Tooth Wear and the "Design" of the Human Dentition: A Perspective From Evolutionary Medicine

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ABSTRACT   Worn, flat occlusal surfaces and anterior edge-to-edge occlusion are ubiquitous among the dentitions of prehistoric humans. The concept of attritional occlusion was proposed in the 1950s as a hypothesis to explain these characteristics. The main aspects of this hypothesis are: 1) the dentitions of ancient populations in heavy-wear environments were continuously and dynamically changing owing to life-long attritional tooth reduction and compensatory tooth migration, 2) all contemporary humans inherit these compensatory mechanisms, and recent reduction in wear severity has resulted in failure to develop attritional occlusion, and 3) this failure leads to an increased frequency of various dental problems in modern societies. Because of the potential significance of this concept, we review and synthesize relevant works and discuss attritional occlusion in the light of current knowledge. Available evidence, on balance, supports the first and second points of the hypothesis. As noted by many workers, the human dentition is basically "designed" on the premise that extensive wear will occur, a conclusion that seems reasonable when one realizes that humans evolved in heavy-wear environments until relatively recently. Some dental problems in contemporary societies appear to reflect the disparity between the original design of our dentition and our present environment, in which extensive wear no longer occurs, but this possibility still needs further investigation. Yrbk Phys Anthropol 46:47–61, 2003.   © 2003 Wiley-Liss, Inc.

The dentitions of prehistoric humans differ strikingly from those of contemporary people in terms of degree of tooth wear. Wear that was sufficiently severe to obliterate cusp morphology and flatten the occlusal surfaces of teeth was ubiquitous and normal in virtually every prehistoric society of the world (for reviews, see Brace, 1977; Molnar, 1972). Interproximal wear was also very severe compared with that observed in contemporary populations (Wolpoff, 1971) (Fig. 1). Relatively recent hunter-gatherer populations such as indigenous Australians and Eskimo experienced considerable tooth wear before being influenced by the Western way of life. A similar condition existed in the ancestors of present-day urban populations who consumed less refined and processed foods. Fossil remains of various extinct hominid species also show remarkable tooth wear,

and Kaifu (2000a) documented this trend in our genus, *Homo*, over more than 2.0 million years. Extensive tooth wear, both occlusal and interproximal, is also a common observation among various mammalian species, including fossil and extant primates. Therefore, tooth wear appears to have been a persistent feature in the lineage leading to humans from early stages of mammalian evolution, although its severity may have been more or less variable during the course of evolutionary history.

From a broad perspective, the severity of wear has reduced somewhat since the development of agriculture, and most dramatically since the industrial revolution. The dentitions of prehistoric hunter-gatherers are characterized generally by heavy wear across the arch. Probably the first indication of a decrease in tooth wear was a drop in wear of the anterior teeth of early agriculturists (Hinton, 1981; Smith, 1983; Kaifu, 1999). The decrease in wear observed over the entire dentition seems to be a phenomenon of modern industrialized societies (e.g. Kaifu, 1999). Some workers related this change to an increased frequency of various dental problems in modern societies. Begg (1954) and Begg and Kesling (1977) systematically and comprehensively discussed this issue, and others also contributed to the discussion (Linghorne, 1938; Klatsky, 1939; Campbell, 1939;
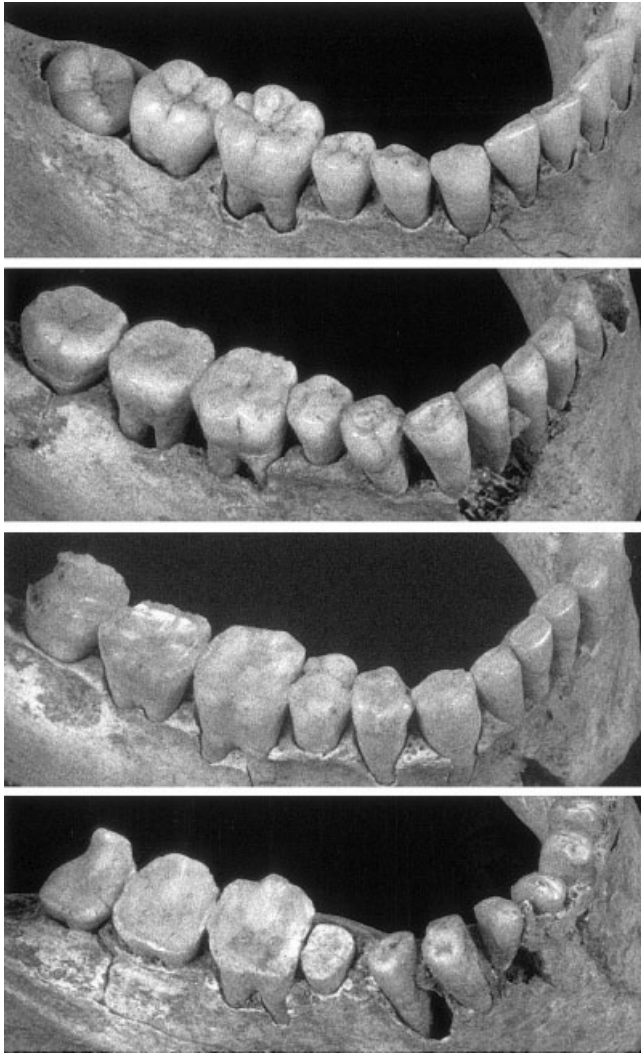
Fig. 1. Progress of tooth wear observed in Holocene prehistoric hunter-gatherers of Japan (Jomon people, ca. 2,300–12,000 years ago). Second specimen from top represents a typical example of occlusal wear selected from a sample of adults with nearly perfect mandibular dentitions (Kaifu, 2000a).

Fig. 2. Two cases of attritional occlusion seen in prehistoric hunter-gatherers in Japan. Top: Moderately worn dentition from archaeological site of Jomon period (western Japan, ca. 6,000–7,000 years ago). Below: Extensively worn dentition from an archaeological site of Okhotsk culture (northernmost Japan, ca. 5–12th centuries AD). Published descriptions and photographs of various human populations in heavy-wear environments indicate that individuals with moderate or extensive tooth wear in such populations show several common occlusal features. Such features include flatly worn occlusal surfaces of teeth, development of a reversed Monson curve in posterior teeth (occlusal plane that inclines downward to buccal), extensive interproximal wear, and anterior edge-to-edge occlusion. More upright positioning of anterior teeth and a nearly flat occlusal plane in lateral view may be added to this list. Same characteristics are also ubiquitous among fossil hominids. Well-preserved fossils of Neandertals and fragmentary fossils of various other fossil human taxa suggest that this type of occlusion has been normal in human lineage.

Sicher, 1953; Barrett, 1958; Murphy, 1964; Dickson, 1970, 1979; Berry and Poole, 1974, 1976; Lombardi, 1982; Dubrul, 1988).

