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G. J. Armelagos

*Department of Anthropology, University of Massachusetts, Amherst, USA*

D. P. Van Gerven

*Department of Anthropology, University of Colorado, Boulder, USA*

A. H. Goodman

*School of Natural Sciences, Hampshire College, USA*

J. M. Calcagno

*Department of Sociology and Anthropology, Loyola University of Chicago, USA*

# Post-Pleistocene Facial Reduction, Biomechanics and Selection Against Morphologically Complex Teeth: A Rejoinder to Macchiarelli and Bondioli

MACCHIARELLI & BONDIOLI (1984, 1986) argue that post-Pleistocene cranio-facial reduction cannot be explained by biomechanical factors related to change in the diet (CARLSON, 1974; CARLSON & VAN GERVEN, 1977) or to facial reduction related to the selective advantages of smaller, morphologically simpler teeth (GREENE, 1967; VAN GERVEN, ARMELAGOS & ROHR, 1977). Instead, they maintain that facial reduction is a mere side-effect of a reduction in overall body size. Our analysis of skeletal and facial reduction in post-Pleistocene Sudanese Nubia suggests that MACCHIARELLI & BONDIOLI's interpretation is incorrect for two reasons. First, the reduction in facial morphology (at least since Mesolithic times) is greater by several orders of magnitude than the reduction in general body size. Second, the dentition not only shows a greater size reduction than does general body size, but a shifting pattern of dental reduction rather than a general decrease across all teeth.

## Introduction

MACCHIARELLI & BONDIOLI (1984, 1986) argue that the decrease in dental and facial size observed in post-Pleistocene populations is a result of an overall decrease in body size and not the result of natural selection favoring either smaller teeth or mechanically modified facial architecture. In support of their argument they assert that the well documented reduction in dental size following the Pleistocene has been incorrectly attributed to what are essentially two principal mechanisms: 1) a dietary shift toward higher carbohydrate, less abrasive foods that in turn favored smaller, morphologically simpler and less caries-prone teeth, and 2) a reduction in the functional demads placed on the masticatory complex resulting in reduced growth of the maxillo-mandibular complex. MACCHIARELLI & BONDIOLI question the likelihood that a shift in diet could have accelerated facial reduction and specifically doubt the possibility that the 15% reduction in occlusal surface area (from 2319 mm$^2$ to 1971 mm$^2$) reported by FRAYER (1978) could have been responsible for a «completely different survival capacity» over the last 10,000 years. The authors argue that the selectionist interpretation has resulted from an abundance of dental remains that do indeed show size reduction but a paucity of skeletal material necessary to support the selectionist view.

The existence of a large series of skeletal remains from Sudanese Nubia spanning a time period from Mesolithic (c 12,000 BP) through Christian (14th century) times provides an excellent test case against which MACCHIARELLI & BONDIOLI's criticisms can be examined.


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## Materials and Methods

The cranial, skeletal and dental measurements used in this study are derived from materials excavated by the University of Colorado Nubian Expedition from the Wadi Halfa area of the Republic of Sudan. The sample includes skeletal material spanning more than 13,000 years from Mesolithic (c. 11,000 B.P.) through Christian (A.D. 1450) periods.

The Mesolithic material derives from a population representing a hunting and gathering adaptation typified by a low density, dispersed populational pattern associated with large body size by MACCHIARELLI & BONDIOLI. During the succeeding A-Group (3400-2400 B.C.) and C-Group (2400-1200 B.C.) periods, barley, millet and sorghum were increasingly cultivated and there was an intensification of herding. This cultural transition would be expected to push these ancient Nubians in the direction of a higher density central-place cultural pattern associated by MACCHIARELLI & BONDIOLI with reduced body size and, as a side effect, reduced tooth size.

In 1000 B.C. lower water levels in the Nile led to an abandonment of Lower Nubia. This hiatus ended with the introduction of the water wheel (*shaduf*) during the Meroitic period (350 B.C. — A.D. 350). With the advent of irrigation made possible by the *shaduf*, Meroitic populations extended political control and occupancy of the Nile valley from Meroe, a capital far to the south.

