
Hominoid Dietary Evolution [and Discussion]

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Hominoid dietary evolution

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SUMMARY

During the later Palaeocene and early Miocene, catarrhine primates and the evolving hominoids had adaptations for frugivorous diets, with the emphasis on soft foods. Early in the middle Miocene the hominoids underwent a major shift, both in morphology and in habitat, with the morphology characterized by thickened enamel on the molars, enlarged incisors and massive jaws. The diet indicated by this morphology is interpreted as still mainly frugivorous but with changed emphasis, possibly towards harder objects. The thick-enamelled hominoids are found associated with more open forest habitats, and the distribution of food resources in equivalent habitats today is discontinuous both in time and in space, leading to evolutionary pressures particularly affecting locomotion, brain size and social behaviour. The earliest known hominid fossils differed little in dental and mandibular morphology from the middle Miocene apes, and the implied dietary similarity, together with ape-like patterns of dental development and retained arboreal adaptations of the postcrania, suggests little change in the foraging strategies of the earliest hominids compared with their ape ancestors and further suggests similarity in evolutionary grade. This similarity may have extended to other aspects of behaviour, for example to patterns of tool making and use, which may have been similar in the common ancestor of apes and humans to the pattern shared by the earliest australopithecines and chimpanzees.

1. INTRODUCTION

Hominoid primates are known from the Miocene to the Present. Relationships among extant hominoids are resolved with some degree of certainty, but the timing and location of most evolutionary events leading to the living apes and humans are not known precisely. We are taking as a starting point the phylogeny that we have formulated in a series of earlier papers (Andrews 1978, 1985; Martin 1983, 1985; Martin & Andrews 1984; Andrews & Martin 1987*a, b*). The phylogeny shown in simplified form in figure 1 is based on two sources of evidence: the branching pattern of the extant hominoids, giving their evolutionary relationships, was first established by reference to recent taxa only; the timing of the evolutionary events, and the fine detail of morphological change, was then interpreted by fitting fossil hominoids into the pattern already established. We propose to follow the same model in interpreting the nature of dietary change in the course of hominoid evolution.

By necessity we will be using adaptationist models for inference of diet, as morphology provides the only positive source of dietary information for fossil animals by analogy with the morphology–diet correlations observed in living primates. In this regard, however, it is important to distinguish what might be called primary adaptation from heritage characters, the former being a direct response to environmental conditions, improving the fitness of individuals relative to others lacking the adaptation, whereas the latter are retained unchanged from an ancestor, and may not be

directly linked with changing diet. This distinction may be important in interpreting morphological change in fossil apes, although it has been found that living ape morphology is more closely linked to dietary function than to phylogenetic history (Hartman 1988).

Morphology provides our principal source of evidence from fossils, although palaeoecology and dental microwear are also important. All of these, however, reflect only the principal (and probably most recent) diet of the species in question, whether recent or fossil, and they cannot at present take account of elements that constitute minor parts of all hominoid diets (Ghiglieri 1987). By these criteria, it may be concluded that hominoid primates are a mainly frugivorous group (see Tutin *et al.*, this symposium), and this feeding category can be further subdivided into ‘hard’ and ‘soft’ groups: hard food includes seeds, nuts and unripe fruit, and may also include non-fruit items such as hard-carapaced insects; soft food includes ripe fruit and soft-bodied insects (Lucas & Luke 1984). Both categories can be distinguished from other food categories such as tough (leaves and animal flesh), or large and hard (bones).

2. MORPHOLOGICAL CORRELATES OF DIET

In most groups of mammals, dental morphology is correlated with diet at a general level. In this paper we provide evidence for enamel thickness for all stages of hominoid evolution (Martin 1983, 1985), and this will

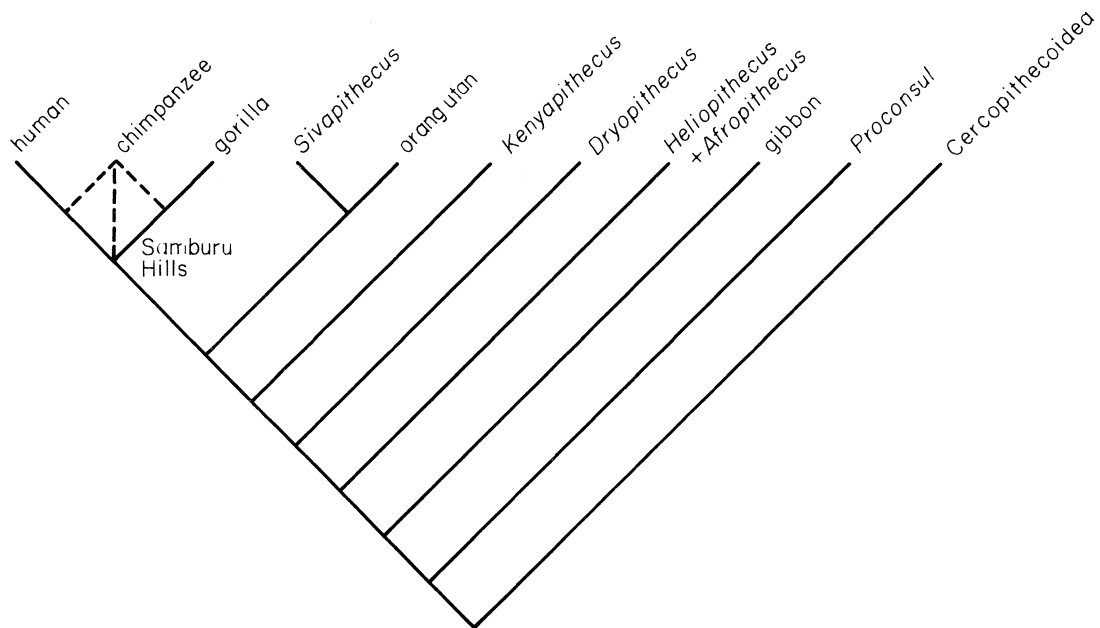


Figure 1. Cladogram showing relationships of fossil and recent hominoids.

be supplemented by other lines of evidence where available. Early work on enamel thickness based on worn teeth and natural breaks in teeth provided some insights into variations in enamel thickness (Kay 1981; Beynon & Wood 1986), but we base our present work on the physical sectioning of teeth and measuring the cross-sectional area of the enamel (Martin 1983). This area is divided by the length of the enamel–dentine junction to produce an average thickness, and further divided by the square root of the dentine area exposed in the same section to derive a size-standardized thickness. It might be argued that absolute thickness of enamel is the appropriate measure in relation to feeding studies, and we would agree if rates of tooth wear were being considered, but we maintain that relative enamel thickness is more useful for comparisons between animals differing in size, masticatory forces and longevity (Martin 1985).

Other lines of evidence, unfortunately still far from complete, are as follows.

1. Body size can be related to diet in a general way. There is progression upwards in size from insectivory in small animals to herbivory in large animals, with frugivory in between (Walker 1981; Andrews 1983). The largest living primate that has an insectivorous diet has a mass of no more than 250 g, and, in the animal kingdom as a whole, the few insectivorous species larger than this have developed highly specialized collecting strategies for diets of ants or termites. Conversely, the smallest living folivorous primate has a mass of 700 g, and, for energetic reasons relating to digestion times where cellulose is the main food source, most folivores are considerably larger.

2. Robusticity of the mandible is related to both diet and body size. The relation is complex, however, and regressions have been calculated separately both for the three main groups of higher primate and for males and females (Alcock 1984). Residuals from these lines were then calculated, but none were found to be significant at the 95% level.

3. Incisor size relative to body size (or its correlate, M1 size) is indicative of the type of food processing. Frugivores have relatively small molars and large incisors, whereas in folivores the proportions are reversed. The ratio of incisors to molars differs markedly, therefore, for the two dietary types.

4. Crown height and molar occlusal area are potentially important attributes of molar teeth, but little comparative information exists for primates. Australopithecines are said to be megadont, and large species have relatively larger teeth for their size than do smaller species, but this appears likely to be a unique character of this group and its significance is disputed (Kay 1985).

5. The lengths of the shearing crests on the occlusal surfaces of molars have been combined in a shearing quotient (Kay 1977; Maier 1984). Long shearing blades may be combined with high crowns and thin enamel, and this combination is characteristic of diets with high fibre content, such as folivory. In this morphology, advancing wear maintains or increases the shearing blades, whereas for thick-enamelled teeth with little cusp relief, advancing wear flattens the occlusal relief.

6. Patterns of microwear can be observed through differences in numbers and sizes of wear striations, as well as relative proportions of pits as opposed to striations (Walker *et al.* 1978). These patterns can be related to a number of dietary differences in living animals, such as browsing against grazing, forest against open-country herbivory, feeding on vertebrates against invertebrates (Teaford 1988). The patterns show a high degree of regularity, but non-dietary factors have also been found to influence them (Gordon 1982).