Begg (1954) paid attention to a series of characteristic features seen in the severely worn dentitions of pre-European-contact indigenous Australian skulls, and developed the concept of "attritional occlusion" (Fig. 2). Attritional occlusion, according to Begg (1954), changes continuously due to attritional tooth reduction and compensatory physiological tooth migration that occurs throughout life. The latter functions to maintain contact between adjacent teeth by closing the spaces generated by the former, ensuring that occlusal function is maintained. Importantly, Begg (1954) did not regard this as peculiar to indigenous Australians. He thought that attritional occlusion was the original type of human occlusion, and insisted that a reduction in wear and resultant failure to develop attritional occlusion was
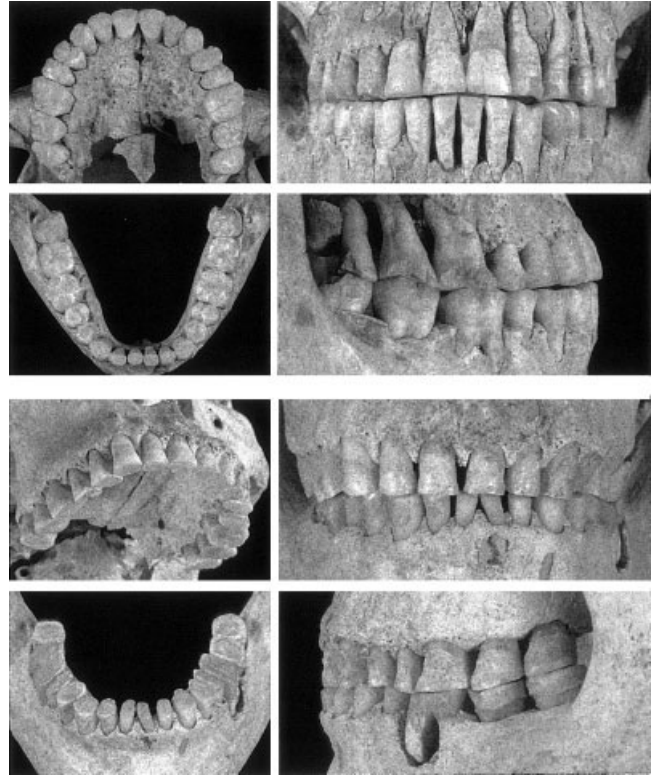
the primary cause of increases in various dental problems in contemporary societies. He regarded attritional occlusion as the "anatomically and functionally correct occlusion" of humans and "nonattritional textbook normal occlusion" as an erroneous concept.

Following the nomenclature of Begg (1954), we use the term "attritional occlusion" to refer to dentitions affected by tooth wear that may have resulted from a variety of processes, including: tooth-to-tooth contact (often referred to as attrition in clinical dentistry); friction of exogenous material forced over tooth surfaces, e.g., during mastication, or the use of teeth as tools (usually referred to as abrasion); and chemical dissolution of tooth surfaces, e.g., from highly acidic diets (usually referred to as erosion). These different types of tooth wear

may occur together or separately, but all result in loss of tooth substance. The main cause of tooth wear in prehistoric populations appears to have been due to some combination of friction of exogenous material forced over tooth surfaces and an increase in the number of power strokes during mastication when less refined, tougher foods are consumed (Saitou, 1987). Our usage of "wear" in this review includes both occlusal and interproximal wear.

The argument by Begg (1954) offers an important insight into understanding the nature of human occlusion. His hypothesis provides us with a key to understanding why the dentitions and occlusion of prehistoric and contemporary people differ, and how we should interpret this fact. Because there is no substantial biological difference between contemporary humans and the latest Pleistocene and early Holocene humans who comprised the Upper Paleolithic, Epipaleolithic (Mesolithic), and Neolithic communities, our knowledge of the human dentition and occlusion can benefit by careful descriptions of the apparent differences between them. Nevertheless, this hypothesis has so far received much less attention than it deserves (Corruccini, 1999, p. 107). This is probably because many points in the argument of Begg (1954) were based on untested observations or inferences. In particular, his argument lacks quantitative documentation of the processes involved in the development of an attritional occlusion. Also, it does not provide evidence of the universality of these processes among populations other than indigenous Australians (Cordato, 1990).

Since the publication of Begg (1954), individual aspects of attritional occlusion were investigated extensively. Some aspects of his argument have gained empirical support, others have been questioned, and several new issues have emerged. Here, we review and synthesize these recent works and discuss attritional occlusion in the light of current knowledge (Begg's theory on orthodontic technique is outside the scope of this review). This paper addresses two aspects of attritional occlusion, namely, the dynamic processes involved in attritional occlusion of the permanent dentition, and the question of whether or not attritional occlusion can be regarded as "correct occlusion" for humans. Some important aspects of the possible impact of a reduction in tooth wear on our oral health are also discussed. Our aim is to highlight the potential significance of the concept of attritional occlusion rather than to provide a comprehensive review of the concept, and we focus on the permanent dentition. The deciduous dentition also changes with wear, and the facial skeleton adapts to some extent (Richards, 1985), but little information about these topics has been published to date.

PROCESS OF ATTRITIONAL OCCLUSION

Demonstration of the actual processes involved in observed wear-related changes in the dentition is central to an understanding of attritional occlusion. Evidence concerning processes of change in the permanent dentition and their universality among human populations are reviewed here. Universality of a process is supported when the following situations are confirmed: 1) the process is observed ubiquitously in ancient populations with heavy wear, and 2) recent populations in which wear severity is variously reduced show the same change process within the limits that their degree of wear permits.

Some of the change processes discussed below are direct consequences of tooth wear, but others are not. In the latter cases (mesial drift, continuous eruption, incisor lingual tipping, and forward shift of the mandibular teeth; see below), tooth wear is not the direct driving force, but it provides space for each process to occur. For these processes, there is an additional criterion to confirm universality: 3) the driving force of the process should be genetically based, or regulated primarily by some intrinsic mechanism(s). Although the mechanisms described here may be shared mammalian traits that evolved early during mammalian evolution, our focus in this review is the human dentition.

Mesial drift

The term "mesial drift" refers to the bodily mesial migration of individual teeth within the alveolar bone, and not to displacement of the whole dentition as a part of skeletal growth processes. As a result of this process, interproximal spaces generally do not occur, even in individuals with advanced interproximal wear.

Extensive interproximal wear and reduction in dental arch length are observed in the dentitions of a wide variety of fossil and living hominids and pongids (Wolpoff, 1971), but interproximal spaces are rarely recognized among them (Fig. 2). This observation is usually accepted as evidence of mesial drift. In several cross-sectional studies of ancient skull materials, mesial drift of the molars with wear was measured relative to various reference structures of the skull (Fig. 3). Such observations have been made on the skulls of Native Americans from New York State (10–19th centuries) (Fishman, 1976), Indian Knoll in Kentucky (ca. 5,000–4,000 years ago) (Hylander, 1977), and Japanese prehistoric hunter-gatherers (ca. 5,000–2,500 years ago) (Nara et al., 1998). Although Lysell (1958a) reported that the tendency in medieval Swedish skulls was not statistically significant, a close examination reveals that his results do not provide clear evidence of the absence of mesial drift in the molars ($P = 0.05$, one-tailed t-test, d.f. = 28). Contrary to the commonly held assumption that mesial drift is solely responsible for closing interproximal spaces, recent studies suggest that the anterior teeth tip lingually with wear, and this process plays an important role in closing spaces in the anterior arches (see "Incisor lingual tipping," below). In two studies of ancient populations with severe wear, arch breadths be-
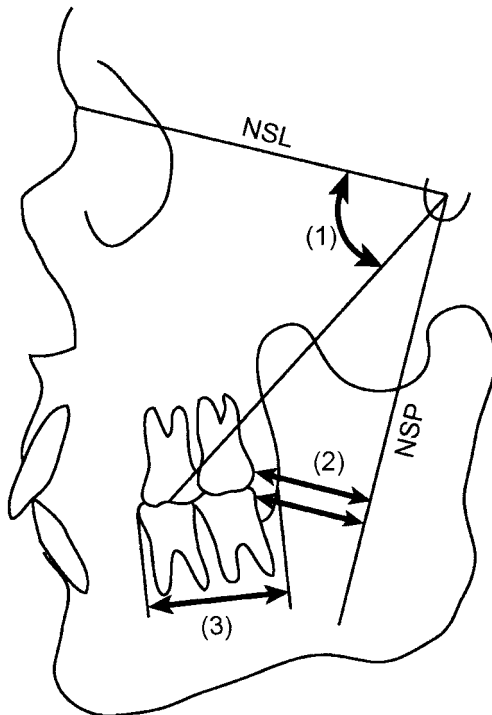
Fig. 3. Selected variables used in documentation of mesial drift of first and second molars. Reference lines: NSL, nasion-sella line; NSP, line passing through sella and perpendicular to the NSL. Variables are as follows: 1, Fishman (1976); 2, Hylander (1977); 3, Nara et al. (1998). In these studies, variable 1 was smaller, and variables 2 and 3 were larger in subgroups with advanced wear than in those with lighter wear. Although possible mandibular lengthening due to continuing bone growth at the condyle (Murphy, 1958; Hylander, 1977) may explain these results partly, the magnitude of detected changes and other evidence (see text and Hylander, 1977) indicate mesial drift of molars.

