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Facial growth and remodeling in the australopithecines – a review

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Abstract

The purpose of this paper is to review the previous investigations of the facial growth and remodeling patterns of early hominids (the australopithecines), and to present some of the problems that arise from these kinds of analysis.

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Introduction

Growth of the face is influenced by a variety of factors which play different roles in different stages of development. It appears that during the late prenatal and early postnatal stages, the dominant factor contributing to facial growth is the growth of the cranial base, including the nasal capsule, and the nasal septum. Later, growth is known to occur by remodeling processes (apposition and resorption), sutural growth, neural and synchondroseal growth, dental development, and the development of the maxillary alveolar process. By age seven, once the anterior cranial base has become stable, the growth of the midface is influenced mainly by the process of downward and forward displacement and periosteal remodeling [CARLSON 1985].

The basic concept of the growth and remodeling of the craniofacial skeleton originated more than 200 years ago with the pioneer works of J. Hunter [HUNTER 1771]. In the 1920s and 1930s Brash revised and developed Hunter's "remodeling" theory claiming that cranial growth was due to ectocranial apposition and endocranial resorption [BRASH 1934]. During the 1940s–1960s three hypotheses were put forward to explain the mechanisms influencing midfacial growth. These were: the sutural hypothesis (see e.g. PRITCHARD *ET AL.* [1956]), the nasal septum hypothesis [SCOTT 1953], and the functional matrix hypothesis [MOSS 1976].

Other major contributions to the study of facial growth were made in the 1960s and 1970s by Enlow and Björk. Enlow's contribution consisted in making major generalizations about the facial growth of both humans and rhesus monkeys. In 1966 the author wrote: *Detailed studies of remodeling patterns in the facial skeleton of extinct members of the genus Homo as well as other related genera*

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and species, both living and fossil, are now needed. It should be determined if the distinctive resorptive nature of the forward part of the maxillary and mandibular arch is a specific characteristic of H. sapiens. [ENLOW 1966a, p. 302]. Following this directive, T. Bromage performed studies to answer the question of how bones of the face grew and remodeled in extinct australopithecine species.

The purpose of this paper is to review the previous investigations of the facial bone growth processes of early hominids, and to present some of the problems that arise from these kinds of analysis.

Facial growth of *Homo* and *Macaca*

According to Enlow [ENLOW 1968; ENLOW & HARRIS 1964; ENLOW & BANG 1965; DUTERLOO & ENLOW 1965], three principles apply to bone growth and remodeling: (1) The concept of "area relocation" (the changing relative positions of all areas within a bone); (2) The principle of the "V" (the enlarging V involves deposition on its inner surface and resorption on its outer surface); and (3) The principle of "cortical drift" (surfaces that face the actual direction of growth are depository, while surfaces that face away from the direction of growth are resorptive; the result is a drift movement of the bone in the direction of the depository surface).

One of the major points made in Enlow's generalization is that the maxilla grows downward and forward by a process of bone deposition on the posterior and superior surfaces. There are two major areas of maxillary growth: the maxillary tuberosity, and the roof of the oral cavity, both of which receive new bone deposits. In contrast, the anterior surface of the maxillary complex is resorptive in character. The mandible, like