7. Some aspects of positional behaviour are closely associated with feeding. Below-branch arm hanging is part of a greater range of positional behaviour that has been observed in apes and is associated with small terminal branch feeding (Aiello 1981). Hand function

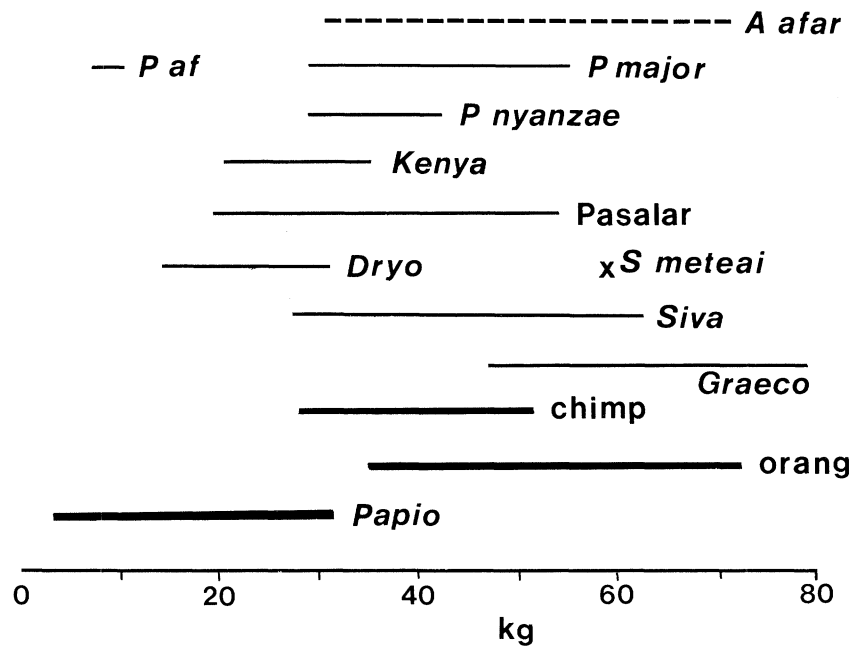


Figure 2. Body mass distributions of fossil and recent hominoids. Reading from the top, *Australopithecus afarensis*, *Proconsul africanus*, *P. major*, *P. nyanzae*, *Kenyapithecus africanus*, the sample of 'Sivapithecus' from Paşalar, *Dryopithecus fontani*, *Sivapithecus meteai*, *Sivapithecus sivalensis*, *Graecopithecus freybergi* from Greece (= '*Ouranopithecus macedoniensis*'), chimpanzee *Pan troglodytes*, orang utan *Pongo pygmaeus*, *Papio cynocephalus*. Body mass of recent taxa and *Proconsul* from Ruff *et al.* (1989), and the others calculated from the regression of M_3 on body mass; \log_{10} body mass = $2.86 \log M_2 \text{ length} + 1.37$.

and degree of manipulative ability are also important factors, and in apes this is closely related to thumb length (Marzke 1983). Manipulative ability is also a significant factor in the use of tools for food processing, and this needs to be considered not just for later hominoids but also for earlier stages of hominoid evolution.

3. EVOLUTIONARY TRENDS IN PRIMATE DIETS

Dietary interpretations will be reviewed chronologically, based on the results given in tables 1–3 and figures 1–4.

(a) Eocene and Oligocene

During much of the early stages of primate evolution, primates were small insect-eating animals. During the Eocene, some primates increased in body size, from an average of well below 1 kg in the early to early middle Eocene to an average slightly above 1 kg in the late Eocene and Oligocene, and at the same time there was a shift from primarily insectivorous diets in the early Eocene at about 50 Ma BP, to primarily frugivorous in the middle Eocene at about 45 Ma BP, to primarily herbivorous by the late Eocene 35–40 Ma BP (Hooker 1991). The Eocene to Oligocene primates of the Fayum showed a variety of diets (Kay & Simons 1980), and molar morphology and lack of shearing blades on the teeth of *Propithecus* and the other hominoid-like species known from the Fayum suggest soft-tissue diets, probably of fruit (Kay & Simons 1980). These taxa are

close to the ancestry of Old World monkeys and apes, that is, to the Catarrhini, and they show great morphological and functional similarity to the apes. It is likely, therefore, that the ancestral pattern for catarrhine diets was some form of soft-fruit frugivory.

(b) Early Miocene

Two groups will be discussed from early Miocene deposits, the *Proconsul* group dating from 18 to 20 Ma BP, and the *Afropithecus* and *Heliopithecus* group from 17 to 18 Ma BP. *Proconsul* is recognized as a stem hominoid (figure 1), part of the superfamily Hominoidea but not related to any one part of the monophyletic clade (Andrews 1985; Martin 1986). Most of the genera in this group of primates are associated with tropical rain forest habitats (Andrews *et al.* 1979). They were arboreal quadrupeds living in the upper canopies much like New World monkeys today (Napier & Davis 1959; Walker & Teaford 1989). The other group combines a different set of ancestral and uniquely derived characters that places it at the stem of the great ape and human clade – Hominidae of some authors (Andrews 1985) – but its ecological affinities are not clear. *Dryopithecus* appears to be a later European derivative of this group.

(i) *Proconsul* faunas. During the early part of the early Miocene in East Africa, there was an abundance of hominoid and hominoid-like primate species. At several sites there were five to six hominoid species commonly present (Andrews 1978; Harrison 1988) together with three to six non-hominoids, with a size distribution similar to African primate faunas today (Fleagle 1978).

Table 1. *Relative enamel thickness in fossil and recent hominoids*

taxon	$(c/e)/\sqrt{b}$	s.d.	<i>n</i>	category
<i>Proconsul africanus</i> ^c	8.54	—	1	thin
<i>Gorilla gorilla</i> ^a	10.04	1.74	17	thin
<i>Pan troglodytes</i> ^a	10.10	2.09	14	thin
<i>Hylobates lar</i> ^a	11.02	—	1	thin
<i>Dryopithecus fontani</i> ^c	12.74	—	1	int. thin
<i>Proconsul major</i> ^c	12.84	—	1	int. thin
<i>Oreopithecus bambolii</i> ^c	15.46	—	1	int. thick
<i>Pongo pygmaeus</i> ^a	15.93	2.51	17	int. thick
<i>Heliopithecus leakeyi</i> ^d	17.35	—	1	int. thick
Paşalar hominoids ^a	19.71	2.49	6	thick
<i>Sivapithecus</i> ^a	19.73	(3.33)	3	thick
<i>Australopithecus africanus</i> ^b	22.17	—	2	thick
<i>Homo</i> ^a <i>sapiens</i>	22.35	6.23	13	thick
<i>Graecopithecus freybergi</i> ^c	28.34	—	1	thick–hyper thick
<i>Paranthropus crassidens</i> ^b	29.61	—	1	hyper thick
<i>Paranthropus robustus</i> ^b	31.32	—	1	hyper thick
<i>Paranthropus boisei</i> ^b	34.91	—	2	hyper thick

^a Martin (1983).^b Grine & Martin (1988).^c New data.^d Andrews & Martin (1987*b*).Table 2. *Comparison of mesiodistal lengths of upper central incisors with first upper molars for recent and fossil hominoids (I^1/M^1); *n* is the sample size.*

taxon	mean	range	<i>n</i>
orang utan	1.13	0.95–1.22	16
chimpanzee	1.09	0.95–1.24	8
gorilla	0.90	0.84–0.96	12
<i>Proconsul</i>	0.93	0.90–0.98	3
<i>Afropithecus</i> ^a	0.98	—	1
<i>Sivapithecus</i> ^b	0.98	0.98–0.99	2
<i>Graecopithecus</i> ^c	0.84	0.82–0.87	2
<i>Dryopithecus</i>	0.81	—	1
<i>Australopithecus africanus</i> ^d	0.81	0.76–0.89	3
<i>A. afarensis</i> ^d	0.89	0.86–0.93	2
<i>Paranthropus boisei</i>	0.60	—	1

^a Leakey & Leakey (1986).^b Includes ‘*Ankarapithecus*’ (Martin & Andrews 1984).^c de Bonis *et al.* (1990).^d White (1977).

Enamel thickness data are reported here for the first time for *Proconsul africanus* and *P. major*. *P. africanus* has thin enamel (table 1), which is the inferred ancestral condition for the hominoid clade (Martin 1985; Andrews & Martin 1987*a*), while *P. major* has slightly thicker enamel. Incisor size (table 2) in most Miocene species is slightly larger than the condition interpreted as primitive for the Hominoidea (Andrews 1985). The I1 is also more spatulate, as in living hominoids, and both features are indicative of fruit processing. Shearing quotients are mostly low, suggesting non-fibrous diets (Kay 1977). They group around values for gibbons, chimpanzees and frugivorous New World monkeys, and some form of soft-fruit frugivory would therefore appear to be indicated for *Proconsul* species and *Limnopithecus*. *Rangwapithecus gordonii* has both more

cuspidate teeth and a higher shearing quotient than other early Miocene hominoids, and on these grounds it may be presumed to have been more folivorous.

The morphology of the hand in *Proconsul africanus* contrasts with the living apes in retaining a primitively longer thumb. It is approximately 50% of the length of the third digit, the same as in modern humans. The angle of the trapezium was at least as great as in chimpanzees (Napier & Davis 1959), so that, in combination with the longer thumb, the fossil ape may have had manipulative ability exceeding that of living apes. The combination of many primitive characters of the hand must make any functional inferences very tentative (Beard *et al.* 1986), but manipulative ability in the hand of *Proconsul* may have been closer to australopithecines than to extant apes.

(ii) *Afropithecus* faunas. Towards the end of the early Miocene there occurred a recently described group of hominoid primates from East Africa and the Arabian peninsula. *Afropithecus turkanensis* was a large species, with massive jaws and robustly built skull. It had enlarged incisors (table 2) and molars with low rounded cusps (Leakey & Leakey 1986). *Heliopithecus leakeyi* from Arabia is similar to it in both age and morphology, but is considerably smaller. The enamel is of intermediate thickness (Andrews & Martin 1987*b*), thicker than in the living African apes and *Proconsul*, and at the top end of the range for orang utans (table 1). The significance of thicker enamel will be discussed in the next section, but the combination of characters seen in *Afropithecus* and *Heliopithecus* leaves little doubt that fruits were a major part of their diet.

