

# The Morphogenetic Relationship of the Temporal Muscle to the Coronoid Process in Human Embryos and Fetuses<sup>1,2</sup>

MEROPI N. SPYROPOULOS<sup>3,4</sup>

*Department of Orthodontics, The University of Michigan, Ann Arbor, Michigan 48109*

**ABSTRACT** The purpose of this investigation was : (a) to study the developmental relationships of the temporal muscle and the coronoid process during the critical initial stages of morphogenesis and (b) to correlate the developmental stages of the muscle and the bone with data describing the functioning of the muscles of mastication in utero.

The heads of 41 human embryos and fetuses, 6 to 11 weeks, estimated fertilization age, were sectioned and examined under light microscopy. The findings are described in terms of six successive stages, each characterized by a major developmental change occurring during that stage.

The data indicate that the temporal and masseter muscle anlagen begin to develop prior to the skeleton to which they ultimately become attached. The coronoid process differentiates subsequently as a discrete entity within the mass of the temporal muscle anlage at an estimated fertilization age of 7 to 7.5 weeks (23-24 mm CRL). At approximately eight weeks of age, the coronoid process unites with the main portion of the mandibular ramus. The findings here presented do not support the conclusion that the coronoid process is self-differentiating as Washburn ('47) contended. Instead, the development of this feature of the human mandible represents a response that follows the differentiation of the temporal muscle. This conclusion is consistent with the observations drawn from a number of investigations concerning structural and functional development of the face.

One of the major areas of concern in the study of craniofacial growth is the relationship between form and function. Does functional activity affect the size, shape and orientation of skeletal units, and if so, to what extent and what is the *modus operandi*? These are some of the fundamental questions underlying the developmental phenomena leading to harmony or disharmony in the various components of the human face.

Efforts to explore and investigate the mechanisms of action have led to the advancement of various theories. Primary among these are: (a) the importance of the cartilaginous nasal septum as a primary growth center (Scott, '54), (b) the intrinsic growth capacity of the bony sutures (Weinmann and Sicher, '55) or of the osseous unit (Latham and Burston, '64), and (c) the primary role of functional matrices in facial growth (van der Klaauw, '48-'52; Moss, '62; Moss et al., '69).

In nature, a functioning bone-muscle com-

plex is always present so that the relative roles of intrinsic factors in the bone, on one hand, and functional influences, on the other, are difficult to evaluate. Experimental and other investigations have tended to support the concept that function influences the growth and form of related skeletal units. Extirpation experiments (Pratt, '43; Horowitz and Shapiro, '55; Avis, '61; Moore, '73) have documented the fact that certain morphological elements of the mandible are specifically associated with muscles and diminish in size if these muscles are removed. Masticatory

Accepted April 28, '77.

<sup>1</sup> Condensed from original thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Orthodontics in the Rackham School of Graduate Studies of the University of Michigan, Ann Arbor, 1976.

<sup>2</sup> This investigation was supported in part by Public Health Service Research Grant DE 03443 from the National Institute of Dental Research.

<sup>3</sup> Permanent address: 41 Ventouri Street, Holargos, Athens, Greece.

<sup>4</sup> Visiting Assistant Professor, Department of Orthodontics, The University of Michigan.

muscle activity has also been evaluated by feeding animals diets of different physical consistency and observing the effects on the size and form of the associated skeletal elements (Watt, '51; Moore, '65; Whitley et al., '66). Again, the findings were consistent with the concept that reduced muscular function influences the underlying skeletal units. The effects of paralysis or hypoplasia of the muscles of mastication on the skull were described by Rogers ('55, '58). Hall ('75) also studied the effects of long-term muscle paralysis on bone growth in embryonic chicks. Nanda et al. ('67) studied the effect of masseter repositioning on the skeletal form and structure of the dog. Eschler ('61) extensively studied the effect of position and direction of muscle pull on the position and shape of the mandible in humans. Moss and Simon ('68), in a functional analysis of the angular process of the human mandible, concluded that the alteration in the geometry of the bone-muscle relationship influences bone morphology.

Focusing specifically on the coronoid process of the mandible and the temporal muscle, Washburn ('47), through extirpation experiments, came to recognize three classes of morphological features in the craniofacial skeleton: (1) those which never appear unless the muscles are present, e.g., temporal line, nuchal crest, mastoid crest, (2) those which are self-differentiating but require the presence of muscle to persist, e.g., coronoid process and (3) those which are largely independent of the muscles which happen to be associated with them, e.g., brain case.

Washburn made his experiment on 1-day-old rats and his observations are directly relevant to the postnatal relationship between the functioning temporal muscle and the coronoid process. The recent well documented evidence of functional activity of the muscles of mastication in utero (Hooker, '58; Humphrey, '68, '71) throws a new light on the prenatal sequence of events as far as initiation and differentiation are concerned. The question which comes into focus is whether, in fact, the coronoid process of the mandible "has an early intrinsic initiation and differentiation" as Washburn contended. Alternatively, one must consider the possibility that the initiation and differentiation are evoked by functional muscular activity already present in utero. The removal of the temporal muscle after birth cannot provide a

basis for evaluating the relative importance of self-differentiation and function in the prenatal period.

Washburn's contention that the size and form of the coronoid process depend upon muscle activity after birth has been corroborated by various experimental studies on animals (Horowitz and Shapiro, '51; Avis, '59; Schumacher, '68; Schumacher and Dokládál, '68; Moss and Meehan, '70; Moore, '67, '73). The conflicting opinion expressed by Boyd et al. ('67), to the effect that Washburn's observations resulted from an interference with the blood supply to the bone, was refuted by Warner ('69). The problem, however, of the initiation and differentiation of the coronoid process has not yet been resolved.

