DENTAL MICROWEAR AND DIET IN *GRIPHOPITHECUS ALPANI.*

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ABSTRACT

Examination of microscopic wear marks on the surface of teeth (dental microwear) provides information about the main components of an animal's diet. Inferences can be made about the diet of extinct species by comparing the dental microwear patterns of fossil samples with those of present-day groups whose diet is known. This thesis examines the dental microwear of *Griphopithecus alpani*, a 15 Ma fossil hominoid from the Miocene site of Pasalar in north-western Turkey. The microwear patterns of *G. alpani* are compared to three extant hominoid taxa - *Gorilla gorilla gorilla*, *Pan troglodytes verus*, and *Pongo pygmaeus pygmaeus.*

Results indicate that there is no close dietary analogue to the fossil hominoids among the extant groups. However, the analysis suggests that the diet of *Griphopithecus alpani* was more similar to that of *Pongo*, which consumes mainly fruit and the occasionally hard and unripe fruits and nuts, than to the other living hominoids examined in this study. The high percentages of pits displayed by *G. alpani* indicate that it was ingesting harder fruits and/or objects than the extant hominoids, and it is similar in this respect to *Graecopithecus freybergi*, a Miocene hominoid from Greece. There were consistent variations in microwear patterns between the different facets examined in this study. The results of this study do not indicate variation in dental microwear according to sex or age.

Experiments were carried out to investigate the effects of taphonomic agents, such as exposure to acids or abrasion by sediment, on dental microwear. Results indicate that post-mortem processes can be readily identified. This study also develops a procedure and software for the correction of foreshortened microwear features. Feature types and dimensions may vary before and after correction, but frequencies of features do not differ.

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CHAPTER 1: INTRODUCTION

Knowledge of an animal's diet allows inferences to be made about its environment, ecological niche, biology and behaviour. During the past twenty years dental microwear analysis has been developed for the examination of diet in extinct and extant species (see Gordon, 1988; Teaford, 1988, 1991, and 1994 for reviews). Dental microwear analysis rests on the principle that mastication leaves microscopic wear marks on teeth. These wear patterns can be quantified and used to make dietary inferences about fossil species. The work presented here is a study of the dietary preferences of *Griphopithecus alpani*, a 15 Ma hominoid from the Miocene site of Pasalar, Turkey, based on dental microwear analysis.

The origins of the Hominoidea date back to early Miocene sites in East Africa dating to between 22 and 17 Ma (Pickford and Andrews, 1981). The hominoids are represented by the genus *Proconsul* and there was high species diversity in these early Miocene apes (Andrews, 1992). Two forms have been recognised and this distinction is partly based on size. At Rusinga Island a large species with an estimated body weight of between 26-38 kg, and a small species with an estimated weight of 9 kg have been identified (Ruff *et al.*, 1989). The post-cranial evidence suggests that the locomotion of these hominoids was a type of arboreal quadrupedalism (Aiello, 1981). The environment of *Proconsul* was, for the most part, forested (Andrews, 1992) and it has been proposed that this taxon ingested a diet of leaves and soft fruit (Kay, 1977a).

During the middle Miocene there was a second radiation of hominoids which spanned the time period 17 - 12 Ma. Andrews (1992) has distinguished three different tribes of hominoid which belong to the sub-family *Dryopithecinae*. These are the Afropithecini, the Kenyapithecini, and the Dryopithecini. The Afropithecini are known from Africa and Arabia and date to 17 Ma. Three genera have been recognised. The Afropithecini are characterised by thickened molar enamel in comparison to *Proconsul* (Andrews and Martin, 1991), enlarged premolars and broadened molars, flattened occlusal surfaces, and hyper-robust canines (Andrews, 1992). The first two characters may be related to a change in the diet of these hominoids, and Andrews (1992) suggests that this may be the ingestion of a larger amounts of hard fruits. The post-cranial remains indicate a similar type of locomotion to *Proconsul* (Rose, 1989). The environment of the Afropithecini seems to have been one of dry seasonal tropical deciduous forests (Evans, *et al.*, 1981). The Kenyapithecini date to approximately 15 Ma and two taxa are recognised (Andrews, 1992). The fossil record becomes sparse in East Africa after about 14 Ma and fossil hominoids are known mainly from Eurasia (Andrews, 1992). The Kenyapithecini are also characterised by thickened molar enamel (Andrews and Martin, 1991; Martin, 1985) and postcrania which was similar to the Afropithecini (Andrews, 1992). The palaeoenvironments of the Kenyapithecini were also like those of the Afropithecini (Andrews, 1992). The third tribe, the Dryopithecini, dates between 8 and 12 Ma and is known from mainly European sites. They are characterised by thin molar enamel like *Proconsul* (Andrews and Martin, 1991) and possibly some similarities in the cranium to the African apes and humans (Begun, 1992, 1994). In the postcrania the

Dryopithecini display characteristics of the arm and elbow which suggest below branch suspensory behaviours similar to the extant great apes (Rose, 1989). The palaeoenvironment of these hominoids was a forested one which was probably subtropical, seasonal, and partly deciduous (Kretzoi, *et al.*, 1974).

The relationship of the orang-utan, African apes and humans to the middle Miocene hominoids discussed above is unclear. The orang-utan has affinities in its subnasal morphology with *Sivapithecus* (Andrews and Cronin, 1982), and both these hominoids have been assigned to the sub-family Ponginae (Andrews, 1992). *Sivapithecus* is known from Eurasia and dates from 12 - 8 Ma (Kappleman, *et al.*, 1991). The Homininae, the African apes and human clade (Andrews, 1992) comprise two groups of fossils - *Graecopithecus freybergi*, known from Greece, and dated to approximately 9 Ma (Andrews, *et al.*, 1996), and a 9 Ma unnamed maxilla from Samburu Hills in Kenya (Ishida, *et al.*, 1984).

In the present study the dental remains of fossil hominoids belonging to the species *Griphopithecus alpani* are examined for the first time. This species is attributed to the Kenyapithecini and is known from the 15 Ma site of Pasalar in north-western Turkey. The locality was discovered in 1969 by German geologists (Andrews and Tobien, 1977). Almost 100 hominoid teeth were recovered during two seasons of excavation in the 1960s. After this systematic excavations were resumed until 1983 and they continue to the present day (Alpagut, 1990). Since then 52 mammalian species have been recovered from the site (Andrews, 1990) and published material includes over 600 isolated hominoid teeth, 3 maxillae, 2 mandibles, and 11 postcranial elements

(Alpagut, *et al.*, 1990). These have been assigned to two species - *Griphopithecus alpani* and *Griphopithecus sp.* (Martin and Andrews, 1993). As so few postcranial remains have been preserved at this site the large number of isolated teeth provide the main source of information about the behaviour and ecology of *Griphopithecus alpani*, as well as its relationship with other hominoids.

1.1 PROJECT AIMS

The principle aim of this study is to investigate the diet of the fossil hominoid *Griphopithecus alpani* on the basis of its dental microwear patterns using a comparative sample of three extant hominoid taxa with known diets. A number of factors which have the potential to influence dietary differences among species will also be examined. Variations among different molar wear facets, sex differences in microwear, and age-related variation in microscopic wear will be investigated.

A second aim of this thesis is to examine possible sources of error which may affect dietary reconstructions that are based on dental microwear analyses. The influence of taphonomic agents will be investigated as processes because they may modify existing microwear patterns (Gordon, 1983, 1984b; Puech *et al.*, 1985). Images of microscopic wear surfaces are complex to record and measure. This study will for the first time document intra-observer error in the measurement of microwear features. As molar wear surfaces are inclined relative to the occlusal plane microwear features present on tilted surfaces will appear shorter than they are in reality (Gordon, 1980, 1982), and software and a procedure to correct foreshortened measurements will be developed in this study. A comparison will be then be made between the uncorrected and corrected microwear measurements to assess the degree to which distortion due to facet tilt can affect microwear variables.

1.2 THESIS ORGANISATION

A discussion of molar wear facet formation and the mastication process is presented in Chapter 2, as well as a general overview of microwear studies which have been carried out to date. The samples and methodology employed in this study are discussed in Chapter 3. In this chapter the habitats and diets of the extant hominoid species used in this study are presented. The Pasalar hominoids sample is discussed as well as the formation of the deposits and the environment of the fauna at the site. Sample sizes for each hominoid species, specimen selection and facets examined. The replication process used to make positive casts of specimens and the scanning electron microscope techniques used to examine dental microwear patterns are also presented in Chapter 3. This chapter also discusses how microwear features were classified and measured, and develops a procedure and software to correct foreshortened microwear features. A comparison between corrected and uncorrected microwear features is also carried out. Presented in Chapter 3 is an examination of intra-observer error in the recognition of microwear features and their measurement. The last section in this chapter outlines the statistical analysis - analysis of variance - which was performed on the microwear data are presented here.

Chapter 4 examines the affect of taphonomic agents on dental microwear. Several experiments to investigate the modifications caused by two different acids (citric acid and hydrochloric acid), alkali, and three different sizes of sediment were carried out. A comparison between the experimental modifications and microscopic marks seen on some of the Pasalar hominoid teeth is presented in this chapter.

The statistical analyses performed on the microwear data are presented in chapters 5, 6, and 7. Chapter 5 contains descriptive statistics for each hominoid species and facet, and for each wear stage (age) (all species) and both sexes (the extant taxa only). Presented in Chapter 6 is a factorial analysis of variance (ANOVA). The analysis is divided into two parts. The first section examines species and facet differences in dental microwear, and the second part investigates the effect of sex and wear stage (age) on microwear features in *Pongo* only. As one of the assumptions of ANOVA - that of independence of data - may have been violated in Chapter 6 a modified ANOVA model is presented in Chapter 7. This is a split-unit ANOVA. As in Chapter 6, Chapter 7 is divided into two parts - one which investigates the effect of species and facet type, and the other which examines sex and wear stage differences in microwear (for *Pongo* only).

Chapter 8 examines the relationship between diet and the formation of pits. It has been suggested that hard object feeding produces a greater number of large pits than the ingestion of soft objects which results in more small pits, and that two different wear processes are responsible for the production of small and large pits. However, contradictory experimental evidence has been provided by Maas (1994). The dimensions and frequencies of pits for all four hominoid taxa examined in the present study are investigated in this chapter. A comparison with other microwear analyses of wild and laboratory primates which present pit dimensions and discussion of the relationship between pit sizes and diet (e.g. Teaford and Walker, 1984; Teaford and Oyen, 1989b; and Teaford and Runestad, 1992) is carried out.

The results of this study and their implications for microwear studies are discussed in Chapter 9. Factors affecting microwear formation, causes of microwear, and sources of error in dental microwear analyses are discussed. Evidence for the dietary preferences of *Griphopithecus alpani* is presented and the microwear patterns of this hominoid are compared with other Miocene hominoids. Palaeodietary reconstruction of the faunas at Pasalar and the microwear of two suoid species are also discussed in this chapter.

Overall conclusions about the work presented in this thesis are presented in Chapter 10. The implications of the effect that taphonomic agents can have on dental microwear are discussed. Conclusions about sources of error, such as molar facets which are tilted relative to the occlusal plane, and intra-observer error in the recording and measurement of microwear features are presented. Species and facet differences in dental microwear patterns are discussed, as well as sex and wear stage variations in microwear patterns. Conclusions are made regarding the two analysis of variance models used in this study - factorial ANOVA and split-unit ANOVA. The relationship between pit dimensions and diet are discussed. Finally, conclusions about the diet of *Griphopithecus alpani* are presented.

CHAPTER 2: LITERATURE REVIEW

The study of molar morphology and gross wear can provide information about an animal's dietary adaptations and feeding behaviour (e.g. Fleagle, 1988; Kay, 1981; Kay and Covert, 1984; Ungar and Kay, 1995). In recent years microscopic wear analyses have been used to provide insight into jaw movements during the chewing cycle, and diet in present-day and fossil species.

2.1 JAW MOVEMENTS, THE CHEWING CYCLE, AND WEAR FACETS

2.1.1 Wear Facet Studies

In a study of the deciduous molars in *Perissodactyla* Butler (1952) noted that the examination of the wear on molar teeth could yield information about jaw movement. He found features on surfaces of the molars of *Hyracotherium*, which had a transverse orientation, and stated that these could have been formed only by lateral movement of the jaw. He also observed that the position of the wear facets themselves, which are produced by opposing teeth during mastication, suggest that the mandible moves transversely during chewing .

Butler distinguished 10 wear facets for *Hyracotherium* - each facet on a lower tooth corresponded to one on an upper tooth. He linked the formation of wear surfaces with the process of mastication. These facets are described below.

Facet 1. On the upper molars this is a medial facet on the metastylar crest and adjacent parastyle of the posterior molar. In lower molars it is present on the buccal surface of the protoconid.

Facet 2. This an anterior facet on the protoconule and the crest connecting it to the paracone on upper molars, and it occludes with the posterior face of the protoconid, and the posterobuccal surface of the metaconid on the lower molars.

Facet 3. On upper molars this is an anterior facet on the protocone, and on lower molars is located on the posterior surface of the metaconid.

Facet 4. This is a posterior facet on the hypocone of upper molars and occludes with an anterolingual facet on the protoconid.

Facet 5. On upper molars this is a posterobuccal facet on the hypocone, and occludes with an anterolingual facet on the protoconid.

Butler noted that on upper molars these five facets form a basin, which he named the *amphicylix*, and on the lower molars the surfaces are on the trigonid.

Facet 6. This is a posterolingual facet on the paracone of upper molars. It occludes with an anterobuccal face of the hypoconid on the lower molars.

Facet 7. On upper molars this is an anterior facet on the metacone and metaconule. On lower molars this facet is located on the posterior surface of the hypoconid and hypoconulid.

Facet 8. This is an anterior facet on the hypocone and occludes with the posterior surface of the entoconid and the lingual face of the hypoconulid of lower molars.

Facet 9. This is a posterior facet on the protocone of upper molars, and is located on the anterior surface of the entoconid in lower molars.

Facet 10. On upper molars this is a posterobuccal facet on the protocone, and it occludes with an anterolingual facet on the hypoconid of lower molars.

These five facets on the upper molars enclose a basin which Butler named the *mesocylix*, and on the lower molars are on the talonid. Butler described how the wear facets are produced during the chewing cycle, where the mandible carries out a rotary movement in the vertical plane.

Facets 1, 2, 6, and 7

These facets are formed through contact between the buccal cusps of the lower and upper molars when the mandible is in its most buccal position. This is the first phase of chewing and the mandible moves superiorly and medially towards the maxilla. The protoconid and hypoconid contact the paracone and metacone and the tip of the protoconid is adjacent to the parastyle, and the buccal surfaces of the protoconid and the hypoconid shear against the lingual surfaces of the paracone and metacone forming facets 1, 2, 6, and 7.

Facets 3, 4, 8, and 9

When the mandible is in its most buccal position there is also contact between the lingual cusps of the upper and lower molars. The metaconid is level with the protoconule, and the entoconid with the metaconule, and the metaconid slides up in front of the protoconule and passes in front of the protocone, forming facet 3. At the same time the metaconid contacts the posterior surface of the hypocone of the anterior tooth, and facet 4 is formed. In the same way, the entoconid passes between the protocone and hypocone, forming facets 8 and 9.

Facets 5 and 10

The mandible then moves towards the lingual cusps of the upper molars. This is last phase of mastication. Contact is made between the buccal cusps of the lower molars and the lingual cusps of the upper molars, and facets 5 and 10 are formed as the anterolingual face of the hypoconid slides down the posterobuccal face of the protocone, and in the same fashion, the protoconid slides over the hypocone.

Butler observed that during the most lingual (and last) phase of mandibular movement, the metaconid and entoconid pass out of contact with the upper teeth. He suggested that the greatest vertical pressure is applied when the jaws are closed in the middle phase of occlusion. This is also when the greatest amount of transverse shear occurs. The greatest vertical shear occurred during first phase, when the buccal cusps of the lower and upper teeth are in contact.

Butler (1980) suggested that all these facets can be homologised in different mammals because all mammal molars are derived from the basic tribosphenic morphology. Thus, wear facets in primates and ungulates can also be recognised in paramyid and sciurid rodents. He also observed that differences in molar patterns result in differences in the relative size and orientation of the facets.

An alternative facet nomenclature was devised by Crompton (1971) who described six wear facets on the teeth of *Didelphodus*. Kay and Hiiemae (1974) further developed and expanded this system in a study of primates and described three more wear surfaces. These ten facets are described below using the definitions of both sets of authors (Crompton (1971) and Kay and Hiiemae (1974)) for the first six wear surfaces.

Facet 1: This facet is located on the posterior surface of the trigonid of lower molars, and it occludes with two shearing facets on the upper molars - the leading edge of facet 1a on the paracrista, and facet 1b on the preparaconule crista.

Facet 2: On the lower molars this facet is on the paracristid , and matches two shearing facets on the upper molars - the leading edge of facet 2a on the postmetacristid and 2b on the postmetaconule crista.

Facet 3: This is found on the cristid obliqua on the lower molars. Again, this facet on the lower molars occludes with two surfaces on the upper molars - the leading edge of facet 3a is located on the postparacrista and facet 3b on the postparaconule crista.

Facet 4: On the lower molars this surface is located on the posterior face of the hypoconid and hypoconulid, and matches two facets on the upper molars. The leading edge of facet 4a is found on the premetacrista and facet 4b is located on the premetaconule crista.

Facet 5: This facet is located on the posterior surface of the trigonid medial to facet 1 on the lower molars. The leading edge of this surface is located on the preprotocrista on the upper molars.

Facet 6: On the lower molars this facet is located on the talonid crest which runs anteriorly from the hypoconulid to the entoconid, and on to the base of the posterior face of the trigonid. The leading edge of this facet on the upper molars is the postprotocrista.

Facet 7: This is located on the mesial surface of the metaconid on the lower molars, and the distal part of the hypocone on the upper molars (except for

Palenochtha where facet 7 on the upper molars lies on the nannopithex fold mesial to the hypocone).

Facet 8: On the lower molars this facet is found on the distal entoconid and occludes with the mesial side of the hypocone in the upper teeth (except for *Palenochtha* and *Gypsonictops*).

Facet 9: This facet is located on the lingual protoconid on lower molars and the buccal hypocone in uppers (this facet is absent in *Palenochtha* and *Gypsonictops*).

Facet 10: On the lower molars this surface is found on the lingual surface of the protoconid the posterior slope of the hypocone (this facet is absent in *Palenochtha* and *Gypsonictops*).

Kay (1977) in a study of catarrhine molar occlusion made further modifications to the facets defined by Kay and Hiiemae (1974). Facet 7 in *Aegyptopithecus* was named facet 7n because Kay (1977) suggested that it was not homologous with facet 7 in the primitive primates, and is located on the posthypocrista (see Hunter and Fortelius (1994) for further discussion of this issue). Kay (1977) also corrected an error in the definition of facet 8 in *Aegyptopithecus*. Facet 10 in the catarrhine primates was named 10n by Kay (1977) as he suggested that it is not homologous with facet 10 in primitive primates. He also described a new facet which was found in *Aegyptopithecus* and other derived primates - **facet x**. This facet is formed between the anterolateral surface of the protocone and the posteromedial slope of the protoconid.

2.1.2 The Masticatory Cycle

In a study of occlusion in primates Mills (1955) further developed Butler's (1952) scheme. He proposed that wear facets correspond to two phases in the chewing cycle - the buccal phase and the lingual phase.

Buccal Phase

During this phase the mandible moves superiorly and medially and passes over the maxillary cusps into centric occlusion. The wear facets formed during this phase are present on the buccal and lingual cusps. (Facets 1,2,6, and 7, which Butler (1980) names the "B-B" facets, due to contact between the buccal cusps; and the "L-L" facets 4,3,8, and 9, due to contact between the lingual cusps).

Lingual Phase

During this phase the mandibular cusps slide downwards and medially over the maxillary cusps, and out of centric occlusion. The wear facets formed here are present on the buccal cusps of the lower molars and the lingual cusps of the upper molars. (These are facets 5 and 10, which Butler (1980) named "L-B" facets).

These two phases correspond exactly to Butler's (1952) earlier description of wear facets and Mills (1955) found that all facets on the molar teeth fall into either of these two phases in the mastication cycle. Mills also suggested that the two phases of mastication take place simultaneously on opposite sides of the jaw - a "balancing occlusion". That is, as one side of the jaw is involved in the buccal phase of mastication the other side will be engaged in the lingual phase. Mills observed that all buccal phase facets have scratch marks which run almost transversely, and are produced by rotation about the ipsilateral condyle. All lingual phase facets have scratch marks which are oriented anterolingually and which are produced by rotation around the contralateral condyle.

Mills (1955) also suggested that canine size and cusp morphology limit the degree of lateral excursion (during chewing the mandibles of most mammals do not move up and down in a straight vertical line but also deviate laterally). In New World monkeys, for example, those species with large canines tend to have blunt cusps, and those species with small canines have steeper cusps.

Mills (1955) compared the occlusal morphology and the chewing cycle in *Gorilla*, *Tupaia*, Old World monkeys, and humans, and found that the pattern of occlusion is very similar among primates. During the buccal phase of occlusion *Gorilla* molars function in a scissor-like way during the buccal phase and suggested that this may facilitate the ingestion of fibrous particles of food such as, leaves and fruit. In *Gorilla* the lower molars engage in a more horizontal type of shear during the lingual phase, when they move against the buccal face of the upper lingual cusps producing a single facet on each cusp. This may facilitate the chewing of harder items by crushing and grinding. The molar cusps of *Tupaia* project steeply in comparison to *Gorilla*, and the path of movement in during chewing in the former would have a greater vertical component.

Mills (1955) observed that Old World monkeys differ from other mammalian families in occlusal morphology in that the lingual cusps have an increased importance during the buccal phase. The lingual cusps of the lower molars are higher relative to the buccal cusps so that contact with the upper molars is maintained until the end of the buccal phase. In most other mammals the lower lingual cusps are lower than the buccal cusps and so lingual cusp contact is lost much earlier than buccal cusp contact. In addition, the lingual phase of the chewing cycle has decreased importance in the Old World monkeys compared with most other primates - contact between the upper lingual and lower buccal cusps is quickly lost. Mills (1955) suggested that balanced occlusion does not occur in the Old World monkeys. He also found that the upper lingual cusps are anteriorly displaced and lower buccal cusps are posteriorly positioned. In these primates during the lingual phase the lower buccal cusps slide between the upper lingual ones. This results in the same effect as that produced during the buccal phase and produces two facets on each cusp instead of one as for other primates. There is thus, scissor-like shearing action in both phases of occlusion which Mills suggested would be appropriate for ingesting a folivorous diet.

Mills (1955) suggested that a whole range of movements intermediate to the two phases of chewing is possible in humans because they have small and blunt cusps. He found that although large numbers of parallel scratches are found on human wear facets they are not as numerous as those of the lower primates. Mills (1955) found that the lower molars are tilted lingually and the upper molars are bucally. He suggested that this is so that occlusion is maintained during the chewing cycle, as the reduced prognathism of humans has resulted in the upper dental arch being narrower than the lower arch (the condylar fossae have migrated laterally relative to the dentition).

Crompton and Hiiemae (1969a and b, 1970) began to examine the chewing cycle in live mammals using cinefluorography and proposed an alternative system of wear surface nomenclature. This system was based on an examination of occlusion and jaw movements in *Didelphis marsupialis* and the authors described 6 molar wear facets which could also be identified in early therian dentitions. Crompton and Hiiemae also found no evidence that that chewing occurs on both sides of the mouth simultaneously and that before molars can come into close enough contact for the two phases of chewing to occur food must be sufficiently broken down by a puncturing and crushing stroke.

Crompton (1971) developed another wear facet nomenclature. He described 6 molar wear facets using the primitive tribosphenic molars of *Didelphodus.* In a study of extant and fossil primate molars Kay and Hiiemae (1974) further developed Crompton's (1971) system of wear facet nomenclature. Crompton's work had been based on primitive molars where the hypocone had not developed. The study by Kay and Hiiemae (1974) identified facets 7-10 which are connected with the development of the hypocone, and with what Mills (1955) described as the lingual phase of chewing (Hunter and Fortelius, 1994).

Kay and Hiiemae (1974) described two stages for the chewing cycle or power stroke - Phase I, and Phase II. Before mastication can take place however, food must initially undergo "puncture-crushing" (Crompton and Hiiemae, 1970) which breaks it down enough for close contact between upper and lower teeth chewing to occur. After this the power stroke takes place. During Phase I (this corresponds to Mills', 1955, "buccal" phase) tooth-food-tooth, or tooth-tooth contact occurs between the laterally positioned lower molars which move upwards and anteromedially into centric occlusion (where the protocone is located in the talonid basin). Phase II (which corresponds to Mills' (1955), "lingual" phase) begins at centric occlusion and the mandible moves downwards and anteromedially out of contact with the upper teeth. The authors suggest that these two phases are continuous in contrast to Mills' (1955) conclusion that the two phases are discontinuous. Kay and Hiiemae observed that puncture-crushing results in abrasion which ultimately leads to the blunting and pitting of the occlusal surfaces. When the teeth are in much closer contact attritional wear (either through tooth-food or through tooth-tooth contact) where mandibular movement is by molar crown morphology. Attritional wear occurs on the slopes of cusps, in the basins, and behind the leading edges of ridges.

Kay and Hiiemae (1974) suggested that wear facets can be examined in terms of three types of chewing action. "Shear" (which results from stresses which have a parallel component relative to the contact plane), "crushing" (which is caused by forces exerted in an almost perpendicular direction relative to the plane of contact), and "grinding" (which is a result of stresses which have both perpendicular and parallel elements relative to the plane of contact).

Kay and Hiiemae (1974) found that shearing occurs during tooth-tooth contacts between the leading edges of crests. These edges are concave on both the upper and lower molars so that contact areas are minimised when they pass each other during chewing. Two areas of contact between the edges and food occurs - one which is moving distally and the other proximally. As this happens the food will tend to force the shearing blades apart perpendicular to their direction of movement, and therefore muscular force is needed to maintain contact between the shearing blades. As primate molars have several shearing blades this stress is minimised by the arrangement of the blades such that they are not perpendicular to each other. As one pair of blades is forced apart others are forced into contact. Kay and Hiiemae observed that the blades of the upper molars come into "serial" contact with a single blade on a lower molar, as these slopes are often duplicated in the upper teeth to form dorsal and transverse arrangements.

Kay and Hiiemae (1974) observed that crushing will occur between planar surfaces, for example on cusp tips, or the basins between cusps, where forces are applied in a direction which is perpendicular to the plane of contact. They suggest that an increase in the amount of crushing activity would be expected to result in the increasing of the crushing facets during evolution.

Grinding involves both crushing and shearing and Kay and Hiiemae (1974) stated that the appropriate morphologies for both these actions would be included in grinding areas. the authors suggested that as primates eat a wide range of foods their teeth have kept features associated with crushing, grinding and shearing.

Kay and Hiiemae (1974) observed that in primates the upper molar occludes with a lower molar of the same position as well as the one behind it. 10 molar wear facets are outlined in their scheme, several of which had evolved in many placental mammals by the Upper Cretaceous (facets 1-6 and 9-10).

Kay and Hiiemae (1974) suggested that an important functional change in food preparation in the primates had begun by the Palaeocene. This change was the introduction of Phase II where food is ground. In *Palaenochta*, a Palaeocene primate which had primitive molars, food was sheared in Phase I, and crushed and ground in a very short Phase II. In primates with more advanced dentitions, Phase I combines cutting and compression (through pulping/crushing), through the simultaneous rather than sequential contact between the shearing surfaces, and grinding of food in Phase II. The introduction of Phase II meant that such the crowns of the teeth took on a twofold function - the basins of the lower molars which functioned in Phase I for pulping and crushing, could also be used in Phase II for grinding. The protocone and hypocone shifted from their function as "pistons" in Phase I to acting as "pestles" in Phase II. Kay and Hiiemae suggested that this scheme may have been appropriate for cutting and pulping food with a high water content.

Kay and Hiiemae (1974) also found contrary evidence to Mills' (1955) suggestion that the active side in mastication rotates about the ipsilateral condyle. *Ateles* was the only primate species for which this occurs. Kay and Hiiemae suggest that the centre of rotation is located anteromedial to the condyle, posteromedial to M3, and (in most of the primates) above the occlusal plane. It was also suggested that the condyle is of little importance for control during the power stroke. Moreover, Kay and Hiiemae found that "bilateral contact", or balancing occlusion, does not take place simultaneously as Mills (1955) suggested.

Kay (1977b) revised the 1974 scheme by Kay and Hiiemae, in a paper in which he described 11 wear facets for *Macaca mulatta.* Some facets in later primates were found not to be homologous to primitive primates as originally thought (Kay and Hiiemae, 1974), and were re-defined in Kay's (1977b) system. Kay (1977b) also identified another Phase II surface - facet "x". This surface is located distolingually to the protoconid (Gordon, 1980) and anterolingually to the protocone. Kay described this facet as an anterior extension of facet 9.

Some of the above conclusions have been applied by Grine (1981) to a study of the differences between the deciduous molars of the 'gracile' and 'robust' australopithecines. He has observed that the gracile specimens show a higher cusp relief in moderate-heavily worn crowns whereas the robust specimens show a low relief, the implication being that there would have been a steeper inclination into centric occlusion in the gracile deciduous teeth. The lower molars show differences in the relative sizes of Phase I and II facets, and the degree of angulation between them. The robust specimens (from Kromdraai and Swartkrans) possess larger Phase II facets (relative to Phase I) than the gracile specimens. This Grine correlates with the increased reliance on Phase II activity in the robust australopithecines. For the Swartkrans specimens there is more grinding activity in Phase I which implies that Phase I and II chewing activity is more similar in these specimens. The Kromdraai specimens show more shearing activity in Phase I and seem to be intermediate between the Swartkrans specimens and the gracile australopithecines. Gracile Phase I facets appear to be polished and very finely scratched, according to Grine (1981). There is, however, a certain amount of pitting, especially on the buccal sides of the protoconid, hypoconid and hypoconulid, as well as on the lingual sides of the protocone and hypocone. The degree of scratching can vary. The moderately worn teeth show few pits, whereas the heavily worn ones show a higher degree of pitting. Grine (1981) suggests that the more heavily worn cusps provide a "flatter and larger" surface on which greater perpendicular masticatory forces may be exerted. For the robust specimens more and heavier pitting is present and the scratches are deeper. Phase II facets show that for both groups the pitting is more concentrated at the bases of cusps. For the gracile australopithecines scratches and pits are more numerous than in Phase I, and often the pits overlay and erase scratches. There is more pitting on robust specimens Phase II facets than on homologous facets on the gracile teeth.

Hunter and Fortelius (1994) have made a comparison between Butler's (1952) system for wear facet nomenclature and identification and that of Kay and Hiiemae (1974) and Kay (1977b). They observed that some of the definitions of facets by Kay and Hiiemae (1974) cause confusion, for example facets 7 and 8. Confusion also arises because Kay and Hiiemaes' (1974) system was developed using specific specimens rather than a sample of molars from each group examined. Hunter and Fortelius prefer Butler's (1952) system because of the clarity of facet definitions and because this system can (and has) be applied to a range of tooth types (for example, *Hyracotherium* (Butler, 1952); North American Tertiary primates (Butler, 1973); rodents (Butler, 1980); hominoids (Butler, 1986); and pigs (Hunter and Fortelius (1994)).

Hunter and Fortelius in a study of two sympatric species of *Listridon* (1994) suggested that most striations do not directly show the path of jaw movement. This pattern can only be seen through the passage of food during chewing. Striations were observed parallel to the direction of movement but the authors also stated that when striae are formed the occlusal surfaces do not come into close enough contact to trap food between them. During pit formation surfaces do approach each other closely and the food is embedded into the enamel (or dentine). Thus, higher stresses are exerted during the formation of pits. Hunter and Fortelius (1994) noticed that most facets display both kinds of microfeatures (pits and striations), but these appear in various combinations. Finally, it was observed that three factors characterise the pattern and nature of occlusal events. These are "force", "area of contact", and "energy absorbed by the strain and fracturing of food". The interplay of these factors during the power stroke is complicated and is influenced by muscle forces, the size and orientation of wear surfaces, the relative movement of the dentition, and the flow of food. This situation may vary from one chewing stroke to another. Hunter and Fortelius (1994) also observed that striations are produced early on in the chewing bout and pits are formed at a later stage when there is very close occlusal contact.

2.1.3 Attrition and Abrasion

Crompton and Hiiemae (1970) observed that during the early stages of the chewing cycle food is “puncture-crushed” which allows the upper and lower molars to approach each other closely after which food is reduced by a shearing action. The wear produced by puncture-crushing is known as *abrasion*, and this wear between teeth and food (or sand or grit for that matter) results in the cusps wearing down leaving unstriated surfaces (Crompton and Hiiemae, 1970). The wear process associated with shearing, and the chewing of food, is known as *attrition*. Crompton and Hiiemae (1970) observed that as a result of attrition facets are formed on the slopes of the cusps which are striated and which can show the direction of jaw movement. Kay and Hiiemae (1974) suggested that the striations are produced either by tooth-food-tooth contact or by tooth-tooth contact. There is debate however, about the nature of tooth-tooth contacts during the chewing cycle. Gordon (1980, 1982) questioned the validity of the strict distinction between striated ("attrition") facets and nonstriated ("abrasion") surfaces. She found that all occlusal surfaces she examined in a study of chimpanzee microwear were striated. Gordon suggested that the terms "attrition" and "abrasion" were inappropriate for the high magnifications used in microwear analyses although, at low magnifications using a binocular microscope the abrasion facets did appear to be less striated. Teaford (1988) questioned whether, at a microscopic level, tooth-tooth contacts do occur or whether, there is a "thin film" (Hiiemae and Kay, 1973) of food which remains between the occlusal surfaces. Teaford and Walker (1983) in a study of still-born guinea-pigs found that pure attrition does not produce microwear features such as striations or pits. Only through the ingestion of food are these features formed. Teaford (1988) also observed that some nonhuman primates (in this case, *Cercocebus albigena* which displays similar microwear patterns to laboratory primates which are known bruxists) may be experiencing significant tooth-tooth contacts during the ingestion of hard objects.

Hunter and Fortelius (1994) suggested that attrition produces a featureless wear and causes the flattening of the wear facets. Abrasion, on the other hand, is caused by hard particles in the dietary regime, and produces the characteristic microwear features, such as pits and striations. The authors observed that pure abrasion occurs away from the occlusal facets where enamel surfaces approach each other closely but do not actually contact.

2.1.4 Comminution

Research has also focused on the physical properties of food and the nature of food break-down. Citing the work of Epstein (1947) Lucas and Luke (1983a) reported that comminution is dependant on two factors - *selection* (the positioning of the particle in comminution apparatus) and *fragmentation* (the degree of breakage of the particle, which is in effect, the size distribution of the broken pieces). Lucas and Luke (1983a) found that the breakdown of a carrot during human mastication selection of particles was mainly dependant on particle size - larger particles were chosen. Breakage, however, was independent of particle size. The experiments conducted by Lucas and Luke suggested that carrot particles are subjected to one breakage per chew, and the number of pieces produced per breakage is small. Using the results from these experiments Lucas and Luke (1983b) developed a computer simulation of the break-down of carrot particles. They found that there was a good match between the real particle-size distributions and those produced by the computer simulations.

Lucas and Luke (1984) citing earlier work by Lucas (1979) state that two typesof simple tooth shape can be derived for the comminution of food given two extremes in fractive behaviours - a pair of sharp, opposing blades, and blunt convex surfaces (like a pestle and mortar). The authors noted that different equipment shapes can have different effects on foods depending on the physical properties of the food. For example, a pair of sharp blades could slice a peanut, but the breakdown rate would be faster if the peanut was shattered using a mortar. Raw meat, on the other hand, cannot be shattered but can be broken down by the action of sharp blades. Lucas and Luke suggested that hard and brittle foods, as well as juicy foods could be efficiently broken-down using flat surfaces, whereas tough and/or soft foods would need to be sliced by sharp, opposing blades.

Fortelius (1985) suggested that for a given combination of food type and dental morphology there is a an optimum number of chews which corresponds to a minimum particle size. Further chewing beyond which this will result in a waste of energy. Lucas and Luke (1983a) found that for the human mastication of carrots as little as ten chews may be the optimum.

2.1.5 Summary

Two systems of wear facet nomenclature have been discussed above. The first was described by Butler (1952). This scheme originally identified 10 wear facets for *Hyracotherium* but was later applied Early Tertiary primates (1973), rodents (1980), and higher primates (1986). Butler's system was later developed by Mills (1955) who related the formation of these facets to a 2-phase masticatory scheme ("buccal" and "lingual" phases).

Crompton (1971) developed an alternative system of wear facet nomenclature. Kay and Hiiemae (1974) and Kay (1977b) expanded this scheme in a description of primate occlusal relationships. Kay and Hiiemae (1974) defined 10 facets which correspond to the 10 facets described by Butler (1952), although the numbering of surfaces is different. Kay (1977b) further refined the nomenclature of Kay and Hiiemae (1974) and described an additional surface associated with Phase II. These facets are also associated with a 2-phase process of mastication (Phase I and Phase II), but there are some differences between this scheme and that of Mills (1955).

The facets which are associated with both Butler (1952)/Mills (1955) scheme of wear facet nomenclature and the masticatory cycle, and the Kay and Hiiemae (1974)/Kay (1977b) scheme are listed in Table 2.1 (*after* Hunter and Fortelius, 1994).

Table 2.1. Wear facet nomenclature.

	BUTLER (1952)	KAY (1977b)
Buccal/Phase I	**1, 2, 3, 4, 6, 7, 8, 9**	**1, 2, 3, 4, 5, 6, 7n, 8**
Lingual/Phase II	**5, 10**	**9, 10n, x**

On the lower molars, these facets are located on the buccal edges of the buccal cusps, and the lingual surfaces of the lingual cusps. On the upper molars, these facets are located on the lingual surfaces of the buccal cusps, and the buccal side of the lingual cusps. Mills (1955) observed that the striations present on these facets are transversely oriented.

On the lower molars facets 5 and 10/ 9 and 10n are located on the anterolingual slopes of the buccal cusps, and the posterolingual surfaces of the lingual cusps of the upper teeth. Facet x (Kay, 1977b) is located distolingual to the protoconid for the lower molars, and anterolingual to the protocone for the upper teeth. Mills (1955) noted that the lingual phase facets possess striations which are anterolingually oriented.

2.2 DENTAL MICROWEAR AND DIET

2.2.1 Molar occlusal microwear and diet

One of the earliest studies dental microwear studies was carried out by Dahlberg and Kinzey (1962) who conducted an examination of the occlusal surfaces of various human populations using a light microscope. These authors observed that the surface of a tooth possesses a number different features such as striations, pits, and cracks, and they suggested that the examination of such features could give information about diet.

Walker (1976) examined the striations present on the incisors of a number of Old World monkeys. He found that terrestrial species have more striations on their teeth than arboreal monkeys due to the feeding substrate (the presence grit on food items), siliceous matter in food, and the mechanical demands placed on the teeth by the type of the particular food ingested. Walker also found that the orientation of striations could distinguish between the teeth of *Cercopithecinae* and the *Colobinae*. He concluded that the frequency of striations in Old World monkeys can be linked with habitat preferences and the physical properties of the food ingested.

Grine (1977) carried out a preliminary examination of hominid deciduous molar wear using a scanning electron microscope (SEM), which set a trend of SEM use for the examination of dental microwear which has continued to the present day. Grine investigated the microwear of "robust" and "gracile" australopithecines. The gracile specimens displayed striations which had a strong buccolingual orientation, whereas the striations present on the molars of the robust group were more randomly oriented. Grine attributed this difference to variation in molar morphology (the gracile specimens had higher cusp relief than differences in diet) rather than a different dietary regime in the two groups.

Rensberger (1978) also conducted one of the earliest studies of microwear using a scanning electron microscope. He studied microwear in herbivorous and partially insectivorous rodents and classified distinctive characteristics in wear on the occlusal surfaces and related differences in wear to chewing rates, dietary regime, occlusal pressures, and molar morphology. Rensberger suggested that abrasion polished the enamel, while striations were formed by hard detrital particles. Resistent food particles produced wedge-shaped fissures in the enamel, and randomly organised small, shallow pits were the result of high occlusal stresses.

Walker, Hoeck, and Perez (1978) undertook an analysis of two sympatric species of hyrax in the wild whose microwear patterns were linked to significant dietary differences. It was found that *Heterohyrax brucei*, a browser, had highly polished occlusal wear facets which were dominated by pits, and did not display any seasonal variation in microwear patterns. Examination of the dental microwear of *Procavia johnstoni*, a grazer, revealed seasonal differences its microwear patterns. During the wet season, heavy microwear was present on the teeth consisting of many fine, parallel striations with occasional larger scratches. Large amounts of phytoliths were found in the faeces of this grazer. Grasses contain larger amounts of opal phytoliths than other plants, and Walker *et al.* suggest that this is the abrasive agent in the diet of *P. johnstoni*. During the dry season, when *P. johnstoni* is forced to a browse, its microwear closely resembled that of *H. brucei*. Walker *et al.* concluded that microwear may be used to show dietary differences in extinct species, but they caution that microwear studies can only give an indication about an animal's dietary regime just prior to death.

Ryan (1979) conducted two experiments to produce unidirectional microwear striations on unworn human teeth. In the first experiment he drew teeth over a glass surface which was covered in sand. In the second experiment a machine was used to pull teeth across a glass surface covered with different grit sizes of silicon carbide powder. In many cases the experiments produced striations which began with broad pits and have extending grooves which become narrow. Many striations, however, did not have a pit at the point of contact or a narrowing, extended groove, but were linear. Ryan suggested that these wear mark characteristics indicate the direction of jaw movement during chewing. He also found a relationship between pit size and particle size at the point of contact. Pit size was consistently smaller than the particle size, although the two variables were highly correlated. The experimental wear patterns were similar to those present both on human archaeological dentitions, and on the teeth of *Phenacolemur*, a Palaeocene primate.

In a three-month study of the microwear of American opossums Covert and Kay (1981) examined the effects of a diet containing grit, fibre and chitin. They observed that herbivores and insectivores could not readily be distinguished by their microwear (as fibre and chitin have no distinct effect on microwear patterns), and that grit produces a similar effect to opal phytoliths.

Gordon and Walker (1983) observed that Covert and Kay's (1981) experiment was flawed. For example, the opossums were fed cat food containing the abrasives (grit, fibre and chitin) and because the texture of this food was soft and sticky it was likely that little chewing occurred. Therefore, the additives would have had much less impact than they would have had if the animals were fed a diet closer to reality. Gordon and Walker also observed that the duration of the experiment was too short. As the opossums chewed less and at a slower rate than the hyraxes used in the study by Walker *et al.*, (1978) the experiment by Covert and Kay (1981) should have run for a much longer period of time (years not months). The final criticism by Gordon and Walker (1983) was that the results had not been quantified.

The first quantitative study to document intraspecific differences in microwear patterns was made by Gordon (1982) who undertook a rigorous analysis of the dentitions of Liberian chimpanzees (*Pan troglodytes verus*). Facet type, the position of the molar in the mandible, age and sex were found to influence feature frequency, density, and dimensions. Gordon suggested that variations in these variables may be linked to the interactions of two mechanical factors - shear (parallel movement of two opposing surfaces during mastication), and compression (perpendicular forces during chewing) exerted onto these surfaces during occlusion. Due to the functional morphology of the mandible amounts of shear and compression are not the same on all molar facets. The greater the distance between a molar and the condyle of the active side, the greater the shearing potential. In contrast, Gordon observed that bite force (compression) is at its greatest at M3. Thus, the greatest shear potential is at M1 and compression is at its greatest at M3. Gordon observed that pits and striations may be the result of two extremes of the same process/continuum - namely, different amounts of shear and compression. This study also suggested that differences in facet orientation can influence gradients of shear and compression and therefore, can affect numbers and dimensions of microfeatures on different (shearing and crushing/grinding) facets. Gordon (1982) observed that the modification potential of a food particle on tooth enamel would be expected to vary under different compression loads. In conclusion, Gordon suggests that intraspecific microwear variability may well be a result of the biomechanics of mastication rather than diet itself, but that these differences are smaller than those displayed between animals exploiting different diets.

Peters (1982) conducted a series of experiments to examine the effects of puncture-crushing bone, hard/tough seeds, and coarse roots on dental enamel. Relative hardness of food items was found to have different effects on enamel. For example, the compression of seeds, as opposed to siliceous particles, resulted in very few scratches. Onions covered with grit produced fewer scratches than hard seeds with less grit. The similarity of scratches produced by grit and those made by opal phytoliths led Peters to suggest that striation morphology alone could not indicate dietary regime. Puncture-crushing of bone and hard legumes resulted in localised fracturing and crazing of enamel.

In a study of adult and still-born guinea pigs Teaford and Walker (1983) found that there was an absence of striations on all the teeth of the still-born animals. The adult teeth however, exhibited a large number of striations. The absence of striations on the still-born teeth indicated that the ingestion of food after an animal's birth causes the formation of striations rather than tooth-to-tooth wear.

Teaford and Walker (1984) continued the precedent set by Gordon (1982) of the quantification of microwear data. They examined different microwear facets on the teeth of a number of primate species including one fossil hominoid - *Sivapithecus indicus* from Pakistan. A number of different facets were compared and results did not indicate any large interfacet variations among the species examined. There were also no significant differences found between the maxillary and the mandibular molars. Interspecific differences in microwear features were found. Numbers of features and feature sizes served to distinguish between groups of primates with different diets. Frugivores and folivores could be distinguished by pit frequency - fruit-eaters had more pits relative to scratches than leaf-eaters. It was also possible to distinguish between hard (such as nuts, seeds and unripe fruits) and soft-object (such as soft, ripe fruits) frugivores - hard-object frugivores had greater frequencies of pits relative to striations than soft-object frugivores. Dimensions of microfeatures also showed differences between frugivorous and folivorous species. The frugivorous species possessed wider and shorter features relative to the folivorous group. *S. indicus* had a microwear pattern intermediate to the frugivorous and folivorous groups, and was most similar to *Pan* in this respect. Thus, according to Teaford and Walker, the occurrence of pits, and the sizes of features on molar surfaces can be used as an indicator of hardness of diet. They concluded that significant interspecific differences were found in this study and that comparisons of homologous facets within the same species are not as great as the variation seen when the same facet is examined for different species.

A study of several species of New World monkey showed that it was even possible to detect dietary differences between closely related species which were collected in different seasons (Teaford, 1985). The microwear patterns of *Cebus apella*, *Cebus nigrivittatus*, and *Cebus capucinus* indicated that interfacet differences in microwear features of the same species were still smaller than interspecific differences when comparing homologous facets. Teaford also observed that differences in diet between these three species may be a result of the presence (or absence) of hard objects.

Using the wear facet classification described by Kay and Hiiemae (1974), Grine and Kay (1988) have developed more sophisticated methods of analysing microwear patterns. In order to try and make the characterisation of microwear parameters more objective and rigorous, Grine and Kay used Fourier transforms for the examination of the microwear patterns and diets of *Paranthropus* and *Australopithecus*. The results showed that *Paranthropus* had a higher pit density (49%) and a wider scratch width than *Australopithecus* (29%). This was taken to indicate that *Paranthropus* had a hard diet similar to extant primate hard object feeders. The diet of *Australopithecus*, on the other hand, was softer and is similar to living primates which are known to feed upon leaves and/or fleshy fruits.

Teaford and Oyen (1989a, b) discovered that turnover of microwear is rapid. This follows the indications from the study by Walker *et al.* (1978). In some cases microwear features were produced and obliterated in as little as 24 hours. Experimental work which involved feeding a hard diet (monkey chow) to one group of laboratory monkeys, and a soft diet (monkey chow softened with water and mixed with fruit purée)showed that molar wear rates and microwear turnover were quicker for the monkeys fed on the hard diet. Wear rates and microwear turnover was also more rapid on crushing/grinding (Phase II) facets. This work indicated that suggest that large samples should be used in analyses of species with variable diets.

Intraspecific variation in dental microwear and diet due to seasonal and habitat differences was investigated by Teaford and Robinson (1989). *Cebus nigrivittatus* specimens were collected from three "ecological life zones" - dry tropical woodland, humid tropical forest, and humid premontane forest, each of which differs in degree of seasonality. The study showed that there were no significant differences in dental microwear between monkeys from different ecological zones, and that microwear patterns varied according to season/year of collection. Specimens from the dry tropical woodland site showed the most consistent differences (e.g. fewer and smaller pits, and more striations during the wet season when softer fruits were available). The humid premontane forest specimens collected during the same season of one year displayed more pits than specimens collected in the same season another year. These differences within zones were of sufficient magnitude to cloud variations between ecological zones. However, Teaford and Robinson conclude that these intraspecific differences were not large enough not to interfere with interspecific differences in microwear.

Investigations using both wild, live-trapped primates and museum samples reaffirmed the importance of considering ecological differences in collection sites when examining microwear patterns of the same species from different sites. Teaford and Glander (1991) found that there were significant intraspecific differences in two groups of howler monkey - *Alouatta palliata* - which were collected from different ecological zones although the basic microwear patterns were similar in the two samples (i.e the dominant feature was scratches). Again, these intra-specific variations in microwear patterns were not large enough to obscure inter-specific differences in dental microwear.

Maas (1991) conducted experimental work to investigate whether factors other than diet might affect the formation of microwear features (in this case striation width). This study showed that different types of enamel respond differently to abrasion by shearing forces (forces parallel to the abrasion surface). Striation width increased with particle size for non-prismatic enamel but not for prismatic enamel and Maas suggested that differences in striation width cannot therefore, be used to indicate differences in diet.

In a study of several Venezualan primates Teaford and Runestad (1992) discussed the need for strict control over sites and dates of collection of museum specimens used in dental microwear analyses. The study, which used primates from humid tropical forest sites, showed that there were few significant seasonal differences in diet within species. There were however, some variations in microwear patterns which could not readily be explained. Teaford and Runestad proposed that the reason for this is that museum collections are limited in the kinds of information they can provide, and it is difficult to detect subtle variations in diet using these specimens. The study also suggested that large and small pits might be formed by different processes, and that striation width is not a good dietary indicator.

Continuing the examination of factors other than diet that can affect dental microwear, Maas (1994) examined the effect of compressive loads (forces perpendicular to the abrasion surface) on different enamel types. She found that pits were the predominant microwear feature which resulted from the compression experiments and that, unlike the striations produced from shearing forces (Maas, 1991), the width of these features was directly related to particle size. This work demonstrated that the width of microwear pits can provide important information about an animal's diet.

The presence of exogenous grit on food as a cause of microwear has continued recently through research on the accumulation of dust in forest environments. Teaford *et al.* (1994) found that during the dry season more microwear features are present on the molars of wild-trapped *Alouatta palliatta*, and this was linked with an increase in dust in the canopy during the dry season. Ungar *et al.* (1995) suggested that dust can accumulate high up in the canopy, and that the concentration of exogenous grit can vary according to habitat and season. The authors proposed that dust might be an important cause of dental microwear in primates.

Lucas (1994) observed that microwear features (pits and striations) can only be produced by particles which are of a sufficient hardness relative to enamel (and dentine). He conducted experiments to examine the physical properties of quartz contained in soil, opal phytoliths, invertebrate exoskeletons, and seed coverings. Only the phytoliths and quartz were hard enough to damage enamel (and produce microscopic pits) but in the process they were also permanently deformed. Lucas also found that hard particles produce microwear features under very low masticatory forces.

Lucas and Teaford (1995) examined the silica content of the most commonly-eaten leaves (*Strebus elongatus* and *Gluta wallichii*) ingested by *Macaca fascicularis* in the Bukit Timah Nature Reserve (Singapore). Both species of leaf contain silica but *S. elongatus* contains silica which is in the form of short, sharp, and densely-packed conical spikes projecting from the underside of the leaves. As a result of this, microwear could be caused by mastication of this species at very low occlusal forces.

It was also observed that ingestion of particles which are harder than enamel causes indentations in the surface. Cracks then form along the edges of indentations and enamel tissue is then lost - pits for example, often display chipping at their margins. Lucas and Teaford also suggest that pits form by indentation before fracture.

Ungar (1996) made a study of several species of European Miocene catarrhines including three hominoid species. Ungar found that bivariate analysis of overall feature widths and lengths indicated the same dietary patterns as the pit to scratch ratios because pit and striations are defined using feature length:width ratios. Ungar also reported that pit and striation dimensions were not useful for differentiating between different diets, as taxa displayed very little variation in feature sizes.

Dental microwear research on the occlusal surfaces of molar teeth has been conducted on a number of fossil primates. Work has been carried out on Eocene prosimians (Strait, 1992), sub-fossil lemurs (e.g. Rafferty and Teaford , 1992), Miocene hominoids (e.g. Covert and Kay, 1981; Teaford and Walker, 1984; Daegling and Grine, 1994; King *et al.*, 1994; and Ungar, 1996), Pleistocene cercopithecines (e.g. Teaford, 1993; and Teaford and Leakey, 1992) . Early hominids have received a great deal of attention from microwear researchers (e.g. Grine, 1977, 1981, 1984, 1986; Kay and Grine 1988; and Walker, 1981) and more recent archaeological human remains (e.g. Harmon and Rose, 1988; Bullington, 1991; Molleson and Jones, 1991; and Molleson *et al.*, 1993).

Dental microwear analyses of many species of extant and extinct mammals have also been carried out. Investigation of the diets of large carnivores (e.g. Van Valkenburgh *et al*, 1990), microchiropterans (Strait, 1993), suids (e.g. Hunter and Fortelius, 1994); ruminants (e.g. Hayek, *et al.*, 1992; Solounias *et al.*, 1988; and Solounias and Moelleken, 1993) have been undertaken.

2.2.2 Non-occlusal molar microwear

A large number of microwear studies have undertaken the examination of non-occlusal microwear on molar teeth. Occlusal molar microwear is determined not only by food itself but also by the mastication process, chewing forces, and occlusal morphology. As a way of overcoming these potentially confounding factors some microwear researchers have turned to the examination of non-occlusal molar surfaces (see Ungar and Teaford, 1996 for discussion). Non-occlusal molar microwear studies until lately had concentrated on hominids, and prehistoric and non-industrial peoples (e.g. Fine and Craig, 1981; Lalueza Fox and Peréz-Peréz, 1993; Puech, et al., 1980). However, non-occlusal molar microwear in non-human primates has recently been documented for the first time by Ungar and Teaford (1996).

2.2.3 Incisor microwear

Incisor microwear has also been investigated for evidence of diet in extant and extinct primate species. Analyses of the incisor microwear patterns of prosimians (e.g.Rose *et al*, 1981), Old World monkeys (e.g. Teaford, 1983), New World monkeys (e.g.Ungar, 1990), great apes (e.g. Ryan, 1981, Ungar, 1992, and 1994), and fossil hominids (e.g. Ryan and Johanson, 1989; Ungar and Grine, 1991) have insights into dietary preferences and feeding behaviour.

CHAPTER 3: MATERIALS AND METHODS

This chapter describes the methods used for the microwear analysis of extant and fossil hominoids. The first section details the samples used, specimen preparation, the use of the scanning electron microscope, and feature recording and measurement. The second section describes the data analysis undertaken.

3.1 THE STUDY SAMPLE

3.1.1 The extant hominoid sample

Three extant hominoid groups were used in this study - the western lowland gorilla, *Gorilla gorilla gorilla* (*G. g. gorilla*), the common chimpanzee, *Pan troglodytes verus* (*P. t. verus)*, and the Borneo orang-utan, *Pongo pygmaeus pygmaeus* (*P. p. pygmaeus*). These species were chosen because they exploit different diets. As the main objective of this study was to reconstruct the diet of an extinct hominoid species it was important to have a comparative base of extant hominoids with different food preferences.

It has been observed that subtle variations in microwear patterns are difficult to detect in museum specimens as opposed to living animals where direct observations on feeding behaviour of particular individuals are available (Teaford and Runestad, 1992). An attempt to tackle this problem was made by controlling for area of capture. Thus, each taxon was derived from a single locality or homogeneous geographical area or ecological zone. It was not possible in every case to obtain specimens with precise dates of collection. Information on the sex of each individual was recorded where it was available.

The tropical rain-forest

The major habitat of all the extant hominoids is tropical rain-forest. The structure of the rain-forest is complex and distinctive, and can vary greatly according to region. Tree crowns are usually stratified into three layers (Richards, 1952). The upper layer is composed of discontinuous emergents (the largest trees) which project above the rests of the canopy. The middle layer is comprised of large trees which have rounded crowns, and this layer, together with the upper layer, forms a continuous canopy. The third layer consists of the crowns of smaller trees, which have vertically extended crowns, and which mature beneath the other two layers. Below the trees is a layer of saplings, shrubs, woody plants, with herbs forming a discontinuous ground covering. In Southeast Asia the *Dipterocarpaceae* tree family dominates the composition of the rain-forest. Rain-forest temperatures are relatively even and high with mean monthly temperatures ranging between 24° C and 28° C (Friday and Ingram, 1985). Annual rainfall in typical rain-forest localities is at least 2000 mm but there is considerable variation (Richards, 1952).

Gorilla gorilla gorilla

The western lowland gorilla inhabits Cameroon, Central African Republic, Zaire, Equatorial Guinea, and Gabon. These countries are part of the rain-forest zone which forms a continuous forested belt extending from Sierra Leone to eastern Zaire (Delany and Happold, 1979).

For this study gorillas from lowland tropical rain-forest in Gabon and Equatorial Guinea were used (Fig. 3.1). Table 3.1 contains information on mean annual temperature and rainfall for a number of areas in Gabon and Equatorial Guinea which are close to some of the localities from which the gorillas used in this study were collected (see Appendix 1). The data were taken from Rudloff (1981). Mean annual temperatures from these selected sites in Gabon and Equatorial Guinea range from 24°C to 26°C, and rainfall varies from 1756 mm to 3120 mm (Rudloff, 1981).

Gorillas have been classed as folivores. However, it has been suggested that resource availability has a strong influence on gorilla diet and the greater diversity in plant species in lowland tropical forests has resulted in the ingestion of larger proportions of fruit by the gorillas in those habitats than is seen in subspecies living in more montane areas (Jones and Sabter Pí, 1971; Sabter Pí, ,1977; Rogers, 1989; Tutin and Fernandez, 1985, 1987).

COUNTRY	MEAN ANNUAL TEMPERATURE	MEAN ANNUAL PRECIPITATION
Gabon		
Makokou (0°34'N 12°52'E)	24°C	1756 mm
Libreville (0°27'N 9°25'E)	26°C	3120 mm
Port Gentil (0°42'S 8°45'E)	26°C	2180 mm
Lambarene (0°45'S 0°14'E)	26°C	2074 mm
Equatorial Guinea		
Bata (1°54'N 9°48'E)	25°C	2209 mm

Table 3.1. Climate data for countries from which *Gorilla* specimens were collected.

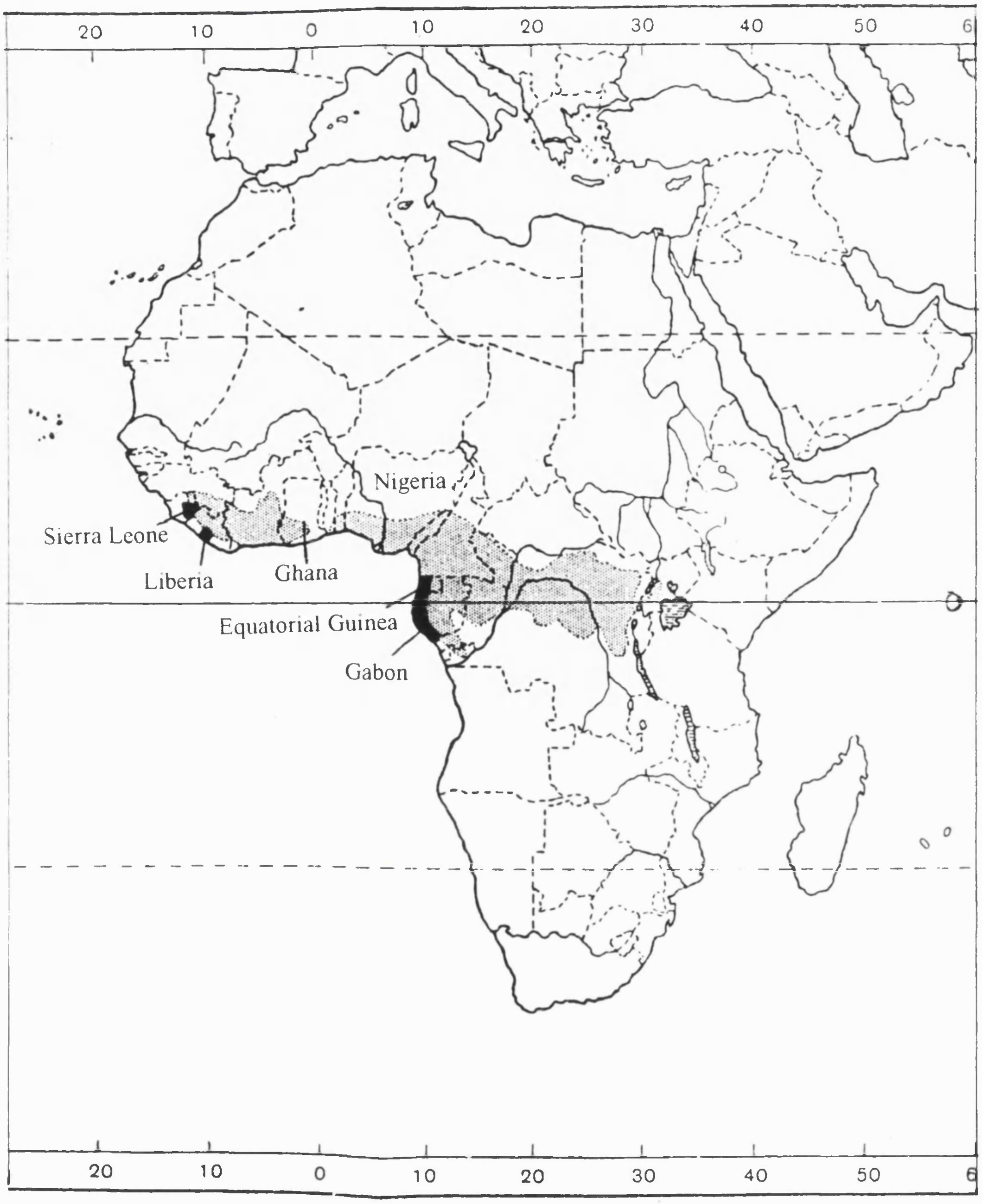


Figure 3.1. Map of Africa showing countries and homogeneous ecological zones from which *Gorilla* and *Pan* specimens were collected. Cross-hatching represents rain-forest distribution. Solid black sections represent localities from which specimens were actually collected. (*After Richards, 1952*).

In fact, the diet of the lowland gorilla is more similar to that of *Pan* than gorillas in other parts of Africa (Rogers, *et al.*, 1990). Ideally the most folivorous subspecies of gorilla (*G. g. berengei*) would have been included in the present study but it was not possible to obtain a large enough sample of these hominoids.