Fig. 4. Selected measurement landmarks used in documentation of continuous eruption in mandibular teeth, and schematic comparisons of their positional relationships between subgroups with little (**A**) and heavy (**B**) wear. OS, occlusal surface; CEJ, cementoenamel junction; AC, alveolar crest; AP, root apex; IAC, inferior alveolar canal; MB, mandibular base. See text for details.

tween the canines or lateral incisors did not show a statistically significant decrease with wear (Hylander, 1977; Kaifu, 2000b).

A large number of papers have described mesial drift in various contemporary human populations, and there is general agreement that it occurs both in developing and established dentitions (Yilmaz et al., 1980). Histological sections of human alveolar bone show that there are signs of bone resorption on the mesial alveolar wall and bone apposition on the distal alveolar wall (Weinmann, 1941; Bhaskar, 1986; Saffar et al., 1997). Other than an observed reduction in arch length (Lammie and Posselt, 1965), mesial drift in the posterior teeth of contemporary humans was detected by a longitudinal cephalometric study (Watanabe et al., 1999), as well as by metric studies using ankylosed deciduous molars as fixed reference points (Yilmaz et al., 1980). There are few data, however, indicating which teeth move, and to what extent (Ash, 1993).

The driving forces of mesial drift are controversial, but there is good experimental evidence that traction of the transeptal fiber system linking adjacent teeth plays a primary role in this process (Moss,
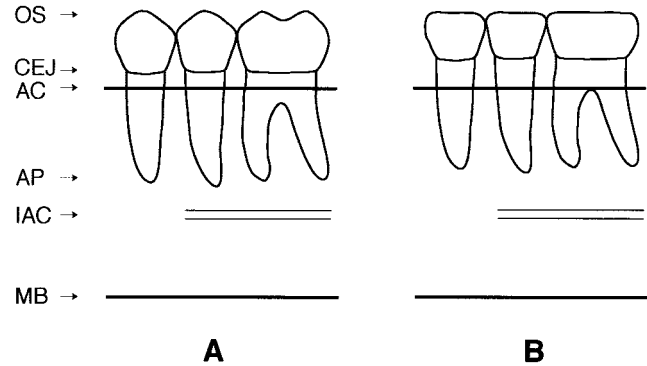
1976; Moss and Picton, 1982; Schroeder, 1986; Robinson and Schneider, 1992; but see Roux et al., 1990). In adult monkeys, "approximal drift" of postcanine teeth was significantly retarded when the interdental soft tissues were surgically traumatized (Picton and Moss, 1973; Moss and Picton, 1974), whereas it was substantially less affected when the forces from occlusion, cheeks, and tongue were controlled (Moss and Picton, 1970; Picton and Moss, 1980). Furthermore, in intact human mandibular arches, the intrinsic approximating force of the second premolar and first molar was measured (Southard et al., 1992). The term "approximal drift" is used here because, in the theory of Moss and Picton (1974), traction of the transeptal fibers causes approximation of adjacent teeth; thus teeth migrate as a group toward a common center, which is the midpoint of the arch in a healthy human dentition.

Continuous eruption

The concept of continuous eruption, or active eruption of teeth throughout life, was first proposed in the 1920s (Gottlieb, 1927), and it has gained wide acceptance. Several metric studies conducted during the last four decades established its occurrence in past populations who experienced heavy wear (Figs. 4, 5). Increase of cementoenamel junction-alveolar crest (CEJ-AC) distance with wear or estimated age was documented directly or indirectly in various teeth of indigenous Australians (Murphy, 1959; Danenberg et al., 1991), Romano-British (Whittaker et al., 1982), and preindustrial Irish populations (Glass, 1991). The same observation was often regarded as being caused by periodontal disease or physiological atrophy of the crestal bone (see reviews in Clarke and Hirsch, 1991; Newman, 1999), but it now appears that this sort of generalized horizontal bone loss does not occur commonly. In various populations, the alveolar bone heights show no significant change (or a slight increase if any
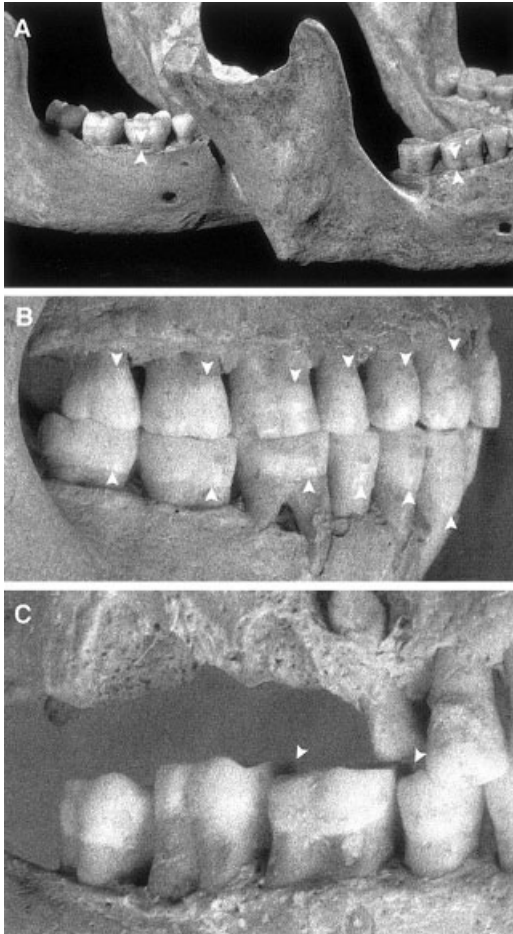
Fig. 5. Evidence of continuous tooth eruption. **A:** Mandibles of young adult (left) and middle-aged (right) individual show differences in degree of root denudation (indicated by arrowheads) (prehistoric Jomon period, Japan). This is reasonably explained by continuous eruption rather than loss of alveolar bone (see text). **B:** Case showing unbalanced continuous eruption in first molars (19th century, Hungary). The arrows indicate cementoenamel junction. Note small crown height in first molars, which show considerably advanced occlusal wear relative to other teeth. If original crown height of this individual was greater in first than in second and third molars, as is usual in humans, only continuous eruption could explain this observation. **C:** Case of overeruption of teeth (19th century, Hungary). Maxillary alveolar bone indicates that second maxillary molar was lost during life, followed by first and third molars. Second maxillary premolar had lost most of its crown for some reason. Note that mandibular molars have overerupted into open space, and mesial interproximal facets of first and second molars (arrows) are now visible above original occlusal surface level.

culties in interpretation of root exposure mentioned above. Continuous eruption of mandibular premolars and molars with wear or age was detected in cephalometric studies of inferior alveolar canal-root apex (IAC-AP) and IAC-CEJ distances for Romano-British, Anglo-Saxon, and medieval populations from Britain (Newman and Levers, 1979; Levers and Darling, 1983; Whittaker et al., 1985), and for another medieval population (Varrela et al., 1989). In addition, continuous eruption of the maxillary and mandibular second premolars was detected in Indian Knoll skulls from the USA (ca. 5,000–4,000 years ago) through an investigation of infraorbital foramen-CEJ and mental foramen-CEJ distances (Hylander, 1977).

