

growth rates under optimal conditions. Some caution is required in interpretation of these effects, because slow growth could be a consequence rather than a cause of resistance. None the less, these findings are crying out for further study at the biochemical level, to understand exactly how these traits are connected to stress resistance. Both mutation and recombination rates often increase in response to stressors such as low and high temperatures. These again could be adaptive mechanisms to increase genetic variation of maladaptive side effects of exposure to stress.

Several lines of evidence suggest that genes causing resistance to stress may incur a pleiotropic cost, because the resistant phenotypes are at a disadvantage to susceptible ones in the absence of the stressor, especially in competitive conditions. This may be another reason why many responses to stress, such as the induction of heat shock proteins, are inducible rather than constitutive. Resistance may be metabolically costly if, for instance, ATP is used to move ions against a concentration gradient, leaving less energy for reproduction. Conflicts between vital processes may also occur. Xeric plants are in general incapable of high rates of photosynthesis, because their stomata are adapted to prevent water loss, which also limits the rate of gas exchange. Resistance may expose organisms to ecological risk. Birds often put on fat in anticipation of acute food shortage, but the extra weight makes them less manoeuvrable and hence more vulnerable to predator attack. Resistance to chemical pollutants such as insecticides and heavy metals often seems to be associated with reduced fitness in optimal conditions, but the reasons are unknown.

The final topic discussed is the role of physical stress in setting the limits to species distributions, and its importance for conservation policy. There is no shortage of hypotheses for why species ranges do not extend further than they do, and empirical studies are few and inconclusive. Gene flow from central areas could prevent further adaptation at the margins of the species distribution, peripheral populations may lack the necessary genetic variability to adapt or there may be absolute physiological constraints on what can be tolerated. Some support for the latter point of view comes from work on the northern limits to the geographic ranges of 50 species of North American birds, where it was demonstrated that the resting metabolic rate at the coldest time of year (January) was about 2.5 times the basal metabolic rate, irrespective of variation in body size or ecology. Intriguing as this finding is, it is a mystery why such a constraint on metabolic rate should occur. Adaptation to stress may or may not be important for the conservation of endangered species. Conservation genetics is going through a period of some turmoil as it is appreciated that magic population numbers for avoiding inbreeding depression and preservation of the right kinds of genetic variability may be much less

important than population dynamics for predicting population persistence. It is not clear where physical stresses will fit in to the final picture, although deterioration in stress-resistance under benign conditions in captivity may well turn out to be an important issue.

I am left with the strong impression that most of the important work on evolutionary responses to stress remains to be done. We are largely in ignorance of the extent to which different stresses are encountered or the mechanisms by which they are combatted in nature. If only by exposing ignorance, Hoffmann and Parsons would have made a valuable contribution, but by collecting together disparate sources of information and pointing some ways forward, they have produced an excellent work of reference.

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The Aquatic Ape: Fact or Fiction? Edited by MACHTELD ROEDE, JAN WIND, JOHN PATRICK and VERNON REYNOLDS. Souvenir Press (E-A) Ltd, 43 Gt Russell St, London WC1B 3PA. 1991. 369 pages. Hardback £20. ISBN 0 285 63033 4.

The Aquatic Ape Theory (AAT), first conceived by Alister Hardy in 1929, proposes that an aquatic stage occurred in the early evolution of man from proto-ape ancestors. Hardy took the advice of colleagues that he would never become a Professor at Oxford or a Fellow of the Royal Society if he published such a controversial idea, and he suppressed it for 30 years until he had achieved these two aims, and then broached the theory cautiously, where it lay dormant for another 10 years until taken up enthusiastically by Elaine Morgan, who promoted it in two books – *The Descent of Woman* (1972) and *The Aquatic Ape* (1982). These caused considerable general interest but were not taken seriously by the palaeoanthropologists.

The book under review contains an updated version of the proceedings of the first international conference (in 1987) on the AAT hypothesis, and presents the views of a number of its proponents and critics. The result is a most useful and entertaining examination of current ideas on early hominid evolution. The argument centres on the evolutionary stage when the hominid line separated from the proto-apes during the late Pliocene in East Africa. Geological evidence suggests that the climate became drier and the forest habitat of the proto-apes receded leaving a woodland-savannah mosaic into which only the hominid line moved successfully. Its descendants were walking upright by nearly 4 million years ago, at the time of the *Australopithecus afarensis* hominids which included 'Lucy' and other fossil fragments from Hadar and Laetoli; but this advanced bipedalism, obviously better adapted to savannah than to arboreal life,

developed while the brain was still small and long before the use of tools or fire. The AAT school consider that Lucy and her predecessors could not have survived and prospered in the open savannah while undergoing the complex evolution of bipedalism, in view of the fast-running predators hunting them. AAT postulates that protection from predators would have required their isolation from the savannah by an environmental change leading to an aquatic or semi-aquatic life-style, in which plenty of food would be easily available from shore and shallow waters.