Research on gorilla diets at the Lopé Reserve in central Gabon and Belinga in north-eastern Gabon has shown that fruit comprises between 45% and 79% of total food ingested, (Tutin and Fernandez, 1985; Tutin and Fernandez, 1987; Tutin *et al.*, 1991). The remainder of the diet of these gorillas is comprised of leaves (mature and young combined) (24.1%), seeds (mature and young) (10.3%), pith (8.4%), bark (4.4%), flowers (1.5%), insects (2.5%), and roots, gall and fungi (3.9%) (Tutin *et al.*, 1991). The gorillas from Lopé ingest a greater diversity of fruit species than sympatric chimpanzees, and consume greater amounts of mature leaves (Tutin *et al*, 1991). They also avoid fruits which have a high lipid content as opposed to the chimpanzees at Lopé (Tutin *et al*, 1991). Research on gorillas at Río Muni in Equatorial Guinea (Sabater Pí, 1977) has shown that fruit comprises about 40% of the diet, leaves form 34%, piths and tender shoots make up 21%, and the remaining 5% is comprised of barks, roots and flowers. As a result of their large size, the gorillas feed on fruits which are available at low heights or which have fallen onto the ground. They also show preferences for sweet and acidic fruits.

For this study a total of eighteen adult wild-shot *G. g. gorilla* specimens were studied. Appendix 1 details the specimens used in the study. Dates, locations of capture (where known), and sex of each individual are taken from Jenkins (1990). These specimens are housed at the Natural History Museum, London.

Pan troglodytes verus

This sub-species of common chimpanzee inhabits western Africa. Ten adult wild-shot animals were used in this study. As very few specimens could be found from one restricted area or even the same country, additional material was used which came from Ghana, Liberia, Nigeria and Sierra Leone (see Figure 3.1). The environment of this sub-species ranges is more mixed and more varied than that of other chimpanzees. As well as inhabiting the tropical rain-forest, *Pan troglodytes verus* is also able to live in more open and arid environments where the majority of the vegetation is savannah (McGrew, *et al.*, 1981). Table 3.2 contains climate data from Rudloff (1981) for areas which are close those from which the specimens were collected.

Very few studies have investigated the diet of *Pan troglodytes verus*. Instead, research has centred on the habitat ((McGrew, *et al.*, 1981) and use of tools (McGrew *et al.*, 1979a; Boesch and Boesch, 1981). The meat-eating habits of *P. t. verus* have also been studied. McGrew *et al.* (1979b) found that mammal remains comprised 2.6% of the faecal remains of *P. t. verus* in Senegal. Aside from documentation of this relatively small component of the diet, there are no other studies which examine the dietary regime of *P. t. verus*. For the present study, dietary preferences in *Pan troglodytes verus* are inferred from dietary information at the species level. In particular, the feeding behaviours of chimpanzees which inhabit areas closest to those of specimens used in the present study (Gabon and Equatorial Guinea). Research at Gombe (Tanzania) and in Gabon has indicated that fruit comprises between 48% (Goodall, 1986) and 68% (Hldadik, 1977) respectively of the diet of *Pan troglodytes*.

COUNTRY	MEAN ANNUAL TEMPERATURE	MEAN ANNUAL PRECIPITATION
Ghana		
Kumasi (6°43’N 1°36’W)	26°C	1465 mm
Liberia		
Monrovia (6°18’N 10°48’W)	26°C	4793 mm
Nigeria		
Lagos/Ikeja (6°35’N 3°20’E)	27°C	1625 mm
Enugu (6°28’N 7°33’E)	27°C	1661 mm
Sierra Leone		
Daru (7°59’N 10°51W)	26°C	2514 mm

Table 3.2 Climate data for countries from which *Pan* specimens were collected.

Leaves and leaf buds form 25% of the diet and 27% is comprised of items such as seeds, blossoms, stems, pith, bark and resin (Goodall, 1986). The chimpanzees at Gombe also supplement their diet with small and medium-sized mammals, birds and birds eggs', and a range of insects (Goodall, 1986).

Recent research at Lopé (Gabon) has shown fruit makes up 67.6% of the diet of the chimpanzees at this site (Tutin *et al*, 1991). Leaves (both young and mature) form 11.3% of the diet, seeds (young and mature) 7%, pith 2.1%, bark 0.7%, flowers 2.1%, insects 5.6%, mammals 2.1%, and roots, gall and fungi combined comprise 1.4% of the food ingested. There is seasonal variation in the diet of *Pan* at Lopé. During the dry season consumption of one species of fruit which is high in lipids is increased, as well as the exploitation of more pith and the young leaves of herbaceous plants (Tutin *et al*, 1991).

The *Pan troglodytes verus* specimens used in this study are listed in Appendix 1. Dates, locations of capture (where known), and sex of each individual are taken from Jenkins (1990). These specimens are housed at the Natural History Museum, London.

Pongo pygmaeus pygmaeus

P. p. pygmaeus is distributed in several areas of Borneo (Figure 3.2). Twenty wild-shot adult specimens which come from Sarawak in Borneo were used in this study. All specimens were collected from the First Division of southern Sarawak which is

*

These specimens are housed at the Natural History Museum, London.

located near Kuching (see Appendix 1. Dates, locations of capture (where known), and sex of each individual are taken from Jenkins (1990)).The habitat is one of tropical rain-forest which is dominated by the *Dipterocarpaceae* tree family. Mean annual temperature for Kuching is 27°C, with 3905 mm mean yearly rainfall (Rudloff, 1981).

Fruit forms the main component part of the diet of *Pongo*. Comparisons across several study sites indicate that fruit forms between 53.8% and 84.7% of the diet of *Pongo* (see figures and references in Rodman, 1988). Leaves and shoots form between 10.2% and 29% of the diet, and bark and wood form between 3% and 14.2% of the foods consumed by *Pongo* (see figures and references in Rodman, 1988). *Pongo* also ingests insects, eggs, fungi, honey, soil, lianas and epiphytes (MacKinnon, 1974).

Pongo has been observed to eat fruits with harder husks and more fleshy pericarps than some of the primates that share its habitat, and ingests unripe fruit more frequently than other sympatric primates (Ungar, 1992, 1995). MacKinnon (1977), who carried out research in Sabah (Borneo) found that *Pongo* ingests hard fruits and also very large fruits. These types of fruits comprised 34.5% of the diet of all fruits eaten (MacKinnon, 1977). It has also been noted that by having an extensive and flexible ranging behaviour, and by being able to ingest sour and bitter, unripe fruits, *Pongo* has a competitive advantage over sympatric fruit-eating animals (e.g. monkeys and birds) (MacKinnon, 1974). The availability of fruits can vary markedly from season to season, and during these months the orang-utans ingest large quantities of leaves and epiphytes (MacKinnon, 1974).

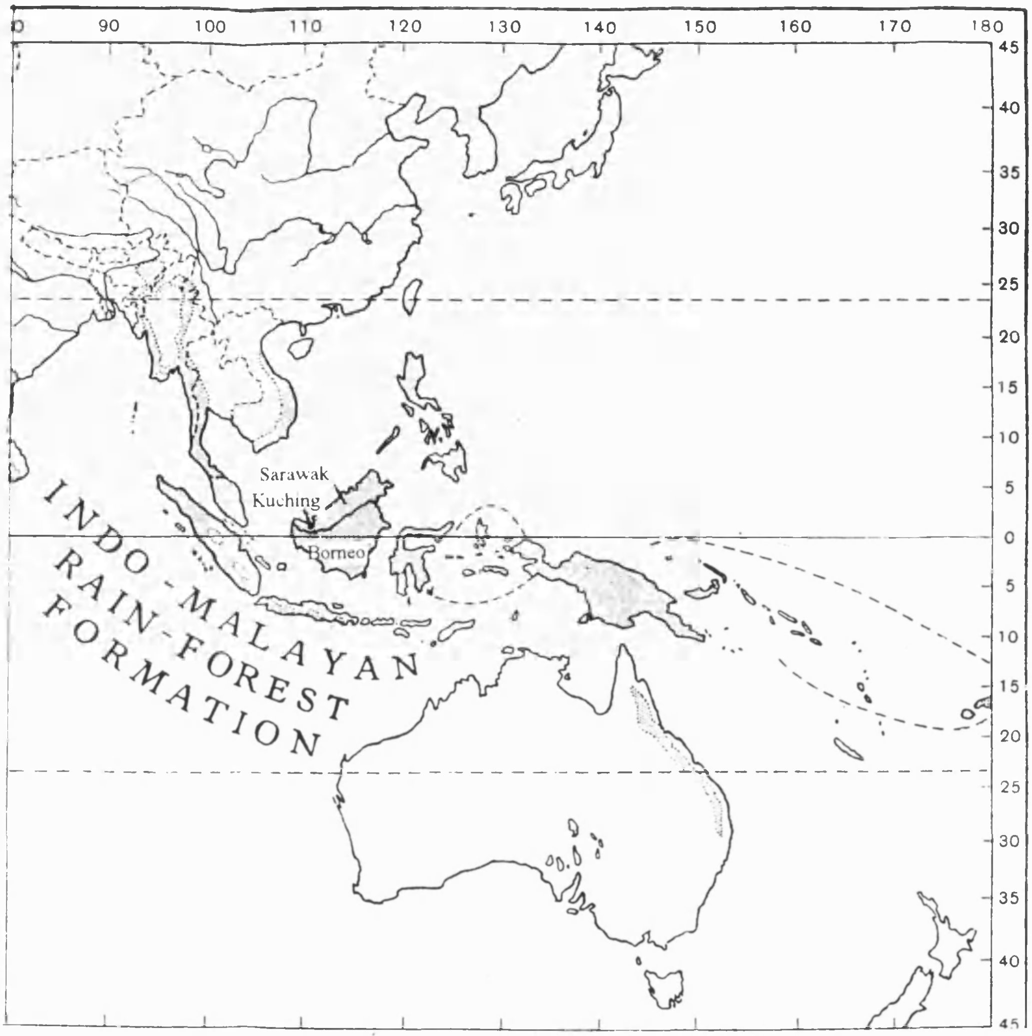


Figure 3.2. Map of Borneo showing locality from which Pongo specimens were collected. Cross-hatching represents rain-forest distribution. (After Richards, 1952).

3.1.2 The fossil sample

The *Griphopithecus alpani* specimens used in this study are all isolated teeth derived from the Miocene site of Pasalar, in north-western Turkey 75 km south-west of the town of Bursa (Figure 3.3). The site was discovered in 1969 by German geologists and excavations were carried out in 1969 and 1970 during which 86 complete hominoid teeth were recovered (Andrews and Tobien, 1977). In 1983 systematic excavations were resumed at the site and continue to the present day (Alpagut, 1990).

Stratigraphy at Pasalar

The deposits at Pasalar form two distinct series - the lower series and the upper series - which are derived from two different sources. The lower series sediments contain two fossiliferous units. Four stratigraphic sections have been described (Figure 3.4) - i) *lower calcareous silt*, ii) *fossiliferous sand*, iii) *upper sand*, and iv) *upper calcareous silt* (Andrews and Alpagut, 1990). The fossiliferous sand is the main fossil-bearing unit and consists of poorly sorted sands, gravel, silt (Andrews and Alpagut, 1990). This unit consists of three levels - the upper level, which contains the lowest concentrations of fossils, and consists of mainly fine sands; the middle section, which is comprised of gravelly, fine sand, and contains large amounts of small mammals and a few larger ones; and the lower half which consists of coarse sands and gravel and contains the greatest proportion of large mammals and hominoids (Fig. 3.4) (Andrews, 1995). The lower series sediments at Pasalar are locally derived.

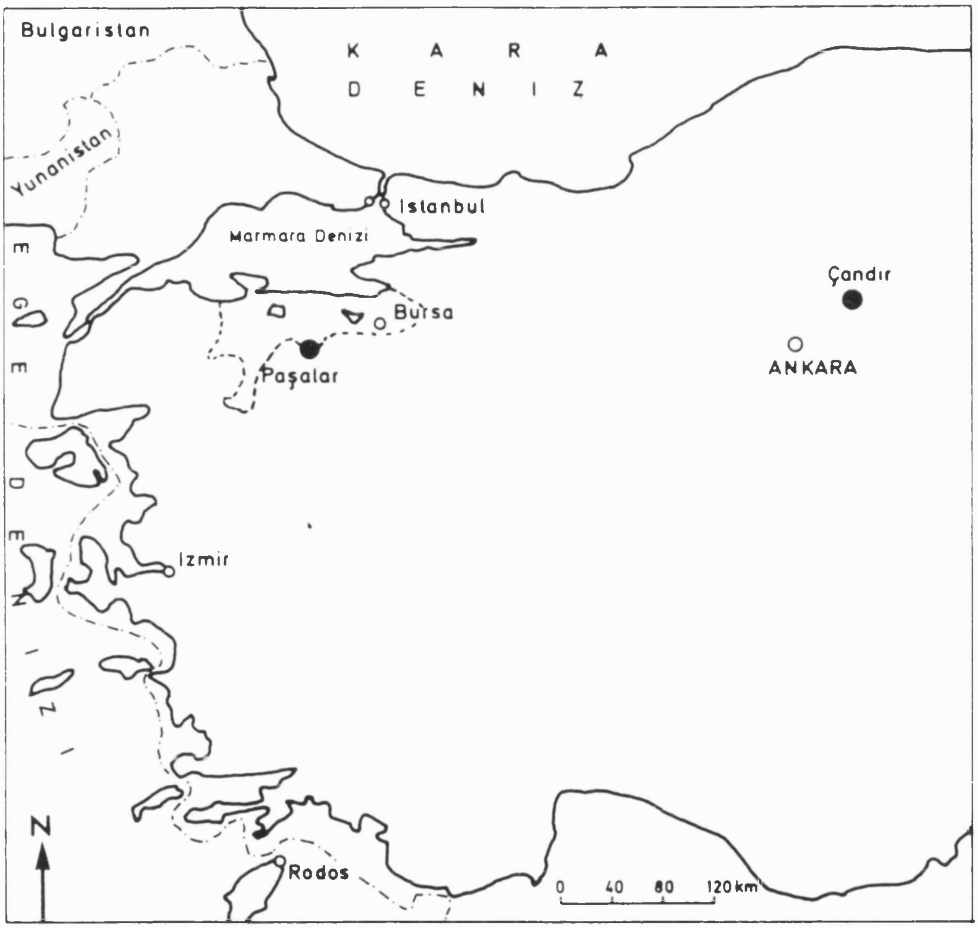


Figure 3.3. Map of Turkey showing the location of Pasalar. (*After Andrews and Alpagut, 1990*).

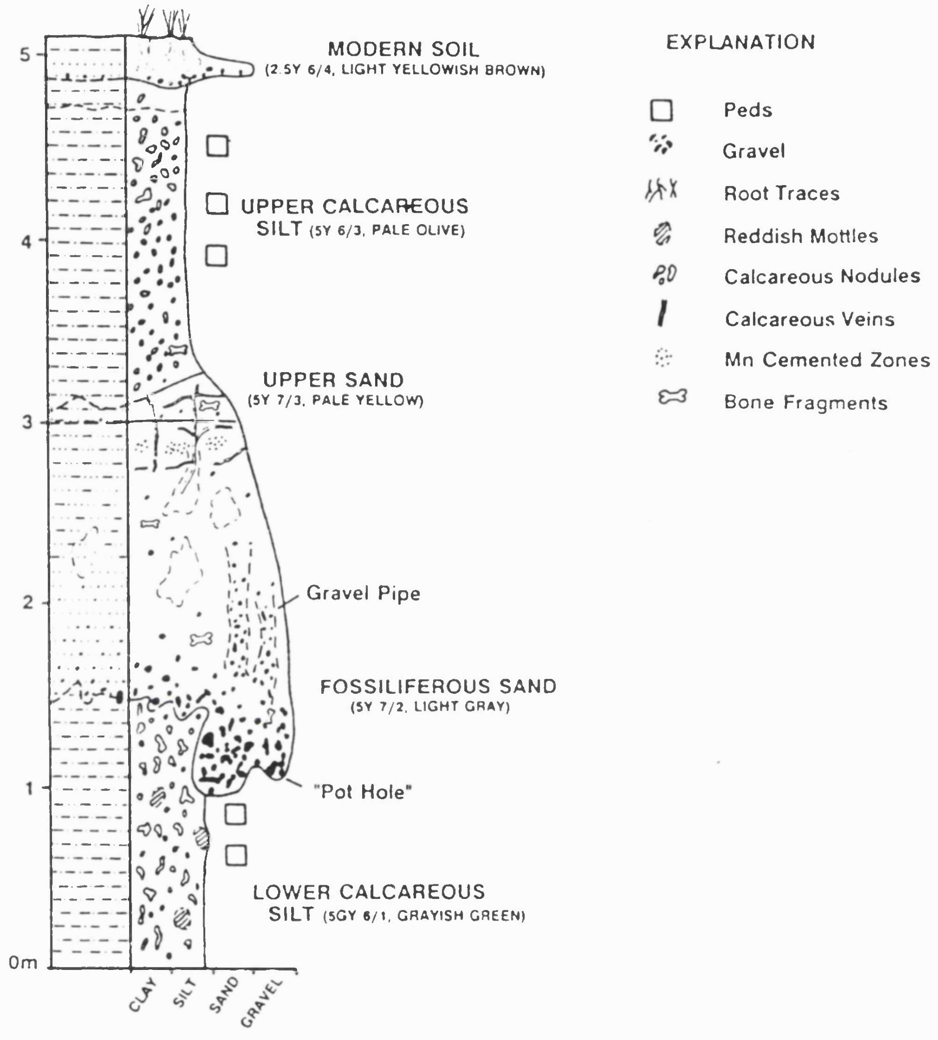


Figure 3.4. Section showing the four stratigraphic layers, including the fossiliferous sand, at Pasalar. (*After Bestland, 1990*).

Two stages of fossil accumulation and deposition have been described for the fossiliferous sands (Andrews, 1995). The first phase involved the accumulation of the bones before burial. The evidence for this comes from the pattern of surface weathering which indicates slow accumulation of bones over a period of perhaps as little as 10-20 years (Andrews, 1995). The fossils were then transported with the sediments to the fossil site and burial occurred rapidly, probably in a matter of days (Andrews and Alpagut, 1990) in a single depositional event. The fauna are thus, restricted in temporal and geographic space.

Pasalar fauna and habitat

52 mammalian species have been identified at Pasalar and the assemblage is considered to be a natural community where many of the species were contemporaneous (Andrews, 1990, 1995). No plant or pollen remains have been discovered from the site. Nor are there any invertebrates. Palaeoecological research therefore, has focused on the mammalian species present at Pasalar (Andrews, 1990) . As mentioned above, the sediments and fossils are limited both in time and space and this means that it is likely that the species were from a single habitat (Andrews, 1990). Comparisons with recent mammalian communities have indicated that the fauna from Pasalar is similar to two habitats - African tropical deciduous forest/woodland, and sub-tropical semi-deciduous monsoon forests in India and Southeast Asia (Andrews, 1990). Deciduous forest/woodland in Africa is highly seasonal with a long dry season (Andrews, 1990). The vegetation is dominated by a single tree canopy comprised of

one or several tree species with grass and shrubs below this layer (Andrews, 1990). Sub-tropical semi-deciduous forest in the summer rainfall belt is similarly characterised by a single main tree canopy comprised of one or several species with a discontinuous lower tree cover, and abundant ground vegetation (Andrews, 1990). Evidence from the number of species present at Pasalar, body sizes (equal numbers of small and large mammals), locomotion (high number of terrestrial species), and diet (the large proportion of frugivores relative to grazers) suggests that of the two recent habitats described above, the Pasalar palaeoenvironment was most similar to sub-tropical semi-deciduous monsoon forest in a seasonal climate with a marked dry season, and with the forest was probably interspersed with rich ground vegetation and grass meadows (Andrews, 1990).

Pasalar hominoid sample

The hominoid specimens from Pasalar include 3 maxillae, 2 mandibles, 603 complete permanent teeth, 42 complete deciduous teeth, and 11 postcranial elements. These specimens are considered to represent at least 35 individuals (Alpagut *et al.*, 1990). These figures are based on material recovered up to 1989 (Alpagut *et al.*, 1990). The number of specimens has increased since then, but these lists remain unpublished at present.

Two species of hominoid are probably represented at Pasalar based on both metrical (upper M1) and morphological variation in the canines and incisors (Alpagut, *et al.*, 1990). 90% of the hominoid sample is represented by one species - *Griphopithecus alpani*- and the remaining 10% has not yet been given a species name, but has been assigned to *Griphopithecus sp.* (Alpagut, *et al.*, 1990). Lower second molars were used in the present study (see section 3.1.2) and the dimensions of these teeth display a bimodal distribution (Alpagut, *et al.*, 1990). Martin *et al.* (1994) have discussed the issue of sexual dimorphism and species recognition and observed that molar teeth are not reliable indicators of sexual dimorphism. The authors state that if a given data set may contain more than one species and has a bimodal distribution then it is not permissible to make any conclusions about sexual dimorphism. Thus, it is not possible to examine sexual variation in dental microwear in the Pasalar hominoid sample.

The molar teeth from Pasalar are characterised by thick enamel (Martin, 1983, 1985). The upper molars possess four cusps and have a simple morphology (Fig. 3.5) (Alpagut, *et al.*, 1990). There is no great size variation in the upper molars - M1 and M3 are equal in size, and both are larger than M2 (Alpagut, *et al.*, 1990). The lower molars, on the other hand, increase in size from M1 to M3 and possess the five cusps which are typical of hominoids (Fig. 3.5) (Alpagut, *et al.*, 1990).

[*] These specimens are housed at the Department of Palaeoanthropology, Dil ve Tarih-Cografya, Facultesi, Ankara University.

3.2 SPECIMEN SELECTION

A number of wear facets on the **second** molar were examined in this study. This molar was selected because previous research has shown that it is intermediate to M1 and M3 in its microwear patterns (see Gordon, 1980, 1982). As a result, this molar is also the one most commonly used for microwear studies (e.g. Grine, 1987; Grine and Kay, 1988; Teaford, 1985; Teaford and Walker, 1984; Teaford and Robinson, 1989; Teaford and Glander, 1991; Teaford and Runestad, 1992; Ungar, 1996; Ungar and Teaford, 1996).

For the *Griphopithecus alpani* sample lower left molars were employed to avoid the inadvertent use of more than one specimen per individual (Figure 3.5). This is because the Pasalar sample used in this study is entirely comprised of isolated teeth. # Only complete, undamaged molars were selected for examination. For the extant hominoid groups associated tooth rows in mandibles or maxillae were available for use. Lower second left molars were taken by preference. However, in some instances the lower left second molar was damaged or missing and lower right molars were selected instead. If neither the left or right second molar was available the upper second left or right molar teeth was used. Out of a total of 65 specimens 1 lower right and 5 upper right molars were used. The remaining 59 specimens were all lower left molars (Appendix 1).

After initial SEM examination some specimens from both the fossil and extant groups had to be discarded. In the case of the extant samples this was due to the presence of

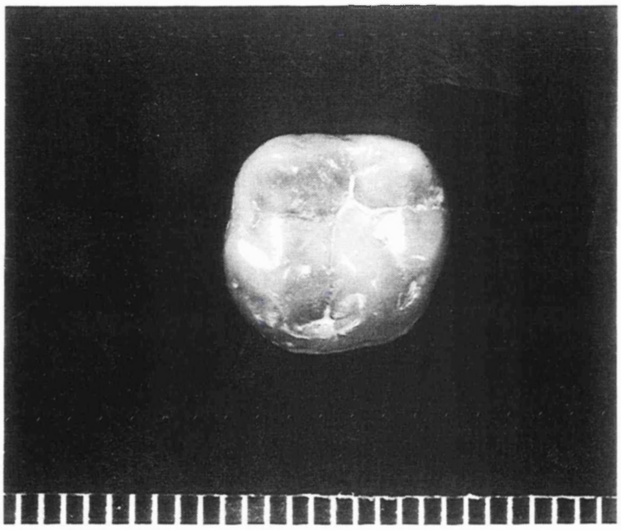


Figure 3.5. Pasalar hominoid lower left second molar.

post-mortem microscopic features which were caused by cleaning/preparing specimens. Some *Griphopithecus alpani* specimens had also been subjected to taphonomic processes (see Chapter 4 for discussion), such as weathering and sediment abrasion, which caused alterations to the dental microwear.

3.3 REPLICATION PROCEDURE

Replicas of the original material were used in this study, although it is possible to use original specimens for SEM examination of microwear . This was due in part to the fact that the *Griphopithecus alpani* sample is housed outside the UK, and because some of the extant hominoid mandibles are too large to fit inside the SEM chamber. Finally, as almost all microwear analyses are carried out using replicas it was decided that use of replicas for this study would ensure consistency with other researchers.

Specimens were cleaned prior to replication as recommended by Gordon (1980 and 1982) with slight modifications. Teeth were first cleaned with tap water and detergent using a sable brush. A 50% solution of household bleach was then applied to the tooth in order to remove any organic matter. The specimen was then rinsed with water and left to dry but covered for protection from dust.

Impressions of the teeth were taken using Coltene President's light body (a polyvinylsiloxane, addition-type silicone elastomer) and soft putty (Coltene (UK) Ltd., 8a Teknol House, Burgess Hill, RH15 9LF). This is a two-part impression material and was chosen because of its high resolution (0.2μm (Beynon, 1987)) and because it remains dimensionally stable (i.e. does not shrink) for at least three years (Beynon, 1987). This means that positive replicas do not have to be made immediately after the moulds are taken, and thus, is very practical for field work, or when working on collections abroad.

Dust was removed from the cleaned specimens using pressurised air. Specimens were mounted onto plasticine to stabilise them and equal amounts of the light body base and catalyst were mixed together using a palate knife. The light body was then applied to the occlusal surface using a sable paint brush. Setting time is approximately 4 minutes and 15 seconds at 23°C. Next, equal quantities of the putty base and catalyst were kneaded together. The putty was placed on and around the tooth crown (without removing the light body), allowed to harden (this takes approximately 6 minutes at 23°), and the impression was carefully removed from the specimen.

Positive replicas were made with Araldite MY 753 epoxy resin and hardener XD 716. This resin is produced by Ciba Polymers (Duxford, Cambridge CB2 4QD, UK) and is mixed using 100 parts base to 38 parts catalyst. The resin was mixed in disposable cups with wooden tongue depressors. Dust was evacuated from inside the impressions with pressurised air. Next, a small amount of resin was applied to the base of the mould using a sable paint brush. This helps to ensure that resin reaches all areas of the tooth crown and also minimises air bubbles. After this the impression was filled to the brim with resin. Each mould was examined and any remaining air bubbles were evacuated using a pin or very fine paint brush. Araldite MY 753 may be cured at room temperature, and although the recommended curing time is 8 days it was found that 10 - 12 days were required to obtain satisfactory replicas. Even then the replicas did not always catalyse fully and had to be re-cast.

Once cured, replicas were mounted onto SEM Cambridge stubs using Ciba-Geigy Araldite epoxy resin adhesive. This glue can take up to three days before it is fully cured. Once the adhesive had hardened dust was removed from the occlusal surface of each specimen using pressurised air. Specimens were then coated with between 20 and 30 nanometres of gold-palladium in a Polaron sputter coater at 2.4 kV in three thirty second bursts. A layer of silver paint running from the base of the stub to two sides of the specimen was applied to ensure better conductivity.

3.4 THE SCANNING ELECTRON MICROSCOPE (SEM)

The SEM is useful in microwear analysis as it has high resolution (20-50 nanometers) and especially good depth of field which is 300 times larger than that available on the light microscope (Bozzola and Russell, 1992). It also has a range of magnifications that are not available on the light microscope, up to a maximum of 200,000x (Bozzola and Russell, 1992). Not only may the SEM be used to examine microwear but it can also take high quality micrographs at the same time. The SEM operates by scanning a focused beam of electrons over a conductive specimen. As the beam touches the surface of the specimen a number of signals are given off. These signals are then collected by a detector, displayed on a cathode ray tube or monitor and translated into a number of pixels which eventually make up an image of the specimen (Bozzola and Russell, 1992).

The Electron Optical Column and Beam Production

The SEM is comprised of several parts. The electron optical column (Fig. 3.6) is responsible for generating the electron beam. It is comprised of an electron gun and several lenses. The electron gun produces a constant source of electrons which give rise to the beam, and is designed so that the maximum current (the greater the current the greater the signal) passes through the smallest probe as this produces the highest resolution (Goldstein and Yakowitz, 1975). The beam itself is produced by heating a filament, usually made of Tungsten and "V" shaped, which eventually leads to the release of electrons by thermionic emission. Due to the application of a negative high voltage the electrons are then accelerated towards the anode. At this stage the spot (beam) size is approximately 50 microns in diameter (Bozzola and Russell, 1992) and requires reduction in size. As mentioned above, small spot sizes are necessary for maintaining good resolutions at high magnifications. A variable number of condenser lenses are responsible for decreasing the spot size. The final lens, which is the strongest, carries out the last demagnification of the spot. It is also responsible for

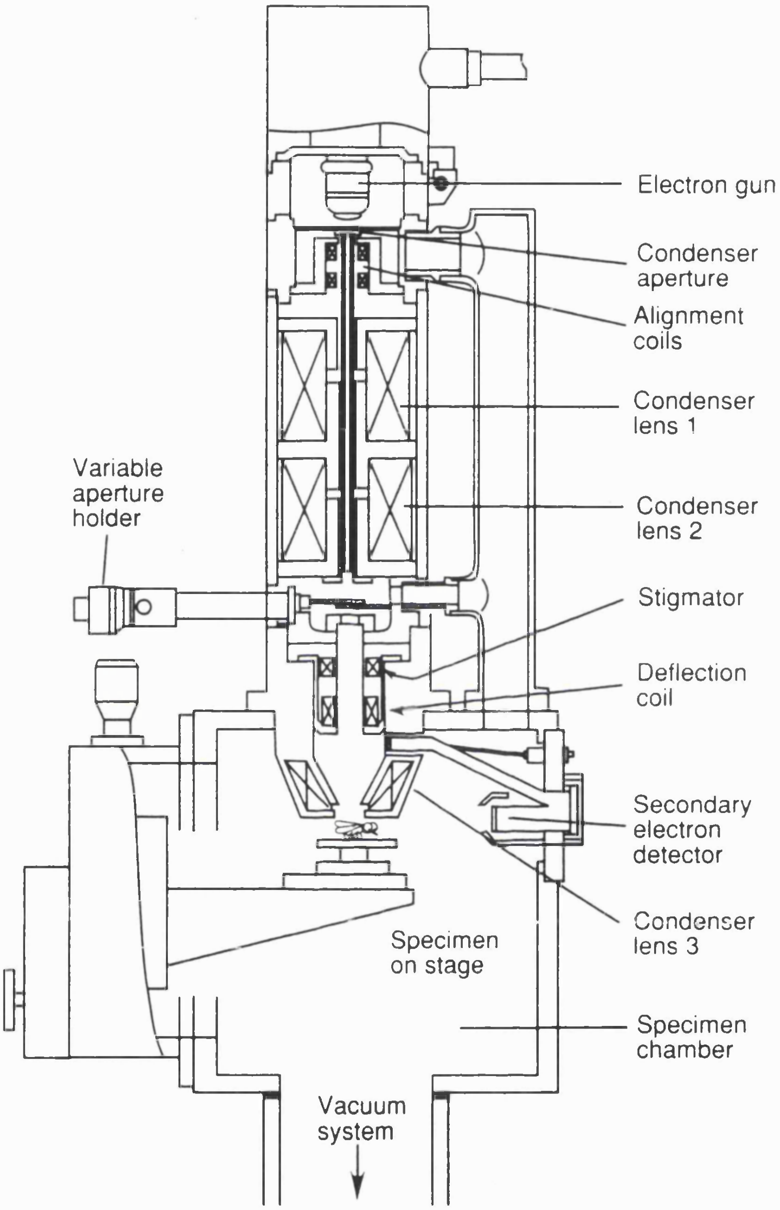


Figure 3.6. The electron optical column. (*After Bozzola and Russell, 1992*).

focusing the image which is eventually displayed on the monitor. Also present in the column are a number of apertures which can be fixed in size and position in the column, or which may be variable and adjustable. These apertures which control the spot size and beam current, as well as depth of field.

Specimen and Beam Interaction

When the beam hits the specimen a number of different types of signal are produced as a result of random scattering of the electron beam as it penetrates the specimen. There are two kinds of electron scattering - **inelastic** and **elastic**. With inelastic scattering the beam interacts with the atoms of the specimen to produce low energy electrons. The most important type of low energy electrons emitted for SEM purposes are *secondary electrons* (SEs) (Taylor, 1986). These electrons leave the specimen at many different, and usually, small angles (Taylor, 1986). They are negatively charged and the detector collects the electrons by having a slight positive bias. The most commonly used detector is the Everhart and Thornley Scintillator (Bozzola and Russell, 1992). This type of detector increases the signal emitted by amplifying the number of electrons which enter it.

With elastic scattering the electrons emitted which are of importance to scanning electron microscopy are *back-scattered electrons* (BSEs). They have a higher energy than SEs and are emitted from deeper within the specimen. They collide with the atoms of the specimen and are emitted whilst retaining their original energy. BSEs are so-called because they retreat from the specimen in the same direction by which they enter it (Bozzola and Russell, 1992). More BSEs are emitted than SEs (see reference in Taylor, 1986). BSEs are emitted at high scattering angles relative to the surface of the specimen and thus, cannot be detected by a SE detector which is positioned to the side of the specimen (Taylor, 1986). BSE detectors are placed directly above the specimen (Fig. 3.7). There are two types of detector which have been specially designed to collect BSEs - the solid state detector (the mostly common type) and the wide-angled scintillator-photomulitplier (for example, the Robinson back-scatter detector). The wide-angled scintillator-photomulitplier works on the same principle as does the Everhart and Thornley Scintillator for detection of SEs, and is more sensitive and also provides better resolution than does the solid state detector (Bozzola and Russell, 1992).

Differences between SE and BSE Imaging

For the most part, SEM studies of dental microwear have used SEs to form an image of the specimen (Ungar, 1994). However, initial examination of replicas using a number of different SEM systems revealed that the BSE produced the best images in terms of contrast and depth of field. Ungar (1992, 1994) has also used BSE imaging for dental microwear analysis and cites work by Boyde and Cowham (1980) when discussing its advantages in terms of increased contrast and depth of field.

The differences between SE and BSE imaging are as follows. With SEs, topographic contrast is used to generate an image of the specimen (Bozzola and Russell, 1992).

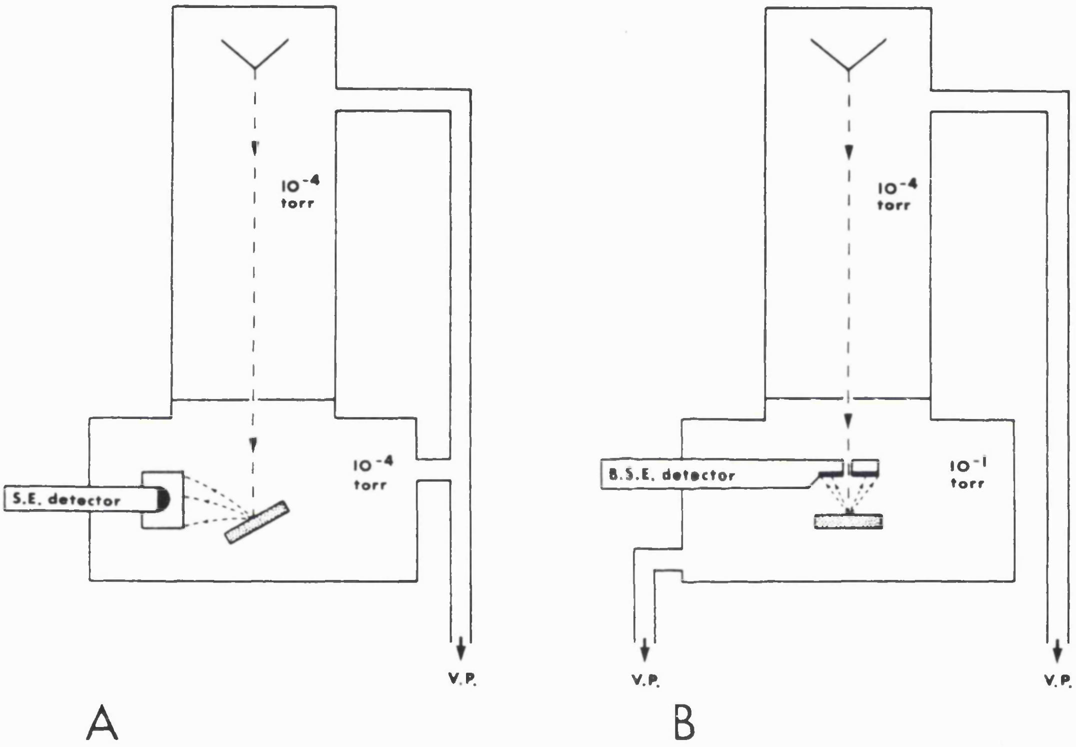


Figure 3.7. Positions of detectors in SE imaging (A) and BSE (B)imaging. (*After Taylor, 1986*).

This is due to the low-angle scattering of electrons. Thus, specimens which are strongly 3-dimensional are suitable for SE detection. For BSE imaging contrast is the result of differences in atomic number of the elements in a specimen. This is known as the "Z" contrast (Bozzola and Russell, 1992). As material which has high topographical relief produces poor images specimens should be as flat as possible as when using BSEs (Taylor, 1986; Bozzola and Russell, 1992). With SEs edges, or raised areas, give greater signal known as "edge effect", whereas this effect is not seen with BSEs. BSEs produce images which are more representative of what is actually seen under a light microscope (i.e. are closer to reality) (Taylor, 1986).

For the present study an ISI ABT-55 SEM fitted with an environmental chamber in BSE mode was used. This type of SEM is usually used for the examination of **original** specimens as there is no need for a conductive coating to be applied to the specimen or for it to be permanently mounted on a stub. However, this SEM system was also found to produce high quality micrographs of **replicas** (although they do require the application of a conductive coating because epoxy resin gives a poor signal (see below)) and so it was used in this study.

This ISI ABT-55 SEM works in the following way. While the electron gun and column are maintained at a high vacuum (10^{-4} Torr (Taylor, 1986)) the specimen chamber is held at a lower vacuum (10^{-1} - 10^{-2} Torr (Taylor, 1986)) than in a conventional SEM. High energy BSEs are used to image the specimen as the increased "noise" (air) in the chamber resulting from the lower vacuum interferes with the signal. The detector is placed directly above the specimen (see Fig. 3.7). The air molecules present in the chamber help to dissipate electrical charge which may build up on the specimen which means that specimens do not need to be coated with a conductor. This has been a very beneficial development in terms of examining valuable fossil material. However, the epoxy replicas used for the present study were given a conductive coating. This is because epoxy resin is largely comprised of carbon which, due to its low atomic number, gives a very poor BSE signal. Fossils and extant material, on the other hand, have a greater mineral content. As this (original) material is higher in atomic number it produces a better BSE signal and thus, no conductive coating is needed to enhance the image.

3.5 SEM Examination Of Specimens

Lower molars were placed inside the SEM chamber in their occlusal position so that the hypoflexid groove (that which runs between the protoconid and hypoconid) was parallel to x-axis of the viewing screen for lower molars, following Gordon (1980, 1982). Upper molars were oriented such that the occlusolingual groove, which runs between the protocone and hypocone (Korenhof, 1960) (Figure 3.8), was aligned parallel to x-axis of the screen. This orientation was used for all SEM examination of microwear and for all photomicrographs taken. The SEM beam was set at an accelerating voltage of 15 kV with the bias (beam current) set at 100, and beam spot size was set at the maximum level available for this low vacuum SEM. A very low

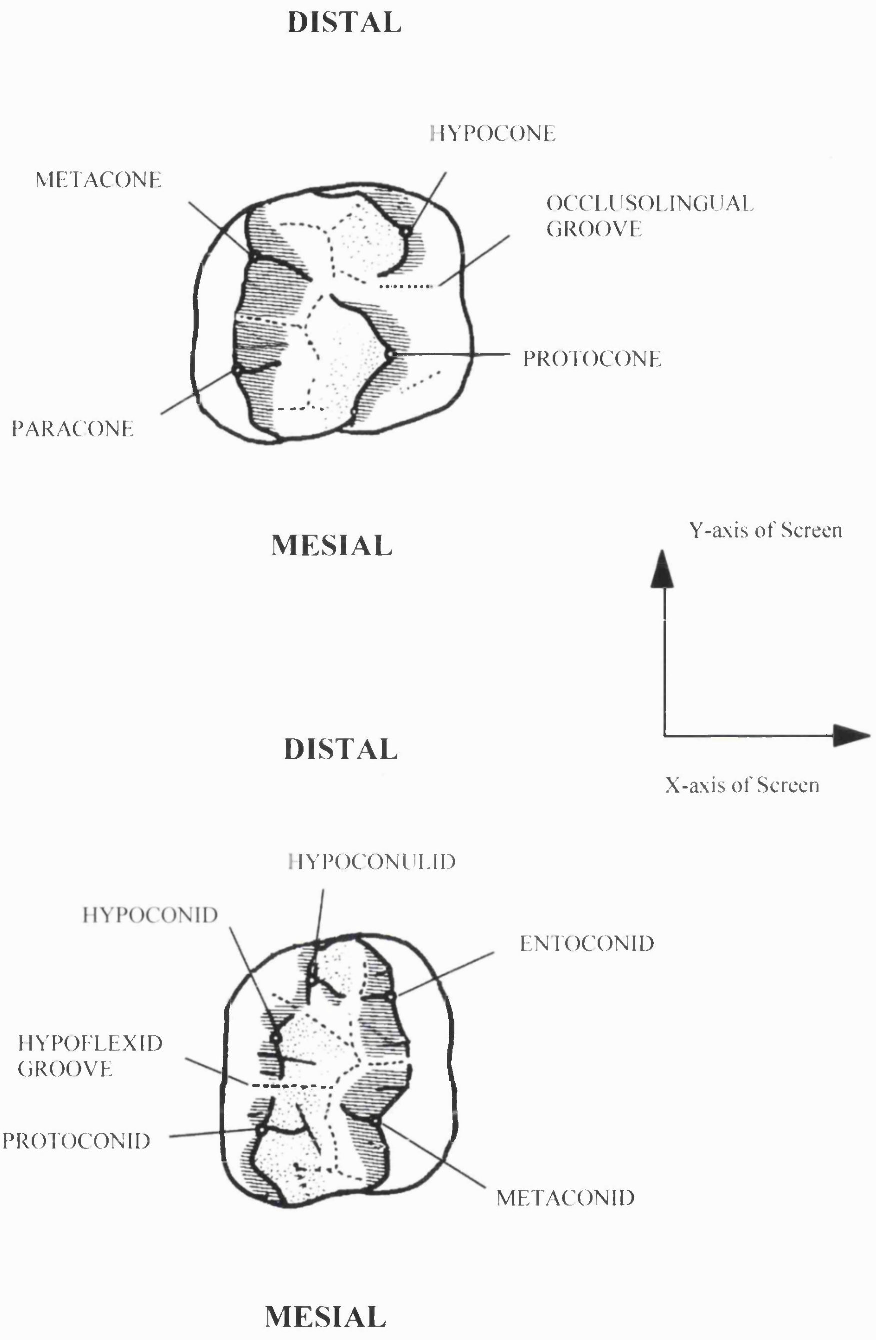


Figure 3.8. Orientation of specimens in the SEM chamber. Upper teeth (above) were aligned so that the occlusolingual groove was parallel to the x-axis of the SEM screen. Lower molars (below) were oriented such that the hypoflexid groove was parallel to the x-axis of the SEM monitor. (*After Kay, 1977b*).

working distance (the area between the top of the specimen and the final condenser lens) was used to orient the specimens inside the chamber, but a working distance of between 20 and 25 mm was used for taking the micrographs used for analysis. This working distance was selected for use as it was the best balance between good depth of field, resolution, and signal strength and the size of the specimen itself. Ungar (1992, 1994) has also found that this working distance represents the best combination of the factors mentioned above.

Microwear researchers tend to use either magnifications of x150-200 (for example, Gordon, 1980, 1982, 1984b, 1988; Grine, 1981, 1984, 1985, 1986, 1987; Ungar, 1992, 1994) or higher ones of x300-500 (for example, Teaford, 1985, 1986, 1993; Teaford and Runestad, 1992; Teaford and Robinson, 1989; Teaford and Walker, 1984). Lower magnifications allow a larger area of the facet to be analysed but have the disadvantage of poorer visibility of smaller features (Gordon, 1988). Higher magnifications allow the resolution of smaller features but sample less of the facet with greater potential to miss significant features or variations within a surface (Gordon, 1988). Ungar (1992) has stated that magnification level may be seen as a balance between resolution and surface area that can be examined. One way to tackle the dilemma may be to take micrographs at lower magnifications and then enlarge the image for data collection following Gordon (1988) and Grine (e.g. 1981, 1986, 1987).

All micrographs used for this study were taken at 200x, although varying magnifications were used initially to orientate each specimen following Ungar (1992).

The SEM micrographs were then enlarged to x400 to facilitate the measurement of smaller features.

3.6 WEAR STAGE

One of the aims of the study is to examine the effect of age on dental microwear. Age was estimated by wear stage using categories of wear identified by Gençtürk (1994) initially. These categories were then condensed into four wear stages as follows:-

Stage 1 - Teeth relatively unworn. Facets often apparent all over the occlusal surface.

Stage 2 - A small dentine exposure on one of the cusp tip areas.

Stage 3 - Enlarged dentine exposures on several/all cusp tips.

Stage 4 - Coalescence of dentine exposures on two or more of the cusps.

All specimens used in this study were assigned to one of the four wear stages (see Appendix 1). The Pasalar sample displayed the least wear and displayed a correspondingly large number of wear stage 1 specimens. Only one wear stage 4 specimen from the whole sample (*Gorilla gorilla gorilla*) was identified (see Appendix 1).

3.7 Surfaces Examined

Three molar wear surfaces on each specimen were examined. Both Phase I and Phase II (Kay, 1977b; Kay and Hiiemae, 1974) facets were included in order to investigate the effect on microwear patterns of the different functions of the occlusal surface during mastication. Facet 1 which is created during Phase I (Kay, 1977b) and facet x which is formed during Phase II (Kay, 1977b) were selected following Gordon (1980, 1982). Facet 9 which is formed during Phase II (Kay, 1977b) was also included in the study for two reasons. First, it was included as a comparison to facet x so that variation in two facets with the same masticatory function could be investigated. Secondly, facet 9 is the surface which is most commonly used for dietary inferences made from microwear studies (e.g. Grine, 1987; Grine and Kay, 1988; Teaford, 1985; Teaford and Walker, 1984; Teaford and Robinson, 1989; Teaford and Glander, 1991; Teaford and Runestad, 1992; Ungar, 1996). Figure 3.9 indicates the location of the three surfaces examined in this study. **Facet 1** on the mandibular molars is located distobuccally to the cusp tip on the protoconid with the hypoflexid (the transverse groove between the protoconid and hypoconid) as a posterior border (Gordon, 1980), and on the upper molars is found on the mesolingual surface of the paracone (Kay, 1977b). **Facet x** on the lower molars is also found on the protoconid and it lies distolingual to the cusp tip with the hypoflexid groove comprising its distal border

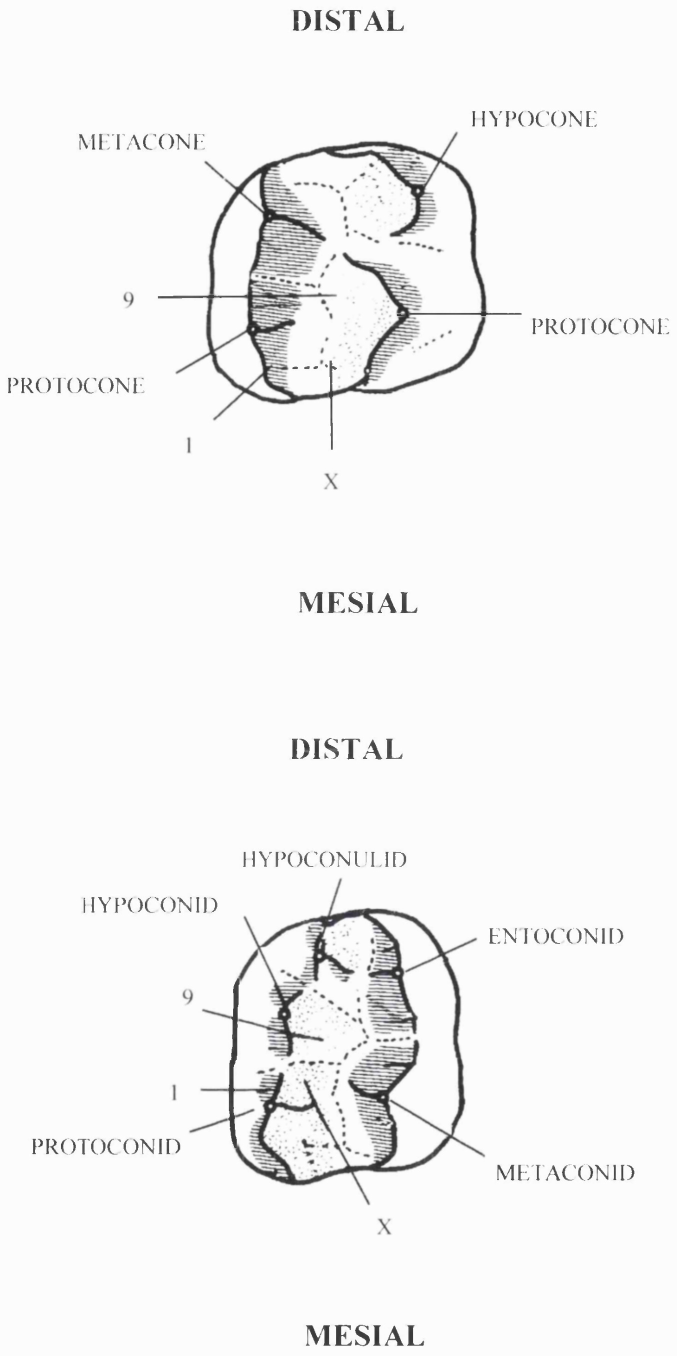


Figure 3.9. Upper (above) and lower molar (below) wear facets. (*After Kay, 1977b*).

(Gordon, 1980). On the upper molars it is located on the mesial portion of the protocone (Kay, 1977b). **Facet 9** is usually a large surface which is located on the lingual surface of the hypoconid in the lower molars and is situated on the distobuccal surface of protocone on the upper molars (Kay, 1977b; Kay and Hiiemae, 1974). It was not possible to take micrographs of the whole facet due to the large size of the surfaces under study. Each facet was first examined at a low magnification and working distance to check for anything unusual, such as taphonomic alterations. If everything appeared normal and the tooth was not heavily worn, a number of micrographs were taken of the approximate centre of the facet. However, if the tooth was very worn, or post-mortem (for example, cleaning) or taphonomic (for example, abrasion of enamel by sediment) damage obscured the middle of the facet, several micrographs were taken of the adjacent areas. In the cases where micrographs could not be taken at the centre of the wear surface, micrographs were taken towards the lingual part of the facet for wear facets x and 9, and of the buccal portion of the surface for facet 1. These areas were chosen to avoid possible encroachment of other wear facets during the wear process (Gordon, 1980). It was for this reason that micrographs of heavily worn specimens were also not taken at the centre of the facet but areas were selected where encroachment by other wear facets was unlikely. It was necessary to take several micrographs of each facet as in many instances some areas exhibited poorer contrast than others, and in this way SEM time could be minimised.

3.8 FEATURE MEASUREMENT

Once the micrographs were taken and developed they were selected for enlargement. As several micrographs were taken per facet a procedure to minimise bias was devised for selection of the micrograph to be used for analysis. This was done by shuffling the micrographs like a pack of cards with the images face down, and selecting one at random. However, the choice of micrograph was often imposed by the fact that there was poor contrast on one of the micrographs, or that there was post-mortem (recovery/cleaning) damage.

Following Ungar (1992, 1994) features within a portion of each micrograph were measured. The portion of the micrograph used by Ungar had dimensions measuring 3.2 x 2.4 inches which represented approximately 0.124 mm^2 of the actual surface of the tooth. As the present study employed 400x magnification, rather than x200 magnification used by Ungar, the dimensions of the field were altered accordingly so that they encompassed the same area used by Ungar. Thus, a 6.4 x 4.8 inch portion of each micrograph was measured which represents 0.000192 $inches^2$ (or approximately 0.124 mm^2) of the actual surface of the tooth. A 6.4 x 4.8 inch acetate grid containing 20 boxes was overlaid on each micrograph to facilitate measuring (Figure 3.10). To avoid observer bias the centre of each micrograph was always selected for measurement. In the event that features in the centre of a micrograph were obscured in any way an adjacent area was selected for measuring. In these cases the area which displayed the best contrast and resolution was selected for measurement. The field chosen for each micrograph was marked so that measuring could be repeated on exactly the same area

Figure 3.10. The 6.4 x 4.8 inch field which was used for measuring features. An acetate overlay (with the dimensions 6.4 x 4.8 inches) with twenty boxes demarcated was placed on top of each micrograph. Features were marked with a pen as they were measured.

at a later date, if necessary. Each micrograph with the 6.4 x 4.8 inch overlay was positioned on the digitser platform with an additional piece of acetate on top. This allowed features to be marked by pen as they were measured to avoid duplicate measuring. A Jandel Scientific graphic digitiser (model number 2210-0.30.C manufactured by the Numonics Corp. (PA 18936, USA)) was used along with DIGITIZE (Version 2.00) (a software programme developed by Earl Weir (Analytical Data Processing, 602 St. Johnsbury Road, Baltimore, MD 21228-4046, USA)) to record and measure features. This digitising programme records the length, width, and orientation of each feature (using four co-ordinates per feature) as well as the total number of features for each micrograph.

Variations in the appearance of microwear features can affect their recognition and recording. These differences can be caused by a number of factors. For example, the degree of contrast and illumination can vary as a result of the day-to-day operation of the SEM, and from specimen to specimen. A very flat facet on a specimen with little topography will give a low signal with this type of low vacuum SEM and detector, and microwear features will be hard to see due to the lack of contrast. Another factor which may cause variation in the appearance of microwear scars is the turnover of microwear features. Features are constantly being reworked through time with certain types of scars becoming "secondarily enlarged and shallowed" (Gordon, 1982) as the tooth and microwear features wear down. The margins of scars become difficult to discern. Recent features are darker in appearance than older scars which are often only faint grey shadows with blurred margins.

As a result of the variation in the appearance of microwear features it has been difficult for researchers to develop a standard method for recording microwear, or producing automated image analysis systems. It was therefore, necessary to develop a protocol for microwear feature recognition and measurement for the present project. The early stages of this protocol were devised with Stan Bloor (pers. comm.). The following protocol was adopted :-

1. Features were measured only if they possessed margins which could be discerned with confidence. Scars which were very small, and/or very faint in appearance were excluded from measurement because they could not be accurately recorded.

2. Often features were truncated (that is, they were cut by the 6.4 x 4.8 inch field) leaving a portion of the scar outside the area used for recording. In this case only the part of the feature which was inside the field was actually measured. In most cases it was **striation length** which was truncated (see section 3.10 for definition) and for this reason scratch lengths were not included in the analysis. Pits (see section 3.10 for definition) were occasionally truncated and this may result in narrower and/or shorter pit dimensions. (Mean percentage of truncated pits as measured on 3 micrographs with varying degrees of wear is 1.8%).

3. Microwear features which had been formed inside existing scars were measured only if their respective margins could be seen clearly and they were not exposed prisms.

4. Linear features which terminated as a non-linear scar were measured as two separate defects if their borders were visible.

5. Linear features which were interrupted along their trajectory at one or more points but appeared to be the same feature rather than a number of different features were measured as a single entity.

6. Artefacts which were produced during the fossilisation process (for example, from sediment abrasion (see Chapter 3)), the initial preparation of specimens (for example, cleaning damage), or the replication process (for example, degassing bubbles) could be easily identified and excluded from measurement (see Gordon 1983, 1984c; Grine 1986 ; Puech *et al.*, 1985; and Teaford, 1988 , 1991, 1994 for discussion). Specimens were excluded from the analysis all together if they displayed several artefacts, or severe damage from one of the processes described above.

7. A time limit of a maximum of one hour was imposed for the measurement of each micrograph as it can often take a long time to digitise a single micrograph. This is because microwear images are extremely complicated and the longer a micrograph is examined the more features come to light. This can lead to several hours of measurement for a single image (see also discussion and references in Teaford 1994). A strict time frame was imposed on the present study. In most cases digitising of a single micrograph took much less than one hour but occasionally a full hour was needed to record all features. Measuring was confined to the most obvious features in each box of the grid in the rare instances where measuring was likely to take more than one hour. The minimum time required to record all scars present on a single micrograph was five minutes. The usual time taken to digitise features ranged between twenty and forty minutes.

A sampling strategy which includes the following 4 steps was used for the measuring of microwear features:-

1. A small area of each facet was imaged using the SEM.
2. After the image had been enlarged features within 6.4 x 4.8 inch overlay were measured.
3. The measuring process itself was restricted to only those features which were visible enough to be recorded with confidence.
4. The time allowed for feature measurement was up to a maximum of one hour per image.

3.9 CORRECTION OF FORESHORTENED FEATURES

Hominoid molars do not have flat occlusal surfaces. The vertical projection of the cusps means that many of the surfaces on the tooth slope relative to the occlusal plane. Microwear features present on an inclined molar surface will be subject to distortion in the form of foreshortening, so that measurements of features will be smaller than they are in reality (Gordon, 1980 and 1982). In addition, the facets slope in more than one direction, so that it is necessary to calculate facet tilt in two axes. For the present study all specimens were examined in their occlusal position. As a result, feature foreshortening due to tilted facets was a potential source of error. A procedure was developed to ascertain the amount of distortion and to correct the foreshortened measurements.

The first step in the tilt correction procedure was to measure the slope of each of the three facets in two dimensions following Gordon (1980, 1982). For this study a Standard Reflex Microscope (Reflex Measurement Ltd., Hadley House, Water Lane, Butleigh, Somerset BA6 8SP, UK) was employed to measure the two tilt angles. The Reflex Microscope is a non-contact instrument which allows objects to be measured directly in three dimensions (see MacLarnon, 1989 for full review). An ordinary stereomicroscope is used to observe the object which is placed in front of a semi-silvered mirror. The three-dimensional properties of the ensuing virtual image can then be seen. A small light spot in the field of view is moved in three dimensions until it corresponds with the desired point on the object's surface and its co-ordinate is then recorded by pressing a switch. The measuring accuracy given by the manufacturers is a repeatability spread (user accuracy) of 5μm (x or y) and 15μm (z), and a standard error of pointing (the accuracy of the instrument itself to resolve a position) of 2μm in x and y and 4μm in z.

Each specimen was placed under the Reflex Microscope in the same orientation as used in the SEM examination (the hypoflexid or occlusolingual groove aligned parallel to the x-axis of the field of view) (Fig. 3.8). This was facilitated by the replica being glued to the SEM stub. Three co-ordinates were recorded for each facet of all specimens.

TAN 1.B, a software programme which automatically corrects foreshortened features, was especially developed for this study (written by Andrew King). The programme works in the following way:-

1. Using the co-ordinates of the three points measured using the Reflex microscope the equation of the plane defined by the facet is obtained (the facets were assumed to be planar).
2. The facet tilt angles in x and y are determined by calculating the angles of orientation the plane makes with the x and y axes of the specimen (in standard orientation, (see Figure 3.8)).
3. The digitising programme outputs a file (containing feature orientations, feature lengths and widths as well as 2 dimensional co-ordinates of each feature) which is read into TAN 1.B (this is known as an 'input' file). By applying standard geometry to the data in the 'input file' and the facet tilt angles (in x and y) the correction utility TAN 1.B then calculates the true lengths and widths of each feature.

A comparison between corrected and uncorrected microwear features was carried out. The correction increased **all** feature lengths and widths although the increase varies due to orientation of the individual features and slope of the facets (see Appendix 2). However, any difference between corrected and uncorrected measurements must be assessed using the microwear variables that will ultimately be used to make dietary inferences. That is, frequencies, proportions, lengths, and widths of "pits" and "scratches" (see section 3.10 for definition)). It can be seen that these decrease as well as increase after correction despite the fact that all lengths and widths of unclassified microwear features show an increase after correction. This is because a feature may be classified differently after correction. That is, a pit may become a scratch and *vice versa*, and there is a risk that different features will be compared in any testing of variation between original and uncorrected microwear variables. An example of this problem is seen in specimen E626 (facet 1) from Pasalar. An examination of the original features reveals the presence of only one pit with a (mean) width of 3.51μm and a (mean) length of 8.22μm (Appendix 3). After the features have been corrected two pits are present on this specimen (Appendix 3). The new mean pit width is 3.21μm and mean pit length is 7.86μm.

As there is variation in the frequencies and dimensions of original and corrected microwear variables in individual specimens it may be more appropriate to use species means. Any irregularities within particular specimens are likely to be balanced out by examining the species mean. In addition, as species means, not individual specimens, will be used in any dietary inferences made in this study, it is important to examine whether the use of original and corrected microwear data result in a difference in species means.

Mean numbers of microwear features and their lengths and widths for each species are given in Table 3.3. Wilcoxon Matched-Pairs Signed-Ranks tests were carried out to compare the original and corrected data for each facet of each species. This test was chosen because most of the data are not normally distributed (see section 3.12) and tests for differences between the signed ranks of the data for each pair.

The results of the Wilcoxon's tests are displayed in Table 3.4. There is no significant difference between original and corrected numbers of pits and scratches (see section 3.10 for definition), or percentage pits (see section 3.12 for calculation of percentage

FACET 9	No. Pits (A)	No. Pits (B)	No. Scratches (A)	No. Scratches (B)	% Pits (A)	% Pits (B)
Gorilla	41.15	40.92	58.08	58.31	33.39	33.21
Pan	53.22	54.11	60.33	61.22	39.03	39.67
Pongo	76.20	76.60	95.55	95.15	43.01	43.05
G. alpani	81.17	80.39	67.50	68.28	55.09	54.61
FACET X						
Gorilla	24.83	24.83	40.33	40.33	32.64	32.64
Pan	46.13	45.87	41.37	41.63	44.23	43.87
Pongo	82.32	81.89	81.84	82.26	48.16	47.99
G. alpani	93.92	93.46	66.00	66.46	58.73	58.70
FACET 1						
Gorilla	7.23	7.69	54.15	54.46	11.38	13.12
Pan	6.00	5.80	46.40	46.60	10.56	9.82
Pongo	20.60	20.50	78.15	78.25	18.11	18.25
G. alpani	19.60	20.40	71.20	70.40	21.02	22.46

FACET 9	Pit width (A)	Pit width (B)	Pit length (A)	Pit length (B)	Scratch width (A)	Scratch width (B)
Gorilla	4.51	4.73	10.31	10.78	2.35	2.67
Pan	5.15	5.63	10.82	11.11	2.32	2.50
Pongo	4.51	4.78	1.75	1.86	1.75	1.86
G. alpani	3.42	3.66	6.83	7.28	1.74	1.92
FACET X						
Gorilla	4.77	4.47	8.93	9.59	2.74	3.00
Pan	5.41	5.90	12.80	14.72	2.85	2.95
Pongo	3.81	3.97	8.04	8.37	1.69	1.77
G. alpani	4.56	4.89	8.64	9.26	1.75	1.87
FACET 1						
Gorilla	2.96	3.86	7.23	9.60	2.36	2.94
Pan	2.85	3.76	7.80	10.25	2.78	3.61
Pongo	4.55	5.44	9.37	11.23	1.76	2.18
G. alpani	4.79	5.45	10.19	11.50	1.71	2.12

Table 3.3. Original (A) and corrected (B) microwear data for each hominoid species.

