Introduction

TIM J. CROW

FEW, IF ANY, SYMPOSIA OR MEETINGS have addressed directly the topic of the speciation of modern *Homo sapiens*. This may be because the concept of speciation as a discrete genetic event has an ambiguous status within evolutionary theory, in part because of the difficulty we have in taking an objective view of the species of which we are members, but also because no member seems to have thought of it as a problem. Yet it is arguable that scrutiny of the origin of our species casts speciation, and maybe evolutionary theory as it now stands, in a critical light.

The meeting that took place under the auspices of the British Academy and the Academy of Medical Sciences on 28 March 2000 at the British Academy, with the subsequent workshop at the Novartis Foundation, had an informal precursor as a 1-day SANE-sponsored conference held at St Anne's College, Oxford, on 30 June 1997 (Maddox, 1997). That meeting introduced the themes of language and lateralisation as putative species characteristics and X–Y homologous genes as a class of potential mediators of change. Several speakers (Derek Bickerton, Nabeel Affara, Chris McManus, James Steele and myself) participated in both events. As reflected in these *Proceedings*, the second meeting added the dimensions of palaeontology (Chris Stringer, Ian Tattersall and Mark Collard), archaeology (Paul Mellars) and neuroanatomy (Detlev Ploog and Norman Cook) to those of linguistics, psychology (Michael Corballis), genetics (Chris Tyler-Smith) and evolutionary theory (Klaus Reinhold).

MAN'S PLACE IN EVOLUTIONARY THEORY—T. H. HUXLEY, C. DARWIN AND A. R. WALLACE

The present *Proceedings* can be placed in the longer time–course of evolutionary debates on 'man's origins'. In *Evidence of Man's Place in Nature*, Huxley (1863) summarised the anatomical and palaeontological case that Darwin (1859) had been reluctant to spell out in the *Origin of Species*, that man has a descent from the great apes. In 1871, Darwin himself approached the issue, which was now the subject of widespread debate, in *The Descent of Man*. One interest of this

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publication is that it linked in a single volume, *The Descent of Man* and *Selection in Relation to Sex*, the anatomical and palaeontological case with Darwin's theory of sexual selection. Was the connection fortuitous; did he, for example, have two different theses that happened to come to fruition at the same time, or were the theses related? In his introduction, Darwin writes that:

> During many years it has seemed to me highly probable that sexual selection has played an important part in differentiating the races of man; but in my *Origin of Species* I contented myself by merely alluding to this belief. When I came to apply this belief to man, I found it indispensable to treat the whole subject in full detail. (Introduction, *The Descent of Man*, pp. 4–5)

Some passages in the second part of the book indicate that Darwin considered the two arguments to be related in a more fundamental way. Thus:

> … Sexual selection has apparently acted on both the male and the female side, causing the two sexes of man to differ in body and mind … [and] has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. Courage, pugnacity, perseverance, strength and size of body … have all been indirectly gained by one sex or the other, through the influence of love or jealousy, through the appreciation of the beautiful in sound, colour and form, and through the exertion of choice … (*Selection in Relation to Sex*, p. 402)

But as to the mechanism, as of course to the genetic basis of natural selection itself, Darwin was unclear. Perhaps the fact that the two arguments are in separate halves of the book reflects Darwin's own uncertainty on the relationship between sexual and natural selection.

The above passage illustrates some of the problems. If we suppose that sexual and natural selection are to some extent based upon distinct principles, do we assume that sexual selection can act separately, '… indirectly gained by one sex or the other …' in the two sexes? One can conjure up an image of almost any bodily feature coming under the influence of capricious mate choice in one sex, and of the two sexes diverging with respect to an array of independent features. But there are clearly limits to the scope of sexual selection. Moreover, A. R. Wallace denied that any separate principle was involved (Cronin, 1991). Then again, if 'Courage, pugnacity, perseverance, strength and size of body' have all been gained through 'the influence of love or jealousy [or] through the appreciation of the beautiful and … the exertion of choice', at what stage did this happen? Do we assume that the courage, pugnacity and perseverance, which are presumably characteristics of males differentially preferred by females, were selected sequentially or as a suite? When did this happen in the history of the species? If strength and size of body are features that differentiate the sexes, are such features species-specific or do the differences that are present in humans reflect a trend that was already present in a precursor hominid or great ape? In short, what is the relationship between sexual selection and speciation?

As is well known, on the topic of speciation Darwin was a gradualist. From the time he became convinced of the mutability of species in 1838, he was at pains to emphasise continuities rather than discontinuities. For natural selection to act it was necessary for there to be variation within populations. No qualitative distinction between variation within and between species was drawn. In the only figure to appear in the *Origin of Species*, population continuities are represented as dotted lines travelling up the page over successive thousands of generations. Lineages separate, and some die out. Some that are close together at the origin are connected to points that are widely separated at the finishing line.

The critical role in Darwin's concept is that of the environment. Populations separate and come under differing selective pressures. Separations are reinforced by geographical barriers. It is the chance isolation of populations which are then subject to divergent environmental selective pressures that is the core of the concept, a concept that has been formalised in the subsequent literature as the 'biological' or 'isolation' species concept (Mayr, 1963). Populations separate and diverge in their genetic complement, and some component of those divergences eventually contributes to hybrid infertility should individuals from the two populations then reassociate.

The attraction of the theory is its simplicity. No arbitrary mechanism of speciation or discontinuity in the flow of natural selection is introduced. There is no need to be overly concerned with the nature of species boundaries. Ring species with continuous clines to infertility at the extremes are well accounted for. What is critical is the environment to which the varieties of organism adapt.

The case of *H. sapiens* raises problems for the isolation species concept. What environment was critical for the transition from a prior hominid species? What is striking about the biological success of the species is its ability to survive in diverse environments (humans are everywhere; Gamble, 1993), and even to change the environment. What specific characteristics of populations (bodily habitus, skin colour, thermoregulatory capacity?) are adaptations to particular environments, and how do these relate to the core characteristic(s) of the species? Diverse hominid species have previously co-existed. Is it just time, or the lack of an isolated population in a sufficiently distinct environment, that has prevented speciation occurring again?