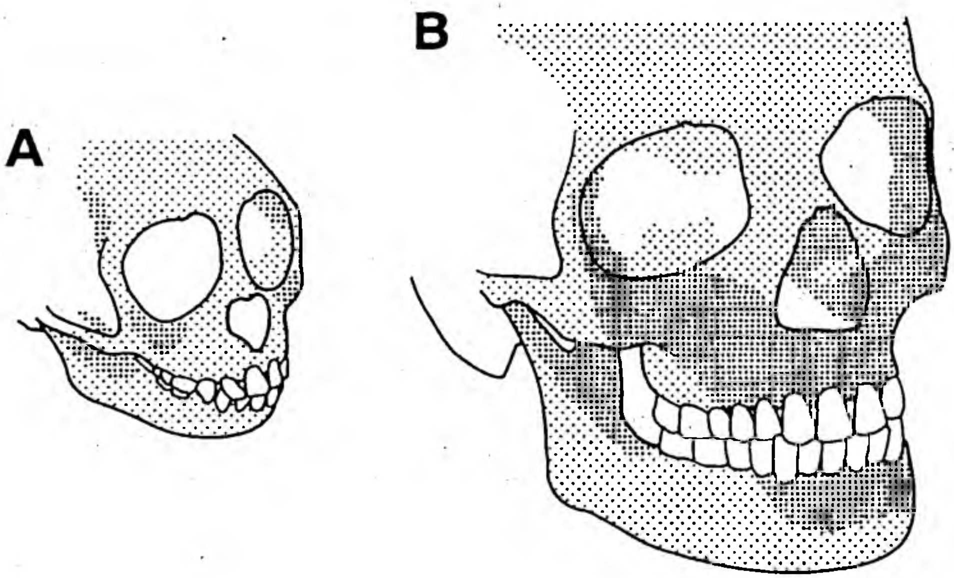

Fig. 1. The distribution of depository (light) and resorptive (dark) surfaces in (A) the rhesus monkey, and (B) human faces. After ENLOW [1966a]

the maxilla, is continuously repositioned in a forward and downward direction as actual new growth proceeds posteriorly; the mandibular condyle represents an important growth site.

ENLOW [1966a, 1970, 1982] compared and contrasted the remodeling changes that occur during the growth of the human and rhesus monkey faces. The detailed distributions of resorptive and depositionary surfaces were determined and mapped in the diagram (Fig. 1). His findings are as follows:

(1) The general plan of facial growth is similar in both species.

(2) The major differences exist in the muzzle area. In the monkey the whole anterior surface of the maxilla is depositionary, while in the human the forward part of the maxillary arch is resorptive. These differences, according to Enlow, provide the basis for the reduced degree of prognathism which is characteristic of the human skull.

(3) The anterior part of the mandible also demonstrates differences. In the rhesus monkey, the entire labial side of the mandible is depositionary, while in the human mandible the alveolar portion located between the mental foramina is resorptive. This could be one of the reasons for chin formation in the human mandible. The opposite (lingual) side of the human mandible is entirely depository, while in the rhesus monkey it is a combination of resorption and deposition. This combined process produces the "simian shelf".

(4) Remodeling differences in the zygomatic area also exist, although the general pattern, i.e., resorption at the anterior surfaces, remains the same for both species.

Facial growth in the australopithecines

Bromage's study [BROMAGE 1985, 1989, 1992] is an "Enlowian" type of study; his interpretations are based on concepts and principles of craniofacial growth and remodeling taken from Enlow's studies of modern humans [ENLOW 1966b, ENLOW & BANG 1965, ENLOW & HARRIS 1964], and from a comparative study of *Homo sapiens* and *Macaca mulatta* [ENLOW 1966a, ENLOW 1982, DUTERLOO & ENLOW 1970].

Bromage used bone surface replicas to study bone formation and resorption with the scanning electron microscope. The periosteal surfaces of immature early hominid specimens were analyzed. The australopithecine specimens were divided into two groups [BROMAGE 1989]: (1) *Australopithecus*, including *A. africanus* and *A. afarensis* (10 specimens), and (2) *Paranthropus*, including *P. robustus* and *P. boisei* (15 specimens). The age range for the first group of the early hominids ("gracile" australopithecines) was from 3.3 to 11.3 years, according to Bromage's estimation based on pongid dental development [BROMAGE 1987, BROMAGE & DEAN 1985], or from 5.0 to 15.6 years based on human-like dental ages at death taken by Bromage from MANN [1975] and SKINNER & SPERBER [1982]. The youngest specimen of this group is one numbered LH 2 (mandible) with complete deciduous dentition and first permanent molars. The oldest specimen, STS 52 (maxilla and mandible), has all its permanent dentition with M3 just erupting. The age range for the second group of early hominids ("robust" australopithecines) is from 1.0 to 11.3 years, based on pongid dental ages

[BROMAGE 1987], or from 2.0 to 15.4 years using the more conventional method of MANN [1975]. The specimen numbered SK 438 (mandibular fragment) with dm2 was the youngest specimen, while SK 52 (maxilla) was the oldest specimen – with complete permanent dentition – considered.

As can be seen in Enlow's work, and also according to Bromage, the bones of the face grow and change shape through a combination of two processes: deposition and resorption. These are said to be the key mechanisms accounting for the different craniofacial forms in each species. *Australopithecus africanus* (the Taung child) was shown by BROMAGE [1985, 1989, 1992] to have an ape-like pattern of facial growth and remodeling, while the facial growth of the "robust" australopithecines (in Bromage's papers *Paranthropus*) resembles that of humans. The different degrees of prognathism between these early hominids can be explained on the basis of different remodeling patterns. Maps of distribution of bone deposits and locations of bone resorption are presented in Fig. 2.