FACET 9	**No. Pits**	**No. Scratches**	**% Pits**	**Pit width**	**Pit length**	**Scratch width**
Gorilla	*p*=0.541	*p* =0.541	*p* =0.721	*p* =0.075	*p* =0.221	*p* =0.541
Pan	*p* =0.109	*p* =0.109	*p* =0.109	*p* =0.089	*p* =0.110	*p* =0.007*
Pongo	*p* =0.477	*p* =0.477	*p* =0.721	*p* =0.000*	*p* =0.000*	*p* =0.000*
G. alpani	*p* =0.241	*p* =0.241	*p* =0.445	*p* =0.001*	*p* =0.003*	*p* =0.000*
FACET X						
Gorilla	*p* =1.000	*p* =1.000	*p* =1.000	*p* =0.002*	*p* =0.005*	*p* =0.134
Pan	*p* =0.465	*p* =0.465	*p* =0.715	*p* =0.012*	*p* =0.012*	*p* =0.112
Pongo	*p* =0.294	*p* =0.294	*p* =0.363	*p* =0.000*	*p* =0.002*	*p* =0.000*
G. alpani	*p* =0.894	*p* =0.894	*p* =0.917	*p* =0.002*	*p* =0.002*	*p* =0.005*
FACET 1						
Gorilla	*p* =0.402	*p* =0.402	*p* =0.345	*p* =0.003*	*p* =0.010*	*p* =0.002*
Pan	*p* =0.655	*p* =0.655	*p* =0.655	*p* =0.068	*p* =0.068	*p* =0.043*
Pongo	*p* =0.906	*p* =0.906	*p* =0.813	*p* =0.204	*p* =0.204	*p* =0.055
G. alpani	*p* =0.086	*p* =0.086	*p* =0.152	*p* =0.004*	*p* =0.008*	*p* =0.001*

Table 3.4 Wilcoxon Matched-Pairs Signed-Ranks probability values for comparisons between original and corrected microwear data by facet for each hominoid species (significant probability values are shown by asterisks).

pits) for any species. There are however, significant differences between original and corrected feature lengths and widths for most species and facets.

Mean pit width

Original and corrected mean pit widths on facet 9 are significantly different in *Pongo* ($p<0.001$) and *G. alpani* ($p=0.001$) (Table 3.4). For facet x original and corrected mean pit widths are significantly different in *Gorilla* ($p<0.05$), *Pan* ($p<0.05$), *Pongo* ($p<0.001$), and *G. alpani* ($p<0.05$) (Table 3.4). Original and corrected mean pit widths on facet 1 are significantly different in *Gorilla* ($p<0.05$) and *G. alpani* ($p<0.05$) (Table 3.4).

Mean pit length

On facet 9 original and corrected mean pit lengths are significantly different in *Pongo* ($p<0.001$), and *G. alpani* ($p<0.05$) (Table 3.4). Original and corrected mean pit widths on facet X are significantly different in *Gorilla* ($p<0.05$), *Pan* ($p<0.05$), *Pongo* ($p<0.05$), and *G. alpani* ($p<0.05$) (Table 3.4). On facet 1 original and corrected mean pit widths are significantly different in *Gorilla* ($p<0.05$), and *G. alpani* ($p<0.05$) (Table 3.4).

Mean scratch width

Original and corrected mean striation widths on facet 9 are significantly different in *Pan* ($p<0.05$), *Pongo* ($p<0.001$), and *G. alpani* ($p<0.001$) (Table 3.4). On facet x original and corrected mean striation widths are significantly different in *Pongo* ($p<0.001$), and *G. alpani* ($p<0.05$) (Table 3.4). Original and corrected mean striation widths on facet 1 are significantly different in *Gorilla* ($p<0.05$), *Pan* ($p<0.05$), *Pongo* ($p=0.001$), and *G. alpani* ($p<0.001$) (Table 3.4).

Although Gordon (1980,1982) has also developed a tilt correction procedure it is not possible to make a comparison with the data presented in this study. This is for several reasons. First, in this study tilt in X and Y was used directly for the correction of microwear features whereas Gordon combined tilt in X and Y. Second, Gordon applied the correction to **lengths** of striations only. In the present study lengths and widths for **all** dimensions were corrected (although scratch length is not included in the main analysis (see section 3.2). Third, in the present study each feature was corrected automatically and the amount of correction applied depended on the orientation of that feature as well as the tilt in x and y of the facet. Gordon, however, calculated the amount of distortion for a given degree of facet tilt and then corrected **all** features on that facet by the same amount. In sum, the methods used in the present study are based on more modern technology and are more exact than those used by Gordon.

3.10 FEATURE CLASSIFICATION

After all the original measurements for a given specimen and facet had been corrected for tilt distortion, microwear features were then divided into types. The two categories mostly commonly used in microwear studies are "pits" and "striations". The relative proportions of pits to striations has been shown to be useful in distinguishing between different facets as well as in discriminating between dietary categories (Gordon, 1988).

Striations and pits are usually defined on the basis of a length:width ratio. Microwear researchers use different ratios to distinguish between scratches and pits, but the most commonly used ratio is 4:1 (e.g. Grine, 1986; Solounias *et al*, 1988; Teaford, 1985, 1986, 1988, 1993; Teaford and Walker, 1984; Teaford and Robinson, 1989; Teaford and Runestad, 1992). All features with a length:width ratio greater than or equal to 4:1 are classified as scratches and all those with a ratio below 4:1 are categorised as pits.

For this study PYTH (a software programme written by Earl Weir (Analytical Data Processing, 602 St. Johnsbury Road, Baltimore, MD 21228-4046, USA)) was used to assign microwear features into the two categories ("pits" and "striations") using a length:width ratio of 4:1.

3.11 INTRA-OBSERVER ERROR

Microscopic wear surfaces are extremely complex images to measure. In order to assess intra-observer error in the measurement of microwear two types of error estimation were carried out - the accuracy of feature measurement, and the ability to recognise the same features were assessed. Measurement error tests were not commenced until measuring had settled into a routine (the fossil species was measured once and then the data was discarded due to the necessity for a slight modification to the digitising programme). After this the microwear of *G. alpani* was measured again and these measurements were used in this study. This repetition allowed a measuring routine to be established before the microwear data was included in the analysis and prior to beginning error tests.

The possibility that the observer could unconsciously memorise a given micrograph and introduce bias into the estimates was also recognised. In order to reduce this risk there was a minimum interval of two months between sets of measurements.

Intra-observer error in measuring

Eight micrographs were chosen at random from the *Griphopithecus alpani* sample. The acetate overlay used for the original data collection procedure was placed on top of each micrograph and twenty features were measured using the digitising methods and software described above. These features were selected randomly in the first session (by dropping a pin once into each of the twenty boxes in the overlay and measuring the feature nearest to the pin point). The features selected were measured once during the same measuring session. The same twenty features on each micrograph were measured again after an interval of at least two months. After another period of at least two months the micrographs were measured for the final time giving a total of three sets of measurements.

After the measurements had been taken the *mean percentage error* was calculated separately for lengths and widths. The mean percentage error was calculated following White and Folkens (1991), and is described below.

a) The overall mean is calculated by summing the three means of each set of measurements and dividing by the number of sets (in this case 3) (A)

b) The mean absolute difference is then calculated. This is obtained by determining the difference between the mean for each set of measurements and the overall mean, and then calculating the mean of these three deviations (B)

c) The mean absolute difference is then divided by the overall mean and the resulting value is expressed as a percentage ((A/B) * 100).

Table 3.5 displays the mean percentage error for lengths and widths for each specimen. The overall mean percentage error for lengths is 8.43% and for widths is

12.05%. Mean percentage error gives an indication as to the magnitude of the error but is influenced by the size of the measurements themselves (Utermole, *et* al., 1983). This means that small measurements will be more greatly affected than larger ones hence, greater error in width measurement than length measurement in the present study.

Specimen	**Lengths**	**Widths**
K1316	5.03	10.28
F107	10.51	12.89
B513	10.96	11.74
K1447	10.17	13.58
H103	7.91	12.56
C207	7.72	11.20
K1367	6.16	11.00
E629	8.96	13.11
Overall mean % error	**8.43**	**12.05**

Table 3.5 Mean percentage error for lengths and widths per specimen, and overall mean percentage error for lengths and widths.

Intra-observer error in recognition of features

Two months after measuring had begun eight micrographs were selected at random from the *G. alpani* sample. The acetate overlay used for the original measurement was placed on each micrograph and all features were measured. Two months later the same eight micrographs were measured again. For the assessment of recognition error the two sets of measurements for each micrograph were compared to the original set of measurements taken which were used in the data analysis in the present study. Thus, three sets of measurements, each taken at a minimum of two month intervals, were available for eight specimens.

Mean percentage error was calculated for the total number of features on each micrograph as well as percentage pits. Table 3.6 displays the mean percentage error for each specimen as well as the overall error in recognising the same features. Overall mean percentage error in the total number of features recorded is 13.93%, and for percentage pits the overall mean percentage error is 16.68%.

Specimen	**% error (% pits)**	**% error (total no. features)**
B510	12.94	36.90
B523	51.89	18.67
E626	13.75	10.60
G1303	12.12	9.57
H272	3.93	5.61
K1394	21.67	14.87
K1399	3.65	11.80
K1447	13.53	3.38
Overall % error	**16.68**	**13.93**

Table 3.6 Mean percentage error in recognition of total number of features and percentage pits for each specimen, and overall mean percentage error for total number of features and percentage pits.

3.12 DATA ANALYSIS

The microwear attributes examined were number of pits, percentage pits, number of striations, total number of features, mean pit width, mean pit length, and mean scratch width per micrograph. These are the most commonly-used variables in the literature (e.g. Gordon, 1982; Teaford and Walker, 1984; Grine, 1987; Teaford and Runestad, 1992; Strait, 1993; Ungar, 1994).

It has generally been found that microwear data do not tend to meet the assumptions of parametric statistical tests and researchers have used various methods to cope with this problem (e.g. Teaford and Walker, 1984 (chi-square and Mann-Whitney tests); Van Valkenburgh *et al.*, 1990 (arcsine and log transformations followed by non-parametric (Kruskal-Wallis) ANOVA); Solounias, *et al.*, 1988, and Teaford and Runestad, 1992 (arcsine transformation). More recently Maas (1989, 1991) suggested that the **rank transformation** procedure (Inman, 1974; Conover and Inman, 1981) is an appropriate alternative. With this procedure each variate is replaced by its rank and parametric tests are then performed on the ranks.

The data for this study were tested for normality using the Lillifors test (this is a modified version of the Kolmogorov-Smirnov, and is used when means and variances must be estimated from the data) and the Shapiro-Wilks' test (which, in relation to other tests for normality, shows good power) (Norušis, 1993a, and reference therein). Since most of the data are not normally distributed, the variates were ranked, and two and three factor analysis of variance was performed following Ungar (1992, 1994). In the event that a variable was normally distributed, analysis of variance (ANOVA) was carried out on **both** the actual data and the ranked values.

Two and three factor analysis of variance (ANOVA) were used in this study. This type of analysis allows the effects of two or more independent variables (for example, facet type, sex, and species) on a response variable (for example, pit width) to be examined. Each independent variable (these are also known as "factors" or "grouping" variables) has a number of **levels**. For example, in this study one of the independent variables is "species" which is comprised of **four** levels - *Gorilla*, *Pan*, *Pongo*, and *G. alpani.*

An important aspect of this statistical method is that it evaluates the **interaction** of the two independent variables (Howell, 1995). An interaction is the dependence of a factor on one level of another (Sokal and Rohlf, 1995). For example, females display greater numbers of pits than males on facet 9, but males have more pits than females on facet x. Thus, any statement about sex differences in number of pits has to be qualified by the facet which is under question. More simply, it is whether the two factors (for example, species and facet) **jointly** have more (or less) of an affect on the response variable (for example, pit width) than if they are considered individually (Norušis, 1993b).

The first step in factorial ANOVA is to identify whether there is an interaction between the two independent variables. If there is a significant interaction it is not useful to then examine the effect of each factor individually. This is because of the reasons mentioned above - any statement about the effect of one factor must be qualified by the other factor levels. However, if there is no significant interaction then the effect of the two independent variables on the response variable is considered **separately**. These are known as the **main effects**.

Where there is a significant main effect (for example, if pit width were to differ significantly according to species) the factor levels are tested to identify the source of the variation. This is done by carrying out comparisons between all possible combinations of **pairs** of levels. In this study pairwise comparisons with Bonferroni corrections were performed using the SPSS (Version 6.0 for Windows) software programme. "Simple" contrasting, which uses the mean of one factor level as a reference group and compares all the other levels to it was selected for this study. By changing the reference level category one or two times more and re-running the ANOVA every possible pair of factor levels was compared and variation could be assessed.

All microwear variables presented in this study were calculated for each micrograph. The data were analysed in two parts as follows.

3.12.1 Analysis of microwear characteristics

Two factor ANOVA was carried out to determine firstly, whether there is an interaction between **facet** and **species** with respect to microwear characteristics. That is, whether these two factors jointly have more of an affect on the response microwear variables than if they are considered separately. Secondly, where there was no significant interaction between the independent variables, **facet type** and **species** were examined separately to assess whether they have a significant effect on microwear attributes. Two-way ANOVAs were carried out on the following response variables:-

1. **Pit density** - calculated as the number of pits per 6.4 x 4.8 inch field for each micrograph

2. **Percentage pits** - calculated as (number of pits ÷ total number of features) x100, per 6.4 x 4.8 inch field for each micrograph

3. **Striation density** - calculated as the number of striations per 6.4 x 4.8 inch field for each micrograph

4. **Total number of features** - calculated as the number of features per 6.4 x 4.8 inch field for each micrograph

5. **Mean pit width** - calculated as the average maximum pit width per 6.4 x 4.8 inch field for each micrograph

6. **Mean pit length** - calculated as the average pit length per 6.4 x 4.8 inch field for each micrograph

7. **Striation width** - calculated as the average maximum striation width per 6.4 x 4.8 inch field for each micrograph.

3.12.2 Sex and Wear stage

To determine whether microwear features are response on sex and/or age as well as facet type, three factor ANOVA was carried out. Facet, sex and wear stage (see section 3.6) were used as the independent variables, and the same seven response variables as discussed in section 3.12.1 were employed. Only *Pongo* was used in this analysis as sample sizes for sex and wear stage samples within the other species were small. Rank-transformed values were used for the response variables. In addition, where the data has a normal distribution the analysis was also performed on the actual data.

CHAPTER 4: THE EFFECTS OF TAPHONOMIC PROCESSES ON DENTAL MICROWEAR

4.1 INTRODUCTION

During an animal's lifetime microscopic alterations to its teeth are made by food. However, after death a number of agents have the potential to cause damage to the enamel which are not related to the ingestion of food. Taphonomic processes are those which affect the bones of an animal after its death through to fossilisation, and recovery and conservation of the remains. Sedimentary abrasion, weathering, and exposure to an acidic environment are just a few of the taphonomic agents that can come into force before burial and during the fossilisation process. These taphonomic agents can cause the alteration or obliteration of existing microscopic features, and they may need to be taken into consideration by researchers making dietary inferences from dental microwear analysis. In addition, specimens may be damaged during and after recovery, for example, cleaning can often affect enamel but these types of post-mortem damage are not under investigation here.

Several experiments have been done to simulate taphonomic processes and to document their effects on enamel and dental microwear features (e.g. Gordon, 1983, 1984a; Puech *et al.*, 1985). In an investigation of the effects of sedimentary transport on microwear, Gordon (1983 and 1984a) tumbled human teeth in four different types of dry sediment, and in aqueous mixtures of these sediments. She found that microwear features were altered and in some circumstances completely obliterated, with the amount of alteration to the microwear being positively correlated with the size of the sediment particles. There was no evidence, however, that new features were added to existing microwear patterns. Puech *et al.* (1985) also conducted an experiment in which a tooth was abraded with an air-propelled stream of sand. At first the enamel became pitted, and then it took on a rough, eroded appearance, often with the abrasive damage following the orientation of the enamel prisms. Striations were formed when sand particles were rubbed across the enamel surface of another specimen. These authors observed that aprismatic enamel was eroded after a tooth was tumbled in water only, and that the superficial enamel on another specimen was dissolved, with remaining features being blunted after tumbling in sea water. When quartz was added to the sea water the tooth became rounded, and some pieces of enamel were chipped away from the surface. A number of striations were formed similar to those produced by the sand abrasion experiment. As the distance travelled by the tooth in the tumbler increased so the abrasion process became more rapid (exponentially, as the speed of abrasion was not greatly accelerated until after 400 km of tumbling). The total distance that the specimen travelled was 4000 km although the time taken for this is not given the authors.

The effect of chemical erosion of enamel was also investigated by Puech *et al.*(1985) who etched a tooth with a 30% solution of phosphoric acid for 60 seconds. Initially shallow pits appeared in the enamel which, with repeated applications of acid, then enlarged to expose a network of enamel prisms. Eventually the prisms could no longer be distinguished and no features could be seen at all.

As fossil specimens from the Miocene site of Pasalar (Turkey) dated to 15 million years are used in the dental microwear analysis in this study, the possibility that microwear on some of the specimens had been altered by a taphonomic process was considered. Taphonomic agents which may have acted upon the fossils from Pasalar include weathering, transport, *in situ* abrasion, and even digestion. During initial SEM (scanning electron microscope) examination of Miocene fossil hominoid (*Griphopithecus alpani*) specimens from Pasalar features were found on some of the specimens which differed from the microwear associated with diet and/or jaw movement. These different marks were suspected to be a result of a taphonomic process. Therefore, a series of experiments was conducted to simulate the effects of various taphonomic agents on dental microwear with the aim identifying the origin of these marks on some of the Miocene fossil hominoid material from Pasalar.

4.2 THE PROBLEM

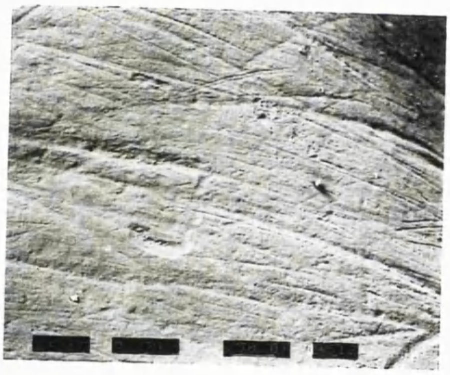
The occlusal Phase 1 wear facet (facet 1) (Kay and Hiiemae, 1974) on specimen H272 (Figure 4.1a) from Pasalar displays a number of striations which run parallel to each other, and the surface is rough and abraded in appearance. This is in contrast to the usual appearance of this facet which is characterised by the presence of striations which run parallel to each other on a **polished** surface (specimen K1367, Figure 4.1b).

Figure 4.1. *Griphopithecus alpani* molars from Pasalar suspected of having been modified by taphonomic processes. (a) Facet 1 of specimen H272 has a rough surface texture indicative of possible abrasion by sediment (scale bar represents 50 μm); (b) "normal" facet 1 of specimen K1367 with smooth surface texture (scale bar represents 50 μm); (c) specimen K1375 may have been etched by acid (scale bar represents 20 μm).

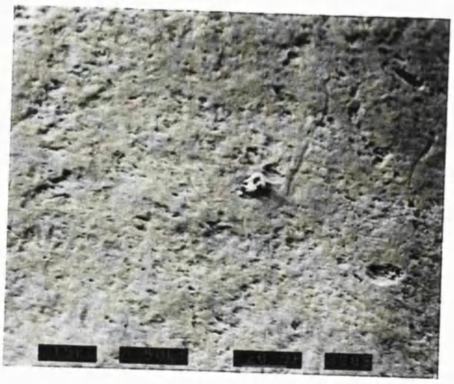
These specimens are housed at the Department of Palaeoanthropology, Dil ve Tarih-Cografya, Facultesi, Ankara University.

a

b



c



*
These are isolated, uncatalogued teeth which are housed at the Natural History Museum, London.

It was suspected that the abrasion seen on the specimen in Figure 4.1a may have been the result of the post-mortem processes (for example, physical abrasion by sediment) rather than being caused by diet during life.

On another specimen from Pasalar (K1375, Figure 4.1c) a number of round pits can be seen on the surface which are aligned in a uniform manner. These pits are part of the enamel structure (enamel prisms) and the enamel appears to have been etched by acid thereby exposing the enamels prisms. It is necessary to know whether the apparent acid etching had occurred during the animal's life (i.e. through the ingestion of acidic fruits) or as a result of post-mortem exposure to an acidic environment.

4.3 MATERIALS AND METHODS

Six human lower molar teeth (with the roots still attached) from the late Neolithic cave burial site of Burmegnez in south east Malta (see Keith, 1924 for details of this site) were used for 3 taphonomic experiments.* The specimens were first cleaned following the method of Gordon (1980, 1982) in order to remove any dirt which might have obscured microscopic damage. This entailed gently brushing the teeth with water and detergent with a sable paint brush, then applying a 50% solution of household bleach, to lift any organic matter, and a final rinsing with water.

The occlusal surfaces of the teeth were examined using a scanning electron microscope (SEM) using the same system and settings as for the main microwear study presented in this work (see Chapter 3). However, in contrast to the main study, specimens were oriented so that the mesial edge of the occlusal surface was aligned at the top of the viewing screen of the SEM, and magnification, which ranged from x7 to x200, varied from specimen to specimen but was always standardised for each individual tooth. This range of magnification was used so that general picture of the modification of larger areas of the enamel surface could be seen, as well as details of smaller patches of the enamel . Micrographs were taken of an area on the hypoconid of each specimen which would be readily identifiable as the experiments progressed.

4.3.1 Acid erosion

Hydrochloric acid

One specimen was placed in a 2.5% solution of hydrochloric acid (HCL) (pH 0.66) in order to simulate the effects of digestion by a predator. The tooth was left for 30 minutes and was then examined using a light microscope to check for any gross damage which might have occurred. No alteration was apparent the specimen was then placed in the acid for another hour and checked again. It was then immersed in the acid for a further hour, rinsed with water and examined in the SEM. The total time of immersion in the acid was 2 hours and 30 minutes.

Citric acid

A second experiment was conducted using acidic fruit. This was to simulate acidic etching which may have occurred during chewing in the mouth as well as digestion in the stomach. A specimen was placed in concentrated citric acid (lemon juice, pH 2.16) to simulate the effects of acidic fruit on dental microwear. The tooth was left in the acid for an uninterrupted time of 46 hours after which it was rinsed in water and examined in the SEM.

4.3.2 Alkali erosion

As the deposits at Pasalar are alkaline an experiment was carried out to investigate the effects of alkali on enamel and dental microwear. A tooth was placed for a total of 238 hours into an aqueous solution of carbonatite ash (with a pH of 10.54) from OlDonyo Lengai, a volcano in Tanzania. The specimen was inspected under a light microscope after 2, 4, 8, 16, 32, 64, and 128 hours to identify any gross damage which might have occurred. As none was apparent the tooth was examined in the SEM after 168 hours and 238 hours.

4.3.3 Sediment abrasion

The effects of sedimentary transport and deposition on dental microwear defects were investigated using a commercial tumbler. Three different types of sediment were used to examine the effects of different sized sands:-

i) **Quartz pebbles** - grain diameters ranged from 2000µm to 11000µm

ii) **Coarse sand** - grain size varied from 500µm to 1000µm

iii) **Medium sand** - grain diameters were between 250µm and 500µm.

One tooth was placed in 3 barrels each containing one of the three types of sediment. A small amount of water was added to render the sediment fluid. Each barrel was placed on a rotary tumbler which spun at 35 revolutions per minute. The circumference of the barrels was 48.5 cm and the linear velocity was 28.3 cm/second or just over 1 km per hour. Specimens were initially rotated for two hours after which they were inspected under a light microscope for any gross modifications which might have taken place. As none was apparent the specimens were tumbled for another two hours. As there was still no alteration apparent the teeth were rotated for periods of time which increased on a $\log_2$ scale - 2, 4, 8, 16, 32, 64, 128, and 256 hours. This gave a total number of 512 hours abrasion, by which time the specimens had travelled 521 km. At the end of each abrasion session the specimens were checked under a light microscope for any damage. In addition, they were examined in the SEM at 4 intervals - 16, 64, 256, and 512 hours.

4.4 RESULTS

4.4.1 Acid erosion

Hydrochloric acid

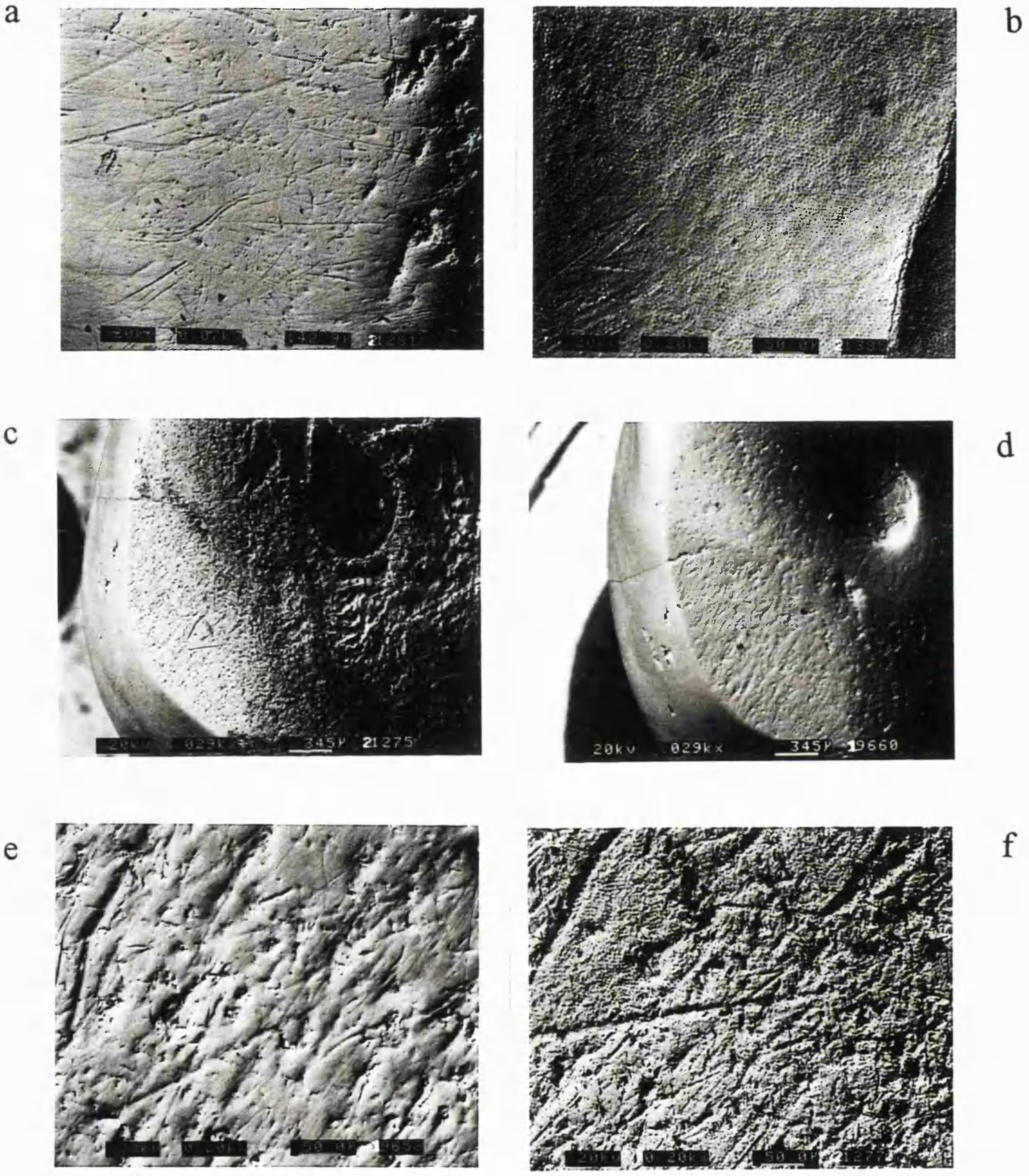
The enamel surface of the tooth before it was immersed in the hydrochloric acid was smooth and polished with the presence of microwear features- striations and pits (Figure 4.2a). After two hours immersion in hydrochloric acid, almost all of the microwear features were removed (Figure 4.2b). The acid exposed a uniform honeycomb pattern of enamel prisms over the entire wear surface. It was not possible to find the exact area on the tooth where the original SEM examination was carried out because of the obliteration of microwear features and the alteration of the enamel surface.

Citric acid

Microwear features could be seen all over the enamel surface of the specimen before it was placed in concentrated citric acid (Figures 4.2c and 4.2d). After 46 hours of immersion in citric acid, damage to the enamel occurred around the area of exposed dentine (Figure 4.2e) and enamel prisms are revealed (Figure 4.2f). Only the finer microwear features have been removed by the citric acid, and the remaining defects have become deeper with sharper margins. The alteration of the enamel by the citric

Figure 4.2. The effect of acid on dental microwear. (a) Tooth *before* (scale bar represents 143 μm); and (b) *after* two hours of immersion in hydrochloric acid (scale bar represents 50 μm); (c) tooth *before* and (d) *after* exposure to citric acid for forty-eight hours (scale bars represent 345 μm); (e) specimen *before* and (f) *after* exposure to citric acid for forty-eight hours (scale bars represent 50 μm).

(An isolated, uncatalogued tooth from Burgmenez, Malta was used in this experiment).


a
b
c
20kv
345μ
21275
d
20kv
029kx
345μ
19660
e
f

acid etching was not so extensive as that caused by hydrochloric acid. There was not such a uniform exposure of the enamel prisms in the specimen which was exposed to citric acid as compared to that which was immersed in hydrochloric acid even after immersion for a much longer period of time (Figure 4.2b).

4.4.2 Alkali erosion

The enamel surface of a tooth before it was immersed in carbonatite ash for 238 hours was smooth with microwear features present (Figure 4.3a). No modification to the enamel or microwear occurred after the specimen was exposed to carbonatite ash (Figure 4.3b). In fact features can be seen more clearly than before immersion in the alkali.

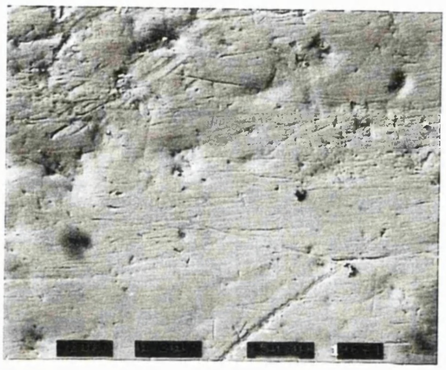
4.4.3 Sediment abrasion

Quartz pebbles

Microwear features are present all over the surface of the tooth before it was tumbled with quartz pebbles (grain size 2000μm to 11000μm) (Figure 4.4a). After 64 hours the enamel had been lightly polished, and some of the finer and more shallow microwear features has been eroded (Figure 4.4b). Further polishing occurred in the remaining tumbling sessions and is documented by SEM micrographs taken after 256 (Figure 4.4c), and 512 hours (Figure 4.4d). The polishing and erosion which occurred

Figure 4.3. The effect of alkali on dental microwear. (a) Tooth *before* and (b) *after* immersion in an aqueous solution of carbonatite ash (scale bars represent 50 μm). (An isolated, uncatalogued tooth from Burgmenez, Malta was used in this experiment).

a



b

Figure 4.4. The effect of abrasion by quartz pebbles on dental microwear. (a) Specimen *before*, and *after* (b) 64 hours (c) 256 hours and (d) 512 hours of abrasion (scale bars represent 50 μm).

(An isolated, uncatalogued tooth from Burgmenez, Malta was used in this experiment).

a

b

c

d

in this experiment was not extreme. Only the finer features which had little depth to them were removed giving the enamel a smoother appearance on some areas of the enamel surface.

Coarse sand

No modification to the enamel occurred on the specimen that was tumbled in coarse sand (grain size 500μm to 1000μm). Before the experiment the tooth exhibited microwear features over the entire enamel surface (Figure 4.5a). At no stage during the experiment, even after 512 hours of abrasion by the coarse sand was there any obliteration of the microwear (Figures 4.5b, 4.5c, 4.5d, and 4.5e).

Medium sand

The most noticeable alteration to the teeth used for the sediment abrasion experiments occurred when the specimen was tumbled with medium sand (grain size 250μm and 500μm). Microwear features were present on the surface of the tooth before the experiment began with a dentine exposure on the cusp tip (Figure 4.6a). After 16 hours of abrasion a large pit and damaged area appeared below the exposed dentine (Figure 4.6b). No other modification occurred. The pit was slightly larger after 64 (Figure 4.6c) and 256 hours (Figure 4.6d) the pit had further enlarged as had the damage just below the dentine exposure. The most dramatic change occurred after 512 hours (Figure 4.6e) with extensive pitting all over the buccal face of the cusp (i.e.

Figure 4.5. The effect of abrasion by coarse sand on dental microwear.

(a) Tooth *before* and *after* (b) 16 hours (c) 64 hours (d) 256 hours and (e) 512 hours of abrasion (scale bars represent 50 μm).

(An isolated, uncatalogued tooth from Burgmenez, Malta was used in this experiment).

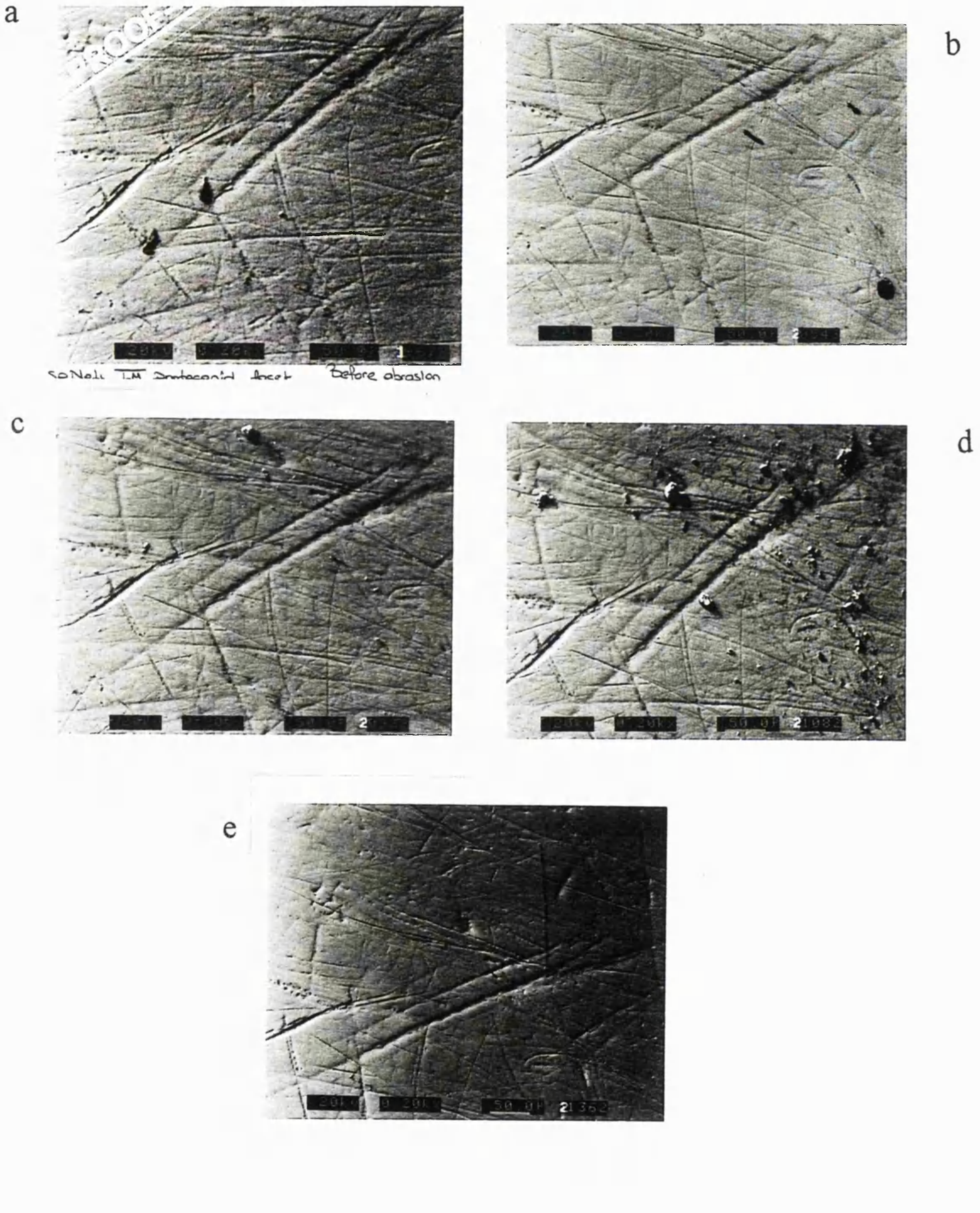
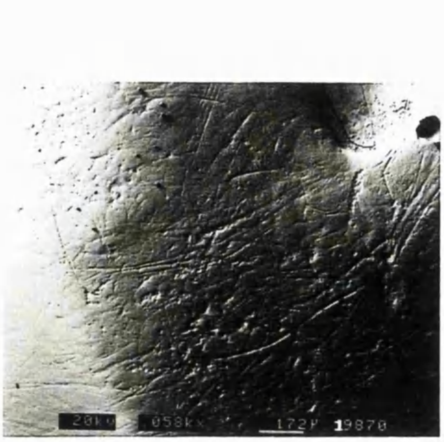

a
b
50 No.1 TM Protoconid facet Before abrasion
c
d
e

Figure 4.6. The effect of abrasion by medium sand on dental microwear.

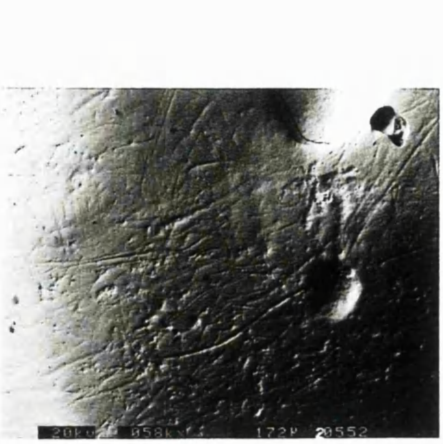
(a) Tooth b*efore* and *after* (b) 16 hours (c) 64 hours (d) 256 hours and (e) 256 hours (scale bars represent 172 μm); (f) detail of obliteration of the microwear features (x 200 magnification) (scale bar represents 50 μm); (g) coalescence of large abrasion pit with dentine exposure (scale bar represents 556 μm).

(An isolated, uncatalogued tooth from Burgmenez, Malta was used in this experiment).

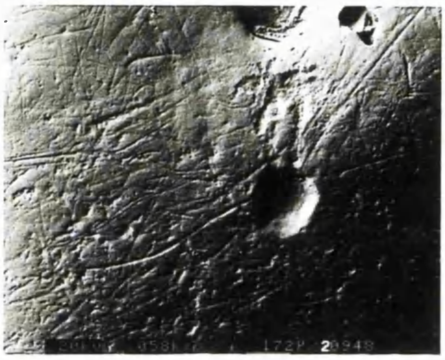
a


20kV .058kX 172µ 19870

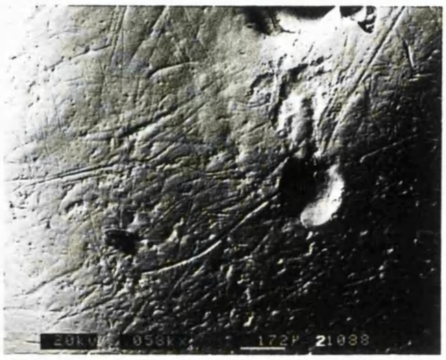
b


20kV .058kX 172µ 20552

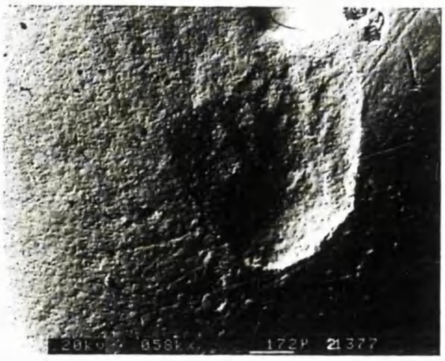
c


20kV .058kX 172µ 20948

d


20kV .058kX 172µ 21088

e


20kV .058kX 172µ 21377

f

g


20kV .018kX 556µ 21501

the left half - from top to bottom of the micrograph). The pits are small - the majority are smaller than about 5μm. The texture of the enamel is rough and lacks any polishing at all. The mastication process usually produces some polishing of the enamel. Most microwear features have been obliterated and any remaining in this area have been eroded (Figure 4.6f). The large pit is now approximately five times bigger than it was after 256 hours of abrasion (see Figure 4.5d), and has coalesced with the dentine exposure (Figure 4.6g).

Heavy pitting caused by abrasion is evident on the buccal portion of the cusp and it can also be seen inside the pit. However, the lingual face of the cusp, towards the centre of the occlusal surface of the tooth, (i.e. to the right of the micrograph) has remained unaltered and microwear features can still be seen here. The same pattern of heavy pitting caused by abrasion on the outer areas of the occlusal surface but not towards the centre of the tooth was seen also on each of the cusps (hypoconid, hypoconulid, metaconid; and entoconid). One possible explanation for is that the long axis of the tooth affected the way the tooth rotated in the sediment and so controlled the distribution of abrasion. The roots of the tooth were intact on the specimen used in this experiment, so the long axis of the specimen ran from the top of the crown to the base of the roots, so that it is possible that the tooth rotated around the long axis , with maximum damage occurring around the outside of the tooth.

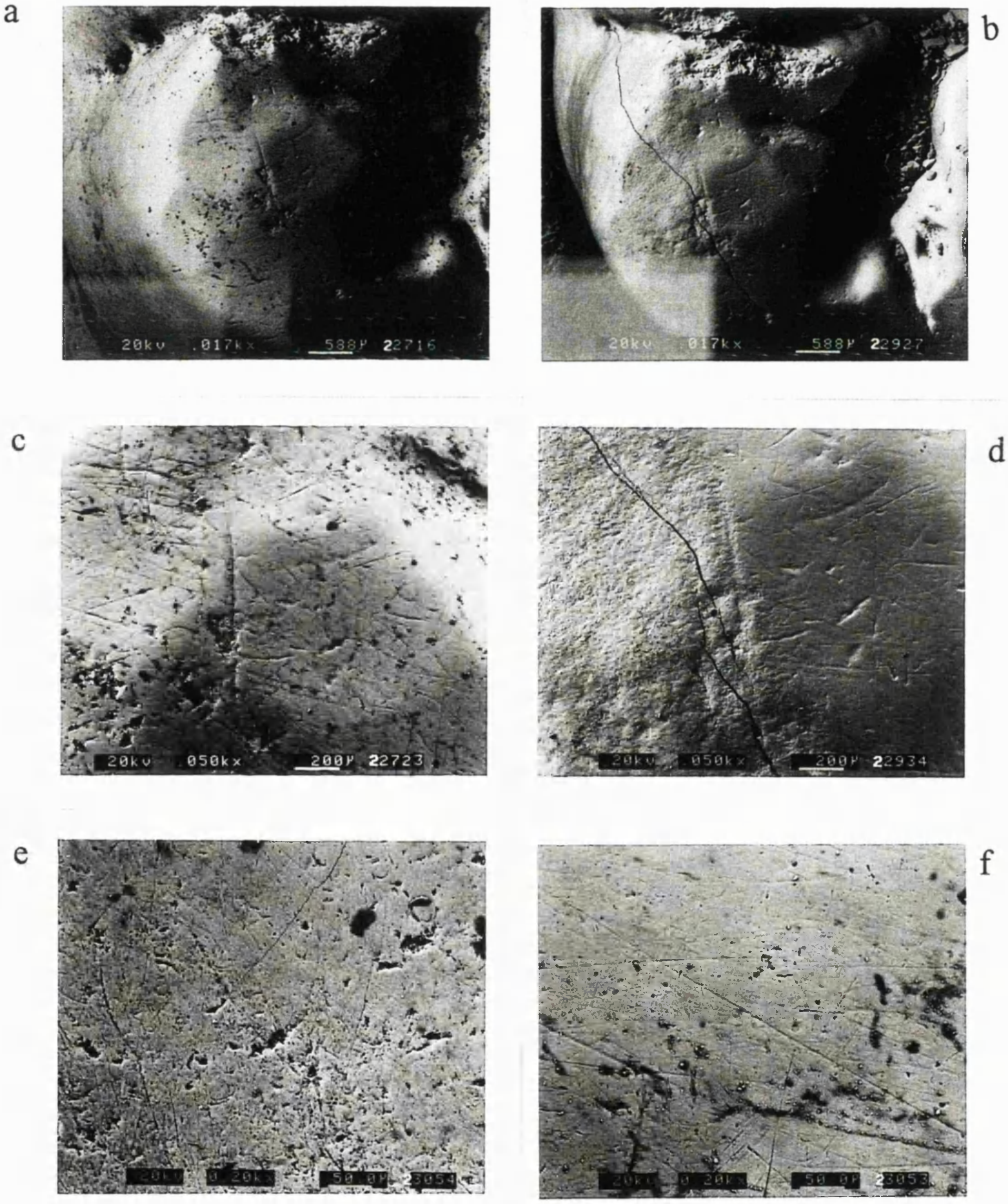
In order to try to clarify this pattern of abrasion a further experiment was conducted. This time an extracted human right lower molar was used, and the roots of the specimen were removed to change the long axis of the tooth to mesiodistal. The specimen was tumbled for 16 hours in the same quantity of medium sand and water as for the previous experiment. This amount of abrasion time was chosen as it was after this length of time that the first SEM examination of the specimen in the first experiment took place. This allowed direct comparison of the two sets of micrographs.

Before the experiment began microwear features could be seen on the enamel surface of the protoconid cusp (Figures 4.7a and 4.7b). After 16 hours abrasion in medium sand extensive abrasive pitting can been seen (Figures 4.7c and 4.7d, and Table 4.1) with the obliteration of the microwear features. The abrasion has followed the same pattern as the first experiment. That is, pitting is present on the buccal facets of the occlusal surface of the cusp but is not present on the lingual face (Figure 4.7c and 4.7d).

The non-occlusal surfaces of the extracted tooth were also investigated. The mesial contact facet (Figures 4.7e) both superiorly and at its centre and the buccal surface of the protoconid (Figure 4.7f) did not display the same heavy abrasive pitting which was present on the occlusal surface.

These experiments indicate that sediment can cause abrasion of enamel. Table 4.1 summarises the effects of the three types of sediment on the enamel and dental microwear features after SEM examination at various intervals. The largest size particles (quartz pebbles) polished the enamel and removed some of the finer and

Figure 4.7. The effect of medium sand on dental microwear (second experiment). (a) Tooth *before* and (b) *after* abrasion (scale bars represent 588 μm); (c) tooth *before* and *after* (d) abrasion (scale bars represent 200 μm); (e) mesial contact facet (f) and buccal (non-occlusal) surface of the protoconid (scale bars represent 50 μm).


a
b
c
d
e
f
20kv .017kx 500µ 22716
20kv .017kx 500µ 22927
20kv .050kx 200µ 22723
20kv .050kx 200µ 22934

more shallow features. No alteration to the enamel or microwear features occurred when a specimen was abraded with coarse sand. The smallest particles used in this study - medium sand - caused the most damage to the microwear features and enamel. The abrasion resulted in complete removal of microwear features, and extensive pitting was produced.

ABRASION TIME	QUARTZ PEBBLES	COARSE SAND	MEDIUM SAND (First experiment)	MEDIUM SAND (Second experiment)
16 hours	Enamel polishing and feature removal	No alteration	Appearance of pit below dentine exposure	Extensive pitting over enamel surface but not on lingual face of cusp
64 hours	Enamel polishing and feature removal	No alteration	Enlargement of pit	—
256 hours	Enamel polishing and feature removal	No alteration	Further enlargement of pit	—
512 hours	Enamel polishing and feature removal	No alteration	Further enlargement of pit and coalescence with dentine exposure. Extensive pitting over enamel surface but not on lingual face of cusp	—

Table 4.1. Effects of three sediment types on dental microwear.

4.5 COMPARISON WITH PASALAR

Table 4.2 details all specimens from Pasalar examined to date which appear to have been altered by the taphonomic processes examined in this chapter. One specimen from the Pasalar sample (BP1312) displayed a similar type of etching pattern to that caused by the hydrochloric acid. The top layer of enamel on the paracone cusp tip has been removed and the network of interconnected enamel prisms has been exposed (Figures 4.8a and 4.8b). The hypocone of the same specimen also displays this pattern of prism exposure (Figures 4.8c and 4.8d).

SPECIMEN	ACID	ALKALI	SEDIMENT
BP36	√	x	√
BP61	√	x	x
BP65	√	x	x
BP1312	√	x	x
F184	√	x	x
K1375	√	x	x
C99	x	x	√
H272	x	x	√

Table 4.2 List of modified specimens from Pasalar

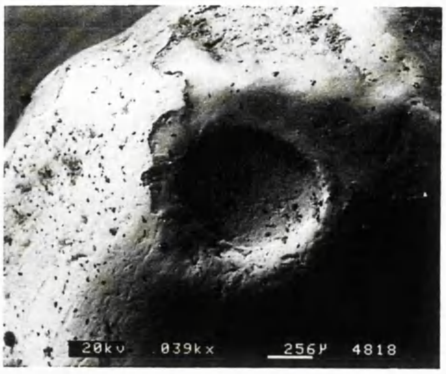
Two molars from Pasalar (BP36 and K1375) display a similar pattern of enamel etching as the specimens which were immersed in citric acid (Figures 4.8e and 4.8f).

Figure 4.8. Pasalar hominoid molars which have been taphonomically modified. Acid etching of paracone cusp tip area (a) (scale bar represents 256 µm)and (b) (scale bar represents 55.6 µm), and hypocone cusp tip region (c) (scale bar represents 263 µm) and (d) (scale bar represents 55.6 µm) of specimen BP1312*; (e) acid erosion over entire occlusal surface of specimen K1375** (scale bar represents 50 µm). Sediment abrasion of specimens (f) BP36* (scale bar represents 55.6 µm) and (g) C99** (scale bar represents 50 µm).

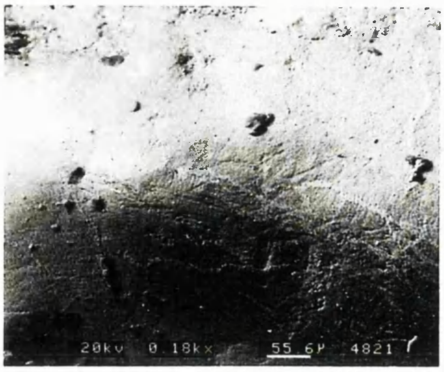
* These specimens are housed at the Natural History Museum, London.

** These specimens are housed at the Department of Palaeoanthropology, Dil ve Tarih-Cografya, Facultesi, Ankara University.

a


20kv 039kx 256µ 4818

b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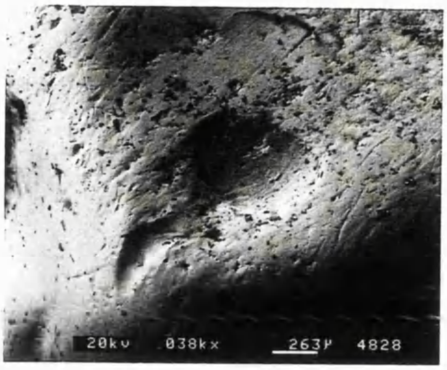
c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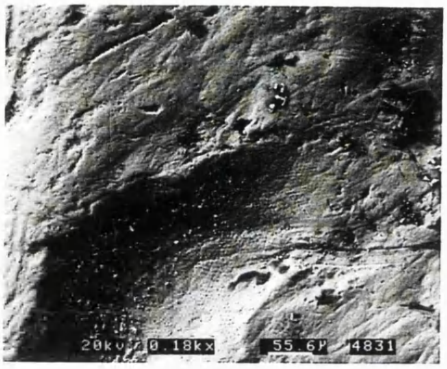
d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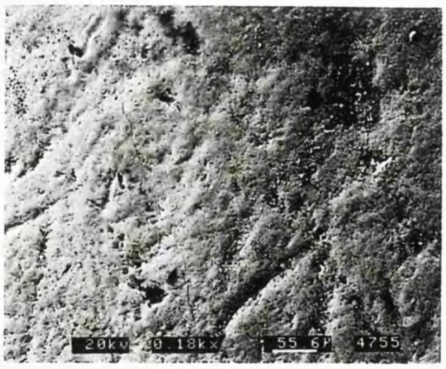
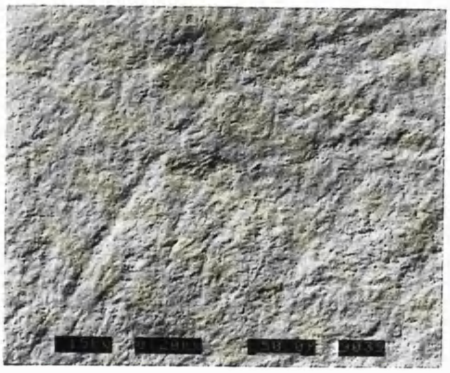
e

f


20kv 0.18kx 55.6µ 4755

g



The finer microwear features have been removed and there are patches of exposed enamel prisms. The features which have not been obliterated (especially specimen BP36, Figure 4.8e) are eroded and do not have accentuated margins as can be seen on the tooth which was etched with citric acid.

Two specimens from Pasalar display a similar pattern of pitting to that of the specimens which were experimentally abraded with medium-sized sand. Very few microwear features can be seen on specimen and C99 (Figure 4.8g) and those which are present are extremely eroded. There is a general rough, pitted appearance to this specimen that is similar to modifications caused by abrasion, although the experimentally produced alteration is much heavier than seen in the fossil tooth. It is therefore, likely that tooth C99 from Pasalar has been abraded by sediment. A second specimen from Pasalar (BP36, Figure 4.1b) also has a similar aspect to the specimens which have been abraded by medium-sized sand but to a much lesser extent than C99. Microwear features have not been eroded away but the texture of the enamel appears rough and pitted and is reminiscent of the specimens which were experimentally abraded by sediment.

4.6 DISCUSSION

The purpose of the experiments reported here was to investigate the effects of various taphonomic processes on dental microwear patterns on fossils. Microscopic features which were suspected of being caused by taphonomic processes have been found on some of the fossil teeth from Pasalar (Turkey). As these marks could potentially confound any dietary reconstruction it was important to ascertain whether they had been produced during the lifetime of the hominoids (i.e. by diet) or whether they were caused by processes which took place after death.

4.6.1 The effect of acids on dental microwear

The experiments conducted demonstrate that acids do affect enamel and dental microwear by removal, in varying degrees, of the features and exposure of enamel prisms. Specimens which have been acid-etched can be readily identified and when encountered should be excluded from analyses from which inferences about past diets are made.

Hydrochloric acid caused heavy erosion of the microwear and enamel. Lighter etching resulted from immersing a specimen in citric acid. Both these types of erosion have been found in the Pasalar sample.

These two kinds of alteration can be easily identified in fossil samples. In the extreme case, as with hydrochloric acid, almost all of the microwear features are removed and the enamel is etched such that the underlying enamel prism network is exposed in a uniform manner over the whole surface of the tooth. Puech *et al.*, (1985) also found this pattern of prism exposure when they etched a tooth with a 30% solution of phosphoric acid. With the lighter erosion, as seen in the citric acid experiment, the finer microwear features are removed and the margins of the remaining ones are sharpened, and there are localised patches of prism exposure. This pattern of removal of the more delicate microwear features has also been documented by Teaford (1994) in an experiment which investigated the effect of a 2-3 second etching of enamel with a 30% solution of phosphoric acid.

4.6.2 The effect of sediment on dental microwear

Apart from the occurrence of polishing by the quartz pebbles, only the medium-sized sand was found to modify the microwear features within the times and degrees of abrasion used in these experiments. The enamel surface was roughened by extensive abrasion pitting and the microwear features were completely removed. This type of abrasion has been seen in three specimens from the Pasalar sample.

It is not clear why abrasion should occur after different periods of time in the two experiments using medium-sized sand. The archaeological tooth was modified after 16 hours as seen by the appearance of a large pit close to the dentine exposure.

However, extensive abrasion was not seen until 512 hours of abrasion had taken place. Similar extensive abrasion of the extracted molar occurred after just 16 hours tumbling in medium-sized sand. Why there should be such a difference in the time taken to cause the same amount of damage to these two specimens is not evident. It could be related to different enamel hardness in the two specimens, or the fact that one is an archaeological specimen and the other was relatively recently extracted. In any case, although further work is needed to clarify this issue it does not alter the fact that this size of sand particles did abrade the enamel surface, and that this type of abrasion can be recognised.

The experiments described above indicate that although sediment has the potential to alter dental microwear patterns, the modification is in the form of **obliteration** of features rather than secondary alteration of the existing microwear patterns or the formation of new features. Thus, enamel which has been abraded by sediment can be detected and the specimen excluded from further analysis. This conclusion is consistent with that Gordon (1984a), although these results contrast with that of Gordon in another aspect (see below). Apart from the slight polishing of enamel which resulted from tumbling a specimen with quartz pebbles, the most significant alteration to dental microwear occurred after abrasion by the smallest (medium-sized sand) sediment particles but Gordon (1984a) found that the degree of modification to the dental microwear was positively correlated with the size of the abrasive particle. However, Gordon does not give enough detail about the sizes of sediments she used in her experiments for any discussion of the reasons why her results contrast with those in the present study.

4.7 SUMMARY

The experiments conducted here indicate that dental microwear patterns tend to be obliterated rather than secondarily modified by taphonomic processes. These results are reassuring in that taphonomically-altered dental microwear patterns can be readily identified. With careful examination of fossil material dietary inferences are not likely to be clouded by the effects post-mortem processes.

The experiments carried out for this study were as follows:-

1. A 2.5% solution of hydrochloric acid for two hours produced extensive erosion of most of the dental microwear features resulted and the underlying uniform enamel prism structure was revealed. One specimen from the Pasalar hominoid collection displayed a similar erosion pattern.

2. Immersion in concentrated citric acid for 46 hours removed most of the finer microwear features and the margins of the larger remaining features were sharpened. Less alteration to the microwear features was encountered with the citric acid than with the hydrochloric acid and enamel prisms were revealed only in patches rather than in a uniform manner across the surface as with the previous experiment. Several Pasalar hominoid specimens display this type of pattern of alteration of the dental microwear.

3. No alteration to the dental microwear occurred when a specimen was exposed to an aqueous solution of carbonatite ash.

4. Polishing of the enamel and removal of finer dental microwear features occurred when a specimen was tumbled with quartz pebbles (the largest sediment particle size used in these experiments) for 512 hours. No alteration to the microwear patterns was observed when a specimen was abraded with coarse sand particles (the medium sediment particle size employed). The greatest modification to dental microwear features occurred after tumbling with the smallest sediment particles - the medium-sized sand - for 512 hours where complete obliteration of microwear features was observed.

CHAPTER 5: RESULTS PART 1 - DESCRIPTIVE STATISTICS

In this chapter the microwear patterns of the three extant and one fossil hominoid are described. The first section examines the microwear patterns for all facets of each species. The next two sections investigate sex and wear stage differences in microwear. Sample sizes within some wear stages and for some of the sex data are too small to include in an analysis of variance. As a result, descriptive statistics are used in this chapter to examine microwear variables in relation to sex and wear stage. These factors have the potential to confound dietary reconstructions which are based on dental microwear.

Both the median and the mean are used as the measures of central tendency in this chapter. The median is used most commonly for data which is not normally distributed, and which require non-parametric statistical testing. As most of the microwear data presented in this study do not have a normal distribution (see Chapter 3), the median is therefore, used in this chapter. The median is also a more representative measure of location in circumstances where the data have a skewed distribution (Sokal and Rohlf, 1995). Many of the microwear variables used in this study have a positive skew (see Chapter 7).

Many microwear studies however, have used the mean as a measure of central tendency (e.g. Teaford and Walker, 1984; Teaford and Runestad, 1992; Grine and

Kay, 1988; Ungar, 1992) and to ensure comparability with these researchers the mean is also reported in this chapter.

Mann-Whitney U (also known as Wilcoxon Rank Sum) statistical tests were used to identify any significant differences between species, sex and wear stages for each facet. This is a non-parametric test which examines differences between two samples using the sums of the ranks of the data in each group (Norman and Streiner, 1994)..

5.1 FACET AND SPECIES VARIATION IN MICROWEAR CHARACTERISTICS

5.1.1 Total number of microwear features

Total incidence of microwear features varies according to species and facet (Table 5.1, Figure 5.1). *Pongo* and *G. alpani* display high numbers of microwear features. Mann-Whitney U tests indicate that *Pongo* has significantly greater frequencies of microwear features than *Gorilla* on facets 9 and 1 ($p<0.05$), and facet x ($p=0.05$). *Pongo* also has significantly more features on facet 1 than *Pan* ($p=0.05$). *G. alpani* displays significantly more features than *Pan* on facet x ($p<0.05$) and *Gorilla* on facets 9 and x ($p<0.05$). There is no significant difference between *G. alpani* and *Pongo*, or between *Pan* and *Gorilla* in total number of microwear features on any of the three facets. Facet 1 displays the least microwear of all three facets, and facets 9 and x show little variation in amount of microwear features.

Facet 9

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	99.2	71.0	80.0	275.0	61.5	122.5	61.0
Pan	9	114.4	99.4	85.0	265.0	37.0	200.5	163.5
Pongo	20	171.8	100.0	149.5	366.0	93.5	237.0	143.5
G. alpani	18	148.7	53.1	150.0	221.0	108.8	183.3	74.5

Facet x

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	12	65.2	37.4	61.5	124.0	32.5	94.0	61.5
Pan	8	87.5	58.7	67.5	162.0	49.3	149.0	99.7
Pongo	19	164.2	127.2	136.0	421.0	52.0	266.0	214.0
G. alpani	13	159.9	176.0	87.8	281.0	74.0	228.5	154.5

Facet 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	60.3	32.1	46.0	87.0	35.0	101.	66.0
Pan	5	52.4	26.7	46.0	66.0	29.0	79.0	50.0
Pongo	20	98.8	55.2	88.5	206.0	61.5	135.3	73.8
G. alpani	15	90.8	53.8	78.0	166.0	46.0	129.0	83.0

Table 5.1. Descriptive statistics for total number of microwear features. (Q_L, Q_U, and QRange refer to the lower quartile, the upper quartile, and the interquartile range (the difference between the lower and upper quartiles) respectively).