In order to explore this problem, this investigation was designed: (a) to study the relative timing of morphogenesis of the temporal muscle and the coronoid process in human embryos and fetuses at the critical initial stages of development, and (b) to correlate the developmental stages of the muscle and the bone with the available data concerning the functioning of the muscles of mastication in utero.

As the areas of the temporal muscle and the coronoid process were studied, other associated structures were closely involved, such as the masseter muscle and the zygomatic arch; their various stages of development were assessed as well.

#### MATERIALS AND METHODS

Heads of 41 embryos and fetuses, free from gross developmental anomalies, were selected from the Embryological Research Collection, Department of Anatomy, The University of Michigan. The specimens were selected to demonstrate sequentially the developmental stages from the first morphogenetic indication of muscle differentiation through the stage of well advanced development of both the muscle and the coronoid process. The specimens ranged in size from 17.8-64 mm crown-rump length (CRL) and in age from the early sixth to the eleventh week (estimated fertilization age). The age of the specimens was established on the basis of CRL and external characteristics as described by Moore ('73). The CRL, the estimated age and the plane of sectioning for each specimen are listed in table 1.

Each specimen was routinely fixed in 10%

TABLE 1

*Size and age of specimens analyzed*

No.	Embryo number	CRL (mm)	Est. fert. age (wks)	Plane of sectioning
1	E.H. 249	17.8	Early 6	Sagittal
2	E.H. 278	18	Early 6	Frontal
3	E.H. 459	19	6	Sagittal
4	E.H. 253	20	6.5	Frontal
5	E.H. 567	20	6.5	Sagittal
6	E.H. 600	20.5	6.5	Frontal
7	E.H. 231	21	7	Frontal
8	E.H. 592	21	7	Frontal
9	E.H. 884	21	7	Frontal
10	E.H. 598	22	7	Frontal
11	E.H. 590	22	7	Frontal
12	E.H. 739	22	7	Frontal
13	E.H. 419	23	7+	Frontal
14	E.H. 594	23	7+	Sagittal
15	E.H. 242	23	7+	Sagittal
16	E.H. 880	24	7.5	Frontal
17	E.H. 704	24	7.5	Frontal
18	E.H. 426	24	7.5	Frontal
19	E.H. 352	25	7.5	Frontal
20	E.H. 1018	25	7.5	Frontal
21	E.H. 908	25	7.5	Frontal
22	E.H. 938	26	7.5	Frontal
23	E.H. 658	26	7.5	Sagittal
24	E.H. 455A	26	7.5	Frontal
25	E.H. 1159	27	8	Frontal
26	E.H. 892	27	8	Frontal
27	E.H. 1069	27	8	Frontal
28	E.H. 840	28	8	Frontal
29	E.H. 1420	28	8	Frontal
30	E.H. 1373	28	8	Frontal
31	E.H. 882	29	8	Frontal
32	E.H. 552	29	8	Frontal
33	E.H. 512	29	8	Frontal
34	E.H. 777	30	8+	Sagittal
35	E.H. 883	30	8+	Frontal
36	E.H. 785	35	8.5	Frontal
37	E.H. 1310	42	9	Frontal
38	E.H. 1178	47	9.5	Frontal
39	E.H. 806	52	10	Frontal
40	E.H. 786	57	10+	Frontal
41	E.H. 1262	64	11	Frontal

neutral buffered formalin, prepared histologically and serially sectioned at either 10 or 15  $\mu$ m in the frontal or the sagittal plane. The term frontal is used here as synonymous with coronal (Kraus et al., '66) and is commonly defined as a vertical plane parallel to the coronal suture of the head. The posterior end of the nasal cavity, the center of the soft palate, the end of the palatal processes and the end of the soft palate were used to orient the sections.

After serial mounting, alternate sections were stained with Masson trichrome connective tissue stain or with hematoxylin and eosin. Using light microscopy, sections were read sequentially, focusing primarily on the

region of Meckel's cartilage. Observations were tabulated and schematic drawings and photomicrographs were made from the original slides.

Starting from 17.8 mm CRL, three embryos were examined for each millimeter of increase in size up to 29 mm CRL. At this size the morphogenesis of the coronoid process was well established. From 29 mm onwards (estimated fertilization age, 8 weeks), the fetuses examined were successively 4-5 mm larger; one or two fetuses from each size group were selected randomly for study. This procedure was used to avoid the introduction of errors resulting from the use of specimens exhibiting extreme variations during the critical stages of de-

velopment. Minor differences in the developmental stage observed in the three specimens of equal size were evaluated, in determining the modal description of the developmental status. In order to reaffirm the typicality of the description, each group of equal size was further compared with the orderly smaller and larger specimens. Ultimately, this procedure resulted in the determination of the developmental trajectory for the sample.

The nomenclature suggested by Boyd ('60) was used to describe the histogenetic stages of muscle differentiation; thus the terms premyoblast, myoblast, myotube, and muscle fiber, imply an order of increasing maturity. The terms are defined as follows:

- (1) *Premyoblasts* are the primordial muscle cells which appear in the undifferentiated mesenchyme; they are round or oval cells condensed at the site where the muscle anlage forms but cannot be differentiated from fibroblasts with light microscopy.
- (2) *Myoblasts* can be classified into early, middle and late stages (Gasser, '67); it should be recognized, however, that only the early and late stages are clearly discernible, while the middle stage represents an intermediate gradation. Early myoblasts appear under light microscopy as short spindle-shaped cells with an ovoid or ellipsoid nucleus and a basophilic cytoplasm containing chromatin, dense basophilic granules and very few myofibrils (Rayne and Crawford, '71). Late myoblasts appear as long multinucleated spindle shaped cells with oblong nuclei and more myofibrils. When grouped and cut longitudinally they appear as parallel ribbons.
- (3) *Myotubes* are multinucleated, very long cells containing myofibrils with light striations at the periphery.
- (4) *Muscle fibers* are cells containing a very large number of peripheral nuclei and distinct transverse striations.