(c) *Middle Miocene*

Thick-enamelled hominoids, such as *Kenyapithecus* from East Africa and ‘*Sivapithecus*’ from Paşalar and

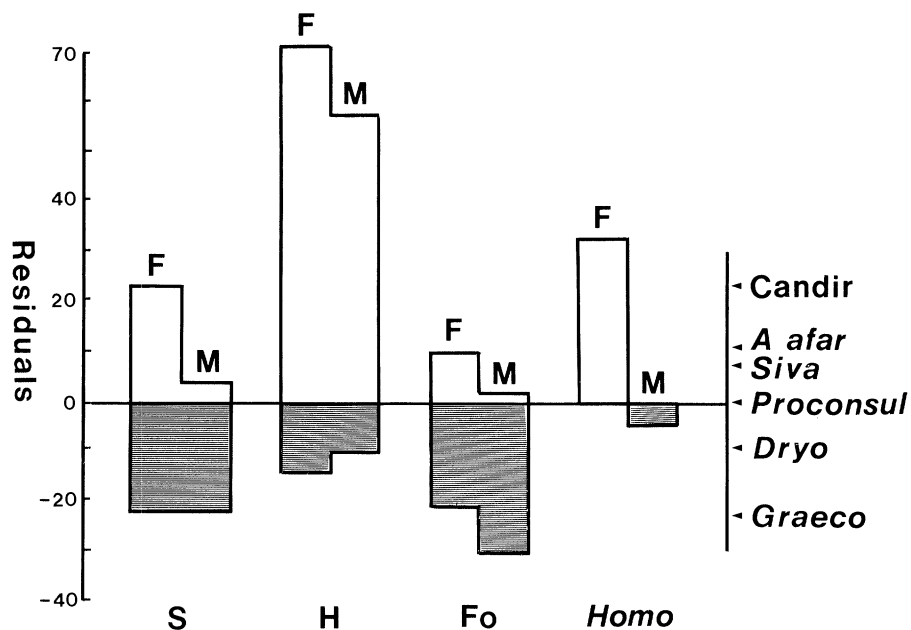


Figure 3. Mandibular robusticity based on residuals from the regression lines of horizontal section modules of the mandible on an estimate of body size – the area of the molar tooth row (Alcock 1984). Separate regressions were calculated for New World monkeys, Old World monkeys and hominoids. Results are for ‘*Sivapithecus*’ from Candir, *Australopithecus afarensis*, *Sivapithecus*, *Proconsul*, *Dryopithecus*, *Graecopithecus*; S, anthropoids with soft fruit diet; H, anthropoids with hard fruit diet; FO, anthropoids with folivorous diet; M, male; F, female.

Candir in Turkey, both dating to about 15 Ma BP, first appeared in the middle Miocene. They are seen as a continuation of the early Miocene trend towards thickening enamel initiated in the progression from *Proconsul* to *Afropithecus* and *Heliopithecus*. They were associated with more open habitats than were the early Miocene hominoids: tropical to subtropical deciduous forest is indicated for both (Andrews *et al.* 1979; Andrews 1990), with a strongly seasonal climate and hence seasonal supplies of fruit. Derived from this group are the sivapithecines, now seen as related to the orang utan clade (Andrews & Cronin 1982; Ward & Pilbeam 1983) and including, for our purposes here, the Greek genus *Graecopithecus* (Martin & Andrews 1984).

(i) *Kenyapithecus* faunas. The fossil hominoids from the middle Miocene of Kenya and Turkey are characterized by thick enamel on their molar teeth. Thick enamel can only be inferred for *Kenyapithecus* based on radiographs and broken teeth, but a sample of the Turkish teeth has been sectioned (table 1, figure 4). The set of characters shared by *Kenyapithecus* and the Turkish ‘*Sivapithecus*’ also includes molars with flattened occlusal surfaces, especially after some wear, robust but still single-cusped P_3 s, and robust maxillary and mandibular bodies (figure 3). The maxillary body is deep with wide separation between the alveolar border and the floor of the maxillary sinus, and the mandible has a massively elongated symphysis, much longer than deep (Alpagut *et al.* 1990). No associations are known of incisors with molars, but based on means of isolated teeth their size relative to the molars appears little different from that seen in *Proconsul*, but there is an indication that the upper central incisors are much larger than the laterals, a characteristic of the orang utan clade.

The postcranial remains of *Kenyapithecus* suggest generalized arboreal quadrupedalism in this genus (Rose 1983) of a type similar to that of *Proconsul* but with no exact parallel today. No hand bones are known.

(ii) Orang utan lineage. Thick enamel is present also in the hominoids that are phylogenetically linked with the orang utan, such as *Sivapithecus* and its included genus *Ramapithecus*. New data presented here suggest the presence of even thicker enamel in *Graecopithecus* (table 1). The presence of thick enamel at this stage would appear to be a retained character from a thick-enamelled ancestor of the middle Miocene of Kenya or Turkey, and thick enamel may have either retained its adaptive function in *Sivapithecus*, or be a heritage character whose function has changed. There is, however, some additional evidence for *Sivapithecus* from the microwear on the molars. The relative proportions of pits and scratches, as well as lengths and breadths of defects, on *Sivapithecus* molars match the soft-fruit pattern and is similar to that observed today in chimpanzees (Teaford & Walker 1984). It is significantly different (Teaford 1988) from the pattern observed in animals that eat hard fruit (which is the function assigned by Kay (1981) to thick enamel). Teaford & Walker (1984) conclude from this that the function of thick enamel is uncertain, but it is also possible that its function when it first evolved was, as Kay suggested, for grinding hard objects, but later hominoids changed diet to softer fruits as in chimpanzees without at first losing thick enamel. Study of the microwear of *Heliopithecus* or *Kenyapithecus* would help to resolve this issue.

The upper central incisors of *Sivapithecus* are robust teeth with massive lingual cingula. The same tooth in *Graecopithecus* is extremely low crowned (de Bonis *et al.*

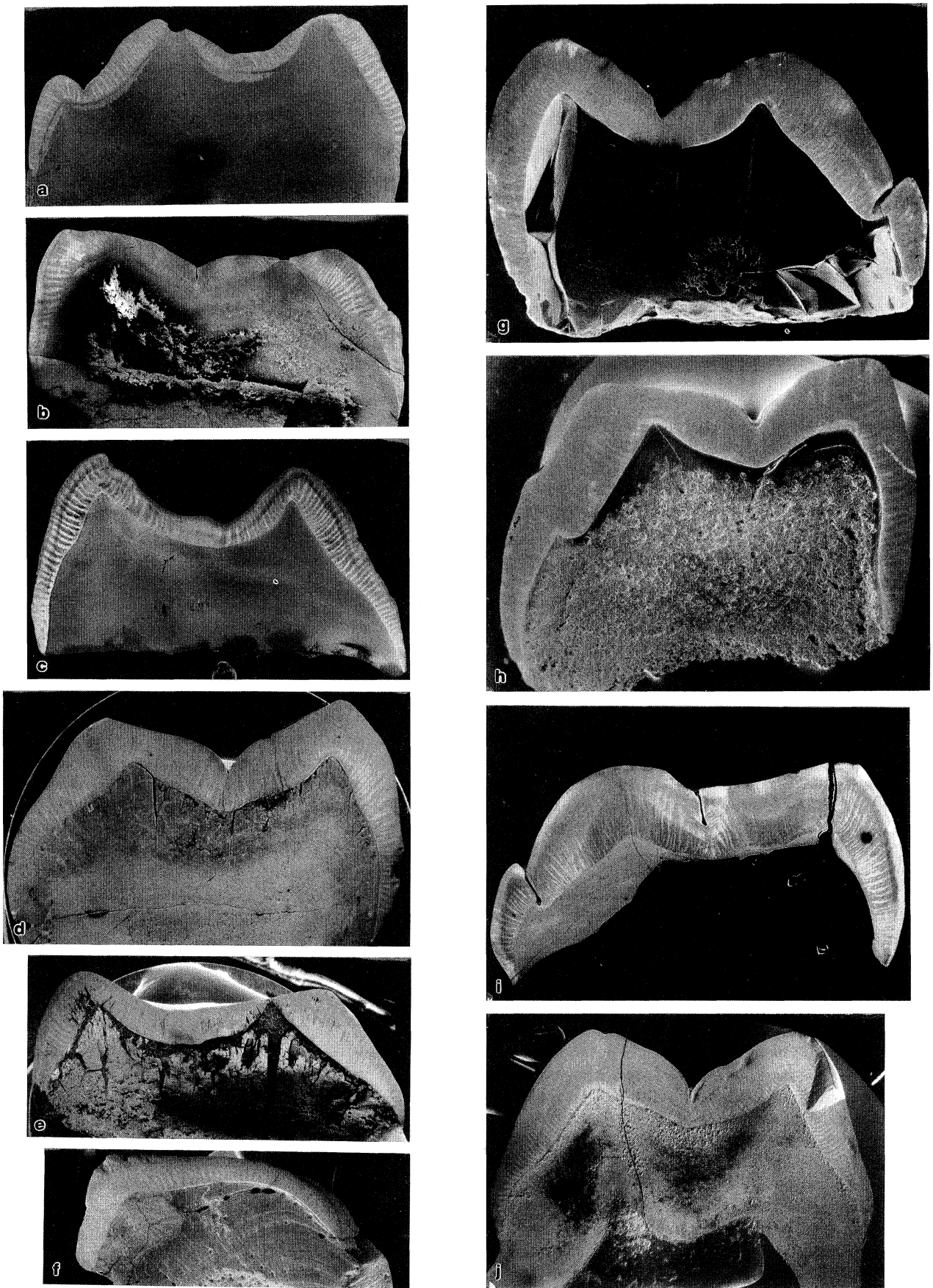


Figure 4. For description see opposite.

1990), and it is smaller relative to first molar length (table 1). In both cases the central incisor is very much larger than the lateral incisor, a specialization seen in living orang utans but not in any other group, living or fossil. Although it would appear to be an important adaptation for fruit processing, the differing proportions from all extant hominoids makes interpretation difficult. Postcranially, *Sivapithecus* was functionally similar to extant cebids, generalized quadrupedalism with a varied positional repertoire and none of the specializations of living apes or monkeys (Rose 1989).

(d) Late Miocene and Pliocene

Compared with the early stages of hominoid evolution, and in particular with the origin of the orang utan lineage, there is practically no fossil evidence for these periods. This is all the more regrettable in that it covers the time of human and African ape divergence (figure 1). Eleven fragmentary fossils are known prior to 4 Ma BP (Hill & Ward 1988), some of them probably pre-dating the splitting of the human lineage. Dental specimens retain thick molar enamel, judging from the external appearance of the teeth, but no measurements have been made. Thick enamel even appears to be characteristic of the Samburu Hills maxilla (Hill & Ward 1988), which we consider to be phylogenetically linked with the gorilla, and this is partial confirmation of Martin's (1983) prediction (Andrews & Martin 1987*a*) of thick-enamelled ancestry for the African apes. The mandibles from Tabarin and Lothagam, however, are probably early members of the hominid clade. They have low robust mandibular bodies (figure 3), and in size and morphology they closely resemble *Australopithecus afarensis* from Laetoli (White 1977).