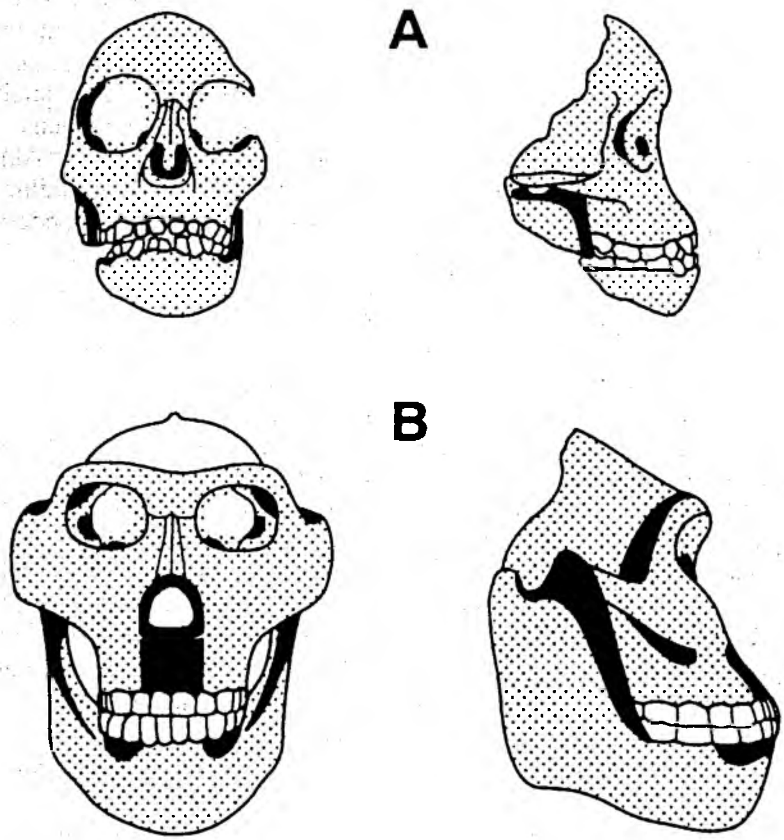

Fig. 2. Frontal and lateral views of (A) *A. africanus*, and (B) *A. robustus* facial remodeling. Light represents areas of deposition, and dark represents areas of resorption. After BROMAGE [1989]

As can be seen from Figure 2, *Australopithecus africanus*' facial growth is characterized by bone deposition on the whole of the anteriorly-facing aspect of the face. The "robust" australopithecines differ from the former by having resorptive areas on the anterior wall of the temporal fossa, the "nasoalveolar clivus", and the anterolateral corners of the mandibular corpus. The two latter features are said to correspond to remodeling patterns that are characteristic of modern humans [BROMAGE 1989]. Downward facial growth in the "robust" australopithecines is opposed to downward and forward facial growth in *A. africanus.*

Remodeling fields have four main attributes, according to BROMAGE [1985]: size, shape, placement, and rate of activity. Bromage suggests that the first three are the same for the Taung baby and the chimpanzee. Differences in the last one, i.e., the rate of activity of remodeling fields, show that the Taung baby is not an ape.

Discussion

As was mentioned before, Enlow's contribution to the study of facial growth and remodeling was making generalizations about these processes. His studies were based on looking at the surface of the bone to establish whether it was resorptive or depository. According to Enlow [e.g. ENLOW & BANG 1965], not much growth occurred in the sutures, and therefore practically all the growth was the result of remodeling (deposition and resorption). After SCOTT [1953] put forward the hypothesis that the maxilla grew in length by apposition of its anterior surface, Enlow [e.g. ENLOW 1966b] was the first to report that the surface of the human maxilla was not depository but resorptive.

Another series of major contributions to our understanding of facial growth and remodeling was made by BJÖRK and SKIELLER [1972, 1976]. Their longitudinal studies of a group of children, using metallic implants as reference points, focused on individuals, and not on averages. Their findings were that while remodeling played a role in craniofacial growth, sutures were important too. The midface increases in height (vertically), depth (anteriorly) and width. An increase in maxillary height takes place by sutural growth and by apposition. Growth in width is not only a result of remodeling processes but occurs by growth of the median suture as well. In addition, growth in length of the maxilla occurs suturally (toward the palatine bone) as well as appositionally in the maxillary tuberosities.

