

The Problem of Parallelism in Relation to the Subspecific Taxonomy of Homo Sapiens

BY L. OSCHINSKY

RÉSUMÉ

L'étude taxinomique des sous-espèces de l'Homo Sapiens se butte à certains problèmes. Pour les résoudre, l'auteur affirme l'importance des caractères morphologiques pris comme groupe et démontre les conditions requises pour que ces caractères soient valables en taxinomie.

It has been emphasized by many authors that the subspecies is frequently the incipient or potential new species which makes its study crucial in evolutionary investigations. (Darwin 1866, 1871; Rensch 1960; Simpson 1943, 1945, 1949, 1950, 1951, 1953a, 1953b, 1959, 1960, 1961) This has in part been denied by Mayr (1963), Brown (1958a, 1958b) and Livingstone (1962, 1963) who have stressed the "swamping" effect (Mayr 1942, 1963; Brown 1958a, 1958b) of a series of hybridizing subspecies. It seems reasonable that both phenomena can occur and that it does not strain the biological imagination to conjure up a situation where one segment of a polytypic species, due to continued isolation, develops a new morphological pattern which finally crosses the species boundary.

Concurrent with the evaluation of the role of the subspecies in biological studies, is the question of parallelism. As Simpson (1950:59) has clearly indicated when he points out that:

The basis of parallelism is initial similarity of structure and adaptive type, with subsequent recurrent homologous mutation, and similar direction of natural selection.

He restates the problem in a later publication (Simpson 1961:78).

Parallelism is the development of similar characters separately in two or more lineages of *common ancestry* and on the basis of, or channeled by, characteristics of that ancestry.¹

Parallelism on the other hand, is not to be confused with convergence which is the development of similar characters separately in a group of lineages *without common ancestry*. Simpson (1961:87) gives the following interesting example of convergence in two lineages of ungulates (litopterns and horses) which are very distinctly removed from each other phylogenetically, yet markedly similar morphologically in regard to certain "horselike" features.

The discoverer of thoatherium, Florentio Ameghino, an evolutionary taxonomist capable in his time (1854-1911), concluded that the resemblances are homologous and that litopterns (the group to which thoatherium belongs) and horses had a common ancestry closer than that, for instance, between horses and rhinoceroses.

The discussion of parallelism has been more or less restricted to higher categories such as, the species, genus, family, order, etc. (Oschinsky and East, in press). Concurrently with this, the lack of attention that has been paid to evolution and taxonomic theory of the various subspecies of Homo sapiens has created the confusion already alluded to by Oschinsky and East.

The studies of Beigert (1957, 1960). Boule and Vallois (1957), Cain and Harrison (1960), Cain (1954), Dobzhansky (1951), Mayr (1942), Simpson (1961), Breitinger (1957, 1959), Heberer (1959a, 1959b), Strauss (1949), Schultz (1936, 1950a, 1950b), Vallois (1958), and Weiner (1958) have mainly been concerned with parallelism on the specific and supraspecific level, and the anthropologists among these authors have dealt with hominid evolution on the same levels. Mayr (1950) has been one of the few who has touched on the taxonomy of the human subspecies in any detail. Concerning these groups, Mayr (1950:114) remarks as follows:

Man as he exists today, has pronounced racial groups, such as the Whites, Negroes, and Mongoloids, which might well deserve subspecific recognition. But there are minor racial differences within each

¹ Italics added.

of these subspecies. Furthermore, preceding modern man there have been types of Homo sapiens that are now extinct, like Cro-Magnon man and his contemporaries. This, no doubt, is a different level of subspecies from those of living man.

In his classification of fossil hominids on the supraspecific level, Mayr has lumped the Australopithecines, the Pithecanthropines, the Neanderthals and the Cro-Magnons all in the same genus; namely, Homo. In other words the hominid family is a monogeneric family with three species, transvalensis for the Australopithecines, and erectus for the Pithecanthropines. The Neanderthals are included with Homo sapiens in the same species.

This latter situation creates a problem in subspecific taxonomy. If Neanderthal man and Homo sapiens are reduced to subspecies then the racial differences become reduced to a category below the subspecies, which is unwarranted in terms of the degree of difference between them. This is also clear when this situation is compared with zoological practice in such groups as the caribou (Banfield 1961) and the bears (Simpson 1945).