A. afarensis has a pattern of microwear on the anterior teeth that has a combination of gorilla-like and unique features. Even when the P_3 is single-cusped and the canines high crowned and projecting, they are not used in the same way as in great apes to slice and shear food, but rather they function to puncture-crush food. Moreover, the presence of both polishing, and pitting and micro-flaking, on the incisors suggests food procurement from different sources (Ryan & Johanson

1989). The proportions of the incisors of *A. afarensis* appear primitive (table 2), and the molars appear to retain primitively thick enamel. There is no evidence from the molar or mandibular morphology of any major dietary change from the pattern observed in thick-enamelled apes during the preceding 10 Ma. Most interpretations of Laetoli and Hadar palaeoenvironments, where *A. afarensis* has been discovered, suggest either open savanna habitats (Leakey & Harris 1987) or more wooded habitats with seasonally deciduous woodland or forest (Andrews 1989). There are also indications that the hominids retained a considerable arboreal capacity (Stern & Susman 1983). Later species of australopithecine have extensive modifications of their teeth, particularly the robust australopithecines (Grine 1986; Kay & Grine 1988; Grine & Martin 1988), but these will not be discussed here.

4. HOMINOID DIETARY TRENDS

Several trends have become apparent from the foregoing descriptions of hominoid tooth morphology. The most notable of these was the increase in enamel thickness during the early to middle Miocene, coupled with the development of flattened molar occlusal morphology, and these were often accompanied by premolar enlargement and increase in mandibular robusticity, as seen in the sequence: *Proconsul-Heliopithecus-Kenyapithecus*. The dietary significance of these changes is far from certain, as the functional significance of thick enamel is still being debated. It has been claimed to be associated with terrestrial foraging (Jolly 1970) as an adaptation for hard abrasive foods found on the ground, but Kay (1981) rejected the terrestrial aspect of this idea, claiming that hard and brittle foods alone may have provided the selective impetus for thick enamel, regardless of where they occurred. Kay (1984) also found that enamel thickness varies inversely with shearing lengths, and as wear proceeds the occlusal surfaces of thick-enamelled teeth become smoothly rounded. Small but hard objects make up a large part of the diet of the orang utan, which also has moderately thick enamel, whereas the folivorous gorilla has the

Figure 4. Coronal sections through the mesial cusps of fossil hominoid molars. Block faces revealed by a wire saw cut through the mesial cusps in a coronal plane. Faces were oriented perpendicular to the incident electron beam in an AMR 1810 Scanning Electron Microscope and imaged using secondary electrons. The images in this plate have been printed to a magnification such that all of the teeth have approximately equal cervical diameters, i.e. the pictures are scaled to a constant tooth size rather than being printed at a uniform magnification. Fieldwidths are given separately for each image and are the width of the entire image field. (a) *Proconsul africanus* right M^1 (M 14081) mesial posterior face, fieldwidth = 8.62 mm. (b) *Proconsul major* left M_3 (M 32237) mesial anterior face, fieldwidth = 13.65 mm. (c) *Dryopithecus fontani* right M^1 (IPS 68) mesial anterior face, fieldwidth = 10.6 mm. (d) *Sivapithecus sivalensis* right M^1 (M 13366) mesial anterior face, fieldwidth = 12.94 mm. (e) *Sivapithecus punjabicus* left M_3 (M 13367) mesial anterior face, fieldwidth = 11.92 mm. (f) *Heliopithecus leakeyi* right M^3 (M 35146). Fracture face of the lateral paracone, which has been polished to smooth the rough, fractured surface. The fracture passes through the tip of the paracone, but runs somewhat obliquely relative to both coronal and sagittal planes so that the plane runs somewhat distally as it moves towards the cervix. Fieldwidth = 8.45 mm. (g) Paşalar hominoid right M_1 (BP 13) mesial anterior face, fieldwidth = 9.08 mm. (h) Paşalar hominoid left M_1 (BP 14) mesial anterior face, fieldwidth = 7.64 mm. (i) *Graecopithecus freybergi* right M_1 (RPL 641) mesial posterior face, fieldwidth = 16.59 mm. (j) *Australopithecus africanus* left M^2 (Stw 284) mesial anterior face, fieldwidth = 16.82 mm.

thinnest enamel and the longest shearing crests seen in extant apes (Kay 1977; Martin 1985). Similarly, with monkeys, the species with diets of hard fruit have the thickest enamel, whereas folivorous species have the thinnest enamel (Kay 1981, 1985).

The dietary category of ancestral catarrhines and earliest hominoids is widely interpreted as soft-fruit frugivory, and the trend towards increasing enamel thickness probably suggests a shift to hard-fruit frugivory rather than any substantive change in diet. The evidence of microwear on later Miocene thick-enamelled hominoids is most similar to that seen today on soft-fruit eaters (Teaford & Walker 1984), which suggests no change from their thin-enamelled ancestors, but no work has yet been done on such fossils as *Heliopithecus* and *Kenya-pithecus* where the trend of increasing enamel thickness is first observed. Diets of the later sivapithecines may have changed, as indicated by the microwear, without apparent change of the enamel, and it is on the teeth of the fossil hominoids where thick enamel is first observed that the significance of thick enamel is most likely to be understood.

Another interpretation of thick enamel is that it was an adaptation for a more varied diet. This would have been the product of increasingly seasonal climates and habitats, the seasonality being in part the result of topographic change within the tropics, producing more open and seasonally varied habitats at *Kenya-pithecus* localities such as Fort Ternan and Maboko Islands (Andrews *et al.* 1979), and in part latitudinal, as hominoids spread northwards beyond the tropics (Andrews 1990). Chimpanzees living today in seasonal habitats have been observed to have more varied diets than forest chimpanzees (Collins & McGrew 1988), and during the dry season they eat dry fruits, hard seeds and hard-shelled fruits. Even so, they are restricted to areas of mosaic habitat, depending on locally wetter areas, such as gallery forest, during the dry season. They occur at lower population densities, and they move about their enlarged home ranges to a greater extent; here their increased body size is an advantage, giving them greater mobility and the capacity to feed on larger food items than possibly competing cercopithecoid monkeys (Wrangham 1980; Andrews 1981). In this scenario, thick enamel is coupled with increased body size in seasonal mosaic habitats.

A further possibility is that thick enamel did not evolve in response to dietary shifts at all but was co-opted for diet after its appearance (Martin 1983). Developmentally the increase in thickness during the early to middle Miocene appears to be the result of a lengthened period of enamel accretion, which may reflect a grade shift in general body growth between thin-enamelled ancestral hominoids and later thick-enamelled species (Martin 1983). Such a fundamental reorganization is unlikely to have been the result of dietary pressures alone, for its ramifications for systems other than the dentition are considerable (Martin 1983).

Thick enamel appears to have been retained in the ancestors of both the orang utan and the hominid

clades. After the branching of the orang utan clade, the limited fossil evidence available indicates retention of the thick enamel and robust jaw adaptations in the ancestors of the African ape and human clade. The early australopithecines maintained this ancestral pattern, with the inference of no dietary change from ape ancestors, despite the evidence for increasingly seasonal habitats associated with hominid fossils. This conclusion is supported by microwear studies (Grine 1986), and similar conclusions emerge from other lines of inquiry, for example the retained adaptations for ape-like arboreality in the postcrania of *A. afarensis* (Stern & Susman 1983) and the short developmental period of tooth crown formation in australopithecines, again a retained ape characteristic (Beynon & Dean 1988).

The lack of morphological change in the teeth and jaws of the earliest hominids suggests that the dietary heritage from thick-enamelled apes was sufficient for dietary needs during the early stages of human evolution. Subsequently, divergence within the australopithecines occurred, with further change leading to the genus *Homo*, and the manufacture and use of tools both made possible the expansion of human diet into areas not possible for our ape ancestors and brought about the reduction of certain physical attributes no longer needed for food preparation, for example, reduction in tooth size and robusticity and bodily strength. It is reasonable to ask, however, if the earliest hominids used or made tools, and if so, were they different in these respects from their ape ancestors.

Chimpanzees have a great breadth of intelligence and culture, and their use of tools parallels that of early hominids (McGrew 1987; Wynn & McGrew 1989). These authors demonstrated high levels of similarity between chimpanzee technology and the early hominid Oldowan industry, with tool use and manufacture function-related to particular tasks in both chimpanzees and early hominids. Both select appropriate raw materials for making tools, and they make the tools opportunistically without a pre-conceived plan other than to produce a shape or cutting edge that will perform the task in hand. Two differences between apes and the makers of the Oldowan industry, however, are that apes do not use stone for tool manufacture, and they do not use tools to make tools. It is also possible that the hominids used tools in a more sophisticated way, for instance in meat processing (Potts 1988) and even more significantly for obtaining meat during hunting (Wynn & McGrew 1989), with subsequent changes in food processing and diet.

The use of space, in the sense of food preparation areas, is also similar in chimpanzees and early hominids (Potts 1988). Potts shows that the artifact accumulations of early hominids at Olduvai do not represent home bases or workshops but were areas to which both animal remains and raw material for stone tools were transported. He compares this with the transport of nuts and hammer stones to suitable anvils by chimpanzees, or alternatively an anvil and hammer stones carried to the source of nuts (references in Potts (1988)). Both require forward planning, and the only difference from the archaeological situation is the distance the

objects are carried, up to 500 m in the case of the chimpanzees and 2–10 km for the hominids.

Because of these characteristics shared by hominids and their nearest ape relatives, it is very likely that they were also present in the common ancestor of apes and humans in the Miocene. There is no preserved cultural record from this far back in time, but neither is there any cultural record from the time of the earliest hominids. It would be surprising, however, if *Australopithecus afarensis* had not achieved at least the degree of tool use and manufacture of chimpanzees, and there is every reason to expect that the common ancestor of humans and chimpanzees had done likewise. The material used, however, would have been biodegradable tissues rather than stone, and to detect their presence we must look to indications from behaviour and morphology of the fossil hominoids.

There are a number of indications from such factors as body size, brain size and morphology, diet, manipulative ability and foraging strategy to provide some insights into the potential for tool use in early hominoids. Larger species are normally dominant over smaller species, have greater control over their environment, are more mobile, and have longer periods of gestation and infancy. As a result, family units may persist longer, and there is a general increase in social behaviour. Larger species also have absolutely larger brains and longer periods of maternal dependence and life spans during which to acquire learned behaviour. Being large also entails an increase in the absolute amount of food needed and a larger supplying area to provide it, and the latter is related to an increase in comparative brain size (cbs (Clutton-Brock & Harvey 1980)). Home range size is also related to the dispersal of resources within it, being necessarily larger when resources are more widely dispersed (Macdonald 1983).

