PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1981 **292**, 57-64
doi: 10.1098/rstb.1981.0013

Phil. Trans. R. Soc. Lond. B **292**, 57–64 (1981) [57]
Printed in Great Britain

DIET AND TEETH

Dietary hypotheses and human evolution

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[Plates 1 and 2]

Hypotheses concerning the diet of early hominids have played an important role in discussions on human evolution. Three investigations have helped define the extent to which dietary hypotheses may be taken and still be testable. Comparative anatomy is a fairly coarse approach, which despite convergences allows only the most specialized diets to be ruled out. A biomechanical analysis makes it clear that the changes in jaw and tooth form are subtle and outside the resolution given by present understanding of cranial function. Analysis of the microscopic tooth wear of extant species has been carried out. Major dietary types can be distinguished by their microwear. The microwear on fossil hominids appears to rule out certain diets that have been proposed for them.

Introduction

Several of the most important discussions on human evolution have been concerned with our ancestral dietary adaptations. At the simplest level, this has been caused by the preponderance of jaws and teeth in the fossil record, but more importantly it reflects the fact that the feeding habits of any species have profound consequences for many aspects of its biology. Particular dietary régimes impose constraints upon such things as body size, locomotor behaviour breeding strategy and social behaviour. They also limit a species to a geographic range, at one end of the scale, and to particular habitats, at the other. Because dietary habits so powerfully determine many aspects of a species' life style, it is not surprising that theories based on dietary models have been very important in the study of human origins.

Dart's ideas based on the notion that *Australopithecus* was a predator (Dart 1953, 1957, 1959) proved to have consequences that affected much of the thinking in the behavioural sciences and which, through popularization by the late Robert Ardrey (1961, 1976), were placed before a large general audience, Dart conceived of *Australopithecus* as

> '. . . carnivorous creatures, that seized living quarries by violence, battered them to death, tore apart their broken bodies, disembodied them limb from limb, slaking their ravenous thirst with the hot blood of victims and greedily devouring livid writhing flesh.' (Dart 1953, p. 209).

The evidence for carnivory in *Australopithecus* included fractures in the bones of that species, an analysis of the bone collection from the Makapansgat cave deposit, and the general feeling that there was little else it could have fed on in the area at the time.

METHODS, PROBLEMS AND EVIDENCE

There are, in fact, several ways in which we might determine the diets of extinct hominids, some of them more useful than others, but all with their own difficulties.

Among the methods that possibly can be applied to the fossil record are the following:

(1) interspecific comparisons of tooth morphology;
(2) biomechanical reconstruction;
(3) inspection of tooth microwear;
(4) carbon isotope analysis;
(5) trace element analysis;
(6) application of ecological 'rules';
(7) analysis of 'food refuse' from archaeological sites;
(8) diagnosis of cases of metabolic diseases caused by diet.

Interspecific comparisons of tooth morphology involve an understanding of dental adaptations to particular diets. If one bears in mind that mammals use their teeth for many purposes and that the teeth of mammals are only a part of the digestive system, it should be possible to make generalizations concerning dental adaptations. For instance, species that graze have, with few exceptions, hypsodont teeth in which the enamel is placed in plates or rods normal to the occlusal plane; these plates are separated by dentine or cement or both. This common, basic pattern can be found in the teeth of horses, elephants, certain rodents, and warthogs, although these groups are easily distinguishable from one another. The limits to which adaptations in different groups of mammals may converge are set in many ways, one of which involves the influence of heritage characters. For instance, the herbivorous panda bear, the carnivorous polar bear, the omnivorous grizzly bear and the termite-eating sloth bear have different tooth morphologies, but these must all function with a basic carnivore temporomandibular joint. Herbivory has not led the panda to evolve a more freely mobile mandibular condyle as it has mammalian groups long committed to herbivory. It is also apparent that the size of an animal may influence tooth shape, so that, for instance, a grazing hyrax may not develop the extremes of hypsodonty and enamel folding that are found in a horse, presumably because the smaller animal can select less abrasive grass parts while the horse must inevitably take some quantity of less desirable food with each large bite.

Examples of several mammalian dentitions are given in plate 1. Although there seem to be several examples of convergent adaptations that can be related to diet, features fundamental to each phylogenetic group impose constraints such that a grazing pig has teeth that are still recognizably pig teeth. These heritage features are the ones that make the comparative method of limited usefulness to the student of any one order of mammals. For the student of the Hominidae, it is extremely unlikely to have any useful resolving power. If, for example, a mammologist who knew nothing about hominids were asked which mammalian molars most resembled those of *Australopithecus*, the answer would probably be orang-utan molars. If asked to look outside the order Primates, the answer would probably be the molars of the sea otter (*Enhydra lutra*). This species possesses small anterior teeth, and large, broad, flat molars with thick enamel. Claims that *Ailuropoda* teeth resemble those of *Australopithecus* (see, for example, Du Brul 1977) are, I feel, not only based on a rather superficial analogy, but also depend on a *comparison* between two bear species and two *Australopithecus* species. Similarly, Jolly's (1970) model depended on a comparison between two baboon species and a hominoid/hominid pair of

