situation with a greater amount of pene-contemporaneous erosion is suggested by the superimposition of Burdigalian and Pontian mammalian faunas on Maboko Island near Kisumu. At Tinderet, the later outwellings of phonolitic nephelinites, nephelinites, through Kenya-type phonolites to basanites and tephrites as described by Binge[11], are probably all of post-Miocene age.

Fauna

At each locality every fossil fragment seen was collected, whether identifiable or not. The results of the 1961 collections are recorded in Tables 1 and 2, and in Table 1 are compared with the figures for Napak I 1958. The following tentative conclusions are drawn concerning the nature of the assemblages:

(1) There are two distinct types of preservation and assemblage represented. In Table 1 are included only those sites where fossils were stratified beneath a mantle of calcareous sub-aerial pyroclastic material. In this group it is notable that skulls, teeth and jaws comprise 12–25 per cent of the total finds. The 'Better' bones, that is, post-cranial bones preserving recognizable facets and form, show a similar range.

The fact that far too many skulls, teeth and jaws are represented when considered in relation to the number of bones, would seem to imply selective preservation. This presumably reflects the scavenging activities of carnivores and rodents in removing a large proportion of the more edible bones from the debris which lay on the temporary land surfaces. This is supported by the fact that many of the bone fragments retain signs of gnawing and chewing. From the Table 1 localities the non-mammalian fossils collected include fossil wood, seeds, fruits and land gastropods.

(2) The sites included in Table 2 are situated at the base of the main volcanic series, and the fossils occur in calcareous sands and grits resting unconformably on the basement complex and consisting largely of quartzose fragments derived from these rocks. The very different percentage of skulls, teeth and jaws, ranging from 1–6 per cent, reflects in part a more correct proportion of cranial to post-cranial fragments, but also the much poorer preservation resulting in the fragmentation of the majority of the specimens.

The contrast in lithology between the two groups of sites is seen also in the non-mammalian fauna. These basal grits characteristically yield fossils of crocodile and chelonia. At Ombo, fish were represented in the form of jaws of *Protopterus*, and at two of the Napak sites valves of an oyster were found. Also, at Ombo and Mariwa the mammals included *Dinotherium*. These are all absent from the sub-aerial volcanic environments, and provide evidence in support of a fluviatile origin for the basal deposits.

Table 2. GRIT DEPOSITS ON BASEMENT SURFACE

	Napak 1961				Moroto 1961		1961
	Napak II	Napak VI	Napak VIII	Total Napak basal levels	Moroto I	Moroto II	Ombo and Mariwa
Total	103	696	647	1,446	818	286	82
Unidentifiable bone fragments	91	685	600	1,376	733	260	72
'Better' bones	6	2	38	46	69	17	—
Skulls, teeth and jaws	6	9	9	24	16	9	10
Details of skulls, teeth and jaws							
Mastodon	4	8	—	12	10	6	6
Rhinocerotid	1	1	4	6	—	—	—
Primate	—	—	—	—	1	2	—
Others	1	—	5	6	5	1	4

Table 3. TOTAL ASSEMBLAGES COMPARED

	Napak upper level 1958–61 (%)	Songhor I, II and III 1961 (%)	Koru 1927–32 BM collection (%)	Mfwanganu (Whitworth 1961) (%)	Napak basal levels 1961 (%)	Moroto I and II 1961 (%)
Percentages of total Mammalia						
Unidentifiable bone fragments	64·4	43·3	×	×	97·0	90·1
'Better' bones	20·3	31·7	×	×	2·0	7·7
Skulls, teeth and jaws	15·3	25·0	×	×	1·0	2·2
Total number of skulls, teeth and jaws	312	120	208	303	Only 24	Only 25
Percentages of skulls, teeth and jaws						
Rodent	42·6	82·5	86·5	68·6	—	—
Mastodon	29·5	—	—*	0·3	50·0	64·0
Ruminant	7·1	10·0	0·5	14·5	—	—
Primate	5·8	2·5	4·3	3·0	—	12·0
Carnivore	3·5	0·8	2·4	3·0	—	—
Suid	2·2	0·8	3·4	2·0	—	—
Others	9·3	3·3	2·9	8·6	50·0	24·0

* At another site near Koru several specimens of *Dinotherium* were found in sediments with a different lithology.

