Parallelism, Homology and Homoplasy in Relation to Hominid Taxonomy and the Origin of Homo Sapiens

BY L. OSCHINSKY, P. GALL, J. MACDONALD, L. NIEMANN, M. SPENCE AND S. WILSON

RÉSUMÉ

Le concept de parallélisme qui, jusqu'à date avait été inclus dans la catégorie "homoplasie", est maintenant placé sous la rubrique "homologie". On a conçu aussi une nouvelle sous-catégorie de "l'homologie", "l'isomorphisme", afin de mieux rendre compte de la similitude due à l'ascendance commune.

In a previous paper, the possibility of parallelism on the subspecific homo sapiens level was indicated (Oschinsky 1963) since many examples are present in the literature of physical anthropology which have confused the categories of isomorphism with those of parallelism. Part of the reason for this confusion is the lack of appreciation of the quasi-arbitrary aspect of all taxonomic procedures as well as the unwarranted expectation of uniqueness in the characters used in lower categories.

In other words, characters which are very variable in time and space have been utilized as if they were relatively invariable. The New World has been populated by "Melanesians" and "Australoids" (Rivet, 1925; Tenkate, 1885; Hrdlicka, 1935) due to the uncritical use of dolichocephaly, sagittal keel, prognathism, and brow ridges and the consequent neglect of the diagnostic total morphological pattern of zygo-maxillary configuration (Oschinsky, 1962 and 1963; Oschinsky and East, in press).

Further confusion is caused by the definition and interpretation of the concept of parallelism, particularly in relation to the concepts of homology and homoplasy. Simpson, in his discussion of homologous and non-homologous similarity utilizes the term "homoplasy" as a collective concept which includes parallelism, convergence, analogy, mimicry and chance similarity. He defines homoplasy as "resemblance not due to inheritance from a common ancestor" (Simpson 1961:78). He defines parallelism as "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" (Simpson 1961:78). He further points out that convergence is the development of similar characters separately in two of more lineages without a common ancestry. Certain difficulties are created by the inclusion of parallelism under the rubric of homoplasy which. as demonstrated in the definition above. is a collective term for similarities not indicative of common ancestry.

Homoplasy in subdivided by Simpson further into the categories of analogy, mimicry and chance similarity, which are equivalent in classificatory grade to parallelism and convergence. It would seem that analogy defined as "functional similarity not related to community of ancestry" and mimicry, as well as chance similarity, can occur in related, as well as unrelated groups, and as such, would be subdivisions of both parallelism and convergence. For comparative purposes, both Simpson's classification and the authors' revised version are reproduced below.

TABLE I

Simpson (1961:78)

- A. Homology (similarities due to common ancestry)
- B. Homoplasy (similarities not due to common ancestry)
 - 1. parallelism
 - 2. convergence
 - 3. analogy
 - 4. mimicry
 - 5. chance similarity

TABLE II

Revised version (Oschinsky et al.)

- A. Homology (similarities due to common ancestry)
 - 1. Isomorphism similarities due to immediate common ancestry
 - 2. Parallelism similarities due to less immediate common ancestry.
 - i. archaeomorphism
 - ii. neomorphism
 - iii. paramorphism
 - iv. random metrical and morphological distribution.
- B. Homoplasy (similarities not due to common ancestry)
 - 1. Convergence
 - i. archaeoid
 - ii. neoid
 - iii. paroid
 - iv. convergent mimicry
 - v. convergent random metrical and morphological distribution.

A. Homology

Simpson defines homology as "resemblance due to inheritance from a common ancestry" (Simpson 1961:78; this meaning is retained here). This includes characters taken as individual traits or as parts of total morphological patterns. There are two types (according to the authors) of homology: isomorphism and parallelism. Isomorphism is similarity due to immediate common ancestry. These are the result of functional requirements having remained the same, and thus represent part of the identical total morphological patterns. It represents the majority of similarities in related animals which have immediate common ancestors; for example, canines in anthropoid apes and cercepithecoid monkeys. Parallelism is similarity due to less immediate common ancestry and involving traits part of separate common, not identical. morphological patterns; for example, canines in Old World and New World Monkeys. There are several subdivisions of parallelism: archaeomorphism, neomorphism, paramorphism, random metrical and morphological similarities. Archaeomorphism is "the parallel retention of archaic features in groups which have been separated geographically for relatively long periods of time"

