Suid Evolution and Correlation of African Hominid Localities: An Alternative Taxonomy

Abstract. *New phylogenies were recently proposed by White and Harris, who recognized 7 genera and 16 species of fossil and extant suids from sub-Saharan Africa. This scheme is regarded here as oversimplified and an alternative is suggested, in which 9 genera and 21 species are recognized. The taxonomic and phylogenetic differences do not have any significant effect on the stratigraphic interpretations offered by White and Harris.*

The fossil Suidae were evolving and diversifying rapidly in Africa during the Pliocene and Pleistocene, and, as their remains are also plentiful and widespread, they are of particular value for correlation and relative dating. Many deposits of this age contain important hominid fossils and artifacts, and so the correct interpretation of the suid fossils is of special significance. White and Harris (*1*) have recently presented their views, and their article contains so much with which I agree that I regret the need to present an alternative interpretation of the taxonomy and phylogeny. Our measure of agreement stems largely from the fact that we recognize basically the same morphological entities in the strata from different areas and hence arrive at similar conclusions regarding the most probable correlations. Accordingly, their correlation does not differ greatly from ones presented in 1971 and 1972 (*2, 3*) except for their valuable clarification of the status of the important deposits in the area east of Lake Turkana ("East Rudolf") and of the Laetolil Beds. Their placement of the South African deposits is in accord with views that I expressed in 1970 (*4*) and elaborated slightly a year later (*2*). However, there are some instances in which I disagree with their identifications—as they clearly do with some of mine—and my taxonomy differs from theirs in a number of points, to which attention should be drawn. In part this is due to our having rather different basic philosophies on the nature of species in paleontology, and thus many of our differences are semantic rather than real. My main purpose in presenting this alternative here is to enable future workers to equate the two schemes and make up their own minds about which they prefer.

Accordingly, Fig. 1 presents a summary of my own interpretation of the phylogeny and taxonomy, set out so as to place the various taxa as nearly as possible in the same relative positions as in figure 1 of White and Harris, with which it should be compared. White and Harris avoided chronometric scaling because of uncertainties in a few of the radiometric dates, but I have inserted a time scale that I believe is consistent with most of the radiometric and paleomagnetic work and with the faunal correlations between the area east of Lake Turkana and the Omo area. Figure 2 presents my interpretation of the correlation between the most important stratigraphic sections in East Africa.

In what they term group 1, White and Harris place the genera *Nyanzachoerus* and *Notochoerus*, which they rightly regard as essentially Pliocene, with *Nyanzachoerus* seemingly "related to *Bunolistriodon* species from the Miocene" (*1*, p. 13). I agree that there are resemblances to the Miocene buno-listriodont, but the name *Libycochoerus* predates *Bunolistriodon* for the African forms (*5*) and I suspect that this genus, in turn, is congeneric with *Kubanochoerus* Gabunia, 1955, from the Caucasus (*6*). I consider that another upper Miocene fossil from Bou Hanifia in Algeria, described by Arambourg (*7*) as *Propotamochoerus devauxi*, should properly be placed in *Nyanzachoerus* and is probably ancestral to the three major Pliocene species. A lower jaw from Sahabi, described by Leonardi in 1952 (*8*) as *Sivachoerus syrticus*, is clearly a *Nyanzachoerus* very close to the species named *Ny. tulotos* in 1972; unfortunately, the type—and only—specimen of *Ny. syrticus* is missing and under the circumstances it is not possible to establish specific identity and inappropriate to use the earlier name. There is also a skull from Sahabi that seems to represent an early form of *Ny. jaegeri*, thus leading me to regard the latter as having diverged at an early stage rather than as having been derived from "*Ny. kanamensis*" as White and Harris indicate. I would place the typical Langebaanweg *Nyanzachoerus* as close to the origin of both lineages; it retains the first premolars, as in *Ny. tulotos*, whereas this tooth is lacking in the other species.