(3) Table 1 records the characteristic high percentage of rodents preserved in all the sub-aerial tuff environments. In Table 3, percentages of the main mammalian groups in the assemblages of skulls, teeth and jaws at Napak and Songhor are compared with similar figures for Mfwanganu[14], and Koru (based on collections made between 1927 and 1932 housed in the Department of Palæontology, British Museum (Natural History)). The proportions of the main groups reveal a remarkably constant picture at the four sites, and contrast sharply with the figures for the more sparse basal assemblages at Napak and Moroto where the small fauna is completely absent.

(4) That collection failure is also a factor to be considered, is shown in Table 1. Practically all the easily seen mastodont fragments from Napak I were collected in 1958 and only an additional eight fragments were found on return in 1961. By contrast, only one-fifth of the 1958 finds were small rodents although they represent three-fifths of the 1961 total, and were often represented by isolated incisors.

(5) The fossils from Napak I, IV and V are from identical lithologies on the same stratigraphical horizon and are virtually contemporaneous. They must represent very similar environments within one mile of each other on the slopes of the periodically active volcano. Yet there are significant differences in the mammalian assemblages which must imply local ecological changes. Rodents form 80 per cent of the fauna at Napak IV but only 30 per cent at Napak I. Ruminants account for almost 30 per cent of the total at Napak V but only 2 and 4 per cent at Napak I and IV. Primates are most numerous at Napak V where they represent almost 15 per cent of the total.

In assessing the abundance of different groups, it has been assumed that each find represents one individual. Only in the case of the primates at Moroto II and of the large primate from Napak V, does it seem probable that several finds represent only one individual.

(6) At Songhor, it is more difficult to give full weight to the percentages shown in Table 3, as a great deal of collecting has been already made. However, the broad similarity both in actual genera and species and in the relative proportions of the different family groups, between the finds from Songhor and those from Napak, Koru and Mfwanganu, is very striking.

(7) At one locality in the main Songhor I exposure, from an isolated area of fine-grained reddish tuffs known as the 'Red Outlier', which measures only some 10 ft. in diameter, 97 mammalian fossils were collected during September 1961. These included 46 unidentifiable bone fragments, 22 better-preserved bones, and 29 skulls, teeth and jaws. This was the richest deposit which we studied, although the outcrop at Songhor II (Table 1) suggested a similar local fossiliferous patch within the tuff. At these sites again too many skulls, teeth and jaws (30 and 25 per cent of the total finds respectively) were associated with too few post-cranial bones. The Red Outlier assemblage showed the usual domination by rodents with 23 out of the 29 cranial fragments.

These fossiliferous patches within the tuffs recall on a small scale the local concentrations of fossils at Napak I, IV and V. These three areas, each with a maximum diameter of less than 50 yards, yielded the vast bulk of the fauna from the Napak upper level although there was well over a mile of good exposure in beds which appeared to be of identical lithology.

(8) The Napak sites I, IV and V have now yielded a faunal list of at least 29 genera or species as follows: primates 6, insectivores 1, rodents 6, carnivores 6, anthracotheres 1, artiodactyls 4, perissodactyls 3, proboscideans 1, hyraxes 1. The majority of the genera and species is also recorded from the other Lower Miocene (Burdigalian?) assemblages at Rusinga, Mfwanganu, Songhor and Koru, but these contrast sharply with the Fort Ternan assemblage. It therefore seemed desirable to collect where possible specimens of potassium-bearing volcanics associated with the various fossiliferous horizons, with the view of potassium-40/argon-40 dating. The specimens are being dated by Drs. J. F. Evernden and G. H. Curtis of the Department of Geology, University of California, Berkeley, and Dr. P. Damon, University of Tucson, Arizona, to whom we are indebted.

It is hoped that the association of the dates with the faunal evidence will be of assistance in assessing the reliability of these techniques when applied to Tertiary volcanic deposits. Also, as more absolute ages become available it may be possible to review the palæontological data for the various localities. It seems desirable to record differences in abundance, as in Tables 1–3, in addition to identifying lists of species. This is essential if the faunas are to yield evidence on rates of evolutionary change and on the relative importance of ecological differences between the various sites.

(9) The finds from Uganda included 13 primate specimens from Napak and 3 from Moroto. This brings the total of primate finds from the Napak upper level to 18, of which at least 9 represent the genus *Proconsul*. The two finds from the new Moroto II site included the left maxilla of a large *Proconsul*. A further expedition to this locality in December 1961 by Prof. D. B. Allbrook and other members of the Department of Anatomy, University College, Makerere, yielded several more *Proconsul* fragments, including the right maxilla of the original individual. These primate specimens, together with those from Napak, will form the subject of a further publication shortly.