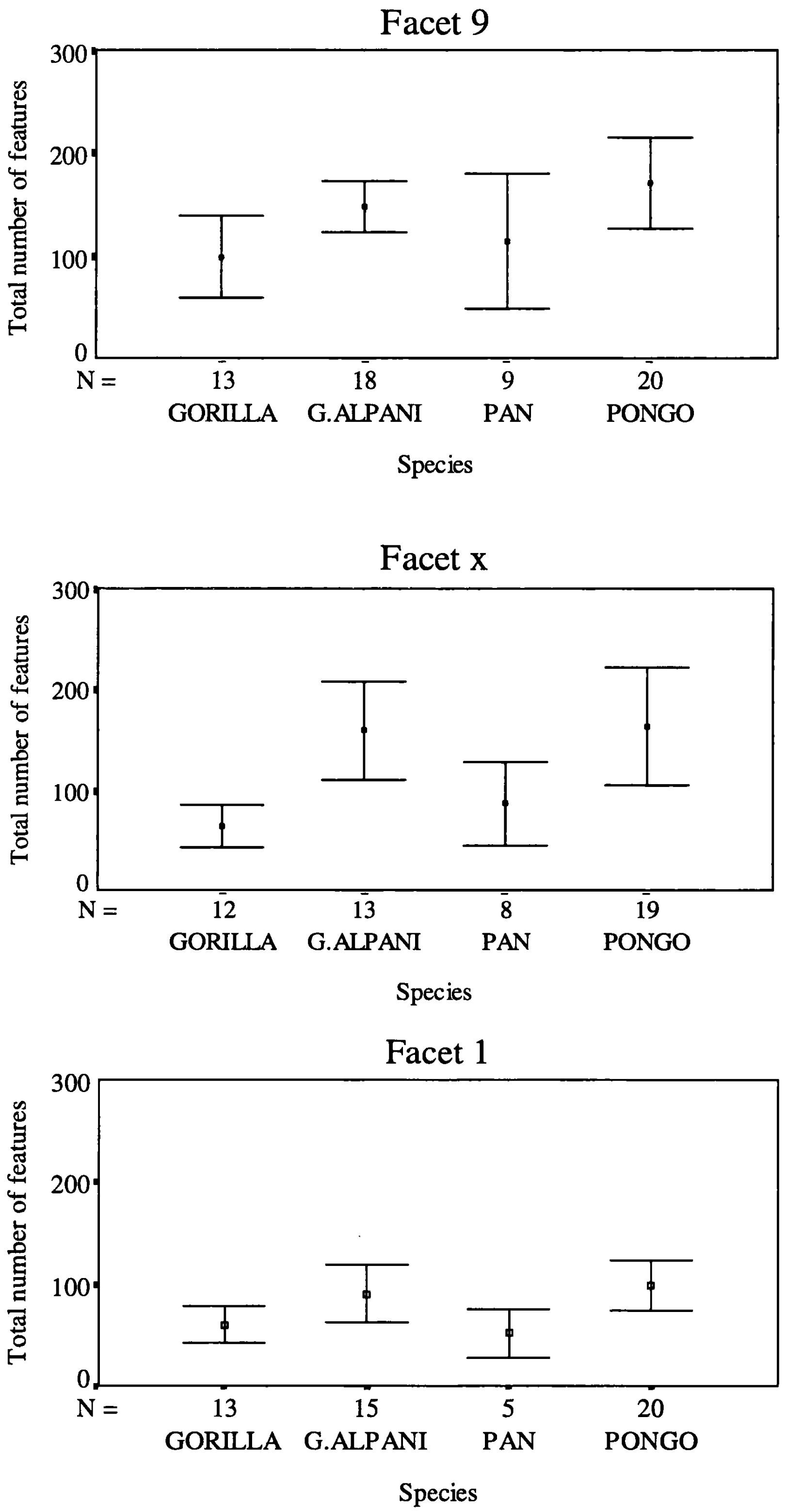


Figure 5.1. Total number of features for all species and each facet (mean +/- 2 S.E.).

(N = number of specimens).

5.1.2 Number of pits

Pit frequency differs depending on species and facet (Table 5.2, Figure 5.2). *Pongo* and *G. alpani* display high numbers of pits. *G. alpani* has significantly greater numbers of pits on facet 9 (p=0.001), facet x (p<0.001), and facet 1 (p=0.01) than *Gorilla*, and significantly more pits on facets x and 1 (p<0.05) than *Pan*. *Pongo* displays significantly greater numbers of pits than *Gorilla* on facets 9 (p<0.05) and x (p=0.01). There is no significant difference between *Pan* and *Gorilla*, *Pongo* and *Pan*, or *Pongo* and *G. alpani.*

5.1.3 Number of striations

There is less variation in striation frequency according to facet than in the variables previously described (Table 5.3, Figure 5.3). *Pongo* and *G. alpani* display large numbers of striations. Mann-Whitney U tests indicate that *Pongo* has significantly more striations on facet 9 (p<0.05) and facet 1 (p=0.05) than *Gorilla*. There are no significant differences between *Pongo* and *Pan*, *Pongo* and *G. alpani*, and *Pan* and *Gorilla*, *G. alpani* and *Pan*, or between *G. alpani* and *Gorilla*, in numbers of scratches.

5.1.4 Percentage pits (pits as a percentage of total microwear features)

Percentage pits varies according to species and facet (Table 5.4, Figure 5.4). *G. alpani* displays the highest percentages of pits on all facets, and *Gorilla* has the lowest percent pits except for facet 1. Mann-Whitney U tests indicate that *G. alpani* has significantly

Facet 9

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	40.9	55.1	22.0	208.0	9.5	48.0	38.5
Pan	9	54.1	61.4	22.0	155.0	10.0	107.5	97.5
Pongo	20	76.6	59.9	54.5	215.0	29.3	129.8	100.5
G. alpani	18	80.4	37.6	74.0	134.0	45.8	109.5	63.8

Facet x

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	12	24.8	24.0	19.0	87.0	10.0	30.8	20.8
Pan	8	45.9	50.1	23.5	121.0	16.3	97.5	81.2
Pongo	19	81.9	78.3	57.0	310.0	26.0	133.0	107.0
G. alpani	13	93.5	51.1	91.0	146.0	48.0	139.5	91.5

Facet 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	7.7	5.8	6.0	22.0	4.0	10.0	6.0
Pan	5	5.8	4.0	6.0	10.0	2.0	9.5	7.5
Pongo	20	20.5	25.3	11.5	89.0	5.3	20.8	15.5
G. alpani	15	20.4	20.5	14.0	84.0	8.0	23.0	15

Table 5.2. Descriptive statistics for number of pits.

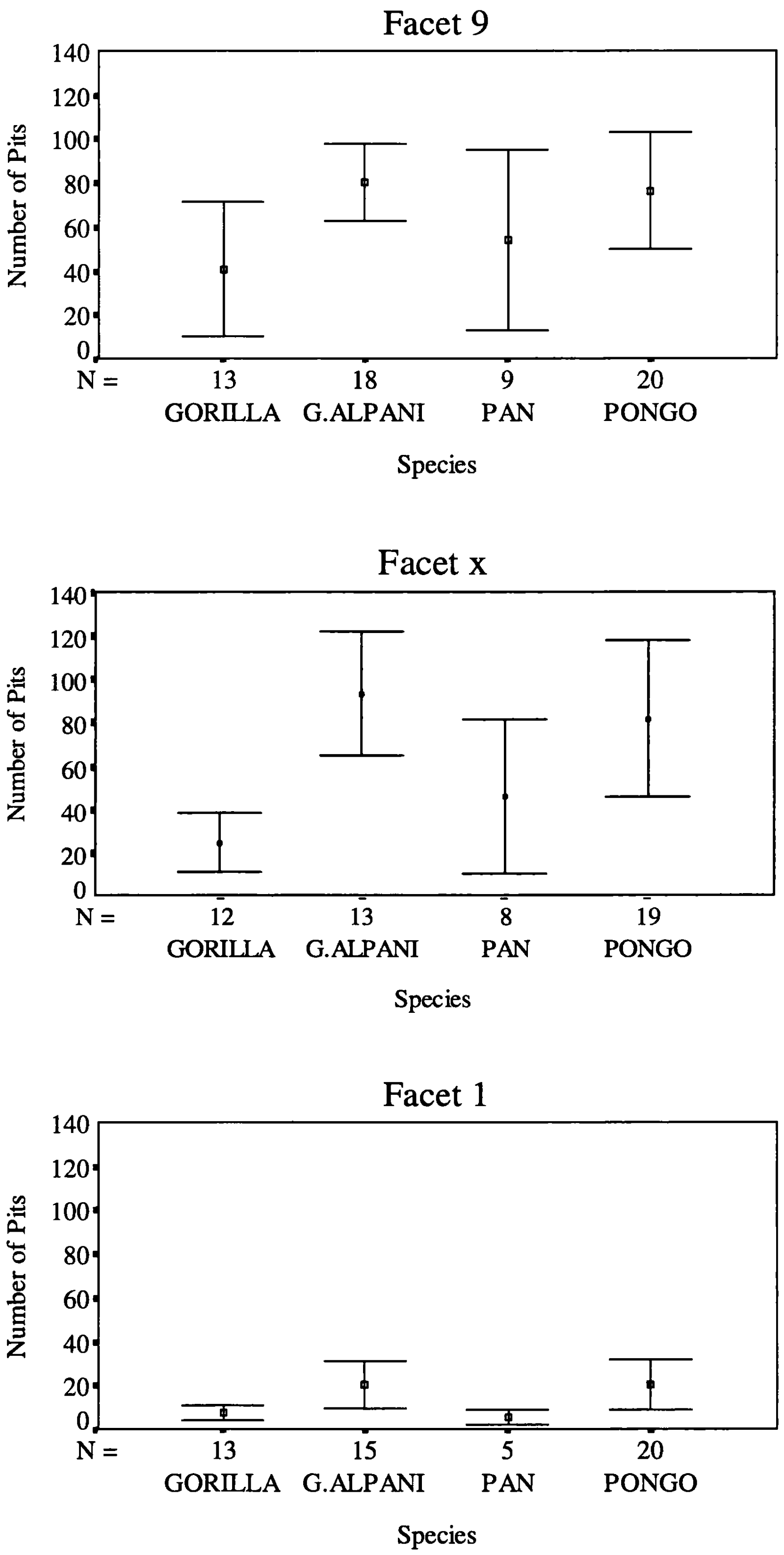


Figure 5.2. Number of pits for all species and each facet (mean +/- 2 S.E.).

Facet 9

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	58.3	23.1	47.0	68.0	39.0	82.0	43.0
Pan	9	60.3	42.5	46.0	130.0	26.5	92.0	2.5
Pongo	20	95.2	58.8	75.0	219.0	57.5	121.5	64.0
G. alpani	18	68.3	37.7	60.0	147.0	43.3	89.5	46.2

Facet x

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	12	40.3	22.8	32.5	75.0	24.5	55.8	31.3
Pan	8	41.6	16.3	41.5	53.0	32.5	53.3	20.8
Pongo	19	82.3	63.8	77.0	216.0	23.0	118.0	95.0
G. alpani	13	66.5	43.3	57.0	149.0	33.0	85.5	52.5

Facet 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	54.2	27.7	44.0	81.0	39.0	87.0	48.0
Pan	5	46.6	22.9	40.0	56.0	27.0	69.5	42.5
Pongo	20	78.3	38.2	70.0	137.0	54.5	108.3	53.8
G. alpani	15	70.4	43.6	56.0	151.0	32.0	106.0	74.0

Table 5.3. Descriptive statistics for number of striations.

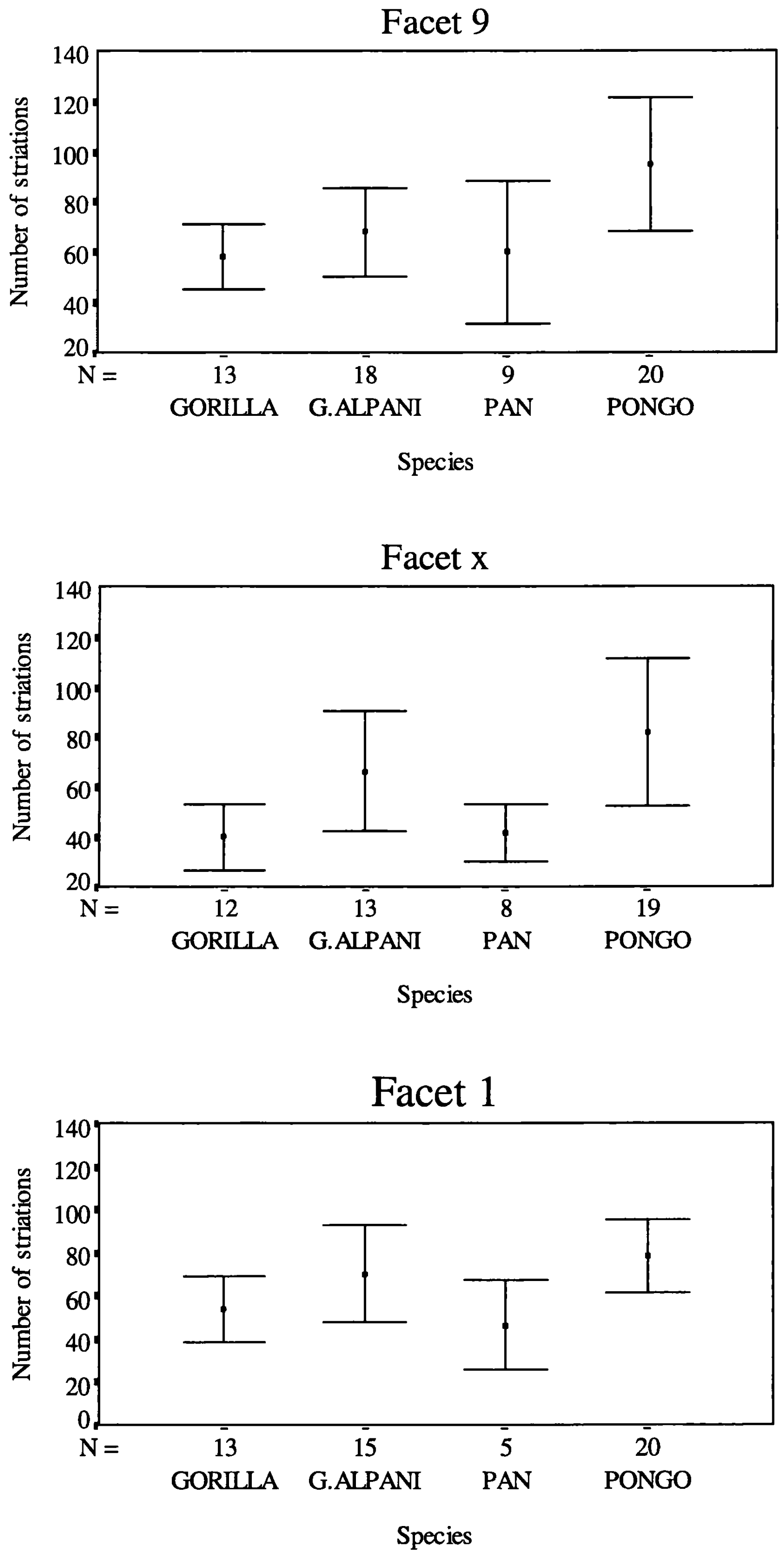


Figure 5.3. Number of striations for all species and each facet (mean +/- 2 S.E.).

Facet 9

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	33.2	17.5	30.1	58.1	18.5	46.6	28.1
Pan	9	39.7	20.6	39.9	56.4	23.2	60.8	37.7
Pongo	20	42.9	17.0	41.8	60.5	30.5	53.4	22.9
G. alpani	18	54.6	15.2	57.2	54.1	43.2	65.0	21.8

Facet x

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	12	32.6	17.9	33.3	68.9	21.5	37.7	16.3
Pan	8	43.9	17.9	37.4	46.4	32.0	64.0	32.0
Pongo	19	48.0	15.4	47.4	53.7	35.9	60.7	24.8
G. alpani	13	58.7	10.0	56.4	28.3	49.7	68.4	18.7

Facet 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	13.1	7.4	14.7	27.3	6.7	17.5	10.8
Pan	5	9.8	5.6	11.8	13.2	5.6	13.1	7.6
Pongo	20	18.1	13.8	13.9	52.6	8.8	24.5	15.7
G. alpani	15	22.5	15.0	17.6	41.7	10.8	41.8	31.0

Table 5.4. Descriptive statistics for percentage pits.

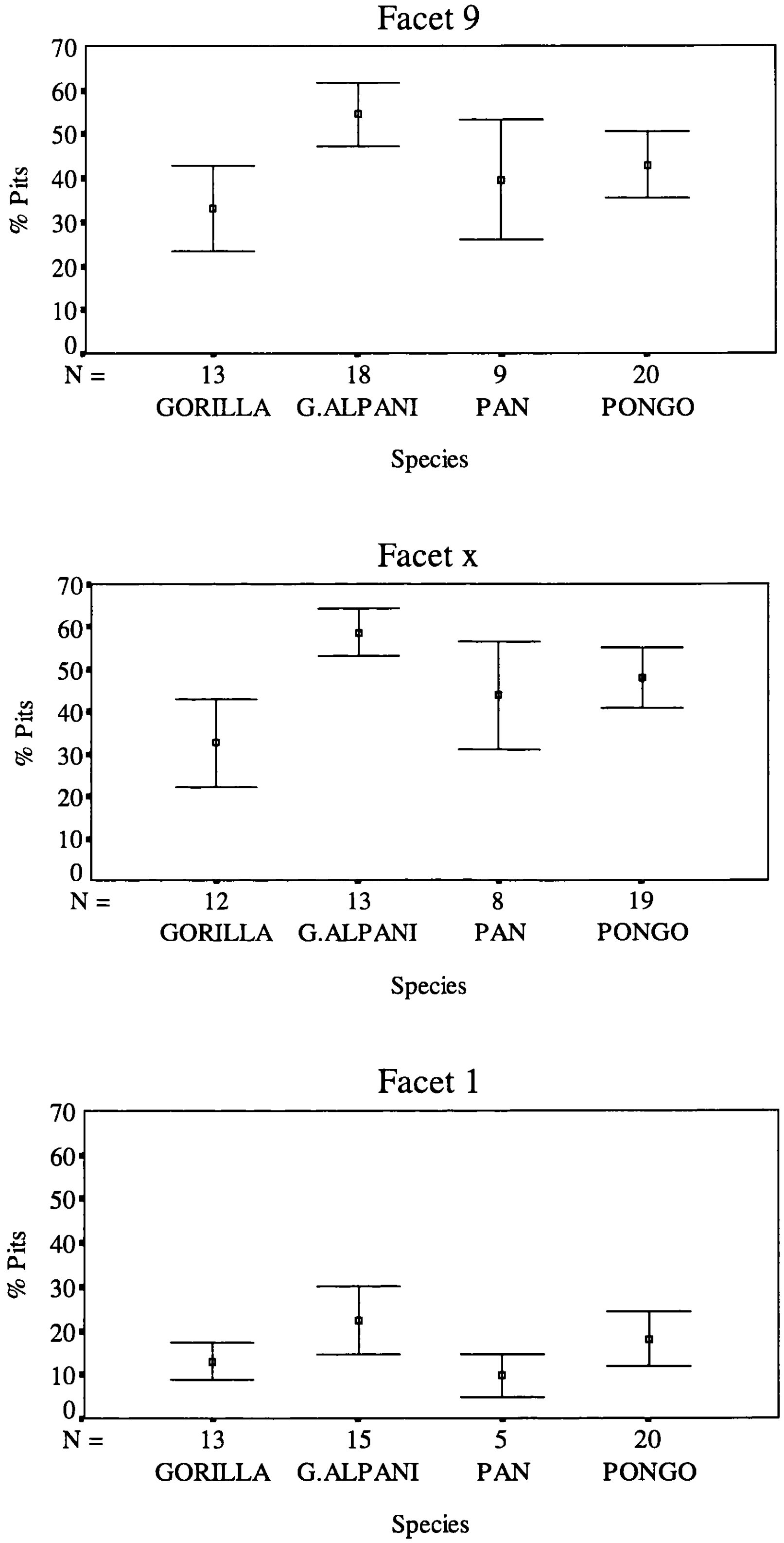


Figure 5.4. Percentage pits for all species and each facet (mean +/- 2 S.E.).

greater percentage pits than *Gorilla* on facets 9 ($p<0.01$) and 1 ($p=0.001$). *G . alpani* also displays significantly higher percentages of pits than *Pongo* on facets 9 ($p<0.05$) and x ($p<0.05$). *Pongo* has higher percentage pits on facet x ($p<0.05$) than *Gorilla*. There is no significant difference between *G. alpani* and *Pan*, *Pongo* and *Pan*, or *Pan* and *Gorilla*.

5.1.5 Pit width

There is very little variation in pit width across species and facets (Table 5.5, Figure 5.5). *Pan* displays the widest pits for facets 9 and x, and *Gorilla* has the most narrow pits on facet 1. *Pongo* and *G. alpani* have the most broad pits on facet 1. *Gorilla* has the most consistent pit widths across all facets. Mann-Whitney U tests indicate that *Pan* has significantly wider pits than *G. alpani* on facet 9 ($p<0.05$). There are no other significant differences in pit width among the four hominoid species.

5.1.6 Pit length

There is also little difference in pit lengths for all species and facets (Table 5.6, Figure 5.6). *Pan* displays the longest pits on facets 9 and x. *Gorilla* has moderately long pits on facets 9 and x relative to the other species, and the shortest pits on facet 1. *Pongo* and *G. alpani* display the greatest pit lengths on facets x and 1. Mann-Whitney U tests indicate that *Pan* has significantly longer pits on facet x than *Gorilla* ($p=0.05$) and *Pongo* facet x ($p<0.05$). Although not a significant difference, *Pan* shows a trend towards greater pit lengths than *G. alpani* on facet 9 ($p=0.0570$) and facet 1 ($p=0.0596$). *Gorilla* displays longer pits on facet 9 than *G. alpani* ($p<0.05$). There are no significant differences between *Pongo* and *G. alpani* and *Pongo* and *Gorilla*.

Facet 9

Species	**N**	**Mean**	**SD**	**Median**	**Range**	Q_L	Q_U	Q **Range**
Gorilla	13	4.7	2.3	3.9	7.8	3.0	6.3	3.4
Pan	9	5.6	2.08	6.1	6.3	3.5	7.1	3.7
Pongo	20	4.8	3.1	3.5	14.1	2.9	5.8	2.9
G. alpani	18	3.7	1.1	3.5	3.3	2.6	4.8	2.2

Facet x

Species	**N**	**Mean**	**SD**	**Median**	**Range**	Q_L	Q_U	Q **Range**
Gorilla	12	4.8	4.0	3.3	14.9	2.7	5.4	2.7
Pan	8	5.9	3.0	4.8	9.5	4.0	7.2	3.2
Pongo	19	4.0	1.4	3.6	4.5	2.6	4.8	2.3
G. alpani	13	4.9	4.6	3.3	17.7	3.1	4.7	1.6

Facet 1

Species	**N**	**Mean**	**SD**	**Median**	**Range**	Q_L	Q_U	Q **Range**
Gorilla	13	4.2	0.9	3.9	11.7	2.0	4.9	2.9
Pan	5	4.7	5.0	5.0	7.0	2.6	6.5	3.9
Pongo	20	5.4	4.6	3.7	16.1	2.7	6.4	3.7
G. alpani	15	5.4	3.1	4.1	8.8	3.0	7.0	4.0

Table 5.5. Descriptive statistics for pit widths.

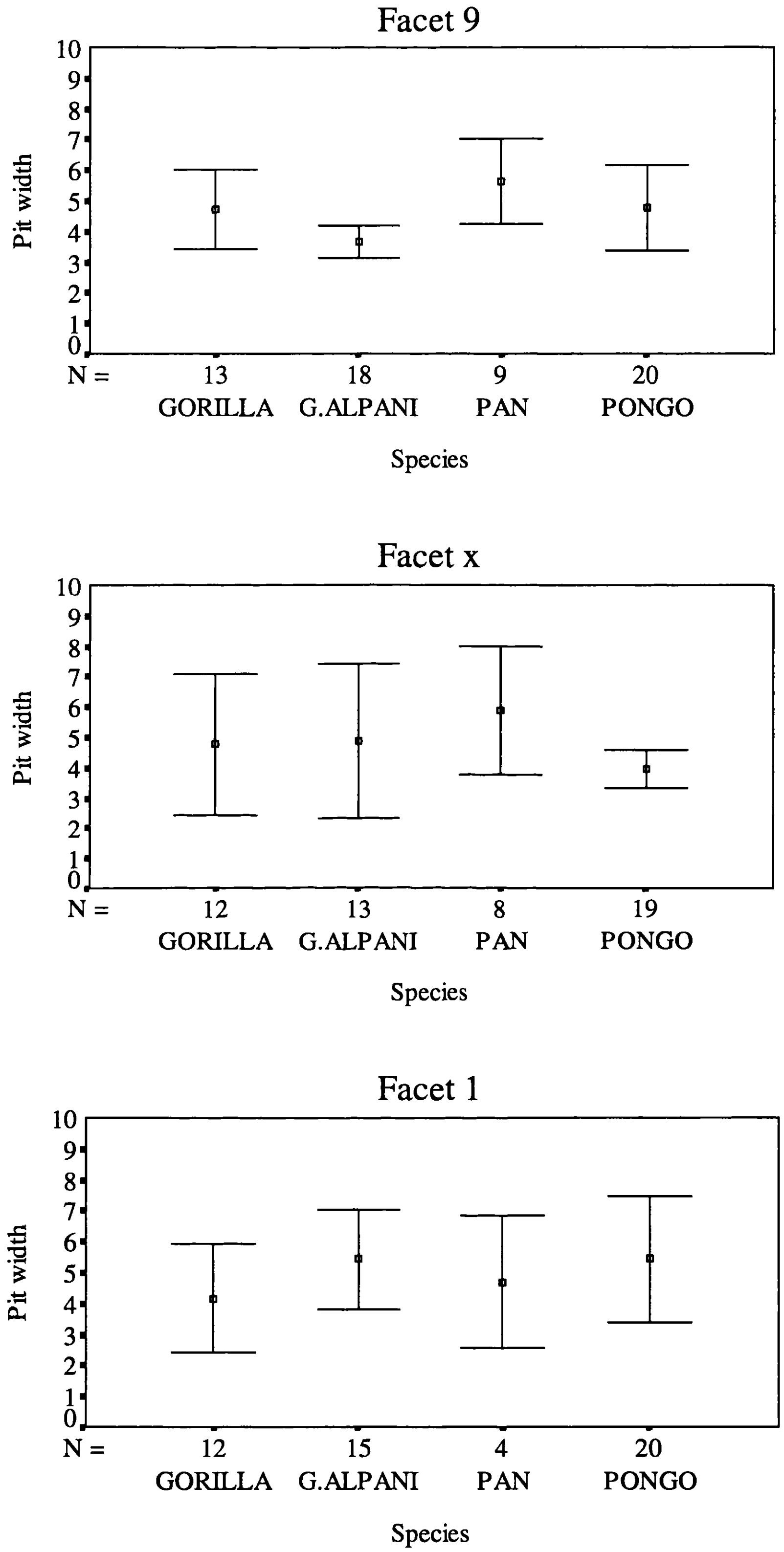


Figure 5.5. Pit widths (μm) for all species and each facet (mean +/– 2 S.E.).

Facet 9

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	10.8	4.6	8.9	16.9	7.4	13.7	6.3
Pan	9	11.1	5.0	10.6	12.5	6.1	15.7	9.6
Pongo	20	9.6	5.2	7.9	21.4	6.2	11.5	5.3
G. alpani	18	7.3	1.6	7.1	4.7	5.9	9.1	3.1

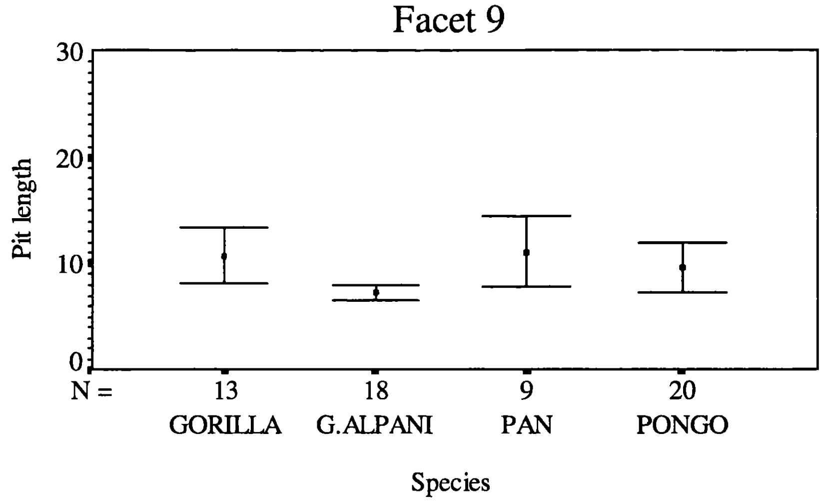
Facet x

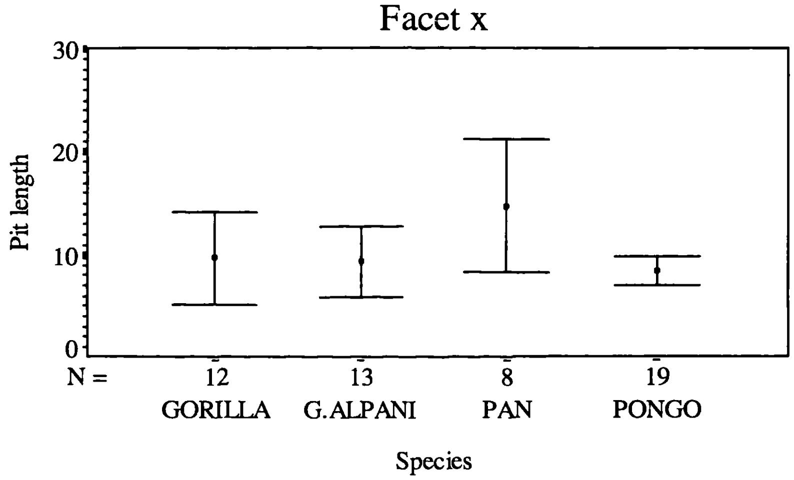
Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	12	9.6	8.0	7.3	31.0	6.2	11.4	5.2
Pan	8	14.7	9.2	13.5	29.3	8.0	17.3	9.3
Pongo	19	8.4	7.4	10.7	11.0	5.7	11.0	5.2
G. alpani	13	9.3	6.3	7.7	24.3	5.9	9.7	3.8

Facet 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	10.4	2.4	8.6	31.8	4.4	12.8	8.4
Pan	5	12.8	3.9	13.0	17.5	5.9	19.6	13.7
Pongo	20	11.2	9.6	7.4	42.2	5.3	13.2	7.9
G. alpani	15	11.5	9.2	9.2	23.2	6.7	14.2	7.5

Table 5.6. Descriptive statistics for pit lengths.





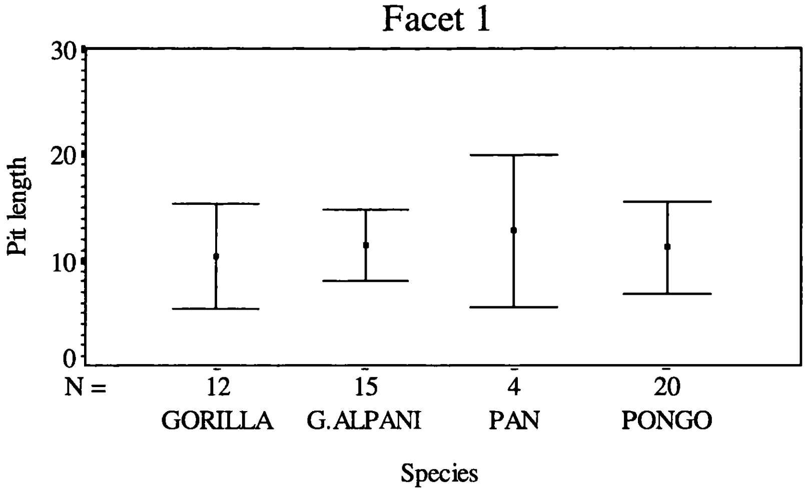


Figure 5.6. Pit lengths (μm) for all species and each facet (mean +/– 2 S.E.).

5.1.7 Striation width

Two species groupings in striation widths are apparent - *Gorilla* and *Pan* display the widest striations, with *Pongo* and *G. alpani* having narrower striae (Table 5.7, Figure 5.7). Mann-Whitney U tests indicate that *Gorilla* has significantly wider striae on facet 9 (p=0.001), facet x (p<0.001), and facet 1 (p<0.05) than *Pongo*. *Gorilla* also displays striations which are significantly wider on facet 9 (p=0.001), facet x (p=0.001), and facet 1 (p<0.05) than those of *G. alpani*. *Pan* has significantly wider striations on facet 9 (p<0.05), facet x (p=0.001), and facet 1 (p<0.05) than *Pongo*. There is also a significant difference between *Pan* and *G. alpani* - *Pan* displays greater striation widths on facets 9, x and 1 (p<0.05) than *G. alpani*.

Facet 9

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	2.7	0.7	2.7	2.6	2.2	3.1	0.9
Pan	9	2.5	0.7	2.3	1.9	1.9	3.3	1.4
Pongo	20	1.9	0.4	1.8	1.5	1.5	2.2	0.7
G. alpani	18	1.9	0.4	2.1	1.4	1.5	2.2	0.7

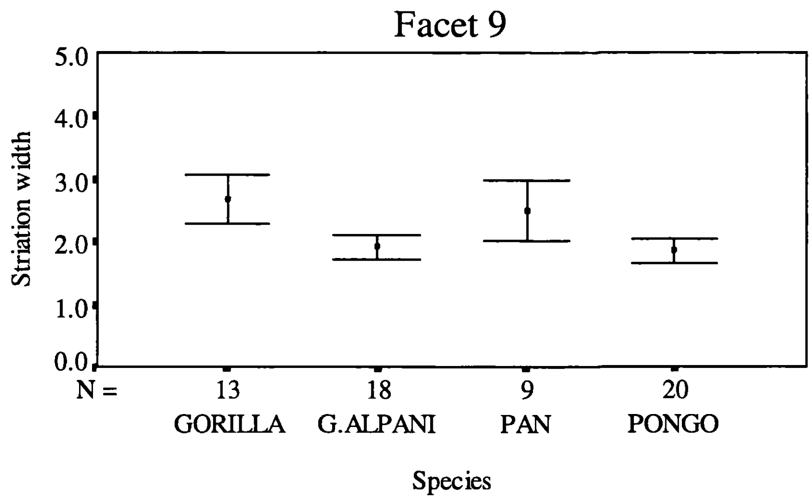
Facet x

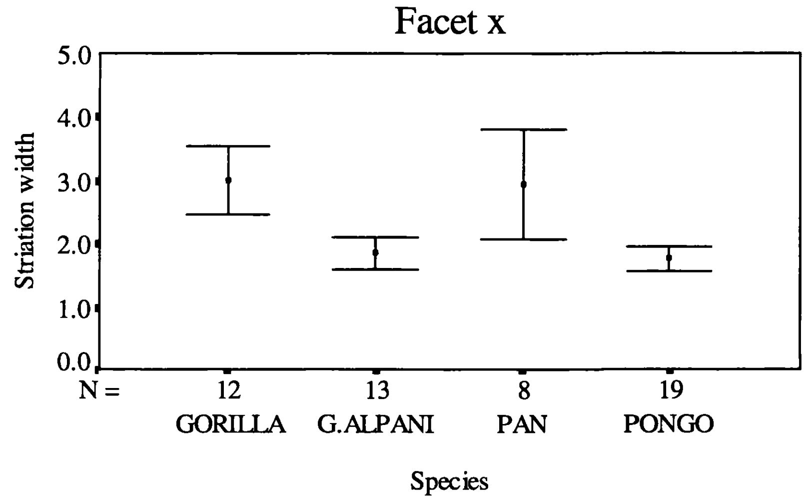
Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	12	3.0	0.9	2.8	2.5	2.1	3.8	1.6
Pan	8	3.0	1.2	2.8	3.8	2.0	3.3	1.3
Pongo	19	1.8	0.4	1.7	1.4	1.5	1.9	0.5
G. alpani	13	1.9	0.5	1.8	1.5	1.5	2.3	0.8

Facet 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	13	2.9	1.2	2.9	4.7	2.1	3.3	1.1
Pan	5	3.6	1.0	3.6	2.5	2.7	4.6	1.9
Pongo	20	2.2	0.7	2.1	2.6	1.6	2.6	1.0
G. alpani	15	2.1	0.5	2.1	1.6	1.7	2.6	0.9

Table 5.7. Descriptive statistics for striation widths.





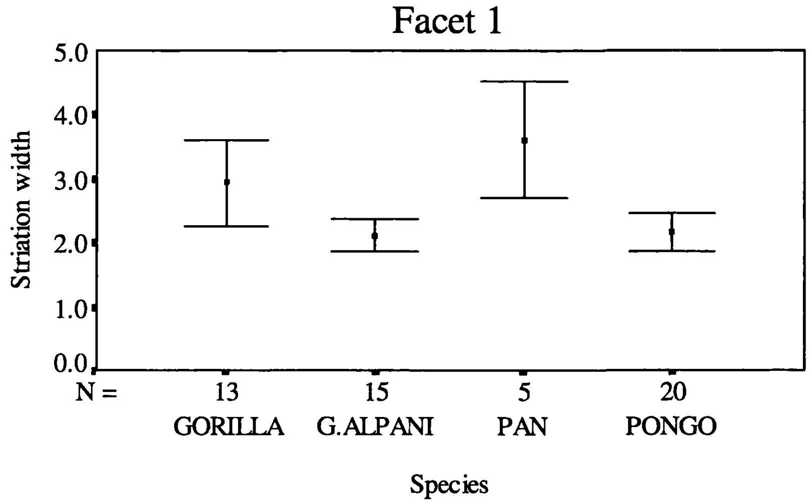


Figure 5.7. Striation widths (μm) for all species and each facet (mean +/- 2 S.E.).

Intra- and inter-specific patterns of microwear

Figures 5.8, 5.9 and 5.10 display the microwear patterns on facets 9, x and 1 for each species of hominoid. Figures 5.11, 5.12, and 5.13 display the microwear patterns for facets 9, x, and 1 for *G. alpani* only. Males and females, and wear stages are shown seperately and differences in microwear between the sexes and wear stages are discussed below.

5.1.8 Summary

Pongo has significantly more microwear features than *Gorilla* (facets 9, x, and 1) and *Pan* (facet 1). *G. alpani* also has greater numbers of all microwear features than *Gorilla* (facets 9 and x), and *Pan* (facet x). None of these differences are highly significant (i.e.< or equal to 0.001). There are no significant differences between *Pongo* and *G. alpani*, or between *Pan* and *Gorilla.*

Numbers of pits also vary between species. *Pongo* displays greater numbers of pits than *Gorilla* (facets 9 and x). *G. alpani* has more pits than *Gorilla* (facets 9 and x (the difference is highly significant) and facet 1) and *Pan* (facets x and 1). No differences were found between *Gorilla* and *Pan, Pan* and *Pongo*, or *Pongo* and *G. alpani.*

Number of striations shows little variation between species. The only significant difference was between *Pongo* and *Gorilla* - *Pongo* has significantly more striations than *Gorilla* (on facets 9 and 1), but this is not a highly significant difference.
G. alpani is conspicuous in the high percentages of pits it displays, however only one of the comparisons is highly significant. *G. alpani* has significantly greater percentage

pits than *Gorilla* (facets 9 and 1), and *Pongo* (facet 9 and x). *Pongo* displays significantly higher percentages of pits than *Gorilla* (facet x). There no significant differences between *Gorilla* and *Pan, Pan* and *Pongo,* or *Pan* and *G. alpani.*

There is little variation in pit widths. The only significant difference in pit widths is indicated between *Pan* and *G. alpani* - *Pan* has wider pits than *G. alpani* on facet 9, but this is not a highly significant difference.

Pit length does not vary greatly between species or facets. *Pan* has significantly longer pits than *Gorilla* and *Pongo* (facet x). *Gorilla* also displays significantly greater pit lengths than *G. alpani* (facet 9). None of these differences are highly significant.

Striation widths differ according to species and facet, with *Gorilla* and *Pan* forming one grouping, and *Pongo* and *G. alpani* making another. *Gorilla* has significantly wider striations than *Pongo* and *G. alpani* (facet 9 and x (highly significant), and facet 1). *Pan* also displays wider striae than *Pongo* (facets 9, x highly significant), and 1).

G. alpani shows the most differences in its its microwear patterns to that of *Gorilla. G. alpani* has the most similar microwear patterns to that of *Pongo* in comparison to the extant hominoids, the only significant difference between these two species is that *G. alpani* has higher percentages of pits than *Pongo* (on facets x and 9). *Pan* displays less differences in its microwear patterns than *Gorilla* but more than *Pongo* in comparison to *G. alpani.*

Figure 5.8. Intra-specific variation in facet 9 microwear patterns.
(Scale bars represent 50 μm).

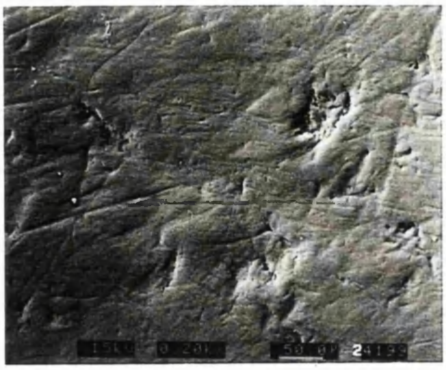
Gorilla **(a, b)** has the lowest frequencies of microwear features, pits and striations, and percentages of pits. It displays significantly less features and pits than *Pongo*, and *G. alpani*, and significantly fewer striations than *Pongo*. *Gorilla* displays significantly lower percentages of pits than *G. alpani*. *Gorilla* has the widest striae of all species which are significantly wider striae than both *Pongo* and *G. alpani*. *Gorilla* has similar pit widths to *Pongo* and displays similar pit lengths to Pan, and has signficantly longer pits than *G. alpani.*

Pan **(c, d)** displays greater numbers of microwear features, pits, striations, and percentages of pits than *Gorilla*, but has relatively lower frequencies and percentages of these features than *Pongo* and *G. alpani*. *Pan* has the widest and longest pits of all species. None of these differences are significant. *Pan* displays relatively wide striations which are significantly wider those displayed by *Pongo*.

Pongo **(e, f)** has the highest numbers of microwear features and striations, and relatively high numbers of pits and percentages of pits, and is similar to *G. alpani* in this respect. It displays significantly more microwear features, and greater numbers of pits and striations than *Gorilla*. It has similar pit widths to *Gorilla* and relatively low pit lengths. *Pongo* displays similar striation widths to *G. alpani*, and has significantly narrower scratches than *Gorilla* and *Pan*.

G. alpani **(g, h)** has relatively high numbers of microwear features and striations, and the highest numbers of pits, and is similar to *Pongo* in this respect. It displays significantly more microwear features and greater numbers of pits than *Gorilla*. *G. alpani* has significantly greater percentages of pits than *Gorilla* and *Pongo*. *G. alpani* has the lowest pit widths and lengths of all species, but these differences are not significant. *G. alpani* displays similar striation widths to *Pongo,* and the dimensions of these features are signficantly narrower than those of *Gorilla*.

a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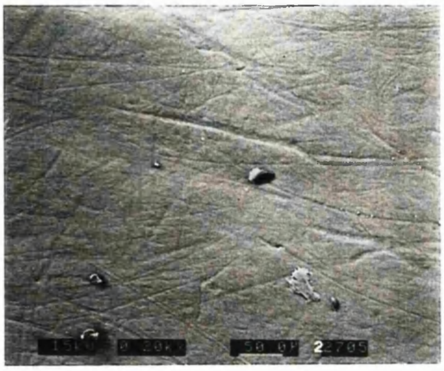
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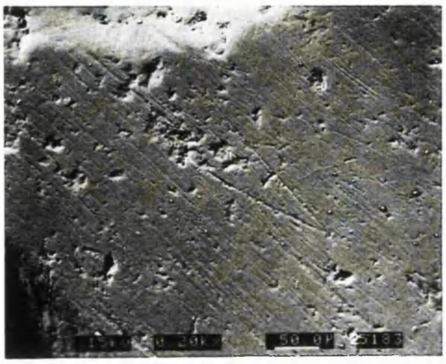
c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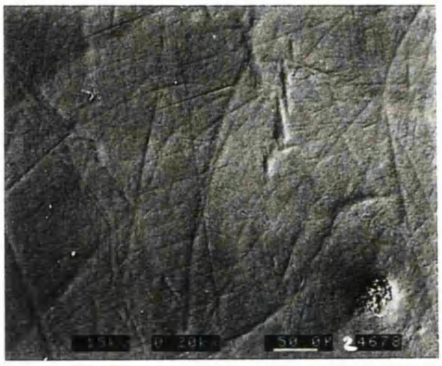
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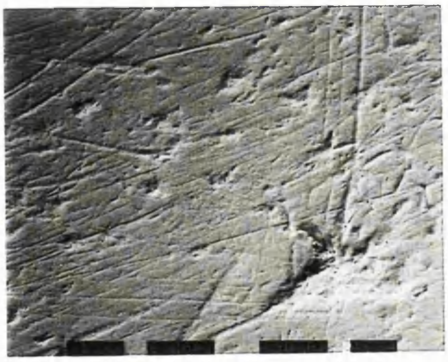
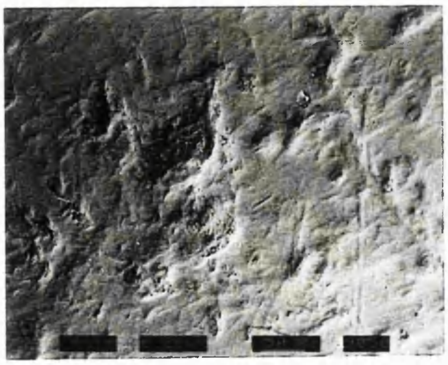
e



f

g



h

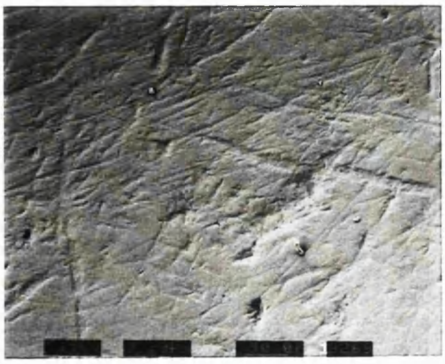


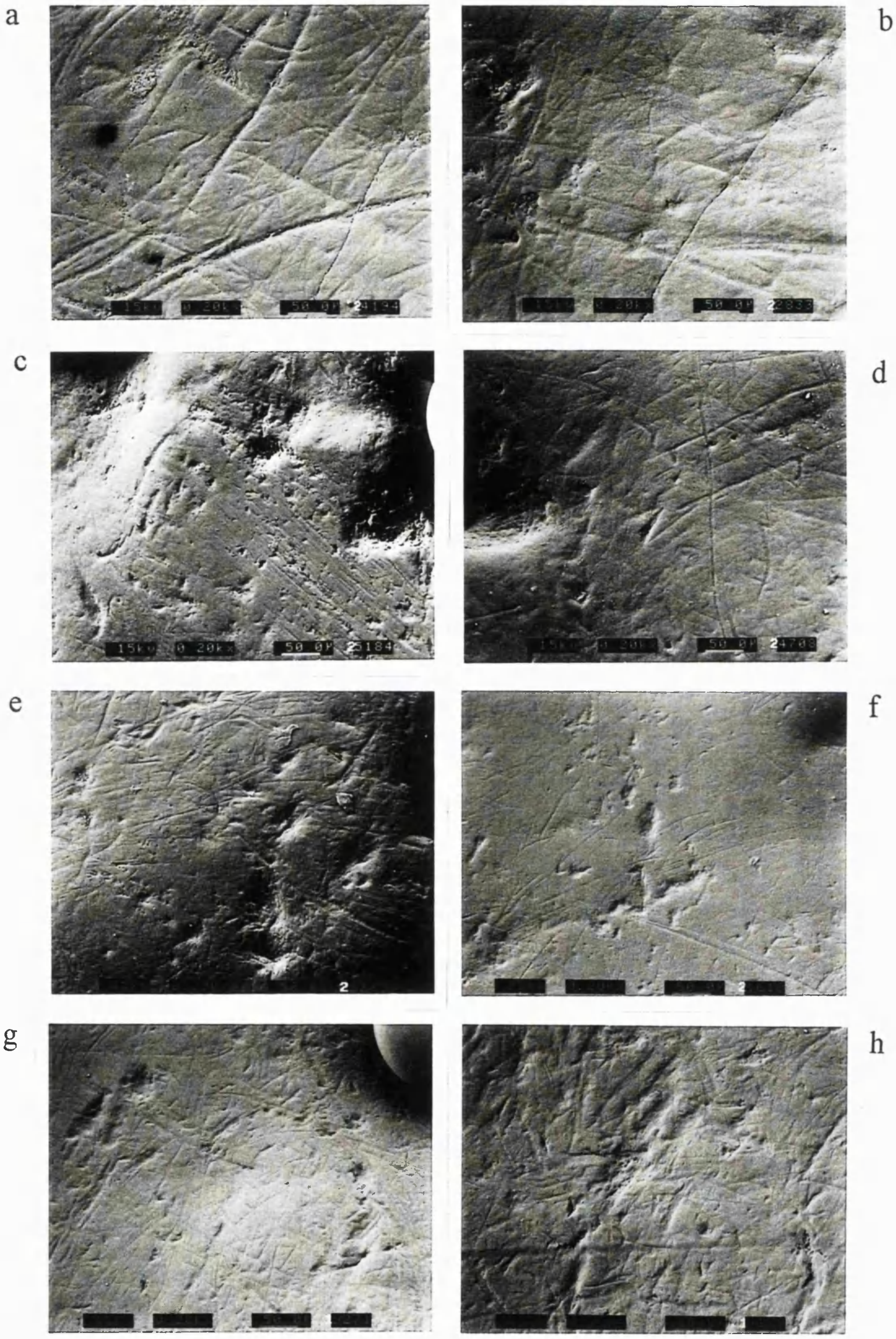
Figure 5.9. Intra-specific variation in facet x microwear patterns.
(Scale bars represent 50 μm).

Gorilla **(a, b)** has the lowest frequencies of microwear features, pits and striations, and percentages of pits. It displays significantly less features and pits than *G. alpani* and *Pongo*. *Gorilla* displays significantly lower percentages of pits than *Pongo*. *Gorilla* has similar striation widths to *Pan* and these features are significantly wider than those displayed by *Pongo* and *G. alpani*. *Gorilla* has similar pit dimensions to those of *G. alpani* which are intermediate in size to those of *Pan* and *Pongo*..

Pan **(c, d)** displays greater numbers of microwear features, pits, striations, and percentages of pits than *Gorilla*, but relatively lower frequencies and percentages of these features than *Pongo* and *G. alpani*. *Pan* has significantly fewer microwear features and less pits than *G. alpani*. *Pan* displays the widest pits of all species but these differences are not significant. *Pan* also has significantly longer pits than *Gorilla* and *Pongo*. *Pan* has similar striation widths to *Gorilla* which are significantly wider those displayed by *Pongo*.

Pongo **(e, f)** has the highest numbers of microwear features and striations, and relatively high numbers of pits and percentages of pits, and is similar to *G. alpani* in this respect. It displays significantly more microwear features, and greater numbers of pits and striations than *Gorilla*. It has the lowest pit widths and lengths of all species but these are not significant differences. *Pongo* displays similar striation widths to *G. alpani*, and has significantly narrower scratches than *Gorilla* and *Pan*.

G. alpani **(g, h)** has relatively high numbers of microwear features and striations, and the highest numbers of pits, and is similar to *Pongo* in this respect. It displays significantly more microwear features and greater numbers of pits than *Gorilla* and *Pan*. *G. alpani* has significantly greater percentages of pits than *Pongo*. *G. alpani* has similar pit dimensions to *Gorilla* which are intermediate in size to the scratch widths displayed by *Pan* and Pongo. These differences are not significant. *G. alpani* displays similar striation widths to *Pongo,* and the widths of these features are significantly narrower than those of *Gorilla*.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24194
b
22833
c
15kV
0.20kX
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25184
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15kV
0.20kX
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24708
e
2
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h

Figure 5.10. Intra-specific variation in facet 1 microwear patterns. (Scale bars represent 50 μm). In general, this facet displays less pits and more striations than facets 9 and x. ***Gorilla*** **(a, b)** has relatively low frequencies of microwear features, pits and striations, and percentages of pits. It displays significantly less features and striations than *Pongo* and fewer pits than *G. alpani. Gorilla* has significantly lower percentages of pits than *G. alpani*. *Gorilla* has relatively wide striations and these are significantly wider than those displayed by *Pongo* and *G. alpani*. *Gorilla* displays smaller pit widths than *Pongo* and *G. alpani* which are similar in size to those of *Pan*. *Gorilla* has the lowest pit lengths for all species, but these differences are not significant. ***Pan*** **(c, d)** displays the lowest numbers of microwear features, pits, striations, and percentages of pits. *Pan* has significantly fewer microwear features than *Pongo* and less pits than *G. alpani*. *Pan* displays smaller pit widths than *Pongo* and *G. alpani* which are similar in size to those of *Gorilla*. *Pan* has the longest pits of all species. These differences are not significant. *Pan* has the widest striations of all species and the dimensions of these features are significantly wider those displayed by *Pongo*. ***Pongo*** **(e, f)** has the highest numbers of microwear features and striations, relatively high numbers of pits similar in number to those displayed by *G. alpani*, and relatively high percentages of pits. It displays significantly more microwear features than *Gorilla* and *Pan*. *Pongo* has significantly more striations than *Gorilla*. The dimensions of the pits displayed by *Pongo* are similar to those of *G. alpani. Pongo* has wide pits relative to those of *Gorilla* and *Pan*. It displays pit lengths which are intermediate to *Gorilla* and *Pan*. These differences are not significant. *Pongo* displays similar striation widths to *G. alpani*, and has significantly narrower scratches than *Gorilla and Pan*. ***G. alpani*** **(g, h)** has relatively high numbers of microwear features and striations, relatively high frequencies of pits which are similar in number to *Pongo*, and the highest percentages of pits. *G. alpani* displays significantly more pits than *Gorilla* and *Pan,* and has significantly higher percentages of pits than *Gorilla*. The dimensions of the pits displayed by *G. alpani* are similar to those of *Pongo*. *G. alpani* has wide pits relative to those of *Gorilla* and *Pan*. It displays pit lengths which are intermediate to *Gorilla* and *Pan*. These differences are not significant. *G. alpani* displays similar striation widths to *Pongo,* and the widths of these features are significantly narrower than those of *Gorilla*.

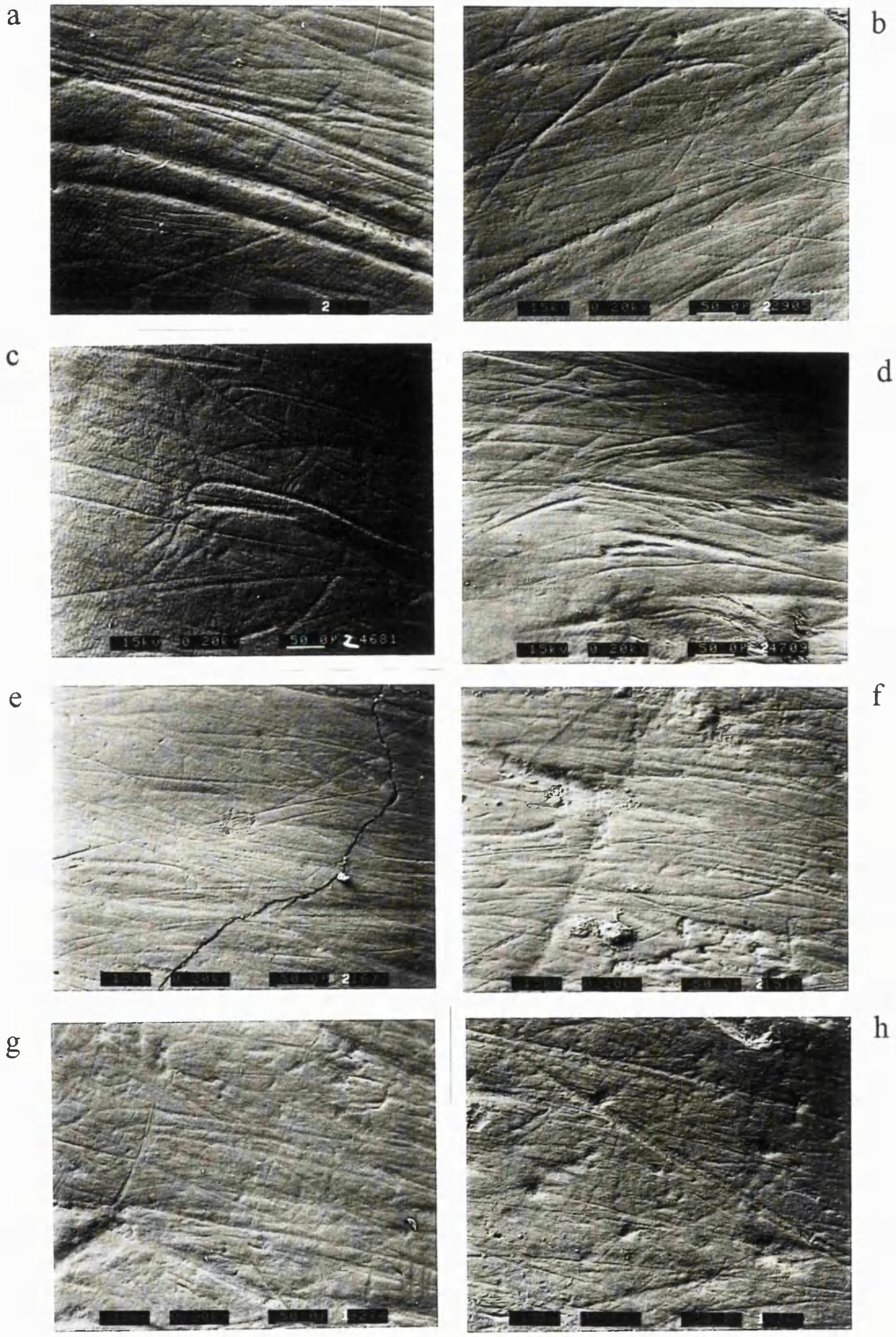
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Figure 5.11. *G. alpani* facet 9 microwear patterns.
Specimens **(a)** D883, **(b)** E626, **(c)** C207, **(d)** H272, **(e)** C206, **(f)** K1316, **(g)** K1394, **(h)** F107. (Scale bars represent 50 μm).

Facet 9 in *G. alpani* is characterised by high numbers of microwear features. It has large numbers of pits and percentages of pits. The dimensions of pits and striations are small. This figure also shows the variability in numbers and sizes of microwear features. In comparison to the extant hominoids examined in this study *G. alpani* displays high total numbers of microwear features and pits in comparison to *Gorilla* and *Pan*. *G. alpani* displays a similar microwear pattern to *Pongo* in the numbers of these microwear features as well as in the narrow striation widths both these species display. *G. alpani* has the smallest pit widths and pit lengths of all species examined. *G. alpani* displays the highest percentages of pits in comparison to all the extant hominoids.

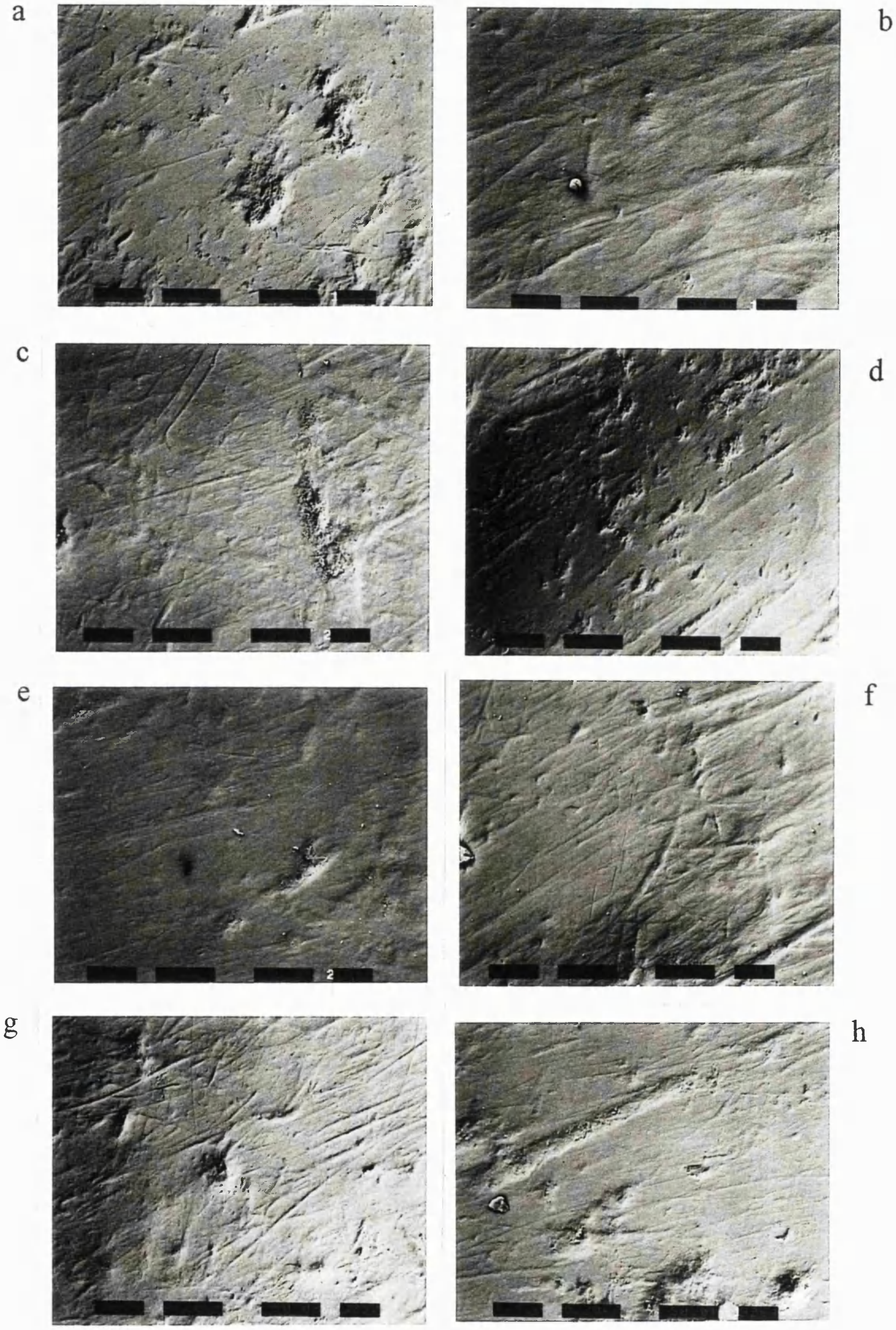
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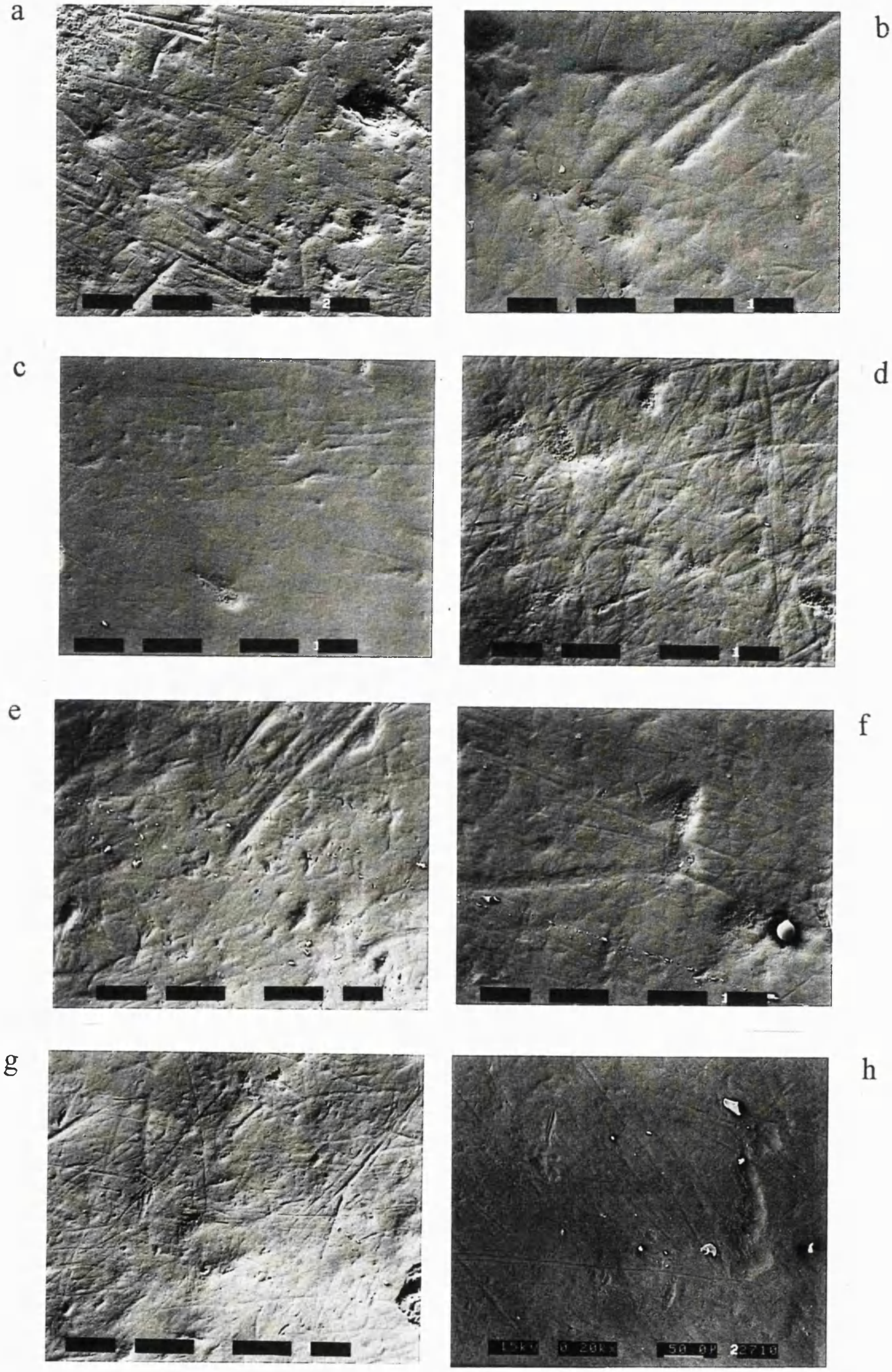
Figure 5.12. *G. alpani* facet x microwear patterns.