Continuous eruption was also documented metrically and histologically in recent populations with limited or virtual absence of wear (Ainamo et al., 1981; Behrents, 1985; Wittaker et al., 1990; Steedle and Proffit, 1985; Marks and Schroeder, 1996). This lends support to the existence of an intrinsic eruption mechanism intended to compensate for anticipated tooth wear and/or continuing vertical jaw growth. In particular, the general observation of supraeruption of unopposed teeth (Ainamo and Ainamo, 1978, 1984) (Fig. 5) suggests that contemporary humans inherit the potential for large-scale eruption as compensation for anticipated heavy wear.

Incisor lingual tipping

Incisor lingual tipping, or more correctly lingual tipping of the anterior teeth, refers to the physiological uprighting movement of the anterior teeth. Compared to mesial drift and continuous eruption, this concept has been much less widely discussed as a part of attritional occlusion.

The phenomenon of incisor lingual tipping in a heavy-wear environment was recently documented in a study of the permanent dentitions of Japanese prehistoric hunter-gatherers (Jomon people, ca. 7,000–2,300 years ago) (Kaifu, 2000b). In this population, the anterior teeth of both jaws were found to be inclined labially when they erupted, but subsequently they appeared to tip gradually lingually with wear until they became nearly upright (Fig. 6). The anterior teeth assumed a normal overlapping relation (scissors occlusion; see Fig. 7 for definition) in younger individuals, so that the maxillary anterior teeth protruded anteriorly more than their mandibular opponents. This initial difference resulted in a greater amount of inclination change in the maxillary central incisors (about 30°) than in the mandibular central incisors (about 10°). These changes appeared to play a role in closing interproximal spaces that rarely occurred in this population, despite substantial attritional reduction of mesiodistal crown dimensions (Fig. 2).

There is some inconsistency in the results of metric studies of incisors in other ancient populations. Slight but significant lingual tipping of maxillary

change is evident) with wear or age during adulthood (Hylander, 1977; Murphy, 1959; Newman and Levers, 1979; Levers and Darling, 1983; Whittaker et al., 1985; Varrela et al., 1989; Tallgren and Solow, 1991). Clarke and Hirsch (1991) suggested that periodontal disease is identified usually in dried skulls as localized alveolar bone defects or modifications around individual teeth.

Occurrence of continuous eruption in preindustrial populations was also documented through other methods that are free from the possible diffi-
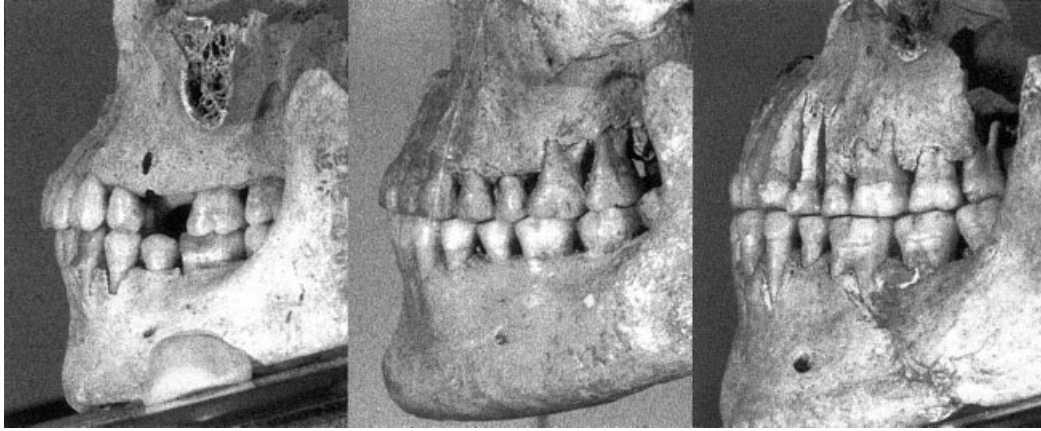
Fig. 6. Wear-related changes in anterior dento-alveolar complex observed in a prehistoric Jomon population of Japan. An adolescent individual with developing dentition (left), an adult individual with moderate wear (middle), and an adult individual with extensive wear (right). Note changes in incisor inclination represented by the angles of the roots, and modification in anterior occlusion, as depicted in Figure 7.
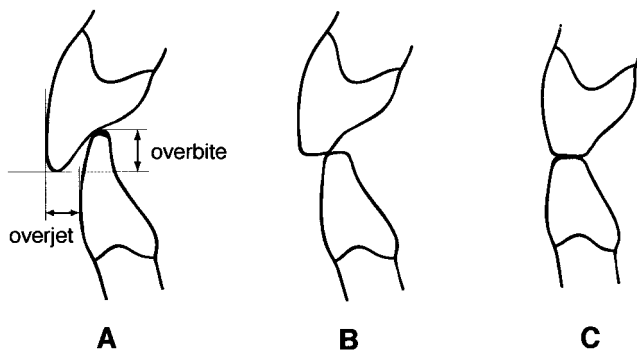

Fig. 7. Three types of occlusal relationship of central incisors, as discussed in text. Vertical and horizontal components of overlap between maxillary and mandibular opposing teeth are called overbite and overjet, respectively. Scissors occlusion (**A**) is the condition where overbite > 0 and overjet > 0 in the anterior dentition. Definition of edge-to-edge occlusion seems inconsistent among workers, but a literal definition is overbite = 0 and overjet = 0 (**C**) (Reinhardt, 1983; Kaifu, 1996). Edge-to-edge occlusion in ancient populations is attained through occlusal modification, with anterior tooth wear and accompanied lingual tipping of anterior teeth. Initial scissors occlusion during the mixed dentition period is modified through an intermediate condition, where overbite = 0 and overjet > 0 (**B**), to edge-to-edge occlusion in adults with advanced wear.

incisors was documented in medieval skulls from Denmark (Lundström and Lysell, 1953), Sweden (Lysell and Fillipson, 1958), and Norway (Hasund, 1965), as well as a prehistoric agricultural and a medieval Japanese populations (Kaifu, 2000b), whereas it was not detected in samples of Native Americans (10–19th centuries AD) (Fishman, 1976) and medieval Swedes (Mohlin et al., 1978). In these studies, mandibular central incisors did not show lingual tipping, or they became slightly procumbent in some cases. On the other hand, significant lingual tipping of both the maxillary and mandibular central incisors was found in a study of Indian Knoll skulls from the USA (ca. 5,000–4,000 years ago) (Hylander, 1977). In this population, the degree of inclination changed with wear, being greater in the maxillary than in the mandibular incisors, as in the Jomon people mentioned above.

These inconsistencies in the behavior of the incisors may well be explained by interpopulation differences in the degree of anterior tooth wear (Kaifu, 2000b). Recent studies of various regional populations strongly suggest the existence of a general tendency for anterior tooth wear to decrease markedly, associated with changes from a hunting-gathering to agricultural subsistence (Hinton, 1981; Smith, 1983; Kaifu, 1999). Unfortunately, the degree of incisor lingual tipping cannot be compared directly among those populations studied by different workers due to methodological differences. It should be noted, however, that the populations who showed significant lingual tipping in both jaws were prehistoric hunter-gatherers (Jomon and Indian Knoll), whereas those that did not were populations of developed agricultural societies. This suggests that significant incisor lingual tipping was not detected in some of the latter populations mainly because the degree of change was small due to limited anterior tooth wear.