(Oschinsky 1963:138). An example would be the retention of prognathism and pre-nasal sulcus in both Australoids and Negroids, from Upper Paleolithic man. Archaeomorphic traits are not a good expression of immediate closeness of phylogenetic relationships because they represent only traits of an earlier total morphological pattern which has been broken up and differentially retained by descendent populations. Neomorphism is "parallel progressive development of features in related groups"; for example, reduction of the alveolar bone in Arctic Mongoloids and Causasoids (ibid:138). Paramorphism is "parallel adaptation to similar environments" (ibid:139). It is thus functional as illustrated by dark skin in Australoids, Negroids and Dravidians. Random metrical and morphological distribution is "similarity due to characters which are not necessarily archaic or progressive, which have not yet been proven to have an adaptive value and which occur in groups relatively widely separated geographically and phylogenetically. A case in point is the pinched nasal bones in Melanesians and Arctic Mongoloids (ibid:139).

B. Homoplasy

Homoplasy is defined by Simpson as "resemblance not due to inheritance from a common ancestry" (1961:78). This meaning has been retained in the authors' revision. Convergence is the sole major division placed under this category in the revision presented here in constrast to Simpson's scheme above.

There are five categories of convergence; archaeoid, neoid, paroid, mimicry, and chance similarity. Except for mimicry, these categories approximate the subdivisions of parallelism, reflecting the fact that these are relative rather than absolute distinctions. Archaeoid convergence is the retention of similar characteristics in unrelated groups, i.e. pentadactyly or reptiles and primates, or the cusp pattern of opossums and certain carnivora. Neoid convergence is parallel progressive development in unrelated groups. An illustration would be the eye of the octopus and man which show the same progressive development of vision using different tissues. Paroid convergence is parallel functional adaptation in unrelated groups, and thus is broadly equivalent to Simpson's usage of the term analogy (1961:79). The stripes in tigers and zebras demonstrate this point, which both serve as camouflage. Mimicry is defined by Simpson as "similarity adaptive as such and not related to community of ancestry" (1961:79). By an examination of the examples used by Mayr to illustrate mimicry (1963:248) it may be concluded that mimicry usually involves an adaptation to the zoological environment of the mimicking organism. Convergent chance similarity involves characters which are not necessarily progressive in several unrelated compared groups i.e. bipedalism in dinosaurs, birds, certain rats, kangaroos, and man; plantigrade foot in bears and Hominids.

A Discussion of the Revised Classification

The extension of the concept of homology to include parallelism, and consequent subdividing of the concept of the process of parallelism as given above, may be felt by some to be pedantic. It is evident however, from Simpson's formulation, that the above given revision was in a sense inevitable. Simpson reflected his own ambivalence concerning the distinction between homology and parallelism in the following quotation:

In the end, parallelism cannot always be distinguished from homology, but that usually does not matter very much. Like homology, parallelism does depend on community of ancestry. At worst, it may exaggerate the degree of propinquity of descent without falsifying its nature or the topological phylogenetic pattern (1961:106).¹

New dilemmas for the concept of parallelism have recently been presented by Coon's (1962) elaboration of Weidenreich's polyphyletic theory of racial origins. Coon contends that Causasoids, Negroids, Mongoloids, Australoids, and Bushmen all crossed the *sapiens* threshold at different periods. This view has been criticized by Dobzhansky (1963:366):

His classification makes *Homo erectus* contemporaneous with *Homo* sapiens for some 200,000 years, although the two lived in different parts of the world. The division of an evolutionary line into species succeeding each other in time is arbitrary, but the division of contemporaneous forms into species is not. If *erectus* lived at the same time as *sapiens*, it must have been genetically isolated from *sapiens*. Yet its

¹ Italics ours.

modern descendants are not genetically isolated; they belong to the same species. For a single species to have arisen from two species that could not interbreed would indeed be extraordinary.²

In other words, the biological laws of chance or coincidence are being stretched too far concerning the five fold crossing of the sapiens threshold at different times and different places. The contentious point in the argument is the confusion of the nature of the processes involved. Parallel development of morphological characters within separate mammalian species is not equivalent to parallelism of the total several separate species themselves. If Coon's contention is correct, then it would be impossible for the various races of mankind to produce fertile offspring, from inter-racial crosses.

