Development and Growth of the Jaws

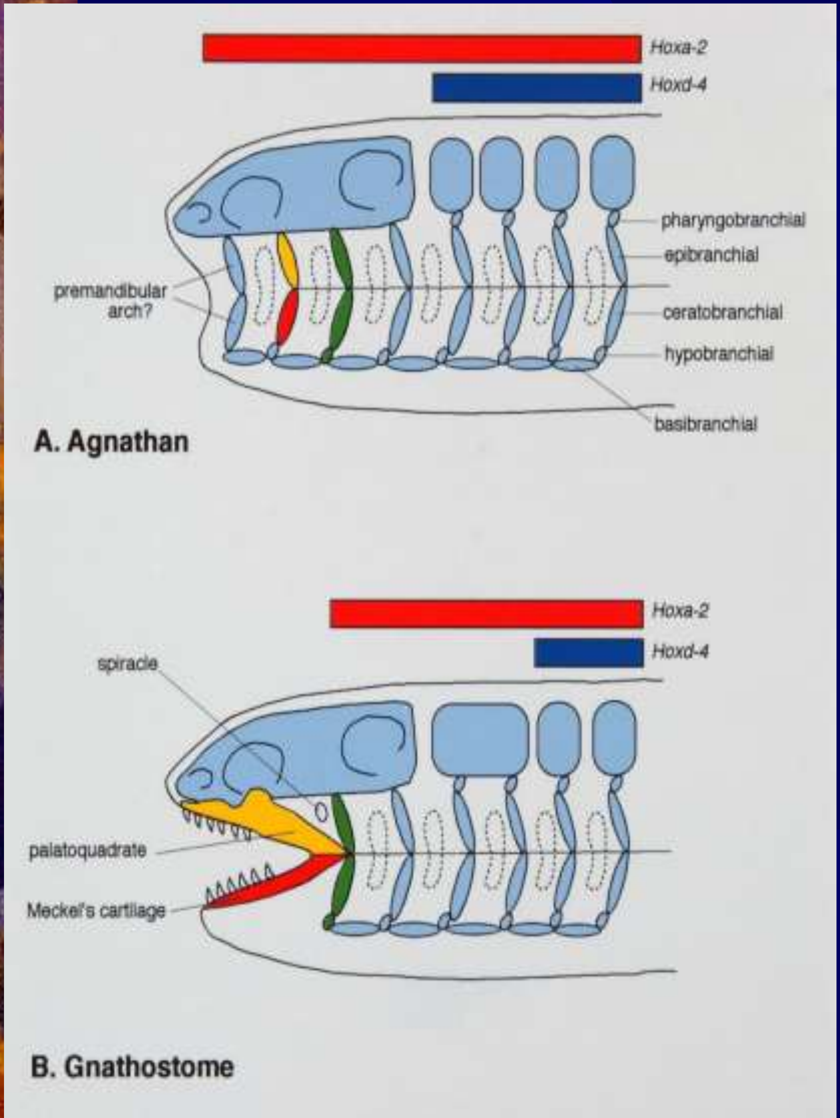
By Murray C Meikle

Biological Foundations of Orthodontics and Dentofacial Orthopaedics

Seminar 6

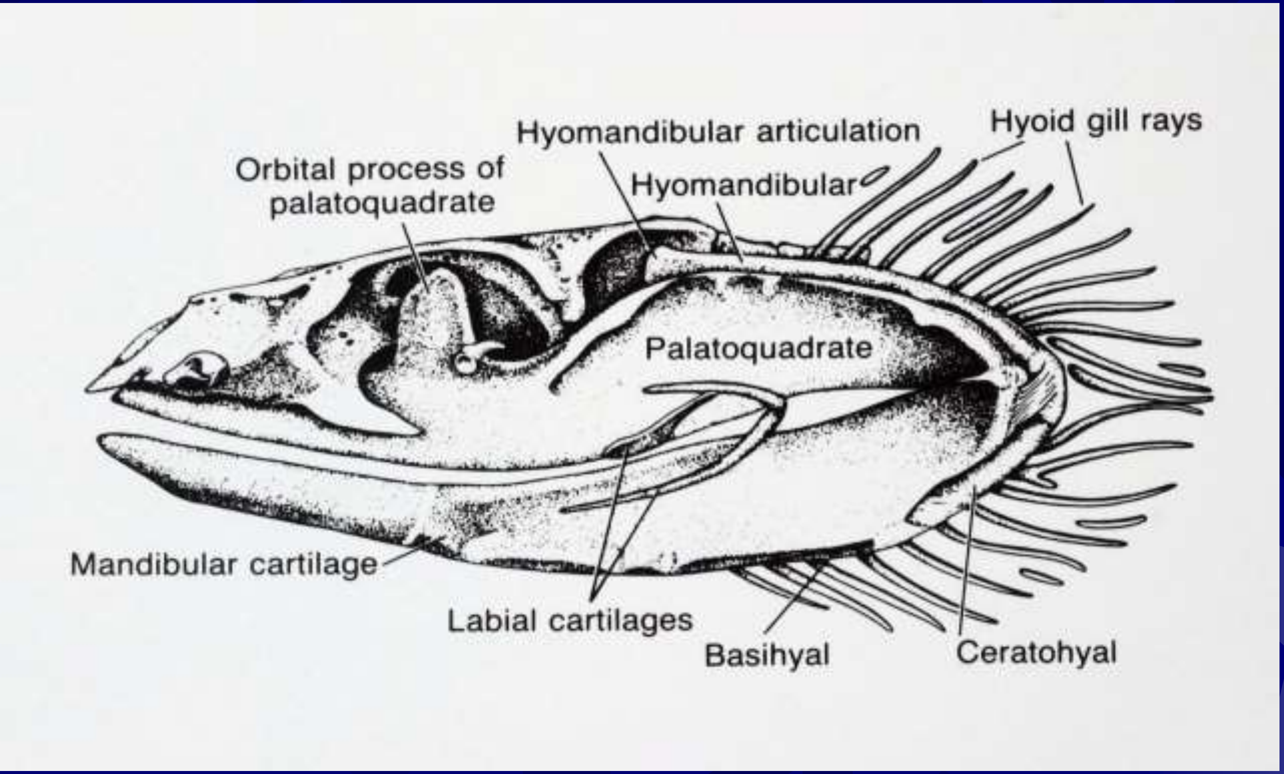
2004

Evolution of the jaws



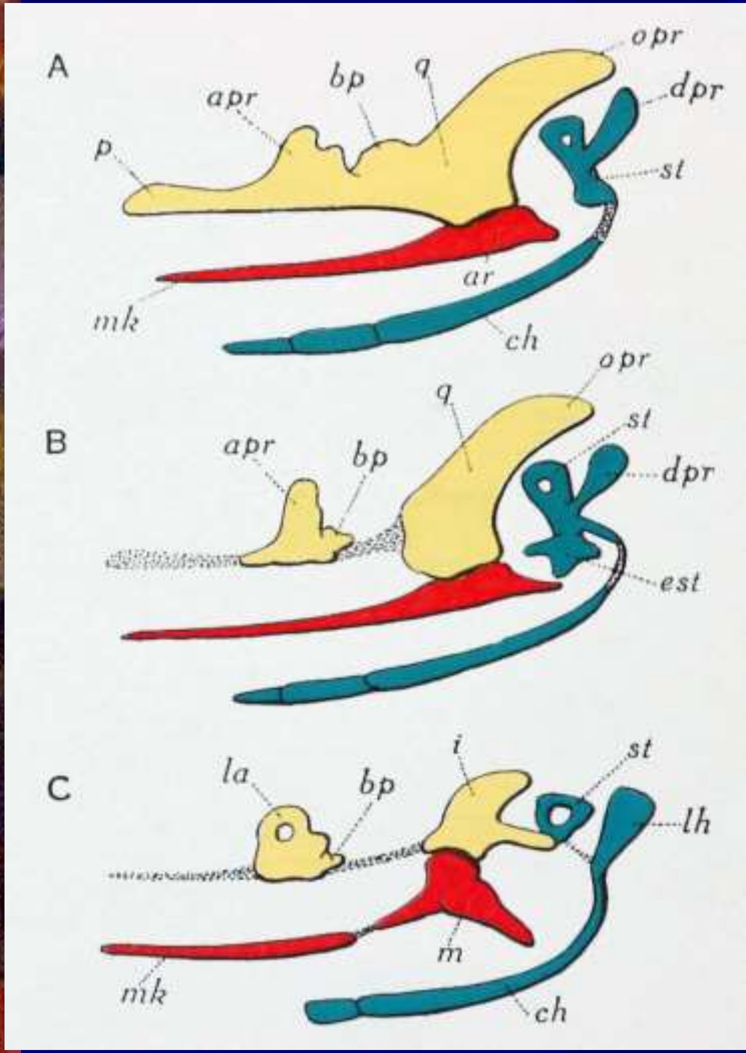
- At the beginning of gnathostome evolution a pair of visceral arch bars adjacent to the mouth appear to have been modified to form the skeletal elements of the jaws; the palatoquadrate and Meckel's cartilages are generally regarded as being homologous with the first arch cartilages of jawless agnathans.