Lingual tipping of the central incisors with wear or age was also observed in great apes (e.g., Dean et al., 1992). In addition, it was indirectly demonstrated in some fossil hominids, i.e., *Australopithecus robustus* and Neandertals. The orientation of the worn incisal surface of their maxillary central incisors changed with occlusal wear from an initial inciso-lingual orientation, to become perpendicular to the long axis of the crown (Ungar and Grine, 1991; Ungar et al., 1997).

Slight lingual tipping of the maxillary central incisors with wear or age was detected in a cross-sectional study of modern Japanese skulls (Kaifu, 2000b), as well as in longitudinal studies of contemporary European and American adults (Forsberg, 1979; Behrents, 1985; Bishara et al., 1994). Sarnäs and Solow (1980) found no significant changes in an adult longitudinal study, but it should be noted that

the period of their study was shorter (21–26 years) than the former three studies (10–80 years, 24–34 years, and 26–46 years, respectively). In addition, in studies of Norwegian and Swedish subjects, the central incisors of the group with advanced wear were more upright than those of the group with lighter wear (Krogstad and Dahl, 1985; Johansson et al., 1993). In contrast, the inclination of mandibular central incisors generally appeared to remain stable or become slightly procumbent in the above studies of modern populations.

The driving forces of incisor lingual tipping are poorly understood. Although there is no corroborative evidence, most workers ascribe it to continuous lip tension counteracting continuous pressures from the tongue (Selmer-Olsen, 1937; Lysell, 1958a; Hylander, 1977; Frederick, 1991). Based on this concept, the following explanatory model can be formed: during development of the dentition, the protruding anterior teeth are in contact with their adjacent and/or opposing teeth in a form of scissors occlusion with no interproximal spaces (see "Anterior occlusion," below). This arrangement may enable the anterior dentition to resist lip forces from causing lingual tipping. These lip forces will tend to cause incisor lingual tipping in heavy-wear environments, as mesiodistal crown diameters and overbite (the vertical component of the overlap between maxillary and mandibular opposing teeth; Fig. 7) decrease with wear. In contrast, in a dentition with limited anterior tooth wear, the mandibular anterior teeth which do not receive direct lip pressure may remain in a stable position or even tip slightly labially as a result of tongue pressure and/or the anteriorly directed component of the forces associated with contact between the mandibular anterior teeth and their maxillary opponents. In this model, the force of incisor lingual tipping is extrinsic. Nevertheless, the universality of this process can be postulated because of the commonality in basic anatomical arrangement of the oral tissues in humans.

Anterior occlusion

It is widely recognized that humans have undergone a transition from edge-to-edge occlusion (overbite = 0 and overjet = 0; Fig. 7) to scissors occlusion (overbite > 0 and overjet > 0) during the last thousand years or so (Brace, 1977, 1986). Evidence so far accumulated has established that a reduction in anterior tooth wear forms the primary foundation of this transition. Populations in heavy-wear environments generally show scissors occlusion during the mixed dentition period; but this form of occlusion is subsequently modified to edge-to-edge occlusion in adults with the advance of wear (Figs. 6, 7). This gradual modification was reported in cross-sectional observations of precontact indigenous Australians, pre- and postcontact Native Americans, recent Aleuts, ancient Nubians, historic British, and prehistoric Japanese (Campbell, 1925; Leigh, 1929; Smyth, 1934; Begg, 1954; Moorrees, 1957; D'Amico,

1958; Hylander, 1977; Reinhardt, 1983; Smith, 1983; Schmucker, 1985; Kaifu, 1996, 2000b).

Brace (1977) reported the presence of edge-to-edge occlusions on subadult and adult unworn dentitions among several populations, and insisted that the decrease in tooth-wear severity had made only limited contribution to the temporal transition of occlusal form, if any (Brace, 1977, 1986; Brace and Mahler, 1971). It is possible that factors other than wear significantly affect anterior occlusal variation at an individual level. This appears true especially for individuals in modern industrialized societies (cf. Corruccini, 1987). On balance, however, published information points to the rareness (if any) of edge-to-edge occlusions in unworn dentitions of ancient people. In her observation of 622 Japanese skulls, Seguchi (2000) reported that 3 prehistoric and 7 historic Japanese specimens with minimum wear showed edge-to-edge occlusion. One of us (Y.K.) reexamined all of these specimens and found that these observations were based on inappropriately reconstructed dentitions (incorrect positioning and inappropriate gluing of some teeth) and/or failure to identify the individuals' habitual occlusal position (maximum intercuspation). After careful restoration and reexamination, it was found that these specimens actually display scissors occlusion, except for two historic individuals whose anterior tooth wear was not minimal but moderate (the labiolingual thickness of exposed dentin on the incisal edge of the maxillary incisors was 0.4–0.7 mm; one individual showed class I molar relation, but the other showed class III). In a process of occlusal change from scissors to edge-to-edge occlusions during growth, contrary to the hypothesis of Brace (1977, 1986), anterior tooth wear is indispensable.

The transition from scissors to edge-to-edge occlusion during growth requires changes in two components: overbite and overjet. In attritional occlusion, overbite decreases as a result of occlusal wear on the anterior teeth, and as suggested by the above discussion, overjet reduces primarily as a result of the difference in the amount of incisor lingual tipping between the jaws (see also "Forward shift of the mandibular teeth," below). In the Jomon population of Japan, the time of attainment of zero overjet approximately coincided with the time when the maxillary central incisors had reached a nearly upright state through lingual tipping (Kaifu, 2000b).

As tooth wear decreased over time in Japan, common adult occlusion changed from edge-to-edge occlusion in Jomon hunter-gatherers, through an intermediate condition (overbite = 0 and overjet > 0) in prehistoric agriculturists, to scissors occlusion in medieval and later populations (Kaifu, 2000b). As for the non-Japanese populations cited in the above discussion of incisor lingual tipping, prehistoric hunter-gatherers (Indian Knoll) showed occlusal modification to edge-to-edge occlusion with wear (Hylander, 1977), whereas scissors occlusion or intermediate conditions were more common in more

recent agriculturists or medieval villagers (Fishman, 1976; Lundström and Lysell, 1953; Lysell, 1958b). This pattern of occlusal variation is what might be expected if anterior tooth-wear severity was actually decreased in the latter populations, as inferred from the suggested global pattern of wear reduction (see "Incisor lingual tipping," above).

Forward shift of the mandibular teeth

The relatively anterior position of the mandibular teeth involves two concepts: forward drift of the mandibular teeth compared with the maxillary teeth (Begg, 1954; Begg and Kesling, 1977), and forward positioning of the whole mandibular arch as a result of continuing bone growth at the mandibular condyle (Murphy, 1958; Hylander, 1977). These processes are thought to occur when the interlocking cusp relations between the arches are eliminated by wear. The former infers that there is labial tipping of the mandibular incisors, but there is no objective evidence that such a change actually occurs in populations with severe anterior tooth wear (see "Incisor lingual tipping," above). Both processes are accompanied by a change in anteroposterior molar relations, but this supposed change has been poorly documented and remains a matter of debate. In various studies it was either observed (Begg and Kesling, 1977) or not observed (Campbell, 1925; Fishman, 1976; Kaifu, 2000b). Smith (1983) detected a 1–2 mm increase of the mesial step (the distance between the mesial points of the maxillary and mandibular first molars) in her sample of prehistoric hunter-gatherers. If forward positioning of the mandibular arch actually occurs, this might contribute to some degree to the decrease of overjet in attritional occlusion.