The Meroitic period was followed by two centuries of political frangmentation and regional autonomy. This X-Group period (A.D. 350-550) did, however, continue a subsistence pattern based on intensive agriculture.

The conversion of Nubia to Christianity in A.D. 550 led to a religious and political unification of Upper and Lower Nubia that lasted until A.D. 1323 when Upper Nubia fell under Islamic control and Lower Nubia was quickly annexed by Egypt.

In summary, over some 11,000 years Nubian populations underwent precisely the transition from a low density dispersed pattern to a higher density central place pattern invoked by MACCHIARELLI & BONDIOLI in their hypothesis of body size reduction. The appropriateness of the Nubian remains in an assessment of the body size hypothesis is enhanced further by strong evidence for biological continuity over this time period.

Greene, for example, was able to demonstrate that the Nubian populations used in this analysis share at least thirteen of sixteen discrete dental traits known to be under strong genetic control. This biological evidence was supported by ADAMS (1967) who upon reviewing the archaeological and biological evidence stated:

«We are conscious now of a continuum of cultural evolution within the borders of Nubia, heavily influenced by events and ideas from abroad, but involving the same basic population from beginning to end. There is no reason why the Nubians of today should not claim to the direct descendants, culturally as well as racially, of their Neolithic, and perhaps even of their Paleolithic, forebears (ADAMS, 1966:29).»

## Results and Discussion

The analysis of changes in femur length demonstrate that there has been little decrease in stature from the Mesolithic through Christian periods (see *Table 1*). When post-Mesolithic groups are compared to the Mesolithic, both males and females exhibit a

TABLE 1 - *Stature estimates based upon either the femur [(2.32 X femur length) + 65.53] or humerus [(2.89 X humerus length) + 78.10] (Calcagno, unpublished data).*

| Group | MALES | | | | FEMALES | | | |
|---|---|---|---|---|---|---|---|---|
| | X | s | N | % | X | s | N | % |
| Meso | 174.8 | 3.82 | (15) | — | 168.7 | 3.18 | (12) | — |
| Agri | 169.8 | 5.45 | (86) | −2.9 | 163.4 | 4.58 | (70) | −3.1 |
| Int Ag | 168.1 | 4.90 | (70) | −1.0 | 162.1 | 4.85 | (61) | −0.8 |

maximum reduction of less than 4 percent. Changes in cranio-facial morphology of these same populations have been far more profound and far more complex that would be expected with simple body size reduction (see *Table* 2 for means and standard deviations of cranio-facial measurements). Examination of percent changes in cranio-facial measurements from Mesolithic through Christian times (*Table 3*) reveals three clusters of change. In cluster 1 (composed of facial height, cranial height, parietal chord and frontal chord) there is an actual increase in size of the dimensions involved while in cluster 2 (composed of facial length, cranial length, symphyseal height and mandibular ramus height) there is a slight decrease of from 0.8 to 4.8 percent. In cluster 3 (composed of length of masseter origin; length of mandibular corpus and symphyseal thickness), however, there is dramatic reduction of from 13 to 26 percent between Mesolithic and Christian times.

These data indicate a complex pattern of facial reduction and cranio-facial reorientation through time in ancient Nubia. Of major importance in this transformation of the Nubian skull is a substantial reduction in the attachment of masticatory muscles implying

TABLE 2 - *Means and standard deviations for cranio-facial variables in three Nubian populations (in cm).*