Björk's next finding [BJÖRK & SKIELLER 1976] was that the anterior surface of the maxilla was neither depository nor resorptive, but sagittally stable (from the age of about 4 to 21). Also, the anterior surface (contour) of zygomatic process appears to be stable, in contrast to ENLOW and BANG'S [1965] classical view that the anterior surface of that process is resorptive and the posterior surface is depository. Enlow also postulated that deposition took place on the posterior maxillary surface, Björk argues, however, that this is not the case because sutures are able to grow.

There are other problems with the point of view of Enlow and Bromage. Firstly, these authors establish which portion of a bone is depository and which is resorptive at the point of death of an individual. This does not allow a knowledge of what happened during the lifetime of the individual. Everything, which can be observed, would have happened only recently. The next problem arises from looking at dead bones to determine how much, for how long and how long ago growth occurred. These questions simply cannot be answered from observations of the bones. Yet another problem is that there is age variation in growth patterns. In order to account for this, growth series were studied, but then one general pattern of facial remodeling was presented as if there was no variation, and as if areas of deposition and resorption were immutable for the entire life of an individual. Finally, there is the problem of individual variation. Björk's studies [BJÖRK & SKIELLER 1972, 1976] clearly reveal that not all individuals have the same growth and remodeling patterns.

Bromage has said that the face becomes more prominent during growth if deposition of bone on the front surfaces is combined with resorption of the back. Therefore, according to him [BROMAGE 1992], the Taung face, for example, is typical of a monkey (or ape) because it does not have resorption areas as seen in modern humans. However, as BJÖRK and SKIELLER [1976] noticed, maxillary projection in the face (alveolar prognathism) depends not only on its growth in length, but may also be a result of displacement and rotation of the maxilla. In addition, there is little evidence that surface deposition could account for downward and forward midfacial growth in humans during the first seven years of life [CARLSON 1985]. It has, however, been noticed that in prognathic apes after a certain age, all maxillary growth in length is by surface deposition. In the phylogenetic development of primates, prognathism decreases as a result of shortening of the jaws [BJÖRK 1951].

Among the australopithecines there are differences in the degree of facial prognathism. The *A. africanus* face is prognathic, while the face of the "robust" specimens is considered to be more orthognathic, and therefore more like the *Homo* face. However, as RAK [1983] has pointed out, similar degrees of prognathism in *Homo* and *A. boisei* reflect two different configurations (Fig. 3). In modern *Homo*, it

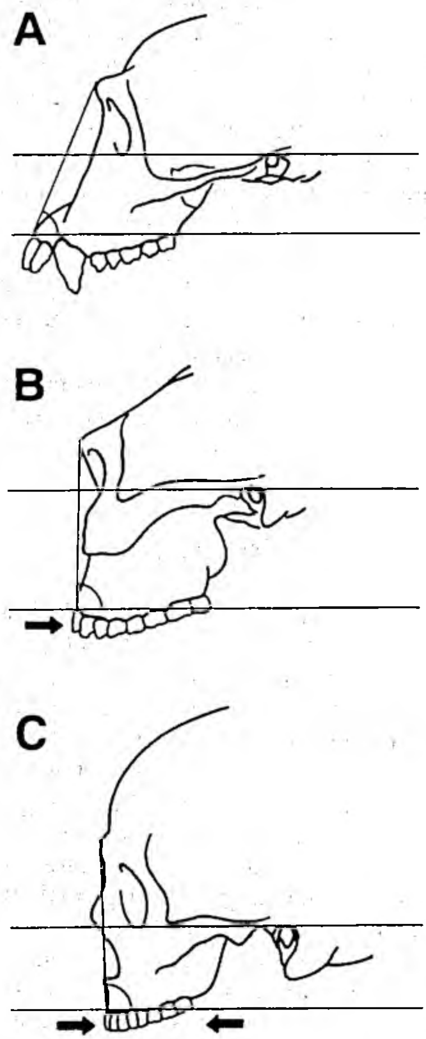

Fig. 3. A comparison between (A) a prognathic chimpanzee, and two orthognathic primates – (B) "robust" australopithecine, and (C) modern *Homo*. After RAK [1983]

is not a result of the retraction of the palate as seen in the "robust" australopithecines, but a result of reduction in the length of the palate. In fact, when the length of the palate is expressed as a percentage of independent measurements, the index value in *A. boisei* does not differ from that of a chimpanzee. In contrast, *A. africanus* has strong facial prognathism – the index of prognathism can be as high as 137% [WOLPOFF 1975]. The upper jaw and therefore the palate, project far anteriorly. The medial part of the midface is located more anteriorly than its lateral (peripheral) portion. Although all the australopithecine faces are prognathic, this feature in the "robust" forms is not as pronounced. The most orthognathic face is that of *A. boisei*, where the index of prognathism can be as low as 113%.