Planes of occlusion

The cusp tips of the posterior teeth usually conform to a smooth curve in the antero-posterior direction that is referred to as the curve of Spee. A transverse occlusal curve also exists normally for each pair of right- and left-side teeth that is concave above and convex below; this is referred to as the Monson curve, or sometimes the curve of Wilson. When an unworn dentition is viewed from the front, with the eye cast along the occlusal surfaces of the teeth on each side, a helicoidal plane may be observed. This results from the increasing axial inclination of molars from the first to third molars (Richards and Brown, 1986; Smith, 1986).

Begg and Kesling (1977) observed in their indigenous Australian sample that the curve of Spee was not as marked as in "textbook normal occlusion." In the sole existing metric study of this phenomenon based on medieval British skulls, there was a weak tendency for the curve of Spee in molar teeth to reduce with increasing wear (Sengupta et al., 1999).

Severely worn dentitions of prehistoric people usually assume a reversed Monson curve, in which the occlusal planes of the first molar region incline downward to the buccal (Tobias, 1980; Osborn, 1982). Smith (1986) and Richards and Brown (1986) showed that, in a wide variety of human populations, this reversal of occlusal surface orientation occurred due to unbalanced wear between the lingual and buccal cusps. As a result of this occlusal surface change, the helicoidal plane increases its expression. However, we should avoid simple generalizations about these occlusal surface changes in populations under heavy-wear environments. Interestingly, the development of a reversed Monson curve tends to be stronger in prehistoric agriculturists than in hunter-gatherers (Smith, 1984). In addition to this subsistence-based variation in wear pattern, intrapopulation variation in dental arch form also affects the transverse orientation of the occlusal surface. Richards and Brown (1986) documented, in a sample of Australian skeletal materials, that this process was accentuated when the differences between maxillary and mandibular arch breadths were greater.

Attritional occlusion: past and present

Available evidence suggests that three kinds of physiological tooth migration, namely, mesial drift of the posterior teeth, continuous eruption of all teeth, and lingual tipping of the anterior teeth, are of primary importance in attritional occlusion. Mesial drift and continuous eruption are well-documented in both ancient and modern populations, though much research remains to be done on the magnitude of tooth movements and the cellular and molecular basis of these changes. So it seems reasonable to posit the universality of these processes among all human populations. As for incisor lingual tipping, data may still be insufficient to conclude universality, but the available evidence is at least suggestive. Incisor lingual tipping is more easily prevented than mesial drift or continuous eruption when wear is minimal, such that scissors occlusion is maintained throughout life. This is probably the reason why little attention has been paid to this process in the dental literature. With the advance of wear, anterior occlusion is modified from scissors occlusion to edge-to-edge occlusion, and the planes of occlusion are altered. Also, anteroposterior molar occlusal relations may change. Obviously, these changes generate many of the characteristics of ancient human dentitions (Fig. 2).

As assumed by Begg (1954), these findings strongly suggest that a single environmental factor, reduction in tooth wear, is preventing contemporary people from accomplishing attritional occlusion. In other words, all of our dentitions would display the above-described characteristics of attritional occlusion if we had been born in prehistoric times!

It should be noted, however, that the concept of attritional occlusion does *not* explain every morphological difference between ancient and contemporary human dentitions, and this conclusion does *not*

mean that all peculiarities of contemporary human dentitions are generated solely by a reduction in wear. The other important differences, which were not dealt with in this review, may be related to changes in masticatory habits and the resultant underdevelopment of jaw bones (e.g., Corruccini, 1999; Inoue et al., 1986; Kaifu, 1997; Kanazawa and Kasai, 1998). Also, the pattern of tooth wear was variable among ancient populations, depending on the subsistence pattern and living environment. As a consequence, the extent of modifications to the dentition caused by wear may differ among populations, especially between hunter-gatherers and agriculturists. Thus, we do not have to consider the dentition of every ancient human to be similar simply because they have developed in a "heavy-wear environment."

IS ATTRITIONAL OCCLUSION "CORRECT" OCCLUSION?

If we accept that two major types of human occlusion exist (attritional occlusion in ancient populations, and nonattritional occlusion in modern populations), then we need to develop a framework within which to understand the differences between them. Begg (1954) and Begg and Kesling (1977) argued that attritional occlusion was the anatomically and functionally correct occlusion, and implied that this was the case for the following reasons: 1) a lower incidence of dental irregularities and diseases was observed in precontact indigenous Australians compared with modern populations in industrialized societies, 2) a dentition with a flatly worn occlusal surface was more efficient in mastication, and 3) the human dentition had acquired a series of compensatory mechanisms in response to progressive tooth reduction by severe wear. Arguments by other workers can be arranged within one or another of these three categories. Next, the three points of Begg (1954) are examined, and the adaptive significance of attritional occlusion is discussed.

Possible influence of reduction in wear

Severe tooth wear was thought to prevent dental caries and periodontal disease to some extent, mainly because it has a cleansing effect on dental plaque and also because it reduces interproximal spaces where plaque may accumulate (Linghorne, 1938; Campbell, 1939; Klatskey, 1939; Begg, 1954; Begg and Kesling, 1977; Berry and Poole, 1974, 1976). Several studies of populations with severe wear showed that common sites of dental caries formation tended to be on the grooves and fissures of less worn crowns (Davies and Pedersen, 1955; Varrela, 1991; Larsen, 1997, p. 67). Similarly, there are reports that accumulation of plaque tends to be more marked in individuals with limited wear than in individuals with relatively heavier wear (Ainamo, 1972; Newman, 1974). However, tooth wear itself does not ensure protection from these diseases. Caries, for example, tends to be prevalent even in populations with severe wear, if the diet is high in carbohydrate content (Larsen, 1997, p. 67). It is still unclear what proportion of dental disease described in ancient populations is prevented by severe wear, tough dietary texture, nutritional constituents, and other factors such as the pattern of mastication (cf. Newman, 1974, 1990).

The etiology of malocclusion is one of the most controversial issues in the hypothesis of Begg (1954). Begg (1954) assumed that a human jaw bone was programmed to grow with the prospect of tooth reduction due to wear, so that its size was originally "designed" to be smaller than the total size of unworn teeth. While the teeth form an orderly arch when wear progresses as expected, he proposed that various malocclusions (such as anterior tooth crowding, tooth rotation, third molar impaction, and bimaxillary protrusion) may occur if the degree of wear is insufficient (Begg, 1954; Begg and Kesling, 1977).

The model of Begg (1954) may not explain the severe crowding occasionally seen in contemporary humans. This is highlighted in a recent study which showed that the incidence of crowding increased only slightly in modern indigenous Australian populations with reduced wear (Corruccini et al., 1990; see also Brace, 1977, and Proffit and Fields, 1993, p. 100). In his examination of the dentitions of a recent indigenous Australian population, Corruccini (1990) could not find support for most of expectations drawn from the model of Begg (1954). He also pointed out other problems of the explanation of Begg (1954), including the overemphasis on the amount of attritional shortening of the dental arches in a heavy-wear environment, and difficulty in postulating enough attritional reduction of the permanent incisors and premolars prior to the canine eruption. These observations are at variance with the model of Begg (1954), which proposes a significant dimensional reduction of the earlier erupting teeth to allow space for later erupting teeth during the formation of the permanent dentition (Fig. 1, top: note that the adolescent dentition displays good alignment of the erupted permanent teeth, even though there is little interproximal wear). Furthermore, from the preceding discussion, some of the important mechanisms postulated in the model of Begg (1954) regarding the process of crowding (existence of a mesially directed intrinsic pushing force in the first molar, and physiological labial tipping of the mandibular anterior teeth, which furnishes more space in the mandibular arch) are actually not present in our dentitions (see "Mesial drift" and "Forward shift of the mandibular teeth," above). It would seem, therefore, that there are a number of limitations in the explanation by Begg (1954) for dental crowding.

