sure pulses were analyzed at different contraction frequencies (Fig. 3). The duration of the systole varied much less with the contraction rate than did duration of the diastole. For both systole and diastole the greatest dependency was exhibited at frequencies below ten beats per minute. Thus the change in contraction frequency of the contractile pumping mechanism depends more closely on a changing duration of the diastole than on a changing duration of the systole, a feature that is basic to all circulatory pumps, invertebrate or vertebrate. The broken line (Fig. 3) shows that the relative duration of systole is only slightly dependent on contraction frequency except at the lowest values. Systole thus makes up a rather constant proportion of the cycle length (20 to 27 percent) at frequencies between 10 and 50 beats per minute.

Rhythmical hemolymph pressures of the magnitude recorded from *P. polymerus* are highly unusual among invertebrates. Indeed, rhythmical contractions of this magnitude involved with circulation and not with burrowing or other locomotory events are unique. Crustaceans generally show hemolymph pressures less than 15 cm-H_2O (*7*). In the large barnacle *Balanus nubilus*, however, internal pressures reach values matching those presently recorded when the animal responds to disturbance by strong muscular contraction (*8*).

The pulsatile pressure in *Pollicipes polymerus* no doubt reflects the contractions of a muscular pumping mechanism, propelling hemolymph unidirectionally. The large pulse pressures suggest circulation in a system of high peripheral resistance. An anatomical basis for such a highly organized circulation in *P. polymerus* has recently been described (*3*).

The identity and location of the contractile pump, however, remains conjectural. The finding of large pressure amplitudes in the rostral sinus supports Cannon's view (*4*) that the rostral sinus, with its valves and encircling muscles, functions as the main propulsive organ in gooseneck barnacles. Further studies are needed to learn whether functional hearts are widespread among cirripeds and other groups of animals that lack obvious tubelike or chambered hearts.

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Photosynthesis and Atmospheric Oxygen

The significance of photosynthesis as a source of atmospheric oxygen was questioned by Van Valen (*1*) who pointed out that the oxygen separated from carbon dioxide by a plant in photosynthesis is necessarily stoichiometrically equivalent to the carbon fixed in the plant cells and is therefore just sufficient to balance the plant's respiration and to oxidize the plant after death, processes in which the carbon recombines with oxygen to form carbon dioxide. From this reasoning he concludes that plants cannot produce a net change in oxidation and that the origin of atmospheric oxygen is unknown. Similar statements have been made by others (*2*).

One important factor is overlooked in this line of reasoning: The rate of cycling or the residence time of carbon in the reduced, "organic" part of the carbon cycle. As long as the carbon is reduced, its equivalent oxygen can remain elsewhere in the system, for example in the atmosphere. Van Valen considers the short life-span of plants and animals (maximum of a few hundred years), but, while he mentions the organic carbon buried in sediments, he appreciates neither its mass nor the time that it remains isolated from oxygen in the atmosphere.

Rubey estimated the mass of carbon now contained as organic debris in sedimentary rocks, dominantly shales, as 68×10^{20} g (*3*). This mass of carbon is the stoichiometric equivalent of 182×10^{20} g of oxygen. The total oxygen in the atmosphere is 11.8×10^{20} g (*4*). Thus the oxygen in the atmosphere can be more than accounted for by carbon fixation by plants in photosynthesis. The balance of the oxygen liberated in photosynthesis, some 15 times that now in the atmosphere, has presumably gone into oxygen sinks such as oxidation of iron, sulfur, and volcanic gases. Cloud examined the balance between the total carbon and the total oxygen in the atmosphere, hydrosphere, biosphere, and sedimentary lithosphere and found that they are approximately in the proportions which would combine to form carbon dioxide (*5*). Although the assumptions are many in such calculations, the approximate balance lends strength to the argument that photosynthesis could account for the oxygen in the atmosphere.

The rate at which organic carbon is being buried in sediments of the deep oceans indicates that only 4 of every 10,000 g of carbon produced by photosynthesis becomes part of sedimentary rocks (*6*). Although this fraction is small, the great length of time which the reduced carbon resides in sedimentary rocks before it is eroded and oxidized accounts for the huge carbon mass which has accumulated and helps stabilize the free oxygen reservoir.

The length of the residence time is determined by the average rate of recycling of shales by erosion which has been estimated by Garrels and Mackenzie to correspond to a "half-mass life" of 600 million years (*7*). This means that only half of the carbon stored in shales would be subjected to weathering and oxidation in 600 million years, and it would presumably be replaced by about the same amount of carbon buried with new shales formed during this period.