| Variables | Mesolithic | | A-C Group | | MXCh Group | |
|---|---|---|---|---|---|---|
| | mean | s.d. | mean | s.d. | mean | s.d. |
| 1. Cranial length | 18.58 | 0.32 | 18.18 | 0.64 | 18.27 | 0.82 |
| 2. Cranial height | 12.75 | 0.56 | 13.91 | 0.66 | 13.64 | 0.64 |
| 3. Frontal chord | 10.57 | 0.29 | 11.70 | 0.45 | 11.47 | 0.55 |
| 4. Parietal chord | 11.32 | 0.35 | 12.48 | 0.49 | 12.35 | 0.70 |
| 5. Facial length | 10.36 | 0.35 | 10.00 | 0.47 | 10.28 | 0.57 |
| 6. Upper face height | 6.63 | 0.33 | 6.68 | 0.40 | 6.66 | 0.43 |
| 7. Cheek height | 2.57 | 0.23 | 2.42 | 0.26 | 2.37 | 0.27 |
| 8. Masseter origin length | 4.31 | 0.52 | 3.38 | 0.34 | 3.18 | 0.32 |
| 9. Ramus height | 4.75 | 0.62 | 4.51 | 0.42 | 4.55 | 0.45 |
| 10. Corpus length | 9.25 | 0.41 | 7.37 | 0.57 | 7.20 | 0.50 |
| 11. Symphysis height | 3.35 | 0.22 | 3.19 | 0.38 | 3.28 | 0.37 |
| 12. Symphysis thickness | 1.69 | 0.17 | 1.48 | 0.14 | 1.44 | 0.18 |
| 13. Ramal width | 4.29 | 0.37 | 3.70 | 0.38 | 3.73 | 0.30 |
| 14. Sigmoid notch height | 4.67 | 0.64 | 4.40 | 0.40 | 4.28 | 0.37 |
| 15. Coronoid process height | 6.14 | 0.54 | 5.98 | 0.53 | 5.95 | 0.53 |
| 16. Total face height | 10.92 | 0.60 | 11.55 | 0.60 | 11.46 | 0.65 |

MXCh = combined Meroitic, X and Christian samples. Modified from CARLSON & VAN GERVEN (1977: 497).

TABLE 3 - *Temporal changes in cranio-facial measurements.*

| | Variables | Mesolithic to A-C mean | A-C Group to MXCh Group | Mesolithic to MXCh Group |
|---|---|---|---|---|
| 1. | Cranial length | −2.2 | 0.5 | −1.7 |
| 2. | Cranial height | 8.4 | −2.0 | 6.4 |
| 3. | Frontal chord | 9.7 | −2.0 | 7.9 |
| 4. | Parietal chord | 9.3 | −1.1 | 8.4 |
| 5. | Facial length | −3.5 | 2.8 | −0.8 |
| 6. | Upper face height | 0.8 | −0.3 | 0.5 |
| 7. | Cheek height | −5.9 | −2.1 | −7.8 |
| 8. | Masseter origin length | −21.6 | −6.0 | −26.3 |
| 9. | Ramus height | −3.8 | −0.5 | 4.3 |
| 10. | Corpus length | −20.4 | −2.4 | −22.8 |
| 11. | Symphysis height | −4.8 | 2.8 | −2.1 |
| 12. | Symphysis thickness | −12.5 | −2.8 | −15.3 |
| 13. | Ramal width | −13.8 | 0.9 | −13.1 |
| 14. | Sigmoid notch height | −5.8 | −2.8 | −8.4 |
| 15. | Coronoid process height | −2.7 | −0.6 | −3.1 |
| 16. | Total face height | 5.5 | −0.8 | 4.8 |

Changes are in percent. MXCh = combined Meroitic, X-Group and Christian samples. Modified from CARLSON & VAN GERVEN (1977: 500).

a reduction in their size. Secondary to these masticatory changes is a slight increase in cranial height and a decrease in cranial length. This complex of changes can be explained by a reduction in masticatory musculature and bony attachments resulting in a smaller face which is rotated to a more inferior and posterior position. Thus, the crania is transformed into a higher and more spheroid form. This complex pattern of morphological transformation, while difficult to explain in terms of simple body size reduction is, never the less interpretable in light of alternative hypotheses.

Two hypotheses have been proposed to account for these changes. The «masticatory function hypothesis» (CARLSON & VAN GERVEN, 1977) and the «caries-resistance-dental reduction hypothesis» (ARMELAGOS, 1968:397; CALCAGNO, 1984; GREENE, 1970; GOODMAN *et al.*, 1986) (see *Figure 1*). The masticatory function hypothesis suggests that the masticatory complex will undergo reduction (with associated cranio-facial remodeling) with a reduction in heavy chewing, which in itself is a result of changing subsistence patterns. With the consumpion of «softer» more culturally processed foods there is a corresponding reduction in growth of the masticatory complex. This reduction leads to a secondary reorientation of the face and vault as described in the preceding data. The key to this hypothesis is that while it does not preclude the possibility or importance of genetic changes in facial reduction, the hypothesis does not invoke genetic evolution as the entire source of long term cranio-facial evolution.