The type species of the genus *Nyanzachoerus* is *Ny. kanamensis*, represented by a right mandibular ramus and some isolated fragments from Kanam, the exact age of which is uncertain. The type has the enlarged third and fourth premolars characteristic of the genus, but the third premolar is longer and the fourth premolar relatively narrower than in any of the material from Kanapoi to which Cooke and Ewer (*9*) attached the specific name *pattersoni*. Material from Hadar has the same features as that from Kanapoi (*10*) but in the moderately large combined sample it is not possible to match the elongate, narrow third premolar of the type of *kanamensis* or the long narrow first molar, whereas the other teeth lie near or just outside the range of variation for the major sample. Of all the known material, the closest is an isolated lower third premolar from Nyawiega in the "Earlier Kaiso" assemblage (*11*), but this is better placed with the *pattersoni* material; cheek teeth from the "Later Kaiso" assemblage match very well with the Kanam specimens. I infer that *Ny. kanamensis* is a late form, most probably a side branch, and I am reluctant to merge them as long as the rather characteristic Kanam material is outside the field of variation encountered in a moderately large sample of "*pattersoni*." White and Harris may very well be correct, but I believe that more material is needed to resolve the issue. In any case, I do not regard *Ny. pattersoni* as derived directly from *Ny. tulotos* but rather as already a separate line when *Ny. tulotos* first appears at Lothagam.

As far as the genus *Notochoerus* is concerned, our respective interpretations differ very little. I prefer to derive *Not. euilus* as a branch from within a *Ny. jaegeri* stock rather than as a lineal continuation, and I consider *Not. capensis* and *Not. scotti* as somewhat divergent but with a close relationship. Remains of *Not. capensis* are rather rare and it is difficult to resolve the question, especially as *Ny. jaegeri* is also very imperfectly known.

In the interpretation of the complex consisting of group 2 (plus group 4), my views differ notably from those of White and Harris, who lump nearly all the abundant material into a single species, "*Mesochoerus limnetes*." Their phylogeny fails to include the genotype species *paiceae*, nor do they mention this South African form in their correlations. The genus *Mesochoerus* was established by Shaw and Cooke in 1941 (*12*) for a species that Broom, 10 years earlier (*13*), had placed in *Notochoerus*. *Mesochoerus paiceae*, however, now proves to be a synonym of *Kolpochoerus sinuosus*, established by Van Hoepen and Van Hoepen in 1932 (*14*). Thus, *sinuosus* is a junior synonym of *paiceae*, but this does not invalidate the genus *Kolpochoerus*, which has priority over *Mesochoerus* and must replace it. Also be-

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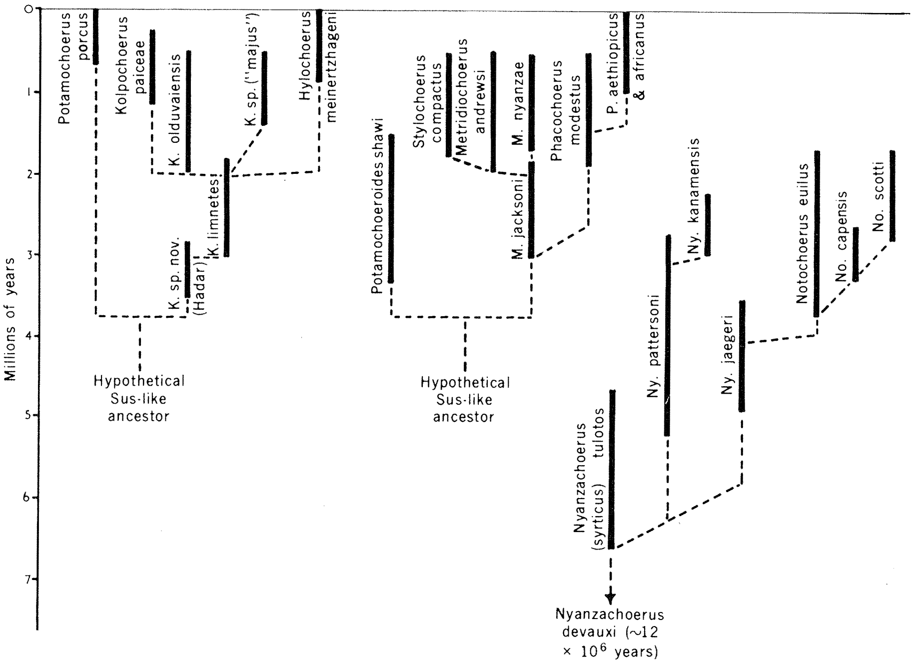

Fig. 1. Proposed phylogeny and taxonomy of late Cenozoic African suids.

longing to *K. paiceae* is a moderately large sample from Hopefield (Elandsfontein) in the southwestern Cape of Good Hope, in which the cheek teeth are generally similar to some from Olduvai (*K. olduvaiensis* in my usage); however, features of the canines and jaw morphology show that they are at least specifically distinct and suggest that *K. paiciae* evolved independently in South Africa.