The histogenetic stages of bone development were assessed according to Patten's ('68) description of intramembranous primary cancellous bone formation. The sequence of changes comprises five main phases as follows:

- (1) *Phase of early preparatory changes.* During this phase an abundance of mesenchymal cells congregates and numerous

small blood vessels are present. Here and there the mesenchymal cells exhibit a tendency to cluster in strung-out groups running in various directions, but with a suggestive definitive plan of organization in each group. An axial fibrous strand becomes more distinct in the late stages of this phase, with a row of cells flanking it on either side when it is cut longitudinally.

- (2) *Phase of ossein framework production.* During this phase, there is saturation and matting together of the original collagenous fibers with osseomucoid, forming the ossein or osteoid framework into which calcium deposition will take place.
- (3) *Phase of deposition of calcium salts.* Calcium deposition begins on the older part of a strand while its younger end is still being extended by the condensation of more mesenchymal cells. The cells at the older end are rounded, have a more deeply staining cytoplasm than their undifferentiated mesenchymal precursors and are termed osteoblasts.
- (4) *Phase of lamellae and trabeculae formation.* This phase is characterized by bone matrix formation replacing the original fibrous strand. Entrapment of bone cells within the lamellae is also observed.
- (5) *Phase of coalescence of the trabeculae.* The growing trabeculae in the area of developing bone come into contact and constitute a continuous system which is known as the primary cancellous bone.

## RESULTS

The sequence of developmental events observed in this investigation is here described in terms of six successive stages. Each stage is designated by the major developmental change occurring during that period.

### *Stage I: Muscle initiation*

CRL: 17.8-20 mm; est. fert. age: early sixth week. (E.H. 249, 278, 459, 253, 567).

Embryos of this size and age revealed an indication of condensation of premyoblasts at the future location of the temporal as well as the masseter muscles (figs. 2A,B).

In sagittal sections, the cells that would eventually give rise to the temporal muscle were oriented in a fan-shaped area equidistant

between the eye and the external ear. An oblong extension of cell condensation constituting the precursor of the masseter muscle was observed at almost a right angle to the fan-shaped area.

In frontal sections, it was observed that the condensation of the anlage of the temporal muscle constituted a thin lamina, while that of the masseter muscle was relatively thick. The masseter anlage was in close proximity to the mesenchymal mass forming the bony anlage of the mandible. The orientation of the premyoblasts was distinctly different from that of the mesenchymal cells; while the mesenchymal cells were oriented vertically, the masseter premyoblasts were directed laterally following the general axis of the future muscle.

In the area corresponding to the future angle of the mandible, the mesenchymal bony anlage was in an advanced stage of the early preparatory phase. This was indicated by the presence of an axial fibrous strand in the middle of the abundantly congregated mesenchymal cells (Patten's First Phase). At this stage of development, the forming buccal wall of the future mandible exhibited only a slight suggestion of lateral convexity.

A nerve fiber was invariably found in close proximity to the lateral border of the bony anlage and inside the mass of premyoblastic condensation of the future masseter muscle.

#### *Stage II: Shaping of the mesenchymal bony anlage of the mandible*

CRL: 20.5-22 mm; est. fert. age: 6.5-7 weeks. (E.H. 600, 231, 592, 884, 598, 590, 739).

During this stage, the temporal lamina was growing downwards but was still at a considerable distance lateral to the superior border of the bony anlage of the mandible. A well defined masseteric aggregate of premyoblasts separated the developing bony anlage and the most ventral extension of the temporal lamina.

The mesenchymal bony anlage at the area corresponding to the future angle of the mandible had begun to demonstrate a definite buccal curvature. In this area the phase of ossein framework production has been initiated and a well defined central core could be observed. Surrounding the core, a relatively thick layer of cellular condensation could be observed

which would ultimately form the periosteum.

At this stage of development, no indication of initiation of the coronoid process was revealed in the examination of sequential sections.

At the location of the future zygomatic arch, inferior to the temporal lamina, a condensation of mesenchymal cells had formed.

#### *Stage III: Central condensation in the temporal muscle*

CRL: 23-24 mm; est. fert. age: 7-7.5 weeks. (E.H. 419, 594, 242, 880, 704, 426).

During this stage, a triangular mass appeared in the center of the temporal muscle anlage. This mass was lined by a zone of condensed and thickly packed, round and ovoid cells and was clearly apparent in sagittal sections (figs. 3A,B). In frontal sections (figs. 4A,B) this feature appeared as a central oblong mass inside the temporal muscle anlage. In contrast to the previous stage, where only premyoblasts were present, the temporal muscle primordium was now of considerable thickness and consisted also of myoblasts.

Although the configuration and continuity of the temporal and masseter muscle anlagen were very similar to those observed in stages I and II, the direction of the myoblasts was now more distinctly oriented towards the sites of the future muscle attachments.

Analysis of sequential sections revealed further shaping of the bony anlage in the area of the future angle of the mandible and a mild elongation upwards, suggestive of initiation of ramal formation.