Specimens **(a)** K1399, **(b)** E626, **(c)** B523, **(d)** B510, **(e)** K1316, **(f)** E629, **(g)** K1394, **(h)** K1447. (Scale bars represent 50 μm).

Facet x in *G. alpani* is characterised by higher numbers of microwear features, numbers of pits, percentages of pits, and pit dimensions than facet 9. The dimensions of striations are the same in facet x as facet 9. Again, this figure gives an indication of the intra-specific variability in microwear features in this species. *G. alpani* similarly high total numbers of microwear features and pits as *Pongo* in comparison to *Gorilla* and *Pan*. *G. alpani* displays relatively high numbers of striations, which are similar in width to those of *Pongo*. Pit dimensions are most similar to *Gorilla*. *G. alpani* displays the highest percentages of pits relative to all the extant hominoids on facet x.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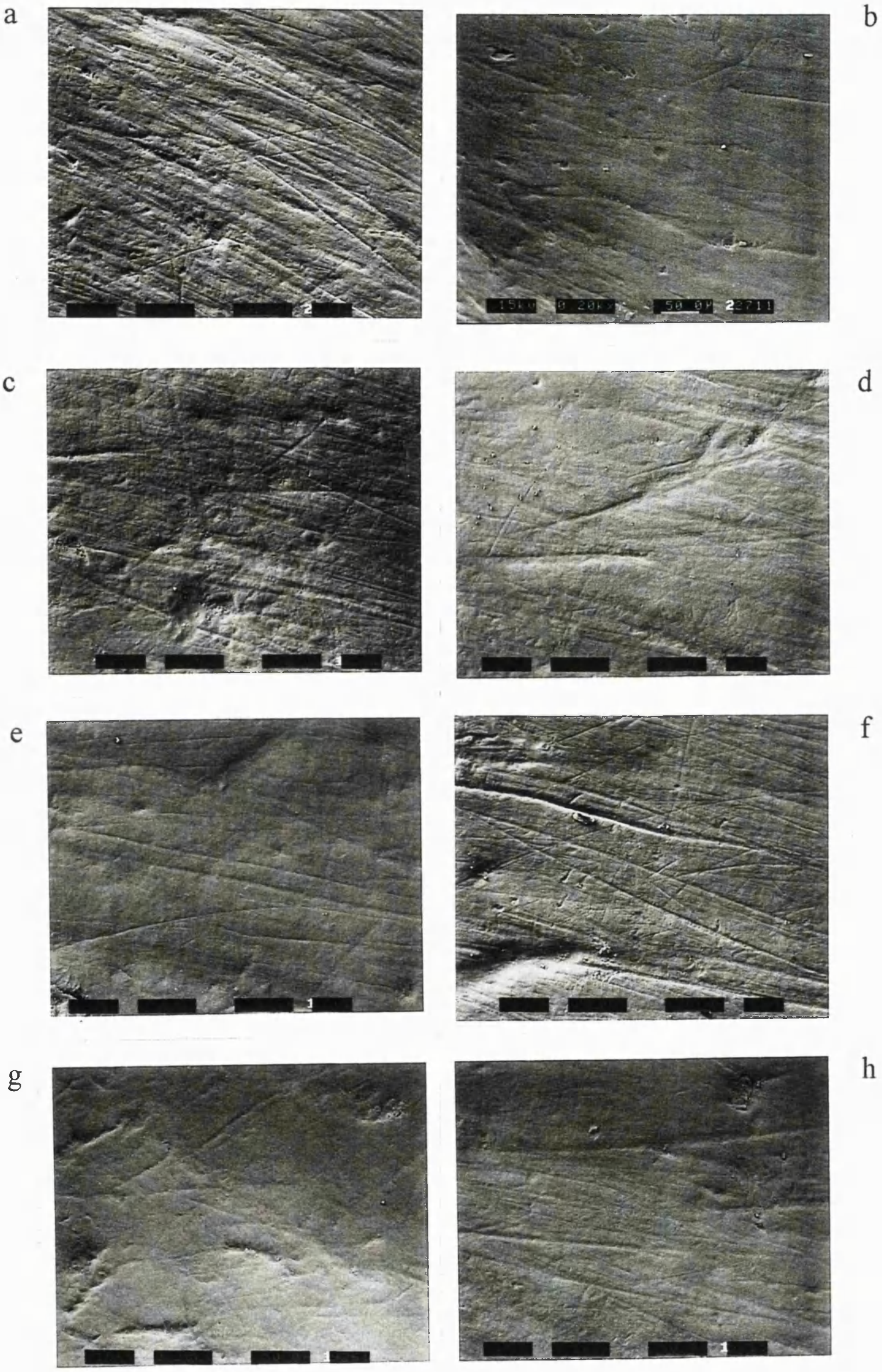
15kV
0.20kx
50.0µ
22710

Figure 5.13. *G. alpani* facet 1 microwear patterns.

Specimens **(a)** 1399, **(b)** K1447, **(c)** B510, **(d)** K1316, **(e)** B523, **(f)** K1394, **(g)** F107, **(h)** E626. (Scale bars represent 50 μm).

Facet 1 in *G. alpani* is characterised by lower numbers of microwear features, numbers of pits, and percentages of pits than facets 9 and x. The dimensions of pits and striations tend to be larger than those seen on facets 9 and x. This shows the variability in microwear features in this species. *G. alpani* displays the most similarity to *Pongo* on this facet than to the other extant hominoids. It has larger numbers of features, more pits and striations, higher percentages of pits than *Gorilla* and *Pan*. *G. alpani* and *Pongo* have wider pits than *Gorilla* and *Pan*, pit lengths which are intermediate to those of *Gorilla* and *Pan*, and smaller striation widths than *Gorilla* and *Pan*.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0.20kx
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22711
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5.2 SEX DIFFERENCES IN MICROWEAR PATTERNS

Information on the sex of individuals was available for the entire *Pongo* sample. The sex of 9 *Gorilla*, and 6 *Pan* specimens was also known. Sex differences are explored using two of the most commonly employed primate microwear variables - percentage pits and pit width (e.g. Teaford and Walker, 1984; Teaford, 1985; Grine and Kay, 1988; Teaford and Runestad, 1992; Ungar, 1996).

5.2.1 Percentage pits

Sex differences in percentage pits are displayed in Tables 5.8, 5.9 and 5.10 and Figure 5.14. There are no significant differences between *Gorilla* males and females for any facet, although males do display greater percentages of pits than females. *Pan* males have greater percentage pits on facets 9 and x than females, and females have higher percentages on facet 1, although sample sizes were too small to perform statistical tests. *Pongo* males have higher percentages of pits than females on facets 9, x, and 1, and this difference is statistically significant for facet 1 ($p<0.05$).

Females

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	36.0	2.19	36.2	39.8	17.2	54.6	37.4
Pan	1	28.6	-	-	-	-	-	-
Pongo	10	37.4	14.6	39.5	51.3	27.5	43.7	16.2

Males

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	40.3	23.7	40.9	58.1	17.9	62.0	44.1
Pan	5	41.6	24.6	52.0	56.4	16.2	61.8	45.6
Pongo	10	48.5	18.1	47.2	54.6	36.4	66.1	29.7

Table 5.8 Male and female percentage pits descriptive statistics for facet 9.

Females

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	3	27.3	18.1	29.4	36.0	8.3	-	-
Pan	1	32.0	-	-	-	-	-	-
Pongo	9	47.1	16.4	45.5	53.7	37.7	60.7	23.0

Males

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	3	32.6	5.9	35.2	11.0	25.8	-	-
Pan	5	44.5	16.1	40.0	40.2	33.4	57.9	24.5
Pongo	10	48.8	15.3	53.9	39.4	34.0	61.9	27.9

Table 5.9 Male and female percentage pits descriptive statistics for facet x.

Females

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	14.4	10.0	13.2	23.3	5.7	24.3	18.6
Pan	1	13.0	-	-	-	-	-	-
Pongo	10	12.3	10.5	9.5	36.6	6.8	13.0	6.3

Males

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	17.4	3.1	16.7	6.7	14.8	20.6	5.8
Pan	2	5.6	7.8	5.6	11.1	0.0	-	-
Pongo	10	24.0	14.7	18.7	49.0	15.2	31.0	15.8

Table 5.10 Male and female percentage pits descriptive statistics for facet 1.

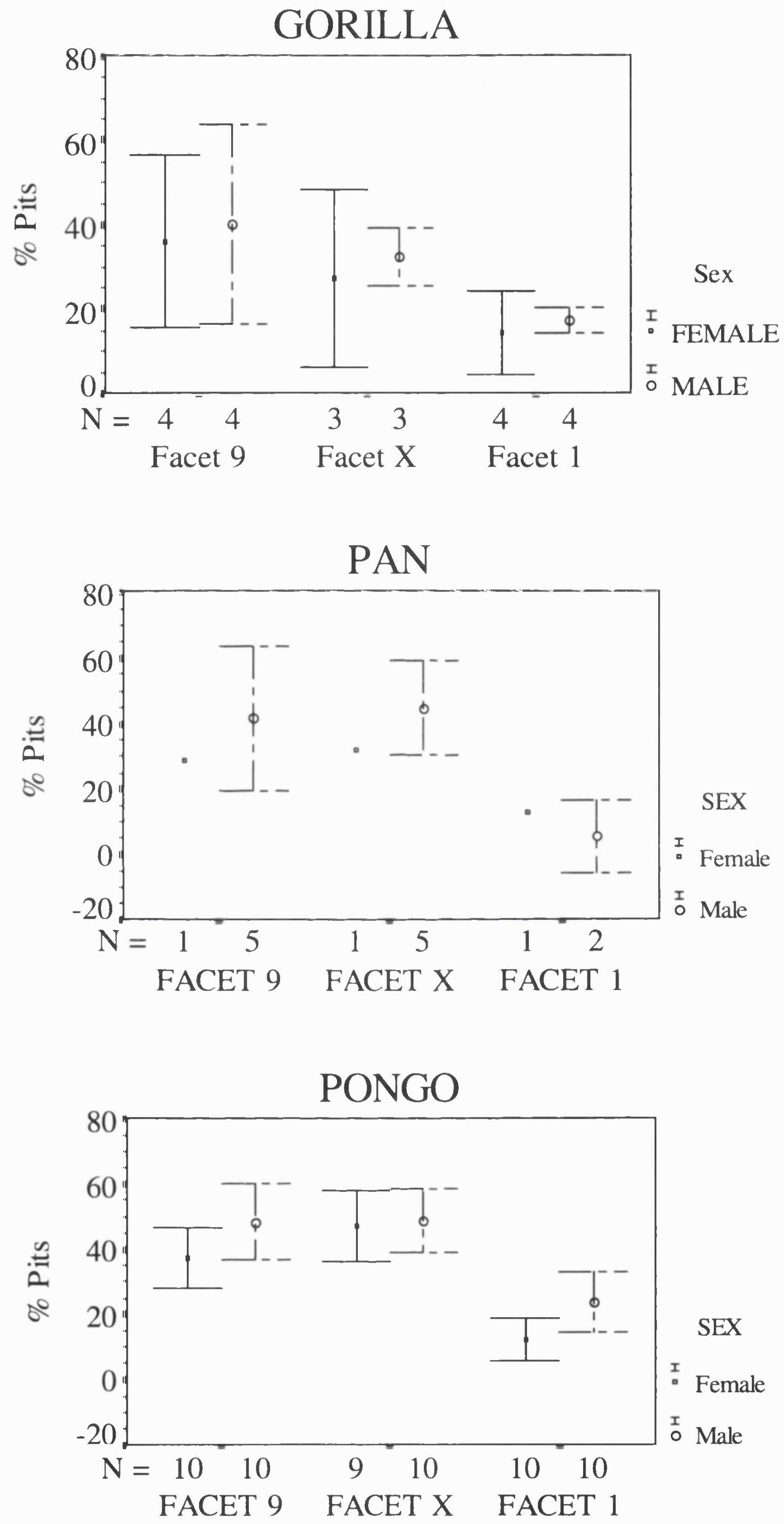


Figure 5.14. Male and female percentage pits (mean +/– 2 S.E.).

5.2.2 Pit width

Sex differences in pit width are displayed in Table 5.11, 5.12, and 5.13 and Figure 5.15. *Gorilla* males have wider pits on all facets than females, although these are not statistically significant differences. *Pongo* males show the same trend on facets 9 and x, while females display wider pits on facet 1 than males. Again, this is not a significant difference. *Pan* sample sizes were too small to perform statistical tests. However, female pit width is wider than that of males on all facets.

Figure 5.16 displays males and female facet 9 microwear patterns for each species of extant hominoid.

Females

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	3.8	2.2	3.3	5.1	2.0	6.0	4.0
Pan	1	8.8	-	-	-	-	-	-
Pongo	10	4.0	1.4	3.5	3.9	2.7	5.3	2.6

Males

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	4.5	1.5	4.7	3.2	2.9	5.8	2.9
Pan	5	5.2	1.6	6.1	3.5	3.5	6.5	3.0
Pongo	10	5.5	4.2	4.0	14.1	3.2	7.0	3.8

Table 5.11 Male and female pit widths (μm) for facet 9.

Females

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	3	3.1	1.9	2.2	3.5	1.8	-	-
Pan	1	12.4	-	-	-	-	-	-
Pongo	9	3.7	1.1	3.6	3.1	2.5	4.8	2.3

Males

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	3	4.3	2.3	3.2	4.2	2.8	-	-
Pan	5	5.1	1.9	4.9	4.6	3.4	6.9	3.5
Pongo	10	4.2	1.6	3.8	4.5	3.2	5.8	2.7

Table 5.12 Female and male pit widths (μm) for facet x.

Females

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	3.2	2.2	3.0	4.9	1.2	5.4	4.2
Pan	1	7.0	-	-	-	-	-	-
Pongo	10	5.9	4.9	4.5	16.0	2.6	7.7	5.1

Males

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	4	6.0	4.4	4.0	9.1	3.6	10.5	6.9
Pan	1	5.0	-	-	-	-	-	-
Pongo	10	4.9	4.5	3.5	15.4	2.9	5.2	2.2

Table 5.13 Female and male pit widths (μm) facet 1.

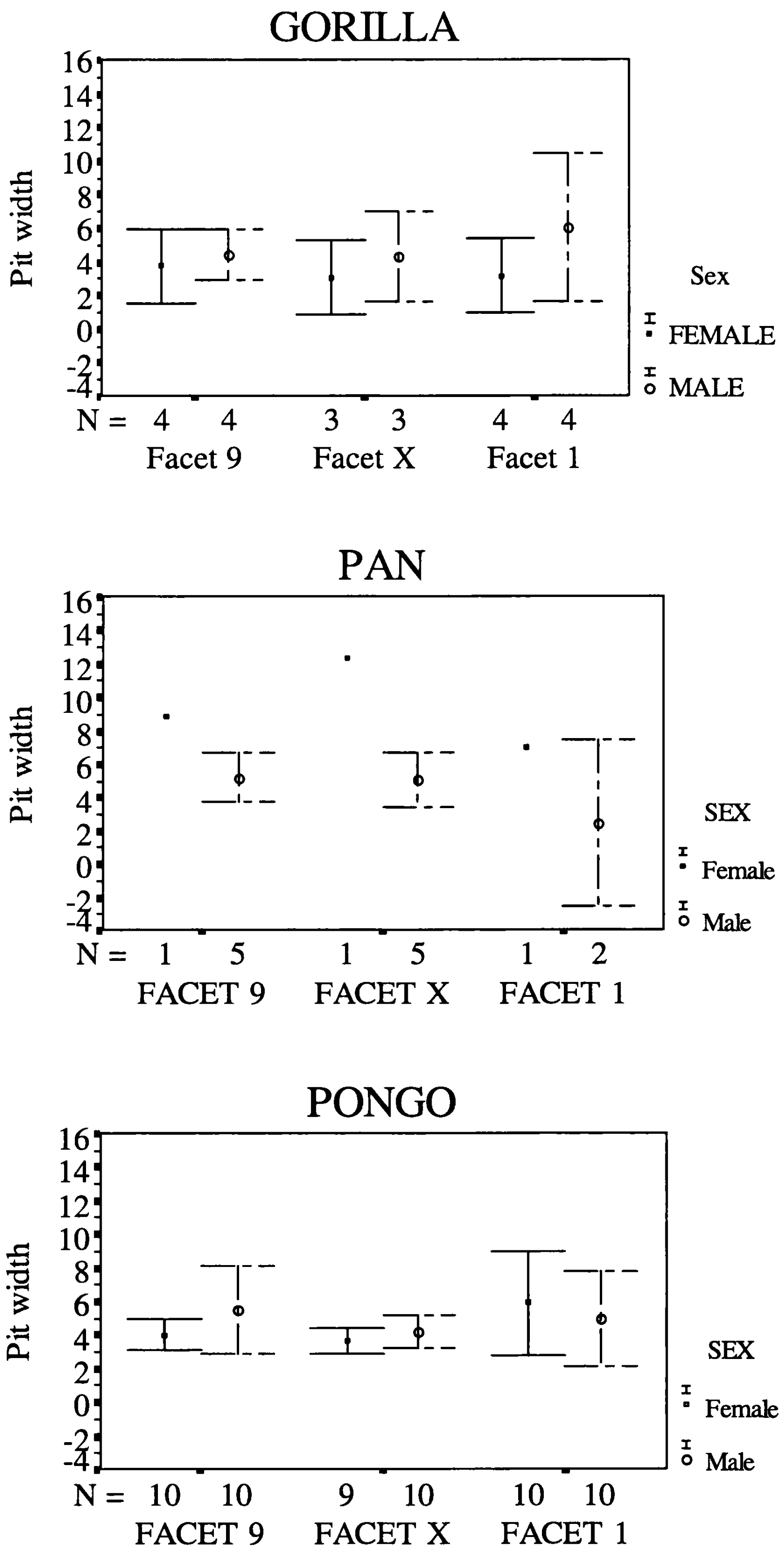
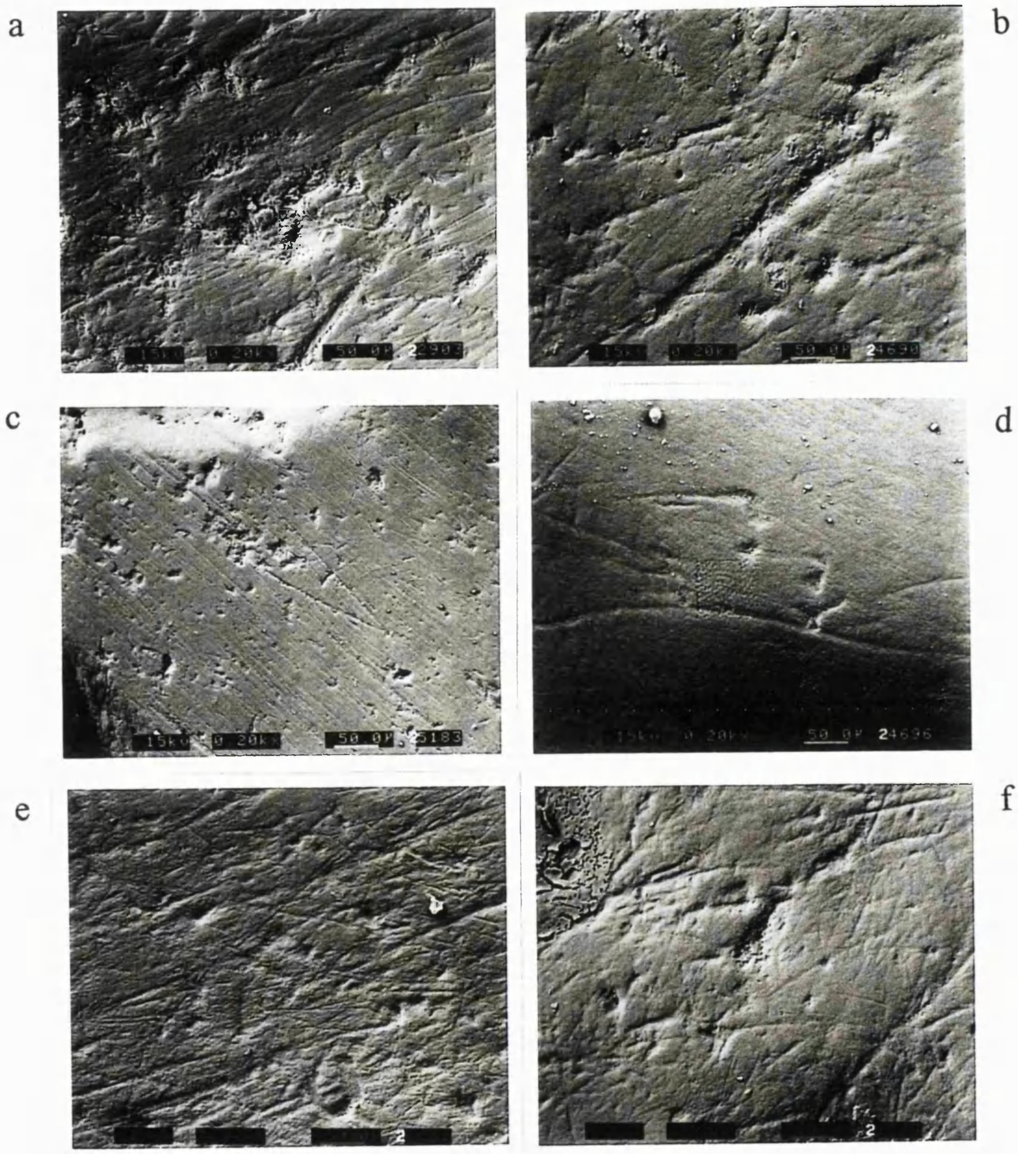


Figure 5.15. Male and female pit widths (µm) (mean +/– 2 S.E.).

Figure 5.16. Male and female facet 9 microwear patterns. ***Gorilla*** (a) males and (b) females; ***Pan*** (c) males and (d) females; and ***Pongo*** (e) males and (f) females. (Scale bars represent 50 µm).

Pongo males have higher percentages of pits and wider pits than females, although this is not a significant difference. *Gorilla* males also show this trend but although again, there were no significant differences between the two sexes. Although sample sizes were too small to perform statistical tests, *Pan* males display higher percentages of pits than females, while females have wider pits than males.


a
15kV
0.20kX
50.0µ
22903
b
15kV
0.20kX
50.0µ
24690
c
15kV
0.20kX
50.0µ
5183
d
15kV
0.20kX
50.0µ
24696
e
2
f
2

5.2.3 Summary

Only one significant difference was found for sex differences in percentage pits. *Pongo* males have higher percentages of pits than females (facet 1, although this is not a highly significant difference). No significant differences in pit widths were found between the sexes for any species. This suggests that sex is not an important determinant of microwear formation. However, one significant difference was found in *Pongo* and this raises the possibility that a larger sample size might reveal more sex differences in microwear patterns.

5.3 WEAR STAGE DIFFERENCES IN MICROWEAR PATTERNS

All specimens were assigned to 1 of 4 wear stages (see Chapter 3). These categories represent teeth which range from only lightly worn (Wear Stage 1) to heavily worn (Wear Stage 4). Only one specimen from the entire hominoid sample was assigned to the heaviest wear stage, all other specimens fell into wear stage categories 1 - 3.

As with the description of sex differences variation in wear stages is explored using percentage pits and pit width.

5.3.1 Percentage pits

Tables 5.14, 5.15, and 5.16 and Figure 5.17 display wear stage differences in percentage pits. *Gorilla* specimens at wear stages 1 and 3 specimens have higher percentage pits than wear stage 2 molars on facets 9 and x, and there is very little difference between percentage pits for all stages of wear on facet 1. However, sample sizes in *Gorilla* were too small for statistical testing. *Pan* wear stages 1 and 3 molars, which have greater percentages of pits than the wear stage 2 specimens, display little variation in percentages of pits when compared to each other on facet 9. Wear stages 2 and 3 molars, while they display similar percentages of pits to each other, have lower percentages than wear stage 1 specimens. Percentage pits is higher on wear stages 1 and 2 specimens than on wear stage 3 molars on facet 1. Statistical tests could not be performed for *Pan* wear stage comparisons as sample sizes were too small. *Pongo* wear stage 1 specimens display significantly greater percentages of pits on facet 9 than wear stage 2 molars ($p<0.05$). Wear stage 1 specimens also have higher percentage pits than wear stage 3 molars, although this is not a significant difference. Percentage pits varies little among the three wear stages on facets x and 1, no significant differences were indicated.

G. alpani displays little variation in percentage pits on facets 9 and x. Facet 1 wear stages 1 and 2 molars have lower percentages of pits than wear stage 3 specimens, and wear stage 1 specimens display higher percentage pits than wear stage 3 molars. Wear stage 2 sample size was too small for statistical testing, but no significant differences were indicated for comparisons between wear stage 1 and 3 specimens.

Wear stage 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	2	37.0	7.1	37.0	10.1	31.9	-	-
Pan	2	45.6	24.0	45.6	33.9	28.6	-	-
Pongo	7	53.6	19.0	54.8	55.8	41.8	68.1	26.3
G. alpani	13	54.1	15.9	57.0	54.1	42.4	66.7	24.4

Wear stage 2

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	1	15.9	-	-	-	-	-	-
Pan	1	26.3	-	-	-	-	-	-
Pongo	6	32.6	13.0	35.0	33.5	19.3	43.5	24.1
G. alpani	2	55.5	25.3	55.5	35.8	37.6	-	-

Wear stage 3

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	9	30.4	15.6	25.4	45.1	17.7	45.5	27.8
Pan	6	39.9	22.6	46.0	55.0	16.5	60.7	44.1
Pongo	7	41.1	13.1	40.9	42.4	31.8	46.0	14.2
G. alpani	3	56.4	10.7	62.2	19.0	44.0	-	-

Table 5.14. Wear stage differences in percentage pits for facet 9.

Wear stage 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	2	34.1	3.9	34.1	5.5	31.3	-	-
Pan	2	52.1	28.4	52.1	40.2	32.0	-	-
Pongo	7	50.9	17.8	53.0	49.1	36.1	67.3	31.2
G. alpani	8	58.3	9.1	55.7	22.8	49.9	68.0	18.1

Wear stage 2

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	1	8.3	-	-	-	-	-	-
Pan	1	40.0	-	-	-	-	-	-
Pongo	6	49.6	16.0	44.7	38.8	35.4	67.3	31.8
G. alpani	2	59.8	13.6	59.7	19.3	50.1	-	-

Wear stage 3

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	8	35.0	7.1	32.4	67.2	21.5	42.7	21.3
Pan	5	41.4	17.6	34.7	45.0	28.9	57.2	28.3
Pongo	6	43.1	13.4	43.4	31.0	28.1	57.1	29.0
G. alpani	3	59.1	14.7	66.7	26.3	42.2	-	-

Table 5.15 Wear stage differences in percentage pits for facet x.

Wear stage 1

Species	**N**	**Mean**	**SD**	**Median**	**Range**	Q_L	Q_U	Q **Range**
Gorilla	2	14.0	1.0	14.0	13.3	-	-	-
Pan	2	12.4	0.8	12.4	1.2	11.8	-	-
Pongo	7	15.0	9.5	12.1	24.1	7.1	26.3	19.2
G. alpani	11	22.8	14.1	17.6	38.8	12.0	41.8	29.8

Wear stage 2

Species	**N**	**Mean**	**SD**	**Median**	**Range**	Q_L	Q_U	Q **Range**
Gorilla	1	15.4	-	-	-	-	-	-
Pan	1	11.1	-	-	-	-	-	-
Pongo	6	17.4	11.9	14.8	32.4	8.6	23.8	15.2
G. alpani	1	44.5	-	-	-	-	-	-

Wear stage 3

Species	**N**	**Mean**	**SD**	**Median**	**Range**	Q_L	Q_U	Q **Range**
Gorilla	9	11.7	8.4	10.9	27.3	5.4	17.5	12.1
Pan	2	6.6	9.3	6.6	13.2	0.0	-	-
Pongo	7	21.8	19.0	15.7	52.6	10.1	40.0	29.9
G. alpani	3	13.7	14.7	7.9	27.6	2.8	-	-

Table 5.16 Wear stage differences in percentage pits for facet 1.

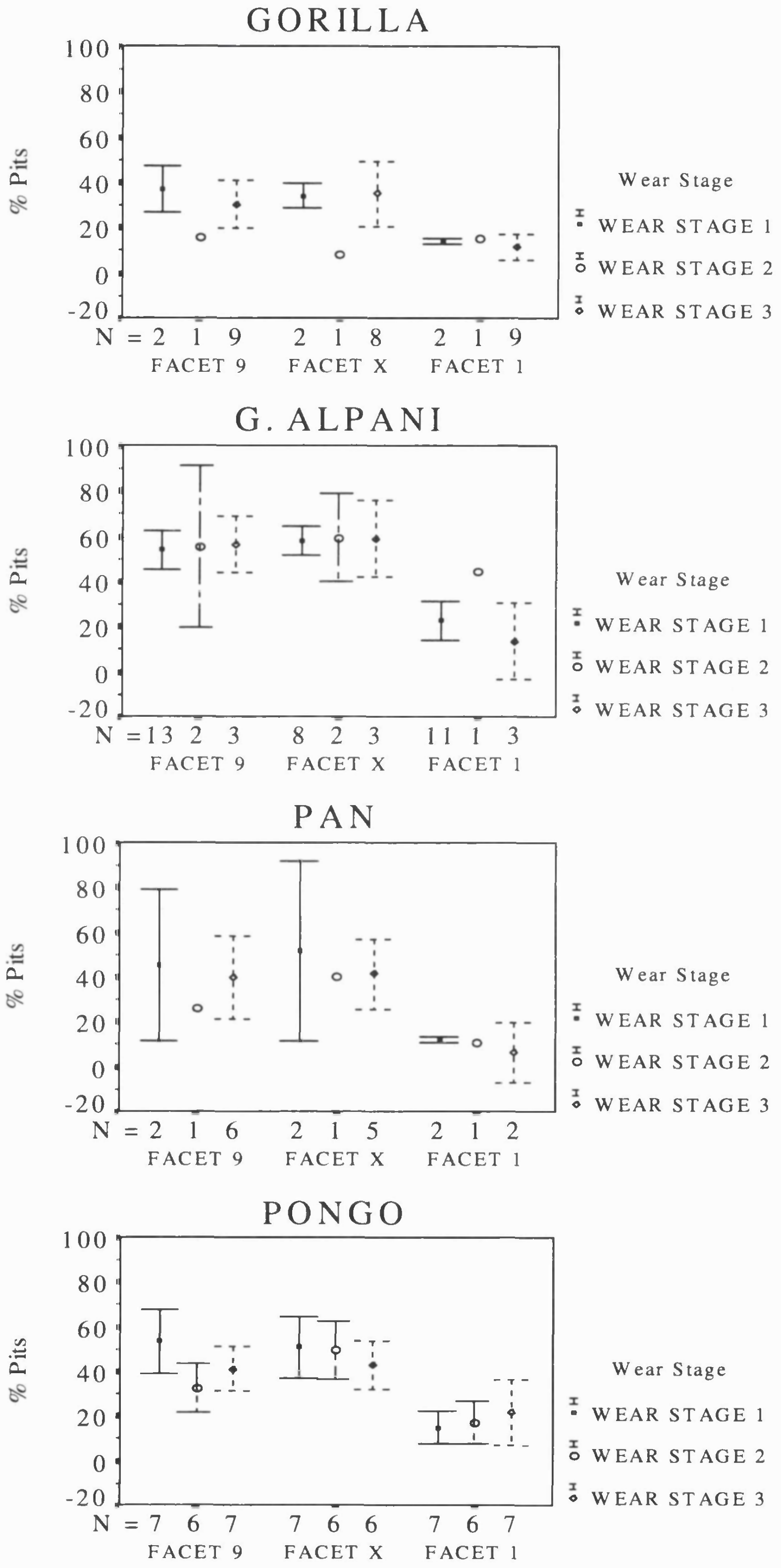


Figure 5.17. Percentage pits for wear stages 1, 2 and 3 (mean +/- 2 S.E.).

5.3.2 Pit width

Wear stage differences in pit width are shown in Tables 5.17, 5.18, and 5.19 and Figure 5.18. *Gorilla* wear stage 1 and 3 specimens, while they display wider pits than wear stage 2 molars, show little variation in pit width across all three facets, although this is not a significant difference (sample sizes were too small for statistical comparisons). *Pan* shows little variation in pit width across all facets. Wear stages 1 and 2 specimens display wider pits than stage 3 molars on all three facets. Pit width is also wider in wear stage 1 molars in comparison to the wear stage 2 specimens on facets 9 and x. The wear stage 2 specimen has wider pits on facet 1 than wear stage 3. Again, statistical comparisons could not be carried out due to small sample sizes. *Pongo* shows little variation in pit width between wear stage 1 and 2 specimens on facet 9. Wear stage 3 specimens display wider pits than the other two wear stages on facet 9. There is little difference in pit width between all three wear stages on facet x, but a similar pattern as that displayed on facet 9 is apparent - widths are greater on wear stage 3 specimens. Wear stage 2 and 3 molars, while they greater pit widths than wear stage 1 specimens on facet 1, show little variation in pit width when compared with each other. None of the differences seen in wear stage pit width comparisons in *Pongo* are statistically significant.

G. alpani shows little variation in width for all stages of wear but wear stage 3 specimens display a small increase in pit widths relative to molars from the other two wear stages on facets 9 and x (wear stages 1 and 3 only could be compared statistically). Wear stages 1 and 3 specimens have greater pit widths than wear stage 2 specimens on facet 1, although this could not be tested statistically due to small sample sizes. There is no significant difference in pit width between wear stage 1 and

Wear stage 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	2	6.7	1.9	6.7	2.6	5.5	-	-
Pan	2	7.5	1.9	7.5	2.7	6.1	-	-
Pongo	7	3.9	1.5	3.4	3.9	2.3	4.1	2.8
G. alpani	13	3.6	1.1	3.3	2.9	2.6	4.8	2.2

Wear stage 2

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	1	1.7	-	-	-	-	-	-
Pan	1	6.7	-	-	-	-	-	-
Pongo	6	3.9	2.0	3.5	5.4	2.6	4.6	2.0
G. alpani	2	3.2	1.0	3.2	1.5	2.5	-	-

Wear stage 3

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	9	4.7	2.3	3.6	6.9	3.0	6.3	3.4
Pan	6	4.8	2.0	4.6	5.0	3.1	6.6	3.5
Pongo	7	6.4	4.6	4.1	13.6	3.5	6.7	3.2
G. alpani	3	4.1	1.5	3.9	2.9	2.8	-	-

Table 5.17 Facet 9 wear stage differences in pit width (μm).

Wear stage 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	2	6.2	1.1	6.2	1.6	5.4	-	-
Pan	2	8.1	6.1	8.1	8.6	3.8	-	-
Pongo	7	3.6	1.2	3.5	3.3	2.4	4.8	2.6
G. alpani	8	3.8	1.0	3.6	3.0	3.1	4.8	1.8

Wear stage 2

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	1	2.2	-	-	-	-	-	-
Pan	1	6.2	-	-	-	-	-	-
Pongo	6	3.9	1.2	3.9	3.3	3.0	5.0	2.0
G. alpani	2	3.1	0.2	3.1	0.4	2.9	-	-

Wear stage 3

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	8	4.9	4.9	3.2	14.9	2.7	5.0	2.3
Pan	5	4.9	1.7	4.7	4.6	3.8	6.2	2.5
Pongo	6	4.4	1.8	4.3	4.1	2.5	6.5	4.0
G. alpani	3	9.1	9.4	4.2	16.8	3.1	-	-

Table 5.18 Facet x wear stage differences in pit width (μm).

Wear stage 1

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	2	4.3	1.1	4.3	1.6	3.5	-	-
Pan	1	7.0	-	-	-	-	-	-
Pongo	7	3.4	1.1	3.0	3.1	2.6	3.8	1.2
G. alpani	11	5.1	3.0	4.1	8.6	3.0	6.2	3.2

Wear stage 2

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	1	1.9	-	-	-	-	-	-
Pan	1	5.0	-	-	-	-	-	-
Pongo	6	6.8	5.4	6.0	15.3	2.8	9.3	6.5
G. alpani	1	3.0	-	-	-	-	-	-

Wear stage 3

Species	N	Mean	SD	Median	Range	Q_L	Q_U	Q Range
Gorilla	8	4.4	3.7	3.9	11.7	1.7	5.5	3.7
Pan	0	-	-	-	-	-	-	-
Pongo	7	6.3	5.8	3.6	16.1	3.0	10.6	7.6
G. alpani	3	7.4	3.9	7.0	7.8	3.7	-	-

Table 5.19 Facet 1 wear stage differences in pit width (μm).

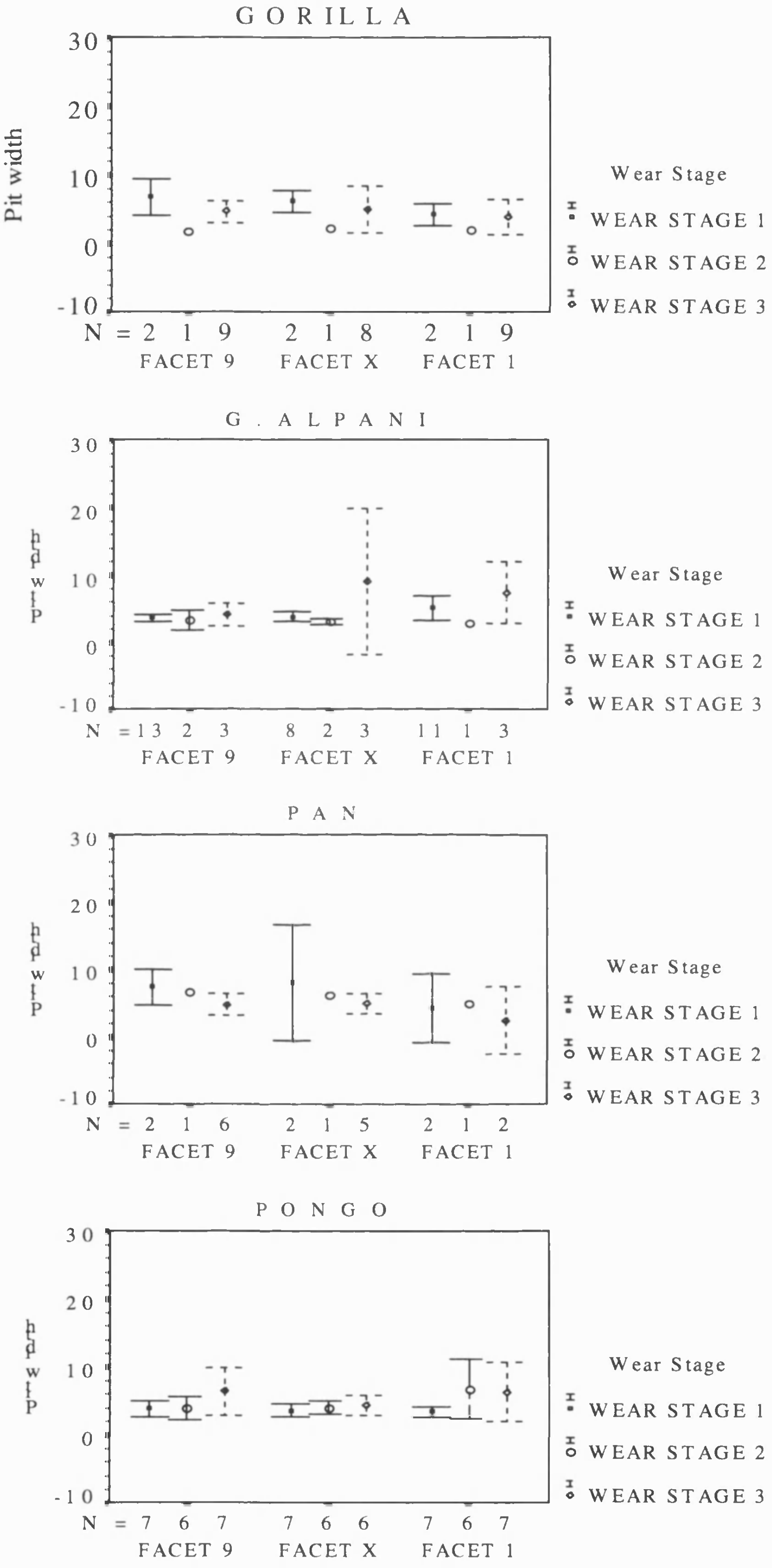


Figure 5.18. Pit widths (μm) for wear stages 1, 2 and 3 (mean +/– 2 S.E.).

wear stage 3 molars on facet 1.

Figures 5.19 and 5.20 display facet 9 microwear patterns for wear stages 1, 2, and 3 for all species of hominoid.

Figure 5.19. Facet 9 variation in microwear patterns according to wear stage (*Gorilla* and *Pan*). ***Gorilla*** (left) wear stages 1 (a) (top), 2 (b) (middle) and 3 (c) (bottom) specimens; and ***Pan*** (right) wear stages 1 (d) (top), 2 (e) (middle), and 3 (f) (bottom) molars. (Scale bars represent 50 µm).

Gorilla wear stages 1 and 3 specimens display higher percentages of pits and wider pits than wear stage 2 molars. *Pan* also shows the same trend as *Gorilla* and in addition, *Pan* wear stage 1 molars have wider pits than wear stage 2 molars. Sample sizes were too small for statistical testing.

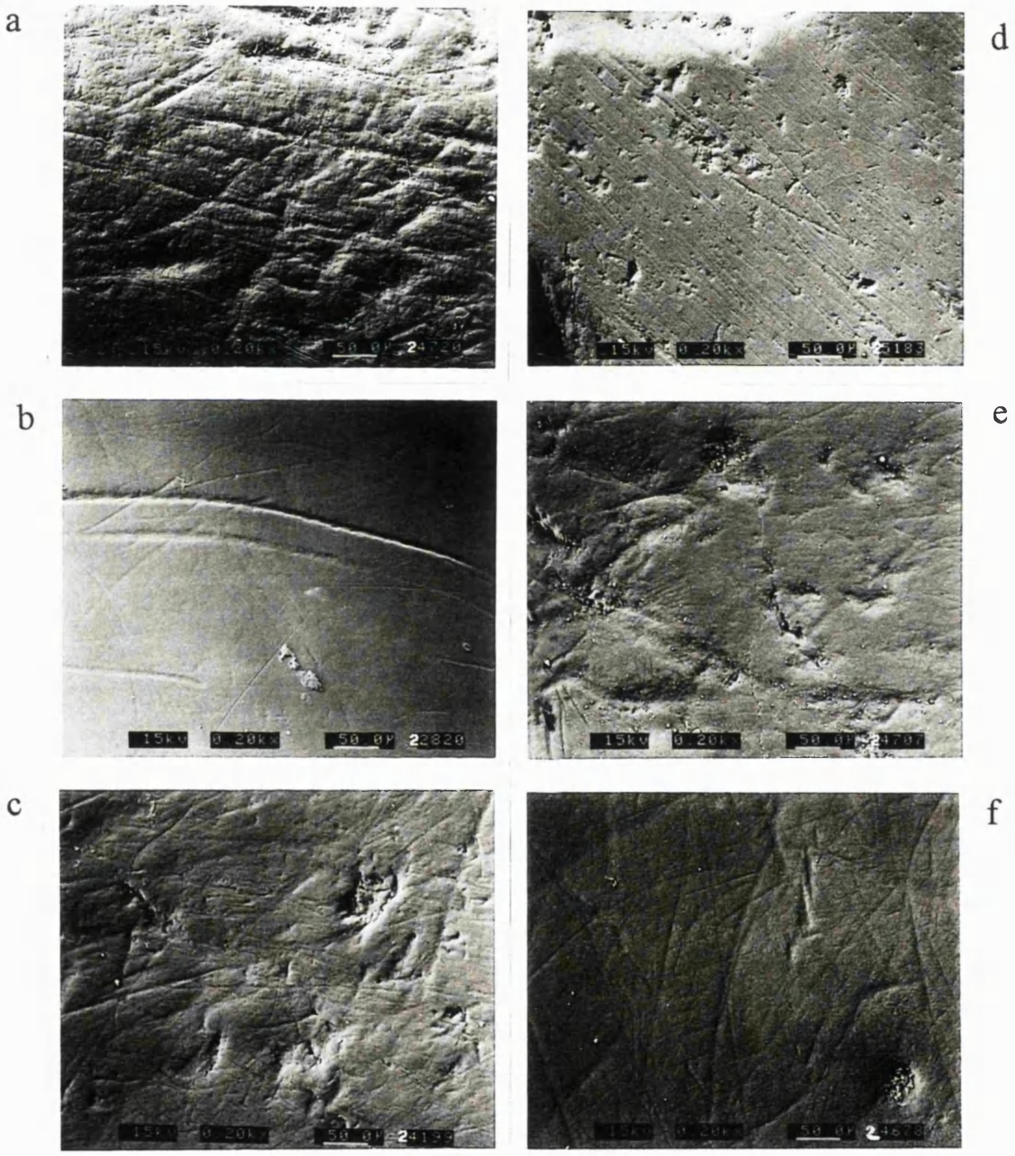
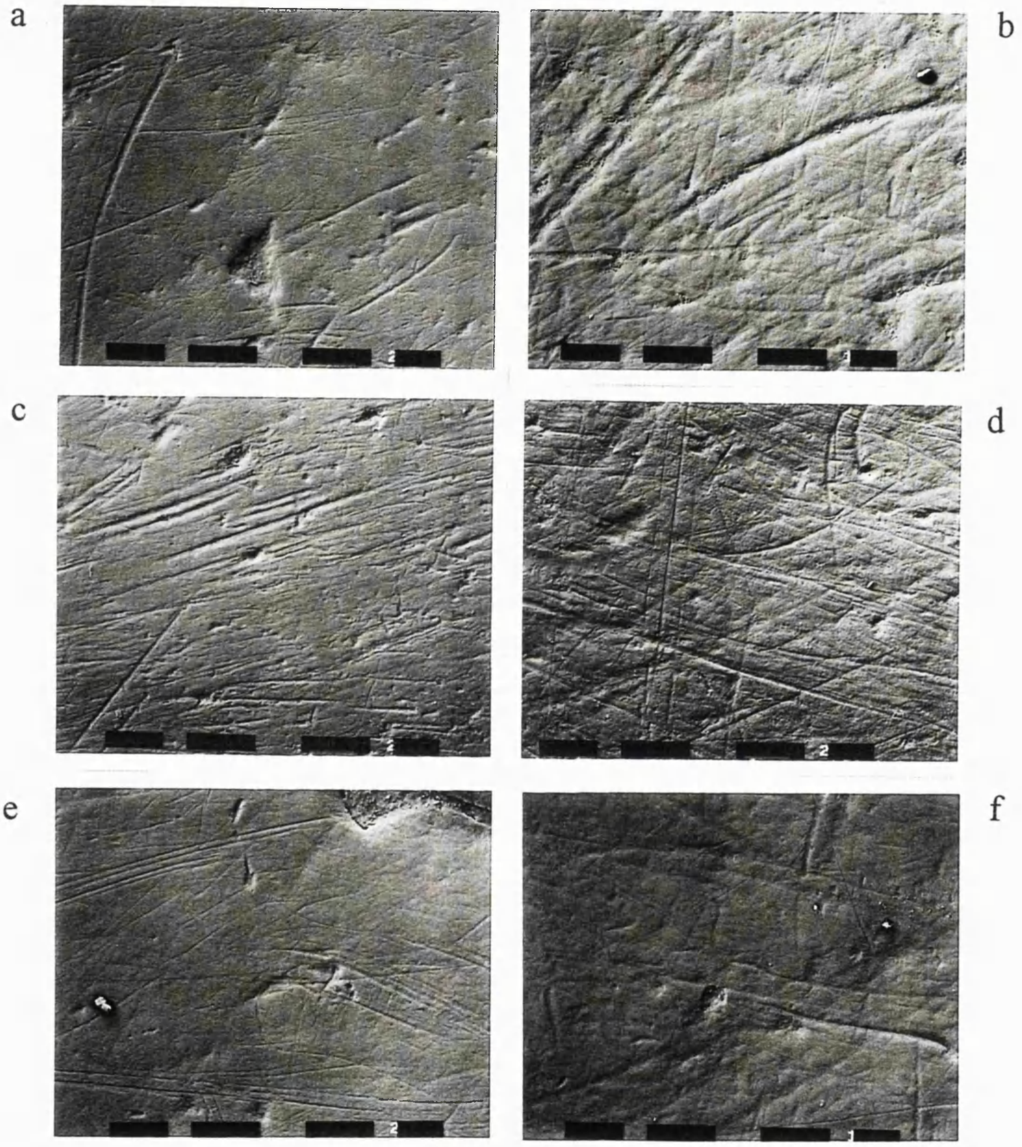

a
15kv 0.20kx 50.0µ
d
15kv 0.20kx 50.0µ 5183
b
15kv 0.20kx 50.0µ 22820
e
15kv 0.20kx 50.0µ 24707
c
15kv 0.20kx 50.0µ 24199
f
15kv 0.20kx 50.0µ 24678

Figure 5.20. Facet 9 variation in microwear according to wear stage (*Pongo* and *G. alpani*). ***Pongo*** (left) wear stages 1 (a) (top), 2 (b) (middle) and 3 (c) (bottom) specimens; and ***G. alpani*** (right) wear stages 1 (d) (top), 2 (e) (middle), and 3 (f) (bottom) molars. (Scale bars represent 50 µm).

Pongo wear stage 1 specimens display significantly higher percentages of pits than wear stage 2 molars. Wear stages 1 and 2 specimens display little variation in pit widths in *Pongo*, while wear stage 3 molars have wider pits than wear stage 1 and 2 specimens, although these are not significant differences. *G. alpani* displays little differences in percentages of pits and pit widths among wear stages on facet 9. Sample sizes were too small for statistical testing.


a
b
c
d
e
f

5.3.3 Summary

The most consistent pattern of microwear variation across species among wear stages is apparent on facets 9 and x. Wear stages 1 and 3 specimens in *Gorilla, Pan* and *Pongo* have higher percentages of pits than wear stage 2 molars on facet 9. In *Pongo* wear stage 1 molars have significantly higher percentages of pits than wear stage 2 specimens. *Gorilla* also shows this pattern on facet x. There are no other significant differences between wear stages.

No significant differences in pit width are indicated between wear stages for any species. Again, the most consistent pattern of variation is seen on facets 9 and x. In *Gorilla* wear stages 1 and 3 specimens display larger pit widths than wear stage 2 molars. In *Pan* wear stages 1 and 2 specimens have wider pits than wear stage 3 molars on both facets 9 and x. In *Pongo* wear stages 1 and 2 molars have smaller pit widths than wear stage 3 specimens.

The most consistent differences in microwear across wear stages in *G. alpani* can also be seen on facets 9 and x. *G. alpani* displays a different pattern of percentage pits to the other hominoid taxa in that it shows little variation in percentages of pits across all wear stages. Pit widths in *G. alpani* show a similar pattern to those of *Pongo* - wear stages 1 and 2 molars display smaller pit widths than wear stage 3 specimens. None of these differences are significant.

This suggests that wear stage is not an important influence on microwear formation. However, one significant difference was found in *Pongo* and larger sample sizes may reveal more wear stage differences in dental microwear patterns.

CHAPTER 6: RESULTS PART 2 - FACTORIAL ANALYSIS OF VARIANCE

Results of the two factor ANOVA performed on the microwear data are reported in this chapter. The first section deals with differences between species and facets for all seven microwear variables detailed in Chapter 3 using two factor ANOVA. In the second section the effects of sex, wear stage, and facet on microwear are examined using factorial (three way) ANOVA. As sample sizes for each sex and wear stage are small for most species used in this study, these analyses are only performed for *Pongo*. Therefore, statements about one factor level differing from another may not be signficantly different. Appendix 2 contains the original data for all specimens and facets.

6.1 MICROWEAR CHARACTERISTICS

6.1.1 Number of pits

The two factor ANOVA carried out on the ranked data does not indicate an interaction between species and facet. Both species ($p<0.001$) and facet ($p<0.001$) have a significant effect on pit numbers (Table 6.1.1).

Table 6.1.1 Number of pits (Two Factor ANOVA)

I. Two factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Species	3	14.81	0.000
Facet	2	42.77	0.000
Interaction			
Species x Facet	6	0.58	0.745
Error	153		

II. Pairwise comparisons

A. Among species

	t	*p*
Gorilla x G. alpani	6.070	0.000
Gorilla x Pan	1.158	0.249
Gorilla x Pongo	4.818	0.000
G. alpani x Pongo	1.688	0.093
G. alpani x Pan	3.838	0.000
Pan x Pongo	2.682	0.008

II. B. Among facets

FACET	*t*	*p*
1 x 9	8.564	0.000
1 x X	7.659	0.000
X x 9	0.690	0.491

Pairwise comparisons indicate that *G. alpani* possesses significantly higher incidence of pits than *Gorilla* ($p<0.001$) and *Pan* ($p<0.001$) (Table 6.1.1). In addition, *Pongo* displays significantly greater pit frequencies than *Gorilla* ($p<0.001$) and *Pan* ($p<0.01$). *Pan* and *Gorilla* however, are not significantly different from each other, nor do *Pongo* and *G. alpani* differ significantly (Table 6.1.1).

Paired comparisons also indicate that different in pit density indicate that both facet 9 and facet x have significantly more pits than facet 1 ($p<0.001$) (Table 6.1.1). Facets 9 and x are not significantly different from each other.

6.1.2 Percentage pits

Two factor ANOVA performed on rank-transformed data does not indicate an interaction between species and facet (Table 6.1.2).

Percentage pits does vary significantly according to species ($p<0.001$) (Table 6.1.2). Pairwise comparisons indicate that *G.alpani* has significantly higher percentage pits than the other three species (*G. alpani* and *Gorilla* $p<0.001$), *G.alpani* and *Pongo* ($p<0.01$), and *G. alpani* and *Pan* $p<0.001$). Results also indicate that *Pongo* has significantly higher percentage pits than does *Gorilla* ($p=0.001$). There is no significant difference between *Pongo* and *Pan*, or between *Pan* and *Gorilla.*

Table 6.1.2 Percentage pits (Two Factor ANOVA)

I. Two factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Species	3	12.19	0.000
Facet	2	53.84	0.000
Interaction			
Species x Facet	6	0.82	0.558
Error	153		

II. Pairwise comparisons

A. Among species

	t	*p*
Gorilla x G. alpani	5.837	0.000
Gorilla x Pan	1.167	0.245
Gorilla x Pongo	3.270	0.001
G. alpani x Pongo	3.058	0.003
G. alpani x Pan	3.636	0.000
Pan x Pongo	1.413	0.160

B. Among facets

FACET	*t*	*p*
1 x 9	8.769	0.000
1 x X	9.483	0.000
X x 9	1.058	0.292

Percentage pits vary significantly by facet (*p*<0.001) (Table 6.1.2). Pairwise comparisons show that facets 9 and x have higher percentage pits than facet 1 (*p*<0.001) but are not significantly different from each other.

6.1.3 Number of striations

Two factor ANOVA carried out on rank-transformed data does not indicate an interaction between species and facet, nor does facet significantly affect striation frequency (Table 6.1.3). Number of striations does vary significantly according to species, however (*p*<0.01).

Paired comparisons of the four species indicate that *Pongo* has a greater number of striations than *Gorilla* (*p*=0.001) and *Pan* (*p*<0.01) (Table 6.1.3). There is no significant difference in number of striations between *G. alpani* and *Pongo*, *G. alpani* and *Gorilla*, *G. alpani* and *Pan*, and *Pan* and *Gorilla*.

6.1.4 Total number of features

Two factor ANOVA performed on rank-transformed data does not indicate an interaction between species and facet (Table 6.1.4).

The analysis indicates that species has a significant effect on total number of features (*p*<0.001) and paired comparisons indicate that *G. alpani* has significantly more features than *Gorilla* (*p*<0.001) and *Pan* (*p*=0.001) (Table 6.1.4). *Pongo* also displays significantly greater numbers of features than *Gorilla* (*p*<0.001) and *Pan* (*p*=0.001).

Table 6.1.3 Number of striations (Two Factor ANOVA)

I. Two factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Species	3	5.11	0.002
Facet	2	2.74	0.068
Interaction			
Species x Facet	6	0.24	0.961
Error	153		

II. Pairwise comparisons

A. Among species

	t	*p*
Gorilla x G. alpani	1.908	0.058
Gorilla x Pan	0.053	0.957
Gorilla x Pongo	3.484	0.001
G. alpani x Pongo	1.542	0.125
G. alpani x Pan	1.526	0.129
Pan x Pongo	2.777	0.006

B. Among facets

FACET	*t*	*p*
1 x 9	1.183	0.239
1 x X	1.022	0.308
X x 9	2.334	0.021

Table 6.1.4 Total number of features (Two Factor ANOVA)

I. Two factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Species	3	9.85	0.000
Facet	2	7.95	0.001
Interaction			
Species x Facet	6	0.37	0.898
Error	153		

II. Pairwise comparisons

A. Among species

	t	*p*
Gorilla x G. alpani	4.186	0.000
Gorilla x Pan	0.140	0.889
Gorilla x Pongo	4.248	0.000
G. alpani x Pongo	0.190	0.849
G. alpani x Pan	3.326	0.001
Pan x Pongo	3.307	0.001

B. Among facets

FACET	*t*	*p*
1 x 9	3.972	0.000
1 x X	2.491	0.014
X x 9	1.463	0.145

There is no significant difference in total number of features between *G. alpani* and *Pongo*, and *Pan* and *Gorilla*.

Two factor ANOVA performed on rank-transformed data also shows that total number of features differs significantly according to facet (p=0.001) (Table 6.1.4). Pairwise comparisons show that facets 9 (p<0.001) and x (p<0.05) have significantly more features than facet 1, but do not differ significantly from each other.

6.1.5 Pit width

Two factor ANOVA carried out on rank-transformed data does not indicate an interaction between species and facet on pit width (Table 6.1.5). There is also no significant difference in pit width among species or facets.

6.1.6 Pit length

Two factor ANOVA performed on rank-transformed data does not show a significant interaction between species and facet (Table 6.1.6). Nor does pit length vary significantly according either to species or facet.

Table 6.1.5 Pit width (μm) (Two Factor ANOVA)

I. Two factor ANOVA for rank-transformed data

SOURCE OF VARIATION		*df*	*F*	*p*
Main effects				
	Species	3	1.31	0.273
	Facet	2	0.44	0.644
Interaction				
	Species x Facet	6	1.04	0.399
Error		153		

Table 6.1.6 Pit length (μm) (Two Factor ANOVA)

I. Two factor ANOVA for rank-transformed data

SOURCE OF VARIATION		*df*	*F*	*p*
Main effects				
	Species	3	0.49	0.692
	Facet	2	0.32	0.729
Interaction				
	Species x Facet	6	1.93	0.079
Error		153		

6.1.7 Striation width

Two factor ANOVA on rank-transformed data does not indicate a species by facet interaction (Table 6.1.7).

Striation width varies significantly according to species (p=0.001) (Table 6.1.7). Paired comparisons show that *Pan* has significantly wider striations than *G. alpani* (p<0.001) and *Pongo* (p<0.001), and that *Gorilla* has greater striation widths than *G. alpani* (p<0.001) and *Pongo* (p<0.001). There is no significant difference in striation width between *G. alpani* and *Pongo*, and *Gorilla* and *Pan*.

Striation width also varies significantly according to facet (p<0.05) (Table 6.1.7). Pairwise comparisons show that facet 1 possesses significantly wider striations than both facet 9 (p=0.01) and facet x (p<0.05). There is no significant difference in striation width between facets 9 and x.