The basic East African member of this genus is *Kolpochoerus limnetes*, which is very well represented in the Shungura Formation and ranges from Member B to Member G, showing a trend toward elongation of the third molars, as I have shown (*15*), and also some tendency toward an increase in the length/breadth ratio, as White and Harris have demonstrated (*1*). White and Harris consider, as I formerly did, that this trend continued in the same stock and that the larger varieties (which I distinguish as *K. olduvaiensis*) are simply part of the same direct lineage.

Even if this were so, I should prefer to retain *olduvaiensis* as the best label for the larger forms, which are far removed from the small and simple teeth in the lower part of the range of *K. limnetes* sensu stricto. The literature teems with arguments about the problems involved in attempting to subdivide a continuously evolving lineage and, as McKerrow has pointed out (*16*), it is necessary "to realise that specific names in palaeontology are frequently only applicable to fixed points in a plexus of evolving organisms." Extension of a single species name to a complex that is changing morphologically over a period of time avoids (or rather evades) the problem but ceases to be useful when the end members of the lineage are so different that it is inconceivable that they would, or could, belong to the same biospecies if they had lived at the same time. As Neville George put it (*17*), "If a spade were always called a spade no doubt correlation would be greatly eased, though it might not be very exact if the spade were anything from a steam shovel to a teaspoon."

Be that as it may, there are other reasons for regarding *K. olduvaiensis* as a distinct species. Apart from the enlarged talon in the third molars, there are changes in the morphology of the skull, such as elevation of the orbits and raising of the zygomatic arches. However, perhaps more significant is the indication that, both in Member G of the Shungura Formation and in Bed I–lower Bed II at Olduvai, the two species were contemporary. Furthermore, the *limnetes* stock [represented in Bed I by the material that Leakey (*18*) called *Promesochoerus mukiri*, *Ectopotamochoerus dubius*, and *Potamochoerus intermedius*] must at this stage also be giving rise to another rather compact and conservative species of *Kolpochoerus* that occurs in the upper part of Bed II and elsewhere (the "*Mes. majus*" of White and Harris); very possibly, the *Hylochoerus* stock also branched off at this time as the later forms would not serve so well as ancestors. Thus the picture is one of divergence and is more complex than would be inferred from the simplistic phylogeny of White and Harris. (I may add that I regard the type specimen of Hopwood's "*Potamochoerus majus*" as inadequate and best regarded as a *nomen vanum*, but I recognize the existence of the entity itself.)

White and Harris state that "*Potamochoerus* specimens are abundant in the Laetolil Beds and Hadar Formation" (*1*, p. 15). I have not seen the new material from Laetolil, except for one mandible, but I have recently described the Hadar suids and consider that the small form found there is a very early *Kolpochoerus*, probably ancestral to *K. limnetes* (*10*). Although there is undoubtedly a resemblance to the bushpig in size and in some aspects of the skull structure, this species retains all four premolars, which are morphologically *Sus*-like, especially the fourth premolars, and this suggests a derivation from a *Sus*-like ancestor. These *Sus*-like characters of the premolars are also seen, but more modified, in *K. limnetes*. I regard the Hadar *Kolpochoerus* as derived from *Sus* but close to the point at which *Potamochoerus* may have branched off. The contemporary existence of *Potamochoerus* at Laetolil is feasible, and I await with interest the publication of fuller details.