In the condensation of cells at the location of the future zygomatic arch, a more advanced preparatory phase was observed.

#### *Stage IV: Communication of temporal muscle anlage with precursor of mandibular ramus*

CRL: 25-28 mm; est. fert. age: 7.5-8 weeks. (E.H. 352, 1018, 908, 938, 658, 455A, 1159, 892, 1069, 840, 1420, 1373).

Muscle differentiation was accelerated during this stage and myotubes were observed in both the temporal and masseter anlagen.

A communication was apparent between the temporal muscle anlage and that of the mandibular ramus. A close spacial relationship was developing between the temporal mass and the future periosteum of the mandible.

ble. Some myoblasts and myotubes were observed to be gaining access into the primordium of the periosteum.

The triangular structure, observed inside the temporal mass in the preceding stage, became progressively more distinct and pointed (figs. 5A,B). The fact that this tissue stained blue with the Masson technique suggested an early preparatory phase of bone formation. Around this coronoid anlage, the direction of the myoblasts (now in a late stage of development) and of the myotubes of the temporal muscle was very distinct.

In sagittal sections, the anlagen of the temporal and masseter muscles appeared as a continuous element. Also, the precursor of the coronoid process exhibited a continuity with the cellular condensation surrounding the osseous framework of the main portion of the future ramus.

With progression in size and age, an increase in the number of temporal myotubes became evident and an enlarged area of attachment to the differentiating periosteum of the mandible was observed.

The zygomatic arch was in a stage of osseous formation and an attachment of masseter late-stage myoblasts and myotubes was apparent. The configuration of the superior border of the ramus (not yet in direct continuity with the coronoid process), although more sharply defined than in the preceding stage, still presented a blunted or rounded appearance.

*Stage V: Establishment of continuity of coronoid process with main portion of ramus*

CRL: 29-35 mm; est. fert. age: 8-8.5 weeks. (E.H. 882, 552, 512, 777, 883, 485).

Continuity of the central condensation (i.e., coronoid process) within the temporal muscle with the rest of the mandibular anlage was well established in this stage. The development of the muscles was well advanced in both size and maturity. This was indicated by the presence of a greater number of myotubes. Due to their varied orientation the myotubes were cut through different planes, ranging from cross sections through longitudinal sections.

The precursor of the coronoid process was still in the late preparatory phase of bone formation, judged histogenetically. Morphogenetically, however, it had achieved a distinct

shape and was elongated, projecting upwards into the mass of the temporal muscle (figs. 6A,B).

Osseous formation was well advanced in the zygomatic arch and in the main portion of the mandibular ramus; in both structures mineralization had been initiated.

*Stage VI: Progressive maturation and growth of muscular and bony elements*

CRL: 36-64 mm; est. fert. age: 8.5-11 weeks. (E.H. 1310, 1178, 806, 786, 1262).

From this stage onwards, the changes observed were associated with maturation and increase in size of the differentiated muscular and skeletal elements. By 42 mm, CRL, a very distinct insertion of the myotubes of the temporal muscle into the periosteum of the coronoid process could be observed. The interface between the muscle and the periosteum extended over an elongated area, but the actual nature of the attachment of the muscle to the bone was ill-defined. No Sharpey's fibers extending from the muscle and investing the bone were yet discernible.

As the size and age of the fetuses increased, muscle fibers appeared in progressively greater numbers. The ossification process was progressing concurrently in both the coronoid and the zygomatic arch and, by the eleventh intrauterine week, the stage of trabecular formation had been achieved (figs. 7A,B).

With the upward elongation of the coronoid process, a coordinated migration of the insertion of the temporal muscle took place. A sharp boundary distinguishing the periosteum from the contiguous muscle fibers had not yet been established at this stage.

The primary developmental features described in the six stages here reported are summarized schematically in table 2 and figure 1.

DISCUSSION

The findings of the present investigation indicate that the temporal and masseter muscle anlagen begin to develop in the human embryo before the skeleton to which they ultimately become attached. These findings agree with the observations of Rayne and Crawford ('71), based upon their study of the development of the muscles of mastication in the rat. The coronoid process of the human mandible differentiates as a discrete entity within the mass of the temporal muscle

TABLE 2  
Schematic summary of the six developmental stages of bone-muscle relationships in the face

	Stage I	Stage II	Stage III	Stage IV	Stage V	Stage VI
CRL	17.8 - 20 mm	20.5 - 22 mm	23 - 24 mm	25 - 28 mm	29 - 35 mm	36 - 64 mm
Est. fert. Age	6 - 6.5 wks	6.5 - 7 wk.	7 - 7.5 wks	7.5 - 8 wk.	8 - 8.5 wks	8.5 - 11 wks
Sagittal Sections						
Frontal Sections						