Although recent studies indicate that reduction in wear was not the primary cause of severe malocclusion (e.g., Proffit and Fields, 1993; Corruccini, 1999), it is still possible that some more minor aspects of

malocclusion have been affected by this factor. For example, reduction in wear may have enhanced third molar impaction (Odusanya and Abayomi, 1991; Rajasuo et al., 1993; Beeman, 1999). In a severely worn dentition, the dental arch length from the second molar forward reduces considerably due to mesial drift of the teeth, thereby providing space for third molar eruption (Begg, 1954; Begg and Kesling, 1977), although the original estimate by Begg (1954) of the amount of this attritional shortening has been questioned (Kaul and Corruccini, 1992). Furthermore, reduction in wear may have something to do with the development of malocclusion in a different way from the model of Begg (1954). There is evidence that traction of the transeptal fibers is continuously acting to maintain contacts of adjacent teeth (see "Mesial drift," above). In the absence of severe interproximal wear, this force, in conjunction with other forces from the soft tissues and occlusion, may cause slippage of approximal contacts in the anterior teeth, where contact points are smaller and the crowns are more tapered (Moss, 1976; Southard et al., 1992; Richardson, 1994; see also Rhee and Nahm, 2000). This hypothesis explains why dental crowding tends to increase with age in contemporary people, not only during the teenage period but also during adulthood (Bishara et al., 1994). Detailed investigation into the correlation between changing patterns in malocclusion and the reduction in wear over time is necessary to confirm these possibilities.

In summary, reduction in wear may well have contributed to a deterioration in oral health in several ways, but most of the proposed possibilities remain to be tested rigorously. For example, a causative relationship was suggested between the interference of unworn cusps and temporomandibular disorders (TMDs) (Kirveskari, 1978, 1999). However, if occlusal factors are associated with TMDs in modern populations, they are likely to represent variables other than those associated with tooth wear, as discussed above.

Wear and masticatory efficiency

Advocates of attritional occlusion insist that human masticatory efficiency increases when the teeth are worn to flat surfaces (Sicher, 1953; Barrett, 1958; Dickson, 1979; Berry and Poole, 1974; Begg and Kesling, 1977; Brace, 1977; Mills, 1988). The first major basis for this view is the possibility of enhanced mobility of the mandible in mastication, with the elimination of interlocking cusp relations. The second is the fact that, in various mammalian teeth, wear is essential to achieve full efficiency. These advocates argue that there is no reason to regard humans as being exceptional in this respect. Some have insisted further that the only advantage of high cusps in humans is to help guide the teeth into their occlusal relationships during eruption.

There seems to be no serious objection to the existence of a guiding function for cusps. The analogy

of functional morphology of the teeth between humans and other animals, however, should be viewed with caution (D'Amico, 1958; Kirveskari, 1979; Luke and Lucas, 1983). Primatologists showed an association between cuspal features and the type of food preferred in various primate species (e.g., Kay, 1975; Sheine and Kay, 1977; Maier, 1984; Fleagle, 1999), indicating that the cusps of primates have functional significance in mastication. Although wear may work to maintain shear efficiency of molars in some species of leaf-eating monkey (Williamson et al., 2000; Fleagle, 1999), this pattern of wear is different from the flat wear in humans. Also, the fact that teeth were regularly worn down in function does not mean that cusps are harmful or useless (Kirveskari, 1979). Importantly, a close look at the structure and variation of enamel thickness over dental crowns has shown that human teeth are basically formed to be wear-resistant (Luke and Lucas, 1983). From the above discussion, it seems reasonable to conclude that our cusps were originally "designed" to be functional in mastication. Still, presently there is no proof whether worn occlusal surfaces are equally functional, and whether release from the interlocking cusp relation increases masticatory efficiency. Further accumulation of data is necessary to enable clearer conclusions to be drawn about the relationship between masticatory efficiency and attritional occlusion (Mohl et al., 1988).

Compensatory mechanisms for wear

Tooth wear continuously alters the external form of teeth. If the human dentition is adapted for severe wear, it is expected to be equipped with some specific morphological and/or compensatory mechanisms to maintain occlusal functionality at any time during the process of wear. The notion that some aspects of the human dentition and occlusion evolved to compensate for severe wear was mentioned by several workers (Campbell, 1939; Sicher, 1953; Murphy, 1959; Berry and Poole, 1974, 1976; Russell, 1987; Dubrul, 1988; Crothers, 1992). Among them, Begg (1954) and Begg and Kesling (1977) presented the most comprehensive list of possible compensatory mechanisms.

The list by Begg (1954) of possible compensatory mechanisms includes two types of physiological tooth migration, i.e., mesial drift and continuous eruption. The foregoing discussion indicates that lingual tipping of the anterior teeth should be added to this category. The hypothesis that the three types of physiological tooth migration evolved as compensatory mechanisms for wear can be tested by examining the universality of these processes among every human population, and noting to what degree the contact relation of adjacent teeth is maintained in dentitions with severe wear under these processes. The universality of these processes was generally supported in the preceding discussion. The rare occurrence of interproximal spacing and open bite in worn dentitions is a familiar observation for
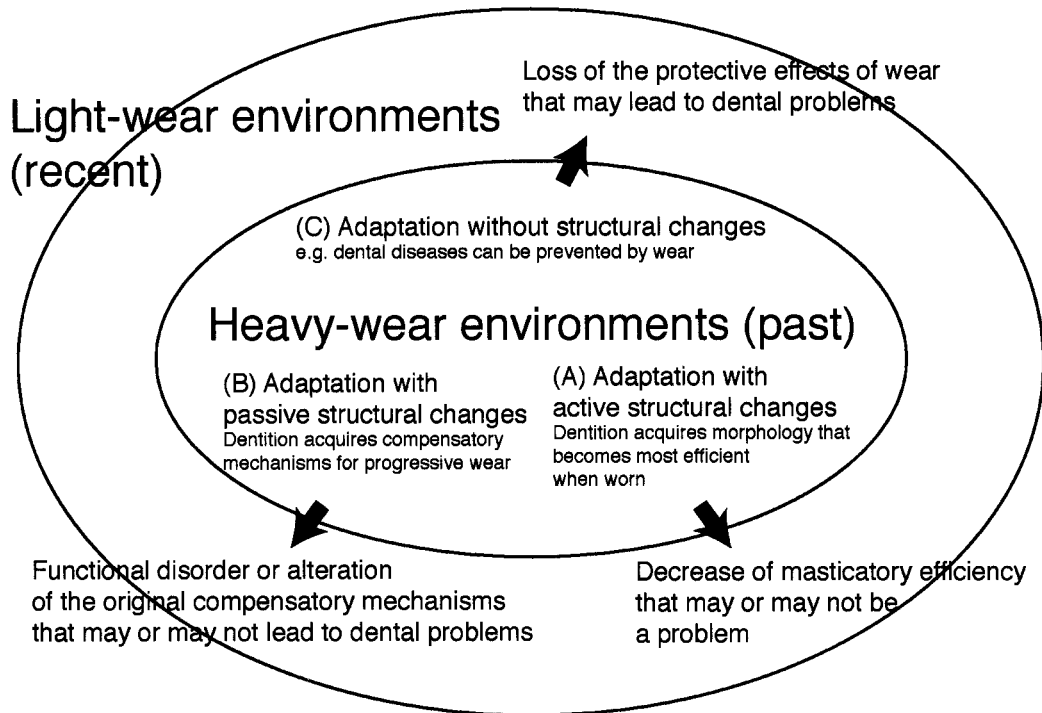
Fig. 8. Theoretically possible responses of human dentition discussed in this paper. Possible adaptive responses to heavy-wear environments in past are in the central circle, and possible consequences of recent reduction in wear are in the periphery. See text for appropriateness of each possibility.

anthropologists studying ancient skeletal remains. This observation is confirmed through numerical data analyses of Japanese dentitions (Kaifu, 2000b, unpublished data).