Group 3 of White and Harris embraces a complex of suids that share a tendency for the second molar to wear rather rapidly to produce a crown consisting of large areas of dentine with residual rings of enamel that I have termed "lakes" (as opposed to the usual enamel "islands"). There is also a trend toward the development of some warthog-like features, both in the skull and in the third molars. The core genus is *Metridiochoerus*, with the genotype species *Met. andrewsi* well represented in the Koobi Fora Formation both by teeth and by skulls. From the Shungura Formation third molars of smaller size occur, and I have used for them the species name *jacksoni* ["*Pronotochoerus*" *jacksoni* of Leakey, 1943 (*19*)], but White and Harris consider this merely an early form of *Met. andrewsi*. However, at Omo skulls both of *Met. jacksoni* and of typical *Met. andrewsi* occur in Member G and are clearly different, although sharing the broad braincase and occiput that I regard as an important characteristic at the generic level. Two species are demanded, although *Met. andrewsi* almost certainly branched off from *Met. jacksoni* at some point.

Furthermore, along with the typical *Met. andrewsi* (and the advanced form at one time distinguished as *meadowsi*), a smaller and more delicate form, very like the typical *Met. jacksoni*, per-

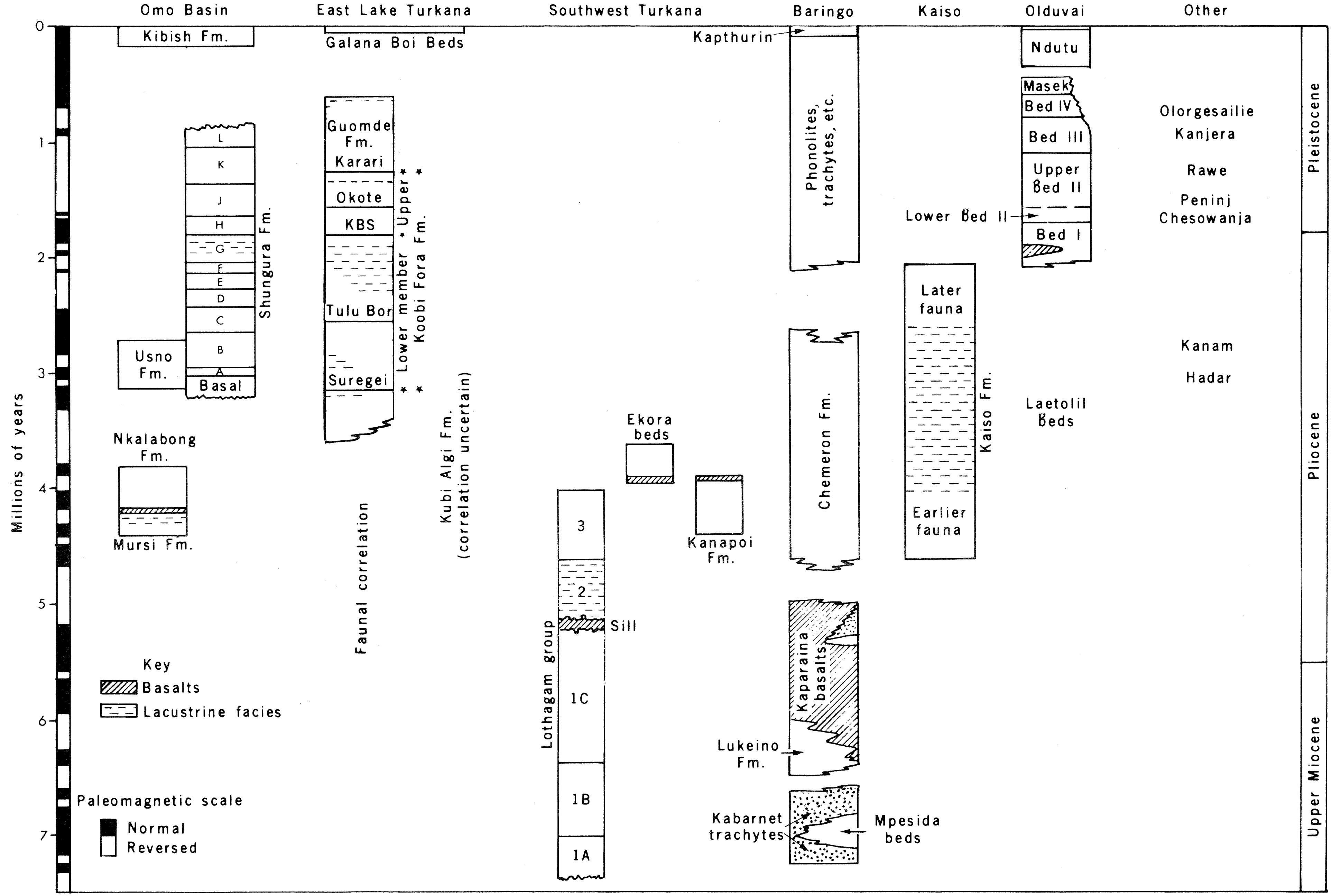

Fig. 2. Provisional correlation of major later Miocene to Pleistocene deposits in East Africa. For the Koobi Fora Formation, the column represents a "best fit" correlation with Omo based on the faunas. [Taken from (*20*)]

sists. I believe that this is a direct descendant of *Met. jacksoni*, and I distinguish it under the specific name *nyanzae* [*"Pronotochoerus" nyanzae*, Leakey, 1958 (*18*)], which has page priority over the rather more typical upper Bed II suid that Leakey called *Notochoerus compactus*. It is not clear where White and Harris place this material, but I suspect that it forms part of what they call "*Met. modestus*," whereas I regard *modestus* as belonging to the genus *Phacochoerus* and to be a synonym of *P. antiquus*. *Phacochoerus modestus* (=*antiquus*) occurs at DK 1 at Olduvai and continues to Bed IV, along with *Met. nyanzae*. I am at a loss to decide what White and Harris mean by *Met. hopwoodi*, the type of which I consider to be a synonym of the advanced *M. andrewsi* (the "*meadowsi*" form).