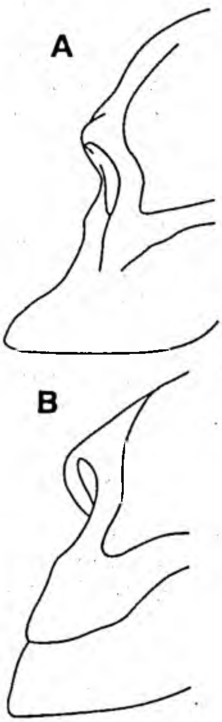

Fig. 4. Lateral view of the face of (A) *A. africanus*, and (B) *A. boisei*. After RAK [1983]

Generally, the medial part of the face and the dental arcade are located more posteriorly in the "robust" specimens, while the lateral part of the face is located more anteriorly. With such a position of the peripheral face, i.e., the zygomatic bones (see Fig. 4), the medial part becomes concave and the nose, in lateral view, is hidden behind it. This configuration is also a reason why the face of the "robust" australopithecines seems to be more orthognathic.

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To sum up, one can say that although Bromage is probably right in what he observes, there are certain problems, as presented in this paper, with that kind of analysis. While bones reflect remodeling processes, the whole of the growth history of bone is not reflected in the tissue itself. Detailed sequences of growth changes, therefore, cannot all be reconstructed.

One additional point can be made here. Even if certain early hominids exhibit remodeling patterns more consistent with macaques, and even if Enlow and Bromage are correct in claiming that this leads to, or is consistent with, greater maxillary prognathism, this means nothing as far as human lineage and adaptation/evolution are concerned. It may simply mean that in order to have prognathism one must have more bone deposition at the labial surface of the maxillary complex. We already know that monkeys and apes tend to be more prognathic than modern humans, so by definition they must exhibit greater bone deposition along the surface of the maxillary complex, if we assume Enlow to be correct. One test of this, which would still not be definitive with respect to questions of lineage, would be to look at remodeling patterns in prognathous vs. ortoganthous primates. Also, it would be interesting to examine the remodeling patterns in different humans with age: prognathous vs. orthognathous.

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Streszczenie

Na wzrastanie szkieletu twarzy wpływa wiele czynników. W fazie okołourodzeniowej głównym czynnikiem jest powiększanie się podstawy czaszki, w tym ścian i przegrody jamy nosowej. Nieco później, rozrost twarzy odbywa się dzięki procesom remodelowania (apozycji i resorpcji), wzrastania śródszwowego i w obrębie chrząstkozrostów, rozwojowi zębów i wyrostka zębodołowego szczęki. Od 7 roku życia na rozrost twarzy zasadniczo oddziałuje już tylko proces dyslokacji ku dołowi i ku przodowi oraz remodelowanie odokostnowe. Podstawowa koncepcja wzrostu i remodelowania szkieletu kraniofacjalnego liczy ponad 200 lat, a rozwój badań nad tą problematyką nastąpił w naszym stuleciu dzięki pracom m.in. Brasha, Pritcharda, Scotta, Mossa, Enlowa i Björka.

Celem przedstawianej pracy jest ocena dotychczasowych badań nad zagadnieniem wzrostu i remodelowania szkieletu twarzy u naszych przodków – australopiteków i zaprezentowanie niektórych problemów, które powstają przy tego rodzaju analizach.