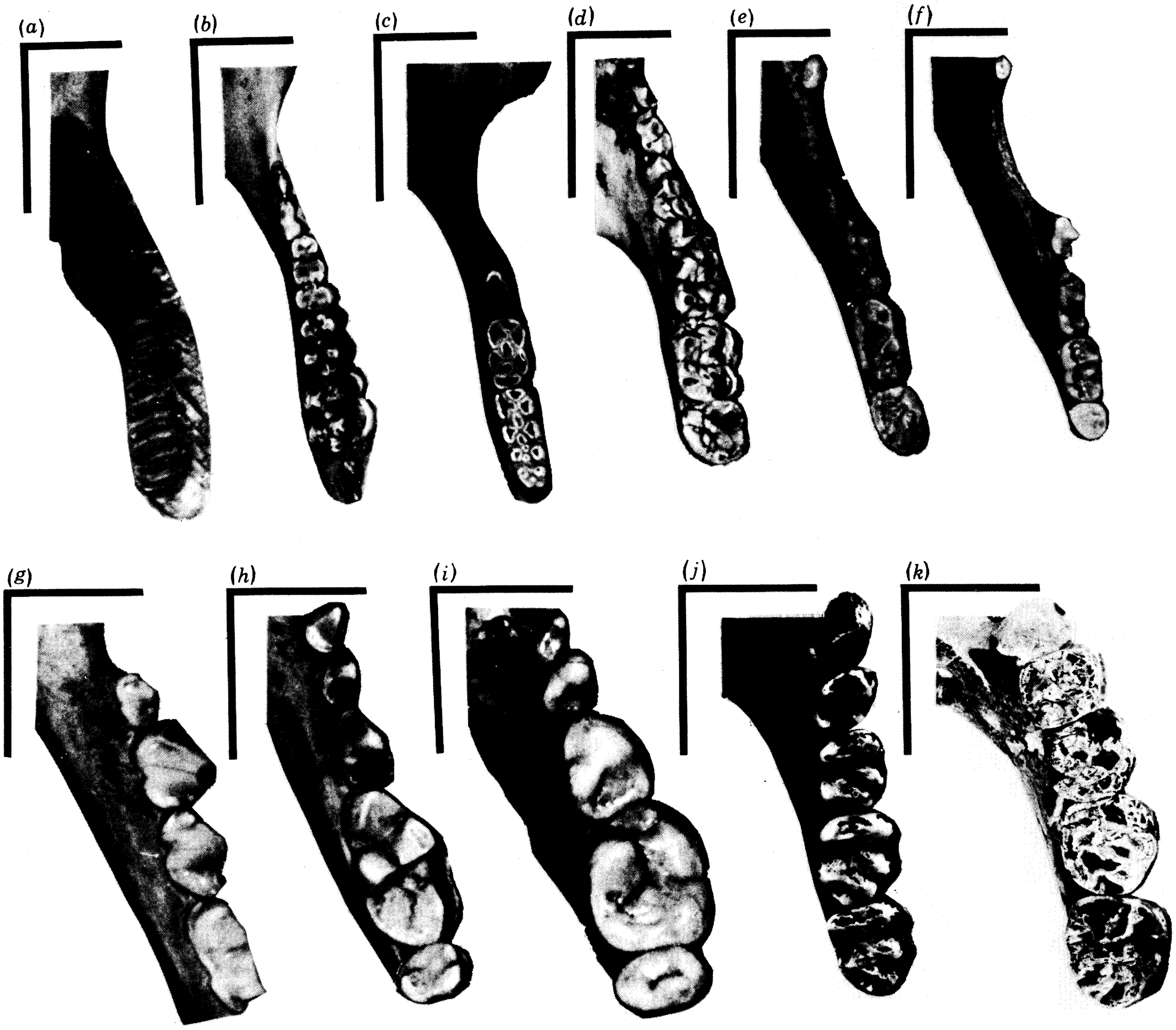

Plate 1. Right mandibular tooth rows of selected mammals. All reduced to the same canine to third molar length. (*a*) Capybara; (*b*) bushpig; (*c*) warthog; (*d*) giant panda; (*e*) grizzly bear; (*f*) polar bear; (*g*) spotted hyena; (*h*) otter (*Lutra* sp.); (*i*) sea otter; (*j*) gorilla; (*k*) robust *Australopithecus*.