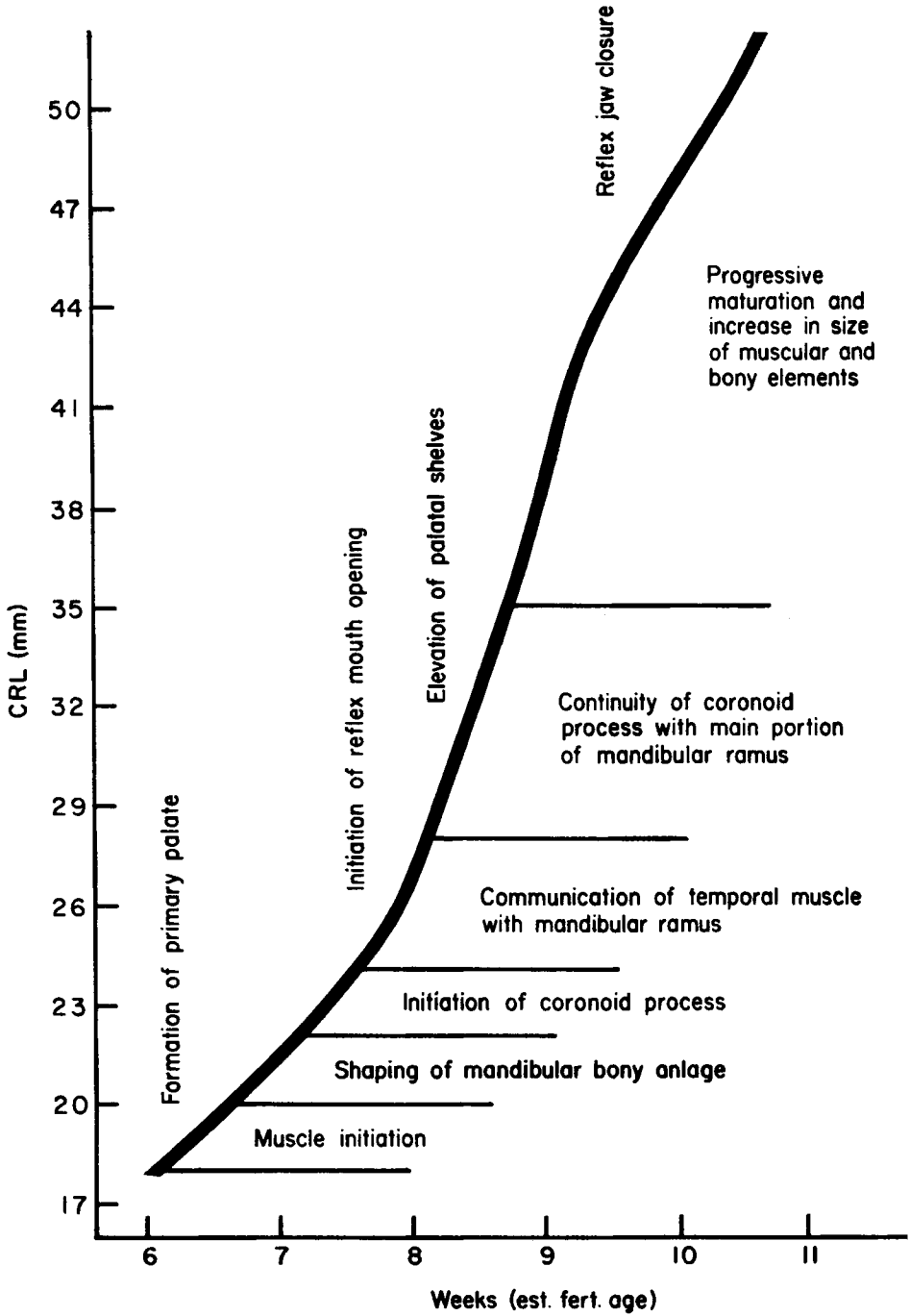


Fig. 1 Timing of the six developmental stages in the morphodifferentiation of the temporal muscle and the coronoid process as compared to other known events of facial development.



anlage at a very early age (estimated fertilization age 7-7.5 weeks and 23-24 mm CRL).

The relative timing of initiation of the temporal muscle and the coronoid process, as well as their interaction during differentiation have relevance for the fundamental issue concerning the autonomy of development of the coronoid process. While premyoblastic condensation at the future location of the temporal muscle is already evident at the beginning of the sixth intrauterine week, the first evidence of a precursor of the coronoid process is only apparent about a week later, at a CRL of 23-24 mm. At this stage, inside the temporal muscle anlage, an indication of mesenchymal differentiation first appears, suggesting the origin of the future coronoid process.

Differentiation proceeds in both the muscle and the bony anlagen with advancing size and age of the embryo; nevertheless, the muscle is consistently more advanced in its maturation until the age of about 9.5 weeks. At this stage, at an approximate CRL of 47-52 mm, both the muscle and the bone have achieved coordinate levels of differentiation. Subsequent changes are associated with an increase in size of the muscle mass and the coronoid process.

The time-space relationships here observed, at the gross histological level of investigation, suggest the existence of an "inductive" mechanism acting upon the undifferentiated mesenchyme incorporated within the very mass of the temporal muscle anlage.

The correlation of the morphogenetic events with the concurrent physiologic events observed during the various stages is pertinent to the study of the factors involved in the initiation and differentiation of the temporal muscle and the coronoid process. Humphrey ('71), continuing Hooker's work ('54, '58) on muscular activity through stimulation of living embryos, has provided evidence that reflexes involving the oral region start at about 8 to 8.5 weeks (menstrual age) and a CRL of 25.0-26.0 mm. (Although Humphrey used menstrual age for the classification of her specimens, the fact that she used CRL measurements permits comparisons to be made satisfactorily). Humphrey stated that at the menstrual age of 8.5 to 9.5 weeks (CRL 27.51-35.0 mm), stimulation of the fetus caused a more complete mouth opening, as compared to the previous stage. Mouth closure at this stage, as judged by the much

longer time interval required when compared with mouth opening, was evidently a passive return to position (Humphrey, '68, '70). This period corresponds to stages IV and V described in the findings presented here. Morphologically, these stages are characterized by the communication of the temporal muscle anlage with the precursor of the mandibular ramus and the establishment of the continuity of the coronoid process with the main portion of the ramus.