In his latest work, Mayr (1963) revises his view and goes back to the older taxonomy in which the Australopithecines have their own genus. He does not agree with Robinson that there is justification for three genera. (Robinson 1954a) The Pithecanthropines in this new revision are still promoted to the genus Homo, and the Neanderthals are still in uneasy partnership with Cro-Magnon man. His original reason for putting the Australopithecines in the genus Homo was his overemphasis of the importance of the erect posture and a concordant neglect of the more or less pongid ratio of splanchno-cranium to neurocranium. In the case of the lumping of the Neanderthals with the Upper Paleolithic Homo sapiens, the same criticism might be made. The Neanderthaloid splanchno-cranium, as in La Chapelle-aux-Saints. is very massive and still anterior to the neurocranium. The zygomatic arches are very gracile and the suborbital maxillary region shows no trace of a canine fossa and bulges anteriorly. The nasal aperture is enormous, and the orbits are high and round. There is a massive supraorbital torus and a very slight forehead. The teeth are very large and the palate is U-shaped. The basi-occipital basi-sphenoid articulation does not show the typical sapiens flexion. The foramen magnum is relatively long and narrow. The mastoids are rudimentary and there is a marked occipital torus. The occipital condyles are small and the foramen magnum is still posteriorly displaced. The mandible has a low and broad ascending ramus, shallow incisurae mandibulae, the necks of the condyles are short and stubby, the gonial angles are semi-lunar in form. The coronoid processes are short and dull. The corpora are thick and the mental foramena are placed inferior to the usual sapiens position.

Mayr (1950) points out that the cranial capacity of Neanderthal man is higher than that of Upper Paleolithic Homo sapiens and this is not the first time in the history of taxonomy, that an abstract numerical value cloaks a morphological difference (Le Gros Clark 1955).

The Neanderthaloid neurocranium still preserves the archanthropine form, i.e. frontal constriction, modest height and a brain with simple convolutions and as such, it can not be equated morphologically with that of Homo sapiens. The fact that the so-called classic types of Neanderthal are later in time than the Steinheim, Fontéchevade, and Skhul does not mean necessarily that they developed from these so-called "sapiens-like" types. There is a possibility that their gerontomorphic ancestors have not yet been found, since material from the Mindle-Riss period is not too abundant. In any case, except for the Steinheim skull, these other crania are rather fragmentary. They consist mostly of calvaria and it is difficult to know such crucial relationships and features as splanchno-cranial relationship to neurocranium, foramen magnum position, relative size of mastoid, and mandibular morphology.

The only complete Neanderthaloid specimen that shows morphological overlap with Homo sapiens is that of the population of Skhul where the presence of a high neurocranium, well developed forehead, and the posterior oriented splanchno-cranium is practically underneath the neurocranium rather than anterior to it as in La Chapelle-aux-Saints. The form of the foramen magnum and the flexion of the basi-occipital, basi-sphenoid junction is sapiens-like. There is no occipital torus and the occipital-parietal arc in the mid-sagittal plane is high rather than low and compressed as in the "Classic" Neanderthals. As any inspection of the casts will demonstrate, the form of the mandible also shows sapiens features. The ascending ramus is high and narrow. The gonial angle is sharp, rather than crescentic, as in La Chapelle and there is a definite chin. All the remaining Upper Paleolithic and Mesolithic Homo sapiens specimens from Europe, North Africa and Eastern Asia are perfectly modern in their splanchno-cranial-neuro-cranial relationships, and are within the range of modern man. (Boule and Vallois 1957; Briggs 1955) Because of these facts, it is considered arbitrary to include Homo Neanderthalensis in the same species as Homo sapiens.

The above excursion into the realm of supraspecific taxonomy may seem a digression, but is unavoidable since it is necessary to highlight some of the problems at those levels in order to appreciate the issues of the lower categories.

Elsewhere, Mayr (1942:155) has stated that:

All differences between species are subject to geographic variation; there is no difference of kind between specific and subspecific characters.

The difference is, thus, more a quantitative one. Fewer characters are diagnostic of the subspecies. Simpson (1953a, 1961) has pointed out that in the definition of higher categories, the characters used are fewer but are relatively exclusive to the taxa. In the case of lower categories, the distinguishing characters are more numerous and less exclusive.