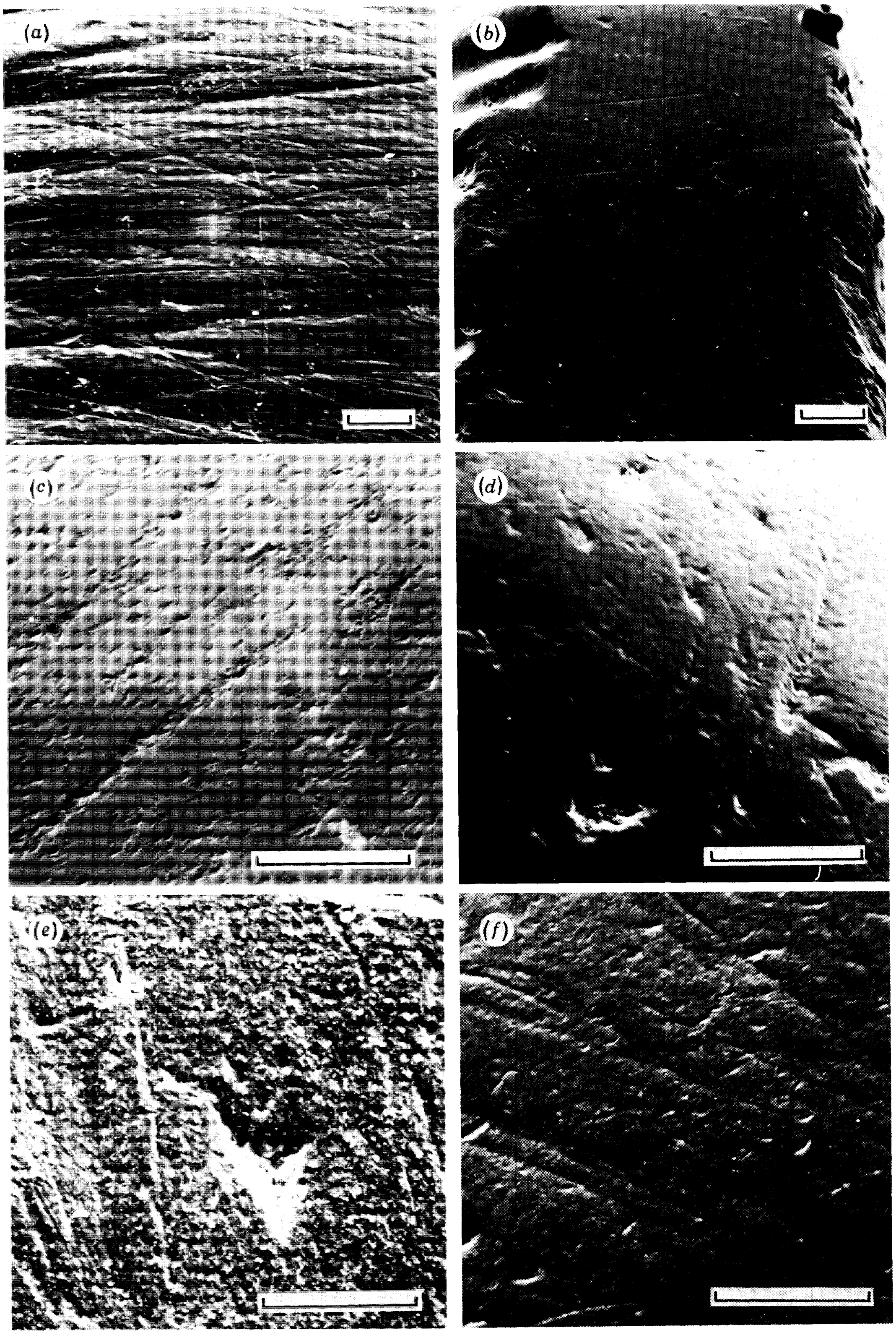

Plate 2. Representative scanning electron micrographs of the occlusal surfaces of the teeth of selected mammals: (*a*) white rhinoceros (grazer); (*b*) giraffe (browser); (*c*) cheetah (carnivore); (*d*) orang-utan (frugivore) (*e*) spotted hyena (scavenger, bone eater); (*f*) robust *Australopithecus*. Scale bars: 200 μm.

species. It does not necessarily follow that, because pairs of species have *similar differences* in the morphology of their teeth and jaws, their dietary régimes are also similar. This is not to deny that similar selective pressures might have affected both pairs similarly, but the constraints of a common heritage may mean that the morphological changes that accompany a dietary change in one pair might accompany a different dietary change in the other.

Biomechanical reconstructions have some value in palaeontology. They can redefine the questions being asked and, if successful, may set limits on the mechanical characteristics of foods eaten. As with many efforts in palaeontology, the anatomy of the modern species being used for comparison is too often inadequately understood.