While in no way opposing the masticatory function hypothesis, the dental reduction hypothesis has placed greater emphasis on the genetic evolution of tooth size. The hypothesis proposes that the dietary shift away from highly abrasive foods toward high carbohydrate foods following the Mesolithic, shifted the selective advantage away from large morphologically complex teeth capable of resisting wear toward smaller, simpler teeth more resistant to dental caries. The selective shift toward genetically smaller, less

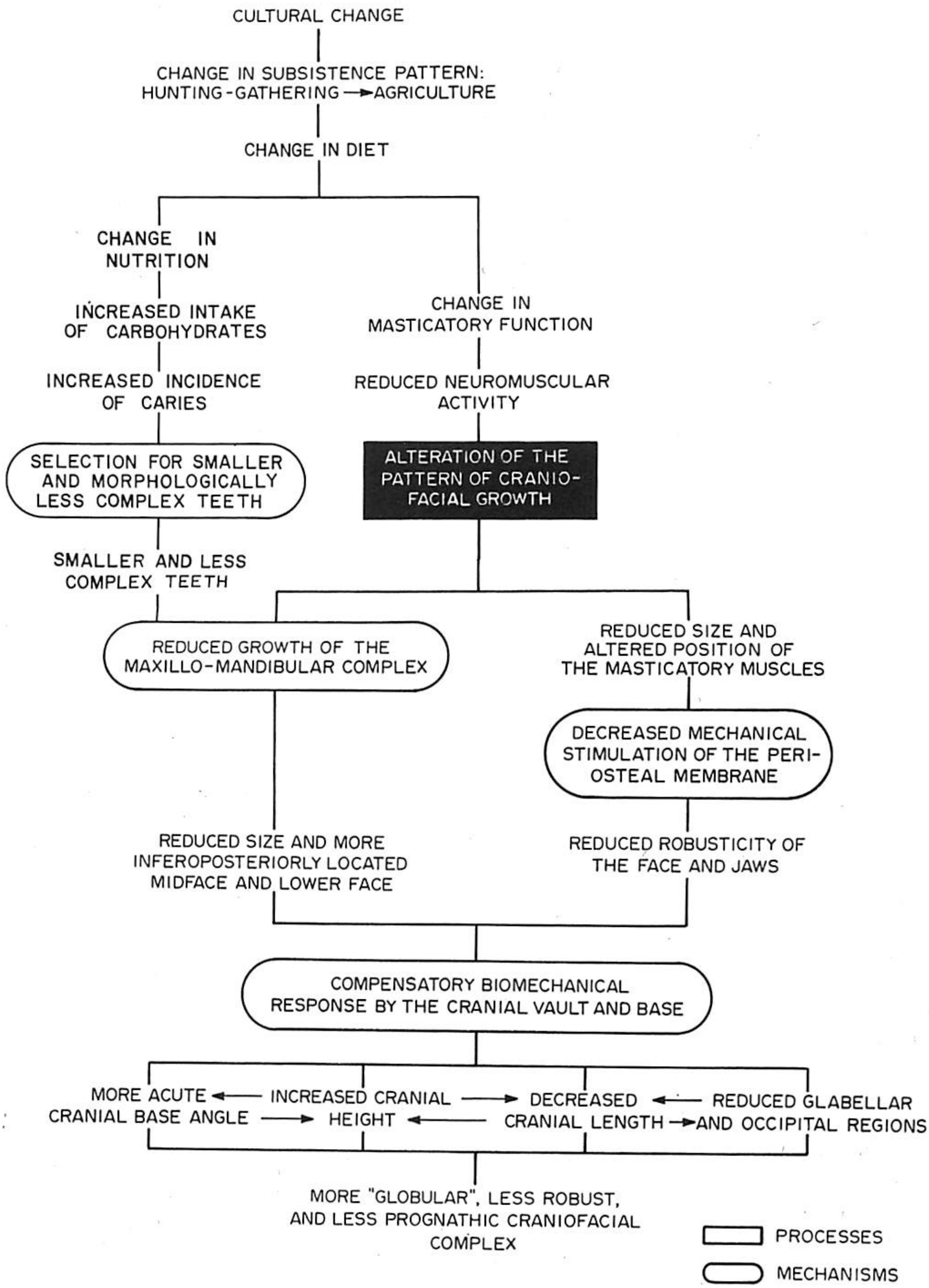


Figure 1. - Alternative hypothesis for facial reduction. Modified from Carlson.