Table 6.1.7 Striation width (μm) (Two Factor ANOVA)

I. Two factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Species	3	22.69	0.000
Facet			
Interaction	2	3.43	0.035
Species x Facet	6	0.88	0.511
Error	153		

II. Pairwise comparisons

A. Among species

	t	*p*
Gorilla x G. alpani	5.599	0.000
Gorilla x Pan	0.297	0.767
Gorilla x Pongo	6.603	0.000
G. alpani x Pongo	0.715	0.476
G. alpani x Pan	4.946	0.000
Pan x Pongo	5.690	0.000

B. Among facets

FACET	*t*	*p*
1 x 9	2.485	0.014
1 x X	2.070	0.040
X x 9	0.366	0.716

6.1.8 Summary

No significant interaction effects between species and facet are indicated for any of the microwear variables examined.

A number of microwear variables vary significantly according to species. Total number of features is differs significantly according to species. *G. alpani* has greater numbers of features than *Gorilla* and *Pan*. *Pongo* also displays more features than both *Gorilla* and *Pan*. *Pongo* and *G. alpani* have greater numbers of pits than *Pan* and *Gorilla* (these differences are highly significant). *G. alpani* has higher percentage pits than *Gorilla*, *Pan*, and *Pongo* (a highly significant difference). *Pongo* has a greater percentage of pits than *Gorilla* (a highly significant difference). Striation frequency also differs significantly according to species - *Pongo* has greater numbers of pits than *Gorilla* (highly significant), and *Pan*. *Pan* and *Gorilla* have wider striations than *G. alpani* and *Pongo*.

Microwear variables also differ significantly according to the facet examined. Facet 9 and x have greater numbers of features, more pits, and higher percentages of pits than facet 1 (these are highly significant differences). Facet 1 displays wider striations than both facet 9 and x.

The two factor ANOVA indicated that neither species nor facet have a significant effect on pit width or pit length.

The microwear patterns of *G. alpani* differ from those of the extant hominoids in the following respects. *G. alpani* has significantly more microwear features and greater numbers of pits than *Gorilla* and *Pan*. *G. alpani* displays higher percentages of pits than *Gorilla* (a highly significant difference), *Pan*, and *Pongo*. *G. alpani* also has significantly narrower striations than *Gorilla* and *Pan*.

6.2 SEX AND WEAR STAGE

Three factor ANOVA was performed on the *Pongo* sample to investigate the effects of sex and wear stage on microwear patterns using rank-transformed data. The same variables were used as in Section 6.1 with facet, sex and wear stage as the independent factors. Both first-order (an interaction between two factors for all levels of the third factor combined, i.e. facet X sex for all wear stages combined; facet X wear stage for both sexes combined; or sex X wear stage for all facets combined) and second-order interactions (an interaction between all three factors, i.e. facet X sex X wear stage) were examined. Where no interaction (facet, sex, and wear stage) was indicated the effects of facet, sex and wear stage on microwear characteristics (the response variables) were examined separately. Pairwise comparisons were carried out to determine the sources of significant variation. Where the data have a normal distribution three factor ANOVA was also performed on the original data.

6.2.1 Number of pits

No interactions among the independent factors are indicated for number of pits (Table 6.2.1). Facet has a significant effect on pit frequency ($p<0.001$).

6.2.2 Percentage pits

Three factor ANOVA performed on rank-transformed data do not show any interactions between factors (Table 6.2.2).. Facet however, does have a significant effect on percentage pits ($p<0.001$) (Table 6.2.2).

As the data have a normal distribution three factor ANOVA were also carried out using the original data (Table 6.2.2). The same results are indicated as for the rank-transformed analysis - no significant interactions between factors, and only facet has a significant effect on percentage pits ($p<0.001$) (Table 6.2.2).

6.2.3 Number of striations

No interactions between variables are indicated by three way ANOVA on rank-transformed data (Table 6.2.3). Nor do any of the variables have a significant effect on striation frequency (Table 6.2.3).

Table 6.2.1 Number of pits (Facet, Sex & Wear stage: 3 Factor ANOVA)

I. Three factor ANOVA for rank-transformed data

SOURCE OF VARIATION		*df*	*F*	*p*
Main effects				
	Facet	2	15.08	0.000
	Sex	1	0.35	0.558
	Wear stage	2	2.11	0.135
First-order interactions				
	Facet x Sex	2	0.26	0.774
	Facet x Wear stage	4	1.07	0.384
	Sex x Wear stage	2	2.04	0.142
Second-order interactions				
	Facet x Sex x Wear stage	4	0.33	0.859
Error		41		

II. Pairwise comparisons

FACET	*t*	*p*
1 x 9	5.00	0.000
1 x X	4.43	0.000
X x 9	0.46	0.646

Table 6.2.2 Percentage pits (Facet, Sex & Wear stage: 3 Factor ANOVA)

I. A. Three factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Facet	2	22.13	0.000
Sex	1	3.04	0.089
Wear stage	2	0.69	0.505
First-order interactions			
Facet x Sex	2	0.60	0.554
Facet x Wear stage	4	1.13	0.354
Sex x Wear stage	2	0.38	0.689
Second-order interactions			
Facet x Sex x Wear stage	4	0.25	0.911
Error	41		

B. Pairwise comparisons

FACET	*t*	*p*
1 x 9	5.21	0.000
1 x X	6.16	0.000
X x 9	1.05	0.299

Table 6.2.2 Percentage pits (continued)

III. A. Three factor ANOVA for original data

SOURCE OF VARIATION		*df*	*F*	*p*
Main effects				
	Facet	2	19.75	0.000
	Sex	1	3.03	0.089
	Wear stage	2	0.65	0.527
First-order interactions				
	Facet x Sex	2	0.34	0.713
	Facet x Wear stage	4	1.21	0.319
	Sex x Wear stage	2	0.44	0.646
Second-order interactions				
	Facet x Sex x Wear stage	4	0.26	0.899
Error		41		

B. Pairwise comparisons

FACET	*t*	*p*
1 x 9	4.86	0.000
1 x X	5.85	0.000
X x 9	1.09	0.281

Table 6.2.3 Number of striations (Facet, Sex & Wear stage: 3 Factor ANOVA)

I. Three factor ANOVA for rank-transformed data

SOURCE OF VARIATION		*df*	*F*	*p*
Main effects				
	Facet	2	0.31	0.738
	Sex	1	2.20	0.146
	Wear stage	2	2.89	0.067
First-order interactions				
	Facet x Sex	2	0.18	0.834
	Facet x Wear stage	4	0.42	0.795
	Sex x Wear stage	2	2.31	0.112
Second-order interactions				
	Facet x Sex x Wear stage	4	0.22	0.926
Error		41		

6.2.4 Total number of features

A significant first-order interaction between sex and wear stage (for all facets combined) is indicated (*p*<0.05, Table 6.2.4). Figure 6.2.1 displays this interaction graphically. Significance tests were not performed to determine sources of variation as no underlying pattern to the differences is evident. The following description should therefore, be treated with caution. This graph represents the means of subsets of data (known as cells) which are grouped by particular combinations of levels for two factors, across all levels of the third factor. (Examples of cell means used in this analysis are the average number of microwear features for male wear stage 1 specimens, mean number of features for female wear stage 1 molars, mean total number of features for male wear stage 2 specimens, and so on). Indication of an interaction between sex and wear stage is given by the degree to which the lines are non-parallel (Sokal and Rohlf, 1995).

Figure 6.2.1 shows how total number of microwear features varies according to wear stage and sex. Male wear stage 1 specimens have greater number of microwear features than female wear stage 1 molars. However, male wear stage 2 and 3 specimens have less microwear features than female wear stage 2 and 3 molars. Total numbers of features in males decrease with age, whereas female wear stage 2 specimens have more microwear features than wear stage 1 and 3 molars, such that wear stage 1 and 3 female molars display similar amounts of microwear.

Table 6.2.4 Total number of features (Facet, Sex & Wear stage: 3 Factor ANOVA)

I. Three factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Facet	2	3.08	0.057
Sex	1	0.61	0.440
Wear stage	2	3.08	0.057
First-order interactions			
Facet x Sex	2	0.00	0.997
Facet x Wear stage	4	0.85	0.502
Sex x Wear stage	2	3.32	0.046
Second-order interactions			
Facet x Sex x Wear stage	4	0.37	0.828
Error	41		

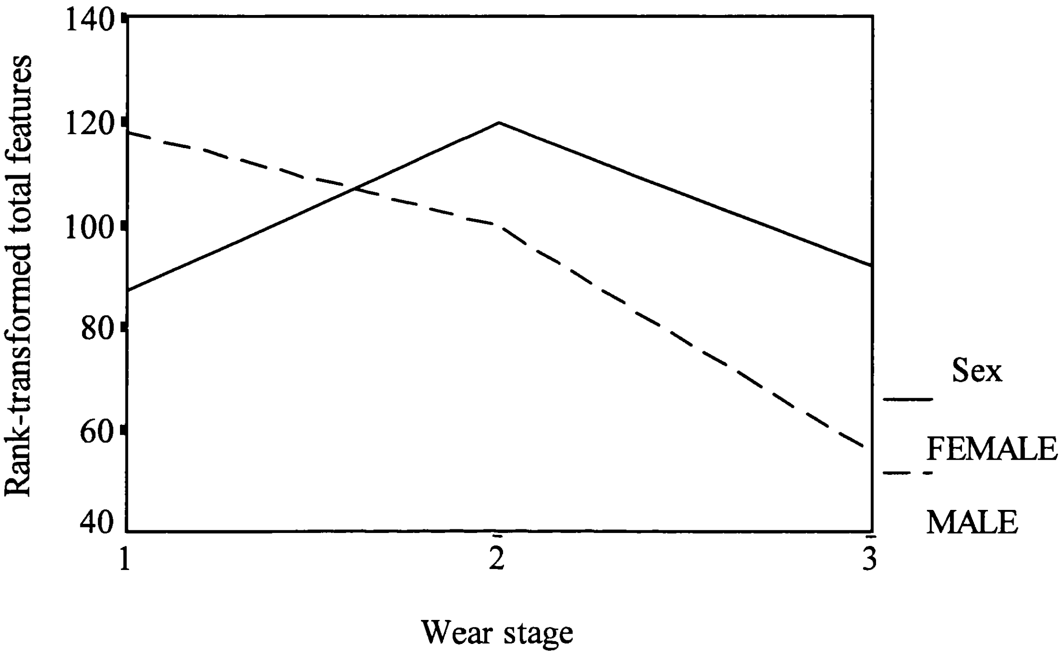


Figure 6.2.1. Two factor (first-order) interaction effect of sex and wear stage on total number of features.

6.2.5 Pit width

A first-order and a second-order interaction is indicated from the three factor ANOVA performed on pit width (Table 6.2.5). The first-order interaction is between sex and wear stage ($p<0.05$) (Table 6.2.5) and is depicted in Figure 6.2.2. Again, the description should be treated with caution as signficance testing was not carried out to determine the sources of variaiton. Female wear stage 1 specimens have wider pits than the equivalent male molars. Pit width in female wear stage 2 and 3 specimens in narrower than male wear stage 2 and 3 molars. In females pit width decreases from wear stage 1 to wear stage 2 specimens, and shows an increase from wear stage 2 to wear stage 3 molars. The reverse is seen in males where pit width increases from wear stage 1 to wear stage 2, but then show a decrease from wear stage 2 to wear stage 3.

There is also a second-order interaction between facet, sex and wear stage ($p<0.05$) (Table 6.2.5), which is shown in Figure 6.2.3. The interaction is depicted from one perspective - by facet. Each facet shows a different pattern for mean pit width according to sex and wear stage. Facet 9 female wear stage 1 specimens have wider pits than the equivalent male molars, but female wear stage 2 and 3 teeth have smaller pit widths than male wear stage 2 and 3 specimens. Female facet 9 specimens show a decrease in pit width from wear stage 1 to wear stage 2, and an increase in pit width from wear stage 2 to wear stage 3. Male facet 9 molars show an increase in pit width with increasing wear stage.

Table 6.2.5 Pit width (Facet, Sex & Wear stage: 3 Factor ANOVA)

I. Three factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Facet	2	0.52	0.599
Sex	1	0.80	0.375
Wear stage	2	1.88	0.165
First-order interactions			
Facet x Sex	2	0.40	0.675
Facet x Wear stage	4	0.88	0.483
Sex x Wear stage	2	5.85	0.006
Second-order interactions			
Facet x Sex x Wear stage	4	4.19	0.006
Error	41		

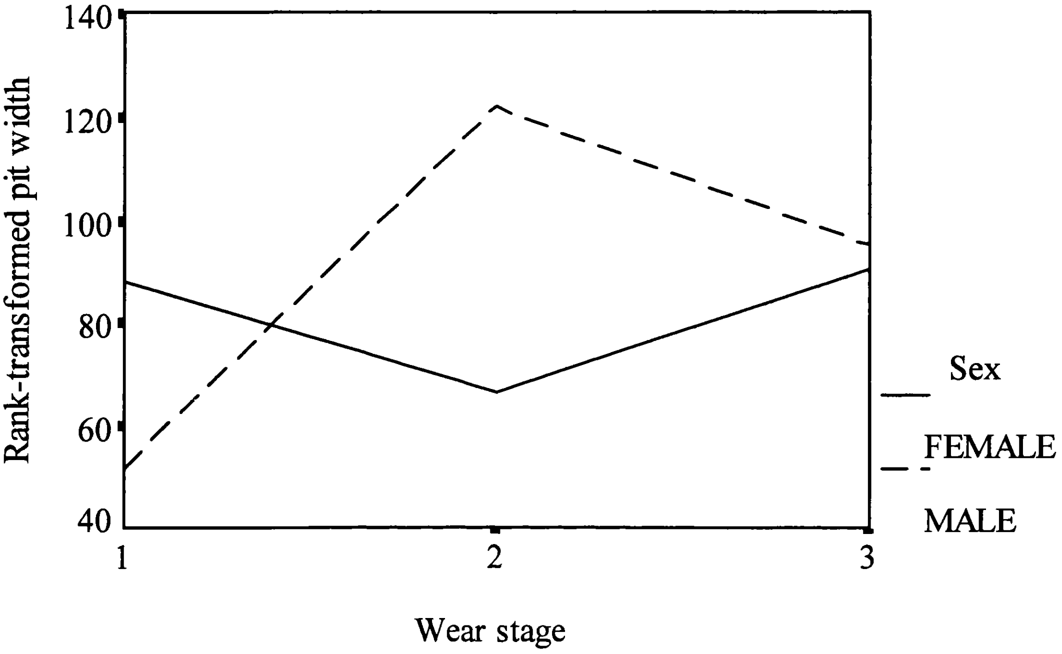
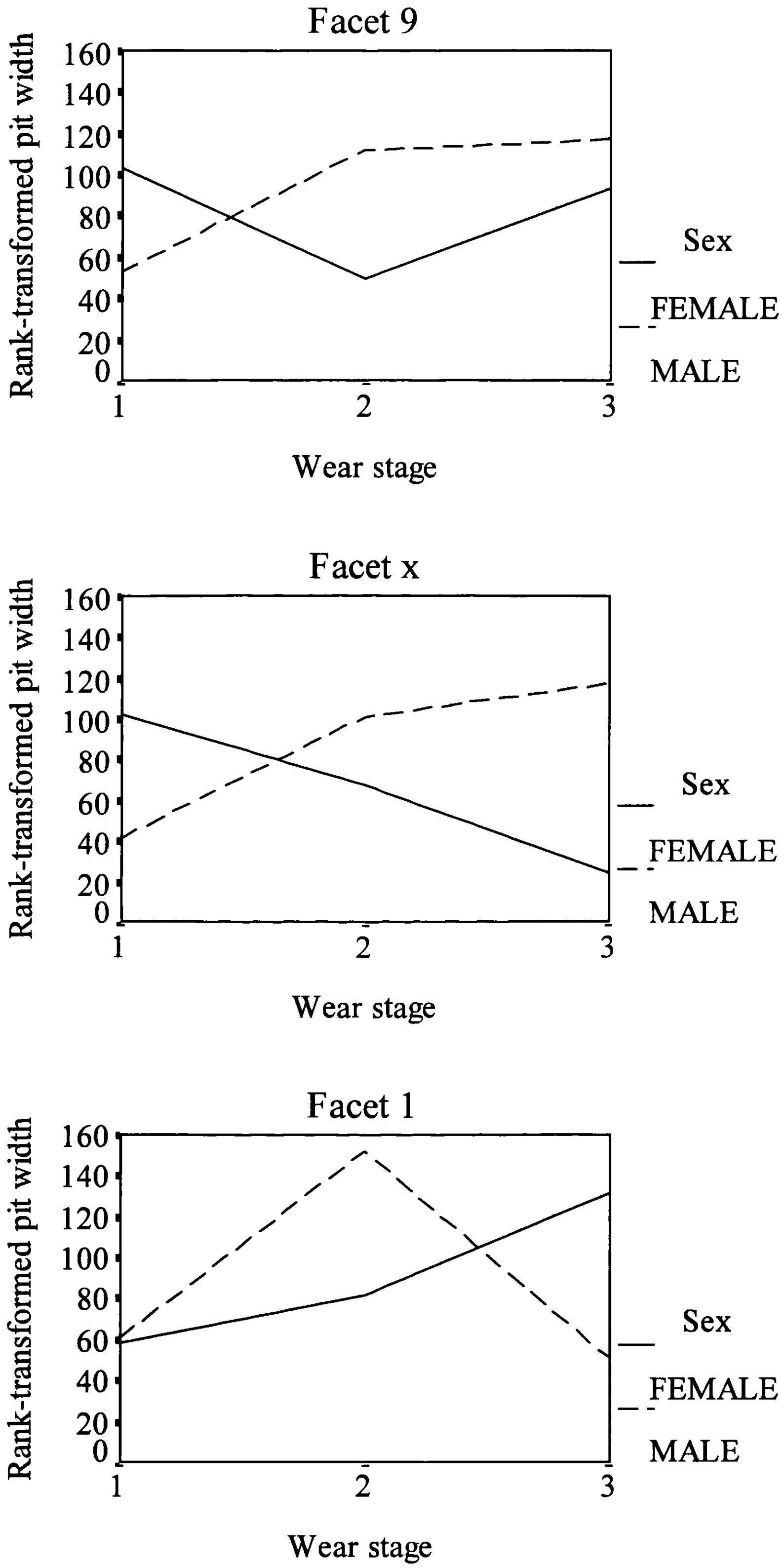


Figure 6.2.2. Two factor (first-order) interaction effect of sex and wear stage on pit width.


Facet 9

Facet x

Facet 1

Figure 6.2.3. Three factor (second-order) interaction effect of facet, sex and wear stage on pit width.

Female facet x specimens display a decrease in pit width with increasing wear stage, whereas males show the reverse - pit width increase with wear stage. Female wear stage 1 molars display wider pits than male wear stage 1 specimens, but have narrower pits present narrower pits on wear stage 2 and 3 dentitions than the equivalent wear stages in males.

Female wear stage 3 specimens have wider pits than the equivalent male molars, but female wear stage 1 and 2 specimens have smaller pit widths than male wear stage 2 and 3 molars. Female facet 1 molars display an increase in pit width as wear stage increases. Male wear stage 2 specimens have wider pits than wear stage 1 and 3 molars.

6.2.6 Pit length

As with the pit width results, two sets of significant interactions are indicated by the three factor ANOVA. A first-order interaction between sex and wear stage ($p<0.05$) (Table 6.2.6) is displayed in Figure 6.2.4. It shows a similar pattern to the first-order interaction effect between the same factors on pit width. Female wear stage 1 specimens display longer pits than the equivalent male molars, but have shorter pits on wear stage 2 and 3 teeth than male wear stage 2 and 3 specimens. Pit length in females decreases from wear stage 1 to wear stage 2 specimens, and increases from wear stage 2 to wear stage 3 molars. The reverse is true for males - pit length increases from wear stage 1 to wear

Table 6.2.6 Pit length (Facet, Sex & Wear stage: 3 Factor ANOVA)

I. Three factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Facet	2	0.72	0.493
Sex	1	0.68	0.416
Wear stage	2	1.90	0.162
First-order interactions			
Facet x Sex	2	0.44	0.644
Facet x Wear stage	4	1.36	0.265
Sex x Wear stage	2	3.69	0.034
Second-order interactions			
Facet x Sex x Wear stage	4	2.65	0.047
Error	41		

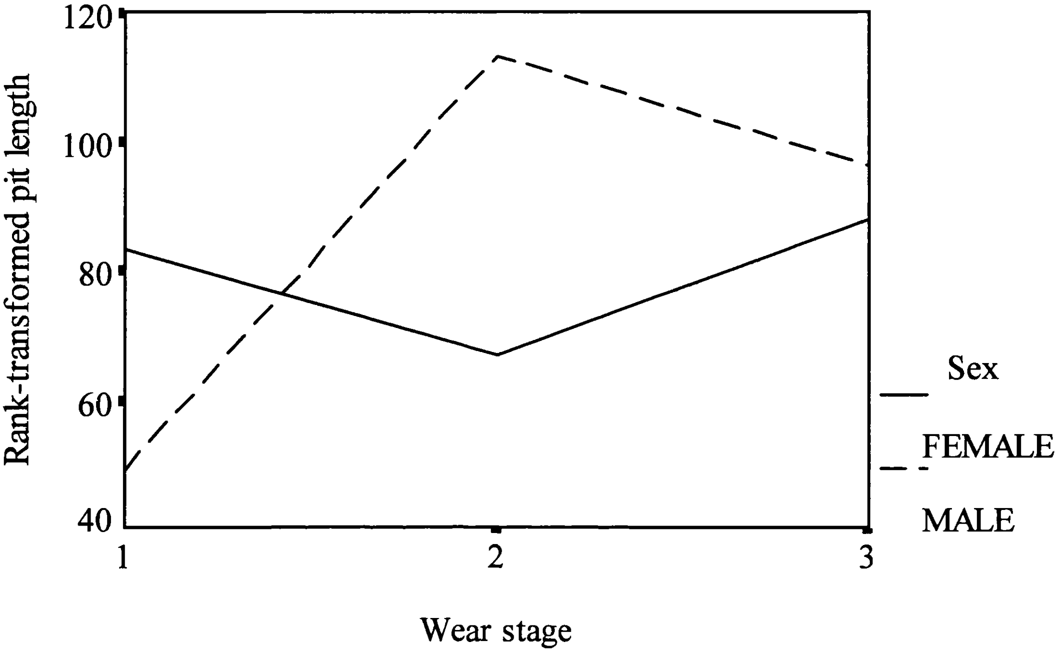


Figure 6.2.4. Two factor (first-order) interaction effect of sex and wear stage on pit length).

stage 2, but decreases from wear stage 2 to wear stage 3.

A significant three way (second-order) interaction between facet, sex and wear stage is also indicated for pit length (p<0.05) (Table 6.2.6). Figure 6.2.5 displays this interaction from a single standpoint - by facet. Each facet shows a different pattern for mean pit width according to sex and wear stage. Again, the pattern is similar to that seen in the second-order interaction effect between these factors on pit width. Facet 9 female wear stage 1 specimens have longer pits than the equivalent male molars. Female wear stage 2 and 3 teeth have shorter pits than male wear stage 2 and 3 specimens. Pit length in female facet 9 specimens decreases from wear stage 1 to wear stage 2, and increases from wear stage 2 to wear stage 3. Male facet 9 molars show an increase in pit length with increasing wear stage.

Pit length in female facet x specimens decreases with increasing wear stage, whereas males show the reverse - pit length increases with wear stage. Female wear stage 1 specimens have wider pits than the equivalent male molars, but female wear stage 2 and 3 teeth have smaller pit widths than male wear stage 2 and 3 molars. Male wear stage 1 specimens display shorter pits than female wear stage 1 molars. However, wear stage 2 and 3 molars have longer pits than the equivalent wear stage teeth in females.

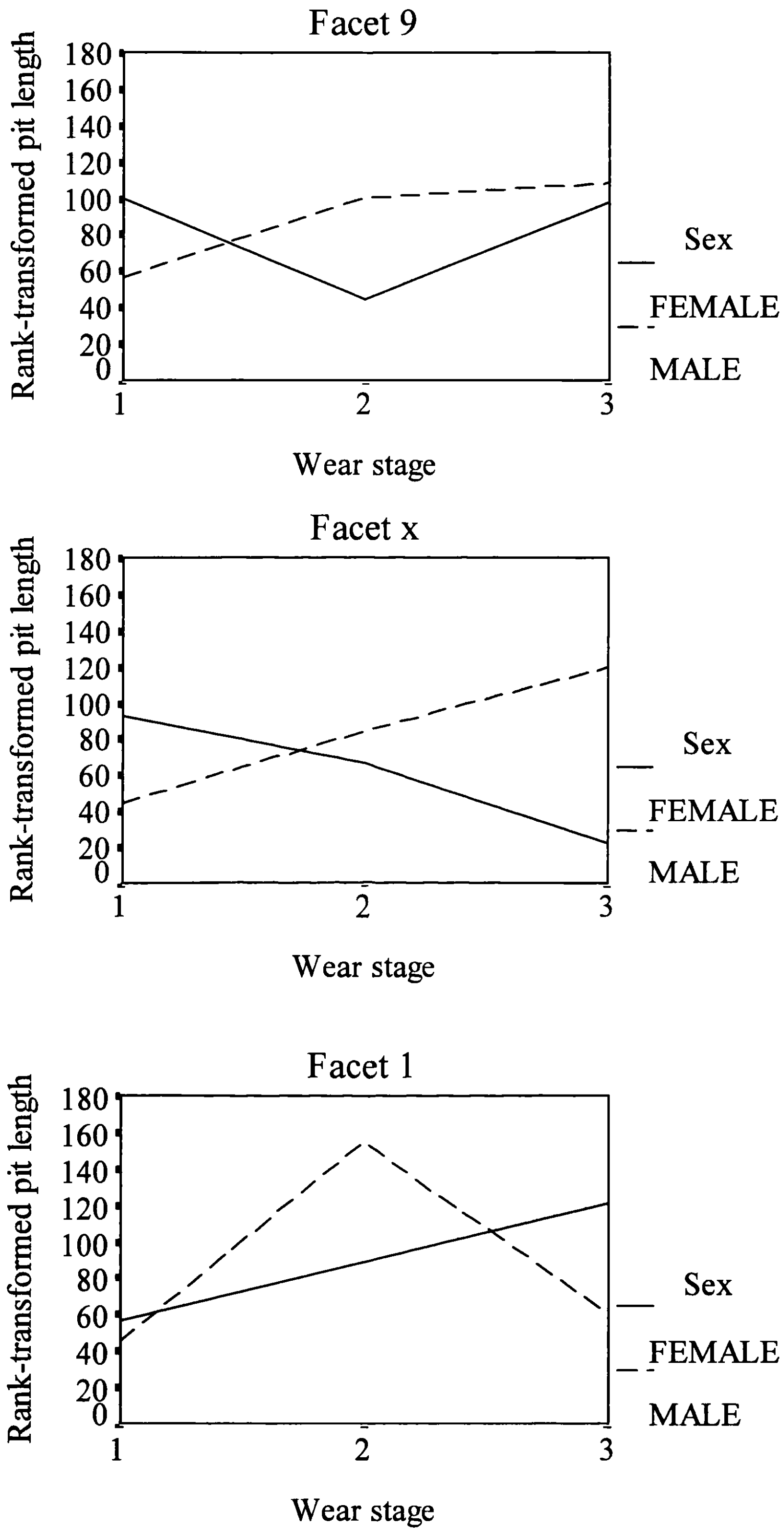


Figure 6.2.5. Pit length three factor (second-order) interaction effect of facet, sex and wear stage.

Female facet 1 molars, while they display an increase in pit width as wear stage increases, have narrower pits than male wear stage 2 specimens. Male wear stage 2 specimens have wider pits than wear stage 1 and 3 molars.

6.2.7 Striation width

Three factor ANOVA performed on striations width indicates a significant first-order interaction between sex and wear stage ($p<0.05$) (Table 6.2.7). Figure 6.2.6 displays this interaction from one perspective - that of facet. A similar pattern is indicated as seen in the interaction effect between the same factors on pit width and pit length. Female wear stage 1 specimens have wider striations than male wear stage molars. Male wear stage 2 and 3 specimens display wider pits than the equivalent wear stages in female specimens.

Table 6.2.7 Striation width (Facet, Sex & Wear stage: 3 Factor ANOVA)

I. Three factor ANOVA for rank-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Main effects			
Facet	2	2.86	0.069
Sex	1	5.41	0.025
Wear stage	2	0.56	0.576
First-order interactions			
Facet x Sex	2	0.79	0.461
Facet x Wear stage	4	0.40	0.807
Sex x Wear stage	2	4.64	0.015
Second-order interactions			
Facet x Sex x Wear stage	4	0.58	0.681
Error	41		

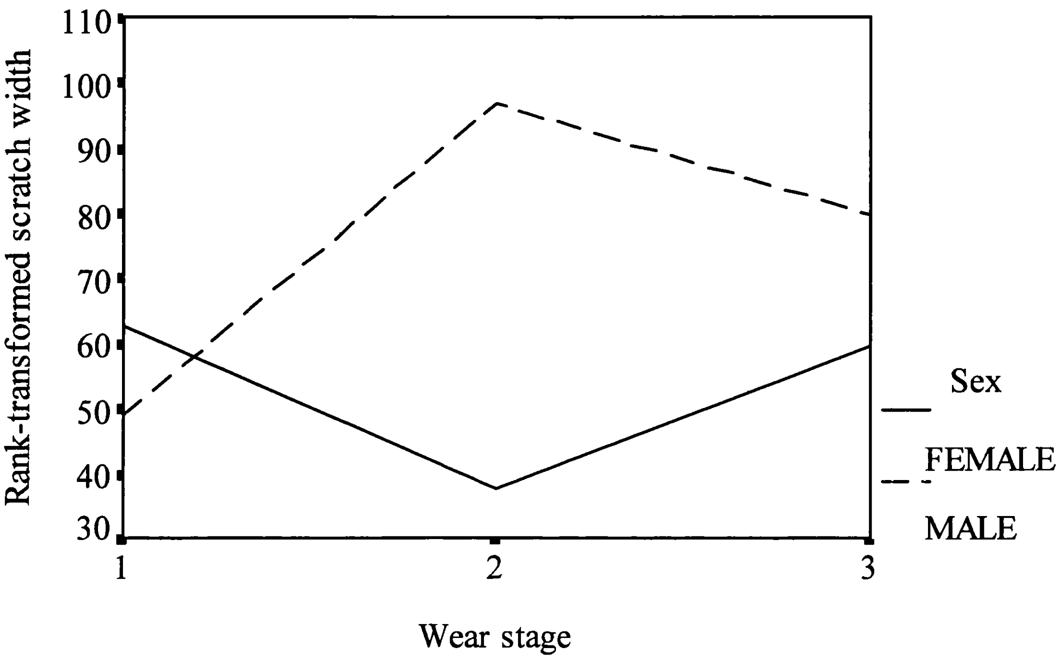


Figure 6.2.6. Two factor (first-order) interaction between sex and wear stage on striation width.

6.2.8 *Summary*

Significant first-order interactions between sex and wear stage (for all facets combined) were found for three of the microwear variables - total number of features, pit width, pit length, and striation width. The interactions show that these microwear variables differ according to particular combinations of levels of sex and wear stage. Significant second-order interactions between all three independent variables - facet, sex, and wear stage - were also found. Pit width and pit length vary significantly according to facet, sex and wear stage. When considered seperately, neither sex nor wear stage have a signficant effect on any of the microwear variables.

CHAPTER 7: RESULTS PART 3 - SPLIT-UNIT ANALYSIS OF VARIANCE

It is not reasonable to assume that the microwear data used in the analysis in Chapter 6 are independent. This is because three facets (and therefore, three measures) per individual (specimen) were used in the analysis as independent data points. As a result, one of the important assumptions of analysis of variance may have been violated. In order to correct this, another analysis of variance is presented in this chapter based on a **split-unit** design (Armitage and Berry, 1987). In this type of analysis the data are arranged into main units and sub-units, such that levels of some factors are spread across larger units, and levels of other factors are spread across smaller units within the larger ones (Armitage and Berry, 1987). Comparisons between species (or sexes and wear stages) were made **between** individual specimens (the main units in this analysis). Contrasts between facets (the sub-units) were made **within** individuals.

The analysis presented in this chapter examined the same response variables and factors as those in Chapter 6. The data however, were transformed differently. The symmetry of the distributions of each response variable were examined for skewness. Most response variables are positively skewed, and an appropriate transformation for this kind of distribution is the **logarithimic transformation** (Sokal and Rohlf, 1995). All response variables, except percentage pits, have a skewed distribution and were therefore, log-transformed. As percentage pits has a symmetrical distribution it was not transformed despite the fact that it does not have a normal distribution. However, ANOVA is not heavily dependant on the assumption of normality (Norušis, 1993b). It is however, important that residuals fit the normal distribution as this indicates that the model fits the data (see below for discussion of this issue for each response variable) and that the assumptions of the test have been met (Sokal and Rohlf, 1995).

In a split-unit ANOVA missing data becomes a problem. In many instances in this study it was only possible to obtain data for one or two facets for a given individual, instead of all three facets (see Chapter 3 for discussion). As the split-unit design compares the response of microwear variables for each facet *within* individuals, if the data are missing for one or more facets for a specimen the analysis becomes problematic. There are several methods for dealing with this issue, such as removing that specimen from the analysis altogether (see Sokal and Rohlf, 1995, for other ways to solve this problem). Removal of specimens however, would have resulted in loss of information, and would have seriously affected sample sizes in this study. In this analysis an alternative method was used. An *unbalanced* ANOVA design using the approximate *F* test - under the assumption that the data are missing at random - was employed.

The first section in this chapter is an analysis of the differences between species and facets for all seven microwear variables detailed in Chapter 3. The second section investigates the effects of sex, wear stage, and facet on microwear. As in Chapter 6, the sex and age effects are only examined in *Pongo* due to small sample sizes in the other species. The data were analysed using SAS (6.11). Where there were no significant interactions paired comparisons, with Bonferroni corrections, were performed. Appendix 2 contains the original data for all specimens and facets.

After both of the split-unit analyses had been performed, the residuals were examined for possible outliers. The outliers were then removed and the analysis was performed again. Both sets of analyses (with and without the outliers) are presented. An objective criterion was used for the identification of outliers - any value which was above or below 3 times the residual standard deviation was removed from the second analysis.

7.1 MICROWEAR CHARACTERISTICS

7.1.1 Number of pits

This variable displays positive skew. The data were **log-transformed** but as some of the values are zero the transformation required the addition of 1 before logging. This transformation succeeded in normalising the data and the distribution of the residuals.

An interaction between facet and species is not indicated by the split-unit ANOVA (Table 7.1.1). Number of pits varies significantly according to species ($p<0.001$) (Table 7.1.1).

Table 7.1.1 Number of pits (Split-unit ANOVA)

I. Split-plot ANOVA for log (+1) transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	57.87	0.000
Species x Facet	6	0.89	0.507
Between individuals			
Species	3	8.27	0.000

II. Pairwise comparisons: Among species

	t	*p*
Gorilla x G. alpani	4.47	0.000
Gorilla x Pan	0.86	1.000
Gorilla x Pongo	3.63	0.004
G. alpani x Pongo	1.05	1.000
G. alpani x Pan	2.90	0.031
Pan x Pongo	2.13	0.221

III. Pairwise comparisons: Among facets

FACET	*t*	*p*
1 x 9	9.91	0.000
1 x X	9.12	0.000
X x 9	0.54	1.000

G. alpani has significantly more pits than *Gorilla* ($p<0.001$) and *Pan* ($p<0.05$). *Pongo* also greater frequencies of pits than *Gorilla* ($p<0.05$). There are no significant differences between *Gorilla* and *Pan*, *Pongo* and *Pan*, or between *G. alpani* and *Pongo*.

Number of pits is also significantly affected by facet ($p<0.001$) (Table 7.1.1). Facets 9 ($p<0.001$) and x ($p<0.001$) have significantly greater numbers of pits than facet 1, and there is no significant difference between facets 9 and x.

Outliers

One outlier was identified (*Pongo*, specimen 1431, facet 1) and the analysis was carried out again without this individual. The results are displayed in Table 7.1.2. Removal of the outlier does not alter the relationships seen in the original analysis in any way.

7.1.2 Percentage pits

As the data are not skewed no transformation was performed. The residuals are normally distributed, indicating that the model fits the data. No interaction between facet and species is indicated by the analysis but both main effects are significant (Table 7.1.3). Percentage pits varies significantly according to species ($p<0.001$) and paired comparisons indicate that *G. alpani* has significantly higher percentage pits than *Gorilla* ($p<0.001$). There are no other significant differences among species.

Table 7.1.2 Number of pits (Split-unit ANOVA) (outliers removed)

I. Split-plot ANOVA for log (+1) transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	64.53	0.000
Species x Facet	6	1.10	0.371
Between individuals			
Species	3	7.95	0.000

II. Pairwise comparisons: Among species

	t	*p*
Gorilla* x *G. alpani	4.45	0.000
Gorilla* x *Pan	0.88	1.000
Gorilla* x *Pongo	3.45	0.006
G. alpani* x *Pongo	1.20	1.000
G. alpani* x *Pan	2.87	0.033
Pan* x *Pongo	1.97	0.321

III. Pairwise comparisons: Among facets

FACET	*t*	*p*
1 x 9	9.64	0.000
1 x X	10.48	0.000
X x 9	0.57	1.000

Table 7.1.3 Percentage pits (Split-unit ANOVA)

I. Split-plot ANOVA for original data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	61.54	0.000
Species x Facet	6	1.07	0.388
Between individuals			
Species	3	6.96	0.000

II. Pairwise comparisons: Among species

	t	*p*
Gorilla x G. alpani	4.50	0.000
Gorilla x Pan	1.28	1.000
Gorilla x Pongo	2.39	0.119
G. alpani x Pongo	2.38	0.123
G. alpani x Pan	2.49	0.094
Pan x Pongo	0.65	1.000

III. Paired comparisons: Among facets

FACET	*t*	*p*
1 x 9	9.5	0.000
1 x X	10.2	0.000
X x 9	1.1	0.841

Facet also has a significant effect on percentage pits ($p<0.001$) (Table 7.1.3). Facets 9 ($p<0.001$) and x ($p<0.001$) have higher percentages of pits than facet 1. No significant

difference between facets 9 and x is indicated by this analysis. No outliers were identified in this analysis.

7.1.3 Number of striations

As the data are right-skewed the log-transformation was performed. This transformation succeeded in normalising both the data and the residuals. No interaction between species and facet is indicated by this analysis, nor does species have a significant effect on striation frequencies (Table 7.1.4). Numbers of striations do vary significantly according to facet ($p<0.05$) (Table 7.1.4). Paired comparisons indicate that facet x has significantly greater numbers of striations than facet 9 ($p=0.05$). There are no other significant differences between facets.

Outliers

One outlier was identified in this analysis (*Pongo*, specimen 1436, facet 1). When it was removed from the analysis number of striations varied significantly according to species ($p<0.05$) (Table 7.1.5). This effect was only just non-significant in the first analysis ($p=0.06$) (Table 7.1.4). Paired comparisons show that the Bonferroni correction has resulted in the loss of significance in the comparison between *Pongo* and *Gorilla* (the probability of the uncorrected t value is 0.01, and after adjustment $p=$ 0.083).

Table 7.1.4 Number of striations (Split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	3.17	0.050
Species x Facet	6	0.39	0.882
Residual error	91		
Between individuals			
Species	3	2.56	0.063
Residual error	61		

II. Pairwise comparisons among facets

FACET	*t*	*p*
1 x 9	0.68	1.000
1 x X	1.59	0.349
X x 9	2.48	0.050

Table 7.1.5 Number of striations (Split-unit ANOVA) (outliers removed)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	3.59	0.032
Species x Facet	6	0.35	0.909
Between individuals			
Species	3	2.84	0.045

II. Pairwise comparisons: Among species

	t	*p*
Gorilla x G. alpani	1.34	1.000
Gorilla x Pan	0.11	1.000
Gorilla x Pongo	2.53	0.083
G. alpani x Pongo	1.18	1.000
G. alpani x Pan	1.25	1.000
Pan x Pongo	2.25	0.168

III. Pairwise comparisons: Among facets

FACET	*t*	*p*
1 x 9	0.47	1.000
1 x X	1.87	0.196
X x 9	0.47	1.000

This indicates that any statement about the species effect on number of striations should be made cautiously as the effect is not strongly significant. The only other difference between this analysis and the original one is that the significance of the paired comparison between facet 1 and 9 is now <0.05 (Table 7.1.5) instead of being equal to 0.05 (Table 7.1.4).

7.1.4 Total number of features

The data used in this analysis were positively skewed the log-transformed was carried out, and the transformation succeeded in normalising the data and the residuals. No interaction between facet and species is indicated (Table 7.1.6). Total number of features varies significantly according to species ($p<0.05$) (Table 7.1.6). Paired comparisons indicate that *G. alpani* ($p<0.05$) and *Pongo* ($p=0.01$) have significantly more features than *Gorilla* but there are no other significant differences between species.

Number of microwear features also varies significantly according to facet ($p<0.001$) (Table 7.1.6). Paired comparisons indicate that facets 9 ($p<0.001$) and x ($p<0.05$) have significantly more features than facet 1 but there is no significant difference between facets 9 and x.

Table 7.1.6 Total number of features (Split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	12.05	0.000
Species x Facet	6	1.18	0.326
Between individuals			
Species	3	5.32	0.003

II. Pairwise comparisons: Among species

	t	*p*
Gorilla* x *G. alpani	3.16	0.015
Gorilla* x *Pan	0.50	1.000
Gorilla* x *Pongo	3.29	0.010
G. alpani* x *Pongo	0.18	1.000
G. alpani* x *Pan	0.02	1.000
Pan* x *Pongo	2.17	0.204

III. Paired comparisons: Among facets

FACET	*t*	*p*
1 x 9	4.91	0.000
1 x X	2.94	0.013
X x 9	2.02	0.140

Outliers

One outlier was identified (*Pongo*, specimen 1436, facet 1). Another analysis was performed which excluded this specimen. The results of this analysis (Table 7.1.7) do not differ with those from the original ANOVA (Table 7.1.6).

7.1.5 Pit width

The data are positively skewed so the log-transformation was performed, but this did not succeed in normalising the distribution of the data or that of the residuals. No interaction between species and facet is indicated (Table 7.1.8). Moreover, neither facet nor species have a significant effect on pit width in either analysis (Table 7.1.8).

Outliers

The presence of three outliers was identified (*Pongo*: specimen 1425, facet 9; *Gorilla*: specimens 932 facet x, and 1857.11.23 facet 1), and removal of the outliers from the analysis resulted in normalising the residuals indicating that the data now fit the model . Results indicate no differences among variable relationships as compared with the original test (Table 7.1.9).

Table 7.1.7 Total number of features (Split-unit ANOVA) (outliers removed)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	12.05	0.000
Species x Facet	6	1.18	0.326
Between individuals			
Species	3	5.32	0.003

II. Pairwise comparisons

A. Among species

	t	*p*
Gorilla x G. alpani	3.16	0.015
Gorilla x Pan	0.50	1.000
Gorilla x Pongo	3.29	0.010
G. alpani x Pongo	0.18	1.000
G. alpani x Pan	0.02	1.000
Pan x Pongo	2.17	0.204

B. Among facets

FACET	*t*	*p*
1 x 9	4.91	0.000
1 x X	2.94	0.013
X x 9	2.02	0.140

Table 7.1.8 Pit width (Split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	0.09	0.916
Species x Facet	6	1.12	0.356
Between individuals			
Species	3	0.56	0.646

Table 7.1.9 Pit width (Split-unit ANOVA) (outliers removed)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	0.16	0.853
Species x Facet	6	2.00	0.075
Between individuals			
Species	3	1.21	0.316

7.1.6 Pit length

As the data are positively skewed the analysis was performed on log-transformed values. Neither the data nor the residuals however, are normally distributed. No interaction between species and facet is indicated (Table 7.1.10). Neither facet nor species have a significant effect on pit length (Table 7.1.10). As the log transformation did not succeed in normalising the residuals before the outliers were removed the validity of these results is questionable. However, the reason that the residuals are not normally distributed is related to the presence of outliers (see below).

Table 7.1.10 Pit length (Split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	***df***	***F***	***p***
Within individuals			
Facet	2	0.13	0.881
Species x Facet	6	1.45	0.204
Between individuals			
Species	3	0.68	0.566

Outliers

Four outliers were identified from the original analysis (*Pongo*: specimens 1423 facet 1, and 1425 facet 1; *Gorilla*: specimens 932 facet x, and 1857.11.23 facet 1). The analysis was performed again excluding these outliers, and this resulted in normalising the residuals. This indicates that the data now fit the model.

A significant interaction is indicated by this analysis between species and facet ($p<0.01$) (Table 7.1.11) which was not apparent in the original results (Table 7.1.10). This interaction is depicted in Figure 7.1.1. It should be noted however, that statistical tests were not performed to determine the signficant sources of error, and therefore, the following comments should be treated cautiously. *Pan* displays pits of a similar length on facets 9 and 1, with the longest pits on facet x. *Pongo* shows the reverse pattern - pit lengths, while they are similar on facets 9 and 1, are smaller on facet x. *G. alpani* shows an increase in pit length from facet 9, to facet x, to facet 1. *Pan* has the longest pits of all the hominoid species for all facets. *Gorilla* has relatively long pits on facet 9, and *G. alpani* has the shortest pits on this facet, with *Pongo* intermediate. *Gorilla* has the shortest pits on facet x, and only slightly longer pits on facet 1. *G. alpani* has relatively long pits on facet x. *Pongo* displays pit lengths on facets x and 1 which are intermediate to *Gorilla* and *G. alpani.*

Table 7.1.11 Pit length (Split-unit ANOVA) (outliers removed)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	0.19	0.824
Species x Facet	6	3.25	0.006
Between individuals			
Species	3	1.04	0.382

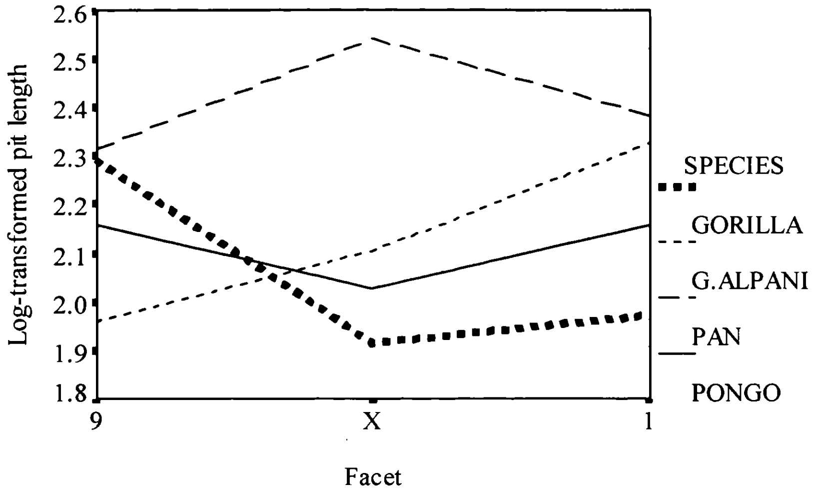


Figure 7.1.1. Interaction effect of facet and species on log-transformed pit length (split-unit ANOVA).

7.1.7 Striation width

The ANOVA was performed on log-transformed data as it is positively skewed. The transformation was successful as both the data and the residuals now have a normal distribution. No interaction between species and facet is indicated by the analysis (Table 7.1.12). Striation width does vary significantly according to species (p=0.001) (Table 7.1.12). Paired comparisons indicate that *Gorilla* has significantly wider striations than *G. alpani* (p=0.001) and *Pongo* (p<0.001), and striation width in *Pan* is significantly than in *G. alpani* (p<0.01) and *Pongo* (p=0.001). There is no significant difference in striation width between *G. alpani* and *Pongo.*

Striation width also varies significantly according to facet (p=0.001) (Table 7.1.12). Pairwise comparisons indicate that facet 1 has significantly wider striations than facet 9 (p=0.001) and facet x (p<0.01), but there is no significant difference between facet 9 and facet x.

Outliers

Two outliers are indicated (*Pongo*: specimen 1417 facet 1; and *Gorilla* specimen 927 facet 1). The ANOVA was performed again without these outliers. There are no large differences between the two analysis (Table 7.1.13). One variation is that the significance of the facet effect is now <0.001 (Table 7.1.13) whereas in the previous analysis it was

Table 7.1.12 Striation width (Split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	7.80	0.001
Species x Facet	6	0.87	0.518
Between individuals			
Species	3	11.14	0.000

II. Pairwise comparisons: Among species

	t	*p*
Gorilla x G. alpani	4.03	0.001
Gorilla x Pan	0.31	1.000
Gorilla x Pongo	4.40	0.000
G. alpani x Pongo	0.24	1.000
G. alpani x Pan	3.75	0.002
Pan x Pongo	4.04	0.001

III. Paired comparisons: Among facets

FACET	*t*	*p*
1 x 9	3.76	0.001
1 x X	3.15	0.007
X x 9	0.53	1.000

Table 7.1.13 Striation width (Split-unit ANOVA) (outliers removed)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	10.15	0.000
Species x Facet	6	0.83	0.552
Between individuals			
Species	3	12.49	0.000

II. Pairwise comparisons : Among species

	t	*p*
Gorilla x G. alpani	4.32	0.000
Gorilla x Pan	0.05	1.000
Gorilla x Pongo	4.83	0.000
G. alpani x Pongo	0.38	1.000
G. alpani x Pan	3.75	0.002
Pan x Pongo	4.15	0.001

III. Paired comparisons: Among facets

FACET	*t*	*p*
1 x 9	4.33	0.000
1 x X	3.54	0.002
X x 9	0.73	1.000

equal to 0.001 (Table 7.1.12). Also, the significance of the paired comparisons between facets 1 and 9 is equal to 0.001 in the original analysis (Table 7.1.12) but is <0.001 when the outliers are removed (Table 7.1.13). Finally, the significance of the paired comparisons between *Gorilla* and *G. alpani* in the first analysis is =0.001 (Table 7.1.12) but when the outliers are removed the significance level is <0.001 (Table 7.1.13).

7.1.8 Summary

Only one significant interaction effect between facet and species is indicated for any of the microwear variables examined in this study. After removal of outliers, a highly significant interaction effect is indicated between facet and species on pit length.

A number of microwear variables did vary significantly according to species. Total number of microwear features varies significantly according to species - *G. alpani* and *Pongo* have significantly more features than *Gorilla.* Removal of outliers did not change these results in any way. *G. alpani* has significantly more pits than *Gorilla* (this is highly significant), and *Pan. Pongo* has significantly more pits than *Pan.* Removal of outliers does not change the results in any way. *G. alpani* has significantly higher percentages of pits than *Gorilla*, and there were no outliers. *Gorilla* and *Pan* have significantly wider striations than *Pongo* (these are highly significant differences). *Pan* has significantly wider striae than *G. alpani.* No important changes occurred with the removal of outliers for these microwear variables. However, when outliers were removed from striation frequency analysis the species effect became significant. This result should be treated with caution as it is not highly significant and the Bonferroni adjustment resulted in the loss of significance in the comparison between *Gorilla* and *Pongo*. Pit widths do not vary significantly according to the species examined.

Several microwear variables did vary significantly according to the facet under examination. Facets 9 and x are have significantly more microwear features, greater numbers of pits, and higher percentages of pits than facet 1 (highly significant). Striation frequencies vary significantly according to the facet examined - facet x has significantly more striations than facet 9 (this is not a highly significant difference). Striation widths also differ significantly according to facet type - facet 1 has significantly wider striae than facet 9 and facet x (highly significant). Removal of outliers did not change these results. Pit widths do no differ significantly according to the facet examined.

The microwear patterns of *G. alpani* differ from the extant hominoids in the following respects. *G. alpani* has significantly more microwear features and higher percentages of pits than *Gorilla*. *G. alpani* has significantly larger numbers of pits than both *Gorilla* and *Pan*. Striation widths displayed by *G. alpani* are significantly smaller than those of *Gorilla* and *Pan*.

7.2 SEX AND WEAR STAGE

The effects of sex and age on microwear were also examined. As with the analysis presented in Chapter 6, facet, sex and wear stage were used as the independent variables (or factors) and their effects on the same response variables as those used in section 7.1 were investigated. First-order interactions investigated were between facet and sex, facet and wear stage, and sex and wear stage. Second-order between facet, sex and wear stage interactions were also examined. If no interaction was indicated the effect of each factor was examined individually. Paired comparisons were performed to identify significant differences between factor levels. To avoid repetition of the results presented above and in Chapter 6 paired comparisons between facets are not reported in this analysis. Outliers were identified for one analysis only - striation width.

7.2.1 Number of pits

No first- or second-order interactions are indicated by the analysis (Table 7.2.1). Facet has a significant influence on pit frequencies ($p<0.001$) (Table 7.2.1), but no other significant effects are indicated. The residuals have a normal distribution.

Table 7.2.1 Number of pits (Facet, sex, and wear stage: split-unit ANOVA)

I. Split-plot ANOVA for log (+1) transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	29.19	0.000
Facet x Sex	2	1.22	0.312
Facet x Wear stage	4	1.87	0.146
Facet x Sex x Wear stage	4	0.98	0.438
Between individuals			
Sex	1	0.05	0.831
Wear stage	2	0.59	0.566
Sex x Wear stage	2	1.83	0.198

7.2.2 Percentage pits

No significant interactions are indicated by this analysis, nor are there any significant main effects (Table 7.2.2). The residuals have a normal distribution indicating that the data fit the model.

7.2.3 Number of striations

No first- or second order interactions are indicated by the ANOVA, nor do any of the factors have a significant effects on number of striations when examined individually (Table 7.2.3). A normal distribution is indicated for the residuals.

7.2.4 Total number of features

The analysis does not indicate any first- or second-order interactions (Table 7.2.4). Number of features does vary significantly according to facet (p<0.01) (Table 7.2.4), but none of the other factors have a significant effect on total number of microwear features. The residuals are distributed normally.

Table 7.2.2 Percentage pits (Facet, sex, and wear stage: split-unit ANOVA)

I. Split-plot ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	37.33	0.000
Facet x Sex	2	0.40	0.674
Facet x Wear stage	4	2.62	0.058
Facet x Sex x Wear stage	4	0.44	0.781
Between individuals			
Sex	1	1.66	0.219
Wear stage	2	0.36	0.792
Sex x Wear stage	2	0.24	0.792

Table 7.2.3 Number of striations (Facet, sex, and wear stage: split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	0.54	0.589
Facet x Sex	2	0.03	0.967
Facet x Wear stage	4	0.89	0.485
Facet x Sex x Wear stage	4	1.23	0.323
Between individuals			
Sex	1	2.24	0.157
Wear stage	2	0.73	0.498
Sex x Wear stage	2	2.06	0.165

Table 7.2.4 Total number of features (Facet, sex, and wear stage: split-unit ANOVA)

I. Split-plot ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	5.77	0.008
Facet x Sex	2	0.17	0.848
Facet x Wear stage	4	1.39	0.264
Facet x Sex x Wear stage	4	1.26	0.310
Between individuals			
Sex	1	1.33	0.269
Wear stage	2	0.90	0.848
Sex x Wear stage	2	2.75	0.099

7.2.5 ***Pit width***

A significant second-order interaction ($p<0.05$) between all three factors - facet, sex, and wear stage - is indicated when the analysis was performed using original data (Table 7.2.5). Figure 7.2.1 depicts this interaction from the perspective of facet using the log- transformed data. Again, it should be noted that significance testing was not performed because no pattern to the variation. The following description should therefore, be treated cautiously. Female wear stage 1 and 3 specimens have greater pit widths than wear stage 2 specimens on facet 9. Males show an increase in pit width with increasing wear stage, and male wear stage 1 molars possess longer pits than female wear stage 1 specimens on this facet. On facet x female pit width decreases with increasing wear stage, while males show the reverse pattern. Female wear stage 1 and 2 specimens have greater pit widths than males. Females show an increase in pit width with increasing wear stage on facet 1. Female wear stage 1 and 3 molars display greater pit widths than the equivalent wear stages in males on this facet. Male wear stage 1 and 3 specimens, while displaying similar pits widths to each other, have shorter pits than wear stage 2 molars. No other interactions or main effects are significant (Table 7.2.5). The residuals have a normal distribution.

Table 7.2.5 Pit width (Facet, sex, and wear stage: split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	0.98	0.390
Facet x Sex	2	0.31	0.736
Facet x Wear stage	4	1.28	0.305
Facet x Sex x Wear stage	4	4.91	0.004
Between individuals			
Sex	1	0.26	0.620
Wear stage	2	1.80	0.202
Sex x Wear stage	2	3.31	0.067

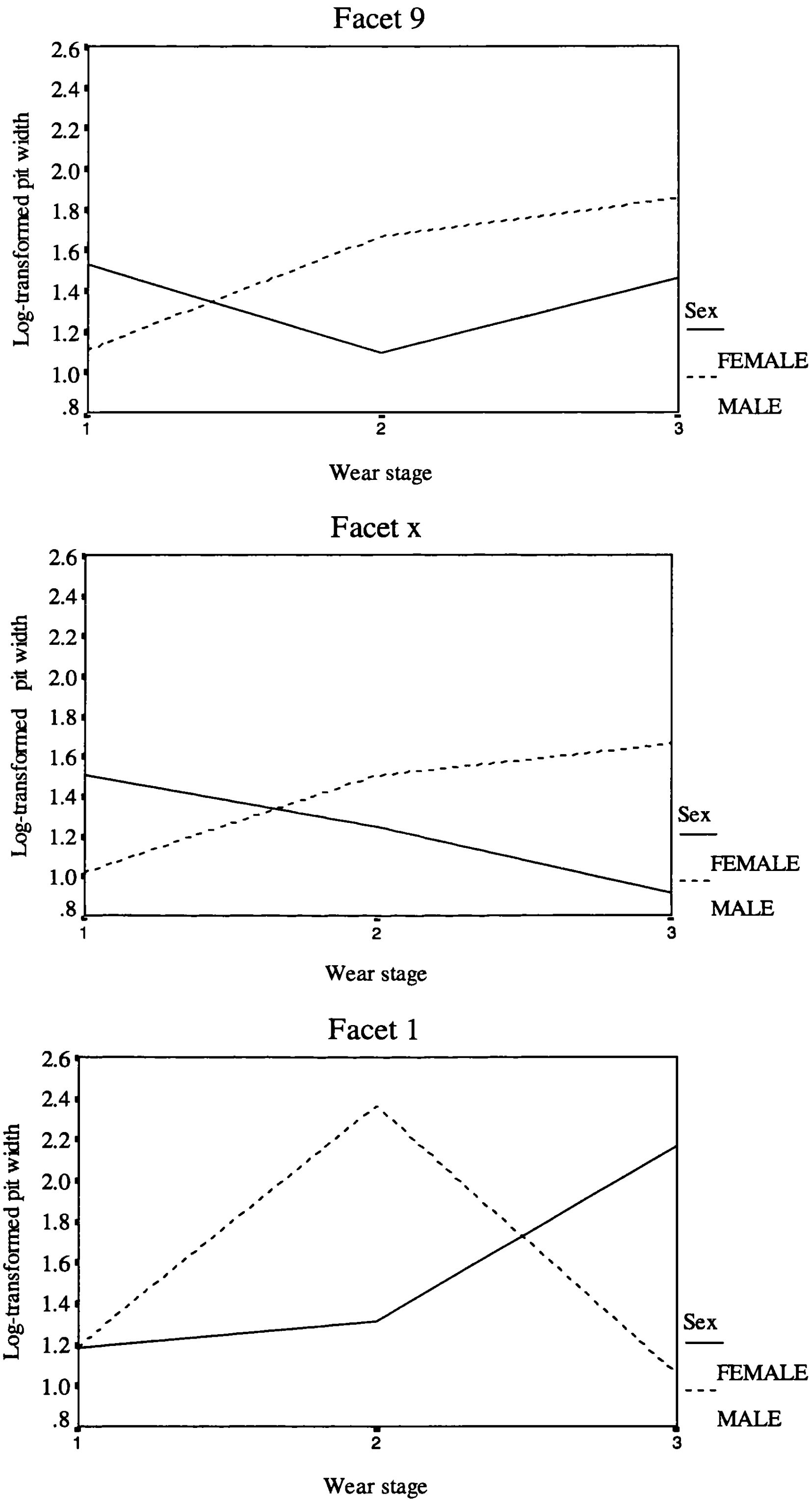


Figure 7.2.1 Second-order interaction effect of facet, sex, and wear stage on pit width (split-unit ANOVA).

7.2.6 Pit length

The analysis shows that there is a significant second-order interaction between facet, sex, and wear stage ($p<0.05$) (Table 7.2.6). Figure 7.2.2 displays this interaction by facet. As significance testing was not performed because no pattern was apparent in the variation, the following description should be treated with caution. The pattern of pit lengths across all wear stages, facets, and both sexes is the same as that seen in pit widths. Female wear stage 1 and 3 specimens have greater pit lengths than wear stage 2 specimens on facet 9. Males show an increase in pit length with increasing wear stage, and male wear stage 1 molars possess longer pits than female wear stage 1 specimens on this facet. On facet x female pit length decreases with increasing wear stage, while males show the reverse pattern. Female wear stage 1 and 2 specimens have greater pit lengths than males. Females show an increase in pit length with increasing wear stage on facet 1. Female wear stage 1 and 3 molars display greater pit lengths than the equivalent wear stages in males on this facet. Male wear stage 1 and 3 specimens, while displaying similar pits lengths to each other, have shorter pits than wear stage 2 molars. No further significant interactions or main effects are indicated (Table 7.2.6). The residuals for this analysis have a normal distribution.

