failed to tie the origin and initial diversification of multicellular animals either to the end of the Precambrian, or to particular latitudinal zones. Evolutionary diversification must have been taking place at that time because once initiated, it is continuous. Eucaryotic unicellular organisms dependent on oxygen were living at least 300-400 Myr before the beginning of the Cambrian<sup>3</sup>, and the fully aerobic environment in which they existed<sup>4</sup> was equally suitable for multicellular animals. That this was the situation for at least 100 Myr before the end of the Precambrian is shown by the presence of fossils of a variety of soft-bodied metazoans in late-Precambrian rocks in several parts of the world<sup>5,6</sup>. These late-Precambrian organisms were, however, already complex forms, so that the evolution of metazoans from protists<sup>4</sup> clearly took place still earlier in the Precambrian, and was not connected in any way with environmental conditions at the end of the Precambrian.

The concept of a sudden diversification of life at the end of the Precambrian derives from the time when it was widely believed (from the lack of fossil evidence) that metazoans evolved only shortly before the beginning of the Cambrian. Thus, Cambrian strata, in contrast to apparently unfossiliferous Precambrian rocks, were known to contain abundant fossils representing the principal animal phyla now inhabiting the world as well as extinct ones. The abundance of fossils at that time was a result of the acquisition of preservable hard parts independently by many groups of organisms. Although the latter was not synchronous, it seemed more nearly so when the Lower Cambrian was believed to represent a period of 30 Myr as against the currently recognised 50 Myr (ref. 7). The complex multicellular organisms that developed hard parts were, however, not living in the surface water of the ocean but on the sea floor, and so they were derived from less complex forms already adapted for a benthic existence. Hence, the sudden diversification of life attributed to the end of the Precambrian or to early Cambrian time refers only to the bottom-dwellers that acquired skeletons, as little is known about the variety of soft-bodied benthic and pelagic animals also living at that time.

Restriction of oxygen, before the beginning of the Cambrian, to surface or near surface water<sup>8</sup> (above or within the pycnocline) or, in high concentration, to certain latitudinal zones, implies lack of disturbance of the density layers by currents like those of today which move water from one region to another or from one depth to another, and result in a mixing of water and distribution of oxygen to nearly all parts of the ocean. An ocean in which movement of water bodies was too slow to significantly affect the stratification would require a more uniform heat distribution than there is at present; such conditions

could only exist in the absence of continents (differential heating giving rise to complex wind patterns, movement of water bodies, and so on) or even of significant rises on the sea floor, that is, the ocean would have to have been global and of more or less uniform depth<sup>9</sup>. Emergence of continents took place long before the end of the Precambrian<sup>10,11</sup>, and oceanic conditions would then have been comparable to those existing today. During the Lower Cambrian the world consisted of at least five continents separated by oceans<sup>12,13</sup>, and in the latter, multicellular animals existed at both high and low latitudes<sup>12</sup>. Colonisation of the sea floor and overlying waters took place more than 100 Myr before the beginning of the Cambrian as the oldest known metazoan faunas include both benthic and pelagic forms<sup>6,15</sup>; some of them lived in shallow water whereas others inhabited relatively deep water<sup>6</sup>. Consequently, as far as the fossil record of Precambrian multicellular animals goes back, oxygen was present in water well below the level of the pycnocline.

If multicellular animals, from the time of their origin until 600 Myr ago, had been restricted to the surface water of certain latitudinal zones because oxygen was not available in sufficient concentration elsewhere in the ocean<sup>1</sup>, either near the surface or below the level of the pycnocline, diversification would have been inhibited. as their migration (actively, or passively by currents) into other environments where they could survive and where adaptive evolution could take place would have been impossible.

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B. AND A. HENDERSON-SELLERS REPLY-Many of Anderson's points are outside the scope of our paper<sup>1</sup>, as the temporal evolution from single- to multicellular life within the evolving oceanatmosphere system is a wide topic and is discussed in more detail elsewhere<sup>2</sup>. The choice of 600 Myr ago as an example of our model results<sup>2</sup> was intended to illuminate the discussions of evolutionary processes current in the literature. Many of his points are, of course, still widely contested. However, we attempt to answer the most obvious below. The question of oceanic stratification at our chosen period is still unresolved. Degens and Stoffers3 discuss the anoxic conditions at depth resulting from the chemistries associated with the two layers. Although the permanency of this stratification is in doubt, its certain occurrence lends credence to our model and provides at worst error bars on the timing. Hargraves<sup>4</sup> postulation of a global sea, although recently criticised<sup>5</sup>, seems to be supported by more recent evidence and discussion<sup>6,7</sup>.

The existence of a pycnocline, at least for long periods during the ocean's history, implies that the build up of oxygen in the upper layers did occur at times up to and including the diversification and emergence of land animals. Our article was intended to illustrate an additional and important factor in the total description of the complicated process of global evolution. The dynamic feedbacks between life, ocean and atmosphere during the evolution of the Earth will not be simply resolved.

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<sup>1.</sup> Henderson-Sellers, B. & Henderson-Sellers, A. Nature 272, 439-440 (1978).