White and Harris designate the very distinctive suid that I term *Stylochoerus compactus* as *Met. compactus*. This involves a taxonomic problem if the material termed *"Notochoerus" compactus* actually belongs within the genus *Metridiochoerus*, whether as a synonym of *Met. nyanzae* or of *"Met." modestus*. As I regard this peculiar suid as deserving separation at the generic level because of the unusual structure of its canines and the fact that they emerge at right angles to the axis of the skull and at an angle of about 45° to the palatal plane, the nomenclatorial problem does not arise in my taxonomic scheme.

Finally, in this group I place as a separate genus and species, confined to South Africa, the Makapansgat suid *Potamochoeroides shawi*. White and Harris apparently consider it a synonym of *Met. andrewsi* and regard it as representing a stage in this lineage corresponding to Omo Member C. It is true that there are some structural features of the molar dentition that resemble early stages of the line leading to *andrewsi*, and I believe that these resemblances demand descent from a common ancestor.

However, there are also major differences that cannot be overlooked when one considers the skull and dentition as a whole. At least three premolars are retained in the adult (sometimes also the upper first premolar), and they are normal teeth, much the same size as in *Sus scrofa* and with somewhat *Sus*-like morphology, although stouter and with the fourth premolars a little modified; in contrast, even fairly early *Metridiochoerus* specimens have only the third and fourth premolars, both of which are reduced. The muzzle in *Potamochoeroides* is shorter than in the bushpig, with little or no constriction of the mandible or palate in the region of the canines. The facial profile is steep. The parietal constriction is narrow and the occiput is also constricted, as in *Sus* and quite unlike the broad occiput characteristic in *Metridiochoerus*. The upper canines are short, stout, strongly curved teeth, with a broad ventral band of ribbed enamel, unlike the more or less phacochoerine canines of *Metridiochoerus*. It is thus very difficult to place the Makapansgat type in the same genus as *Metridiochoerus jacksoni* (or early *andrewsi*), let alone in the same species. Furthermore, this form is not confined to the Makapansgat locality, which could be contemporary with the early Shungura and thus provide a possible early stage. It is also found at Bolt's Farm and Gladysvale and may possibly occur at Taung. *Metridiochoerus andrewsi* (sensu stricto) occurs at Bolt's Farm, and so does *Phacochoerus modestus* (= *antiquus*), although they are from different patches of breccia and are not necessarily contemporary. It thus seems preferable to maintain *Potamochoeroides shawi* as a distinct form, confined to South Africa; unfortunately this placement precludes its use for comparisons of age, except in a very general way.