The work was financed by a scientific grant-in-aid from the Royal Society. We also thank the Directors of the Uganda and Kenya Geological Surveys, the Trustees of the Uganda Museum (for valuable assistance with equipment and personnel), Dr. and Mrs. M. Posnansky of Kampala, Mr. and Mrs. R. O. Doenhoff and Mr. and Mrs. J. McLeod of Songhor, Mr. F. Wicker of Fort Ternan, and Mr. and Mrs. S. Stevenson of Irire, Karamoja, for much personal kindness. Finally, we thank Prof. T. Neville George for his critical reading of the text, and the numerous people who helped in various ways or who are at present actively concerned in further specialist studies in preparation for the full report on the work.

1 For distribution of localities, see Maps (Fig. 1) in Bishop (refs. 2 and 3).

2 Bishop, W. W., *Nature*, **182**, 1480 (1958).

3 Bishop, W. W., *Rec. Geol. Survey Uganda*, 1957–58 (1962).

4 Mr. Wilson's finds from Moroto I will be described together with the new material in a forthcoming *Occ. Paper Uganda Museum*.

5 Leakey, L. S. B., *Ann. Mag. Nat. Hist.*, **4**, 689 (1962).

6 Various publications. *Fossil Mammals of Africa* (Brit. Mus. (Nat. Hist.), 1950 onward).

7 Kent, P. E., *Quart. J. Geol. Soc. Lond.*, **100**, 85 (1944).

8 Shackleton, R. M., *Quart. J. Geol. Soc. Lond.*, **106**, 345 (1951).

9 McCall, G. J. H., *Rep. No. 45, Geol. Survey Kenya* (1958).

10 Saggerson, E. P., *Rep. No. 21, Geol. Survey Kenya* (1952).

11 Binge, F. W., *Rep. No. 50, Geol. Survey Kenya* (1962).

12 Trendall, A. F., Geology of Sheet 35 (Napak), *Rep. Geol. Survey Uganda* (in the press).

13 Curtis, G. H., and Evernden, J. F., *Nature*, **194**, 611 (1962).

14 Whitworth, T., *Overseas Geol. and Min. Res.*, **8**, 150 (1961).

MOLECULAR ORIENTATION OF SOME KERATINS

By DR. C. EARLAND, P. R. BLAKEY and J. G. P. STELL

Department of Textile Industries, Institute of Technology, Bradford

WOOL and related hairs (α-keratin) show no birefringence in transverse section, and it is concluded that the preferred molecular orientation must lie in the direction of the fibre axis. In the case of feather, however, which is substantially in a β-configuration, Astbury and Bell[1] observed more than twenty years ago that the molecular orientation of a thin outer layer of quill was at right angles to the feather axis. Recently, we have[2], using the polarizing microscope, found that in the transverse section of goosewing quill, the region showing transverse orientation represented approximately the exterior third of the calamus (root-end) wall, reducing to one-seventh at the rachis. Preliminary X-ray diffraction work also indicated that the pattern of calamus is in fact composite and arises from two structures at right angles to each other.

Thick tactile whiskers, such as those of lion and tiger, exhibit Maltese-cross birefringence when a transverse section is viewed in polarized light, and it has been concluded that in these structures it is the interior region surrounding the medulla that possesses tangential orientation at right angles to the axis[2].

In the present investigation an examination has been made by X-ray diffraction and polarizing microscopy of a number of keratinous materials to determine the extent to which molecular orientation at right angles to the longitudinal axis is general in these structures. The materials examined included hairs, cattle horn and mammalian quills as these are representative of a wide range of keratinous structures. Baleen plate of whale ('whalebone') and rhinoceros horn have been studied also as these materials are interesting in that their complex structures may be regarded as intermediate between normal horn and hair. Some further observations on tactile whiskers and feather calamus are included in the present communication as they have confirmed the conclusions put forward previously regarding the molecular orientation of these structures.

The calamus was isolated from white goose feathers with scissors. Shavings of rhinoceros horn were taken near the root and both from living animals and museum specimens. Strips of commercial 'whalebone' were used with the fringe fibres attached. Although it has been suggested that hydroxyapatite may be present in the whalebone fringe fibres of the fin whale[3], it was found that the calcium phosphate content of the baleen used in this work was 1·0 per cent only. Prior to examination, all materials were degreased by Soxhlet extraction with alcohol and then with ether.

Transverse sections were obtained by hand-sectioning with a razor blade or by the use of a microtome. Specimens were mounted in xylene and viewed in ordinary and convergent polarized light. Examination at elevated temperature was made by enclosing the specimen in an electrically heated aluminium block, the apparatus being similar to that used for observing the shrinkage temperature of collagen.