The more fundamental question is the nature of a species. Is there a speciation characteristic? What holds a species, for example humanity, together? The notion seems contrary to the Darwinian continuity principle. Indeed, in the case of humans Wallace had difficulty in accepting Darwin's thesis that:

> man's whole nature—physical, mental, intellectual, and moral—was developed from the lower animals by means of the same laws of variation and survival; and, as a consequence of this belief, that there was no difference in *kind* between man's nature and animal nature, but only one of degree. My view, on the other hand,

> was, and is, that there is a difference in kind, intellectually and morally, between man and other animals; and that while his body was undoubtedly developed by the continuous modification of some ancestral animal form, some different agency, analogous to that which first produced organic *life*, and then originated *consciousness*, came into play in order to develop the higher intellectual and spiritual nature of man. (Wallace, 1905, quoted in Cronin, 1991).

Wallace's unease has a significant parallel in contemporary evolutionary theory. Maynard-Smith & Szathmary (1995) identify eight major transitions—the origin of replicating molecules (RNA, DNA and protein), eukaryotes, sexual populations, cell differentiation and multicellular organisms, colonies, societies and language (which, following Bickerton, they regard as the most characteristic function of *H. sapiens* with consciousness as an epi-phenomenon)—as critical discontinuities in evolutionary history. But one can ask why these eminent evolutionary theorists have not treated the origins of language as another speciation event, analogous, say, to the separation of the New from the Old World monkeys or to the diversification of Darwin's finches on the Galapagos islands? The answer, it seems, is twofold. First, that the jump seems too big (Wallace's point). Secondly, that these authors, as inheritors of the most rigorous and 'gene-centred' version of Darwinism, have down-played the discontinuous nature of speciation events (Maynard-Smith, 1993). The outcome is that, as in Wallace's case, the explanation of the origins of *H. sapiens* acquires the status of mystery.

LANGUAGE AS THE DEFINING CHARACTERISTIC: F. M. MULLER'S CRITIQUE OF DARWINIAN THEORY

The concept that language is the defining characteristic of humanity has an ancient origin:

> In most of our abilities we differ not at all from the animals; we are in fact behind many in swiftness and strength and other resources. But because there is born in us the power to persuade each other and to show ourselves whatever we wish, we not only have escaped from living as brutes, but also by coming together have founded cities and set up laws and invented arts, and speech has helped us attain practically all of the things we have devised. (Isocrates, BC 436–338, quoted in Harris & Talbot, 1997)

Darwin can be quoted as in agreement with this view. On page 53 of *The Descent of Man* he writes that language 'has justly been considered as one of the chief distinctions between man and the lower animals' but he seems not to have regarded this as a particular difficulty. In 1873, within 2 years of the publication of *The Descent of Man*, Friedrich Max Muller (Muller, 1996), who held the chair of Philology in the University of Oxford, delivered a series of three lectures at the Royal Institution in which he drew attention to the problems that language raises for Darwin's theory:

> My object is simply to point out a strange omission, and to call attention to one kind of evidence—I mean the evidence of language—which has been most unaccountably neglected, both in studying the development of the human intellect, and determining the position which man holds in the system of the world.

Muller placed Darwin's theory in the philosophical tradition of Locke (1690) and Hume (1739) without regard for the achievements of Kant (1781, 1788). He complained that Darwin's theory that 'man being the descendant of some lower animal, the development of the human mind out of the mind of animals, or out of no mind, is a mere question of time, is certainly enough to make one a little impatient'. The problem according to Muller was that the contents of human consciousness were not merely, as maintained by Locke and Hume, those that arose from the sensations but also from the framework (the 'pure intuitions') of space and time that is intrinsic to the human mind:

> If we are to become conscious of anything … we must place all phenomena side by side, or in space; and we can accept them only as following each other in succession, or in time. If we wanted to make it still clearer, that Time and Space are subjective, or at all events determined by the Self, we might say that there can be no There without a Here, there can be no Then without a Now, and that both Here and Now depend on us as recipients, as measurers, as perceivers.

In other words, there must be a deictic frame, and that frame is intrinsic to the capacity for language.

In the second lecture Muller addresses the problem:

> There is one difficulty which Mr Darwin has not sufficiently appreciated … There is between the whole animal kingdom on the one side, and man, even in his lowest state, on the other, a barrier which no animal has ever crossed, and that barrier is—*Language* … If anything has a right to the name of specific difference, it is language, as we find it in man, and in man only … If we removed the name of *specific difference* from our philosophic dictionaries, I should still hold that nothing deserves the name of man except what is able to speak … a speaking elephant or an elephantine speaker could never be called an elephant. Professor Schleicher, though an enthusiastic admirer of Darwin, observed once jokingly, but not without a deep meaning, 'If a pig were ever to say to me, 'I am a pig' it would ipso facto cease to be a pig'.

Muller considers how far Darwin had gone towards conceding the point: 'Articulate language is peculiar to man' (Darwin, 1871: 54), and 'It is not the mere power of articulation that distinguishes man from other animals, for, as everyone knows, parrots can talk; but it is his large power of connecting *definite sounds with definite ideas*'.

Muller writes:

> Here, then, we might again imagine that Mr Darwin admitted all that we want, viz. that some kind of language is peculiar to man, and distinguishes man from the other animals … but, no, there follows immediately … 'This obviously depends upon the development of the mental faculties'.

Muller asks:

> What can be the meaning of this sentence? … If it refers to the mental faculties of man, then no doubt it may be said to be obvious. But if it is meant to refer to the mental faculties of the gorilla, then whether it be true or not, it is, at all events, so far from being obvious, that the very opposite might be called so—I mean the fact that no development of the mental faculties has ever enabled one single animal to connect one single definite idea with one single definite word.
>
> I confess that after reading again and again what Mr Darwin has written on the subject of language; I cannot understand how he could bring himself to sum up the subject as follows: 'We have seen that the faculty of articulate speech in itself does not offer any insuperable objection to the belief that man has been developed from some lower animal'.