The first step in a biomechanical reconstruction is the choice of an appropriate modern analogue. The closest living relative is often, but not always, the best choice. To take the example of *Australopithecus robustus*, the closest living relative is *Homo sapiens*. In many respects, such as the configuration of the temporomandibular joint, the form of the teeth, and the small canines, the morphological similarities are close enough to make the analysis possible without omission of any major variable because it is found in only one of the two species. But is the modern analogue adequately understood in this instance? Our knowledge of the masticatory anatomy of *Homo sapiens* is exhaustive and years of dental research have led to an understanding of normal occlusal relationships and functions. The biomechanics of human chewing are understood in part, but not in whole, because of the peculiar nature of humans as experimental animals. Humans are suitable experimental subjects because they can respond to verbal directions to perform certain actions, yet invasive techniques can be used only rarely in humans. More is known about the forces acting on the mandible in galagos or monkeys than in people, simply because strain gauges can be applied directly to bone in living, non-human animals (Hylander 1979). Although electromyographic studies have been carried out on human volunteers (see Moller 1966), the study of bite forces can only be made under unusual circumstances (Graf 1976). However, biomechanical analyses of human biting and chewing have been made (see Walker (1978) for a review of the literature).

By modelling the muscles on a reconstructed skull of a robust *Australopithecus* (based on KNM-ER 406 and KNM-ER 729), the major lines of action of the masticatory muscles can be determined and the values for their contractile forces estimated from cross-sectional areas (figure 1). The results are somewhat surprising. Given that the skulls of *Australopithecus* and *Homo sapiens* are obviously different, it is a surprise to find that the lines of action of their muscles of mastication are very similarly arranged. Apparently, the way in which bite forces can be applied to food are the same in both, yet the muscle forces produced in *Australopithecus* were much larger than in humans. But since these bite forces are used to generate *pressures* over occlusal surfaces, the area of the loaded teeth is criticial. In the fossil hominid, the occlusal area is very much larger, maybe four or five times larger than in humans. Thus, with similar lines of muscle action, *Australopithecus* would have had to generate four or five times the bite force to create the same pressures as are recorded in modern humans. The question, then, can be rephrased. Formerly, the anatomy of robust *Australopithecus* led to the intuitive question: 'What were they eating that was so hard?' Now we see that the appropriate questions is, instead: 'What were they eating that could be masticated by modern humans as well that *Australopithecus* needed to process in greater quantities?' The answer might be a food substance that contains a large proportion of indigestible material.

Tooth microwear studies (Walker *et al.* 1978; Walker 1980) are beginning to yield results that may help to resolve the choice between major dietary types. In a study on two sympatric species of hyrax, Walker *et al.* (1978) showed that grazers and browsers could be distinguished by the microwear on their teeth. The teeth of grazers are subjected to abrasion by the siliceous phytoliths in grasses. These tiny particles (about 10 μm in diameter) cannot be avoided, and sheep, for example, ingest 10 kg of phytoliths a year (Baker *et al.* 1959). This is, of course, the reason why the teeth of grazers are either hypsodont or continuously growing and why their enamel is orientated normal to the occlusal plane. Little by little, the teeth of grazers are ground away by phytoliths.