Despite the fact that my taxonomic interpretation differs in so many details from the views of White and Harris, I must emphasize that this has little or no impact on the correlations that they have derived, as the correlations are based on the occurrences of similar morphological entities and are little affected by the labels that are attached to those entities, except in a few rare instances. Theirs is the first definitive consideration of correlation problems within the Koobi Fora Formation, and their analysis is both timely and valuable. I await with interest the appearance of the detailed systematic revision to which they refer.

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References

1. T. D. White and J. M. Harris, *Science* **198**, 13 (1977).
2. H. B. S. Cooke, in *Proceedings of the 5th Congrès Néogène Méditerranéen, Lyon 1972* (Mémoire 78, Bureau de Recherches Géologiques et Minières, Paris, 1974), p. 99.
3. ——— and V. J. Maglio, in *Calibration of Hominoid Evolution*, W. W Bishop and A. J. Miller, Eds. (Scottish Academic Press, Edinburgh, 1972), p. 303.
4. H. B. S. Cooke, *Bull. Soc. Vertebr. Paleontol.* **90**, 2 (October 1970).
5. J. Leinders, *Bull. Mus. Natl. Hist. Nat. Sci. Terre Ser. 3* **46** (No. 341), 197 (1975).
6. L. K. Gabunia, *Dokl. Akad. Nauk SSSR* **102**, 6 (1955).
7. C. Arambourg, *C. R. Somm. Soc. Géol Fr.* **4**, 107 (1961).
8. P. Leonardi, *Rend. Accad. Naz. 40 Ser. 4* **4**, 75 (1952).
9. H. B. S. Cooke and R. F. Ewer, *Bull. Mus. Comp. Zool. Harv. Univ.* **143**, 149 (1972).
10. H. B. S. Cooke, *Kirtlandia*, in press.
11. ——— and S. C. Coryndon, *Fossil Vertebr. Af.* **2**, 109 (1970).
12. J. C. M. Shaw and H. B. S. Cooke, *Trans. R. Soc. S. Afr.* **28**, 293 (1941).
13. R. Broom, *Rec. Albany Mus. Grahamstown* **4**, 167 (1931).
14. E. C. N. Van Hoepen and H. E. Van Hoepen, *Paleontol. Navors. Nas. Mus. Bloemfontein* **2** (No. 4), 39 (1932).
15. H. B. S. Cooke, in *Earliest Man and Environments in the Lake Rudolf Basin*, Y. Coppens, F. C. Howell, G. Ll. Isaac, R. E. F. Leakey, Eds. (Univ. of Chicago Press, Chicago, 1976), p. 251.
16. W. C. McKerrow, in *The Species Concept in Palaeontology*, P. C. Sylvester-Bradley, Ed. (Systematics Society, London, 1956), p. 122.
17. T. Neville George, in *ibid.*, p. 123.
18. L. S. B. Leakey, *Br. Mus. (Nat. Hist.) Fossil Mamm. Afr.* **14** (1958).
19. ———, *J. East Afr. Uganda Nat. Hist. Soc. Natl. Mus.* **17**, 45 (1943).
20. H. B. S. Cooke, in *Evolution of African Mammals*, V. J. Maglio and H. B. S. Cooke, Eds. (Harvard Univ. Press, Cambridge, Mass., in press).

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Enkephalin-Like Material Elevated in Ventricular Cerebrospinal Fluid of Pain Patients After Analgetic Focal Stimulation

Abstract. *Enkephalin-like activity has been measured in the ventricular cerebrospinal fluid of patients with intractable pain. Electrical stimulation of periventricular brain sites resulted in significant decrease in persistent pain in these subjects. This analgesia, which was blocked by naloxone in 80 percent of the cases, was accompanied by a significant rise in ventricular enkephalin-like activity, as measured by two different methods. The results present evidence of in vivo release of enkephalin-like material in humans and suggest that stimulation analgesia may be partially due to this release.*

The enkephalins and endorphins (*1*) produce analgesia when administered in pharmacological doses to nonhuman mammals (*2*). The potential role of these endogenous opioids in regulation of pain perception has been suggested (*3*), and an endogenous pain inhibitory system with opioid and nonopioid components has been proposed (*4*). We now report that electrical stimulation of periventricular brain sites in humans suffering from intractable pain leads to relief, and is accompanied by a significant increase in enkephalin-like material

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