It has been pointed out that there has been considerable parallelism in the evolution of the mammal-like reptiles in South Africa, for example, therocephalians, cynodonts, ictidosaurs (Colbert 1955, Romer 1945, Mayr 1963, Simpson 1949). The early mammals of the Jurassic such as the triconodonts, symmetrodonts, pantotheres, multituberculates, are probably the end result of separate therapsid radiations. The evidence seems to indicate that the pantotheres gave rise to the present day marsupials and placentals but that the monotremes probably go back to a separate therapsid ancestor (Colbert, 1955). Just as the several lineages of mammal-like reptiles displayed different mosaics of mammalian and reptilian characters in their skeleton, so the present-day mammalian subclasses (i.e. monotremes, marsupials, plancentals) demonstrate similar mosaicism (i.e. egg-laying and cloaca in the monotremes, immature birth and pouch in the marsupials, and full term birth in placentals). The more unique and specialized a total morphological pattern is, the more unlikely the possibility it can be reproduced exactly by parallelism. The early "parallel" lineages of Therapsids and mammals are really cases of convergence since the morphological mosaics are extremely heterogenous. This means that when the situation of the mammal-like reptiles is compared with the Thoatherium-Equid convergence (or any other intra-mammalian convergence), the biological distance between

² Italics ours.

any of these lineages will not be as great as that between the several convergent mammal-like reptile lineages. All this is perhaps a rather involved way of saying that convergence is a phenomenon of higher categories and parallelism is a phenomenon of lower categories. It was too tempting to resist the opportunity to digress on the hierarchy of convergence, which contains a categorical analogy to the hierarchy found in sub-specific and supra-specific parallelism.

In the light of the above discussion, the following speculations re hominid phylogeny are proposed. The application of the hypothesis of "no identical parallel species" precludes any further development from Rhodesian man, Solo man and the Western Neanderthals. Their total morphological patterns show the retention of archaic characteristics without change for long periods of time. Also, there is no evidence of transitional types of the calibre of the Skhul-Tabun-Jebel Qafzeh, series in Africa, the Far East or Western Europe. The presence of the Niah skull with C14 date of 40,000 years from Borneo (Brothwell, 1960) indicates an early date of sapiens geographical migration. It is probable that Solo Man, Rhodesian Man and the Western European as well as the Eastern Chinese Neanderthals persisted in the geographical fringe areas until eliminated by invading sapiens forms radiating out from their hypothetical Near Eastern centre. So much then for speculation on the supra-specific level. The discussion can now be transferred to the sub-specific level.

A systematic fact that is often neglected is that taxonomic characters can change their diagnostic value in terms of their category level. In a given phylogeny, what today can be designated as a sub-specific taxonomic character of great diagnostic value can very easily have been diagnostic as of a genus or family character in a higher category or in chronological terms, at an earlier period.

All primitive hominids had shovel-shaped incisors (Carbonell 1963). There was no great variability in the distribution among the various forms (i.e. Australopithecus, Pithecanthropus and Sinanthropus). In early Homo sapiens there was also no marked variation in the distribution of shovel-shaped incisors (i.e. Upper

Cave, Choukoutien, Skhul and Cromagnon). However, in recent time, shovel-shaped incisors have become rare in Caucasoids and Negroids but persist in greater frequency and intensity in Mongoloids (Carbonell 1963). This fact makes them useful in present day Homo sapiens subspecific taxonomy. Therefore, to confuse the status of shovel-shaped incisors as generic character in one context, and as a subspecific character in another is very misleading. Especially to apply the name of a contemporary subspecies to that of a variable character which was invariable in the past, as Coon (1962) has done in calling Sinanthropus' shovel-shaped incisors Mongoloid, as well as referring to Sinanthropus himself, as Mongoloid, is confusing. It certainly makes more sense to refer to the present-day frequency and intensity of shovel-shaped incisors in certain Mongoloid populations, as Sinanthropoid, than to refer to these characters in Sinanthropus as Mongoloid. However, either use implies a direct relationship which is difficult to prove. The reason that this relationship is indeterminable is that we are here dealing with the questionable phylogeny of isolated characters rather than total morphological patterns; as Le Gros Clark (1955) has pointed out, homology is only absolutely certain when the phylogeny of total morphological patterns in continuous in the fossil record.

On the subspecific Homo sapiens level a similar problem has been presented by Coon in relation to Mongoloid facial flatness and the anterior zygo-maxillary projection (Coon, Birdsell and Garn 1950; Coon 1962). In both of these works, the view is advanced that Mongoloid facial flatness and anterior malar bone projection is a late development phylogenetically. However, when facial flatness and anterior projection of the zygo-maxillary junction are examined in Upper Paleolithic populations, it is evident that, all members of Upper Paleolithic sapiens have a malar bone which is morphologically indistinguishable from present-day old and new world Mongoloids (Oschinsky 1962: Oschinsky and East in press). Facial flatness as measured by the zygo-maxillary and naso-malar angles is also already present in the Upper Paleolithic population of Choukoutien in the Upper Cave. In accordance with the principle of the opportunism of evolution as enunciated by Simpson (1949, 1953, 1961) it would seem more reasonable to maintain that the Mongoloids have simply retained the Upper Paleolithic facial complex whereas the other racial groups have not.