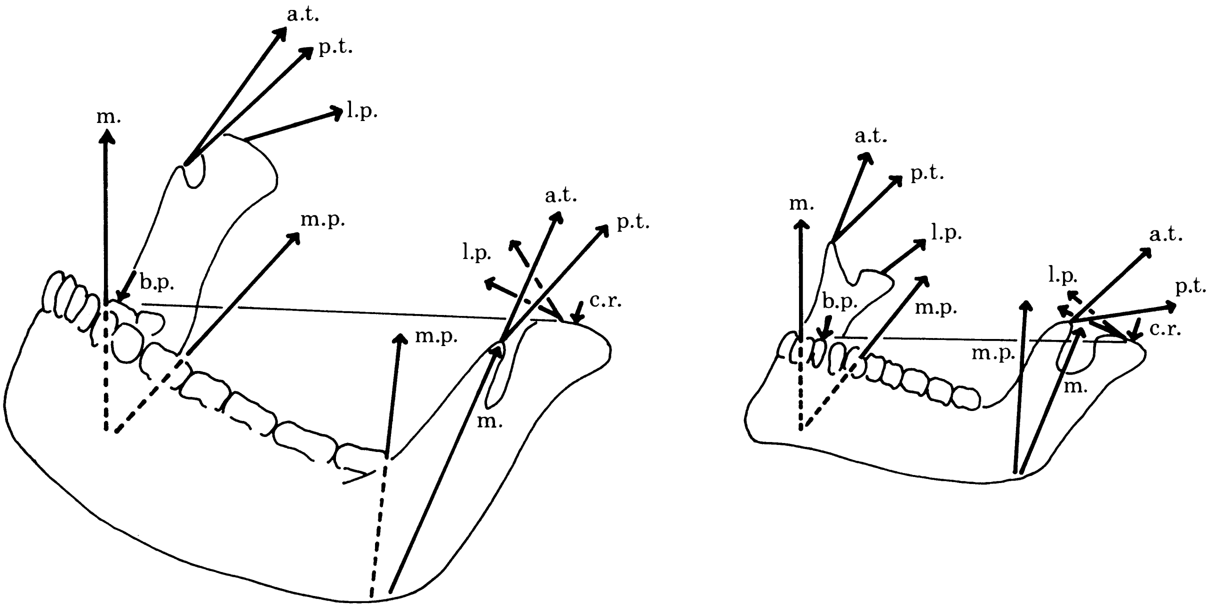

Figure 1. Lines of action of the muscles of mastication in modern human and robust *Australopithecus*. The orientation selected is such that the bite point (second molar) and the balancing side mandibular condyle are in the plane of the page (see Walker (1978) for details). Abbreviations: a.t., anterior temporalis; p.t., posterior temporalis; m., masseter; m.p., medial pterygoid; l.p., lateral pterygoid; b.p., bite point; c.r. condylar reaction point.

Other broadly defined dietary groups can also be recognized on the basis of the characteristic patterns of microwear on their teeth (plate 2). Since high quality replication methods are now available (Walker 1980), fossil specimens may be examined without either any danger to the specimen or the need to cut off small pieces that will fit in the scanning electron microscope chamber. Work is under way to document wear patterns on a series of modern mammals of known, different diets. Quantification of scratch lengths, scratch widths, scratch and pit frequencies and so on may provide a statistical basis for evaluating the probable diets of early hominids. As an example, browsing animals have about five and grazing animals 300 minute scratches per square millimetre. With the research programme at its present stage, only qualitative assessments of the microwear of extinct forms can be made. It appears that grazing (including eating husked grass seeds) and browsing can be ruled out for diet of robust *Australopithecus*. Bone crunching, suggested by Szalay (1975), can also be dismissed, since it produces characteristic wear not found in the fossil species. The dietary pattern most congruent with the observed microwear is frugivory. The microwear on molar teeth from nearly 20 robust

Australopithecus from East Africa cannot, at present, be distinguished from that found in mandrills, chimpanzees and orang-utans.

Carbon isotope analysis of bone promises to be a powerful tool in dietary studies. Laboratory studies have shown that the isotopic composition of carbon in an animal's bones is a function of the isotopic carbon in its diet (De Niro & Epstein 1978). This is true for both the carbonate and collagen fractions of bone. The ratio of ^{13}C to ^{12}C in plants eaten by herbivores depends upon the photosynthetic pathway that the plants use. Most tropical grasses have higher ^{13}C to ^{12}C ratios than most browse plants. This fact was used by De Niro & Epstein (1978) to determine the diets of the same hyrax individuals used in the microwear studies by Walker *et al*. (1978). The method discriminated accurately between individuals that were known to have been grazers and those that were known to have been browsers in a blind test. It may be possible to apply this method to fossil bones if it can be demonstrated that diagenetic changes do not affect the carbon isotope ratios.

Strontium analysis of fossil bone (Toots & Voorhies 1965) is a method that has been used with varying degrees of success to estimate past diets. Plants contain different amounts of strontium; therefore, browsing and grazing animals can be distinguished by the strontium levels in their teeth and bones. Further, although the amount of strontium lost at each trophic level is relatively small, it is significant. Thus the strontium level in herbivores is low, but it is even lower in carnivores feeding on those herbivores. Parker & Toots (1980) review the role of strontium analysis in palaeontology and assess the utility of other trace elements for dietary reconstruction. Schoeninger (1979) has shown that this method can contribute to understanding dietary differences in archaeological samples for which the only other method would be to guess the richness of diets from the accompanying grave goods and/or the burial location. The only attempt to assess the diet of *Australopithecus* by strontium analysis (Boaz & Hampel 1978) yielded uncertain results, possibly because of the taphonomic history of the sample chosen.

There are certain constraints placed upon an animal's dietary habits by its body size. These range from energetic considerations to the relative sizes of the animal and its food. Although such ecological 'rules' cannot be used to predict the diet of any particular species, they can help in setting limits on the number of possible diets to be considered. Kay & Hylander (1978) show that insectivorous and folivorous mammals differ consistently in their body size. They demonstrate that, for insectivores in which the prey are not social insects in local concentrations, the energetic cost of locating enough insects to support a large body size is too great to be practical. Most insectivores are, therefore, small, the exceptions being species that prey on colonial insects. On the other hand, mammalian folivores need to retain food in their digestive tracts for long periods of time for cellulose digestion to take place. Small mammals have short food passage times and high metabolic rates. Thus, a mere increase in body size would be a selective advantage to a folivore, and most folivores are large for this reason. Clutton-Brock & Harvey (1980) have shown that, within taxonomic families, folivores have relatively smaller brains than frugivores. Their explanation for this finding is based on the observation that leaves are an evenly distributed food source whereas fruits are very unevenly distributed in both space and time. Therefore, much more complex information is need to exploit fruit as a food resource than to exploit leaves. The larger brains in frugivores are, by this explanation, required to process this greater amount of information about the environment. Whether or not the relative brain sizes of fossil species may be subject to such analysis depends on the accuracy of body mass estimates. Unfortunately, to date we have no single individual early hominid specimen for which both the brain case and the postcranial bones are complete enough for a reliable estimate of brain size and body mass to be made.