If the organic content of shales has been fairly constant through the past

600 million years as indicated by Ronov (*8*) and the volume of sedimentary rocks has been reasonably stable as implied by Garrels and Mackenzie's model, the reservoir of reduced organic carbon has been large throughout the later part of geologic time. This does not require that atmospheric oxygen has been strictly constant; the other oxygen sinks may be important controls and might fluctuate independently. It does imply, however, that there is no need to call on photodissociation of water or other potential sources for atmospheric oxygen. We can thank green plants.

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I did not say (*1*), nor do I see that I implied, that most or effectively all atmospheric oxygen did not originate by photosynthesis. In fact my concern with the great mass of reduced carbon implies a belief that this was the main origin. However, the continual appearance of new reduced material from outside the photosynthetic cycle causes a problem if there is no other process involved, and analogous problems intrude themselves (*1*) in regulation and at the time of origin of an oxidizing atmosphere. Enos (*2*) does not reach these problems.

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Origin of Mitochondria

The origin of eukaryotic organelles is an intriguing phylogenetic question both because of the antiquity of divergence of eukaryotes and prokaryotes and because of the enormous structural and functional differences between these grades of organization. It is refreshing to find a review (*1*) that opposes the widely publicized notion of the endosymbiotic origin of eukaryotic organelles (*2*). We feel, however, that some of the principles of systematics have been ignored by both those in favor of and against the endosymbiosis hypothesis.

According to Raff and Mahler, the time lag between the 1.8-billion-year-old oxidized red beds (an indication of free O_2 in the atmosphere) and the oldest probable eukaryote fossils (Beck Springs Dolomite, 1.2 to 1.4 billion years ago) discredits the endosymbiosis hypothesis. We find nothing in the hypothesis itself that requires that "eukaryotes acquired aerobic symbionts as free O_2 began to appear." The general biochemical opportunism of prokaryotes (witness their present metabolic diversity) suggests that they would quickly evolve to utilize this O_2. That such aerobic prokaryotes would immediately thereafter enter into an endosymbiotic relationship with biochemically more restricted protoeukaryotes, or that they would immediately begin to evolve into such organisms, however, is not clear. Whether endosymbiotic or not, eukaryotes would follow rather than precede the release of O_2 into the atmosphere. That they may have followed the release of sufficient O_2 by some 4×10^8 years seems not in conflict with either hypothesis. On the other hand, given the difficulties of distinguishing small protoeukaryotes from prokaryotes in the early part of the fossil record, it is possible that the two events were more nearly simultaneous than Raff and Mahler indicate.

More to the point is that eukaryotic cells are not just anaerobic cells with mitochondria (*1, 3*). If it can be shown that an aerobic pathway in the cytoplasm is a primitive feature of eukaryotes inherited directly from their prokaryote ancestors, then the endosymbiotic origin of mitochondria is less likely. A homologous aerobic pathway present both in prokaryotes and in the cytoplasm of eukaryotes (and therefore encoded by the nuclear genome) would be inherited by the eukaryote directly from the aerobic prokaryotic common ancestor of both. The protoeukaryote itself would therefore have been aerobic; as such, it would not need an endosymbiont to provide it with oxidative respiratory functions. Some of the data presented by Raff and Mahler support the primitive aerobiosis of eukaryotic cells, whereas other data can be explained equally well by either hypothesis.

Raff and Mahler did not explain what they mean by bacterial and mammalian superoxide dismutases being "different." If the difference indicates that the loci encoding these enzymes are not homologous and therefore have no common ancestry, this is entirely consistent with the endosymbiosis hypothesis. If, on the other hand, the enzymes are homologous, and "different" only indicates that they have a phylogenetically distant common ancestry and have diverged since, this would not be consistent with endosymbiosis, but then the significance would be in the similarity rather than, as Raff and Mahler stated, in the dissimilarity.

That yeasts ultimately have an absolute requirement for O_2 in their requirement for oleate and steroids (which can only be synthesized aerobically) does not per se refute the endosymbiosis hypothesis, but need only mean that their potential for anaerobic growth arose secondarily after the establishment of aerobic respiration, regardless of whether the latter was by an endosymbiotic event or by progressive evolution. On the other hand, Raff and Mahler's point that steroids are made aerobically in some prokaryotes and in the cytoplasm of all eukaryotes suggests (if the pathways are homologous) that eukaryotes have always been aerobic and have inherited nuclear genes for that biosynthetic pathway from their prokaryotic ancestors. Similarly, that advanced prokaryotes and all eukaryotes utilize the same aerobic pathway to make monounsaturated fatty acids is an important point for establishing the primitive aerobiosis of eukaryotes.

The "considerable amount of evolutionary divergence" between bacterial and mitochondrial cytochromes noted by Raff and Mahler has no bearing on the question of mitochondrial origins. Considerable divergence would be expected by both the endosymbiotic and nonendosymbiotic hypotheses.

Raff and Mahler say that "the widespread occurrence of cytochromes in