetal and adult hemoglobin" in this respect. It is entirely possible that some adult hemoglobin was present along with the embryonic hemoglobin; however, since n for hemoglobin solutions obtained from the embryos was 1.1, as opposed to n = 1.5 to 1.8 for adult and fetal hemoglobin in solution, one can calculate, assuming that n cannot be less than 1.0 for embryonic hemoglobin and that no embryonic hemoglobin is present in adult skates, that at least 80 percent of the hemoglobin present in these embryos is of a distinct type. Further experimentation is limited by the scarcity of egg-cases and the small quantity of hemoglobin available from embryos (0.2 ml of a 1.5 percent hemoglobin solution from a 1.6-g embryo).

Since the skate egg-case, in which the embryos and fetuses remain for 1.5 to 2 years of development, is relatively isolated from the environment except for the diffusion of respiratory gases (the "cleidoic" condition) (8), it might be expected that hemoglobin with high oxygen affinity would be needed throughout not only the embryonic but also the fetal period, in contrast to observed results. However, observations on ten egg-cases indicated the egg-case is a "closed system" only during the first few months of development. When the egg-case is laid, a hole (2 by 4 mm) at each of the four corners is plugged with a very viscous mucus, which is gradually dissolved during development. In all fetuses with adult hemoglobin, the four holes were open; in the embryos weighing 1 to 1.6 g, only two of the holes were still plugged. The oxygen tension [polarographically determined (9)] inside these egg-cases was rarely less than half that of sea-water. The urea retention function of the skate egg-case (8) must take place only during the initial phases of development, although even small embryos



Fig. 2. Oxygen affinity (top) and hemeheme interaction (bottom) as functions of pH for the hemoglobin in solution and in erythrocytes for adult, fetal, and embryonic skates. Conditions: 1.5 to 2 percent hemoglobin solution in potassium phosphate buffer; final ionic strength, 0.267; erythrocyte suspensions in elasmobranch Ringer's solution; temperature, 10 to 11°C.

(wet weight 0.5 g) survived for weeks in running sea-water. The function of the egg-case for the entire 1.5-to-2 year period is protection of the embryo and the external yolk sac from injury; only when the external yolk sac is completely absorbed does the young skate hatch. In contrast to the transient existence of "embryonic hemoglobin" in the oviparous skate, the ovoviviparous shark Squalus suckleyi has a distinct fetal hemoglobin throughout its 23-month gestation period (10).

The widespread phylogenetic distribution of the ability to synthesize a fetal or embryonic hemoglobin of high oxygen affinity in egg-laying vertebrates (skate, bullfrog, terrapin, and chicken) represents a biochemical "preadaptation" (11) which has made possible the development of the oxygen-transfer system involved in the diffusion of oxygen from maternal to fetal blood (1) in the polyphyletic evolution of ovoviviparty and viviparity in many vertebrate groups.

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Density of the Upper Atmosphere

An atmospheric density at an altitude of about 368 km has been inferred from the orbital behavior and physical characteristics of the American artificial earth satellite Explorer I, also denoted as 1958 Alpha. The orbital data as of 1 February 1958 were (1, 2): eccentricity, 0.139; inclination, 33°.2; argument of perigee, 120°.0; anomalistic period, 0^d.0798274; decrease of period 3.9×10^{-7} day per period or about 0s.42 per day. From these one finds a mean distance of 1.22757 earth radii, corresponding to a perigee height above the international ellipsoid of 368 km.

The satellite is a cylinder 80 in. long and 6 in. in diameter, and it has a mass of about 14 kg (3). The area of such an object that is relevant to its air resistance is its area projected on a plane normal to its direction of motion. The average over all possible orientations, for random tumbling, is one fourth of the total superficial area, or 2520 cm². The same value is obtained if the cylinder spins about a transverse axis, randomly oriented with respect to the orbit plane. Averaged over a spin period, over orientations of the spin axis with respect to the orbit plane, and over the motion of perigee, the same projected area has been obtained as for random tumbling, and has been employed. The aerodynamic drag coefficient has been taken to be 2. The density has been inferred by a method described elsewhere (4) from this value, the mass, the average area, the eccentricity, the mean distance, the rate of decrease of period, and the logarithmic derivative of density near perigee given by the ARDC model atmosphere (5).

The density thus found, 1.5×10^{-14} g/cm^3 at a geometric altitude of 368 km (348 geopotential) is about 14 times that predicted by the ARDC model atmosphere. It falls nearly on the middle curve, No. 2, in a study (6) that tentatively suggested a modification of the ARDC atmosphere to satisfy a density 4.5×10-13 g/cm3 at 220 km (213 geopotential) that had been inferred (7) from observations of the U.S.S.R. satellite 1957 Alpha 2. This value was about 9 times the ARDC density. The values $4.5\times10^{\scriptscriptstyle -13}$ and $1.5\times10^{\scriptscriptstyle -14}~{\rm g/cm^3}$ depend somewhat on the gradients of density of the ARDC model employed in the reductions. It seems better to infer the densities at both altitudes from the observations without recourse to model atmospheres, and to proceed by successive approximations until the gradients and densities are consistent. In this way, from the observations of both satellites together, densities have been inferred of about 4.0×10^{-13} g/cm³ at 220 km and about 1.4×10^{-14} g/cm³ at 368 km.

These values do not agree well with densities predicted by Harris and Jastrow (8) as extrapolations from altitudes of about 220 km and below, but they seem to be in surprisingly good agreement with curve No. 2 of reference (6).

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Density Determinations Based on the Explorer and Vanguard Satellites

Minitrack observations on the orbits of Explorer I and Vanguard I permit us to make a rough determination of the density of the atmosphere at latitudes between 33°N and 33°S (1, 2). Our analysis is based on the orbit elements and rate of change of period obtained from Minitrack data for these satellites by the Vanguard Computing Center. The change in period is the direct result of the drag exerted by the atmosphere, which causes the satellite to lose energy continuously during its lifetime. As the energy of the satellite decreases, it falls towards the center of the earth,

Table 1. Orbital periods for Explorer I, derived by the Vanguard Computing Center from Minitrack data. The third column gives the average value of dP/dt, obtained from the tabular differences in the first and second columns.

Date	P (min)	dP/dt (min/day)
5 Feb.	114.95	
0.4	114 54	0.0073
2 Apr.	114.34	0 0097
2 May	114.25	0.0057
		0.0150
17 May	114.13	
Weighted av. (min/day)		$(9^{+6}_{-2}) \times 10^{-3}$
M/C_dA		$(24 \pm 8) \text{ kg/m}^2$

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