One week later (menstrual age 10.5-11.5 weeks, CRL 44.0-56.0 mm), reflex jaw closure has been recorded, which implies primarily masseter and temporal muscle action. This period corresponds to the later part of Stage VI described in the present study. At this time, a very distinct attachment of temporal myotubes to the periosteum of the coronoid process can be observed.

Comparison of the rate of maturation of the temporal and masseter muscles with that of the superficial muscles of the face (innervated by nerve VII), as described by Gasser ('67), suggests that the muscles innervated by nerve V are more advanced in their development. Gasser found the superficial muscles of facial expression to be composed mostly of myoblasts at 41 mm CRL. At this same stage of development, myotubes are already present in both the temporal and masseter muscles. This can be attributed to the fact that reflex muscle activity in utero involves these muscles prior to the muscles of facial expression.

Baume ('55), based upon an investigation of muscle insertion and bone growth in the mandibles of Rhesus monkeys, concluded that muscle has an osteogenic effect. He assumed that the bone resorption resulting from muscle extirpation is due to the absence of a bone-forming organ rather than the lack of function. This concept is consistent with the assumption of an osteogenic influence of the temporal muscle on the underlying mesenchyme. Baume's concept, however, does not account for the bone resorption observed to occur after induced paralysis of an intact muscle (Warner, '69).

The concept of the "biokinetic relationship of differentiations," proposed by Blechschmidt ('74), attributes special emphasis to the metabolic field. According to this author, differentiations are but momentary aspects of metabolic movements, i.e., submicroscopic movements of particles. He believes that,

under normal circumstances, extreme condensations of the mesenchyme are found only when young inner cells have both the opportunity and the immediate inducement to become spherical. This concept is consistent with the assumption that the differentiation of the mesenchyme to form the precursor of the coronoid process is a response to the temporal muscle.

The weight of the evidence in the present investigation and the corroborative data from related studies, here cited, strongly suggest that the coronoid process is not self-differentiating as Washburn contended. Instead, it represents a *developmental response* which follows the differentiation of the temporal muscle within which the coronoid process appears.

#### CONCLUSIONS

The evidence provided by the present investigation leads to the following conclusions:

(1) The temporal and masseter muscle anlagen differentiate in the human embryo before the skeleton to which they ultimately become attached.

(2) The coronoid process of the mandible differentiates as a discrete entity within the mass of the temporal muscle anlage and subsequently becomes continuous with the main portion of the mandibular ramus.

(3) The coronoid process is not self-differentiating; instead, it represents a developmental response that follows the differentiation of the temporal muscle.

(4) The developmental stages here reported may be correlated with functional events occurring in utero.

#### ACKNOWLEDGMENTS

The author gratefully acknowledges Doctor Alphonse R. Burdi for providing material from the Embryological Research Collection of the University of Michigan and for his guidance throughout the study. The deepest appreciation is also expressed to Doctor Melvyn J. Baer for his careful review and most helpful suggestions. Finally, the author wishes to acknowledge the technical assistance of Mr. Paul Schelble.

#### LITERATURE CITED

- Avis, V. 1959 The relation of the temporal muscle to the form of the coronoid process. *Am. J. Phys. Anthrop.*, 17: 99-104.
- 1961 The significance of the angle of the mandible: an experimental and comparative study. *Am. J. Phys. Anthrop.*, 19: 55-61.
- Baume, L. J. 1955 Muskelansatz und Knochenwachstum. *Schwitz. monatssch. f. zahnk.*, 65: 18-26.
- Blechs Schmidt, E. 1974 Humanembryologie. Prinzipien and Grundbegriffe. Hippokrates Verlag, Stuttgart, Germany.
- Boyd, J. D. 1960 Development of striated muscle. *Structure and Function of Muscle*. Vol. 1. Chap. III. G. H. Bourne, ed. Academic Press, New York, pp. 63-85.
- Boyd, J. G., W. A. Castelli and D. F. Huelke 1967 Removal of the temporalis muscle from its origin. Effects on size and shape of the coronoid process. *J. Dent. Res.*, 46: 997-1001.
- Eschler, J. 1961 Muscular abnormalities and functional disorders as a cause of mandibular malposition. *Europ. Orthod. Soc.*, 37th Congress, 168-195.
- Gasser, R. F. 1967 The development of the facial muscles in man. *Am. J. Anat.*, 120: 357-376.
- Hall, B. K. 1975 A simple, single-injection method for inducing long-term paralysis in embryonic chicks and preliminary observations on growth of the tibia. *Anat. Rec.*, 181: 767-777.
- Hooker, D. 1954 Early human fetal activity, with a preliminary note on double simultaneous fetal stimulation. *Res. Publ. Assn. Res. Nerv. Ment. Dis.*, 33: 98-113.
- 1958 Evidence of prenatal function of the central nervous system in man. James Arthur Lecture on the Evolution of the Human Brain, 1957. The American Museum of Natural History, New York.
- Horowitz, S. L., and H. H. Shapiro 1951 Modification of mandibular architecture following removal of temporalis muscle in the rat. *J. Dent. Res.*, 30: 276-280.
- 1955 Modification of skull and jaw architecture following removal of the masseter muscle in the rat. *Am. J. Phys. Anthrop.*, 13: 301-308.
- Humphrey, T. 1968 The development of mouth opening and related reflexes involving the oral area of human fetuses. *Alabama J. Med. Sci.*, 5: 126-157.
- 1970 Reflex activity in the oral and facial area of the human fetus. In: *Oral Sensation and Perception*, Second Symposium. J. F. Bosma, ed. C. C. Thomas Co., Springfield, pp. 195-233.
- 1971 Development of oral and facial motor mechanisms in human fetuses and their relation to craniofacial growth. *J. Dent. Res.*, 50: 1428-1441.
- Kraus, B. S., H. Kitamura and R. A. Latham 1966 *Atlas of Developmental Anatomy of the Face*. Hoeber Medical Division. Harper and Row Publishers, New York.
- Latham, R. A., and W. R. Burston 1964 Effect of unilateral cleft of the lip and palate on maxillary growth pattern. *Brit. J. Plast. Surg.*, 17: 10-17.
- Moore, K. L. 1973 *The Developing Human*. W. B. Saunders Co., Philadelphia.
- Moore, W. J. 1965 Masticatory function and skull growth. *J. Zool.*, 146: 123-131.
- 1967 Muscular function and skull growth in the laboratory rat (*Rattus norvegicus*). *J. Zool.*, 152: 287-296.
- 1973 An experimental study of functional components of growth in the rat mandible. *Acta. Anat.*, 85: 378-385.
- Moss, M. L. 1968 The functional matrix. In: *Vistas in Orthodontics*. B. Kraus and R. Riedel, eds. Lea and Febiger, Philadelphia, pp. 85-98.
- 1969 Functional cranial analysis of the mandibular angular cartilage in the rat. *Angle Orthodont.*, 39: 209-214.
- Moss, M. L., and M. A. Meehan 1970 Functional cranial analysis of the coronoid process in the rat. *Acta. Anat.*, 77: 11-24.
- Moss, M. L., and L. Salentijn 1969 The primary role of