Muller distinguishes between what he describes as emotional and as rational language. The former he relates to the 'bow-wow' or 'onomatopoeic' origins theory of language, 'the power of showing by outer signs what we feel, or, it may be, what we think'. This he regards as shared between man and other animals. Rational language, on the other hand, he relates to the power of forming and handling general concepts, and this he regards as specific to man. He draws attention to the observations of Hughlings Jackson (1868; Taylor, 1932), that the two can be separated by the effect of disease, and that disorders that impair the intellectual and rational expression of speech are, following the observations of Broca (1861), to be found with lesions that affect the anterior lobe on the left side of the brain.

The ability to form 'roots' is what Muller regards as the essence of intellectual or rational language. He describes its significance as follows:

> There is in every language a certain layer of words which may be called purely emotional. It is smaller or larger according to the genius of each nation, but it is never quite concealed by the alter strata of rational speech. Most interjections, many imitative words, belong to this class. They are perfectly clear in their origin, and it could never be maintained that they rest on general concepts. But if we deduct that inorganic substratum, all the rest of language, whether among ourselves or among the lowest barbarians, can be traced back to roots, and every one of these roots is a sign of a general concept … Take any word you like, trace it back historically to its most primitive form, and you will find that besides the derivative elements, which can easily be separated, it contains a predicative root, and that in this predicative root rests the connotative power of the word.

Muller summarised his case:

> If the words of our language could be derived straight from imitative or interjectional sounds, such as bow-wow or pooh-pooh, then I should say that Hume was

> right against Kant, and that Mr Darwin was right in representing the change of animal into human language as a mere question of time. If, on the contrary … after deducting the purely onomatopoeic portion of the dictionary, the real bulk of language is derived from roots, definite in their form and general in their meaning, then that period in the history of language which gave rise to these roots … forms the frontier … between man and beast … That period may have been of slow growth, or it may have been an instantaneous evolution: we do not know … These roots, which are in reality our oldest title-deeds as rational beings, still supply the living sap of the millions of words scattered over the globe, while no trace of them, or anything corresponding to them, has ever been discovered even amongst the most advanced of catarrhine apes.

Muller's notion of the linguistic root as a general concept can be compared with de Saussure's (1916) formulation of the components of the linguistic sign. According to de Saussure it is the arbitrariness of the relationship between the signifier (the sound pattern) and the signifieds (the concepts to which it is attached) that is the first principle of linguistics. Although he seems not to have considered this principle in a comparative context, he regarded arbitrariness of association as fundamental to the human capacity for language. It is necessary to the formation of abstract concepts.

DID LANGUAGE REQUIRE A MACRO-MUTATION?

Subsequent linguists have raised the problem for evolutionary theory in different forms. Chomsky's (1959) critique of Skinnerian operant theory as an explanation of verbal behaviour carried the strong implication that there were principles underlying language that were human specific. The concept of universal grammar as a defining human characteristic and of its generativity have implications for speciation theory, as well as for neuroscience, but these have not been pursued. Linguistics and evolutionary theory have remained separated [see Pinker's (1994) discussion of Chomsky's views below].

Perhaps the most incisive attempt to cross the disciplinary boundary is that of Derek Bickerton in his contributions in *Language and Species* (1990) and *Language and Human Behavior* (1995). Bickerton (1990) distinguishes protolanguage, the use of symbols without grammatical structure, the use of null elements, subcategorisation of verbs and recursiveness, from full language, and attributes the former to trained apes, children under 2, adults who have been deprived of language in their early years, and speakers of pidgin. He dates the origin of language to the origins of modern *H. sapiens* and writes (1990: 190) that:

> The evidence … indicates that language could not have developed gradually out of protolanguage, and it suggests that no intermediate form exists. If this is so,

> then syntax must have emerged in one piece, at one time, the most likely cause being some kind of mutation that affected the organization of the brain. Since mutations are due to chance, and beneficial ones are rare, it is implausible to hypothesize more than one such mutation.
>
> Several factors suggest, indeed, that just such a single mutation gave rise to our species. It is here that problems arise. For our species is distinguished from all others not merely by syntacticized language but also by changes in the features and dimensions of the skull and by our typical supralaryngeal tract.
>
> The problem, bluntly stated, is: How could any single event, whether a point mutation or a re-shuffling of chromosomes, occasion so many and such diverse changes? The problem would be bad enough if only a single principle were required to set syntax in motion. If seven or eight were required, the situation would be still worse.

Bickerton goes on to argue that the critical event:

> could have consisted simply in the linking (or the dramatic strengthening of pre-existing links between) those areas of the brain where the lexicon was stored and those areas where the structure of actions and events was analyzed. These linkages would then have inhibited the random chaining of words and facilitated their rapid and automatic organization into the structural units described.

On the question of the nature of the event Bickerton supposes that the primary change was in the brain itself but:

> the emergence of our species does not seem to have been attended by any conspicuous enlargement, and whatever alterations in the brain's hard-wiring may have been required to initiate syntax, it seems unlikely that there should have resulted from them a change in the shape of the brain sufficient to cause such marked alterations in skull dimensions. Perhaps some additional factor could be found that would underlie all three changes. But at present there are no obvious candidates.

Other linguists have squared up to the evolutionary dilemma. Thus in a chapter entitled 'The big bang' Pinker (1994: 332) outlines the problem:

> Language is obviously as different from other animals' communication systems as the elephant's trunk is different from other animals' nostrils. Nonhuman communication systems are based upon one of three designs: a finite repertory of calls (one for warnings of predators, one for claims to territory, and so on), a continuous analog signal that registers the magnitude of some state (the livelier the dance of the bee, the richer the food source that it is telling its hivemates about), or a series of random variations on a theme (a birdsong repeated with a new twist each time …). As we have seen, human language has a very different design. The discrete combinatorial system called 'grammar' makes human language infinite (there is no limit to the number of complex words or sentences in a language), digital (this infinity is achieved by rearranging discrete elements in particular orders and combinations, not by varying some signal along a