Fruit is a discontinuous resource, both in space and in time (Milton 1988), and being more widely dispersed in the environment than are leaves or grass, frugivores (and predators) tend to have larger home ranges and therefore larger brains (relative to body size) than do folivores and grazers (Clutton-Brock & Harvey 1980). Fruit is also a predictable resource in that fruiting occurs regularly from one year to the next, and this leads to an emphasis on learning and memory together with greater flexibility of behaviour (Milton 1988). It is proposed by Milton, therefore, that larger brains, and by implication greater intelligence, arose initially as a dietary response rather than to facilitate social relations. Many of the thick-enamelled hominoids were large-bodied frugivores close to the ancestry of the great ape and human lineages, and it is likely that they had relatively large brain sizes. Brain size has been calculated for *Proconsul* as 167 cm³ with a cbs of 48.8% (Walker *et al.* 1983): this is comparable to chimpanzees and to australopithecines (Aiello & Dean 1990) but higher than gorillas and monkeys.

Proconsul also provides evidence of possibly high manipulative ability, having a long and opposable thumb. Variety of grip was probably greater than is present today in tool-using and tool-making chimpanzees. A detailed comparison with the hand of *A.*

afarensis would be of interest, for there appear to be considerable functional similarities. In other respects also, australopithecines show little or no change from fossil apes in brain size, dental development, type of diet, overall body size or even, perhaps, in cultural development and tool use, and as a result it may be concluded that they were the same evolutionary grade as the Miocene (and recent) apes. Subsequent brain enlargement, dental reduction and changes in the gut proportions in the genus *Homo* (Milton 1988) suggest a higher quality diet and food processing, which may be the result of increasingly sophisticated use of tools.

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Discussion

L. AIELLO (*University College, London, U.K.*). Do the australopithecines have any hominid adaptations other than bipedalism, and are they in fact just bipedal apes?

P. ANDREWS. Traditionally, hominids have been defined on the basis of three characters: large brains, changes in the teeth, and bipedal locomotion. Recent work has shown that australopithecines are no more encephalized than are some of the apes, for example chimpanzees, and one school of thought also claims that brain structure and complexity are also similar, although there is still some dispute over this. It is shown here that the functional adaptation of the main battery of chewing teeth is essentially unchanged in the early australopithecines from their ape ancestors, although the later australopithecines show some modi-

fications to this pattern, such as the enlargement of the molars and the development of two-cusped third premolars. The incisors of most australopithecines also show no reduction from the ancestral ape condition. We are left, therefore, with bipedalism as the only definitive hominid adaptation, although even here recent work has shown that early australopithecines retain such ape features as shortened hind-limbs and long curved phalanges. It is very likely that the actual appearance of the early australopithecines was ape-like, their manner of life, social grouping and diet also being ape-like, and even their level of intelligence and use of tools was no greater than that of apes, so that the only thing that distinguished the earliest hominids from contemporary species of the ape was their ability to walk or run on two feet instead of four.

A. E. SCANDRETT (*184 Granby Court, Denbigh, Milton Keynes, U.K.*). Does the enamel thickness of incisors and canines correlate with that of the molars?

P. ANDREWS. The authors have not sectioned any incisors or canines, and so have no information on how enamel thickness correlates with that of the molars. It would appear unlikely that there is a strong correlation, as the function of the anterior teeth is different from molar function.

A. E. SCANDRETT. Which teeth were studied to provide data on molar enamel thickness?

P. ANDREWS. Sample sizes for the three lower molars and the three upper molars were as follows: gorilla, 18 teeth sectioned buccolingually, 6 teeth sectioned mesiodistally; chimpanzee, 16 teeth sectioned buccolingually, 5 teeth sectioned mesiodistally; orang utan, 18 teeth sectioned buccolingually, 6 teeth sectioned mesiodistally; humans, 17 teeth sectioned buccolingually, 7 teeth sectioned mesiodistally; fossil hominoids, 17 teeth sectioned buccolingually. For any one tooth for any one species, the usual sample size was four specimens, but for the upper and lower third molars of chimpanzees the sample sizes were two and three respectively.

