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EDITORIAL

Parasites as indicators of human biology and evolution

Thinking about parasitic infections tends to be limited to the problems they cause; to disease, diagnosis and cure. This is to under-rate our guest organisms, and to ignore the many lessons they have for us. Our parasite fauna is more than merely a chance collection, but reflects many of the attributes that make us human. Indeed, one of the most intriguing aspects of the parasites of any animal is the way they and their hosts may have evolved in parallel, so that a phylogenetic analysis of parasites may indicate the phylogeny of their hosts and *vice versa*. Paraphrasing Croll [1], one might claim: 'show me the parasite, and I'll describe the host'.

Early authors attempting to derive human phylogeny from parasites [2–5] were disappointed by the small number of groups that seem to have co-evolved with us and with our close relatives. Only the lice and pinworms seemed to reflect such co-evolution. A comprehensive review of the pinworms [6] appears to confirm the close relationship between ourselves and chimpanzees, *Pan* spp. However, information on lice, which has also been revised recently [7, 8], indicates that we share *Pediculus* with chimpanzees and *Phthirus* with the gorilla *Gorilla gorilla*, so the lice fail to indicate which ape is closer to man.

Garnham [9] tried to use the malaria parasites *Plasmodium* spp. to define our relationship with other primates; Escalante *et al*. [10] have taken up the *Plasmodium* story, concluding that the primate malaria parasites originated in Africa, and that the parasites of both chimpanzees and the gorilla are very similar to our own.

So, other than to confirm that we are closer to the chimpanzees and the gorilla – possibly a little closer to chimpanzees – than to the orang-utan, *Pongo pygmaeus*, phylogenetic study of individual groups of parasites has added little to conventional methods in establishing our phylogeny.

Other authors have looked at the fauna as a whole to dissect the relationships with our primate relatives. In reviewing the history of efforts to apply parasitological knowledge to problems in the phylogeny, ecology and behaviour of primates, Dunn [11] relied on a simple presence or absence formula as a measure of parasitological relatedness between hosts. He was perhaps the first to relate primate parasite faunas to host ecology, finding that arboreal and folivorous habits were associated with restricted parasite faunas.

Glenn and Brooks [12] applied to hominoid primates the methods they had developed for the use of parasites in the construction of phylogenies of other hosts. These methods depend primarily on the analysis of checklists of the widest possible selection of parasites of each host. They used an automated phylogenetic analysis to compare the presence or absence of particular parasites among the hosts' fauna. In contradiction to all conventional phylogenies, they found that the parasite fauna of *Homo sapiens* is more similar to that of baboons (*Papio* spp.) than to those of gorillas or chimpanzees, indicating that *Homo* is more ancient than all other apes, and closer to the cercopithecines. Obviously the method did not work in this instance, and the reasons why it is not applicable to the higher primates may be highly illuminating. Combes [13], for example, makes the point that our wide geographical distribution and diversity of habits have allowed more opportunity for host-transfer to man than to any other animal. He further explains the richness of our parasite fauna on the grounds of our adopting a terrestrial lifestyle, although the timing of our descent from the trees may be disputed (see below).

A serious problem confronted by all earlier authors, including Ashford [14], was the inadequacy of their raw data. The available lists indiscriminately included many rare human parasites and much of the information on parasites of other primates was obtained from captive animals. Therefore, these lists did not differentiate between parasites that might be abundant and host-specific, and those that represent exceptional occurrences.

Improved catalogues, such as that compiled by Coombes and Crompton [15], provide a much more comprehensive list of human parasites and enable us to allocate to each one a degree of dependence on humans for its survival [16]. One astonishing conclusion is that $>80\%$ of the 400 or so species of parasite that infect man are probably purely zoonotic, and that only about 10% specialise in life in man. The remaining 10% are equally happy in human or animal host populations. This is consistent with the idea that we are a recent species to which not many parasites have become adapted.

Of the 40 or so 'human specialists', most have cosmopolitan distributions and their region of origin is obscure, so they give no clue to human origins. Those that are geographically restricted, or whose origins can be otherwise deduced, are predominantly Aethiopian (Africa south of the Sahara). This indicates that we have been in Africa long enough for a few specific host–parasite associations to emerge, and accords with our supposed African origins. However, the 'human specialists' are not concentrated, as might be expected, in the East African savannahs, but in the rain forests of West and Central Africa: the cradle of humanity, according to our parasites, was not Olduvai or the Danakil, but somewhere in Gabon or Cameroon.

In addition to our African guests, there is also a considerable group of human-specialist species that seem to be of Palaearctic (Europe and Asia, north of the Sahara and Himalayas), or Oriental (Asia south of the Himalayas to Wallace's Line) origin. This is clear confirmation that our ancestors have been out of Africa for a very long time. Furthermore, at least five human-specialists (three species of *Taenia* and two of *Sarcocystis*) depend on our eating beef or pork; all of these appear to be of Palaearctic or Oriental origin. Clearly, according to what Brooks and McLennan [17] call 'parascript' (parasites and the language of evolution), not only have we been out of Africa for a long time, but it was only after we had left Africa that we began to be specialist cow and pig eaters.

A surprising number of members of our specialist fauna occur as pairs of closely related forms. Examples include the two lice *Pediculus humanus* and *P. capitis*, the two tapeworms *Taenia saginata* and *T. asiatica* (often considered a subspecies of *T. saginata*), the two follicle mites *Demodex folliculorum* and *D. brevis*, the two entamoebae, *Entamoeba dispar* and *E. histolytica* and even the two bedbugs *Cimex lectularius* and *C. hemipterus*. Were we once two separate populations, in different parts of the globe, which rejoined after a long separation? Our parascript certainly suggests as much.

A final intriguing feature of our specialist parasite fauna concerns the four forms (three *Schistosoma* species and *Dracunculus medinensis*) which depend for their transmission on our entering water. The feminist diatribe of Elaine Morgan [18] suggesting an aquatic phase in our evolution is dismissed by most anthropologists, but in support of this theory, as far as we know, no other primate has indications of such long-standing association with water.

Turning again to the lack of similarity between our parasite fauna and those of our closest relatives, we find a further surprise. The dissimilarity applies mostly to intestinal parasites: ours are much more like those of baboons, whose diet also resembles ours. It seems that the folivorous diet of the great African apes must be a recent specialisation that has developed since our evolutionary paths separated, and that they have acquired their unique parasites (some of whose closest relatives are in horses!) by host transfer, relatively recently. The implication here is that the ancestor of the ape-human had feeding habits more like ours, and those of baboons, than those of any modern ape. The *Homo*/*Pan*/*Gorilla* ancestor of some 5–8 million years ago was therefore an omnivore, so terrestrial, and quite possibly bipedal. We are not, then, according to our parasites, specialised apes, but apes are specialised humans! Since the fossil record is so conspicuously lacking in any ancestry for the African apes, the parasitological evidence may be the best we have.

Now, over to the microbiologists: what do the bacteria, viruses and fungi tell us?

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