It is for this reason that biometrical methods are of limited use above the subspecies level. Le Gros Clark (1955:22-3) states the difficulties as follows:

Apart from the problem of assessing general taxonomy relationships by reference to morphological resemblances so far as these may be determined by direct comparisons, attempts have from time to time been made to estimate degrees of resemblance (and thus, it is assumed, degrees of affinity) on a quantitative basis. This biometrical approach is an attempt to facilitate and place on a strictly objective basis the comparison of one type with another. But unfortunately it is fraught with the greatest difficulties, the main one of which, no doubt, is the impossibility by known methods of weighting each individual character according to its taxonomic relevance. If the measurements of every single morphological character of skull, dentition, and limb bones were of equal value for the assessment of zoological affinities, it might be practicable to assess the latter in strictly quantitative terms. But it is very well recognized that this is by no means the case. It is well known also that the products of convergent evolution may lead to similarities (particularly in general over-all measurements and indices derived therefrom) which, if expressed quantitatively, would give an entirely false idea of systematic proximity. Generally speaking, it is true to say that statistical comparisons of over-all measurements and indices are of the greatest value in assessing degrees of affinity in forms already known to be quite closely related — e.g., subspecies or geographical races, but they become of less and less practical value as the relationship becomes more remote and the types to be compared become more disparate.²

It seems probable that such morphological features as sagittal keel, shovel-shaped incisors and occipital bun are also subject to parallelism since they are present in such distinct groups as Melanesians, Eskimos and South American Indians, where there has been no evidence for close contact over a considerable period.

The case might be stated even more strongly than Le Gros Clark has put it in his delineation of the subspecies as the usual lower category where metrical parallelism is automatically ruled out, due to proximity of ancestry. As has been already pointed out by Oschinsky and East (in press), parallelism can occur on the subspecific level, i.e. palatine and mandibular tori in Eskimos and Vikings; sagittal keel, dolichocephaly, and hypsicephaly in Eskimos. Melanesians and South American Indians. It is only on the level of the "sub-subspecies" or micro-geographical race, that we can assume similarities to be homologous. This is because the groups are contiguous in space, and continuous in time, so that there have been no obvious barriers to interbreeding. This is not true in the case of many sections of the Australoid, Mongoloid. Negroid and Caucasoid subspecies, many of which have been isolated from each other, for perhaps as long as 20,000 years, i.e. Autraloids and Caucasoids; Mongoloids and Negroids, etc., (Coon 1962).

This is sufficient time for parallelism to be developed which can mislead us in our interpretation of similarities between such

² Italics added.

widely separated groups (Oschinsky and East, in press). It is for this reason that Le Gros Clark's concept of "total morphological pattern" is so important in the assessment of affinities between groups in the lower categories. He writes (1955:15)

It seems desirable to stress this concept of pattern rather strongly because the assessment of the phylogenetic and taxonomic status of fossil hominid remains must be based, not on the comparison of individual characters in isolation one by one, but on a consideration of the *total pattern*³ which they present in combination.

Concerning the choice of characters involved in the investigation of affinities between biological groups, Le Gros Clark refers to the "principle of taxonomic relevance". This asserts that those characters are chosen whose taxonomic usefulness has already been established by comparative anatomical and paleontological investigations. The following is his discussion of this principle (Le Gros Clark 1955:25-26)

It may be asked how the distinction is to be made between morphological characters which are relevant or irrelevant for taxonomic purposes. The answer to this question is that each natural group of animals is defined (on the basis of data mainly derived from comparative anatomy and paleontology) by a certain pattern of morphological characters which its members possess in common and which have been found by the pragmatic test of experience to be sufficiently distinctive and consistent to distinguish its members from those of other related groups. The possession of this common morphological pattern is taken to indicate a community of origin (in the evolutionary sense) of all the members of the group, an assumption of which the justification is to be found in the history of paleontological discovery. But, as a sort of fluctuating background to the common morphological pattern, there may be a number of characters, sometimes obviously adaptive, which not only vary widely within the group but overlap with similar variations in other groups. Such fluctuating characters may be of importance for distinguishing (say) one species from another within the limits of the family, but they may be of no value by themselves for distinguishing this family from related families.4

In this context of "total morphological pattern" and "taxonomic relevance" the following remarks of Mayr (1942:19, 21) concerning variability are most appropriate.

³ Italics provided.

⁴ Italics added.

The most practical diagnostic characters are those that relate to some easily visible structure with low variability.

We must search for characters that tend to remain stable, characters that are phylogenetically conservative.⁵

By the application of the principles of "total morphological pattern", "taxonomic relevance", "phylogenetic conservatism" (low variability through time), and geographical conservatism (low variability in space), the true affinities of subspecific and lower categories can be assessed, and the confusing role which parallelism has played in the evaluation of relationships among the various subspecific groups of Homo sapiens can be eliminated.