The remains of the meals of early hominids that are found on archaeological living floors are, of course, direct evidence of diet. However, it is not at all clear in many instances that any or all of the bones were collected by hominids as food. In a discussion of the agencies that may give rise to accumulations of bones in caves, Brain (1980) concludes that several usually act together and that detailed comparative studies on single agents are needed before any particular assemblage can be attributed to hominid actions. For open sites, such as those at Olduvai Gorge (Leakey 1971), where there is an association of bone refuse and stone artefacts, the situation is much clearer. The archaeological record documents that by 2 Ma ago some early hominids were breaking and cutting animal bones for the associated meat and/or marrow (Isaac, this symposium). However, since most plant remains are never fossilized and bones often are, the record of what was eaten is obviously biased in favour of animal food. Also, since at this time robust australopithecines were contemporaries of at least one other hominid species, the question arises as to which indulged in eating animal parts. Some of the objective methods discussed in this paper may help to answer this question.

It is true that several robust bones have been found in association with living floors and it has been hinted (Bishop *et al.* 1975) that this might be taken as evidence that robust australopithecines made the tools. But if we are to take repeated association with tools as evidence of tool-making, then bovids are clearly the best candidates in the Plio-Pleistocene for tool-maker status. It can also be argued that the hominid species found on the sites must be food refuse and that those absent are the most likely tool makers. Ethnoarchaeological studies, such as those by Binford (1978) on the Nunamuit Eskimos, Yellen (1974) on the San Bushmen, and Gifford (1980) on the Dassenetch of Kenya, provide an important perspective on the process of site formation and the intuitive definition of what are called sites by archaeologists. By concentrating on the processes by which sites are formed, such studies have uncovered hidden biases that affect interpretation in archaeology. The advantage in these cases is that the remains left behind by people can be correlated with their use as observed before the site was abandoned.

As an infrequent occurrence, it might be expected that an occasional individual hominid will show signs of disease or disorders related to diet. These might range from gum disorders, affecting the alveolar bone of the jaws, to systemic metabolic diseases with nutritional causes. To follow the example used previously, robust australopithecines show little tooth and gum disease. One individual from East Turkana (KNM-ER 729) had broken the crown from a molar during life, but this episode led only to local alveolar resorption (Leakey *et al.* 1972). In contrast, some individuals of *H. erectus* (e.g. KNM-ER 730) contemporary with robust australopithecines show heavy tooth wear, alveolar resorption, and pocketing (Day & Leakey 1973).

Enamel hypoplasia, resulting from interruptions in the normal developmental process, may be caused by certain diseases or nutritive stresses. Such hypoplasia have been observed in robust australopithecine teeth (Robinson 1956; Tobias 1967; White 1978), and White (1978) has suggested that they might be related to weaning.

A single *H. erectus* skeleton, KNM-ER 1808 (Leakey & Leakey 1978), shows signs of a systemic disorder that resulted in an inflammation of the periosteum shortly before death. The diagnosis most consistent with the distribution and histological appearance of the newly formed bone and with that of the underlying bone of the skeleton is hypervitaminosis A. Further, it is very probable that this disease was of sudden onset. The underlying bone is histologically normal, but the bone resulting from the periostitis is abnormal and highly disorganized. This abnormal bone is found over all long-bone shafts and in places is up to 7 mm thick. Documented occurrences of hypervitaminosis A include many cases of children who were given overdoses of vitamin A by their mothers. These individuals show growth disturbances associated with early ossification of epiphysial cartilages. In this case, however, the individual was fully adult. Although adult examples of hypervitaminosis A are rare in the literature, cases are described in which Arctic and Antarctic explorers were forced by extreme circumstances to eat wild or domestic carnivores (Shearman 1978). The diaries make special mention of eating liver, which was often the only uncooked meat that they could chew. Because carnivore livers contain huge amounts of vitamin A, a single episode of consuming quantities of polar bear, dog, or other liver is sufficient to produce massive subperiosteal bleeding, severe bone pain, and, within a short time, extensive new bone deposition.

Although the diagnosis of a disease in a case of such antiquity cannot ever be made with certainty, the context of this case invites speculation. KNM-ER 1808, as well as being the most complete *H. erectus* skeleton known, is also among the earliest-known individual members of that species. Could it be that, before the use of fire and while butchery practices were in a formative stage, we have the remains of an individual who suffered from over-indulging in liver? Is it too unlikely that, during the transition from a more vegetarian diet to one that involved meat, dietary mistakes might be made? This case will be dealt with more fully in Walker *et al.* (1980).