Wkład Enlowa do badań nad wzrastaniem szkieletu twarzy (lata 60. i 70.) polegał na stworzeniu uogólnień dotyczących zarówno człowieka jak i małp. Jak wynika z jego prac, kości twarzy rosną i zmieniają kształt poprzez kombinację dwu procesów: apozycji i resorpcji. Jest to mechanizm warunkujący międzygatunkowe zróżnicowanie kształtu twarzy. ENLOW [1966a, 1970, 1982] porównał i zestawił przemiany wynikające z remodelowania, które pojawiają się podczas wzrostu twarzy człowieka i małpy rezusa. Oznaczył obszary resorpcyjne i apozycyjne (przedstawione na rys. 1). Wnioski Enlowa są następujące. (1) Ogólny plan wzrostu twarzy u obu gatunków jest podobny. (2) Podstawowe różnice dotyczą okolicy pyska (szczęk). U małp cała przednia powierzchnia szczęki jest miejscem apozycji, podczas gdy u człowieka w przedniej części łuku zębodołowego szczęki zachodzi resorpcja. (3) U rezusa cała policzkowa strona żuchwy jest miejscem apozycji, podczas gdy w przedniej części ludzkiej żuchwy, pomiędzy otworami bródkowymi, kość ulega resorpcji. Przeciwna – językowa – strona żuchwy u człowieka całkowicie podlega apozycji, u małp natomiast jest częściowo resorpcyjna, a częściowo apozycyjna, co powoduje utworzenie tzw. „małpiej półki".

W latach 80. T. Bromage, wzorując się na pracach Enlowa, przeprowadził badania nad wzrostem i remodelowaniem kości twarzy u wczesnych hominidów. Bromage użył odcisków powierzchni kości twarzoczaszek do badań formacji i resorpcji kości, korzystając z elektronowego mikroskopu skaningowego. Wydzielił dwie grupy wczesnych hominidów – „masywne" i „gracylne" australopiteki. U *A. africanus* BROMAGE [1985, 1989, 1992] stwierdził małpi typ rozrostu i remodelowania kości twarzy, podczas gdy u „masywnych" australopiteków – ludzki. Z różnych wzorów remodelowania wynika zróżnicowany stopień prognatyzmu u wspomnianych grup hominidów. Mapy rozkładu apozycji i resorpcji na kościach twarzy u australopiteków prezentuje rys. 2.

Prace i uogólnienia Enlowa nie wyjaśniły jednak wszystkiego. BJÖRK i SKIELLER [1972, 1976], w wyniku badań longitudinalnych grupy dzieci, zwrócili uwagę na dodatkowy aspekt wzrostu i remodelowania kości twarzy – znaczenie wzrostu śródszwowego. Stwierdzili także, że przednia powierzchnia szczęki nie jest ani apozycyjna, ani resorpcyjna, ale strzałkowo stabilna (w wieku od 4 do 21 lat). Są też inne problemy wynikające z przyjęcia punktu widzenia Enlowa i Bromage'a. Po pierwsze, autorzy ci posługiwali się kośćmi zmarłych osobników, z których można odczytać procesy zachodzące krótko przed śmiercią. Na podstawie kości nie można ustalić w jakiej fazie życia i jak długo trwały procesy remodelacyjne. Następnym problemem jest fakt, że istnieje ontogenetyczna zmienność wzorca wzrastania twarzy – nie można w związku z tym przedstawiać jednego ogólnego wzorca remodelowania kości twarzy oraz obszarów apozycji i resorpcji. Jest też problem indywidualnej zmienności – prace BJÖRKA i SKIELLERA [1972, 1976] dobitnie dowodzą, że nie wszyscy osobnicy mają ten sam wzór wzrostu i remodelowania.

Australopiteki mają zróżnicowany stopień prognatyzmu twarzowego. Twarz *A. africanus* jest prognatyczna, podczas gdy twarze „masywnych" australopiteków są bardziej ortognatyczne i w związku z tym bardziej przypominają twarze rodzaju *Homo*. Tymczasem, na co wskazuje RAK [1983], podobny stopień prognatyzmu *Homo* i *A. boisei* wynika z dwu różnych konfiguracji (rys. 3) – u współczesnego człowieka jest wynikiem redukcji długości podniebienia, a u „masywnych" australopiteków, rezultatem cofnięcia podniebienia. Również bardziej przednie położenie bocznych części twarzy (kości jarzmowych) u *A. boisei* potęguje wrażenie ortognatyczności (rys. 4).

Chociaż Bromage ma prawdopodobnie rację w tym, co pisze o remodelowaniu, pozostają pewne problemy. Kość odzwierciedla procesy remodelowania, jednak nie cała historia wzrostu kości jest utrwalona w tkance. W związku z tym, nie wszystkie sekwencje zmian wzrastania można szczegółowo zrekonstruować. Poza tym, nawet jeśli niektóre wczesne hominidy mają wzorce remodelowania zgodne z małpami (co zdaniem Enlowa prowadzi do większego prognatyzmu), nie ma to znaczenia dla rekonstrukcji zmian ewolucyjnych w ludzkiej linii.