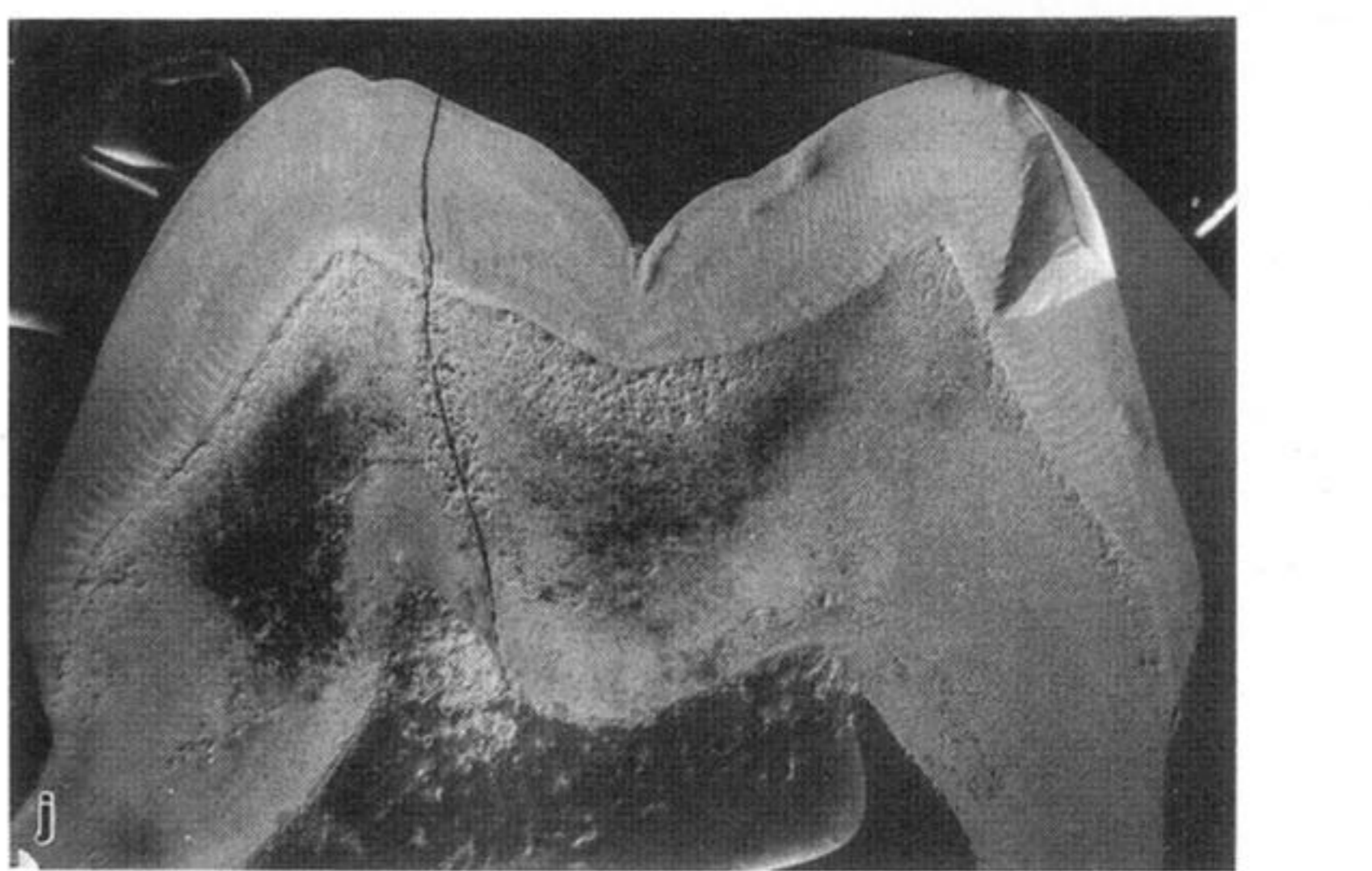
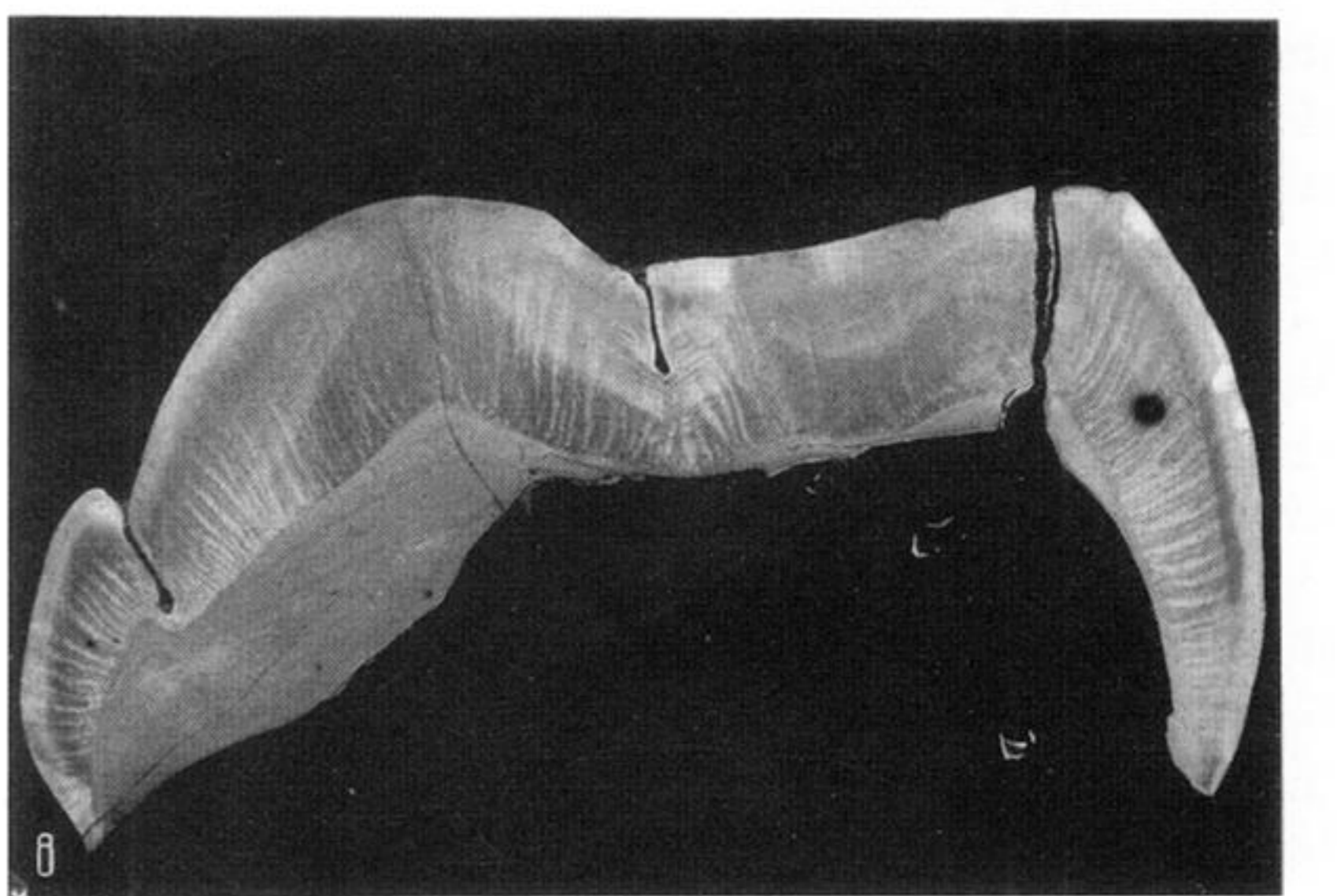
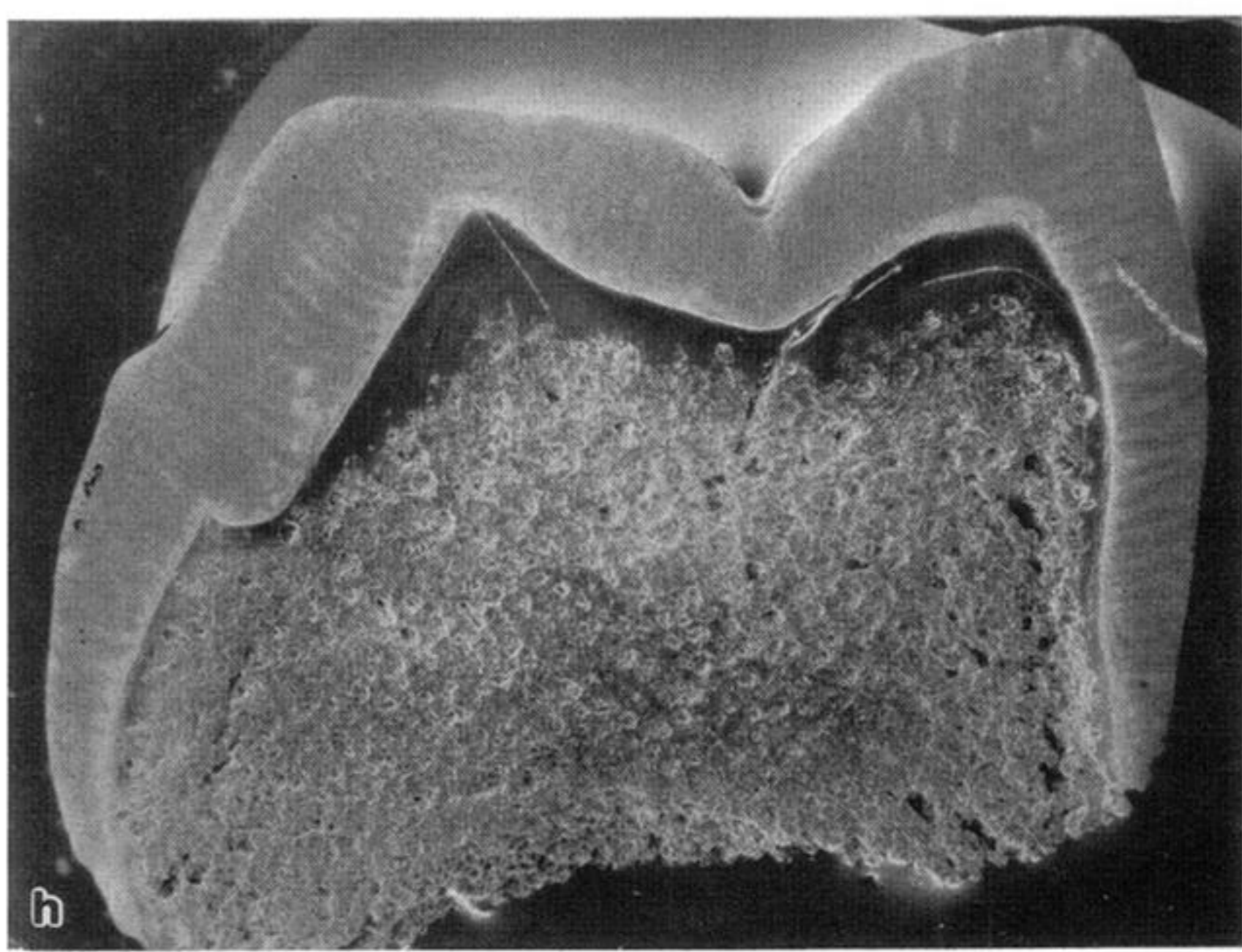
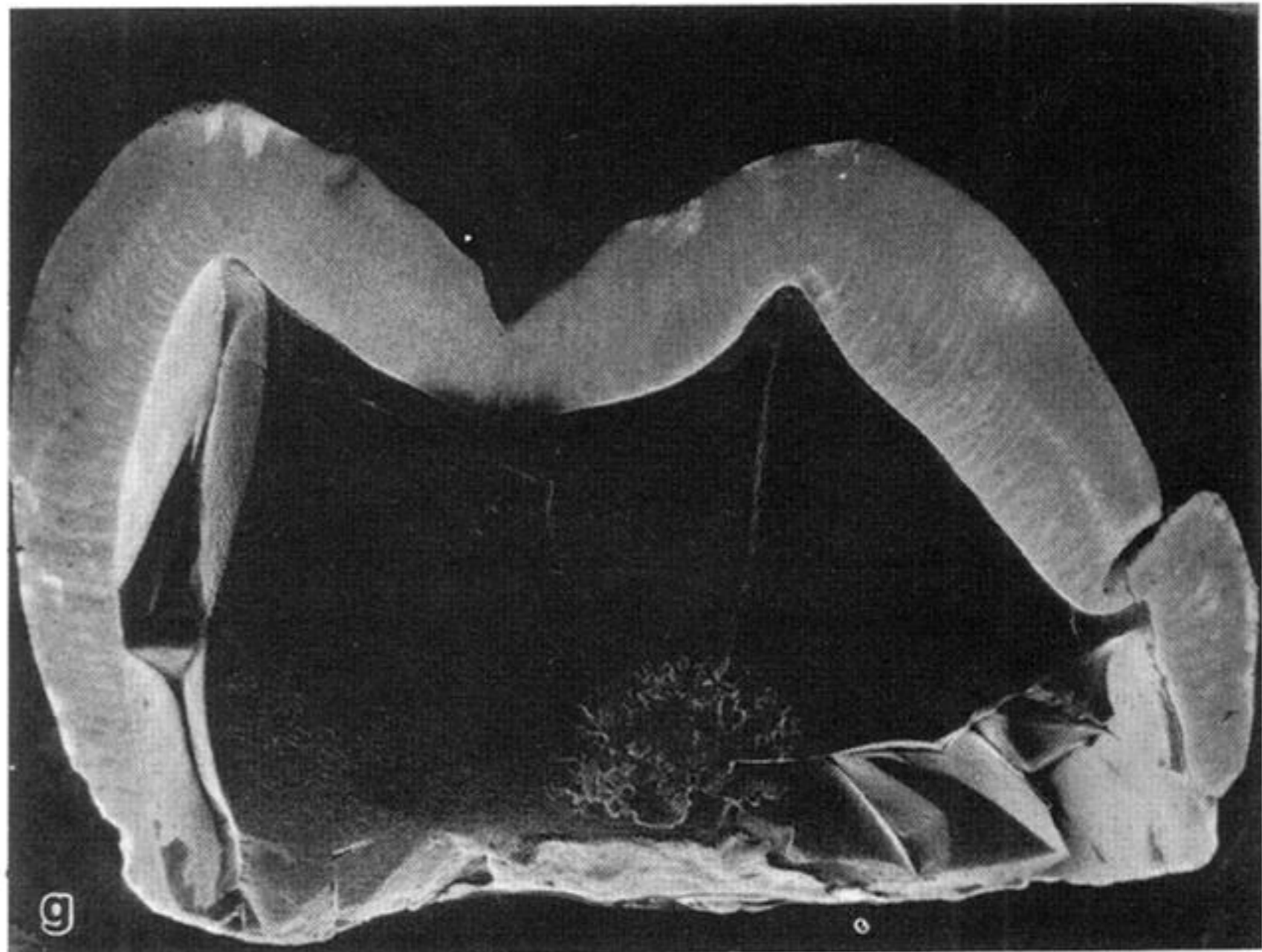