Conclusions

In summary, what can we say about the diet of robust australopithecines? Based upon several lines of evidence, it now seems unlikely that they ate grass seed, leaves, or bone. It is quite likely that they maintained a form of the original hominoid diet, which was based upon a preponderance of fruit (Kay 1977). The fruits of most indigenous African plants are small, largely lacking in fleshy pulp, and are either encased in a hard external shell or pod or consist of small seeds with individual hard, protective cases. The features of the masticatory system and the microwear findings to date are consistent with bulk eating of such fruits without much preparation. By that, I mean that whole fruits (casings, pulp, seeds, and all) were probably masticated, rather than the fruit being shelled, pulped or otherwise prepared. In such a diet, the occasional harder-than-usual particle might cause the sort of microscopic damage seen on the occlusal surfaces of robust australopithecine teeth. Further, it is reasonable to assume that, once in a while, a tooth might be fractured by such a particle even though the teeth were not subjected to heavy wear by mammalian standards. By the comparative method, it was seen that the teeth of the sea otter were the most similar morphologically to robust *Australopithecus* teeth of all non-primates. Sea otters eat the flesh of molluscs, which is not abrasive in itself, but which occasionally contains a very hard fragment of shell or a pearl. The flat, broad teeth with thick enamel that characterizes these two species can be thought of as an adaptation to resist the bending and fracturing that might result from chewing such an object. Thus, although the diets of these two similarly adapted animals might not be the same, the mechanical properties of those diets might well be similar.

I thank Linda M. Perez and Pat Shipman for their help in preparing this paper. The research was supported by the National Science Foundation through grants BNS 75-16879 and BNS 78-24499.

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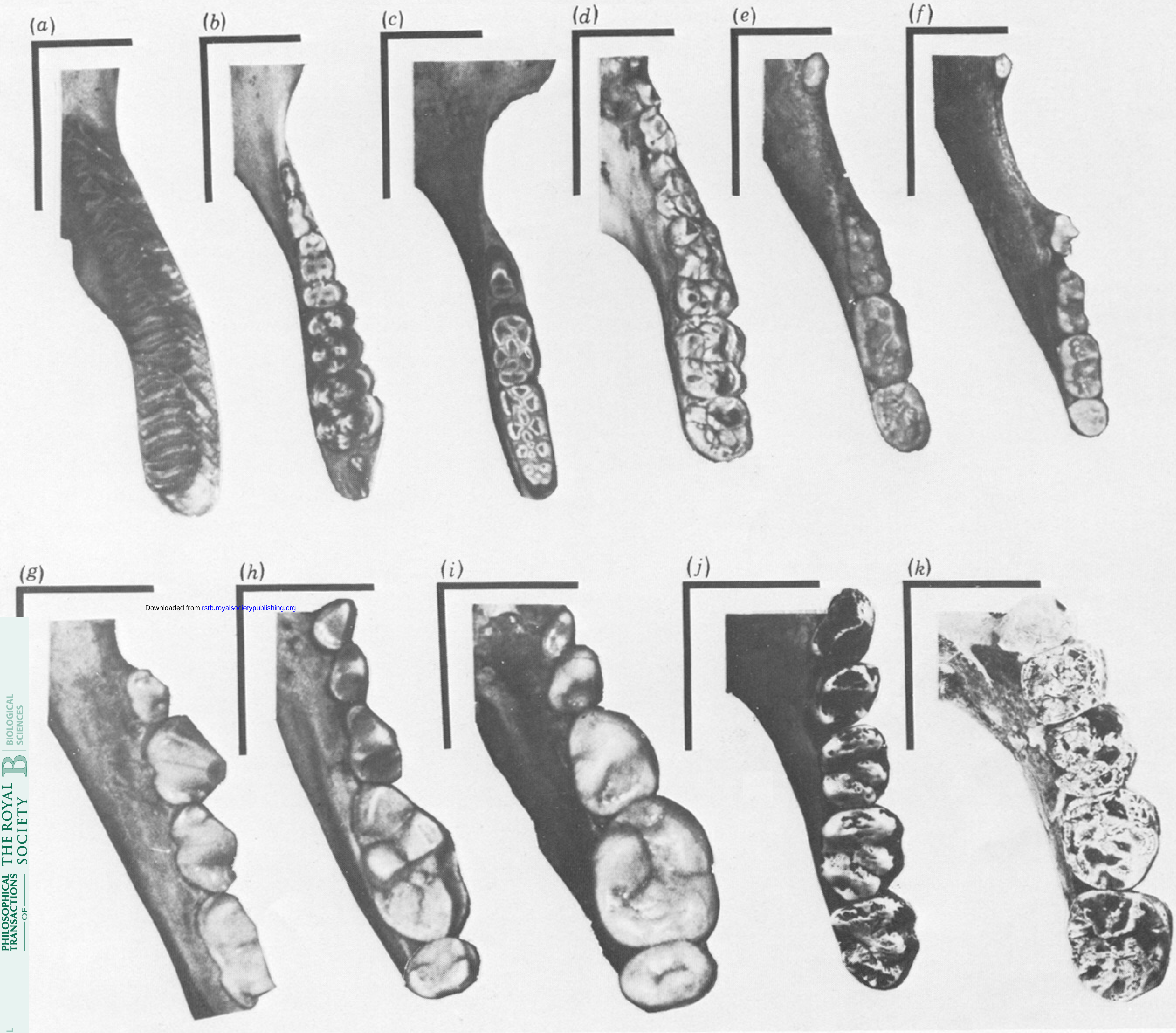