> continuum like the mercury in a thermometer), and compositional (each of the infinite combinations has a different meaning predictable from the meanings of its parts and the rules and principles arranging them).
>
> Even the seat of human language in the brain is special … [see the chapter in these *Proceedings* by Detlev Ploog] The vocal calls of primates are controlled not by their cerebral cortex but by phylogenetically older neural structures in the brain stem and limbic system, structures that are heavily involved in emotion … Genuine language … is seated in the cerebral cortex, primarily the left perisylvian region. (Pinker, 1994: 334)

After an extended discussion of how attempts in the great apes fall short of demonstrating human language capacity, Pinker considers the views of other linguists:

> Elizabeth Bates, a vociferous critic of Chomskyan approaches to language, writes: 'If the basic structural principles of language cannot be learned (bottom up) or derived (top down), there are only two possible explanations for their existence: either universal grammar was endowed to us directly by the Creator [Wallace's explanation], or else our species has undergone a mutation of unprecedented magnitude, a cognitive equivalent of the Big Bang … '

Bates backs off from the Bickertonian scenario into the timid conclusion that the evidence for linguistic and neurological discontinuity cannot be so great as to require so drastic a solution:

> We have to abandon any strong version of the discontinuity claim that has characterized generative grammar for thirty years. We have to find some way to ground symbols and syntax in the mental material that we share with other species.

Pinker contrasts this with one of Chomsky's (1988) infrequent comments on the matter:

> Can the problem [the evolution of language] be addressed today? In fact, little is known about these matters. Evolutionary theory is informative about many things, but it has little to say, as of now, about questions of this nature. The answers may well lie not so much in the theory of natural selection as in molecular biology, in the study of what kinds of physical system can develop under the conditions of life on earth and why, ultimately because of physical principles. It surely cannot be assumed that every trait is specifically selected. In the case of such systems as language … it is not easy even to imagine a course of selection that might have given rise to them.

'What could [Chomsky] possibly mean?', Pinker (1994) asks. 'Could there be a language organ that evolved by a process different from the one we have always been told is responsible for the other organs?'

Pinker considers the alternatives to natural selection but comes up with nothing more striking than Gould & Lewontin's (1979) 'spandrels', the by-products of selection for other targets. He considers the Darwinian refutation of Paley's (1803) argument for design in the evolutionary history of the eye and compares this history with that of language. But the time–course of these developments and their respective scopes are quite different. Language is recent and a species characteristic. Photodetection is ancient and crosses the boundaries of species, orders and even phyla (Quiring *et al.*, 1994). Thus the evolution of the eye, even though it does not qualify as a 'major transition' in Maynard-Smith & Szathmary's (1995) sense, has greater significance in the history of life than the evolution of language. Although the difficulty in explaining the initial change may be as great in each case, the progressive modification of the eye by selection over hundreds of millions of years casts little light on the discontinuity in the evolution of language, that, in its extant form, must be dated at less than two hundred thousand.

Aspects of Pinker's argument fall foul of Bickerton's critique. Pinker (1994) writes:

> Language … is composed of many parts: syntax, with its discrete combinatorial system building words; a capricious lexicon; a revamped vocal tract; phonological rules and structures; speech perception; parsing algorithms; learning algorithms. Those parts are physically realized as intricately structured neural circuits, laid down by a cascade of precisely timed genetic events.

But if these component genetic events are sequential innovations, at what stage and in what order were they introduced? One must assume that they were each selected and that each on its own proved advantageous. But what were the advantages of the individual components unrelated to the other elements of language? What was the order in which the components were selected (Bickerton, 1995: 72)? One must assume that the whole cascade was completed in the transition between the protolanguage that was characteristic of *Homo erectus*, and the capacity for language that is present in modern *H. sapiens*.

In answer to Bates' question 'What protoform can we possibly envision that could have given birth to constraints on the extraction of noun phrases from an embedded clause? What could it conceivably mean for an organism to possess half a symbol, or three quarters of a rule?', Pinker (1994) writes that:

> Grammars of intermediate complexity are easy to imagine [contra Bickerton, 1995: 72]. In a recent book Derek Bickerton answers Bates even more concretely. He gives the term 'protolanguage' to chimp signing, pidgins, child language in the two-word stage, and the unsuccessful partial language acquired after the critical period by Genie and other wolf-children. Bickerton suggests that *H. erectus* spoke in protolanguage. Obviously there is still a huge gulf between these relatively crude systems and the modern adult language instinct and here Bickerton makes the jaw-dropping additional suggestion that a single mutation in a single woman, African Eve, simultaneously wired in syntax, resized and reshaped the skull, and reworked the vocal tract … [W]e can extend the first half of Bickerton's argument without accepting the second half, which is reminiscent of hurricanes assembling jetliners.

Thus Pinker, along with Bates, recoils from the prospect of a big bang mutation. But neither has any answer to the questions about the time–course or the nature of the transition from the protolanguage of *H. erectus* to modern *H. sapiens*. Nor does Bickerton himself offer any hypothesis about the nature of the brain change that he postulates as responsible not only for the innovation in function but also for the change in skull shape and configuration of the vocal tract. Curiously none of these authors considers the possibility raised by Louis Bolk (Bolk, 1926) that some step in the evolution of humans was taken by the process of neoteny, i.e. by a small change in the trajectory of development, for example a delay in the plateau of brain growth that resulted in a prolongation into adult life of some of the features, for example of the face, that are characteristic of infancy in the chimpanzee.

But in discussing Chomsky's views on the evolution of language, Pinker (1994) quotes him as follows:

> These skills [for example, learning a grammar] may well have arisen as a concomitant of structural properties of the brain that developed for other reasons. Suppose that there was selection for bigger brains, more cortical surface, *hemispheric specialization for analytic processing* [italics added], or many other structural properties that can be imagined. The brain that evolved might well have all sorts of special properties that are not individually selected; there would be no miracle in this, but only the normal workings of evolution. We have no idea, at present, how physical laws apply when 10^{10} neurons are placed in an object the size of a basketball, under the special conditions that arose during human evolution.

Indeed this is a curious passage. The first sentence invokes the concept of the spandrel. The second and last sentences postulate selective pressures for brain features that apparently were specific to *H. sapiens* but are unidentified. Pinker comments dismissively on the last sentence 'We may not, just as we don't know how physical laws apply under the special conditions of hurricanes sweeping through junkyards'.