TABLE 4 - *Temporal changes in tooth breadths (in percents).*

| | Mesolithic to A-C Group | A-C Group to MXCh Group | Mesolitic to MXCh Group |
|---|---|---|---|
| ANTERIOR DENTITION | | | |
| Mandible | | | |
| Males | −7.9 | −0.6 | −8.5 |
| Females | −9.6 | −0.5 | −10.0 |
| Maxilla | | | |
| Males | −5.7 | +0.7 | −5.0 |
| Females | −7.5 | +1.6 | −6.0 |
| POSTERIOR DENTITION | | | |
| Mandible | | | |
| Males | −7.5 | −1.6 | −8.9 |
| Females | −8.4 | −1.8 | −10.1 |
| Maxilla | | | |
| Males | −6.6 | −1.1 | −7.6 |
| Females | −6.2 | −1.6 | −7.7 |

Posterior dentition includes premolars and molars. Anterior dentition includes incisors and canines. Modified from CALCAGNO (1984).

complex teeth was also fueled by the reduction in the overall masticatory apparatus and cranial remodeling. It is clear that while the two hypotheses differ slightly in focus, both predict the pattern of change observed in the Nubian data far more satisfactorily than the body size hypothesis proposed by MACCHIARELLI & BONDIOLI.

CALCAGNO (1984) has recently provided dental data from ancient Nubia that make it possible to evaluate the relative roles of facial reduction and dental reduction from Mesolithic through Christian times. By comparing the diachronic order of facial reduction and dental reduction it should be possible to better understand their respective roles in cranio-facial remodelling.

Tooth breadth (one of the most reliable indicators of crown size) decreases at the rate of one percent per thousand years between Mesolithic and A-group -C-group (early agriculturalist) periods (see *Table 4*). As noted by CALCAGNO (1984), this rate of dental reduction argues for strong selective pressure favoring smaller teeth. In addition, reduction is observed for all teeth (anterior and posterior, mandibular and maxillary) in both males and females.

The rate of reduction decreases between early agricultural (A-group-C-group) and later intensified agriculture (Meroitic, X-group and Christian) times. During this temporal phase anterior tooth size approaches stability while posterior teeth continue to reduce but at a slower rate.

This pattern of dental reduction closely parallels masticatory reduction reflected in the third cluster of cranio-facial measurements. As previously discussed, these dimensions show an initial rapid reduction between Mesolithic and early agricultural periods of from 12.5 to 21.6 percent. This, however, is followed by a slower reduction of six percent from early to later agricultural periods.

The strong correspondence between the rate and timing of dental and masticatory features makes it difficult to assess the primacy of either of the selectionist hypotheses. However, the continuing reduction of the posterior dentition may well reflect the continuing advantage of smaller caries-resistant teeth.

Most importantly, however, the inability of these data to separate changes in the dental system from the masticatory features of skull reinforces our understanding of an important biological reality. The dentition, its skeletal support system and associated musculature are a single functional complex that has evolved through time in response to dietary changes. More highly processed cariogenic foods associated with a Neolithic economy may very well have simultaneously shifted the selective advantage in favor of smaller teeth while at the same time contributing to a new nutritional environment in which reduced neuromuscular stimulation and concomitant changes in patterns of bone deposition and cranio-facial growth prevailed. What is clear is that single environmental (mechanical) or genetic causes of cranio-facial evolution in post-Pleistocene populations are unlikely to be found in Nubia or elsewhere and, more importantly, the attribution of complex patterns of cranio-facial evolution and dental reduction to reduction in body size are demostrably unwarranted.

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