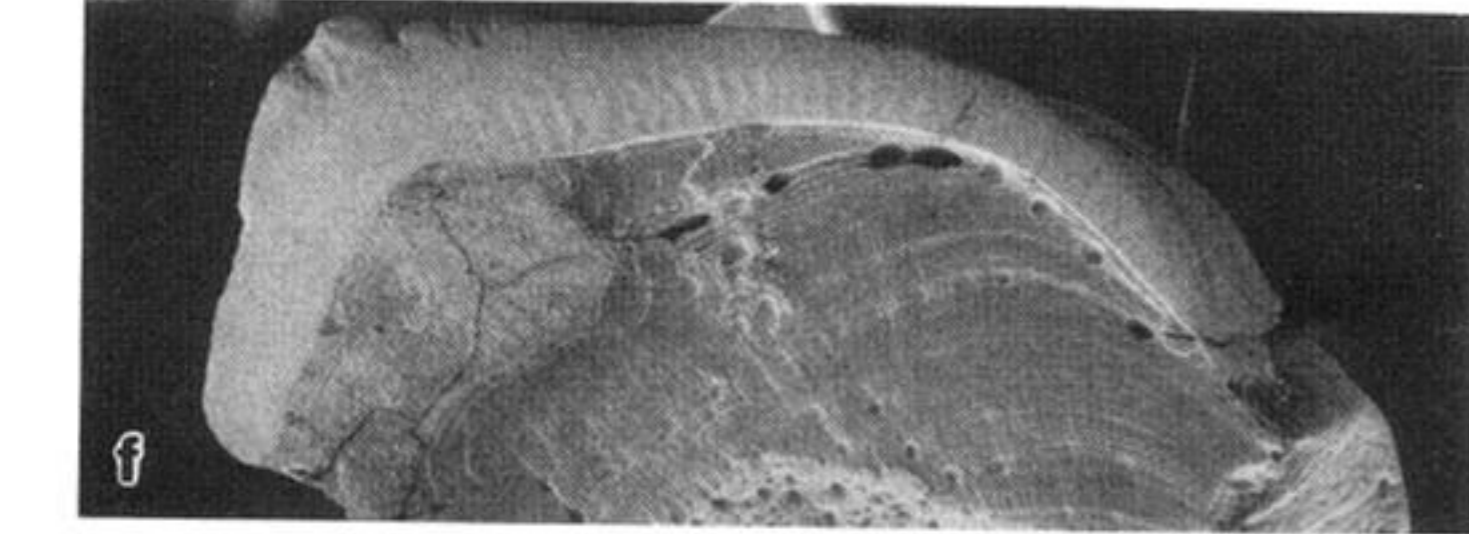
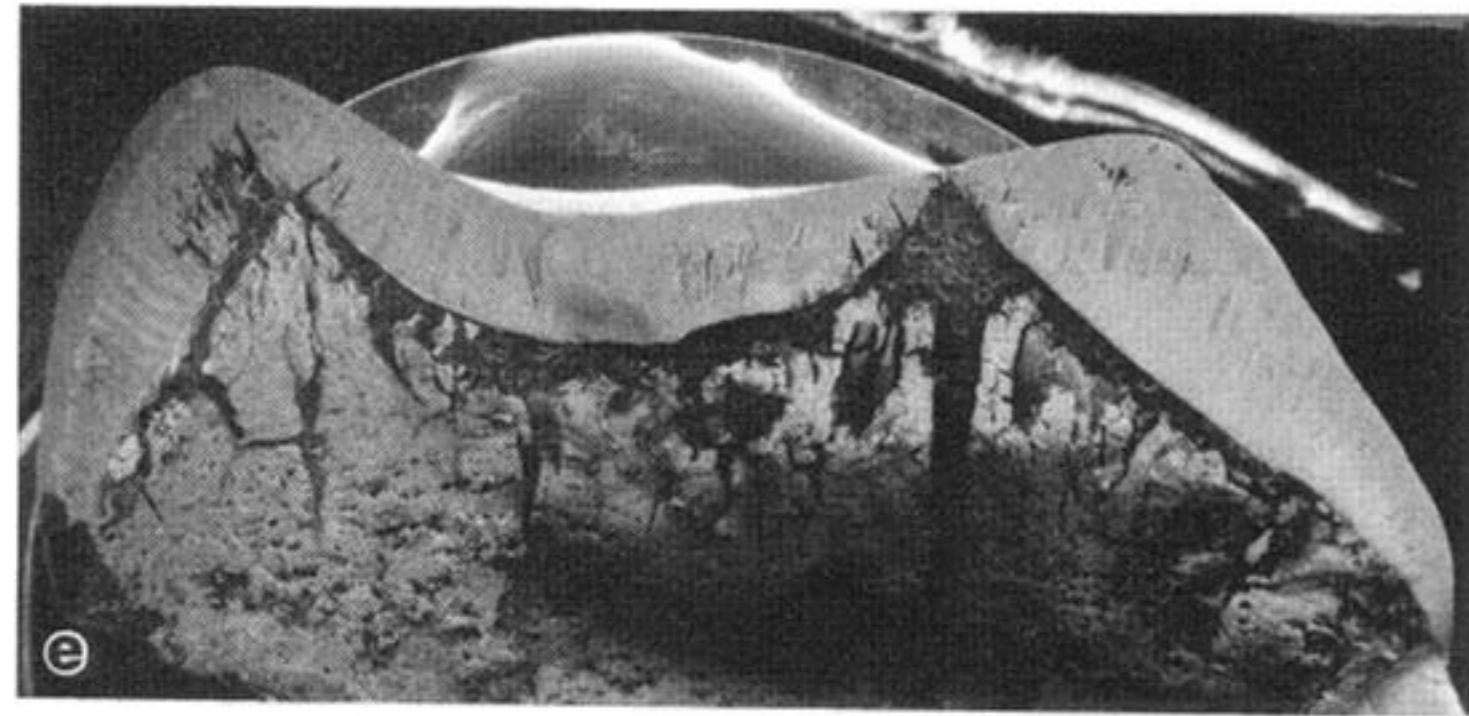
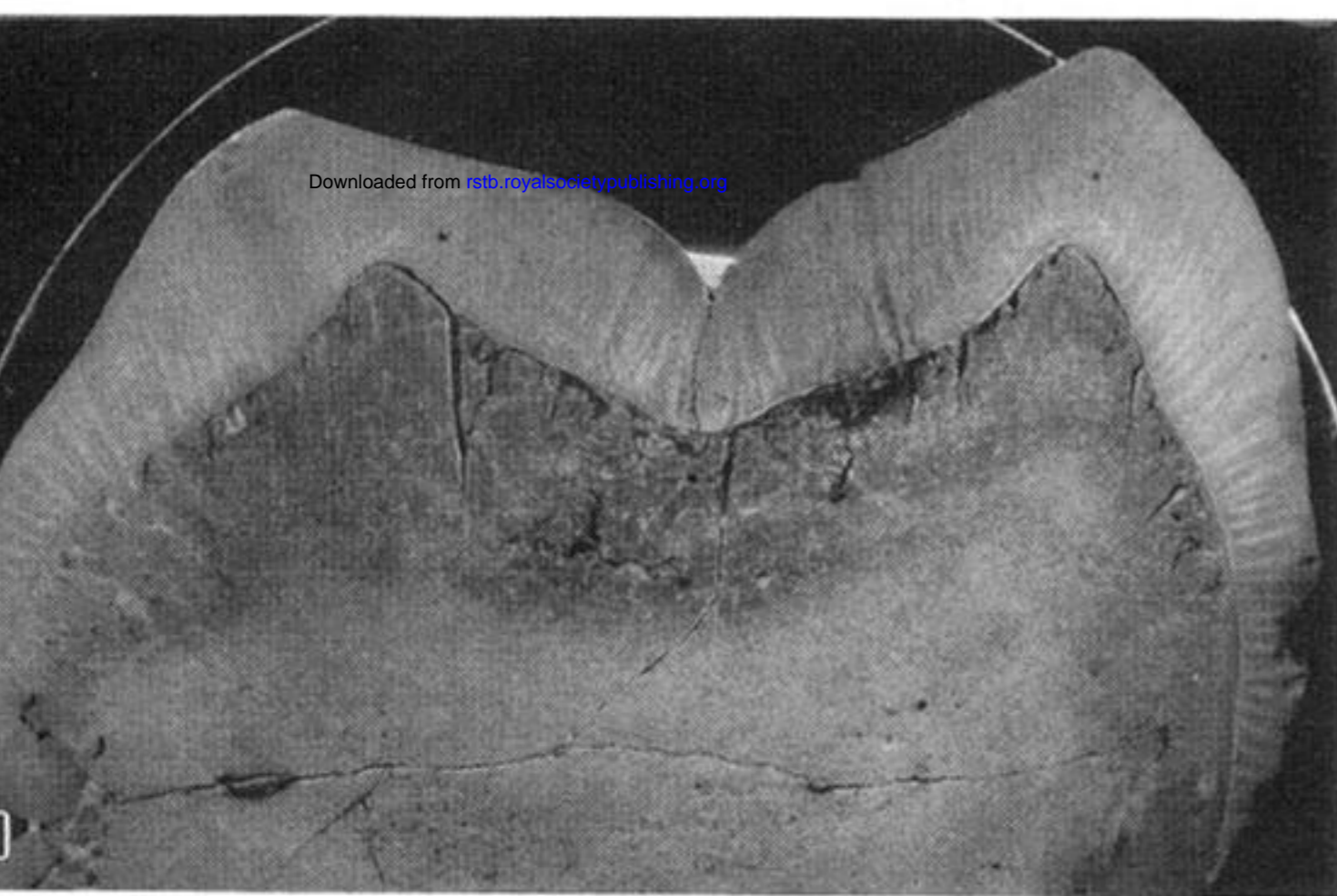