But what this dismissal has overlooked is what (italicised in the passage) has been overlooked by Bickerton, and is so familiar to Pinker (see, for example, the passage quoted above from page 334 of Pinker, 1994) that he and many others have failed to identify it as a potential key to the problem. Language is lateralised, with some critical component being localised in most individuals in the left hemisphere, as we have known since the observations of Dax (1865) and Broca (1861). It is only when it is understood, as Marian Annett has consistently emphasised, that directional handedness on a population basis is specific to *H. sapiens* (McGrew & Marchant, 1997), that it becomes recognisable as the key to the evolution of language and the speciation of *H. sapiens*.

THE STATUS OF SALTATIONS IN EVOLUTIONARY THEORY

To take seriously a structural discontinuity as an explanation for a species difference, it is necessary to consider concepts of evolutionary change other than Darwinian gradualism and the 'biological' or 'isolation' species concept. Bickerton relates how some time between his first (1981) and second (1990) formulations of the evolutionary origins of language, he heard about the theory of punctuated equilibria (Eldredge & Gould, 1972). Penner's (2000) sustained attack on evolutionary theory, on the basis that the theory cannot account for the origins of language, lacks reference even to this modest departure from classical Darwinian orthodoxy. But there have long been challenges to the gradualist version (De Vries, 1901; Bateson, 1894; Goldschmidt, 1940), and some of these have had an explicit genetic basis. Thus White (1978) and King (1993) have argued strongly for a role for chromosomal change in speciation, but their arguments have not overwhelmed the established view. Against this view it is argued (e.g. Coyne & Orr, 1998) that radical rearrangements of the chromosome complement, for example chromosomal fusions, may apparently have few phenotypic effects, and in some cases alternative chromosomal configurations persist, as it were, as a polymorphism within species.

The case for saltational change in species transitions has been argued at a macro-evolutionary level (Stanley, 1998), that the amounts of change seen within species and other taxa are simply insufficient to account for the overall pattern of evolutionary change that is seen over time, and at the level of morphology (Schwartz, 1998) that the intermediate states in the transition between species that are required by the gradualist theory are absent. But all such general arguments come up against the difficulty, in terms of an actual genetic transition, that Goldschmidt's (1940) 'hopeful monster' ran into: the greater the magnitude of the saltational change the less likely it is to have survival value, and the greater the difficulty the hopeful monster will have in identifying a mate. The difficulty is particularly great if the change has the reproductive consequence of reducing fertility in the hybrid state. The possibility that the monster can identify an individual with the same mutation is clearly dependent on reproduction already having taken place, and even then the new mutation is at a severe statistical disadvantage with respect to the existing population.

But here Darwin's (1871) juxtaposition of *The Descent of Man* and the theory of sexual selection offers a way out. If there were some way in which sexual selection and speciation were interdependent this might be relevant both to the problem of the discontinuity of the change and to that of mate selection. The case of cerebral lateralisation in modern *H. sapiens* illustrates the possibility. All authorities on the genetics of lateralisation (Annett, 1985; McManus, 1985; Corballis, 1997) are agreed that there is a sex difference: females are more righthanded than males (although the adult male brain is probably more asymmetrical than that of the female; Bear *et al.*, 1986). The female brain grows faster than that of the male (Kretschmann *et al.*, 1979) and females have greater mean verbal fluency and acquire words earlier (Maccoby & Jacklin, 1975; McGlone, 1980; Halpern, 1992) than males. If language is the species characteristic and lateralisation is the process by which it evolved, these facts are related, and they tell us about the nature of the genetic mechanism. Only two explanations of the sex difference in lateralisation are conceivable, that it is hormonal in origin (Geschwind & Galaburda, 1985), or that it reflects a sex chromosomal locus (Crow, 1993, 1994), and the facts of sex chromosomal aneuploidies (XXY and XXX individuals who differ in hormonal status have similar hemispheric deviations in development) speak decisively in favour of the latter interpretation. The hypothesis that the asymmetry factor is present on both X and Y chromosomes (Crow, 1993; Corballis *et al.*, 1996) can explain the transmission of handedness within families and apparent dosage effects in the aneuploidies. That there are problems (Corballis, 1997) in accounting for persisting variation in males and females in terms of conventional polymorphisms and heterozygote advantage explanations, should not dissuade us from pursuing the line of thought. The genetic principles involved may not be those on which we have hitherto relied.

The paradigm of *H. sapiens* therefore suggests a new version of saltational speciation, that it is not chromosomal changes in general that play a role in speciation but changes on the sex chromosomes, and perhaps particularly changes in regions of X–Y homology that are involved. These regions have a special status because they can account (as in the case of lateralisation in humans) for quantitative differences in a characteristic in males and females, and such quantitative differences are a potential substrate for sexual selection. The Y chromosome itself has a unique role, because it is not necessary for survival. There are interindividual differences on the Y (reviewed here by Chris Tyler-Smith) but there are also large interspecific differences. The Y therefore can be seen as a test-bed of evolutionary change. One possibility is that the primary changes in speciation take place on the Y, but that when they are located in regions of homology with the X there is the possibility of correlated but independent change in the two sexes. Such correlated but quantitatively differing ranges of variation have the potential to explain the type of runaway sexual selection envisaged by Fisher (1958), and this may be what occurred with respect to cerebral asymmetry at some point in hominid evolution (Crow, 1998a, 1998b); the introduction of the dimension of symmetry–asymmetry allowed brain growth to equilibrate at a new point of plateau, and this equilibration took place around successive modifications on the Y and then on the X chromosome.