- functional matrices in facial growth. *Am. J. Orthodont.*, *55*: 566-577.
- Moss, M. L., and M. R. Simon 1968 Growth of the human mandibular angular process: A functional cranial analysis. *Am. J. Phys. Anthropol.*, *28*: 127-138.
- Nanda, S. K., W. W. Merow and V. Sassouni 1967 Repositioning of the masseter muscle and its effect on skeletal form and structure. *Angle Orthodont.*, *37*: 304-308.
- Patten, B. M. 1968 *Human Embryology*. Third ed. McGraw Hill Book Co., New York.
- Pratt, L. W. 1948 Experimental masseterectomy in the laboratory rat. *J. Mammol.*, *24*: 204-211.
- Rayne, J., and G. N. C. Crawford 1971 The Development of the Muscles of Mastication in the Rat. *Advances in Anat. Embryol. Cell Biol.*, Springer-Verlag, Berlin, *44*, No. 5.
- Rogers, W. M. 1955 Experimental changes similar to asymmetry observed in bulbar polio in the skull and mandible of monkey following trigeminal lesions. *Anat. Rec.*, *121*: 357-358.
- 1958 The influence of asymmetry of the muscles of mastication upon the bones of the face. *Anat. Rec.*, *131*: 617-632.
- Schumacher, G. H. 1968 Maxillo-mandibuläre Apparat unter dem Einfluss Formgestaltender Faktoren. *Nova Acta Leopold.*, *33*, No. 182.
- Schumacher, G. H., and M. Dokládal 1968 Über unterschiedliche Sekundärveränderungen am Schädel als Folge von Kaumuskelresektionen. *Acta Anat. (Basel)*, *69*: 378-392.
- Scott, H. H. 1953 The cartilage of the nasal septum. *Brit. Dent. J.*, *95*: 34-48.
- Van der Klaauw, C. J. 1948-52 Size and position of the functional components of the skull. *Arch. neerl. zool.*, *9*, No. 1.
- Warner, W. M. 1969 *The Relationship of the Temporal Muscle to the Form and Architecture of the Skull of the Rat*. M. S. Thesis, University of Michigan, Ann Arbor.
- Washburn, S. L. 1947 The relation of the temporal muscle to the form of the skull. *Anat. Rec.*, *99*: 239-248.
- 1947 The effect of the temporal muscle on the form of the mandible. *J. Dent. Res.*, *21*: 174.
- Watt, D. G. 1951 The effects of physical consistency of food on the growth and development of the mandible and the maxilla of the rat. *Am. J. Orthodont.*, *37*: 895-928.
- Weinmann, J. P., and H. Sicher 1955 *Bone and Bones*, Second ed. The C. V. Mosby Co., St. Louis, pp. 88-91.
- Whitley, A. T., G. S. Kendrick and J. L. Mathews 1966 The effects of function on osseous and muscle tissues in the craniofacial area of the rat. *Angle Orthodont.*, *36*: 13-17.

*Abbreviations*

a, anlage	mc, Meckel's cartilage
ac, auditory canal	mm, masseter muscle
cp, coronoid process	mp, medial pterygoid muscle
e, eye	oc, oral cavity
eo, ear ossicles	za, zygomatic arch
m, mandible	

PLATE 1

EXPLANATION OF FIGURES

- 2A Parasagittal section through the temporal and masseter anlagen in a human embryo of 18 mm, CRL, and estimated fertilization age of early 6 weeks.  $\times 5.3$ .
- B Higher magnification of the same section showing the orientation of premyoblasts constituting the precursor of the temporal muscle.  $\times 21.2$ .
- 3A Parasagittal section through the temporal and masseter anlagen in a human embryo of 23 mm, CRL, and estimated fertilization age of seven weeks. The first indication of a triangular central condensation of the mesenchyme is evident inside the temporal muscle anlage.  $\times 5.3$ .
- B Higher magnification of the same section.  $\times 21.2$ .
- 4A Frontal section through the temporal anlage in a human embryo of 24 mm, CRL, and estimated fertilization age of a little over seven weeks. The condensed central oblong mass of mesenchyme inside the temporal muscle is the precursor of the coronoid process.  $\times 5.3$ .
- B Higher magnification of the same section.  $\times 21.2$ .