Although the transverse sections of whisker were of uniform thickness, the birefringent region exhibited very marked multicolouring when viewed in white light, indicative of optical heterogeneity. In these circumstances no quantitative measurements of birefringence could be made, although the insertion of a quarter wave plate showed that in all cases the birefringence was negative.

X-ray diffraction photographs were obtained using a flat plate camera and copper $K\alpha$-radiation from a Raymax rotating anode crystallographic unit operating at 40 m.amp and 40 kV, with the beam parallel, radial or tangential to the axis. Where comparison photographs were required a quadrant type cassette was used.

(*a*) *Feather calamus.* It had been shown previously that the regions exhibiting differing birefringence were separated by a sharp boundary line[2], and there was no evidence for the two structures merging into each other. This suggested that it should be possible to separate the two phases mechanically and this was, in fact, achieved by the following method. A sample of calamus was mounted in a stretching frame in such a manner that tension could be applied tangentially in the plane perpendicular to the feather axis. The specimen was steamed for about 2 min in this state, when it split spontaneously into its two components. These components were then mounted in the X-ray camera with the direction of the quill axis vertical. X-ray diffraction photographs showed that although the molecules of the two regions possess the same configuration, in the case of the inner region the orientation is parallel to the feather axis, but in the case of the outer region it is perpendicular to this axis.

(*b*) *Tactile whiskers.* It has been reported previously[2] that the interior regions of transverse sections of whiskers of lion and tiger exhibit Maltese-cross birefringence in polarized light. Myelin sheaths however, also exhibit the same phenomenon and it has been concluded that this form of birefringence

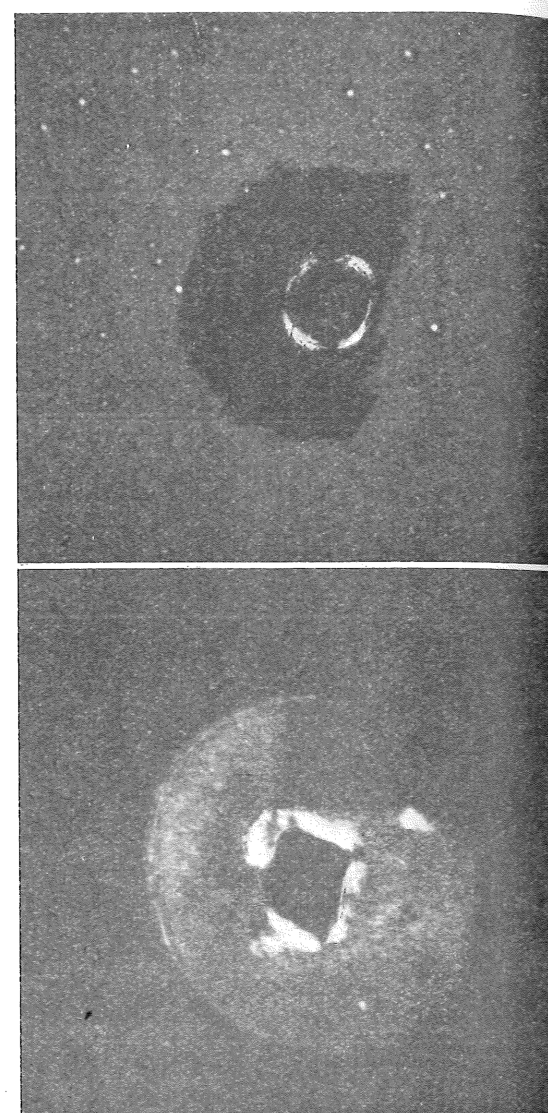


Fig. 1. Top, transverse section of whisker of lion viewed in polarized light at 115° C (×45); bottom, transverse section of horse hair viewed in polarized light (×400)

may arise from two materials within the sheath, the protein molecules which lie tangentially and incrusted lipoid materials with the molecules orientated radially[4]. Since the latter birefringence is reduced by solvent extraction[5], it was concluded that the Maltese-cross birefringence of whiskers was due solely to tangential orientation of protein molecules since the materials used had been extracted thoroughly. However, the region showing this phenomenon is always in the vicinity of the medulla where lipoid materials are very probably present, and therefore the birefringence of these materials was examined at elevated temperatures, since it is known that the birefringence due to lipoids disappears at 100° C (ref. 5). It was shown that a transverse section of lion whiskers viewed in polarized light with the specimen heated to 115° C gave a Maltese cross as sharp as that at room temperature, and it must be concluded that the original views regarding the cause of this birefringence are correct.