There is thus a potential three-way relationship between sexual selection, sex linkage and speciation, in which the pattern suggested by hominid evolution is backed up in the recent literature relating to other species. A role for sexual selection in modifying a primary change in a sexually dimorphic feature to establish a new species boundary has been argued in relation to Hawaiian Drosophilid species by Kaneshiro (1980) and Carson (1997). Similar arguments apply in the case of the prolific speciation of cichlid fishes in the lakes of East Africa (Dominey, 1984; McKaye, 1991) and may also apply in birds (Price, 1998). Some putative speciation loci, for example the Odysseus homoeobox (Ting *et al.*, 1998) and the *per* gene (Ritchie & Kyriacou, 1994) that have been identified in *Drosophila* species, are X-linked. In discussing the relationship between the X chromosome and speciation that she finds in Lepidoptera, Prowell (1998) offers three explanations: (1) that X-linked traits evolve faster, (2) that traits related to speciation tend to be sex-limited, and that sex-limited traits tend to be on the sex chromosomes, and (3) that female-limited X-linked traits undergo faster rates of evolution when, as in the case of Lepidoptera, the female is heterogametic. These explanations are not mutually exclusive. Prowell asks whether the X chromosome bias is unique to Lepidoptera and concludes that none of these explanations is likely to be limited to this order. In discussing Haldane's rule, that when, in a species hybrid, one sex is sterile or inviable it is the heterogametic sex, Coyne & Orr (1998) consider various explanations including faster evolution and recessivity of genes on the X chromosome. While each of these observations and hypotheses is consistent with the generalisation that there is a relationship between speciation and the sex chromosomes, none of the authors considers the more restrictive formulation suggested by the sequence of events (Sargent *et al.*, 1996, 2001; described in these *Proceedings* by Carole Sargent *et al.*) on the mammalian Y chromosome, that it is the interaction between the sex chromosomes, particularly the possibility of transfer of material between them, that is critical in speciation. In this volume Klaus Reinhold considers the case that sexual selection acts selectively on sexual dimorphisms that relate to sex-linked genes, as suggested by Rice (1984).

The sequence of events, including a translocation and a paracentric inversion, suggested by the work summarised by Carole Sargent *et al.* and by the X–Y hypothesis as relevant to the course of hominid evolution, carries the further implication that epigenetic modification is involved in the process of sexual selection and speciation. In mammals genes on one X chromosome are subject to the process of X inactivation, but those gene sequences that are also represented on the Y chromosome are protected from this influence. Such genes are expressed from both X and Y in males and from both Xs in females, a similar dosage thus being maintained in each sex. The mechanism by which this protection is achieved is unknown (Burgoyne & McLaren, 1985; Crow, 1991). Gene sequences that have been transferred from the X to the Y are in a new situation; whatever the mechanism a phase of epigenetic equilibration must be assumed (Jegalian & Page, 1998). If X–Y pairing in male meiosis plays a role, the orientation of the sequence on the Y is also relevant. The paracentric inversion on the Y short arm could be critical.

A magnetic resonance imaging (MRI) investigation in monozygotic twins of handedness and asymmetry of the planum temporale (Steinmetz *et al.*, 1995) indicates that there is room for an epigenetic influence in the determination of cerebral asymmetry, and this may account for the stochastic element that is incorporated in genetic theories (Annett, 1985; McManus, 1985). There is a possibility, therefore, that the genetic mechanisms underlying the development of cerebral asymmetry in humans are a paradigm for a more general interaction between genetic and epigenetic mechanisms in sexual selection and speciation. One can contemplate the hypothesis that sexual selection and natural selection are mediated by distinct but complementary genetic processes, that natural selection reflects the response that ensures the organism's survival, of any part of the genome to environmental change, whereas sexual selection reflects the sequential response of the female genome (for example the mammalian XX complement) to change on the Y chromosome, and that this process involves particularly the epigenetic modulation of genes on the X. According to this concept speciation follows the history of the non-recombining sex chromosome, in mammals the Y.

CONTRIBUTIONS TO THIS VOLUME

These *Proceedings* reflect an attempt to cross the interdisciplinary boundaries between archaeology, palaeontology, neuropsychology, neuroanatomy, genetics and evolutionary theory to approach the problem of the origins of modern *H. sapiens*. Paul Mellars outlines the archaeological evidence (see also Mellars, 1989, 1998) for the relative recency and abruptness of appearance of artefacts associated with the creativity of modern humans. Chris Stringer gives an update on the speciation of modern *H. sapiens* and the Out of Africa hypothesis, for which he has been so effective an advocate (Stringer & McKie, 1996), and Ian Tattersall argues the case that he has previously developed (Tattersall, 1998), that the speciation of modern *H. sapiens* exemplifies the principle of punctuated equilibria, i.e. it is a saltational change. Mark Collard places this discussion within the framework of the present evidence on the longer course and diversity of hominid evolution. These contributions are followed by discussions of the singularity of human language by Derek Bickerton, and of the relevance of cerebral asymmetry by Michael Corballis. In each case they outline their own concepts of the selective advantages of the component functions that they regard as critical. Both authors modify their previous formulations; interestingly neither sees the critical steps as necessitating genetic discontinuities as strongly as some other contributors. James Steele reviews the palaeontological and archaeological evidence that allows us to address the question: when did directional asymmetry enter the record of hominid evolution? The key question here (p. 154) is whether or not directional asymmetry is a derived feature, and if so at what stage?

Detlev Ploog has accumulated a body of evidence on the neuroanatomical basis of language and on the differences between this and the substrate of communicative ability in other primates. These differences require a genetic explanation, and that genetic explanation must be relevant to the nature of species transitions. In amplifying the human case, Norman Cook has built on the arguments that he first deployed in *The Brain Code* (Cook, 1986), that the facts of human brain evolution require that language is represented in both hemispheres and that callosal connectivity is critical to their integration. These arguments are echoed in the recent literature on the role of the right hemisphere in language (Coney & Evans, 2000). When these hemispheric differentiations are recognised as dependent upon language as the speciation characteristic, it will be appreciated, as Chomsky argued, that human psychology has less in common with that of other primates and mammals than is often assumed. New neuroanatomical and neurophysiological principles have been introduced at at least one hominid species boundary.