In the book, after Elaine Morgan's Introduction, AAT proponents discuss where the evolution of the genus *Homo* might have happened (Leon P. LaLumiere); does AAT fit in with marine ecology and primate behaviour? (Derek Ellis); and whether there are aquatic features in fossil hominids (Marc Verhaegen). Later chapters, discussing reactions for and against the aquatic ape theory, range widely and include Graham Richards on the reception of AAT by the scientific community from 1972–87, Martin Pickford on the geological evidence, Alan Turner on adaptation and the aquatic ape, Holger and Signe Preuschoft on epistemological and palaeoanthropological viewpoints, Paul Leyhausen on what constitutes an aquatic mammal, Marc Verhaegen on human regulation of body temperature and water balance, Caroline M. Pond on adipose tissue in human evolution, Peter E. Wheeler on human body hair reduction and tract orientation, John M. Patrick on respiratory adaptations for swimming and diving, Erika Schagatay on the human diving complex, Joseph Ghesquiere and Helene Bunkens on the burden of locomotion in water – could the aquatic ape have overcome it? Jan Wind discusses AAT and the evolution of human drowning and swimming, Machteld Roede asks whether aquatic mammals support AAT, and also discusses aquatic man and his close relationship with the sea, and some short papers include an attempt to combine the aquatic and the savannah theories. The editors finally add some general conclusions. References are given at the end of each chapter, a large number of figures and tables are included and their locations listed after the very helpful list of contents which itemizes the numerous subheadings to each chapter, and there is an index of authors and a very detailed index of subjects (e.g. dogs get 8 and buoyancy 13 references to the text). So my first comment is that the editors are to be strongly commended for taking so much trouble to make the reader's task easier.

Graham Richards' in his article entitled 'The refutation that never was' claims that AAT received no serious academic attention between 1972 and the 1987 meeting, comments being either patronising or contemptuous; and he attributes this 'deafening silence' partly to the fact that the consensus of academic opinion on hominid evolution was breaking down by 1972, so that it was no longer possible to

assume that *Ramapithecus* was the earliest hominid, that the hominid and pongid lines split about 15 million years ago, that hunting was a major feature of early hominid life-style, that bipedalism was directly associated with brain enlargement and linked to stone artifact manufacture – these and other vital questions were already under heated debate. So no one was prepared to help AAT to enter the arena. This academic silence has been complete up to 1987, as one can easily check by studying recent standard texts such as Roger Lewin's *Human Evolution* (Blackwell Scientific Publications, 1984) and the *Encyclopedia of Human Evolution and Prehistory*, edited by Tattersall, Delson and van Couvering (Garland, 1988).

The list of chapter headings I have given above shows that in this volume the battle between pro- and anti-AAT theorists is now properly joined, and the reader has the opportunity to make up his/her own mind or reserve judgement. I would hesitate to give my own opinion when each side is accusing the other of writing 'Just So Stories' and many of the arguments await further research support. The reader will find an interesting example in LaLumiere's article: this suggests a location, the hypothetical Danakil Island/Afar Triangle at the south end of the present Red Sea area, where recurrent tectonic activity could have isolated the hominid ancestors and protected them in shallow waters while the evolutionary step to bipedalism was made. Fossils found in areas suggested by LaLumiere might prove or disprove this hypothesis, if there were funds and the will to mount a large-scale search.

Whether or not Morgan and company are correct, it seems to me that they have done hominid evolutionists a great service in forcing them to either agree with the possibility of AAT or defend their positions. This is evident from the very large amount of information, much of it new I think, gathered in this book and thereby made available to a wide readership. One conclusion which is evident is that, if early hominids went through an aquatic phase in their evolution, it produced only mild anatomical changes compared with those shown by other aquatic mammals. Perhaps this fits in with what is known about the time available for such changes. While the Encyclopedia referenced earlier in this review states that there is a complete hiatus in hominoid fossils over the period 8 to 4 million years ago (approximately), recent molecular evidence from DNA sequence data strongly suggests that the evolutionary lines of hominids and African apes separated about 4–5 million years ago (Hasegawa & Kishino: DNA sequence analysis and evolution of hominoidea, in *New Aspects of The Genetics of Molecular Evolution*, Japan Scientific Societies Press and Springer Verlag, 1991). *A. afarensis* (Lucy and her relatives) are dated to about 3.6 million years BP, relatively soon after the two ancestral lines split, and the selection pressure which led to their development of bipedalism and not extinction presents a major evolutionary problem for speculation.