(*c*) *Miscellaneous animal hairs.* In view of the fact that the very extensive literature on the fine structure of wool makes no mention of Maltese-cross birefringence, it was scarcely surprising that none was found in this investigation. The literature on heavily medullated wools and kemp, which are more akin to the tactile whiskers than the finer wools where medulla is completely absent, however, is less comprehensive and these materials were, therefore, carefully examined but again no birefringence was observed.

Although it was not possible to make a complete survey, a very large number of other animal hairs was also examined, but only one example of Maltese-cross birefringence was found. This was in monster horse hair, and a transverse section taken near the root is shown viewed in polarized light in Fig. 1.

(*d*) *Cattle horn.* X-ray diffraction showed that in the case of horn, which consists of about ten concentric laminates which may be separated readily mechanically, the outer layer has very good orientation with the molecules lying perpendicular to the axis and tangentially. The inner layers, generally, did not show such good orientation, but the orientation showed a tendency to be parallel to the horn axis, although occasionally a region could be found with molecular orientation similar to that in the outer layer. No evidence could be found for a β-configuration.

A transverse section of horn, about 0·001 in. thick, obtained by using a shaping machine, was mounted in xylene and viewed in polarized light. The outer layer, which amounted to about one-third of the thickness of the horn, was highly birefringent whereas the remainder was birefringent to a lesser degree. Thus the molecular orientation as shown optically was consistent with the results obtained from X-ray diffraction.

(*e*) *Baleen plate* ('*whalebone*'). Whalebone, after extraction with alcohol and ether to remove grease, gave a normal α-keratin X-ray diffraction pattern. A transverse section of this material viewed in normal light is shown in Fig. 2, top. In the lower portion the fibres can be seen set in the matrix, and the upper portion consists solely of layers of horny embedding material. The laminated nature of the latter may be seen clearly and it is thus very similar to cattle horn. The same section viewed in polarized light (Fig. 2, bottom) shows that each embedded fibre exhibits a Maltese cross and is very similar to the whiskers of lion and tiger. The fringe fibres which emerge from baleen also show the same effect.

(*f*) *Rhinoceros horn.* There is considerable confusion in the literature regarding the structure of rhinoceros horn and an attempt to clarify the position has been made recently by Ryder[6]. There is no doubt that, whereas cattle horn is composed of sheets of keratinous material, rhinoceros horn consists of longitudinal filaments. These tend to separate, particularly at the proximal end, which, no doubt, gave rise to the earlier statements that rhinoceros horn is composed of matted hair[7,8]. Although the latter is untrue, it has been shown[6] that the inter-filamentous horn is much sparser than, for example, in the case of baleen plate (Fig. 2, top), and the filaments are packed so tightly together that they are often multi-sided rather than circular. Morphologically, it is probably not incorrect to regard both baleen plate and rhinoceros horn as intermediate between hair and cattle horn.