The peculiar genetic history and population characteristics of the Y chromosome are outlined by Chris Tyler-Smith, including the interaction with the X. The small size of the Y and its sex-limited transmission make it at first sight an unlikely vehicle for the determining characteristic of the species. In addition, as Corballis (1997) has argued, there are problems in assuming that a conventional polymorphism will be maintained on the Y and could account for significant and persisting variation in the population. These problems need to be overcome if the X–Y hypothesis of human origins is to be sustained. Sargent *et al.* (1996, 2001) have summarised their own evidence and that of others, that allows one to identify those regions of the Y that may have particular significance in human evolution, including the Xq21.3/Yp11.2 region of homology, following translocation and subsequent paracentric inversion. The identification within this region of protocadherinXY, a gene that codes for a cell-surface adhesion molecule that is expressed in the brain, rescues the theory from the sudden death that would have followed the demonstration that no gene, or a gene that was unexpressed in the brain, was present in the region. I have outlined the theory together with its implications as I see them. Klaus Reinhold discusses evidence and theory on sex chromosomal linkage of sexually selected traits that may be the key to a functional separation of sexual and natural selection.

References

Annett, M. (1985) *Left, Right, Hand and Brain: The Right Shift Theory.* London: Erlbaum.

Bateson, W. (1894) *Materials for the Study of Variation*. New York: Macmillan.

Bear, D.M., Schiff, D., Saver, J., Greenberg, M. & Freeman, R. (1986) Quantitative analysis of cerebral asymmetry; fronto-occipital correlation, sexual dimorphism and association with handedness. *Archives of Neurology*, **43**, 598–603.

Bickerton, D. (1981) *The Roots of Language*. Ann Arbor: Karoma.

Bickerton, D. (1990) *Language and Species*. Chicago: University of Chicago.

Bickerton, D. (1995) *Language and Human Behavior*. Seattle: University of Washington.

Bolk, L. (1926) *Das Problem der Menschwerdung.* Jena: Gustav Fischer.

Broca, P. (1861) Remarques sur la siegé de la faculté du langue. *Bulletin de la Société Anatomique de Paris (2nd Series)*, **6**, 330–57.

Burgoyne, P.S. & McLaren, A. (1985) Does X–Y pairing during male meiosis protect the paired region of the X chromosome from subsequent X-inactivation? *Human Genetics*, **70**, 82–3.

Carson, H.L. (1997) Sexual selection: a driver of genetic change in Hawaiian *Drosophila*. *Journal of Heredity*, **88**, 343–52.

Chomsky, N. (1959) A review of B.F. Skinner's verbal behavior. *Language*, **35**, 26–58.

Chomsky, N. (1988) *Language and the Problems of Knowledge: The Managua Lectures.* Massachusetts: MIT Press.

Coney, J. & Evans, K.D. (2000) Hemispheric asymmetries in the resolution of lexical ambiguity. *Neuropsychologia*, **38**, 272–82.

Cook, N.D. (1986) *The Brain Code: Mechanisms for Information Transfer and the Role of the Corpus Callosum*. London: Methuen.

Corballis, M.C. (1997) The genetics and evolution of handedness. *Psychological Review*, **104**, 714–27.

Corballis, M.C., Lee, K., McManus, I.C. & Crow, T.J. (1996) Location of the handedness gene on the X and Y chromosomes. *American Journal of Medical Genetics (Neuropsychiatric Genetics)*, **67**, 50–2.

Coyne, J.A. & Orr, H.A. (1998) The evolutionary genetics of speciation. *Philosophical Transactions of the Biological Society of London*, **353**, 287–309.

Cronin, H. (1991) *The Ant and the Peacock*. Cambridge: Cambridge University Press.

Crow, T.J. (1991) Protection from X inactivation. *Nature*, **353**, 710.

Crow, T.J. (1993) Sexual selection, Machiavellian intelligence and the origins of psychosis. *Lancet*, **342**, 594–8.

Crow, T.J. (1994) The case for an X–Y homologous determinant of cerebral asymmetry. *Cytogenetics and Cell Genetics*, **67**, 393–4.

Crow, T.J. (1998a) Sexual selection, timing and the descent of man: a genetic theory of the evolution of language. *Current Psychology of Cognition*, **17**, 1079–114.

Crow, T.J. (1998b) Why cerebral asymmetry is the key to the origin of *Homo sapiens*: how to find the gene or eliminate the theory. *Current Psychology of Cognition*, **17**, 1237–77.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection: Or, the Preservation of Favoured Races in the Struggle for Life.* London: John Murray.

Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex.* London: John Murray [New Jersey: Princeton University Press: 1981 facsimile of original]

Dax, M. (1865) Lésions de la moitié gauche de l'éncephale coincident avec l'oubli des signes de la pensée [Read at congrés méridional at Montpelier in 1836]. *Gazette Hebdom Méd Chirurg*, **11**, 259–60.

De Vries, H. (1901) *Die Mutationstheorie*. Leipzig: Verlag von Veit.

Dominey, W.J. (1984) Effects of sexual selection and life histories on speciation: species flocks in African cichlids and Hawaiian *Drosophila*. In: *Evolution of Fish Species Flocks* (eds A. A. Echelle & I. Kornfield), pp. 231–49. Maine: Orino Press.

Eldredge, N. & Gould, S.J. (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: *Models in Palaeobiology* (ed. T. M. Schopf), pp. 82–115. San Francisco: Freeman Cooper.

Fisher, R.A. (1958) *The Genetical Theory of Natural Selection*, 2nd Edn. NY: Dover.

Gamble, C. (1993) *Timewalkers: The Prehistory of Global Colonization*. Bath: Sutton.

Geschwind, N. & Galaburda, A.M. (1985) Cerebral lateralization. Biological mechanisms, associations and pathology: a hypothesis and a program for research. *Archives of Neurology*, **42**, 428–654.

Goldschmidt, R. (1940) *The Material Basis of Evolution*. New Haven: Yale University Press [reprinted 1982].

Gould, S.J. & Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian program: a critique of the adaptationist programme. *Proceedings of the Royal Society of London*, **205**, 281–8.

Halpern, D.F. (1992) *Sex Differences in Cognitive Abilities*. New Jersey: Erlbaum.

Harris, R. & Talbot, T.J. (1997) *Landmarks in Linguistic Thought.* London: Routledge.