The physical anthropology of the nineteenth century perhaps has also contributed interpretive obscurity due to its neglect of the concept of subspecific parallelism. It was automatically assumed that any archaic feature characteristic of a population automatically relegated that population to a more primitive phylogenetic grade. Unconscious taxonomic weight was given to combinations of prognathism and presence or absence of brow ridges so that racial family trees were reproduced in many of the text books of the period which relegated the Negroid to a more primitive status because of prognathism than Cromagnon man because of its absence (Osborn, H.F., 1947). From this it would seem that prognathism had greater taxonomic weight in determining primitivity of the taxonomic status than brow ridges. It seems more plausible to view the present day distribution of archaic traits in Homo sapiens specific groups as a mosaic of remnants of what was once a total morphological pattern which is now redistributed in several new total morphological configurations. Examples are prognathism among Australoids and Negroids, large brow ridges among Australoids and Caucasoids, shovelshaped incisors among Mongoloids and Australoids, mandibular tori among Arctic Mongoloids and north European Caucasoids. Is it biologically meaningful to argue that Negroids and the Australoids are especially closely related because they both have prognathism or that the Australoids and the Caucasoids are more closely related because they both have brow ridges? All recent evidence seems to indicate that there has been no contact for perhaps as long as 20,000 years between these various groups (Coon 1962), therefore there has been little chance of intraspecific genetic exchange. On the other hand, the presence of brow ridges, prognathism and shovel shaped incisors in geographically contiguous populations such as Australoids, Melanesians and Polynesians would indicate that these distributions are the result of hybridization rather than parallel retention of archaic characters which were once part of an ancient total morphological pattern which has since been replaced by another. Thus in the

new total morphological pattern these archaic features are to be considered as general phylogenetic vestiges of higher hominid categories rather than immediate evidence for subspecific close relationship among the contemporary subspecies, unless there has been interbreeding. It is for this reason that perhaps the concepts of parallelism and convergence should include the idea of parallel and convergent retention of characters, as well as parallel and convergent development of characters.

As has already been indicated, the significance of nonhomologous similarities as well as parallelisms are affected by differential antiquity with reference to the time of common origin. Thus, although a character be homologous if it remain relatively unchanged for a long period of time, this extended chronology with the gradual mosaicism that sometimes occurs, creates doubt concerning the morphological equivalents of archaic traits in several long-seperated subspecies. In the previous example of the Australian Aborigine the same archaic characters will belong to different categories depending upon the groups compared. In the case of brow ridges of Australoids and Caucasoids, these would be referred to as examples of archeomorphism, whereas the brow ridges in Australoids and Melanesians and Polynesians would be instances of isomorphism as well. In other words, long separation of subspecific groups with the consequent breaking down of subspecific total morphological patterns creates doubt with reference to the isomorphism or the immediate morphological equivalence of the characters. In the case of the brow ridges among the Australoids, Melanesians, and Polynesians, due to recent genetic exchange, there can be little doubt that the characters are the same in the isomorphic sense.

It should be emphasized again that as there are no sibling species in mammals in general (Simpson, 1961), so there are no interfertile parallel species, nor derived parallel or polytopic subspecies as found in birds (Mayr, 1963), in Homo *sapiens*, as claimed by Coon (1962).

The total morphological and physiological patterns of mammalian species and subspecies are so unique that chances are against total species-subspecies parallelism. This does not preclude the possibility of the occurrence of isolated character complexes of which there is abundant evidence in hominid and other mammalian groups, causing much difficulty in the true assessment of affinities in various related lineages. There is no evidence, however, from neontology or palaeontology that *parallel* development of species has resulted in duplication of species with consequent interspecific fertile breeding potentials.

University of Toronto

REFERENCES

- BROTHWELL, D.R.
 - 1960 Upper Pleistocene Skull from Niah Cave. Sarawak Museum Journal 9:323-349.

CAIN, A.J.

- 1954 Animal Species and Their Evolution. London, Hutchison.
- CAIN, A.J. and G.A. HARRISON
 - 1960 Phyletic Weighting. Proceedings of the Zoological Society of London 135:1-31.
- CARBONELL, V.
 - 1963 Variations in the Frequency of Shovel Shaped Incisors in Different Populations. *In* Dental Anthropology, D.R. Brothwell, ed. London, Pergamon Press.
- CHANG, S. and M.K. KIM
 - 1961 A Note on Shovel Shaped Incisors: Instanding Lateral Incisors and Occlusal Type of Incisors in Koreans. The Seoul Journal of Medecine 2.
- Colbert, E.H.