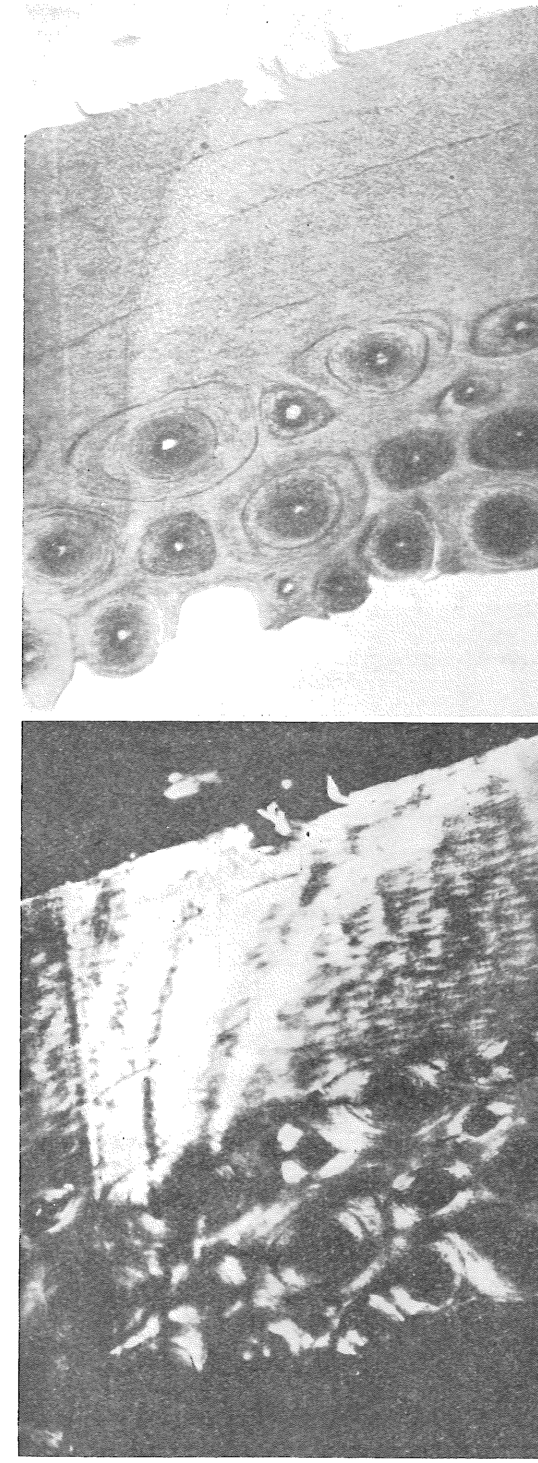


Fig. 2. Top, transverse section of baleen plate viewed in normal light (×60); bottom, similar section viewed in polarized light (×60)

Concurrently with the publication of the discovery of transverse orientation in whiskers of the cat family[2], Ryder[6] published photomicrographs of transverse sections of the individual filaments comprising rhinoceros horn. The latter showed clearly longitudinal cell structures orientated tangentially in the plane of the section and were, in fact, very

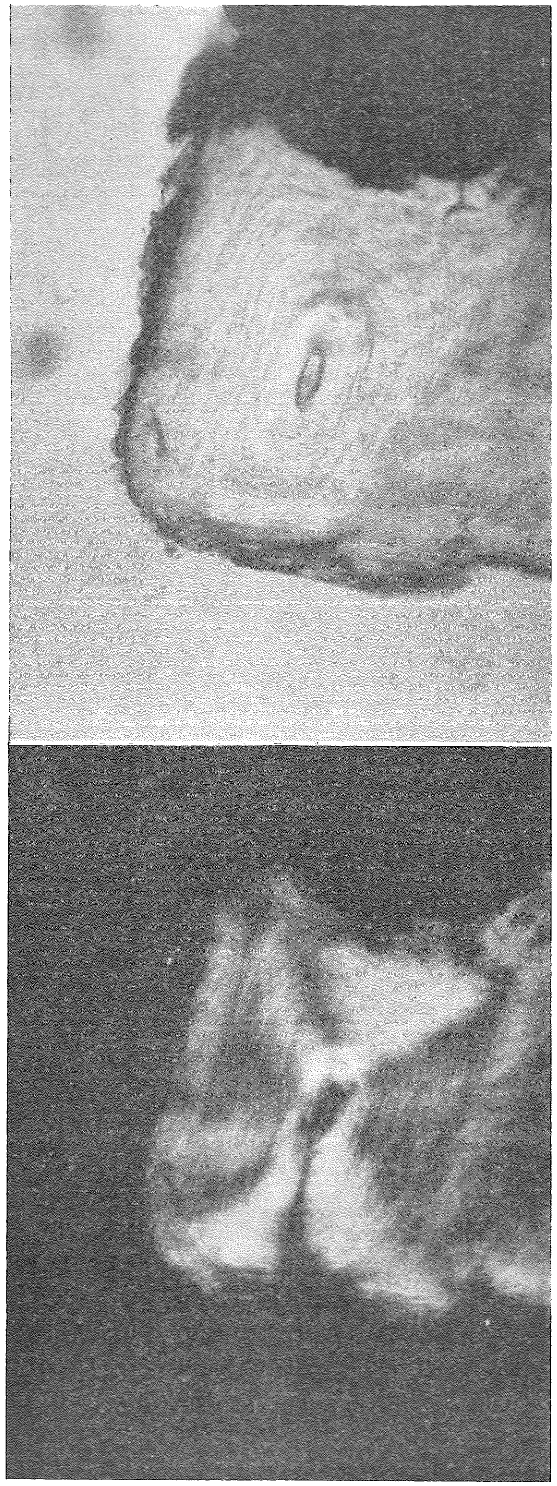


Fig. 3. Top, transverse section of a single filament of the horn of the black African rhinoceros viewed in normal light (× 50); bottom, similar section viewed in polarized light (× 50)

similar to sections of whisker. It was therefore anticipated that these sections would exhibit Maltese-cross birefringence in polarized light. In Fig. 3 is shown a transverse section of a filament from the horn of the black African rhinoceros (*Diceros bicornis*) viewed in polarized light and a similar section taken from the horn of the Indian rhinoceros (*R. unicornis*) in polarized light is shown in Fig. 4.

