

tions were measured on a Rigaku AFC four-circle diffractometer using graphite monochromatised MoK α radiation ($2\theta \leq 50^\circ$).

The structure was solved by the heavy atom method using 1,171 reflections with $2\theta \leq 30^\circ$. The three-dimensional electron density map calculated on the basis of coordinates of the iodine atom revealed the rough structure of the complex. The least-squares refinement of the atomic parameters which were estimated on the electron density map was unsuccessful. The accurate positions and directions of the six glucose units and the *p*-IAN molecule were determined by the block-diagonal rigid-body least-squares technique³. The O₆ atoms and water molecules were found on a difference Fourier synthesis. In successive refinements, one of the O₆ atoms was found to be disordered. Using 3,519 reflections with $|F_0| \leq 3\sigma(F)$, the final block-diagonal least-squares refinement with anisotropic temperature factors reduced the *R* value to 0.072. Fig 1 illustrates the structure of the complex.

Each glucose unit is in the C1 chair conformation, and all glucose units are α -1,4-linked; this result is in agreement with the structures of the other α -CDx complexes which were determined by X-ray analysis³⁻⁵. The *p*-IAN molecule is included in the cavity along the axis of α -CDx. The iodine atom and the benzene ring are situated in the cavity of α -CDx, while the nitrogen atom lies outside the cavity. The shortest distance between the benzene ring and α -CDx is 3.25 Å which is from an O₄ atom to a carbon atom of the benzene ring. This rather short intermolecular distance indicates that *p*-IAN is rigidly fixed in the cavity. The shortest distance from the iodine atom is 3.70 Å which is the distance to the disordered O₆ atom.

In the α -CDx-*p*-IAN complex, the six O₄ atoms of α -CDx lie very near the least-squares plane of themselves, and the maximum deviation from the plane is 0.13 Å. In the α -CDx-potassium acetate complex³ and the α -CDx-H₂O complex⁴, the maximum deviations are 0.01 Å and 0.98 Å, respectively. The average valence angle of α -1,4-linking oxygen atoms is 120° (2) which is in agreement with 119.1° in the α -CDx-potassium acetate complex and 119±3° in the α -CDx-I₂ complex⁵. The distances between oxygen atoms O₂ and O₃ of adjacent glucose units are 2.68, 2.76, 3.00, 2.92, 2.98 and 2.87 Å which are the acceptable distances for hydrogen bonds. On the other hand, in the α -CDx-H₂O complex and the α -CDx-I₂ complex, there exist distances of 3.36 Å and 3.83 Å, respectively. In the α -CDx-*p*-IAN complex, all C₆-O₆ bonds are oriented to the outside of the cavity and the conformation is the same as that found in the α -CDx-I₂ complex; the conformational angles O₅-C₅-C₆-O₆ are -75±8° in the α -CDx-*p*-IAN complex and -70±8° in the α -CDx-I₂ complex.

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¹ French, D., Levine, M. L., Pazur, J. H., and Norberg, E., *J. Am. chem. Soc.*, **71**, 353 (1949).

² Demarco, P. V., and Thakker, A. L., *Chem. Commun.*, **2** (1970).

³ Hybl, A., Rundle, R. E., and Williams, D. E., *J. Am. chem. Soc.*, **87**, 2779 (1965).

⁴ Manor, P. C., and Seanger, W., *Nature*, **237**, 393 (1972).

⁵ McMullan, R. K., Seanger, W., Fayos, J., and Mootz, D., *Carbohydr. Res.*, **31**, 211 (1973).

resemblance to a model species which is unpalatable (that is, distasteful or dangerous)¹⁻³. Predators learn to avoid the unpalatable model species after one or more adverse experiences with it, and any mimic species that resembles the model sufficiently closely will likewise be avoided.

The first examples of mimicry were documented in Brazilian butterflies¹—most additional examples and experimental work have been limited to mimicry in insects. Vertebrates exhibiting mimicry are rare, but include fish⁴, snakes^{5,6} and birds^{7,8}. A single example has previously been described in mammals: Shelford described a series of five squirrel species which mimic unpalatable treeshrew models in Borneo^{9,10}. The case described here is a possible additional example which, if confirmed, extends the phenomenon of mimicry to a large African mammal.

The genus *Hyaena* is represented in Africa today by two species: the striped hyaena, *H. hyaena*, inhabiting northern Africa; and the brown hyaena, *H. brunnea*, limited to southern Africa. Hyenas (the spotted hyaena, *Crocuta*, excluded) weigh 50–60 kg, and inhabit open dry plains and thorn scrub, live singly or in pairs, and are chiefly nocturnal. *Hyaena* has a sloping back, pointed ears, and an erectile mane. It has strong



Fig. 1 External appearance of, a, the aardwolf, *Proteles cristatus*, and, b, the hyaena, *Hyaena hyaena*, both drawn to the same scale. Redrawn by P. Olsen from colour illustrations in Dorst and Dandelot²⁹.

teeth and jaws and it is known to kill live game occasionally, although it is primarily a scavenger.

The aardwolf *Proteles cristatus* is a much smaller, jackel-sized (12–15 kg) mammal with a discontinuous distribution: a northern population is found throughout most of East Africa, and a separate population inhabits southern Africa. *Proteles*, like *Hyaena*, has a sloping back, pointed ears, and a well developed erectile mane along the dorsal spine from neck to tail. This mane is composed of stiff hairs some 20 cm in length and, when erected, makes the aardwolf appear considerably larger than it actually is¹¹. *Proteles* inhabits open

Is the aardwolf a mimic of the hyaena?