COON, C.S.

```
1962 The Origin of Races. New York, Knopf.
```

- COON, C.S., S.M. GARN and J.B. BIRDSELL 1950 Races. Springfield, Thomas.
- Dobzhansky, T.
 - 1963 Possibility that Homo Sapiens Evolved Independently Five Times is Vanishingly Small. Current Anthropology 4:365-366.

EAST, D.A. and L. OSCHINSKY

1958 A Comparison of Serological and Metrical Methods Used in Differentiating Between Certain East African Racial Groups With Reference to D² Analysis. Sankhya 20:31-34.

¹⁹⁵⁵ Evolution of the Vertebrates. New York, Wiley.

- HRDLICKA, A. 1935 Notes on "Melanesians" and "Australians" and the Peopling of America. Smithsonian Miscellaneous Collections 94:1-58. HOOTON. E.A. 1946 Up From the Ape. New York, Macmillan. HUBELL. T.H. 1954 The Naming of Geographic Variant Populations. Systematic Zoology 3:113-121. KROGMAN, W.M. 1960 The Philadelphia Center for Research in Child Growth. Philadelphia, The Growth Center. LEGROS CLARK, W.E. 1920 On a Series of Ancient Eskimo Skulls from Greenland. Journal of the Royal Anthropological Institute 50:281-298. 1955 The Fossil Evidence for Human Evolution. Chicago, University of Chicago Press. 1958a Bones of Contention. In Ideas on Human Evolution 1962, W.W. Howells, ed. Cambridge, Harvard University Press. Originally in Journal of the Royal Anthropological Institute 88:131-145. History of the Primates. London, British Museum of Natural 1958b History. 6th edition. MAYR. E. Systematics and the Origin of Species. New York, Columbia 1942 University Press. 1950 Taxonomic Categories in Fossil Hominids. In Origin and Evolution of Man. Cold Spring Harbour Symposium on Quantitative Biology 15:109-118. Animal Species and Evolution. Cambridge, Harvard University 1963 Press. OSBORN. H.F. The Age of Man. Science Guide 52. New York, The American 1947 Museum of Natural History. OSCHINSKY. L. 1961 A Short Note on Upper Lateral Incisor Tooth Crowding Among the Eskimos. Anthropologica N.S. 3:90-94. 1962 Facial Flatness and Cheekbone Morphology in Arctic Mongoloids: A Case for Morphological Taxonomy. Anthropologica N.S. 4:349-377.
 - 1963 The Problem of Parallelism in Relation to the Subspecific Taxonomy of Homo Sapiens. Anthropologica N.S. 5:131-145.

- OSCHINSKY, L. and D. EAST The Cranial Morphology of Arctic Mongoloids: A Statistical Morphological Study. Ottawa, National Museum of Canada (in press).
- OSCHINSKY, L. and R. SMITHURST
 - 1960 On Certain Dental Characteristics of the Eskimo of the Eastern Canadian Arctic. Anthropologica N.S. 2:105-112.
- SIMPSON, G.G.
 - 1943 Criteria for Genera, Species and Sub-species in Zoology and Palaeozoology. Annals of the New York Academy of Science 44:145--178.
 - 1949 The Meaning of Evolution. New Haven, Yale University Press.
 - 1951 The Species Concept. Evolution 5:285-298.
 - 1953 The Major Features of Evolution. New York, Columbia University Press.
 - 1961 Principles of Animal Taxonomy. New York, Columbia University Press.

RIVET, P.

1925 Les Australiens en Amérique. Bulletin de la Société Linguistique 26:1-43.

Romer, A.S.

1945 Vertebrate Palaeontology. Chicago, The University of Chicago Press.

TEN KATE, H.

1885 Sur les crânes de Lagoa-Santa. Bulletin de la Société d'Anthropologie de Paris. 3^{ème} série 8:240-244.

VAURIE, C.

1949 A Revision of the Bird Family "Dicruridae". Bulletin of the American Museum of Natural History 93:199-342.

Voous, K.H.

- 1951 On the Evolutionary and Distributional History of the Kingfisher Genus "Ceyx" in Malayasia. Ardea 39:182-196.
- 1955 Origin of the Avifauna of Aruba, Curaçao, and Bonaire. Actes du Congrès International Ornithologique XI.

WEIDENREICH, F.

1946 Apes, Giants, and Man. Chicago, The University of Chicago Press.