Of the five living species of rhinoceros, the horns of four were available for examination, the exception being the Sumatran rhinoceros (*R. sumatrensis*). A comparative investigation of these four keratins was therefore made, and the results are summarized in Table 1.

Although Table 1 suggests that the Asian rhinoceroses have horns superficially more resembling

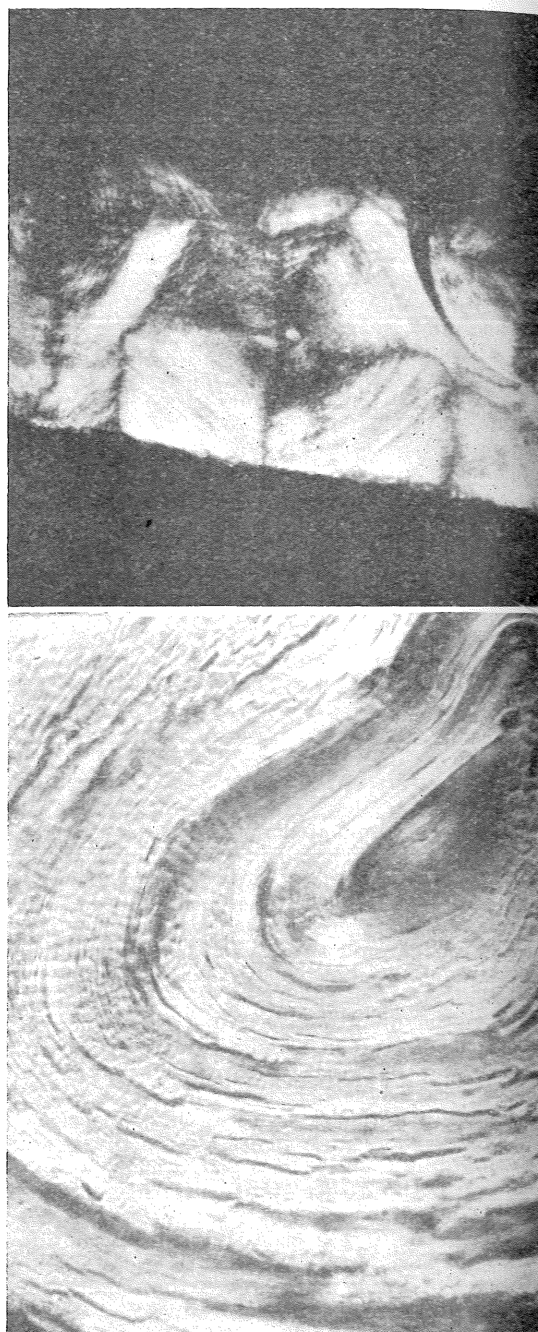


Fig. 4. Top, Transverse section of the horn of the Indian rhinoceros viewed in polarized light (× 50); bottom, transverse section of a portion of a filament of the horn of the white African rhinoceros viewed in normal light (× 400)

Table 1. STRUCTURE OF RHINOCEROS HORNS FROM DIFFERENT SPECIES

Species*	Macro structure	Appearance in polarized light of transverse section	X-ray diffraction pattern
Indian (2) (*R. unicornis*)	General appearance like cattle horn.	Maltese-cross effect (Fig. 4).	Poorly orientated α-pattern. Strong apatite reflexions.
Javan (1) (*R. sondaicus*)	Filaments very firmly embedded in matrix.	Patchy birefringence. Filaments too irregular to produce cross.	Poorly orientated α-pattern. Apatite reflexions absent.
African Black (2) (*Diceros bicornis*)	General appearance like bundle of bristles.	Maltese-cross effect (Fig. 3).	Poorly orientated α-pattern. Apatite reflexions absent.
African White (1) (*Cerathotherium simus*)	Filaments readily separated.	Patchy birefringence. Filaments too irregular to produce cross.	Poorly orientated α-pattern. Apatite reflexions absent.

* The number of specimens examined from different animals is given in parenthesis.

cattle horn that the African species, and *R. unicornis* is the only species containing apatite as a major constituent of its horn, it must be borne in mind that the observations have been made on a small number of animals.