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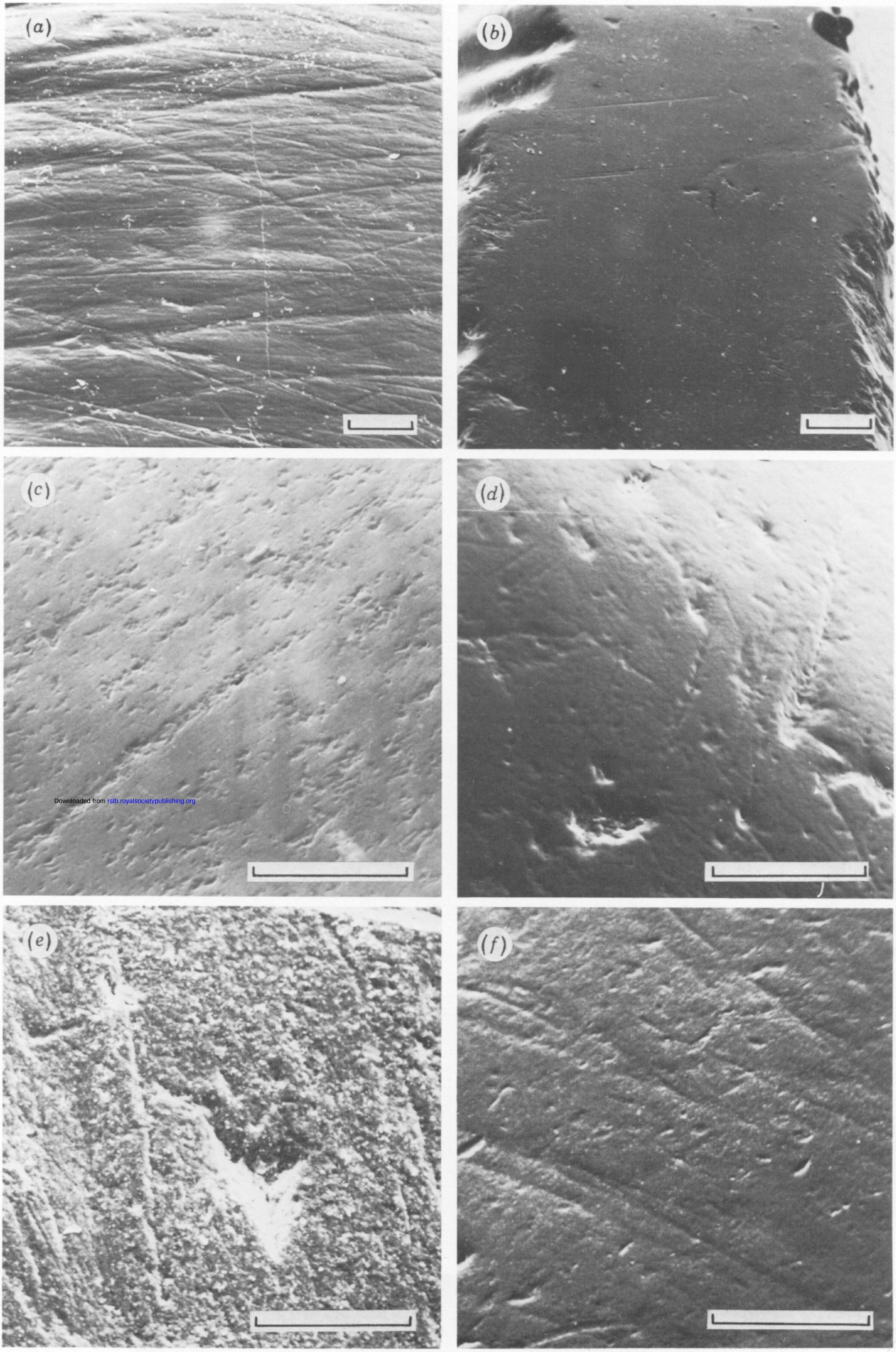

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