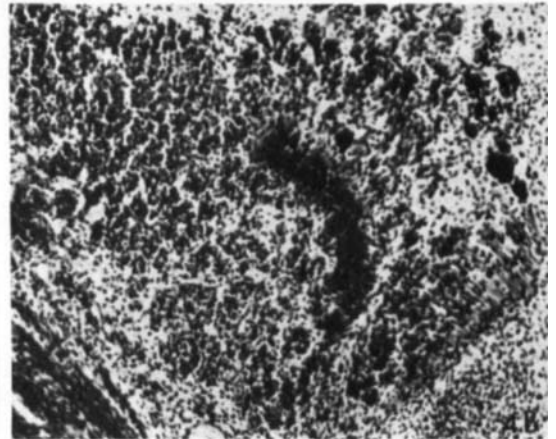
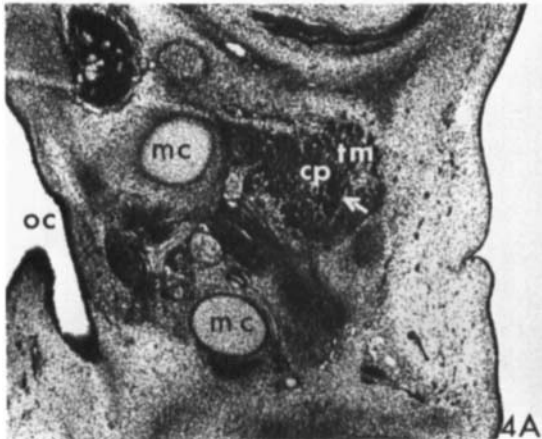
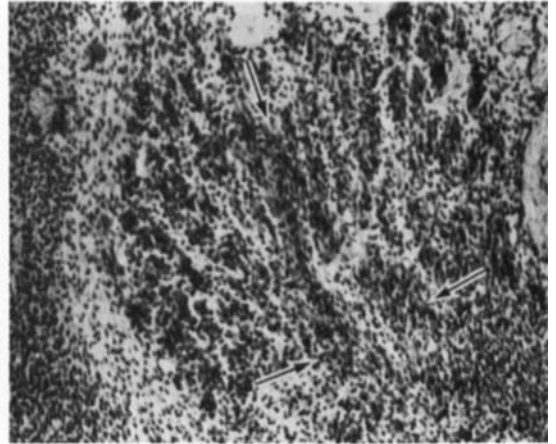
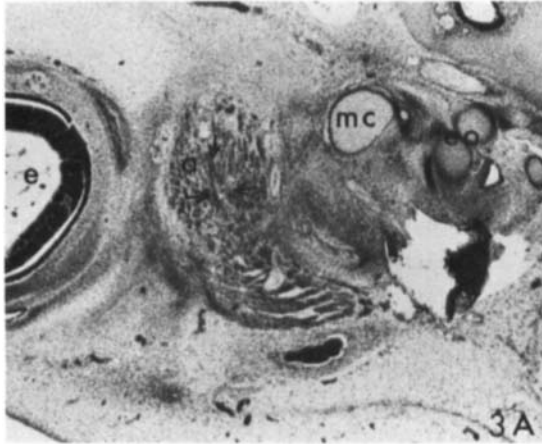
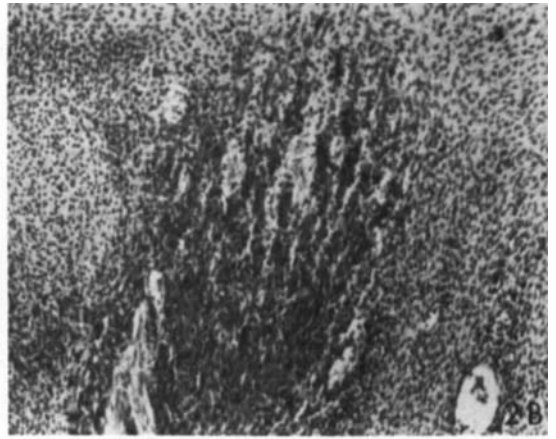


PLATE 2

EXPLANATION OF FIGURES

- 5A Sagittal section through the temporal and masseter muscle anlagen in a human embryo of 26 mm, CRL, and estimated fertilization age of 7.5 weeks.  $\times$  5.3.
- B Higher magnification of the same section showing the distinct anlage of the coronoid process in the center surrounded by the temporal myoblasts and myotubes.  $\times$  21.2.
- 6A Frontal section through the temporal muscle and the mandibular ramus near the posterior margin of the soft palate in a human embryo of 29 mm, CRL, and estimated fertilization age of eight weeks.  $\times$  5.3.
- B Higher magnification of the same section. The coronoid process is clearly discernible inside the myotubes of the temporal muscle.  $\times$  21.2.
- 7A Frontal section through the mandibular ramus at the highest point of the coronoid process in a human embryo of 64 mm, estimated fertilization age of 11 weeks. Mineralization is well advanced in both the coronoid process and the zygomatic arch, where bony trabeculae can be observed.  $\times$  5.3.
- B Higher magnification of the same section showing the elongated muscle-bone interface between the temporal muscle and the coronoid process.  $\times$  21.2.