In feather and cattle horn the keratins possessing transversal and longitudinal orientation are located in well-defined regions. In the case of rhinoceros horn, however, the poor X-ray diffraction pattern produced when the specimen was mounted longitudinally and the extensive but rather ill-defined Maltese-cross pattern shown by a transverse section in polarized light, suggest that the protein molecules showing different orientations are more intimately associated.

(*g*) *Mammalian quills*. The birefringent zones exhibited by transverse sections of porcupine and hedgehog quills in polarized light were less extensive than in the other keratinous structures examined. Nevertheless, the four extinction positions were clearly visible and there can be no doubt that a thin layer possessing transverse orientation is present. If the complex internal structure of quill be regarded as a medulla, the location of this layer is not dissimilar to that in tactile whiskers.

Thus, it has been shown conclusively by X-ray diffraction and polarizing microscopy that feather calamus and cattle horn are polyphase in structure, possessing molecular orientation of the protein molecules at right angles to the main structural axis, in addition to parallel orientation.

Strong evidence has been obtained also from polarizing microscopy that similar structures are present in rhinoceros horn, baleen plate and mammalian quills, but in hair and wool with a single exception the preferred molecular orientation lies exclusively in the direction of the fibre axis.

It is considered that the biological significance of these structures is to prevent the splitting that would occur if the structural elements were laid down exclusively in one direction.

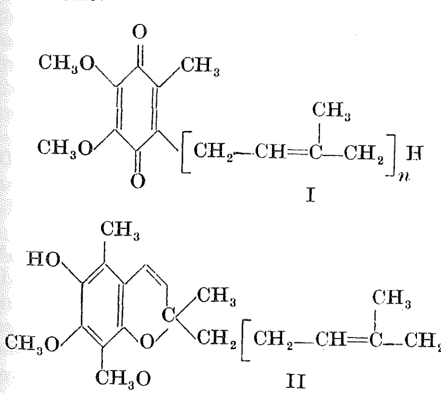
We thank Dr. L. Harrison Matthews and Mr. E. H. Tong of the Zoological Society of London, Dr. G. B. Corbet of the British Museum (Natural History) and Dr. E. Lees of the Department of Biological Sciences, Bradford Institute of Technology, for providing specimens and advice. One of us (J. G. P. S.) is a Wool Textile Research Council Fellow.

[1] Astbury, W. T., and Bell, F. O., *Tabulae Biologicae*, **17**, 90 (1939).
[2] Earland, C., Blakey, P. R., and Stell, J. G. P., *Biochim. Biophys. Acta*, **56**, 268 (1962).
[3] Pautard, F. G. E., *J. Dental Res.*, **40**, 1285 (1961).
[4] Schmidt, W. J., *Protoplasma*, **29**, 435 (1937).
[5] Schmidt, W. J., *Protoplasma Mon.*, **11** (1937).
[6] Ryder, M. L., *Nature*, **193**, 1199 (1962).
[7] Anthony, H. E., *Bull. N.Y. Zool. Soc.*, **31**, 179 (1928).
[8] Beddard, F. E., *Camb. Nat. Hist.*, **10**, 253 (Macmillan, London, 1902).

UBIQUINONE AND UBICHROMENOL

Ubiquinone and Ubichromenol in *Torula* Yeast

UBIQUINONES (I) and ubichromenols (II) are isomeric.



I

II

Ubichromenol$_{10}$ ($n=9$)[1] has been found in various animal tissues and ubichromenol$_7$ ($n=6$) occurs in a *Torula* yeast (commercially dried).

The isomerization can be effected in the laboratory by various procedures involving the use of a catalyst[2,3]. These lead to a racemic product, but the preparations from human kidney[4] and from *Torula* yeast were optically active.

The question whether ubichromenol is or is not a natural product for which it is reasonable to seek a function is not easily settled, although evidence has been reported[5] which supports a natural origin from some animal tissues. It became necessary to investigate the problem in the case of *Torula* yeast.

A commercial, dried *Torula* yeast (*Candida utilis*), kindly given by the Lake States Co., New York, and designated type *B*, was analysed for ubiquinone (UQ) and ubichromenol (UC) with the results shown in Table 1.

Simple extraction of lipid from yeast is an inefficient process[6], and the failure in experiments 1, 2 and 3 to achieve the yields of UQ and UC which occur after alkali digestion (saponification) of the yeast is not surprising. Alkali and heat tend to destroy UQ and UC, and saponification should aim at liberating these substances with minimal destruction. The fact that the ratio UC/UQ in Table 1 is nearly constant argues against conversion of UQ in the saponification