The Aquatic Ape: Fact or Fiction is remarkably cheap at £20 for 369 pages and numerous tables and figures in hardback, and I think it should find its way into most biological libraries and onto the shelves of many biologists.

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The Triumph of the Embryo. By LEWIS WOLPERT.
Oxford University Press. 1991. 211 pages. £14.95.
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How each organism develops into an adult from the single-celled egg must be one of the most fascinating topics in Biology. However, it is often considered inaccessible to the layman. The complex movements to form cell layers and shapes are difficult to describe as the embryo is 3-dimensional and its complexity increases dramatically as it develops. This makes it hard to visualize what is happening and hold it in your mind. Once the descriptive aspects are grasped, trying to understand how this is achieved can seem even more daunting, as we need to know not just about cellular interactions but about the genetic programmes which switch on and off the expression of proteins to ultimately get the right cells to do the right things at the right time and in the right place. There are thousands of cells with hundreds of functions and yet they are carefully integrated to make a functional whole organism.

Professor Wolpert has tried to make this fascinating process accessible to the layman, and he has done a good job of explaining development with a minimal amount of terminology and unnecessary jargon. He makes things as easy as possible describing the early steps in embryonic development in terms such as the conversion from buns to doughnuts – so you immediately visualize what is happening. He also refers to the relationship between faults in developmental pathways and human diseases, thus emphasizing the importance of cellular decisions being executed correctly.

As might be expected much of the book is devoted to the spatial organization of cells, the way each species has its own individual shape and form, and he explains well how sometimes the fate of parts of embryos is fixed and at other times it can alter if normal development is perturbed. We all know that human embryos can be split to produce twins, but this is not true for all organisms, nor does this flexibility last for very long as development proceeds in those species which can regulate. He explains how developmental processes are dependent on decisions within cells, often due to influences from, and interactions with, other cells. He emphasizes the fact that the signals are simple and probably small in number and

that the response of the cells receiving the signal is complex.

Generally, the topics selected for describing how eggs develop into embryos and obtain their form and pattern are good, though a few unquestioned dogmas have slipped in; for example, we are told mammalian eggs have no yolk because nutrients are supplied by the mother. Yet observation of mouse and rat embryos clearly shows the presence of yolk – we just do not know what it is for yet.

The book moves on to a molecular analysis of the control of development. This is important as it is the area in which progress is being rapidly made to unravel the mechanisms behind what we see when we watch an embryo develop or respond to experimental treatments. Whilst this approach is in part descriptive, as Wolpert says, I think it is also a very experimental approach and is unravelling fundamental developmental mechanisms. Many of the molecular experiments being performed interfere with development by expressing a gene in the wrong place or at the wrong time and use the resulting response of the embryo to give clues to underlying mechanisms rather than being only a description of which genes are expressed where and when, as he tends to imply.

The bare essentials of genetics, RNA and protein synthesis and the regulation of gene expression are covered in just 12 pages and really must make these topics, usually covered in much more depth, accessible to everyone. With this information one can readily follow the subsequent sections on the diversity of cells and how they each perform their specialized functions.

There is a chapter on the development of the *Drosophila* embryo. Discussing an insect egg developing may seem odd to the layman but it is an area which, because of the beauty of *Drosophila* genetics followed by the revolution in molecular biology, enables us to understand at the molecular level how a unicellular egg develops first polarity, a head and a tail and then divides it up in segments. Such segments are based on repeating units found throughout biology and not surprisingly some of the genes found in *Drosophila* are found in vertebrates too and are important in the development of their body axis.

The wiring of the brain is of interest to us all, and although it is a highly complex process it is covered in this book. Sex and cancer, two obviously relevant topics are also described though it is a shame that more emphasis was not placed on the rapid molecular advances in these subjects. We now understand quite a lot about the molecular basis of sex determination in a number of organisms and about numerous forms of cancer.

No book by Professor Wolpert would be complete without a section on regeneration, which his laboratory has devoted so much effort to studying. Evolution is also covered and here Professor Wolpert emphasises the concept that there are a few fundamental developmental mechanisms that have been