Table 7.2.6 Pit length (Facet, sex, and wear stage: split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	1.04	0.369
Facet x Sex	2	0.26	0.775
Facet x Wear stage	4	1.59	0.207
Facet x Sex x Wear stage	4	2.90	0.041
Between individuals			
Sex	1	0.14	0.718
Wear stage	2	1.81	0.120
Sex x Wear stage	2	2.86	0.091

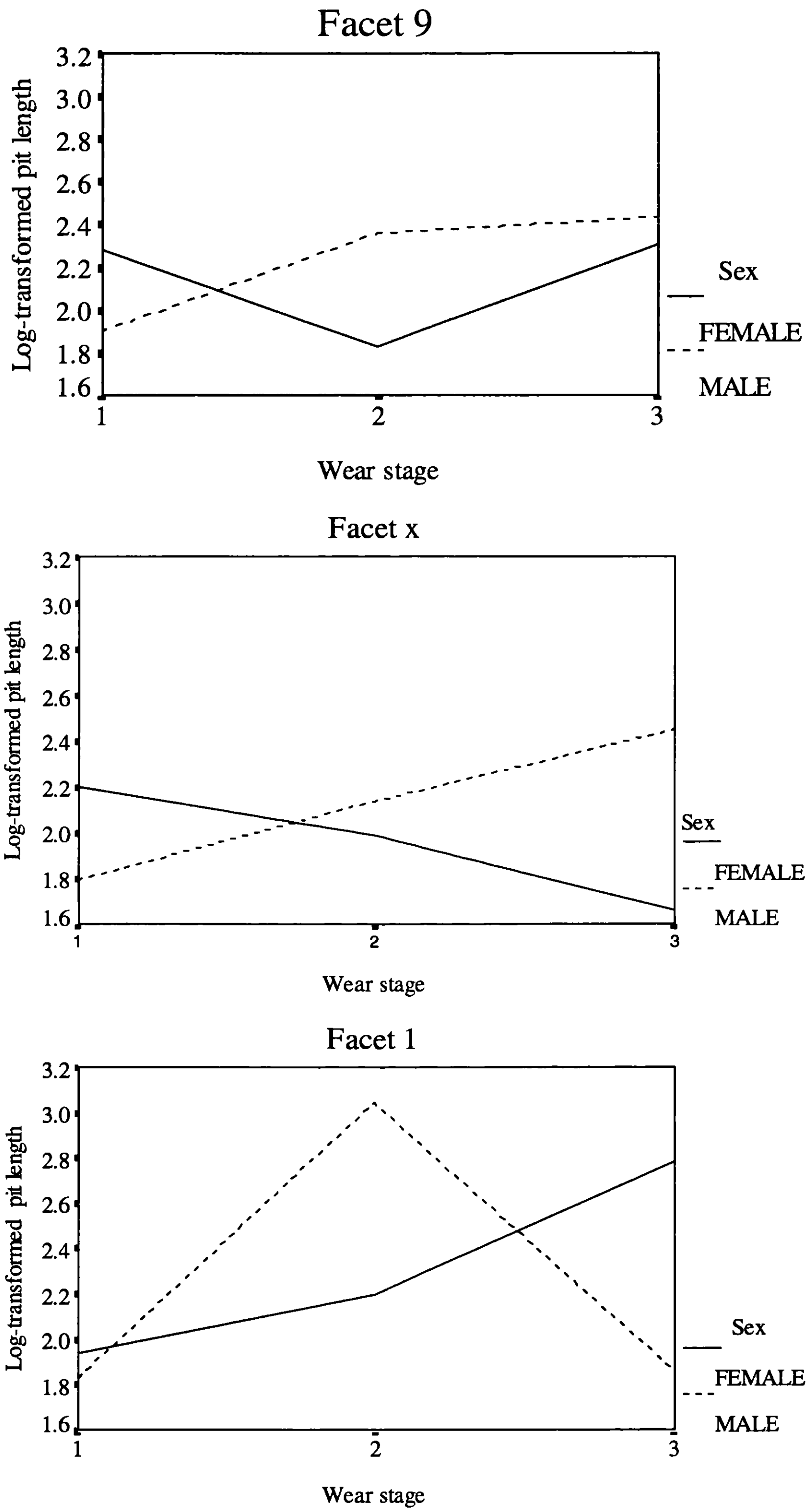


Figure 7.2.2 Second-order interaction effect of facet, sex, and wear stage on pit length (split-unit ANOVA).

7.2.7 Striation width

The ANOVA performed on striation width does not indicate any significant interactions between factors (Table 7.2.7). There are no other significant main effects (Table 7.2.7). The residuals have a normal distribution.

Outliers

One outlier was detected from the original analysis (*Pongo*: specimen 1417 facet 1). The outlier was removed and the analysis was performed a second time. Results do not indicate any differences in the relationships between the response variable and the factors (Table 7.2.8) as compared with the original analysis (Table 7.2.7).

Table 7.2.7 Striation width (Facet, sex, and wear stage: split-unit ANOVA)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	2.96	0.070
Facet x Sex	2	0.49	0.619
Facet x Wear stage	4	0.47	0.756
Facet x Sex x Wear stage	4	0.27	0.896
Between individuals			
Sex	1	1.38	0.260
Wear stage	2	0.49	0.622
Sex x Wear stage	2	1.62	0.233

Table 7.2.8 Striation width (Facet, sex, and wear stage: split-unit ANOVA) (outliers removed)

I. Split-unit ANOVA for log-transformed data

SOURCE OF VARIATION	*df*	*F*	*p*
Within individuals			
Facet	2	2.27	0.125
Facet x Sex	2	0.12	0.889
Facet x Wear stage	4	1.33	0.286
Facet x Sex x Wear stage	4	0.41	0.799
Between individuals			
Sex	1	2.47	0.138
Wear stage	2	0.64	0.542
Sex x Wear stage	2	2.79	0.096

7.2.8 Summary

Significant second-order interaction effects between facet, sex, and wear stage are indicated for pit widths and pit lengths, but these are not highly significant results. The interactions show that these microwear variables differ according to particular combinations of levels of facet, sex and wear stage. Neither sex nor wear stage had a significant effect on numbers or dimensions of any of the other microwear variables examined in this study.

CHAPTER 8: THE RELATIONSHIP BETWEEN PIT DIMENSIONS AND DIET

Research on primate microwear patterns has shown that the frequency of pits relative to scratches can distinguish between different diets (e.g. Teaford and Walker, 1984; Teaford 1985; Grine and Kay, 1988; Teaford, 1988). Frugivores have higher incidences of pits relative to scratches than folivores, and hard object fruit-eaters have more greater proportions of pits to scratches than soft object frugivores.

The relationship between hardness of diet and proportions of microwear pits is also apparent in other mammalian species. Van Valkenburgh *et al.* (1990) have examined microwear and diet in extant and extinct large carnivore species. These researchers found that those carnivores which ingest a hard diet (frequent bone-crushers) have higher proportions of pits to scratches than those which ingest a softer diet. Van Valkenburgh *et al.* found that the microwear of large carnivores is most similar to that of frugivorous primates which are hard-object feeders. Similar work on mammalian faunivores has generally indicated that hard and soft object faunivores may be differentiated by incidence of pits (higher proportions of pits to scratches in the former compared with the latter group), that faunivores and primate frugivores have overlapping pit frequencies, and that hard object faunivores and primate frugivores have similar pit frequencies (Strait, 1993).

However, investigations into the size of pits have indicated that the relationship between microwear (pit frequency) and hardness of diet may not be a simple one. Experimental work has indicated that ingestion of hard objects results in a higher number of large pits (>10μm) than soft object feeding which produces more small pits (<10μm) (Teaford and Oyen, 1989a). This has led to the suggestion that different mechanisms - tooth-tooth wear and compression - are responsible for the production of small and large pits respectively (Teaford and Oyen, 1989a; Teaford and Runestad, 1992). Teaford and Runestad (1992) suggest two possibilities for small pit formation resulting from tooth-tooth wear: adhesion (where enamel is transferred from one tooth surface to another, and this includes an important component of force which is parallel to the enamel surfaces (Maas, 1994, and references therein)) and the fracturing of prisms at their boundaries. Enamel prism boundaries may constitute weak points in the enamel surface, and high pressures resulting from contact between microscopic contact points on two opposing enamel surfaces could result in the fracture of prisms at their borders. Teaford and Runestad suggest that in either case (adhesion or enamel prism fracturing) the results would be a number of pits the size of prisms. The mechanism by which Teaford and Runestad (1992) suggest large pits (bigger than the enamel prisms) are formed is compression. This process involves force a large component of which is perpendicular to the occlusal surfaces (Maas, 1994; also see references therein).

Teaford and Runestad (1992) have suggested that the diets and microwear patterns of New World primates provide further evidence of the differential formation of small and large pits. *Cebus*, which ingests invertebrates, the occasional hard object, and ripe fruit, and *Aloutta*, which feeds on a soft diet of fruit and leaves, both have similar frequencies of pits (Teaford and Runestad, 1992). This unexpected similarity was clarified when the proportions of small and large pits were compared. *Alouatta* had a larger number of small pits and a narrower mean pit width than *Cebus* (Teaford and Runestad, 1992).

Some doubt on this conclusion has been raised by Maas (1994). Maas conducted experiments on the abrasion of different mammalian enamel types under compressive loads. Her results indicated that the process by which pits are formed cannot be resolved by their size and this research showed that the main determinant of pit size dimensions was the size of the abrasive particle itself. Compression of the same abrasive particle size produced pits both larger and smaller than enamel prisms. Moreover, the boundaries of the pits were separate from the borders of prisms. This experimental work also indicated that even though magnitude of compressive force is not a cause of variation in the size of microwear features, it may explain the presence or absence of microwear on tooth surfaces. Maas (1994) suggested that the small bite force which is produced during typical chewing does not consistently result in the formation of pits.

As the relationship between pit formation and diet is more complex than initially thought in early microwear research, an examination of the characteristics of pits was carried out for the present study. Percentages of pits and the proportions of small (prism size) and large pits were compared for the three extant hominoid groups (*Gorilla*, *Pan*, and *Pongo*) and the fossil *G. alpani* following the work of Teaford and

Runestad (1992). In order to be comparable with these researchers data for facet 9 only was analysed. The same cut-off point of 4μm was used to distinguish between small and large pits - all pit widths below 4μm were classed as small pits, and all those pits equal to or greater than
4 μm were categorised as large pits.

Following Teaford and Runestad (1992) the arcsine transformation was performed on the proportions of pits (relative to scratches), as well as the proportions of large pits. The arcsine transformation is an appropriate transformation to use when proportions and percentages are being analysed (Sokal and Rohlf, 1995), and was employed by Teaford and Runestad (1992) because their data did not meet the assumptions of statistical tests requiring normality, homoscedasticity, or independence.

Table 5.4 in Chapter 5 displays the descriptive statistics for percentage pits for each species. Figure 8.1 displays mean percentages of pits (the proportion of pits relative to total microwear features) for each hominoid species. *G. alpani* has the highest percentage pits of all four groups (54.6 %). Percentage pits in the extant hominoids varies from 42.9 % in *Pongo*, to 39.7% in *Pan*, and 33.2% in *Gorilla.*

Table 8.1 displays mean pit widths and their standard deviations, and the arcsine transformation of proportion of pits for each of the four hominoid species. (This transformation results in a slight increase in the proportions, as compared with the original untransformed proportions). A graph of pit width plotted against the arcsine transformed proportion (Figure 8.2) of pits shows that *Pan* has the widest pits of the

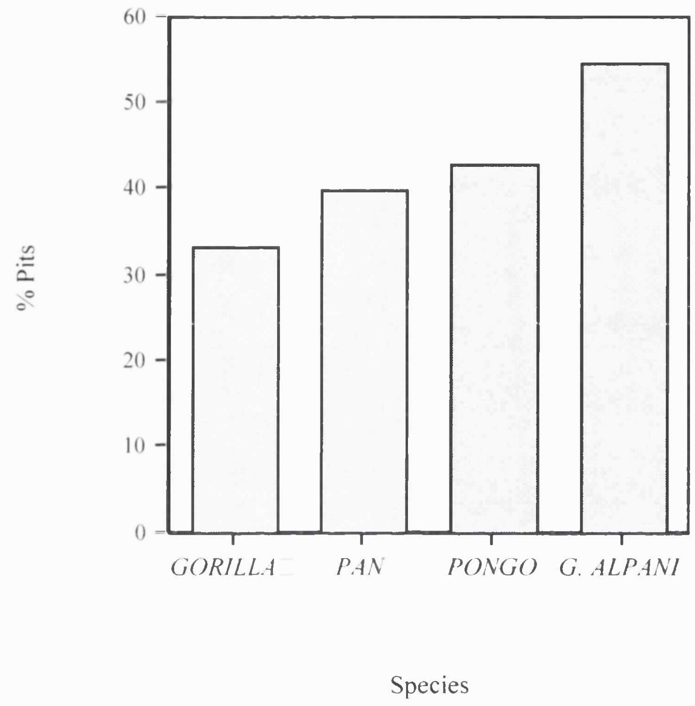


Figure 8.1. Mean percentage pits for all hominoid species.

Table 8.1. Pit widths and arcsine transformation of proportion of pits for each species of hominoid (means and standard deviations).

SPECIES	PIT WIDTH	STD	PROPORTION OF PITS	STD
Gorilla	4.73	2.34	0.34	0.18
Pan	5.45	2.11	0.41	0.21
Pongo	4.78	3.13	0.44	0.17
G. alpani	3.66	1.12	0.58	0.15

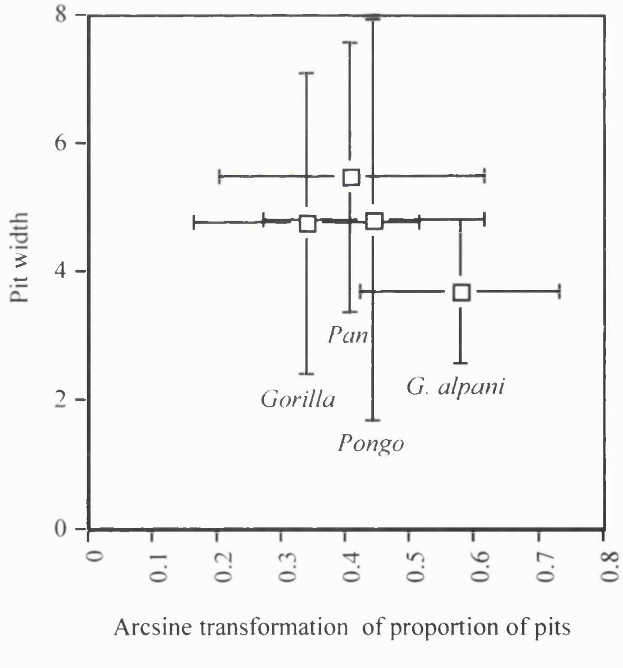


Figure 8.2. The relationship between mean proportion of pits (arcsine transformed) and mean pit width (µm) (mean + s.d.).

four species (5.45μm) and is intermediate to *Gorilla* and *Pongo* in the proportion of pits (0.41) (Table 8.1). *Gorilla* has a mean pit width of 4.73μm and has the lowest proportion of pits (0.34). *Pongo* has the highest proportion of pits (0.44) of all the three extant hominoids, and a mean pit width of 4.78μm. *G. alpani* has the smallest pit widths for all four species (3.66μm) and the highest proportion of pits (0.58).

Chi-square tests did not indicate any significant differences between species in pit width. One Way ANOVA performed on the arcsine transformation of proportion of pits did indicate a significant difference between species (p=0.01) (Table 8.2). Multiple comparisons tests (Tukey's Honestly Significant Difference test at 0.05 significance level) show that *G. alpani* has significantly greater proportions of pits relative to scratches than *Gorilla*, but shows no other significant differences in relation to the other species.

Table 8.2. Results of One-Way ANOVA of arcsine transformed proportions of pits. Three separate tests were performed (one test examined both pit sizes combined together, one test used small pits only, and one test examined large pits) using all species.

VARIABLE	***DF***	***F Ratio***	***p***
Pits	**3**	4.182	0.0097
Small pits	**3**	2.768	0.0501
Large pits	**3**	4.175	0.0097

Table 8.3 contains the arcsine transformations of proportion of small and large pits for each species. Figure 8.3 displays the transformed proportions of small and large pits for each species of hominoid. In all species there are larger proportions of small pits than large pits. The proportions of small and large pits form two species groupings. *Gorilla*, *Pongo* and *G. alpani* display the greatest difference between proportions of small and large pits, and in *Pan* the difference between the two types of pits is more equal. *G. alpani* shows the most extreme difference in proportions of small and large pits, and *Pan* displays the least difference. Wilcoxon Matched-Pairs Signed-Ranks tests were carried out to see whether there were significant differences in the proportions of large and small pits within species. *G. alpani* ($p<0.001$) and *Pongo* ($p>0.001$) both have significantly greater proportions of small pits than large pits, while neither *Gorilla* or *Pan* show a significant difference in pit type. The results for *Gorilla* are strange considering that this species is very similar to *Pongo* in proportions of small and large pits. However, *Gorilla* does display much larger standard deviations than *Pongo* and this may be the reason why no significant differences are seen in *Gorilla* (Table 8.3 , Figure 8.3).

One-Way ANOVA did not indicate a significant difference between species in the proportion of small pits ($p>0.05$) (Table 8.2). However, the probability value was only just outside the 0.05 significance level ($p=0.0501$) (Table 8.2). The multiple comparisons test revealed that *Pan* has a smaller proportion of small pits than *G. alpani*. One-Way ANOVA was also carried out to ascertain whether there were any between-species differences in the frequencies of large pits. A significant difference in the proportion of large pits was indicated.

Table 8.3. Arcsine transformation of proportion of small and large pits (means and standard deviations).

SPECIES	PROPORTION OF SMALL PITS (<4μm)	STD	PROPORTION OF LARGE PITS (≥4μm)	STD
Gorilla	0.82	0.43	0.35	0.27
Pan	0.58	0.28	0.51	0.28
Pongo	0.80	0.23	0.31	0.17
G. alpani	0.78	0.10	0.22	0.10

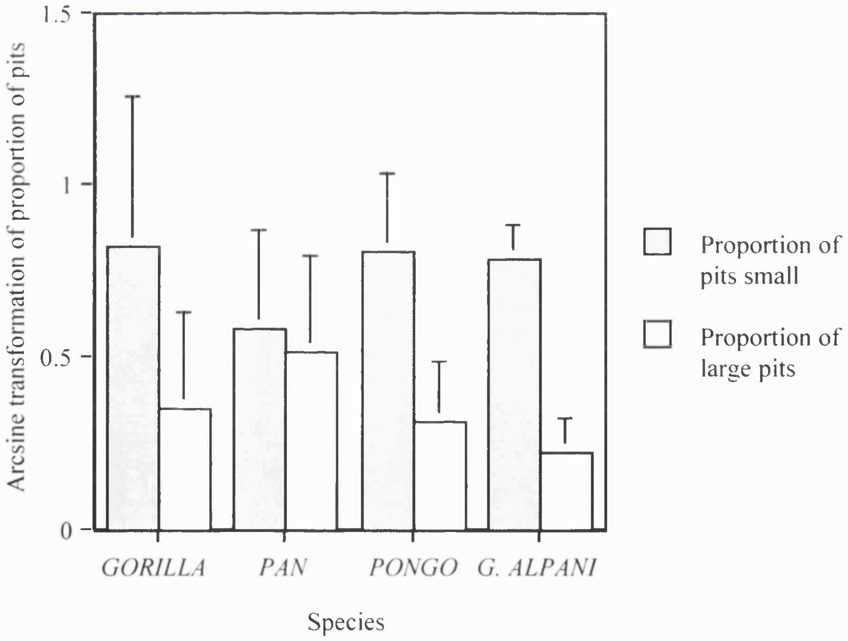


Figure 8.3. Arcsine transformation of proportions of large (≥4μm) and small (<4μm) pits (mean and s.d.).

(*p*=0.01) (Table 8.2) is indicated. Multiple comparisons tests (Tukey's Honestly Significant Difference test with 0.05 significance level) reveal that *Pan* has significantly greater proportions of large pits relative to overall number of pits than *G. alpani*.

Figure 8.4 displays the proportion of large pits plotted against mean pit width. In this figure *G. alpani* has lowest proportion of large pits and the smallest pit width. *Pongo* has a slightly larger proportion, with greater proportions in *Gorilla*, and *Pan* respectively. *Pan* has the largest pit width of all four species, followed by *Pongo* and *Gorilla*.

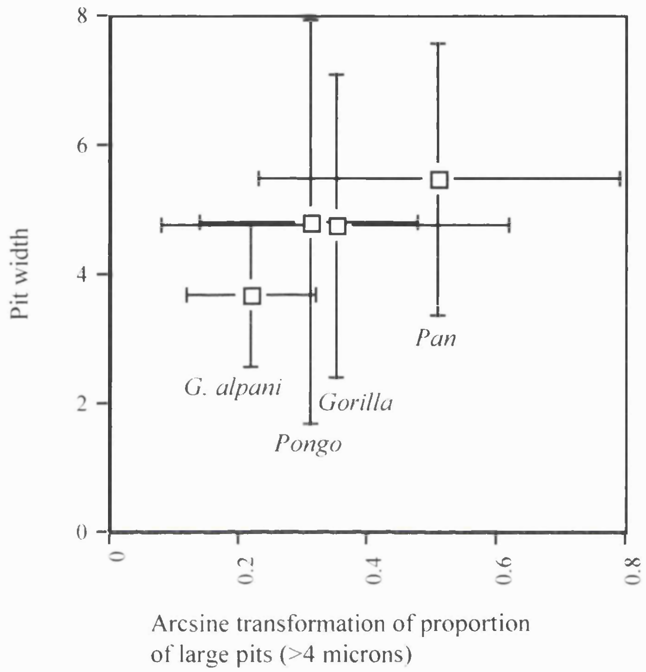


Figure 8.4. The relationship between the mean proportion (arcsine transformed) of large pits (≥4μm) and mean pit width (μm).

Discussion

Although only one significant difference in the ratio of pits to scratches is indicated among the four species examined there is considerable variation in proportions of pits. The fossil hominoid, *G. alpani*, has a larger proportion of pits relative to scratches in comparison to the extant hominoids. No significant differences between taxa are indicated for pit widths. The proportion of small pits relative to large pits was variable across taxa.

All species have greater proportions of small pits than large pits. For *Pongo* and *G. alpani* this difference is significant. *Gorilla* displays similar proportions of small and large pits to *Pongo* but this difference was not significant - this lack of significance may be due to the large standard deviation for proportion small pits for *Gorilla.*

While none of the extant species are hard food specialists, *Pongo* is known to ingest the occasional hard object (Ungar, 1995). *Pongo* however, has more small pits than large pits in comparison to *Pan* (which has been referred to in a previous microwear study as a soft fruit-eater (Teaford and Walker, 1984)). *Gorilla* also has a large number of small pits relative to large pits in comparison to *Pan.* The reason for the large number of small pits in these two species is not clear. As museum samples (in some cases, where little information on locality and date of collection was available) were used in this study, rather than individuals from a known study site which has good information on dietary behaviour, there may be a limit to which dietary inferences can be made using the literature from other research sites. One reason for the large number of small pits in *Gorilla* and *Pongo* may be the fact that they exert greater chewing forces than *Pan* larger mandibles and musculature. Hunter and Fortelius (1994) suggested that pit widths reflect greater occlusal stresses exerted during the ingestion of hard objects.

Experimental evidence provided by Maas (1994) suggests however, that pit sizes do not increase under increasing compressive loads. Another reason why *Gorilla* and *Pongo* might display more small pits than large ones might be related to the amount of lateral excursion they perform during mastication. Mills (1955) has noted that the large canines and high cusps of *Gorilla* limit lateral excursion during mastication. *Pongo* also possesses large canines. This may account for the formation of smaller pit widths in *Gorilla* and *Pongo*. *Pan*, in contrast, has smaller canines than *Gorilla* and *Pan*, and displays a greater number of large pits than the two latter species. *G. alpani* displays the smallest pit widths of all hominoids examined in this study. Mandibular canine dimensions in *G. alpani* are similar to those of *Pan troglodytes* (Waddle, *et al.*, 1995). However, it has not yet been possible to investigate mandibular morphology and dimensions due to the lack of preservation of skeletal parts at Pasalar, and thus, the relationship between canine size and mandibular dimensions is unclear.

The contrasting evidence provided by the experiments carried out by Teaford and Oyen (1989a) and (Maas, 1994) makes it difficult to be certain about the relationship between different wear processes and the formation of small and large pits. Examination of the microwear of New World monkeys with known diets has also provided evidence to support Teaford and Oyens' (1989a) suggestion that small and large pits are formed differently. Further research is needed to clarify this issue.

The results of the present study, and recent work by Ungar (1996), may indicate that pit width is not a useful indicator of food hardness in extant and extinct hominoids. Relative proportions of different feature types (i.e. scratches to pits) may be more useful in dietary interpretations using dental microwear in the hominoids.

Two different conclusions could be made about the diet of *G. alpani* based on the contrasting evidence regarding the relationship between pit formation and hardness of diet. If large pit widths do reflect the ingestion of hard objects, then the large number of small pits displayed in the microwear of *G. alpani* would suggest that it was ingesting soft objects, perhaps soft fruits and leaves as in the case of *Alouatta* (Teaford and Runestad, 1992). On the other hand, if pit size does not reflect feeding object hardness, and wear processes cannot be inferred from pit dimensions (Maas, 1994), the high percentages of pits displayed by *G. alpani* would suggest that it did have a hard object component to its diet.

CHAPTER 9: DISCUSSION

9.1 FACTORS AFFECTING MICROWEAR FORMATION

The predictive relationship between diet and dental microwear may be obscured by factors which are extrinsic to the dietary regime of an animal, such that the causes of tooth wear are perhaps more complex than might initially have been thought. One of the most important factors which is independent of diet but which can have an affect on microwear formation is enamel microstructure.

Enamel formation (*amelogenesis*) is comprised of 2 phases - an organic/matrix production stage and a mineral /maturation phase (Boyde and Martin, 1984; Hillson, 1986). Enamel is formed by a closely connected sheet of cells known as *ameloblasts.*. These cells are long, narrow, and cylindrical in shape, and are packed together so that one of the narrow faces is in contact with the developing enamel. During the organic phase a protein matrix is formed into which crystallites grow. This matrix has similar structures to mineralised enamel but is about 30% organic (Hillson, 1986). The mineral phase involves replacement with apatite. Enamel is approximately 96-97% mineral/inorganic (Hillson, 1986) . The mineral component is an apatitic calcium phosphate (Aiello and Dean, 1990) which varies in purity (Fortelius, 1985; Hillson, 1986). During enamel formation the end of the ameloblast has a process at its secretory end known as a *Tomes' process*, and this fits into a *Tomes' process pit* in the surface of the developing enamel. Crystallites tend to be oriented perpendicular to the secretory surfaces and discontinuities in crystallite orientation exist where the sides of the Tomes' processes meet. These discontinuities are known as *prisms* or *rods*. Enamel is secreted in an incremental way and this is evidenced by markings in the developing enamel. These incremental markings are formed in a regular manner which mirror the acceleration and deceleration of enamel secretion (Aiello and Dean, 1990). Two kinds of incremental lines are produced - brown striae of Rezius (which are known as perikymata on the surface enamel) and cross striations. Both types of marking have a particular periodicity.

Three basic types of enamel prism shape have been defined in mammals (Boyde, 1964), although some intermediate patterns maybe found as these patterns are not totally distinct (Boyde and Martin, 1984). *Pattern 1* enamel is characterised by prisms which have complete boundaries. *Pattern 2* enamel has horseshoe-shaped discontinuities which are incomplete. These prisms are aligned vertically and are interspersed with *interprismatic* enamel (Hillson, 1986). *Pattern 3* enamel is also characterised by prisms which have incomplete boundaries and which are keyhole-shaped in section. It does not have interprismatic enamel (Fortelius, 1985; Hillson, 1986). Incomplete prism boundaries (Patterns 2 and 3) are caused by the ameloblast translating across its secretory product. This means that the prismatic and interprismatic phase become continuous (Fortelius, 1985). Nonprismatic enamel is found in the surface layer of enamel of some species where the ameloblasts no longer have their Tomes' processes (Boyde 1964, Fortelius, 1985).

All three enamel prism packing patterns can be found within a primate species but each species will be characterised by one main pattern. Primates are characterised by a predominance of Pattern 1 and Pattern 3 enamel . *Gorilla*, *Pan*, *Pongo* and *Homo* show a predominance of Pattern 3 prisms (Boyde and Martin, 1984). Boyde (1969) has shown that Pattern 2 is formed by the smallest ameloblasts of all three groups, and Pattern 3 enamel is produced by the largest ameloblasts. Pattern 1 has ameloblasts which are medium-sized in cross-section.

The movement of ameloblasts relative to each other may result in a single or several layers of prisms intersecting each other at an angle. This is known as *decussation* and only occurs with Pattern 2 and 3 enamel as the ameloblasts forming these enamel patterns move relative to each other on the developing surface. When several layers of prisms are involved in decussation they are known as *Hunter-Shreger bands* or *decussating zones*. The most common type of Hunter-Shreger bands are those which are horizontal relative to the root-crown axis of the tooth and are arranged in a concentric spiral around the cusp tip (Fortelius, 1985). The decussating zone is formed parallel to the developing front of the enamel and is also parallel to the striae of Retzius and perikymata (Fortelius, 1985). The other type of decussation occurs is vertical relative to the root-crown axis of the crown, where the Hunter-Shreger bands are aligned radially around cusp tips. These develop transversely relative to the developing front of the enamel and are aligned perpendicular to the striae of Retzius and perikymata (Fortelius, 1985).

Hardness of the enamel itself is an important determinant in the wear resistance of enamel and Fortelius (1985) suggests that this is related to the density of the crystallites. Non-prismatic enamel is more resistant to wear than prismatic enamel which is less dense because of the prism boundaries (Fortelius, 1985).

Decussation is also an important consideration in wear resistance. Fortelius (1985) found evidence that strongly decussating enamel is less wear-resistant than enamel which decussates little. He suggested that this is due to the fact that the prisms in decussating enamel cannot be as tightly packed together as is the case for prisms which are parallel. However, cracks which develop in non-decussating enamel are not likely to continue at length along the planes of the prism boundaries which would result in the removal of large amounts of enamel (Fortelius, 1985).

Crystallite orientation also affects wear resistance. Experimental evidence indicates that that prisms which are sectioned longitudinally by a wear surface are less resistant to wear than those cut transversely (Boyde and Fortelius, 1986).

The differential fracturing and wear properties of enamel microstructure have the potential to confound dietary reconstructions based on dental microwear. Maas (1991) noted that enamel has three structural factors which can influence the wear process. Firstly, differences in prism packing patterns are a cause of potential variation in the wear and fracturing process since they represent planes of weakness in the enamel. This could potentially lead to preferential paths of fracturing. As mentioned above, the three different arrangement patterns vary not only across species but all three types can be found within a single tooth. The second factor is linked to the orientation of the long axes of the prisms relative to the wear surface. Again, this factor varies both across species and within teeth. The third source of potential differential wear concerns the orientation of the crystallites. The orientation varies according to prismatic and interprismatic enamel, and to the three prism packing types. In addition, the influence of all three factors will vary according to the plane of a given wear facet or functional surface.

Maas (1991) conducted a series of experiments to examine the relationship between enamel structure and dental microwear. She looked at the effect of three factors in relation to striation width - species differences in enamel microstructure, the direction of shearing forces relative to the enamel prisms and crystallites, and size of abrasive particles. Maas found that prismatic enamel did not show an association between abrasive particle size and striation width. Nonprismatic enamel, however, did demonstrate a clear relationship between striation width and particle size. Striation width variation according to prismatic and nonprismatic structure seems to be related to their differential responses to direction of shear. Maas found that it is the orientation of the long axes of the crystallites which is the important structural influence on microwear. Crystallite long axes inside prisms are parallel to the prism long axis, but they are oriented in a more apicocervical direction in the interprismatic regions. This resulted in greater striation widths when shear was applied in an apicocervical direction in species which have prismatic enamel. Striation widths were also greater when prism long axes were oriented obliquely relative to the wear surface. In addition, Maas (1991) found that the expression of any one factor (i.e. enamel type, direction of shear, and particle size) was dependant upon the other factor levels. That is, there was a significant interaction between the factors.

The effect on enamel of abrasion compressive forces has also been examined (Maas, 1994). The most common microwear features produced were pits. In these experiments particle size *was* the main determinant of microwear feature size in contrast to the experiments discussed above (Maas, 1991) which examined abrasion under shearing loads.

Martin (1983) and Boyde and Martin (1984) have described the enamel structure of the great apes. All hominoids (including *Griphopithecus alpani*) are characterised by Pattern 3 prism packing in most areas of the deep enamel. There is also a thin layer of Pattern 1 enamel near the enamel-dentine junction. The developing enamel of *Gorilla gorilla* displays prism-packing patterns which were predominantly Pattern 3 and in the mature tissue some areas of Pattern 1 prisms were also found in the sub-surface enamel 3 (Boyde and Martin, 1984). These authors found that there was strong prism decussation in the developing surface and the mature enamel. The developing enamel surface of *Pan troglodytes* indicated a predominantly Pattern 3 organisation of enamel prisms, although there were also number of Pattern 3 variations, and some patches of Pattern 2 enamel 3 (Boyde and Martin, 1984). In the mature tissue Pattern 1 prisms were found in high amounts and the authors attributed this to the fact that they selectively sampled sub-surface enamel. *Pan* also showed well-marked decussation in it mature enamel and daily incremental lines. Both *Gorilla* and *Pan* have a thick layer of Pattern 1 enamel overlying the Pattern 3 enamel (which is about 40% in depth)

(Martin, 1983). The developing enamel surface of *Pongo pygmaeus* displays prisms which are predominantly Pattern 3 in organisation, and most of the mature tissue sampled showed Pattern 3 organisation but there were sub-surface areas of Pattern 1 prisms as well 3 (Boyde and Martin, 1984). Prism decussation in *Pongo* was also strong, and daily incremental marking were also visible. The layer of Pattern 1 enamel which overlies the Pattern 3 prisms is moderately thick (25-30%) (Martin, 1983). Martin (1983) examined the enamel structure of *Sivapithecus alpani* (*Griphopithecus alpani*) and found that, like the extant hominoids, it displayed predominantly Pattern 3 in the mature tissue. Pattern 3 organisation extended to within a short distance of the surface of the enamel, and thus, the layer of Pattern 1 overlying the enamel was thinner in this extinct species than in the present-day hominoids. The microwear patterns of *G. alpani* are more similar to those of *Pongo* than *Gorilla* and *Pan*. Similarities between *G. alpani* and *Gorilla* were found in numbers of striations and the dimensions of pits. *G. alpani* and *Gorilla* display significant differences in the frequencies, dimensions and percentages of four of the microwear variables examined in this study (total numbers of microwear features, frequencies of pits, percentages of pits, and striation widths, as indicated by split-unit analysis of variance, see Section 9.5). The microwear patterns of *G. alpani* and *Pan* are similar in frequencies of microwear features, numbers of striations, percentages of pits, and the dimensions of pits. *G. alpani* and *Pan* also display differences in their microwear patterns - *G. alpani* has more pits and narrower striations than *Pan* (indicated by split-unit analysis of variance, see Section 9.5). Of the extant hominoids the microwear patterns of *Pongo* are most similar to those of *G. alpani*. No significant differences between the microwear patterns of these two species were indicated (see Section 9.5).

The microwear features examined in the present study were classed as "pits" or "striations" and the frequencies as well as dimensions of these variables were recorded and analysed. Maas (1991) found that striation widths were dependant on factors extrinsic to the dietary regime - enamel structure and direction of shearing force - of species which have prismatic enamel. The extant hominoids examined in the present study as well as *Griphopithecus alpani* all have prismatic enamel. Striation widths which were examined here are therefore, unlikely to reflect diet alone and should be treated cautiously. In contrast, Maas (1994) found that pit widths do reflect particle size and are not affected by enamel microstructure. In light of this, pit widths (and lengths presumably) may be used to predict diet.

9.2 WHAT CAUSES DENTAL MICROWEAR?

As Teaford (1988) has pointed out, factors other than gross measures of hardness of food objects themselves need to be taken into account when examining what may produce dental microwear. Lucas (1994) found that microwear can only be formed by particles which are of sufficient hardness relative to enamel (and dentine). In his study he found that of the materials he examined (including seed covering and invertebrate exoskeletons) only quartz and opal phytoliths were capable of damaging enamel. Boyde (1984a and b) has found that abrasives which were softer than fully mineralised enamel were able to abrade enamel. However, Boyde found that enamel is selectively resistant to erosion - enamel at the enamel-dentine junction and the true enamel surface was not abraded, while enamel adjacent to the prism boundaries was eroded by the airpolishing. In addition, enamel was more rapidly removed from prism discontinuities which lay parallel to the surface being abraded. Walker (1984) suggested that the small pits produced in the dentine of baboon canines may have been formed by enamel particles - prism cores which had been "plucked" during tooth-tooth contact.

Walker *et al.* (1978) suggested that opal phytoliths were responsible for the microwear seen on hyrax dentition. Peters (1982) examined the effect of grit adhering to various food items. Relatively soft food items such as onions which were coated with grit, produced fewer striations than harder objects such as seeds which were covered with less grit. This, presumably, is because the onion required less chewing and so the abrasive (grit in this case) caused less damage than mastication of harder objects even though they were covered in a lesser amount of abrasive. Ungar (1992, 1994) suggested that the microwear present on the incisors of four Sumatran anthropoid species was very likely caused by a combination of exogenous grit and opal phytoliths and the phytoliths produced striations which were broader than those made by grit. In his study, primates which fed near the ground had narrower striations than those which fed higher up in the canopy, as a greater proportion of phytoliths would be consumed by the latter species.

In addition to leaves and grasses, opal phytoliths can also be present in large amounts in fruits and seeds. The reproductive structures of plants often contain the same amount of phytoliths by dry weight as leaves (Ungar, 1992). In many cases the silica structures found in the exocarps and mesocarps of fruits are indistinguishable from those found in leaves of the same species (Piperno, 1989). Thus, both hard and soft fruits would contain small and/or angular particles which can abrade enamel. The abrasive particles produce more microwear when they are contained in food items which require extensive preparation before swallowing and digestion, for example hard and/or tough fruits, nuts, and seeds (Peters, 1982). Teaford and Oyen (1989a) also had similar findings from experiments they conducted in which they fed two sets of monkeys a similar diet of monkey chow (biscuits). The only difference between the two groups was that the biscuits fed to one of the groups had been softened with water and fruit purée. The teeth of those monkey fed on the hard (unsoftened) biscuits wore more quickly than those fed on the soft diet. The monkeys raised on the hard diet displayed significantly greater amounts of microwear than those animals which ingested the soft diet (Teaford and Oyen, 1989b). The diets of both groups however, still contained the same amount of abrasives and the only difference between the two diets was in the hardness of the food items.

So far only abrasives in the diet have been considered as causes of dental microwear. Another possible cause of damage to enamel is exposure to acid. Some of the fruits eaten by extant primates are extremely acidic (often because they are eaten when unripe (Ungar, 1992, 1995)). Although mention of the influence of acidic foods on the formation of microwear has been made by some researchers (Teaford, 1988) it has not been fully investigated. Not only can acid have a pronounced effect on enamel (as shown by the experiments conducted in the present study (Chapter 4) on the effect of hydrochloric and citric acid), but it can also result in the accelerated abrasion of enamel (see references and discussion in Teaford, 1988).

9.3 SOURCES OF ERROR

There are several potential sources of error in this study, for example, microscopic features (artefacts) created by post-mortem agents which may obscure those modifications may by food, the distortion of microwear features due to molar morphology and the slope of the facets, and intra-observer error in the measurement of microwear features. Gordon (1983, 1984a), Puech *et al.* (1985), and Teaford (1994) examined the effect of various taphonomic agents on dental microwear. Gordon (1983, 1984a) found that although microwear is modified by sediment abrasion the features are obliterated rather than secondarily altered. Gordon (1980, 1982) also discussed the effect on microwear features of molar facets which are tilted relative to the occlusal plane. She found that features on these tilted facets appear shorter than they should be in reality, and are therefore subject to distortion.

9.3.1 Taphonomic agents

Post-mortem agents such as sediment abrasion, acidic etching, and recovery of fossils may modify microscopic wear marks on the teeth, and could therefore, obscure dietary reconstructions. Initial examination of the Pasalar hominoid dentition revealed a number of specimens which displayed unusual microscopic marks. It was suspected that these specimens had been modified taphonomically.

Several experiments were carried out in this study to examine the effects of taphonomic agents on enamel and microwear. Both the hydrochloric and citric acid eroded the enamel and microwear features. The hydrochloric acid produced a heavier erosion than the citric acid - almost all the microwear features were removed and enamel prisms were uniformly exposed. Only the finer microwear features were obliterated after immersion in citric acid, and there was patchy exposure of enamel prisms. Both these patterns of acidic erosion have also been found in other experimental studies (e.g. Puech *et al.*, 1985; Teaford, 1994).

When enamel was abraded with different size sediment the greatest alteration to the dental microwear occurred after abrasion by the smallest sediment particles - the medium-sized sand. The pre-existing microwear features were completely removed by the abrasion and the enamel surface was covered in extensive pitting. This contrasts with the experiments conducted by Gordon (1984a) who found that the greatest modification to microwear features was produced by the largest sized sand particles in her experiment (pea gravel). However, Gordon does not give detailed information about the sizes of the grains used in her experiments, and so it is not possible to provide an explanation as to why her results are different from those presented here. After 512 hours of abrasion by the medium-sized sediment (grain size ranged between 250 μm and 500 μm) in the first experiment (using human archaeological material), and 16 hours in the second experiment (using an extracted human tooth) the enamel surface was extensively pitted and the microwear features had been completely removed. The pits were small (less than 5 μm) and uniform in size, and were so numerous that they gave the enamel surface a very rough texture, and lacking a certain amount of polishing that is usually seen with microwear made during the life of an animal. This pattern was seen only on the buccal slopes of the cusps and not on the lingual faces or towards the centre of the occlusal surface. Further tests are needed to determine why the extensive pitting appeared so much earlier in the extracted tooth than the archaeological material.

The experiments show that the taphonomic alteration of microwear patterns is distinctive and can be readily identified. Microwear features tend to be *obliterated* rather than secondarily altered by taphonomic processes. Thus, if fossil and archaeological specimens (and recent material which has not been collected immediately after the death of the animal) are carefully examined, and taphonomically damaged specimens are excluded from analysis, inferences about diet are not likely to be obscured by the effects post-mortem processes.

9.3.2 Tilt

Another source of error is produced by molar morphology itself. The cusps on a molar tooth project vertically relative to the occlusal plane. This means that features which lie on an inclined facet will be foreshortened when viewed perpendicular to the occlusal plane. In order to minimise this problem researchers have tended to orientate specimens such that the facet under examination is normal to the SEM beam (e.g. Teaford and Walker, 1984; Grine, 1986; Van Valkenburgh, *et al.*, 1990; Ungar, 1996). In the present study however, molars were examined in their occlusal position in order to keep a standard orientation for all three facets. Microwear features present on these inclined facets were therefore subject to distortion in the form of foreshortening, such that measurements of features will be smaller than they should be in reality.

A procedure was developed to establish the amount of foreshortening and to correct all the distorted measurements. A comparison was then made between original and corrected microwear data. It was found that in some cases same features may change before and after correction (i.e. a pit may become a scratch or *vice versa* after correction, as seen in specimen E626 (Appendix 3). Also, although percentage corrections could be high for some individual specimens, when species means were compared there was little difference between original and corrected feature frequencies and proportions (Appendix 3). Species means for original and corrected feature dimensions however, were often significantly different (Table 3.4). Although the magnitude of the difference was generally small (often less than 0.5 μm) (see Table 3.3), there was nevertheless a consistent and significant difference.

9.3.3 Intra-observer error

SEM micrographs of microwear are complex images to record. Microwear features are constantly being reworked through time as the teeth wear, such that features become secondarily enlarged and shallowed (Gordon, 1980, 1982). Some features will appear dark and are easy to discern, whereas others are faint, and they appear as grey shadows with blurred margins, making it difficult to identify microwear features and their borders. The longer an image is examined, the more features are apparent because of the various shades of grey which represent features in different states of wear. As a result of this there is an element of subjectivity involved in recording these features. Moreover, an investigator's criteria for measuring microwear features may inadvertently vary from one day to next.

Added to these difficulties is the fact that specimens vary in the amount of signal they emit due to individual variation in topography, a result of species differences in molar morphology, and the wear process at a gross level. An image of a relatively worn, flat specimen will be poorer in terms of contrast and light in comparison to a molar which is little worn and has more relief. It is also the case that the SEM itself can differ slightly from day to day in terms of resolution and clarity of images. These factors all contribute to the difficulty in discerning microwear features.

For the purpose of estimating intra-observer error, the standard measuring procedure was followed in all details. Each micrograph was enlarged from x 200 to x 400 to and this allowed a greater area of the facet to be examined initially, followed by greater resolution of features through increased magnification. A 6.4 x 4.8 inch portion (which represents 0. 124 mm^2 of the actual tooth) of each enlarged micrograph was measured. An acetate overlay with a grid containing twenty boxes helped transform daunting microwear images into manageable units for measurement. Shallow features which were being eroded away were not measured if their borders were not sharp and clear. As a result, many features which were visible were not recorded because their margins could not be measured with confidence. Features were sometimes truncated by the boundaries of the 6.4 x 4.8 inch field. In these cases only the portion of the features which was inside the field was recorded. Typically, striation lengths were truncated and for this reason striation lengths were not used as a microwear variable in any analysis which would be used to infer diet. The number of pits typically affected by truncation was very small. A time limit of one hour was imposed, and in the majority of cases this was a sufficient length of time for recording microwear features. In the rare event where there were so many features that it was likely that measuring would take more than one hour, only the most obvious features in each box of the grid overlay were recorded.

Based on these criteria, intra-observer error estimations were performed to evaluate measuring accuracy, and to assess the error in recognising microwear features. Mean absolute percentage error in measurement (an assessment of the variation in measuring the same features on three different occasions) was calculated as 8.43% for widths and 12.05% for lengths. Repeatability in identifying microwear features (the ability to recognise the same features on three successive occasions) was estimated as 13.93% for total number of microwear features, and 16.68% for percentage pits.

There is no standard against which these error estimates can be assessed as no previous work on dental microwear has examined measurement error. A microwear study of deciduous human archaeological teeth by Bullington (1991) is a partial exception. Bullington measured each micrograph three times and then used the average of the three in her dietary analysis. She did not, however, give any error estimations. Nevertheless, the intra-observer estimates presented in this study indicate that the repeatability in feature identification and measurements is subject to a maximum error of 17%. This error must be taken into account when microwear data are used in dietary reconstructions.

The intra-observer error estimations also have implications for inter-observer error in microwear measurements and comparisons between studies conducted by different researchers. Inter-observer error will very likely exceed any intra-observer error. This implies that it would be difficult for one researcher to reproduce another investigator's results. This has implications for both the standardisation of microwear methods among researchers, as well as being a consideration when comparing one microwear study with another.

9.4 THE STATISTICAL ANALYSIS

9.4.1 Comparison between Factorial and Split-Unit ANOVA

Two statistical analyses of the microwear data were performed in this study. The first analysis was a factorial analysis of variance (Chapter 6). As it is not reasonable to assume independence of data in this type of analysis, a split-unit analysis of variance (ANOVA) was also carried out (Chapter 7).

Species and facet differences in microwear

A comparison of the two factor and split-unit ANOVAs revealed that the split-unit ANOVA indicated an interaction between facet and species that was not shown by two-factor ANOVA. Pit lengths vary according to the particular combination of species and facet levels under examination. Two factor ANOVA did not indicate this interaction between facet and species. Split-unit ANOVA also revealed a significant main effect that was not shown in the two factor ANOVA - striation frequencies vary according to the facet under examination. The two analyses were otherwise the same in terms of the influence of species and facet type on the microwear variables examined. The main difference between the two analyses was in the pairwise comparisons between species. Two factor ANOVA found more significant differences between species than split-unit ANOVA. In addition to the higher percentages of pits displayed by *G. alpani* relative to *Gorilla* indicated by both types of analysis, two factor ANOVA also showed that *G. alpani* has higher percentages of pits than *Pan* and *Pongo*. Both types of analysis revealed that, in addition to the greater numbers of microwear features than *G. alpani* and *Pongo* have in comparison to *Gorilla*, *G. alpani* and *Pongo* also display significantly greater numbers of microwear features than *Pan*. As the data used in the two factor ANOVA may violate the assumption of independence of the data, a possible effect of increased sample sizes would be to find more differences between pairs of species than if individual specimens had been controlled for. This appears to be the case with the two factor ANOVA presented in this study.

Sex and wear stage differences in microwear

Three factor ANOVA also found more significant interactions between the independent variables (facet, sex and wear stage) than split-unit ANOVA. Both types of analysis revealed significant second-order interaction effect between facet, sex, and wear stage. Pit widths and pit lengths are dependant on the particular facet, sex, and wear stage examined. Three factor ANOVA also revealed two significant first-order interaction effects between sex and wear stage - total number of microwear features and striation widths vary significantly according to particular combinations of the sexes and wear stages examined. Neither type of analysis found that any of the microwear variables differed significantly according to sex or wear stage.

As it is not certain that the data used in the three factor ANOVA are independent, and because some differences were found between this analysis and the split-unit ANOVA (where the data are independent), the split-unit ANOVA results are taken as being more reliable for indicating differences in microwear patterns in this study.

9.4.2 Species and Facet differences in dental microwear

In general, this study has found that species differences in microwear feature types and sizes are not dependant on the facet examined. This is indicated by the lack of significant interactions between species and facet. Only one significant interaction is shown by the analysis - species differences in pit lengths are dependant on the particular facet under inspection. This means that any attempt to relate pit lengths to diet would also need to take into account the particular facet which was examined, as different surfaces can vary in patterns of pit lengths.

When considered separately both species and facet have a significant effect on the majority of microwear variables. The most consistent species differences which emerge from this study are those between *G. alpani* and *Gorilla*, and *Pongo* and *Gorilla*. *G. alpani* and *Pongo* display significantly greater numbers of microwear features and pits on all facets in comparison to *Gorilla*. *G. alpani* also has significantly higher percentages of pits than *Gorilla*. *Gorilla* has significantly wider striations than *G. alpani* and *Pongo*. There is only one significant difference in microwear variables between *Pan* and the other extant hominoid species - *Pan* has wider striations than *Pongo*. Significant differences in two microwear variables were found between *G. alpani* and *Pan*. *G. alpani* displays more pits and narrower striations than *Pan*.

The microwear patterns of all three hominoids are consistent with the literature on primate microwear and diet. It has been found that primate frugivores have higher proportions of pits relative to striations (e.g. Teaford and Walker, 1984; Teaford 1985;

Grine and Kay, 1988; Teaford, 1988). Moreover, primates which ingest soft fruits can be distinguished from those which feed on harder fruits. The percentages of pits displayed by all three hominoid species examined in this study are consistent with published microwear patterns of homologous facets in primate frugivores (Teaford and Walker, 1984; Teaford, 1988). Both *Gorilla* and *Pan* however, have substantially larger percentages of pits than reported by Teaford (1988) for the same species. In the case of *Gorilla* this difference may well be attributed to the use of different sub-species - *G. g. gorilla* consumes large quantities of fruit in comparison to *G. g. berengei*, for example, although Teaford does not mention which particular sub-species he examined.

The significant differences in numbers of microwear features and pit frequencies seen in *Pongo* and *Gorilla* indicated in the present study by split-unit ANOVA may relate to differences in the consumption of hard and soft fruits. Whilst *Pongo* is not a hard food specialist (Ungar, 1995), it does ingest a certain amount of hard fruits and hard-husked objects (MacKinnon, 1977; Ungar, 1992, 1994, 1995). *Pongo* also feeds on unripe fruit. *G. g. gorilla* also ingests substantial amounts of fruit (e.g. Tutin and Fernandez, 1985, 1987; Tutin *et al.*, 1991) although no study has provided information about the hardness of the fruits eaten by *G. g. gorilla*. Sabater-Pí (1977) reported that this sub-species of *Gorilla* feeds, to a large extent, on fruits which are low-lying and which have fallen on the ground. The latter are likely to be ripe, and therefore, relatively soft, fruits. The microwear patterns of *Pan* appear to be intermediate between those of *Pongo* and *Gorilla* because the analysis presented here does not indicate significant differences between these three species. The only significant difference found between the three species of extant hominoid is that *Pan* has wider striations than *Pongo.* However, sample sizes for *Pan* were smaller than for other species and this may account for the large variation in this species and lack of differences with the other extant hominoid examined in this study. In general then, the results of this study indicate that *Pongo* ingests harder fruits than *Gorilla*, at least some of the time, and that the diet of *Pan* is intermediate between that of *Pongo* and *Gorilla.*

G. alpani has a pattern of microwear that is similar to *Pongo* in many respects and it is suggested that the diet of this Miocene hominoid was predominately fruit. *G. alpani* displays similar differences in microwear in comparison to *Pan* and *Gorilla* as does *Pongo*. *G. alpani* also has significantly greater percentages of pits than *Gorilla* and it is suggested that *G. alpani* ingested, at least some of the time, harder fruits than *Gorilla.* Although split-unit ANOVA did not indicate significant differences in percentages of pits between this Miocene hominoid and *Pan* and *Pongo* it may also be that *G. alpani* fed on harder fruits than these two extant hominoids, due to the high percentages of pits it displays.

Clear differences in dental microwear between facets, regardless of species, have emerged in this study. Facets 9 and x, the Phase II surfaces (Kay and Hiiemae, 1974; Kay, 1977b), display similar microwear patterns to each, but differ in comparison to facet 1, a Phase I surface. Facets 9 and x have significantly greater numbers of all types of microwear features, pits, and percentages of pits than facet 1. Facet 1 has wider striations than facets 9 and x. The two Phase II facets are extremely similar in the amounts and sizes of microwear features and split-unit ANOVA indicates only one significant difference between them - facet x has significantly greater numbers of striations than facet 9. These results are consistent other studies which have reported that Phase I facets display lower numbers of microwear features, frequencies of pits, and percentages of pits than Phase II facets (e.g. Gordon, 1980, 1982; Teaford and Walker, 1984; Teaford, 1985). The results presented here are also compatible with the findings of Gordon (1980, 1982) who reported that while Phase II surfaces display more microwear features in general than Phase I facets, striations occur in approximately the same amounts on both types of facet. This means that the main difference between Phase I and Phase II facets is due to the higher numbers of pits that are present on the latter surface types.

The Mann-Whitney U tests presented in Chapter 6 often show more significant differences between the species than the ANOVA. However, the ANOVA did not investigate differences between species in microwear for a given facet, but instead all facets combined were examined. Also, the paired comparisons between species performed in the ANOVA have been adjusted using the Bonferroni correction. This is because when more than two groups are compared the chance of finding a significant difference is increased by the number of comparisons (e.g. if 6 paired comparisons are carried out then the chance of finding a significant difference will be 0.05 x 6 = 0.30). If the t values presented in the ANOVA tables in Chapter 8 are examined they often indicate significance but this is before the Bonferroni adjustment has be made. After correction the significant difference indicated by the t value may well have disappeared.

9.4.3 Sex and Wear Stage differences in microwear

The examination of the effects of sex and wear stage on dental microwear were performed using the *Pongo* sample only, due to small sample sizes in the other hominoid species (and it has not been possible to assign sexes to the *G. alpani* using only the second molar tooth (see Chapter 3 for discussion). The effect of three factors on dental microwear variables - facet, sex and wear stage - was examined. In general, there were very few significant interactions, or significant effects of the factors. When examined separately sex and wear stage had no significant effect on any dental microwear variables.

Significant second-order interaction effects of facet, sex, and wear stage on pit width and pit length are indicated by two factor and split-unit ANOVA. Differences between facets in pit widths and lengths are dependant on sex and wear stage for their expression. No other significant interactions are indicated from this analysis. When the main effects were considered separately only one factor had a significant effect on two of the microwear variables - total numbers of microwear features and frequencies of pits varied significantly according to the facet examined.

Mann-Whitney U comparisons (Chapter 5) between the same facets for those species with an adequate male and female sample size, do not indicate any significant differences between the two sexes for any microwear variable. Mann-Whitney U tests indicate only one significant differences between wear stages - *Pongo* wear stage 1 specimens display significantly higher percentages of pits than wear stage 2 molars for facet - and this is not a highly significant difference. However, the split-unit ANOVA examines three possible sources of variation simultaneously, and as the addition of more factors can explain more of the variation, it is a more powerful test. Although most microwear variables do not vary significantly, it is apparent that the dimensions of pits are influenced by sex and wear stage, as well as facet. However, sex and wear stage sample sizes used in the split-unit ANOVA are rather small and this analysis also includes only one species. As such, the results presented here should be treated cautiously. The inclusion of species, and larger sex and wear stage sample sizes, may provide more concrete information on this issue in the future.

Ungar (1992, 1994) studied the incisor microwear of four Sumatran anthropoids and found that there was a significant difference between *Pongo* males and females in striation widths - males had narrower striations than females. Exactly what this indicates is not made clear, especially as none of the other three primate species he examined displayed sex differences in microwear. Gordon (1980, 1982) however, did discover sex differences among a single sub-species of chimpanzee - *Pan troglodytes verus*. She found that females have significantly shorter striations than males, and that females display lower proportions of pits relative to scratches on third molars. No variation between the sexes was found in the dimensions of pits however, and Gordon's definition of a pit is different to that used in this study (she classed pits as having approximately equal lengths and widths, the present study used a length to width ration of 4:1. Gordon also found age-related differences in dental microwear. Juveniles had significantly higher numbers of microwear features than adults. Gordon did not relate these findings to diet.

There is evidence from behavioural studies for sex and age differences in the feeding behaviour of *Pongo*. Galdikas (1988) found that adult male orang-utans spent more time feeding on termites and other foods, such as small vines and orchid leaves and stems, and less time eating bark and young leaves than adult females. Rodman (1977) however, found evidence to the contrary - males spent less time feeding on fruit and termites, and more time ingesting fruit. The microwear evidence presented in this study does not, in general, indicate age or sex differences in diet, although it should be noted that the comparative hominoids used in this study did not come from single populations. Differences in pit widths and lengths, however, are dependant sex, wear stage, and the particular occlusal facet under examination.

9.5 OTHER WAYS OF INTERPRETING DIET USING TEETH

Tooth morphology, particularly incisors and molars, provide a vast amount of information about diet. The incisors of frugivores tend to be broader, relative to molar size, than those of than folivores because fruit requires more preparation prior to chewing than leaves. Those primate species which feed on exudates have large, procumbent incisors. Molar morphology (and to a lesser extent, the premolar form) is also linked to the physical properties and structure of the food items consumed. Frugivores tend to have molars with low, rounded cusps, and wide basins where the emphasis is on crushing and pulping (Fleagle, 1988; Kay, 1981) because these food items have a three-dimensional aspect (Kay and Covert, 1984). This morphology is beneficial for the ingestion of both soft fruits, as well as harder nuts and seeds.

However, the digestion of a diet which includes a large amount of structural carbohydrates (for example, leaves, bark, and buds) is greatly enhanced by commminuting the tough food items by shearing them. This is because these food items form almost two-dimensional sheets which are more easily reduced by a cutting/shearing action, thereby increasing their surface area (Kay, 1981; Kay and Covert, 1984; Ungar and Kay, 1995). This is achieved in primates by having molars which posses well-developed shearing crests and cusps of high relief (Fleagle, 1988; Kay, 1981) and this is seen in both folivores and insect eaters. In addition to having well-developed shearing crests, insectivores are characterised by small molars which possess particularly pointed cusps.

Kay (1977a) found that shearing crest development relative to M_2 length could be used to distinguish between folivorous and frugivorous Old world anthropoids - folivorous species have longer shearing blades than frugivorous taxa. More recently, Ungar and Kay (1995) used shearing crest development to reconstruct the diets of several species of European Miocene catarrhines. They found that the pattern of shearing crests development follows that seen in extant hominoids - folivorous species have greater crest development than frugivores.

Another aspect of molar morphology which can give insight into the feeding behaviour of primates is *relative enamel thickness*. Kay (1981) examined the relative enamel thickness of 37 Old world anthropoids and found that those species which are characterised by thick enamel, for example *Cercocebus* and *Pongo*, ingest hard objects such as hard fruits and nuts and seeds. Kay and Covert (1984) also found this pattern in other mammalian species. These authors also found that *relative enamel thickness* is highly negatively correlated with *relative shearing crest development.* That is, well-developed shearing crests are associated with *thin* enamel, and poorly developed shearing crests are linked with *thick* enamel. A marked example of this association is seen in the cercopithecines, which have thick enamel and poorly developed shearing crests, and the colobines which have well-developed shearing crests and thin enamel. The extant hominoids do not show such clear differences, because *Pongo*, for instance, has thick molar enamel but also displays relatively well-developed shearing crests. When *Pongo* was removed from the analysis there was a significant correlation between relative enamel thickness and shearing crest development among the hominoids.

The dietary behaviours of several Miocene hominoids have recently investigated using a combination of incisor morphology, shearing crest development, and relative enamel thickness (Andrews, 1992; Andrews and Martin, 1991). *Proconsul* an early Miocene hominoid is characterised by thin molar enamel and broad incisors, and the authors suggest that this taxon ingested soft fruits. During the middle Miocene there was a second radiation of hominoids. Several taxa are characterised by thickened molar enamel and these hominoids are associated with more open habitats, which were strongly seasonal tropical to sub-tropical forests, than those of the early Miocene hominoids. It has been suggested that although these hominoids underwent a dietary shift, possibly towards harder object frugivory.

9.6 COMPARISON WITH OTHER MIOCENE CATARRHINES

In a study of Old World primates Kay (1981) observed that the molar enamel is thicker among frugivorous species than folivorous ones. He also found that those frugivorous primates with the thickest enamel ingest extremely hard nuts, seed and fruits, while the thinner enamelled species are unable to do so. This led Kay to suggest that the morphology of the molars and the extremely thick enamel on the teeth of *Sivapithecus indicus*, an 8 Ma Miocene hominoid from the Siwaliks (Pakistan) (Opdyke *et al*., 1979) would have ingested a diet consisting of hard seeds, nuts and fruits.

Teaford and Walker (1984) carried out a microwear analysis of eight primate species, including the Miocene hominoid *Sivapithecus indicus*. They found that this hominoid displayed microwear patterns which were intermediate between primate hard and soft fruit-eaters, and was most similar to *Pan troglodytes*. Teaford (1988) re-analysed this data using a different definition of a pit (a length:width ratio of 4:1, instead of 10:1) and taking into account individual variation in microwear. He found that the microwear patterns of *Pan* and *S. indicus* are statistically indistinguishable from those of *Pongo*, Teaford suggested that *S. indicus* may not have been a “classic” hard object feeder.

Ungar (1996) found that the range of variation in percentage pits for a number of these Miocene catarrhines indicates a range of diets similar to those seen in extant anthropoids - that is, hard-object feeders, soft-fruit eaters and folivores. Ungar suggests that *Graecopithecus freybergi* (Ungar refers to this species as *Ouranopithecus macedoniensis*) (which had a high percentage of pits) was a hard object feeder while *Dryopithecus* spp., *Pliopithecus* spp., and *Anapithecus* were probably soft-fruit eaters, and *Oreopithecus* was a folivore. *Griphopithecus alpani* (54.6%) has similarly high percentages of pits as *Graecopithecus* (57.7%). *G. alpani* overlaps with all other species except *Oreopithecus* (Figure 9.1).

In addition, *G. alpani* displays smaller pit widths and lengths than all other species (Figure 9.2). The range of pit widths seen in *G. alpani* overlaps with *Anapithecus*, *Oreopithecus*, and *Graecopithecus*. There is overlap in pit lengths among all taxa.

Ungar (1996) suggested that the lack of species differentiation in pit dimensions may be evidence that pits and striations are distinct entities - rather than being part of a continuum (as Gordon (1980, 1982) has proposed). As the dimensions of the pits did not vary between taxa Ungar suggested this supports the idea that that pits are formed by similar processes (i.e. regardless of diet). Real differences between species were in the proportions of scratches to pits Split-unit ANOVA did not indicate any significant differences in pit widths or pit lengths between any of the species examined in the present study - either extant or fossil. The interpretation of pit lengths however, is complicated by the interaction between facet and species. In this study striation widths were found to vary significantly according to species. However, relating striation widths to diet must be treated with caution as Maas (1991) found that scratch width formation is related to enamel microstructure, rather than the size of the abrasive particle.