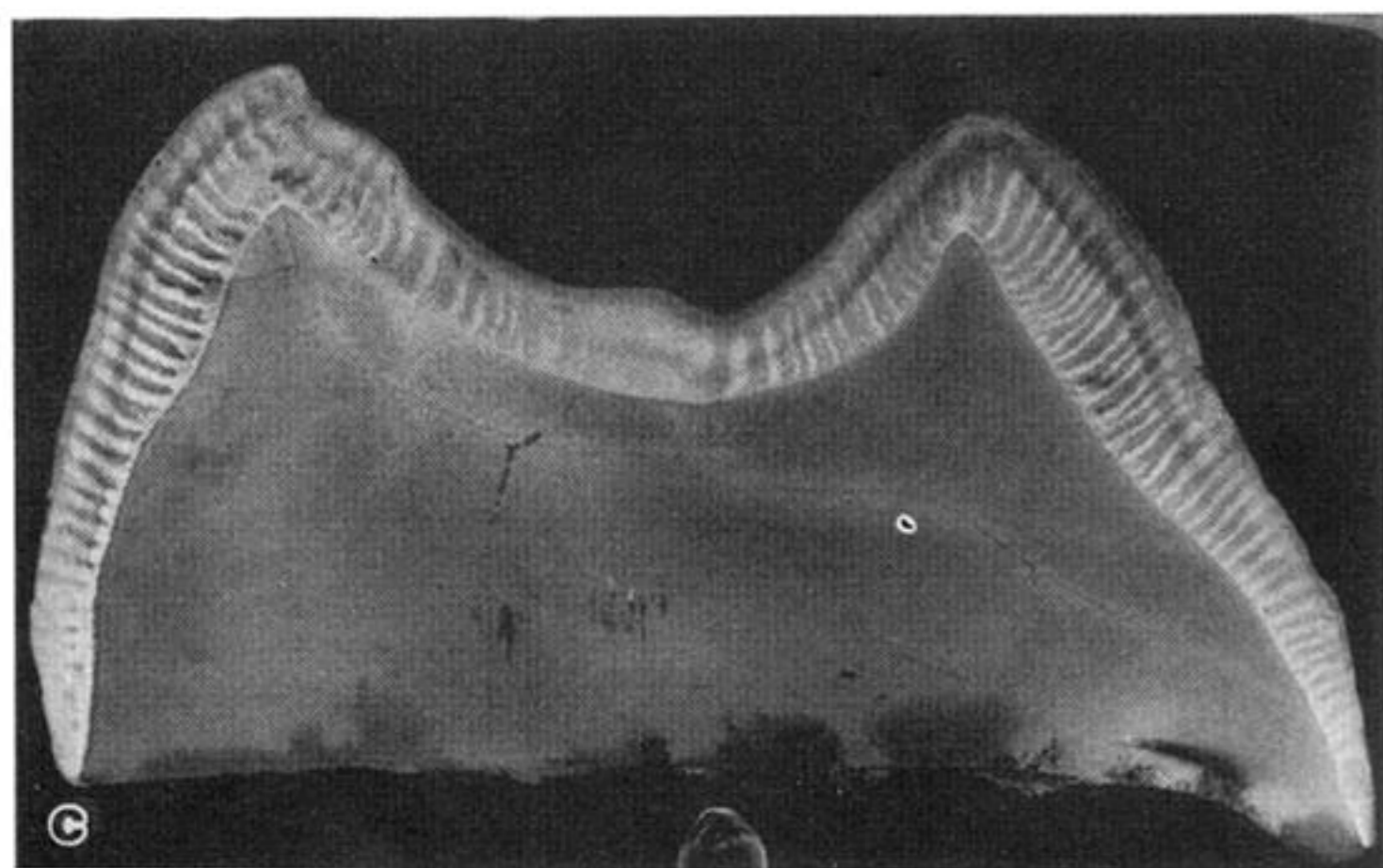
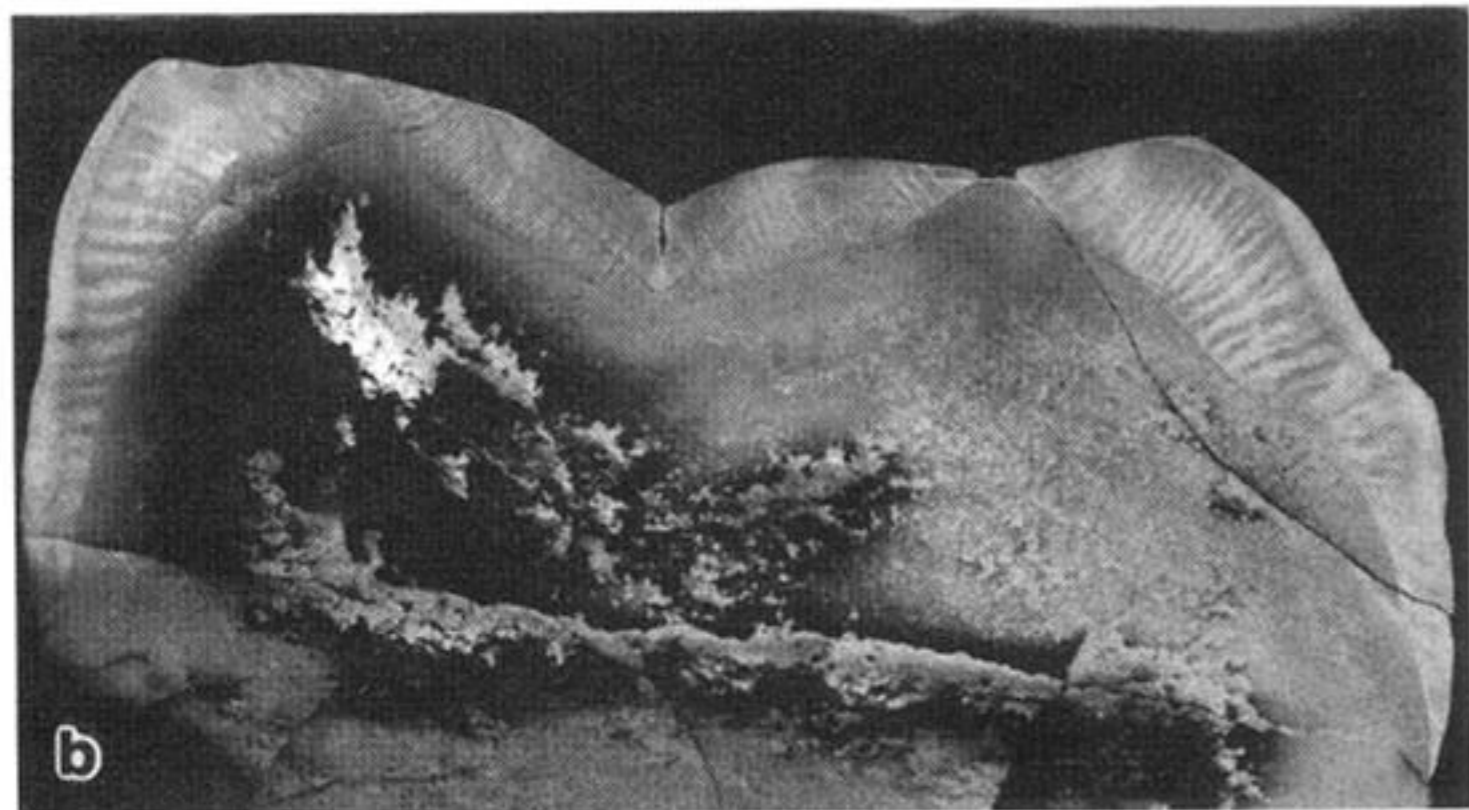
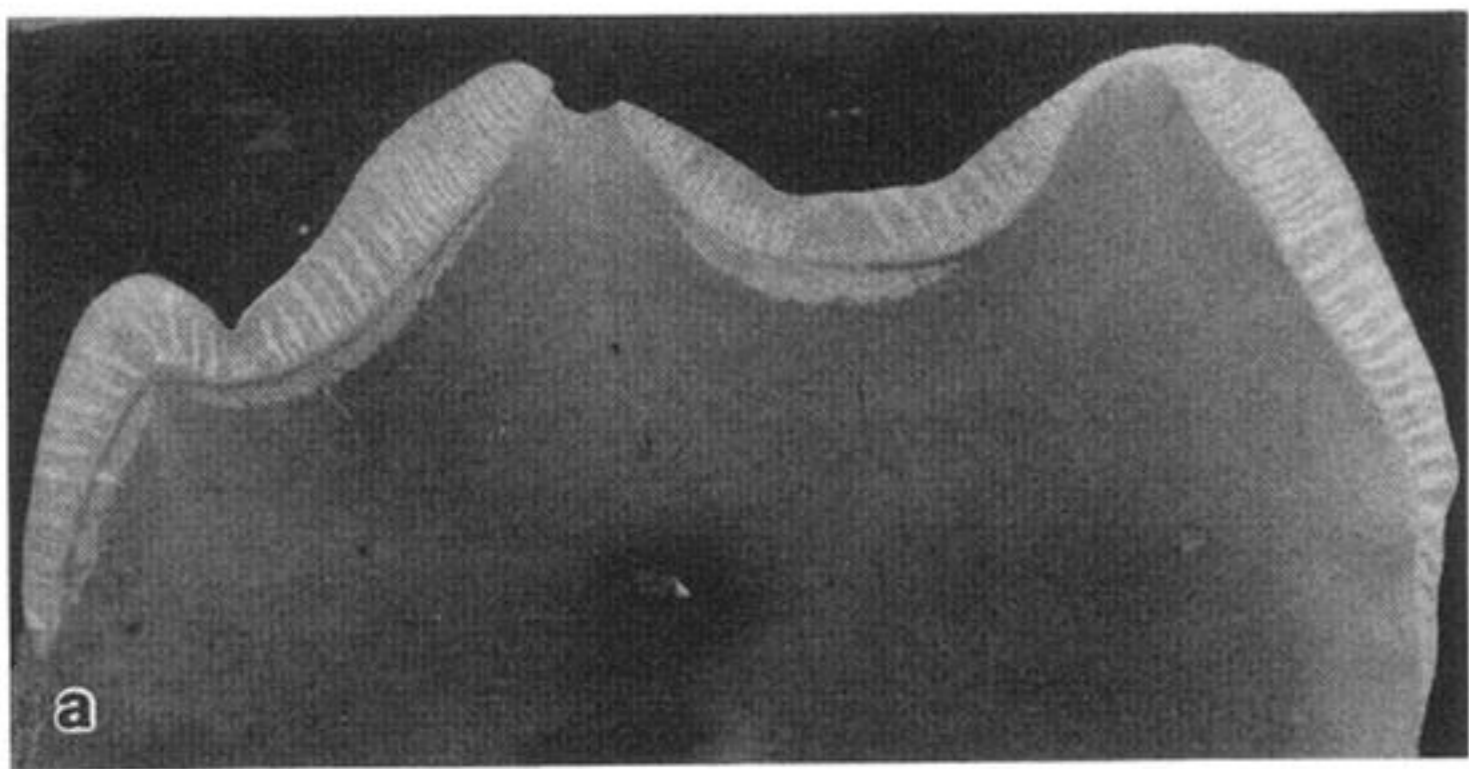


Figure 4. For description see opposite.