Hughlings Jackson, J. (1868) Observations on the physiology of language. *British Medical Journal*, **ii**, 259.

Hume, D. (1739) *A Treatise on Human Nature*. 1978 Reprint. Oxford: Clarendon Press.

Huxley, T.H. (1863) *Evidence of Man's Place in Nature*. London: Williams & Norgate.

Jegalian, K. & Page, D.C. (1998) A proposed mechanism by which genes common to mammalian X and Y chromosomes evolve to become X inactivated. *Nature*, **394**, 776–80.

Kaneshiro, K.Y. (1980) Sexual isolation, speciation and the direction of evolution. *Evolution*, **34**, 437–44.

Kant, I. (1781) *Immanuel Kant's Critique of Pure Reason*. Translated by Norman Kemp Smith 1963. London: Macmillan.

Kant, I. (1788) *Critique of Practical Reason*. Translated by Lewis White Beck 1956. Indianapolis: Library of Liberal Arts.

King, M. (1993) *Species Evolution. The Role of Chromosome Change.* Cambridge: Cambridge University Press.

Kretschmann, H.F., Schleicher, A., Wingert, F., Zilles, K. & Loeblich, H.-J. (1979) Human brain growth in the 19th and 20th century. *Journal of the Neurological Sciences*, **40**, 169–88.

Locke, J. (1690) *An Essay Concerning Human Understanding*. Reprinted 1975. Oxford: OUP.

Maccoby, E.E. & Jacklin, C.N. (1975) *The Psychology of Sex Differences*. Oxford: Oxford University Press.

McGlone, J. (1980) Sex differences in human brain asymmetry: a critical survey. *Behavioral and Brain Sciences*, **3**, 215–63.

McGrew, W.C. & Marchant, L.F. (1997) On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology*, **40**, 201–32.

McKaye, K.R. (1991) Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa. In: *Behaviour, Ecology and Evolution* (ed. M. H. A. Keenleyside), pp. 241–57. London: Chapman & Hall.

McManus, I.C. (1985) Handedness, language dominance and aphasia: a genetic model. *Psychological Medicine Monograph Supplement*, **8**, 1–40.

Maddox, J. (1997) The price of language? *Nature*, **388**, 424–5.

Maynard-Smith, J. (1993) *The Theory of Evolution*. Cambridge: Canto.

Maynard-Smith, J. & Szathmary, E. (1995) *The Major Transitions in Evolution.* Oxford: W. H. Freeman.

Mayr, E. (1963) *Animal Species and Evolution.* Massachusetts: Harvard University Press.

Mellars, P. (1989) Technological changes at the middle-upper palaeolithic transition: economic, social and cognitive changes. In: *The Human Revolution: Behavioural and Biological Perspectives in the Origins of Modern Humans* (eds P. Mellars & C. Stringer), pp. 338–65. Edinburgh: Edinburgh University Press.

Mellars, P. (1998) Modern humans, language, and the 'symbolic explosion'. *Cambridge Archaeological Journal*, **8**, 88–94.

Muller, F.M. (1996) Lectures on Mr Darwin's philosophy of language in Fraser's Magazine volumes 7 and 8, 1873. In: *The Origin of Language* (ed. R. Harris), pp. 147–233. Bristol: Thoemmes Press.

Paley, W. (1803) *Natural Theology*, 5th Edn. London: R. Faulder.

Penner, J.G. (2000) *Evolution Challenged by Language and Speech*. London: Minerva.

Pinker, S. (1994) *The Language Instinct*. Allen Lane: London.

Price, T. (1998) Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society of London (Biological)*, **353**, 251–60.

Prowell, D.P. (1998) Sex linkage and speciation in Lepidoptera. In: *Endless Forms* (eds S. H. Howard & S. H. Berlocher), pp. 309–19. Oxford: Oxford University Press.

Quiring, R.U., Walldorf, U., Kloter, U. & Gehring, W.J. (1994) Homology of the eyeless gene of *Drosophila* to the small eye gene in mice and Aniridia in humans. *Science*, **265**, 785–9.

Rice, W.R. (1984) Sex chromosomes and the evolution of sexual dimorphism. *Evolution*, **38**, 735–42.

Ritchie, M.G. & Kyriacou, C.P. (1994) Reproductive isolation and the period gene of *Drosophila*. *Molecular Ecology*, **3**, 595–9.

Sargent, C.A., Boucher, C.A., Blanco, P. *et al.* (2001) Characterization of the human Xq21.3/Yp11 homology block and conservation of organization in primates. *Genomics*, **73**, 77–85.

Sargent, C.A., Briggs, H., Chalmers, I.J., Lambson, B., Walker, E. & Affara, N.A. (1996) The sequence organization of Yp/proximal Xq homologous regions of the human sex chromosomes is highly conserved. *Genomics*, **32**, 200–9.

de Saussure, F. (1916) *Course in General Linguistics*. Paris: Payot [Illinois: Open Court, translated by R. Harris, 1983].

Schwartz, J.H. (1998) *Sudden Origins: Fossils, Genes and the Emergence of Species.* New York: J. Wiley.

Stanley, S.M. (1998) *Macroevolution: Patterns and Processes*. Baltimore: J. Hopkins.

Steinmetz, H., Herzog, A., Schlaug, G., Huang, Y. & Jancke, L. (1995) Brain (a)symmetry in monozygotic twins. *Cerebral Cortex*, **5**, 296–300.

Stringer, C. & McKie, R. (1996) *African Exodus: The Origins of Modern Humanity.* London: J. Cape.

Tattersall, I. (1998) *Evolution and Human Uniqueness*. Oxford: Oxford University Press.

Taylor, J. (1932) *Selected Writings of John Hughlings Jackson, 2 Volumes*. London: Hodder & Stoughton.

Ting, C.T., Tsaur, S.C., Wu, M.L. & Wu, C.-I. (1998) A rapidly evolving homoeobox at the site of a hybrid sterility gene. *Science*, **282**, 1501–4.

White, M.J.D. (1978) *Modes of Speciation*. San Francisco: W. H. Freeman.