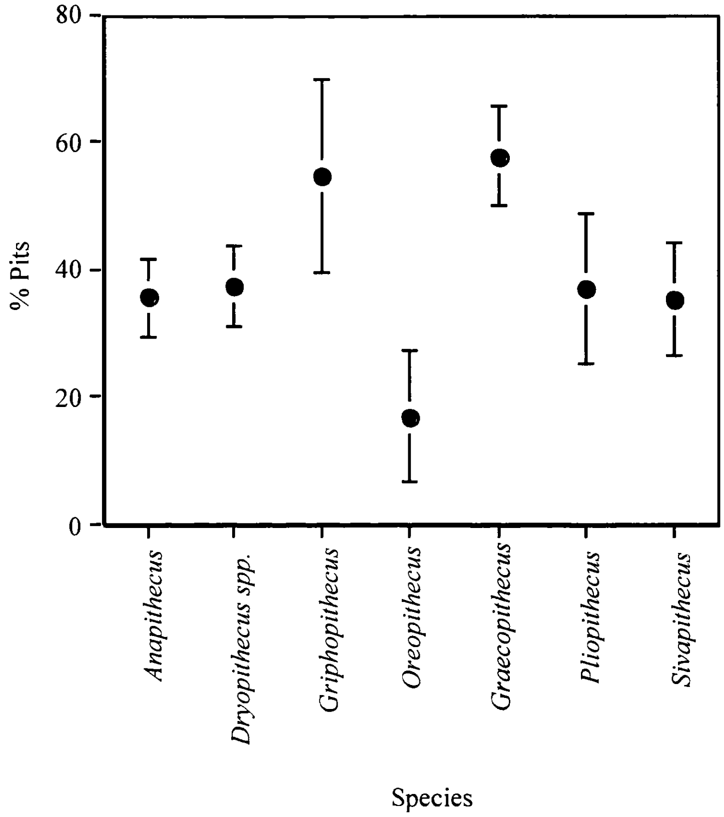


Figure 9.1. Percentage pits for a number of Miocene hominoids including *Griphopithecus alpani.* (Data for *Sivapithecus* from Teaford, 1988. All other hominoid data (excluding *G. alpani*) were taken from Ungar, 1996).

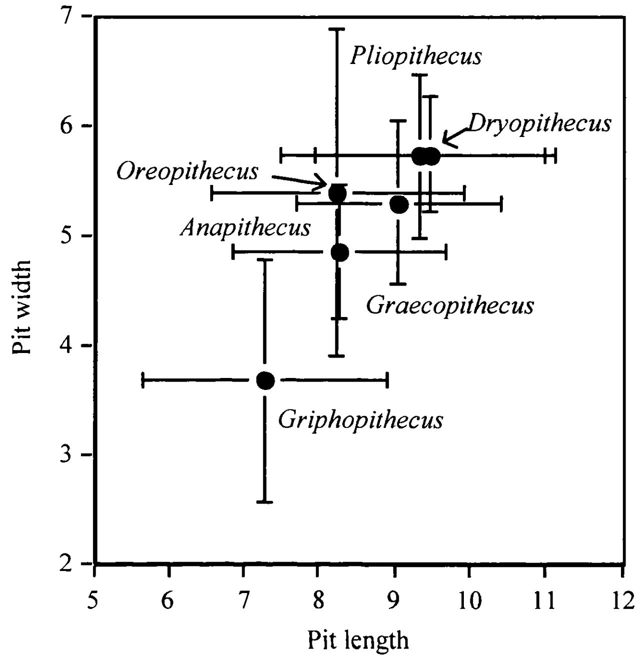


Figure 9.2. Bivariate plot of pit widths and pit lengths (μm) for a number of Miocene hominoid species including *G. alpani*. (Excluding *G. alpani* all data were taken from Ungar, 1996).

The relationship between the dimensions of pits and diet is not a simple one. On the basis of both experimental (Teaford and Oyen, 1989a) and observational (Teaford and Runestad, 1992) data it has been suggested that soft-object feeding produces small pits, and the ingestion of hard objects results in the formation of large pits. These authors proposed that small pits are formed by tooth-tooth wear (either by adhesion or by the fracturing of enamel prisms at their boundaries which constitute weak points) and large pits by compression. Citing research by Misra and Finnie (1981) on wear resistance of metals, Teaford and Oyen (1989a) suggest that the primary wear mechanism - three-body abrasion (where loose particles contact the wear surface (Misra and Finnie, 1981)) - is altered to two-body abrasion (where abrasive particles are held fixed in as they are moved across a surface (Misra and Finnie, 1981)) during the ingestion of soft foods. Maas (1994) on the other hand suggested that the size of pits does not indicate the wear process by which they were formed, as pits which were both larger and smaller than enamel prisms were produced by the same particle size. Although the experiments indicated that average pit area corresponded to the average diameter of the abrasive particle there was variation in feature sizes within each experiment. Therefore, a high number of small pits may indicate the size of abrasive particles within or adhering to food items, rather than a different wear process than that which produces large pits.

According to Maas (1994) this variation reflects irregularity in the shape of the food particles, and the contact area with the enamel, within each particle size class. Moreover, for each size class the pit area observed was less than the average diameter of the particle, and this is related to previous suggestions that the widths of microwear features are approximately 1/10th the diameter of the particle size (Maas, 1994 and reference therein).

Hunter and Fortelius (1994) suggested that pit minimum diameter is an indication of the extent to which a particle is pressed into rather than across the enamel. Thus, pit minimum diameter is a reflection of the size and angularity of the particle, as well as well as the direction and force which act upon it (Gordon, 1982; Maas, 1994). Hunter and Fortelius (1994) suggested that pit and striation widths reflect the greater occlusal stress exerted during the ingestion of hard objects rather than the occurrence of larger hard particles. In contrast, Maas (1994) found that the size of pits (which represented 95% of all the microwear features produced under compressive loads) does not vary with the different compressive loads used in her experiments (50 kg and 100 kg), and she suggested that the loads used represent an upper limit for the effect of different loads on microwear formation. . However, Maas also found that high magnitudes of force were required in order to produce pits consistently, and she observed that below this limit different compressive forces may influence microwear patterns. The low numbers of pits seen on the teeth of typical primate soft food eaters (e.g. Teaford and Walker, 1984; Teaford, 1988) may indicate low masticatory loads. Hylander *et al.* (1987) found that maximum jaw loading during mastication occurred immediately prior to centric occlusion - that is, during Phase I movements. The authors also suggested that the loads exerted during typical Phase II chewing was small. This supports the theory that much of the wear produced on Phase II facets occurs when crushing occurs between these surfaces during Phase I movements. The striations formed during Phase II are formed by relatively low occlusal forces as the jaw adductors relax.

Proportions of large (≥ 4 μm) and small (< 4 μm) pits were examined in the present study. Although *G. alpani* has the highest proportion of pits (all sizes of pit) compared with the other species examined, it has the smallest pit widths. *Pan* displays proportions of pits which are intermediate between *Pongo* (which has the greatest proportions for all the extant taxa) and *Gorilla* (which has the lowest proportion for the extant species), and has the widest pits of all species. All taxa display greater proportions of small pits than large pits. *Pongo* and *G. alpani* display significantly more small pits than large pits. *Pan* displays the least difference between the two sizes of pit, and has significantly greater proportions of large pits than *G. alpani*. Teaford (1988) also found that mean pit widths for *Gorilla*, *Pongo*, and *Pan* overlap in their ranges and while greater differences were indicated for the percentages of pits displayed by these species, *Pan* and *Pongo* were statistically indistinguishable. These results are consistent with the findings of the present study. While living anthropoids may differ in the process by which pits are formed, the evidence is uncertain for such a difference among the extant hominoids, and even less so for *G. alpani* in light of the study by Ungar (1996) on Miocene catarrhines.

G. alpani is similar to *Graecopithecus* in the proportions of pits it displays. Compared with other Miocene taxa *Graecopithecus* has intermediate pit widths, while *G. alpani* displays the smallest pits in comparison to modern hominoids and *Graecopithecus*. The high percentages of pits seen on the molars of *G. alpani* suggest that like *Graecopithecus* it was a hard-object feeder. In fact, *G. alpani* displays similar percentage of pits on its molars as *Cercocebus albigena* (55.2% pits (Teaford, 1988)) which ingests very hard nuts and fruits (Teaford and Walker, 1984). Ungar (1996) proposes a diet of roots, tubers, nuts and seeds for *Graecopithecus* based on its terrestrial adaptations. Although *G. alpani* also has some terrestrial characteristics it may have spent a large amount of time in the trees. Given that most extant great apes are predominantly fruit-eaters it may be that *G. alpani* was also mainly frugivorous and ingested a diet of hard fruits and nuts similar to *C. albigena.* It is also possible that like *Graecopithecus*, *G. alpani* also supplemented its diet with roots and tubers.

9.7 PALAEODIETARY RECONSTRUCTION OF MIOCENE FAUNAS AT PASALAR

Quade *et al.* (1995) have carried out a palaeodietary reconstruction of the Miocene fauna from Pasalar. Stable carbon ($\delta^{13}C$ - the ratio of ^{13}C to ^{12}C (see Quade *et al.* 1995, for the calculation of this ratio)) and oxygen ($\delta^{18}O$ - the ratio of ^{18}O to ^{16}O isotope (see Quade *et al.* 1995, for the calculation of this ratio)) analyses were performed using dental enamel from the fossil mammals to interpret palaeodiet and sources of body water. Carbon isoptopic composition of carbonate in enamel and soil is determined by the carbon isotopic composition of native vegetation. C_3 plants include most trees, shrubs and herbs, and also grasses that prefer cool growing seasons. C_3 plants are predominant in areas where there are mainly winter rains (e.g. the Mediterranean) (Quade *et al.*, 1995, and reference therein). C_4 plants comprise some desert herbs and shrubs, but mainly grasses which favour warm growing seasons, and are common in tropical, subtropical, and temperate regions (excluding forests) where there is monsoon rainfall (Quade *et al.*, 1995). As the $\delta^{13}C$ ratios are dependant on what an animal eats, a low value will indicate a diet which was almost entirely comprised of C_3 plants (Quade *et al.*, 1995). It would also suggest that the animal ingested food from a closed environment because C_4 grasses are not found in these habitats.

Evaporation from leaves results in ^{18}O enrichment of plants, and is at its greatest where the vegetation is most exposed to sunlight (Quade *et al.*, 1995). A high $\delta^{18}O$ may indicate that an animal has been feeding on ^{18}O enriched foliage (Quade *et al.*, 1995). It may also suggest the consumption of C_4 grasses which are richer in ^{18}O than C plants (as C plants are growing in warm conditions and when evaporation will be at its greatest) (Quade *et al.*, 1995).

The $\delta^{13}C$ results indicate that all mammals at Pasalar consumed a diet of predominantly C_3 plants (Quade *et al.*, 1995). There were however, distinct variations in the isotopic patterns among species. *Caprotragoides*, an antelope, had the lowest $\delta^{13}C$ and $\delta^{18}O$ values indicating that it fed in a closed forest setting on C_3 plants which were under low evaporative stress. The giraffid, *Giraffokeryx*, displayed low isotopic $\delta^{13}C$ values indicating that it was feeding on C_3 plants. *Hyposodontus*, a bovid, and *Conohyus*, a suid, had the highest $\delta^{13}C$, indicating that they were feeding on a small amount of C_4 grasses and/or water-stressed C_3 plants, in a more open environment. Quade *et al.* (1995) also found that *Anchitherium*, an equid, *Brachypotherium*, a rhinocerotid, and the proboscidean *Gomphotherium* all had intermediate isotope ratios.

Giraffokeryx displayed a the highest $\delta^{18}O$ values and it is possible it was feeding on leaves from high up in the canopy where there is greater ^{18}O due to increased evaporation (Quade *et al.*, 1995). As modern day giraffes obtain most of their water from foliage rather than from evaporated water sources, the authors suggest that *Giraffokeryx* was also feeding in the same way. *Hyposodontus* also had high $\delta^{18}O$ values, indicating that it was feeding in more open areas. The results for *Conohyus* were mixed, and *Caprotragoides* had low values indicating that it was feeding mainly on vegetation from closed areas.

Listridon, a suid, also displayed low $\delta^{13}C$ and $\delta^{18}O$ values indicating it fed on C_3 plants which were under little evaporative stress in a closed forest environment (Quade *et al.*, 1995). The microwear patterns of two species of *Listridon* (suoids) from Pasalar - *L.* cf. *L. splendens* and *L.* aff. *L. latidens* - have been examined by Hunter and Fortelius (1994). They used a simple method of microwear quantification which produced a measure of the size of the five largest pits using the smallest diameter of each pit. They found that the two species displayed significant differences in microwear which were particularly pronounced in moderately worn (wear stage 2) specimens when all facets were combined - *L.* aff. *L. latidens* had larger pits than *L.* cf. *L. splendens*. The authors suggest that *L.* cf. *L. splendens* had a folivorous diet which (also supported by its bilophodont molar morphology) while *L.* aff. *L. latidens* (which also retains a "pestle and mortar" morphology) ingested a wider variety of foods and included harder particles.

Griphopithecus alpani displayed intermediate $\delta^{13}C$ and $\delta^{18}O$ values which suggests that it was a feeding in both open and closed environments (Quade *et al.*, 1995). Quade *et al.* (1995) suggest that the isotope patterns of the Pasalar species reflect dietary differences in a mainly forested environment. Andrews (1990) conducted an analysis of mammalian species represented at Pasalar and compared them with modern-day species and habitats. He suggested that the palaeoenvironment at this site was most similar to sub-tropical semi-deciduous monsoon forest in a seasonal climate with a marked dry season, and that forest was probably interspersed with rich ground vegetation and grass meadows.

For comparison with the microwear analysis of the two sympatric species of *Listridon* conducted by Hunter and Fortelius (1994), the mean widths of the five largest pits were calculated for *Griphopithecus alpani* and were compared with the pit dimensions minimum diameter for *Listridon* species. (It should be noted that these authors do not state how pits were defined, and that they used minimum pit diameter while pit width was used in the present study). While Hunter and Fortelius found that none of the five largest pits had diameters which were less than 20 µm, the mean dimensions recorded for *G. alpani* specimens on facet 9 was 18 µm. If the dimensions of pits do reflect food particle hardness then this results would indicate that the *Listridon* species were ingesting a harder diet, which possibly comprised larger objects, than that of the hominoids. That Hunter and Fortelius found significant differences between the two species of *Listridon* is of interest in terms of the Pasalar hominoids. Two sympatric species of hominoid have been provisionally recognised at this site - *Griphopithecus alpani*, which comprises about 90% of the sample, and *Griphopithecus sp.* which makes up approximately 10% of the hominoid sample based on differing incisor morphologies. The lower M2s do show a bimodal distribution (Alpagut *et al.*, 1990) but as the morphologies of these molars do not show any variation it is not to possible to distinguish between the two hominoid species on the basis of this tooth. However, it could be that some of the molars that have been examined in the present study belong to the second species of hominoid - *Griphopithecus sp.* It is also possible that, as with the two *Listridon* species, the two hominoid species were exploiting different diets. However, the range of variation seen in the Pasalar hominoid microwear does not exceed that of any of the extant taxa examined in this study, and in contrast to *L.* aff. *L. latidens* and *L.* cf. *L. splendens*, the hominoid molars all have the same morphology which would indicate a similar dietary adaptation. It is therefore, likely that if two species of hominoid were present at Pasalar, they were ingesting the same diet.

CHAPTER 10: CONCLUSIONS

The aim of this study was to examine the dental microwear patterns of *Griphopithecus alpani*, a Miocene hominoid from the site of Pasalar, Turkey, with a view to making inferences about the dietary preferences of this extinct species. The microwear patterns of *G. alpani* were examined in relation to a comparative sample of three species of extant hominoid - *Gorilla gorilla gorilla*, *Pongo pygmaeus pygmaeus*, and *Pan troglodytes verus*. An important part of this study was the development of a rigorous methodology, and an examination of various sources of error which may be introduced and/or which need to be taken into account when analysing dental microwear. The following conclusions are offered.

10.1 TAPHONOMIC AGENTS

The experiments carried out in this study have shown that several taphonomic agents can damage enamel and modify dental microwear. Citric acid and hydrochloric acid both erode microwear features, the latter causing more extensive removal of microscopic wear marks than the former. Sediment abrasion also modified the dental microwear. Three sizes of sediment were used in the experiments - quartz pebbles, coarse sand, and medium sand. The medium-sized sand, the smallest sediment size used in the experiments, caused the most damage to the enamel and the microwear. Microwear features were obliterated and the abrasion produced characteristic pitting over the surface of the tooth. These pits were small and were extensively distributed, giving the enamel a rough texture. The experiments conducted in this study show that the taphonomic modification of dental microwear is distinctive and does not result in the secondary modification or production of microscopic wear marks that could be confused with wear produced during the lifetime of an animal. Instead, microwear features are obliterated. Thus, if fossil material is examined carefully palaeodietary reconstructions which are based on dental microwear will not be clouded by taphonomic processes.

10.2 TILT

A procedure was developed in this study to correct the sizes of microwear measurements which are foreshortened by tilted occlusal wear facets. A comparison between corrected and uncorrected microwear measurements revealed that in some cases frequencies of the two feature types (striations and pits) may change before and after correction. That is, a pit may become a scratch and *vice versa.* Comparisons of species means indicated that frequencies and percentages of microwear features did not vary before and after correction. There was, however, a significant difference between the dimensions of original and corrected feature dimensions. Therefore, any microwear study which examines molar facets which are inclined relative to the occlusal plane (i.e. the molar tooth is in its occlusal position) should take into account the resulting distortion and correct the foreshortened features.

10.3 INTRA-OBSERVER ERROR

Intra-observer error in measuring accuracy and in recognising the microwear features was estimated in this study. Mean absolute percentage error was calculated for both types of error estimation. Measurement accuracy had an error rate of 8.43 % for feature lengths and 12.05 % for widths. Repeatability in feature recognition had an error of 13.93 % for total number of features, and 16.68 % for percentage pits. It is not possible to assess these results any further as no other microwear study has examined intra-observer error. This rate of error also has implications for inter-observer error.

10.4 STATISTICAL ANALYSIS

This study carried out two types of analysis of variance (ANOVA) - factorial ANOVA and split-unit ANOVA - as it was not reasonable to assume independence of data in the former. A comparison between the two tests revealed some differences between the two analyses. In general, the factorial ANOVA found more significant differences between pairs of species than the split-unit ANOVA. It is suggested that the results of the split-unit analysis are more valid than the factorial analysis, and the former type of analysis is preferred.

10.5 SPECIES AND FACET DIFFERENCES IN DENTAL MICROWEAR

The results of this study indicate that species differences in dental microwear are not influenced by the particular facet under examination.

Variation in dental microwear according to facet

Consistent variations in microwear patterns were found between the different facets examined in this study. The two Phase II facets - facet 9 and x - have significantly greater frequencies of microwear features, greater numbers and percentages of pits, and narrower striations than facet 1, a Phase I surface. Only one significant difference between facets 9 and x was revealed in this study - facet x displays more striations than facet 9

Variation in dental microwear according to species

Several microwear variables differed significantly according to species. *Griphopithecus alpani* has greater numbers of microwear features and higher percentages of pits than *Gorilla*, and narrower striations than both *Gorilla* and *Pan. G. alpani* displays significantly more pits than *Gorilla* and *Pan. G. alpani* also has significantly more pits than *Pan.* No significant differences are indicated between *G. alpani* and *Pongo*. There are also very few differences in the microwear patterns of the extant hominoids - most differences are between *Pongo* and *Gorilla*, and there are no differences between *Pan* and *Gorilla.*

10.6 SEX AND WEAR STAGE DIFFERENCES IN DENTAL MICROWEAR

The effects of sex and wear stage were examined for *Pongo* (sample sizes were too small to use any of the other hominoid species). None of the microwear variables varied significantly according to sex or wear stage. The results also showed two sets of significant interaction effects on pit width and pit length - a first-order interaction between sex and wear stage, and a second-order interaction between facet, sex and wear stage. A biological explanation for these interactions is not apparent at this stage.

10.7 THE DIMENSIONS OF PITS AS INDICATORS OF DIET

There were no differences among any of the species examined in this study in pit widths. The results suggested that pit lengths were dependant on the facet and species under examination, but the validity of this result may be weakened by the fact the fact that the residuals were not normally distributed before outliers were removed from this analysis. No evidence was found for the theory that the sizes of pits reflect different wear processes, and that large pit widths indicate hard object feeding. Examination of the proportions of small and large pits indicated that all taxa have greater ratios of small pits, with *Pan* displaying the least difference between the two pit sizes. While none of the extant taxa are hard object specialists, *Pongo* does ingest these food items on occasion, but while it has a high proportion of pits relative to striations, these tend to be small. Thus, while extant anthropoids may differ in the pit formation process the evidence is uncertain for the extant apes, and Miocene catarrhines including *G. alpani*. Pit dimensions may not be the most useful indicators of dietary preferences.

10.8 THE DIET OF GRIPHOPITHECUS ALPANI

It is suggested that *G. alpani* ingested a diet of which the main component was fruit. The high percentages of pits in *G. alpani* (54.6 % on facet 9) compared with the extant hominoids (which ranged between 33.2 % and 42.9 %) study suggest that it may have exploited a certain amount of hard fruits and/or objects as part of its feeding regime because among the living anthropoids *G. alpani* exhibits similar percentages of pits to *Cercocebus albigena* (55.2 %) which ingests hard nuts and seeds (Teaford, 1988b). With regard to other Miocene hominoids the ratio of pits relative to striations displayed by *G. alpani* is similar to *Graecopithecus freybergi* (57.7 %) which has been described as hard object feeder (Ungar, 1996). No differences in microwear were found in the hominoid sample from Pasalar that might indicate the presence of more than one species of *Griphopithecus*.

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APPENDIX 1

Specimens used in this study: information includes localities and dates of collection, sex, wear stage, molar teeth, and facet tilt angles in two dimensions (x and y).

Specimen	Species	Locality & date of collection	Tooth	Sex	Wear stage
B510	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
B513	*G. alpani*	Pasalar, Turkey	Lower Left M2	3	2
B523	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	3
C206	*G. alpani*	Pasalar, Turkey	Lower Left M2	3	1
C207	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
D1132	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
D883	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
E626	*G. alpani*	Pasalar, Turkey	Lower Left M2	3	1
E629	*G. alpani*	Pasalar, Turkey	Lower Left M2	1	3
F107	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
G1303	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
H103	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
H272	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
K1316	*G. alpani*	Pasalar, Turkey	Lower Left M2	2	1
K1367	*G. alpani*	Pasalar, Turkey	Lower Left M2	3	3
K1394	*G. alpani*	Pasalar, Turkey	Lower Left M2	3	1
K1399	*G. alpani*	Pasalar, Turkey	Lower Left M2	3	2
K1447	*G. alpani*	Pasalar, Turkey	Lower Left M2	3	1
ZD.1857.11.2.3	*Gorilla*	Gabon	Lower Left M2	2	3
ZD.1861.7.29.4	*Gorilla*	01,34'S 09,45'E) Gabon	Lower Left M2	1	2
ZD.1939.903	*Gorilla*	Equatorial Guinea, 1926	Upper Right M2	[2?]	1
ZD.1939.904	*Gorilla*	Equatorial Guinea, 1926	Upper Right M2	[1?]	3

APPENDIX 1
(continued)

Specimen	**Species**	**Locality & date of collection**	**Tooth**	**Sex**	**Wear stage**
ZD.1939.905	*Gorilla*	Equatorial Guinea, 1926	Upper Right M2	[1?]	3
ZD.1939.919	*Gorilla*	(c.02,32'S 09,45'E) Gabon	Lower Left M2	[2]	3
ZD.1939.920	*Gorilla*	(c.02,32'S 09,45'E) Gabon	Lower Left M2	2	1
ZD.1939.921	*Gorilla*	(c.02,32'S 09,45'E) Gabon	Lower Left M2	2	3
ZD.1939.922	*Gorilla*	(c.02,32'S 09,45'E) Gabon	Lower Left M2	1	3
ZD.1939.927	*Gorilla*	(0,49'S 09,57'E) Gabon, 15 August 1907	Lower Left M2	1	3
ZD.1939.928	*Gorilla*	Gabon	Lower Left M2	[2]	3
ZD.1939.929	*Gorilla*	Gabon	Lower Left M2	2	4
ZD.1939.932	*Gorilla*	Gabon	Lower Left M2	[2]	3
ZD.1939.934	*Gorilla*	Gabon	Lower Left M2	1	3
ZD.1939.935	*Gorilla*	Gabon	Lower Left M2	[1]	3
ZD.1939.938	*Gorilla*	(0,37'S 10,18'E) Gabon	Lower Left M2	[2]	3
ZD.1948.3.31.2	*Gorilla*	(01,50'N 11,30'E) Equatorial Guinea	Lower Left M2	1	3
ZD.1887.12.2.1	*Pan*	(06,45'N 11,16'W) Liberia, 4 January 1887	Lower Left M2	2 [1?]	3
ZD.1917.12.16.1	*Pan*	(07,59'N 10,50'W) Sierra Leone	Lower Left M2	2	3
ZD.1950.1863	*Pan*	(c.07,50'N 11,10'W) Sierra Leone, May 1948	Lower Left M2	2	2
ZD.1968.7.5.5	*Pan*	(c.07,50'N 11,10'W) Sierra Leone, May 1948	Lower Left M2	1	1
ZD.1968.7.5.7	*Pan*	(07,19'N 11'18'W) Sierra Leone, April 1948	Lower Left M2	[2]	3
ZD1894.7.25.2	*Pan*	(O6,20'N 05,38'E) Nigeria	Upper Right M2	3	3
ZD1976.1797	*Pan*	Ghana, 1969	Lower Left M2	2	3
ZD1976.1798	*Pan*	(06,51'N 02,57'E) Ghana, 1969	Upper Right M2	2	3
ZD1976.1799	*Pan*	(06,51'N 02,57'E) Ghana, 1969	Upper Left M2	2	1

APPENDIX 1
(continued)

Specimen	Species	Locality & date of collection	Tooth	Sex	Wear stage
ZD1976.1802	*Pan*	Ghana, 1969	Lower Right M2	3	1
ZD.1976.1415	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	2
ZD.1976.1416	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	2
ZD.1976.1417	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	2
ZD.1976.1418	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	2
ZD.1976.1419	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	1
ZD.1976.1421	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	3
ZD.1976.1422	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	3
ZD.1976.1423	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	3
ZD.1976.1424	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	3
ZD.1976.1425	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	3
ZD.1976.1426	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	3
ZD.1976.1429	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	1
ZD.1976.1430	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	1
ZD.1976.1431	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	3
ZD.1976.1434	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	2
ZD.1976.1436	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	1
ZD.1976.1439	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	1
ZD.1976.1442	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	1
ZD.1976.1443	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	2	2
ZD.1976.1444	*Pongo*	Sarawak (First Division), Borneo, c. 1949	Lower Left M2	1	1

APPENDIX 1

(continued)

Specimen	Species	Facet 1 Tilt (Y)	Facet 1 Tilt (X)	Facet x Tilt (Y)	Facet x Tilt (X)	Facet 9 Tilt (Y)	Facet 9 Tilt (X)
B510	*G. alpani*	148	164	170	17	161	26
B513	*G. alpani*			176	14	8	27
B523	*G. alpani*	172	161	167	178	9	10
C206	*G. alpani*	5	16				
C207	*G. alpani*			19	-33	14	149
D1132	*G. alpani*	158	155	160	24	5	35
D883	*G. alpani*	141	149	172	34	176	45
E626	*G. alpani*	151	140	163	5	166	21
E629	*G. alpani*	175	175	4	14	180	9
F107	*G. alpani*	149	139	166	2	170	153
G1303	*G. alpani*	149	153	167	33	169	41
H103	*G. alpani*	156	161	171	12	8	16
H272	*G. alpani*			146	32	153	55
K1316	*G. alpani*	159	158	177	16	3	32
K1367	*G. alpani*	143	155	168	162	153	175
K1394	*G. alpani*	163	167	150	31	4	52
K1399	*G. alpani*	154	154	152	0	0	178
K1447	*G. alpani*	121	117	13	167	166	24
ZD.1857.11.2.3	*Gorilla*	3	23	177	146	3	22
ZD.1861.7.29.4	*Gorilla*	131	41	166	164	0	141
ZD.1939.903	*Gorilla*	122	38	15	3	170	149
ZD.1939.904	*Gorilla*	15	30	22	4	167	145

APPENDIX 1

(continued)

Specimen	Species	Facet 1 Tilt (Y)	Facet 1 Tilt (X)	Facet x Tilt (Y)	Facet x Tilt (X)	Facet 9 Tilt (Y)	Facet 9 Tilt (X)
ZD.1939.905	*Gorilla*			4	160	23	27
ZD.1939.919	*Gorilla*						
ZD.1939.920	*Gorilla*	128	167	16	6	179	30
ZD.1939.921	*Gorilla*	132	156			6	33
ZD.1939.922	*Gorilla*					13	15
ZD.1939.927	*Gorilla*	134	155			20	35
ZD.1939.928	*Gorilla*	145	15				
ZD.1939.929	*Gorilla*	111	125	142	173	180	23
ZD.1939.932	*Gorilla*	142	150	4	36		
ZD.1939.934	*Gorilla*	118	146	149	23		
ZD.1939.935	*Gorilla*					168	21
ZD.1939.938	*Gorilla*	157	166	155	23		
ZD.1948.3.31.2	*Gorilla*	146	174	133	20	151	41
ZD.1887.12.2.1	*Pan*	139	148	151	166	11	32
ZD.1917.12.16.1	*Pan*			53	152	20	52
ZD.1950.1863	*Pan*	154	34	147	40	15	163
ZD.1968.7.5.5	*Pan*	135	133	160	166	165	6
ZD.1968.7.5.7	*Pan*			172	58	170	55
ZD1894.7.25.2	*Pan*					1	24
ZD1976.1797	*Pan*	144	127	151	167	152	9
ZD1976.1798	*Pan*			139	9	173	157
ZD1976.1799	*Pan*			3	21	146	170

APPENDIX 1
(continued)

Specimen	Species	Facet 1 Tilt (Y)	Facet 1 Tilt (X)	Facet x Tilt (Y)	Facet x Tilt (X)	Facet 9 Tilt (Y)	Facet 9 Tilt (X)
ZD1976.1802	*Pan*	124	25			173	158
ZD.1976.1415	*Pongo*	170	166	145	4	1	13
ZD.1976.1416	*Pongo*	170	0	2	17	4	17
ZD.1976.1417	*Pongo*	120	133	172	13	4	19
ZD.1976.1418	*Pongo*	159	159	168	8	11	12
ZD.1976.1419	*Pongo*	166	115	169	31	10	21
ZD.1976.1421	*Pongo*	148	162	176	8	180	19
ZD.1976.1422	*Pongo*	171	7	171	7	1	9
ZD.1976.1423	*Pongo*	2	4	160	13	3	14
ZD.1976.1424	*Pongo*	157	159	150	21	8	26
ZD.1976.1425	*Pongo*	160	169	2	0	2	3
ZD.1976.1426	*Pongo*	167	169	174	16	10	17
ZD.1976.1429	*Pongo*	142	140	2	19	4	20
ZD.1976.1430	*Pongo*	165	0	150	1	172	25
ZD.1976.1431	*Pongo*	167	164	158	6	180	13
ZD.1976.1434	*Pongo*	149	153	13	27	6	21
ZD.1976.1436	*Pongo*	163	44	171	19	158	46
ZD.1976.1439	*Pongo*	151	177	7	19	180	39
ZD.1976.1442	*Pongo*	168	17	3	17	1	23
ZD.1976.1443	*Pongo*	158	149	170	19	7	8
ZD.1976.1444	*Pongo*	32	84	174	14	3	13

APPENDIX 2

Mean numbers, percentages, and dimensions of microwear features (before and after the foreshortened measurement were corrected) for each specimen (3 facets per individual) examined in this study.

Specimen	Species	Facet	Total Features	No. Pits (A)	No. Pits (B)	No. Scratches (A)	No. Scratches (B)	% Pits (A)	% Pits (B)	Pit width (A)	Pit width (B)	Pit length (A)	Pit length (B)	Scratch widths (A)	Scratch width (B)	% correction (widths)	% correction (lengths)
B510	*G. alpani*	9	203	107	106	96	97	52.7	52.2	2.21	2.33	4.94	5.19	2.05	2.16	5.58	4.57
B510	*G. alpani*	1	129	20	23	109	106	15.50	17.80	7.19	11.39	13.63	17.27	1.37	2.60	87.14	23.75
B510	*G. alpani*	x	237	113	113	124	124	47.70	47.7	4.83	5.22	9.26	10.02	2.08	2.26	8.32	8.15
B513	*G. alpani*	9	184	135	135	49	49	73.4	73.4	3.64	3.96	6.96	7.71	1.32	1.48	9.01	10.77
B513	*G. alpani*	x	186	129	129	57	57	69.40	69.4	3.16	3.24	6.25	6.45	1.05	1.08	2.85	3.18
B523	*G. alpani*	9	37	23	23	14	14	62.2	62.2	5.52	5.67	8.26	8.51	1.42	1.47	3.11	2.42
B523	*G. alpani*	1	36	1	1	35	35	2.80	2.80	11.21	11.54	24.24	29.35	1.57	1.63	4.07	20.06
B523	*G. alpani*	x	69	46	46	23	23	66.70	66.7	18.65	19.91	27.44	29.37	2.39	2.56	7.17	6.67
C206	*G. alpani*	9	181	40	40	141	141	22.1	22.1	4.67	4.76	9.12	9.35	1.20	1.22	1.59	2.95
C206	*G. alpani*	1	68	12	12	56	56	17.60	17.60	4.74	4.88	9.84	9.96	1.60	1.66	3.53	.88
C207	*G. alpani*	9	132	46	45	86	87	34.8	34.1	4.61	5.22	8.27	9.42	1.80	2.17	17.70	13.03
C207	*G. alpani*	x	176	95	91	81	85	54.00	51.7	4.40	4.98	9.77	11.20	2.13	2.37	11.37	13.96
D1132	*G. alpani*	9	206	158	157	48	49	76.7	76.2	4.68	5.19	8.72	9.73	1.21	1.33	10.30	11.09
D1132	*G. alpani*	1	192	26	23	166	169	13.50	12.00	5.20	6.18	9.37	11.97	1.22	1.29	5.33	24.40
D1132	*G. alpani*	x	244	170	172	74	72	69.70	70.5	2.78	3.04	5.49	5.97	1.83	1.98	9.05	6.48
D883	*G. alpani*	9	183	131	130	52	53	71.6	71.0	2.45	2.68	5.57	6.05	1.85	2.23	11.84	14.02
D883	*G. alpani*	1	78	10	10	68	68	12.80	12.80	2.27	3.01	4.69	6.21	1.36	1.81	33.09	32.05
E626	*G. alpani*	9	108	44	44	64	64	40.7	40.7	2.34	2.43	4.92	5.07	2.00	2.10	4.53	2.75
E626	*G. alpani*	1	38	1	2	37	36	2.60	5.30	3.51	3.21	8.22	7.86	1.90	2.82	46.03	23.94
E626	*G. alpani*	x	89	60	60	29	29	67.40	67.4	2.77	3.21	5.24	5.82	1.63	1.84	16.03	8.86
E629	*G. alpani*	9	73	46	46	27	27	63.0	63.0	3.81	3.86	6.98	7.06	2.10	2.13	1.32	1.18
E629	*G. alpani*	1	46	12	14	34	32	26.10	30.40	3.77	3.70	9.42	9.20	1.79	2.10	4.55	12.84
E629	*G. alpani*	x	73	50	50	23	23	68.50	68.5	4.23	4.24	8.38	8.40	1.48	1.48	.23	.19
F107	*G. alpani*	9	105	61	61	44	44	58.1	58.1	2.92	3.09	6.37	6.58	1.98	2.13	6.99	2.98
F107	*G. alpani*	1	26	6	8	20	18	23.10	30.80	9.95	10.02	14.80	14.22	2.11	2.86	28.22	16.43
G1303	*G. alpani*	9	182	76	80	106	102	41.8	44.0	3.37	3.66	7.05	7.62	2.26	2.42	8.89	4.24
G1303	*G. alpani*	1	93	40	41	53	52	43.00	44.10	3.47	4.11	7.49	7.89	1.84	2.21	19.53	6.47
G1303	*G. alpani*	x	191	96	105	95	86	50.30	55.0	3.99	4.40	8.66	9.37	1.77	1.99	14.75	10.43

APPENDIX 2
(continued)

Specimen	Species	Facet	Total Features	No. Pits (A)	No. Pits (B)	No. Scratches (A)	No. Scratches (B)	% Pits (A)	% Pits (B)	Pit width (A)	Pit width (B)	Pit length (A)	Pit length (B)		Scratch width (B)	% correction (widths)	% correction (lengths)
H103	*G. alpani*	9	109	67	68	42	41	61.5	62.4	4.35	4.54	8.63	8.98	1.60	1.71	5.40	4.98
H103	*G. alpani*	1	129	19	21	110	108	14.70	16.30	3.00	2.95	8.17	8.18	1.62	1.70	4.53	3.57
H103	*G. alpani*	x	220	150	150	70	70	68.20	68.2	3.07	3.30	7.01	7.52	2.26	2.43	7.17	7.17
H272	*G. alpani*	9	159	131	120	28	39	82.4	75.5	3.80	4.75	7.46	9.58	2.13	2.63	21.53	27.89
K1316	*G. alpani*	9	125	64	65	61	60	51.2	52.0	2.28	2.49	5.82	6.32	1.83	2.12	12.61	10.87
K1316	*G. alpani*	1	55	22	23	33	32	40.00	41.80	2.47	2.77	6.00	6.72	2.43	2.91	16.52	12.66
K1316	*G. alpani*	x	110	62	62	48	48	56.40	56.4	3.52	3.81	7.19	7.65	1.65	1.77	8.06	6.87
K1367	*G. alpani*	9	125	57	55	68	70	45.6	44.0	3.05	2.77	7.19	5.86	1.63	1.94	1.00	2.54
K1367	*G. alpani*	1	101	8	8	93	93	7.90	7.90	5.82	7.02	17.01	20.74	1.95	2.35	20.45	22.20
K1367	*G. alpani*	x	64	26	27	38	37	40.60	42.2	3.03	3.10	7.34	7.73	1.79	1.73	.54	.12
K1394	*G. alpani*	9	165	97	94	68	71	58.8	57.0	2.78	3.33	5.86	7.04	1.77	2.21	21.65	19.23
K1394	*G. alpani*	1	130	14	14	116	116	10.80	10.80	2.46	3.39	5.20	6.74	1.33	1.89	41.74	27.09
K1399	*G. alpani*	9	258	97	97	161	161	37.6	37.6	2.48	2.49	5.89	5.90	1.51	1.52	.50	.20
K1399	*G. alpani*	1	191	82	85	109	106	42.90	44.50	2.73	2.97	5.52	6.12	1.68	1.81	9.76	6.27
K1399	*G. alpani*	x	345	186	173	159	172	53.90	50.1	2.67	2.89	5.27	5.82	1.40	1.46	4.27	10.58
K1447	*G. alpani*	9	141	81	81	60	60	57.4	57.4	2.65	2.67	5.01	5.07	1.59	1.61	1.10	1.10
K1447	*G. alpani*	1	50	21	21	29	29	42.00	42.00	4.10	4.54	9.19	10.07	1.94	2.15	10.66	9.63
K1447	*G. alpani*	x	75	38	37	37	38	50.70	49.3	2.13	2.21	5.03	5.08	1.27	1.3	2.49	1.64
ZD.1857.11.2.3	*Gorilla*	9	94	9	10	85	84	9.6	10.6	2.64	2.61	7.11	7.09	2.09	2.20	4.55	2.81
ZD.1857.11.2.3	*Gorilla*	1	55	10	10	45	45	18.20	18.20	12.51	12.59	34.19	34.24	2.41	2.42	.59	.19
ZD.1857.11.2.3	*Gorilla*	x	62	16	16	46	46	25.80	25.8	2.76	2.79	6.03	6.08	2.00	2.03	1.26	.76
ZD.1861.7.29.4	*Gorilla*	9	44	9	7	35	37	20.5	15.9	1.88	1.73	5.03	3.93	2.43	3.00	19.57	18.54
ZD.1861.7.29.4	*Gorilla*	1	26	4	4	22	22	15.40	15.40	1.85	1.94	3.97	4.20	2.91	3.02	4.27	5.85
ZD.1861.7.29.4	*Gorilla*	x	12	1	1	11	11	8.30	8.3	1.97	2.15	2.18	2.23	2.42	2.59	6.90	4.12
ZD.1939.903	*Gorilla*	9	69	21	22	48	47	30.4	31.9	7.12	8.18	18.77	20.84	3.70	4.12	12.41	7.92
ZD.1939.903	*Gorilla*	1	45	4	6	41	39	8.90	13.30	3.97	5.12	8.08	13.45	3.02	4.40	28.64	44.65
ZD.1939.903	*Gorilla*	x	32	9	10	23	22	28.10	31.3	5.03	5.37	11.18	11.55	3.73	4.52	14.42	11.17
ZD.1939.904	*Gorilla*	9	63	15	16	48	47	23.8	25.4	3.53	3.07	10.54	8.27	2.30	2.69	7.21	5.70
ZD.1939.904	*Gorilla*	1	60	12	10	48	50	20.00	16.70	3.65	4.32	9.39	10.93	2.87	2.98	5.70	4.67
ZD.1939.904	*Gorilla*	x	30	3	3	27	27	10.00	10.0	2.54	2.67	7.13	7.50	2.81	2.94	4.79	5.35

APPENDIX 2
(continued)

Specimen	Species	Facet	Total Features	No. Pits (A)	No. Pits (B)	No. Scratches (A)	No. Scratches (B)	% Pits (A)	% Pits (B)	Pit width (A)	Pit width (B)	Pit length (A)	Pit length (B)		Scratch width (B)	% correction (widths)	% correction (lengths)
ZD.1939.905	*Gorilla*	9	63	9	9	54	54	14.3	14.3	9.62	9.53	18.50	17.11	1.83	1.97	3.66	2.20
ZD.1939.905	*Gorilla*	x	95	19	19	76	76	20.00	20.0	3.84	3.94	7.83	7.96	2.33	2.39	2.62	1.68
ZD.1939.919	*Gorilla*	9	60	12	15	48	45	20.0	25.0	2.60	3.04	7.33	8.87	2.37	3.18	7.21	5.70
ZD.1939.919	*Gorilla*	1	44	0	0	44	44	.00	.00					2.92	2.96	1.52	16.79
ZD.1939.919	*Gorilla*	x	50	21	19	29	31	42.00	38.0	3.13	3.33	7.08	7.00	2.97	3.09	4.69	7.86
ZD.1939.920	*Gorilla*	9	112	46	47	66	65	41.1	42.0	5.30	5.54	11.88	12.98	2.12	2.28	7.79	6.58
ZD.1939.920	*Gorilla*	1	109	16	16	93	93	14.70	14.70	1.93	3.54	4.23	7.04	1.66	2.50	58.74	5.85
ZD.1939.920	*Gorilla*	x	136	49	50	87	86	36.00	36.8	6.93	6.99	11.45	11.64	1.95	2.02	3.24	2.20
ZD.1939.921	*Gorilla*	9	133	56	53	77	80	42.1	39.8	5.23	5.83	9.86	12.48	1.93	2.15	11.63	19.86
ZD.1939.921	*Gorilla*	1	46	7	7	39	39	15.20	15.20	3.80	3.80	7.97	7.97	2.07	2.07	.03	.01
ZD.1939.922	*Gorilla*	9	38	8	8	30	30	21.1	21.1	2.81	2.91	6.82	7.42	2.50	2.66	6.20	6.77
ZD.1939.927	*Gorilla*	9	88	51	49	37	39	58.0	55.7	6.30	6.84	12.84	14.38	2.63	2.83	7.35	8.20
ZD.1939.927	*Gorilla*	1	99	4	4	95	95	4.00	4.00	.90	.92	2.34	2.44	1.36	1.39	2.35	4.14
ZD.1939.928	*Gorilla*	1	45	4	3	41	42	8.90	6.70	1.14	1.58	2.99	4.14	1.41	1.81	30.03	52.68
ZD.1939.929	*Gorilla*	9	313	215	215	98	98	68.7	68.7	3.84	3.85	7.38	7.40	1.56	1.56	.24	.29
ZD.1939.929	*Gorilla*	1	103	22	22	81	81	21.40	21.40	3.74	4.18	8.22	9.24	2.02	2.20	9.28	13.92
ZD.1939.929	*Gorilla*	x	91	32	32	59	59	35.20	35.2	2.93	3.19	6.36	6.92	3.41	2.10	8.31	9.35
ZD.1939.932	*Gorilla*	1	104	8	7	96	97	7.70	6.70	2.13	2.21	5.84	5.04	2.30	2.92	25.74	27.32
ZD.1939.932	*Gorilla*	x	65	23	23	42	42	35.40	35.4	15.84	16.69	29.87	33.18	2.03	3.76	9.63	7.02
ZD.1939.934	*Gorilla*	1	22	3	6	19	16	13.60	27.30	2.91	5.86	6.77	16.01	2.87	3.52	48.80	52.27
ZD.1939.934	*Gorilla*	x	34	10	10	24	24	29.40	29.4	1.59	1.77	3.61	3.93	4.28	2.23	10.11	9.65
ZD.1939.935	*Gorilla*	9	133	41	40	92	93	30.8	30.1	4.39	4.72	9.97	10.50	2.23	2.36	5.90	4.19
ZD.1939.938	*Gorilla*	x	114	88	88	26	26	77.20	77.2	2.93	3.11	6.00	6.36	1.95	4.54	6.11	6.13
ZD.1948.3.31.2	*Gorilla*	9	80	43	41	37	39	53.7	51.2	3.33	3.62	8.01	8.82	2.88	3.70	17.43	24.34
ZD.1948.3.31.2	*Gorilla*	1	44	0	5	44	41	.00	10.90	.00	4.09	.00	10.09	2.92	6.06	50.12	12.39
ZD.1948.3.31.2	*Gorilla*	x	61	27	27	34	34	44.30	44.3	4.14	5.29	8.43	10.77	2.96	3.79	27.76	27.82

APPENDIX 2

(continued)

Specimen	Species	Facet	Total Features	No. Pits (A)	No. Pits (B)	No. Scratches (A)	No. Scratches (B)	% Pits (A)	% Pits (B)	Pit width (A)	Pit width (B)	Pit length (A)	Pit length (B)	Scratch width (A)	Scratch width (B)	% correction (widths)	% correction (lengths)
ZD.1887.12.2.1	*Pan*	x	89	23	23	66	66	25.80	25.8	4.63	4.74	12.08	12.55	3.01	3.08	2.31	3.98
ZD.1917.12.16.1	*Pan*	9	36	22	22	14	14	61.10	61.1	6.20	6.35	13.56	14.08	2.75	3.45	2.63	3.75
ZD.1917.12.16.1	*Pan*	x	23	10	10	13	13	43.50	43.5	4.85	4.90	14.37	14.49	5.61	5.66	0.92	0.99
ZD.1950.1863	*Pan*	1	90	10	10	80	80	11.10	11.10	4.33	5.01	11.96	14.12	2.41	2.79	15.53	18.39
ZD.1950.1863	*Pan*	9	38	10	10	28	28	26.30	26.3	6.54	6.74	15.42	15.93	3.02	3.11	3.08	3.33
ZD.1950.1863	*Pan*	x	60	23	24	37	36	38.30	40.0	5.57	6.22	13.36	15.60	2.93	2.99	8.52	9.21
ZD.1968.7.5.5	*Pan*	1	46	5	6	41	40	10.90	13.00	4.22	6.98	13.27	21.39	2.80	5.09	80.55	72.20
ZD.1968.7.5.5	*Pan*	9	35	10	10	25	25	28.60	28.6	7.93	8.83	17.80	18.53	3.03	3.45	12.59	3.67
ZD.1968.7.5.5	*Pan*	x	50	18	16	32	34	36.00	32.0	9.86	12.40	24.97	35.02	2.96	3.37	13.45	37.32
ZD.1968.7.5.7	*Pan*	9	86	52	52	34	34	60.50	60.5	5.53	5.65	10.29	10.57	1.99	2.05	2.52	2.32
ZD.1968.7.5.7	*Pan*	x	185	133	131	52	54	71.90	70.8	4.45	4.62	8.50	8.77	2.52	2.58	2.95	3.63
ZD1894.7.25.2	*Pan*	9	148	53	59	95	89	35.80	39.9	2.35	2.57	5.17	6.06	1.66	1.69	3.04	7.01
ZD1976.1797	*Pan*	1	24	0	0	24	24	0.00	0.00					3.24	3.62	11.65	9.02
ZD1976.1797	*Pan*	9	49	3	3	46	46	6.10	6.1	3.60	3.63	7.08	7.14	2.69	2.71	0.58	0.93
ZD1976.1797	*Pan*	x	49	17	17	32	32	34.70	34.7	7.44	7.55	16.29	17.85	2.06	2.12	2.42	8.57
ZD1976.1798	*Pan*	9	300	156	156	144	144	52.00	52.0	4.43	3.28	9.04	6.13	2.20	2.24	1.55	1.46
ZD1976.1798	*Pan*	x	75	24	24	51	51	32.00	32.0	2.81	2.91	5.51	5.75	1.88	1.93	2.99	1.36
ZD1976.1799	*Pan*	9	253	157	158	96	95	62.10	62.5	3.12	6.13	5.87	6.13	1.43	1.52	6.10	4.48
ZD1976.1799	*Pan*	x	169	121	122	48	47	71.60	72.2	3.64	3.82	7.35	7.69	1.86	1.87	4.66	3.55
ZD1976.1802	*Pan*	1	34	6	4	28	30	17.60	11.80	1.49	1.80	3.80	3.86	2.11	2.55	23.68	33.48
ZD.1976.1415	*Pongo*	1	227	88	91	139	136	38.80	40.10	3.61	1.69	7.09	5.10	1.67	1.43	9.12	6.26
ZD.1976.1415	*Pongo*	9	332	127	132	205	200	38.30	39.8	2.39	2.49	4.97	5.17	1.34	1.45	7.39	4.03
ZD.1976.1415	*Pongo*	x	432	320	315	112	117	74.10	72.9	3.00	3.17	6.04	6.40	1.40	1.47	4.75	6.00
ZD.1976.1416	*Pongo*	1	124	11	11	113	113	8.90	8.90	4.88	5.37	12.77	13.20	1.45	1.63	11.87	1.90
ZD.1976.1416	*Pongo*	9	101	15	15	86	86	14.90	14.9	3.44	3.49	6.81	6.90	1.51	1.54	2.04	0.57
ZD.1976.1416	*Pongo*	x	136	57	57	79	79	41.90	41.9	4.01	4.24	7.63	8.14	1.59	1.66	5.14	7.07
ZD.1976.1417	*Pongo*	1	91	8	7	83	84	8.80	7.70	2.09	6.71	4.34	13.28	1.03	3.75	15.40	37.97
ZD.1976.1417	*Pongo*	9	93	33	28	60	65	35.50	30.1	2.90	3.47	5.95	6.89	1.80	1.84	5.15	12.52
ZD.1976.1417	*Pongo*	x	57	27	27	30	30	47.40	47.4	4.67	4.74	9.88	10.19	1.54	1.55	1.04	3.34
ZD.1976.1418	*Pongo*	1	158	17	19	141	139	10.80	12.00	2.16	3.16	4.81	7.25	1.50	1.32	25.33	11.38
ZD.1976.1418	*Pongo*	9	392	163	164	229	228	41.60	41.8	2.62	2.70	5.96	6.12	1.48	1.53	3.64	2.26
ZD.1976.1418	*Pongo*	x	337	114	115	223	222	33.80	34.1	2.27	2.31	5.31	5.41	1.41	1.45	2.79	1.85

APPENDIX 2
(continued)

Specimen	Species	Facet	Total Features	No. Pits (A)	No. Pits (B)	No. Scratches (A)	No. Scratches (B)	% Pits (A)	% Pits (B)	Pit width (A)	Pit width (B)	Pit length (A)	Pit length (B)	Scratch width (A)	Scratch width (B)	% correction (widths)	% correction (lengths)
ZD.1976.1419	*Pongo*	1	51	2	2	49	49	3.90	3.90	15.07	2.59	35.08	5.82	2.17	1.88	16.15	29.95
ZD.1976.1419	*Pongo*	9	153	30	30	123	123	19.60	19.6	4.83	5.06	11.05	11.48	1.39	1.44	3.66	4.89
ZD.1976.1419	*Pongo*	x	251	133	133	118	118	53.00	53.0	5.18	5.36	9.69	10.12	1.32	1.36	3.33	4.50
ZD.1976.1421	*Pongo*	1	140	22	22	118	118	15.70	15.70	2.07	3.59	5.97	7.25	1.39	1.62	46.79	40.87
ZD.1976.1421	*Pongo*	9	281	110	110	171	171	39.10	39.1	2.44	2.54	5.40	5.65	1.29	1.35	4.19	4.77
ZD.1976.1421	*Pongo*	x	349	145	144	204	205	41.50	41.3	2.27	2.45	4.73	5.08	1.35	1.46	7.46	8.13
ZD.1976.1422	*Pongo*	1	69	7	7	62	62	10.10	10.10	5.03	10.60	12.76	12.96	2.04	2.09	26.40	43.28
ZD.1976.1422	*Pongo*	9	72	30	30	42	42	41.70	41.7	6.33	6.36	15.66	15.73	2.84	2.84	0.30	0.58
ZD.1976.1422	*Pongo*	x	11	5	5	6	6	45.50	45.5	2.52	2.55	5.17	5.49	1.34	1.34	1.21	6.05
ZD.1976.1423	*Pongo*	1	86	3	3	83	83	3.50	3.50	15.98	17.71	24.35	45.34	1.94	2.86	6.34	3.55
ZD.1976.1423	*Pongo*	9	110	35	35	75	75	31.80	31.8	5.00	5.05	11.36	11.51	1.89	1.90	0.77	1.46
ZD.1976.1424	*Pongo*	1	59	6	6	53	53	10.20	10.20	2.29	4.64	3.62	13.24	2.10	2.35	40.68	31.28
ZD.1976.1424	*Pongo*	9	198	82	81	116	117	41.10	41.40	3.25	3.47	7.08	7.50	1.68	1.78	6.28	5.88
ZD.1976.1424	*Pongo*	x	86	25	24	61	62	29.10	27.9	4.76	4.70	11.56	10.95	1.72	1.83	1.06	1.16
ZD.1976.1425	*Pongo*	1	71	11	12	60	59	15.50	16.90	3.36	1.57	5.67	3.18	2.54	1.49	26.36	12.71
ZD.1976.1425	*Pongo*	9	74	17	17	57	57	23.00	23.0	16.00	16.16	25.78	25.96	2.30	2.33	1.19	0.58
ZD.1976.1425	*Pongo*	x	39	11	11	28	28	28.20	28.2	6.42	6.55	14.54	14.94	2.50	2.55	2.04	2.62
ZD.1976.1426	*Pongo*	1	25	10	10	15	15	40.00	40.00	5.49	3.14	11.38	4.86	2.62	2.96	0.71	2.50
ZD.1976.1426	*Pongo*	9	26	17	17	9	9	65.40	65.4	4.34	4.46	8.06	8.44	1.81	1.92	12.01	10.20
ZD.1976.1426	*Pongo*	x	46	26	26	20	20	56.50	56.5	6.13	6.42	13.45	14.07	2.55	2.69	5.29	4.12
ZD.1976.1429	*Pongo*	1	70	3	5	67	65	4.30	7.10	3.24	2.65	8.95	5.25	1.55	1.19	54.47	40.23
ZD.1976.1429	*Pongo*	9	146	60	61	86	85	41.10	41.8	1.95	2.07	4.67	5.00	1.33	1.38	5.33	4.01
ZD.1976.1429	*Pongo*	x	183	66	66	117	117	36.10	36.1	2.26	2.38	5.47	5.73	1.23	1.29	4.98	4.98
ZD.1976.1430	*Pongo*	1	107	13	13	94	94	12.10	12.10	1.40	5.54	2.93	11.65	1.32	2.63	12.35	7.81
ZD.1976.1430	*Pongo*	9	207	135	137	72	70	65.20	66.2	2.91	3.30	5.76	6.63	1.92	2.22	14.78	12.70
ZD.1976.1430	*Pongo*	x	41	28	28	13	13	68.30	68.3	3.55	3.59	6.59	6.66	1.70	1.72	1.10	1.16
ZD.1976.1431	*Pongo*	1	139	81	78	58	61	58.30	56.10	2.17	3.03	4.43	8.41	1.84	2.04	19.83	25.99
ZD.1976.1431	*Pongo*	9	63	29	29	34	34	46.00	46.0	6.53	6.66	10.28	10.46	1.82	1.85	1.94	1.84
ZD.1976.1431	*Pongo*	x	56	33	33	23	23	58.90	58.9	3.82	3.92	7.75	7.95	1.81	1.86	2.67	2.64
ZD.1976.1434	*Pongo*	1	109	19	20	90	89	17.40	18.30	5.45	17.00	12.08	25.20	2.63	2.06	36.58	14.58
ZD.1976.1434	*Pongo*	9	231	48	48	183	183	20.80	20.8	6.32	7.92	14.26	16.91	1.88	2.47	29.51	19.68
ZD.1976.1434	*Pongo*	x	217	81	78	136	139	37.30	35.9	5.03	5.63	10.67	11.66	1.76	1.91	9.71	7.52

APPENDIX 2

(continued)

Specimen	Species	Facet	Total Features	No. Pits (A)	No. Pits (B)	No. Scratches (A)	No. Scratches (B)	% Pits (A)	% Pits (B)	Pit width (A)	Pit width (B)	Pit length (A)	Pit length (B)	Scratch width (A)	Scratch width (B)	% correction (widths)	% correction (lengths)
ZD.1976.1436	*Pongo*	1	21	4	4	17	17	19.00	19.00	1.25	3.04	3.82	5.64	1.05	2.21	35.93	32.76
ZD.1976.1436	*Pongo*	9	305	231	230	74	75	75.70	75.4	2.08	2.32	4.09	4.54	1.28	1.44	12.01	10.20
ZD.1976.1436	*Pongo*	x	196	118	119	78	77	60.20	60.7	1.87	2.09	3.69	4.23	1.24	1.34	10.35	15.01
ZD.1976.1439	*Pongo*	1	80	26	21	54	59	32.50	26.30	2.77	3.81	5.96	6.79	1.36	3.27	14.88	51.06
ZD.1976.1439	*Pongo*	9	185	123	126	62	59	66.50	68.1	3.01	3.44	7.02	8.26	1.77	1.81	12.80	11.97
ZD.1976.1439	*Pongo*	x	266	178	179	88	87	66.90	67.3	3.25	3.42	7.17	7.44	1.89	2.08	6.84	3.77
ZD.1976.1442	*Pongo*	1	211	61	59	150	152	28.90	28.00	3.06	3.81	7.03	7.53	1.27	1.85	1.83	7.64
ZD.1976.1442	*Pongo*	9	239	125	131	114	108	52.30	54.8	4.76	5.10	10.12	10.72	1.78	1.93	5.56	9.67
ZD.1976.1442	*Pongo*	x	286	148	147	138	139	51.70	51.4	3.30	3.49	6.96	7.40	1.80	1.86	4.61	6.20
ZD.1976.1443	*Pongo*	1	91	16	16	75	75	17.60	17.60	2.69	6.68	4.99	17.54	1.96	2.56	0.71	2.50
ZD.1976.1443	*Pongo*	9	95	48	46	47	49	50.50	48.4	3.27	3.55	6.30	6.66	2.30	2.49	7.76	6.54
ZD.1976.1443	*Pongo*	x	52	34	34	18	18	65.40	65.4	3.47	3.58	5.98	6.16	2.19	2.25	2.91	2.97
ZD.1976.1444	*Pongo*	1	46	4	4	42	42	8.70	8.70	6.98	2.43	9.28	5.02	1.78	2.38	15.71	67.82
ZD.1976.1444	*Pongo*	9	132	66	65	66	67	50.00	49.2	5.86	5.97	12.26	12.38	1.68	1.75	1.56	1.95
ZD.1976.1444	*Pongo*	x	78	15	15	63	63	19.20	19.2	4.60	4.83	10.54	11.03	1.85	1.93	4.24	5.35

APPENDIX 3

An example of the different classifications of microwear features depending on whether or not dimensions of features are corrected for distortion in the form of foreshortening. A pit may become a scratch and *vice versa*. Specimen E626 (facet 1) is used in this example. Pits are shown in bold.

Length:width ratio	**Original scratch width**	**Original pit width**	**Original scratch length**	**Original pit length**
100.35	2.08		208.77	
8.93	1.65		14.78	
10.07	1.26		12.67	
10.69	.79		8.44	
4.14	.99		4.11	
22.36	15.40		344.25	
18.72	1.22		22.92	
12.03	1.20		14.49	
23.49	.57		13.33	
11.87	.92		10.97	
53.21	2.41		128.14	
60.91	.82		49.92	
14.19	.91		12.90	
48.42	1.79		86.46	
5.92	1.31		7.76	
10.53	.86		9.02	
53.30	1.26		67.02	
62.91	.73		45.62	
70.41	2.38		167.61	
27.30	6.33		172.87	
133.20	.59		78.07	
6.19	1.57		9.71	
12.97	1.17		15.17	
22.47	.72		16.10	
22.52	1.22		27.56	
14.18	1.29		18.26	
28.96	1.27		36.76	
14.40	1.22		17.63	
22.02	.55		12.14	
79.89	.79		63.06	
20.38	1.99		40.51	
2.34		**3.51**	16.68	**8.22**
21.71	.77			
31.71	2.66		84.38	
18.54	3.41		63.19	
14.45	2.81		40.67	
9.48	1.27		12.03	
8.86	2.12		18.80	
Mean	1.90	3.51	53.32	8.22

APPENDIX 3
(continued)

Length:width Ratio	**Corrected scratch width**	**Corrected pit width**	**Corrected scratch length**	**Corrected pit length**
100.35	2.93		270.98	
8.93	2.43		18.16	
10.07	1.76		16.63	
10.69	1.16		10.36	
4.14		**1.45**		**5.11**
22.36	22.75		419.70	
18.72	1.81		28.02	
12.03	1.75		18.08	
23.49	.83		16.50	
11.87	1.36		13.43	
53.21	3.53		157.78	
60.91	1.18		62.74	
14.19	1.33		15.90	
48.42	2.64		105.41	
5.92	1.91		9.65	
10.53	1.25		11.23	
53.30	1.85		82.09	
62.91	1.07		55.66	
70.41	3.49		206.59	
27.30	9.35		211.02	
133.20	.83		100.23	
6.19	2.30		11.95	
12.97	1.71		18.85	
22.47	1.05		19.87	
22.52	1.81		33.63	
14.18	1.89		22.44	
28.96	1.88		44.82	
14.40	1.80		21.69	
22.02	.79		15.43	
79.89	1.15		78.30	
20.38	2.86		51.12	
2.34		**4.97**		**10.61**
21.71	1.13		20.52	
31.71	3.92		103.31	
18.54	5.02		77.43	
14.45	4.16		49.56	
9.48	1.87		14.65	
8.86	3.10		23.23	
Mean	2.82	3.21	67.69	7.86