The second category in the list of Begg (1954) was possible protective responses of the teeth to prevent exposure of the dental pulp by wear (deposition of secondary dentin and pulpal pain). Begg (1954) believed that these mechanisms had not evolved to protect against caries. According to him, caries was uncommon in indigenous Australians, and pulpal pain would have been of no use as a warning for the encroachment of caries, because it would apply only when caries had advanced to a considerable extent.

Begg (1954) further listed several morphological features of the dentition which were, according to him, adaptive for heavy wear. Among them, two may be of significance: the existence of leeway space (i.e., the excess of combined mesiodistal crown diameters of the three buccal deciduous teeth compared to that of their permanent successors) and the crown height variability that ensures that earlier-erupting teeth are higher occluso-gingivally than later-erupting teeth within each tooth class.

There is another observation supporting the concept that the human dentition evolved under the premise of existence of severe wear. Individuals with considerably broader maxillary arches relative to their mandibular arches are observed in indigenous Australians (Barrett, 1953, 1969; Beyron, 1964; Brown et al., 1983, 1987). This variant of occlusion, termed "alternate intercuspation," is con-

sidered to be functional only under heavy-wear environments where interlocking cusp relations are eliminated (Begg and Kesling, 1977; Brown et al., 1987). If this notion is correct, the emergence of alternate intercuspation may be included as an additional response to heavy-wear environments.

An evolutionary adaptation perspective

A perspective of evolutionary adaptation is essential to provide a fundamental understanding of the morphological and functional significance of organisms. Previous workers evaluated attritional occlusion within parts of the above-arranged frameworks, and failed to put the above three issues (health status, masticatory efficiency, and compensatory mechanisms) effectively in the context of evolutionary adaptation. Figure 8 summarizes theoretically possible responses of the human dentition to heavy- and light-wear environments. Probably throughout the course of human evolution, starting from primitive mammals, our ancestors always experienced environmental conditions in which teeth were worn naturally at a considerable rate. Therefore, there is a sound basis to hypothesize that the dentition of our ancestors had accomplished, possibly as a shared basic mammalian feature, evolutionary adaptation to heavy-wear environments in some of the following ways: A) adaptation with active structural changes, B) adaptation with passive structural changes, and C) adaptation without structural changes. The information in the preceding text was arranged in this framework.

The hypothesis that the human dentition evolved morphology that acquired higher masticatory efficiency when worn corresponds to possibility A. In other words, this hypothesis posits selective advantage in a worn dentition over an unworn counterpart. The foregoing discussion shows, however, that presently there is no persuasive evidence to support this notion.

The hypothesis that the human dentition acquired compensatory mechanisms for wear corresponds to possibility B. The above examination suggests that the three types of physiological tooth migration are such mechanisms. Many recent dental textbooks actually suggest that mesial drift and continuous eruption function to compensate for attritional tooth reduction (Scott and Symons, 1974; Bhaskar, 1986; Avery, 1987; Dubrul, 1988; Schroeder, 1986; Foster, 1990; Proffit and Fields, 1993; Ash and Ramfjord, 1995). Continuous eruption may in part compensate for continuing vertical jaw growth, but this factor is limited compared with the loss of vertical crown height in heavy-wear environments. If possibility B is actually the case, the recent reduction of wear severity should have affected the expression of the original compensatory mechanisms, because contemporary humans may well inherit some or all of these mechanisms despite the fact that severe wear no longer exists in modern industrialized societies. This may or may not have led to some dental problems such as the occlusal irregularities discussed above.

These findings suggest strongly that human dentitions, both ancient and modern, are primarily "designed" for heavy-wear environments. Scissors occlusion and interlocking cusp relations in contemporary adults may represent retention of the juvenile condition which is an unexpected situation, bearing in mind the original "design" of our body. It should be noted, however, that attritional occlusion of humans most likely emerged *not* because it was advantageous over an unworn dentition in past heavy-wear environments, but as a product of compromise in such environments.

The reality of possibility C is evaluated through examination of the presence or absence of some dental problems. Dental caries and periodontal disease are nominated as possibilities in the preceding discussion.

CONCLUDING REMARKS

In recent years, a new school called "evolutionary medicine" is reexamining and providing new insights into the etiology of a number of human diseases from an evolutionary perspective (Nesse and Williams, 1998; Sterns, 1999; Trevathan et al., 1999). The above discussion on attritional occlusion suggests that the human dentition and occlusion could be evaluated from the perspective provided by evolutionary medicine. Our synthesis of the available evidence suggests that the human dentition is "designed" on the premise that extensive wear will occur ("adaptation with passive structural changes" in Fig. 8). Because of a radical reduction in the degree of wear during the last thousand years or so, disparity may be generated between the original "design" of our dentition and our present environment. Therefore, the effect of a reduction in tooth wear is worth testing rigorously.

However, we should distinguish the influence of a reduction of tooth wear on oral health from the adaptive significance of attritional occlusion. Admitting that attritional occlusion is a product of evolutionary adaptation, its absence may not necessarily lead to pathological conditions. Previous advocates of attritional occlusion seem to have overemphasized the etiological significance of a reduction in tooth wear (see above), because this distinction was ambiguous. Although reduction of wear may have affected our dentitions in certain ways as discussed above, the recent proliferation of severely maligned dentitions seems to be associated with other factors, including changes in masticatory habits and the resultant underdevelopment of the jaw bones (e.g., Corruccini, 1999; Inoue et al., 1986; Kaifu, 1997; Kanazawa and Kasai, 1998). Accurate knowledge of the processes of change in the dentition associated with the development of an attritional occlusion is necessary to truly understand how a reduction in wear has affected our oral health. Though we now understand some major aspects of these change processes, the available evidence is still insufficient to draw an indisputable picture about them. Thus, our understanding of the influence of tooth wear reduction remains imperfect at present.

Also, in accepting the adaptive significance of attritional occlusion, it should *not* be regarded as a treatment model for contemporary dentistry unless there is verification from the clinical viewpoint. Begg and Kesling (1977) used the concept of attritional occlusion to justify their approach to the orthodontic treatment of patients, and advocated grinding of more tooth substance and the extraction of more teeth than done by others. They further proposed the use of chewing gum containing carborundum dust to simulate prehistoric wear (Begg and Kesling, 1977, p. 47). A similar proposal was also made by Berry and Poole (1974, 1976), and more recently Neiburger (2002) advocated that the recreation of ancient dental wear patterns can help reduce various modern dental problems. The following important perspective, however, is lacking in these proposals: *Attritional occlusion must have been adaptive and functional under heavy-wear environments in the past, but there is no guarantee that a dentition that is artificially modelled to simulate attritional occlusion will work well in modern societies*.

Finally, how should we evaluate the contribution by Begg (1954) to our understanding of the human dentition and occlusion? Although his theory of attritional occlusion suffers from a number of defects

and is far from perfect, his attempt was the first to interpret systematically and comprehensively some (but not all) of the important aspects of the differences between the dentitions of ancient and contemporary people. Among the contributions so far made by a number of workers to this field, Begg (1954) afforded us a very important key to open the door to evolutionary thinking about human dentition and occlusion.

ACKNOWLEDGMENTS

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