MIMICRY is a phenomenon of evolutionary convergence or parallelism by which an edible mimic species gains some measure of protection from predators by virtue of its close

plains and thorn scrub, lives singly or in pairs, and is chiefly nocturnal. It has only vestigial cheek teeth and feeds largely on termites and other insects, and occasionally on carrion and rodents^{12,13}.

In his initial description of *Proteles*, Geoffroy St-Hilaire¹⁴ noted that its external appearance is very similar to that of *Hyaena*, a resemblance noted in virtually every subsequent description of the aardwolf (Fig. 1). Kruuk¹³ observed that *Proteles* and *Hyaena* look so similar that they are often confused. The resemblance of *Proteles* to *Hyaena* in body, mane and tail colour, and in the colour and development of stripes remains close in spite of considerable clinal variation in these characters; the pattern in each subspecies of *Proteles* resembling closely the sympatric subspecies of *Hyaena*¹⁴⁻¹⁶. Size is the only real difference in the external morphology of the two, and this is a notoriously difficult quantity to perceive in the field in the absence of some fixed comparative scale.

In addition, *Proteles* is found throughout its distribution in the same open plain or thorn scrub habitat as *Hyaena*, and its general behaviour is remarkably similar. The aardwolf and hyaena are both chiefly nocturnal, and live singly or in pairs. Even their kneeling defensive response to attack is similar¹¹.

The external similarity of *Proteles* to *Hyaena* extends also to most of the characters of internal anatomy that have been studied, indicating that *Proteles* is closely related to the hyaenas. The chromosomes¹⁷⁻¹⁹ and haemoglobin mobility²⁰ of *Proteles* are virtually identical to those of *Hyaena* and *Crocuta*, and the gyri and sulci of the cerebral hemispheres of the brain are arranged on exactly the same plan¹¹. The complete dental formula of *Proteles*, though not always fully developed, is the same as that of *Hyaena* and *Crocuta*²¹. The male reproductive tract of *Proteles* appears to be more similar to that of *Hyaena* than to that of *Crocuta*^{21,22}. *Proteles* differs from *Hyaena* principally in having a dentition much reduced in size, and in retaining the pollex (a digit lost in both *Hyaena* and *Crocuta*)²³.

The evolutionary lines leading to *Hyaena* and *Crocuta* appear, from the fossil record, to have been distinct since the Miocene²⁴. Fossils bearing on the evolution of the aardwolf have recently been discovered^{21,25} which indicate a Pliocene or earlier time of divergence of *Proteles* from the ancestral hyaenid stock, but the precise phylogenetic relationships among these three genera of Hyainidae are not yet completely clear.

Two hypotheses of hyaenid relationships seem tenable. *Proteles* may have separated from the common ancestor of *Crocuta* and *Hyaena* before they separated (suggested by the shared loss of the pollex in the latter two genera), in which case the close external resemblance of *Proteles* to *Hyaena* is perhaps convergent. On the other hand, *Crocuta* may have separated from the *Proteles*-*Hyaena* stock before these two became differentiated (suggested by the reproductive tract and the close external resemblance), in which case the external resemblance of *Proteles* and *Hyaena* may reflect a parallel retention from a common ancestor having this appearance.

The nearly complete geographic sympatry, close external resemblance, and similar behaviour of *Proteles* and *Hyaena* are unusual in closely related forms, since speciation normally involves significant divergence in geographic distribution, in external appearance, or in behaviour. All of the conditions of Batesian mimicry are met by *Proteles*, and this may help to explain its distribution, appearance, and behaviour. Only the predator remains to be identified.

Leopards occur throughout the range of *Proteles*, they are most active at night, and they are predominantly visually oriented predators. Leopards routinely prey on jackals^{26,27} and, in view of their wide prey tolerance²⁸, might be expected to prey on *Proteles* as well. Because of its large size and strong skull, a *Hyaena* would be dangerous to an attacking leopard. The much smaller, weaker *Proteles* would be a poor match for a leopard, and it seems that an important component of the aardwolf's defence against predators may be its close external resemblance to the larger, more dangerous *Hyaena*. The ability of *Proteles* to erect its mane when excited would

further confuse a potential predator as to its actual size and identity.

This possible case of mimicry in a large mammal is unique, and deserves further investigation. Unfortunately, low population densities and nocturnal activity patterns make both *Proteles* and *Hyaena* difficult to study in the field. Additional study of their behaviour and ecology will be of great interest, and observation of any interactions with leopards of particular importance.

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Total human body protein synthesis in relation to protein requirements at various ages

THE intensity of body and tissue protein metabolism per kg declines with increased adult body size in mammals¹. This fall parallels a similar progressive decline in the intensity of energy metabolism²⁻⁴. It has also been concluded that protein metabolism per unit of body weight is about four to five times faster in young rats than in adult man¹; this pattern of change extends to cellular and subcellular aspects of protein metabolism, such as plasma albumin synthesis, liver RNA content and enzyme activity^{1,5}. Similarly, the rate of protein synthesis per kg total body weight declines during growth and development within a species, such as the rat⁶. This parameter again parallels the reduction in the intensity of energy metabolism which occurs during the growth period³.

Such surveys provide a general picture of protein metabolism in mammals and help to explain the metabolic basis for differences in dietary protein requirements both within and between the various species. The concepts involved should apply to man at various ages⁷⁻⁹. In previous studies with human subjects, however, different approaches have been used, some of which are no longer considered valid, and insufficient detail has been provided. It is therefore difficult to use the estimates to compare changes in body protein and energy metabolism with those for dietary protein needs throughout a man's life.

Using a common approach, we have tried to characterise the relationship which exists between protein and energy metabolism in man and to examine dynamic aspects of body protein metabolism with reference to dietary protein needs, during the period of rapid growth and development and the later years when senescence dominates body metabolism and function. The procedures, analytical methods and calculations of total body