The following concepts have been devised to clarify the complex nature of subspecific parallelism. First, there is the parallelism which is the result of the parallel retention of archaic features in groups which have been separated geographically for relatively long periods of time. Examples of this would be the incidence of prognathism, pre-nasal sulcus, large teeth, large palates, and broad nasal apertures in Australoids and Negroids. This particular type of parallelism has been termed archeomorphism. Geographical, cultural and archeological evidence all agree that the separation of the Negroes from the Australoids is of great antiquity (Coon 1963), and until evidence can be brought forward that there has been relatively recent interbreeding, say in the past two or three thousand years, it must be at present assumed that these similarities are not due to interbreeding, but to the maintenance of an ancient condition which has shown little change independently in both groups.

A second type of parallelism is *neo-morphism*. This is parallel progressive development in various subspecies such as found in the Arctic Mongoloids and Causasoids in the reduction of alveolar bone. This reduction causes lingual displacement of the lateral incisors in the Mongoloids (Oschinsky and Smithurst 1960; Oschinsky 1961; Shin Yo Chang and Myung Kook Kim 1961) and causes almocclusion in the Caucasoids (Tweed 1945; Krogman 1960).

⁵ Italics added.

The third type of parallelism is called *para-morphism*. These are parallel adaptations to similar environments, such as black skin in the Australoids and the Negroids and Dravidians. If we had data on the antiquity of the black skin, it could be maintained that it was also an archeo-morphic trait.

The last category of parallelism is random metrical and morphological convergence. These are characters which are not necessarily archaic or progressive, which have not yet been proven to have an adaptive function, and which occur in groups widely separated geographically and phylogenetically. Pinched narrow nasal bones in Melanesians and Arctic Mongoloids; dolichocephaly in the Indians of Southern California and the Australoids; hypsicephaly in the Moriori and the Indians of Tierra del Fuego, are examples of this type of parallelism.

In terms of slight obliquity in the vertical plane, the cheek bones of the Melanesian and non-Arctic Mongoloid are rather similar. But closer examination of the principle of total morphological pattern, clearly indicates that this is a random similarity. The projecting cheek bone, or zygo-maxillary junction to be more precise, is characterized by a long zygo-maxillary process of the maxilla and parallel zygomatic arches. The zygo-maxillary tuberosity is large and projects forward anteriorly. In the Old and New World Mongoloids (non-Arctic) the zygo-maxillary junction forms a right angle. When the zygo-maxillary junction of the Melanesians is examined, in the basal view, its shape is manifest as a crescent. The zygo-maxillary process of the maxilla is very short and the zygomatic arches are oblique rather than. parallel when the skull is viewed in the norma basalis (see figure 1; Oschinsky and East, in press). Presumably, the moderate obliquity of the malars (morphological overlap) in Mongoloids and Melanesians is due to different causes which have not yet been ascertained. It is thus evident how important the concept of the total morphological pattern is in deciding the morpholological equivalence of characters used in tracing affinities.

To sum up, then, on the kinds of characters used in taxonomic, subspecific studies; first, it must be ascertained that the characters are morphological equivalents and this is done on the basis of a close examination of the characters in terms of comparative anatomy and paleontology; second, the characters must vary concordantly within a population; thirdly, they must be geographically continuous (to rule out parallelism); fourthly, they must be chronologically continuous and show a gradual trend in a given direction; fifthly, they should have a high frequency within the population; sixthly, they should be relatively unique within the subspecies or other lower category in as far as this is possible in lower categories. If all of these attributes are present, the characters are then considered to be taxonomically relevant.

It is the mode of variation in time and space, manifested by the subspecies which is of taxonomic importance, not knowledge of the mode of inheritance as claimed by Dobzhansky (1951, 1962), Boyd (1950, 1963) and Laughlin (1950, 1962b). Lack of this knowledge did not prevent Darwin (1866) and Darwin and Wallace (1858) from developing their theory of natural selection, nor has lack of knowledge of polygenic inheritance impeded the progress of paleontology as the achievements of Keith (1925a, 1925b, 1931), Boule and Vallois (1932, 1957), Simpson (1943, 1945, 1950, 1951, 1953a, 1953b, 1959, 1960, 1961), Romer (1945, 1959), Le Gros Clark (1920, 1955, 1958a, 1958b) and Robinson (1954a, 1954b, 1961) indicate.

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