- *Hoxa-2* knockouts in mice suggest that a key evolutionary innovation was the retreat of *Hoxa-2* expression which was permissive of jaw formation. A similar retreat of *Hoxd-4* has been proposed to account for the formation of the post-otic skull from the rostral agnathan vertebrae.
- Modified from Romer (1977). *The Vertebrate Body.* Mark *et al*. (1995). *Developmental Biology* **6**, 275–284.

Second arch cartilages



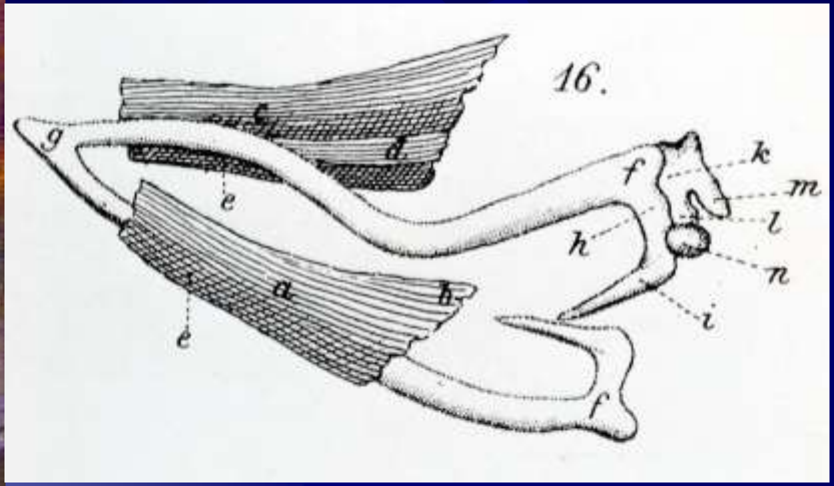
- In fish the second branchial arch cartilages became modified to form specialized jaw supports. The ceratohyal and the basihyal support Meckel's (mandibular) cartilage; the epibranchial (hyomandibular) element supports the palatoquadrate cartilage, braced against the otic region of the chondrocranium.
- From Romer (1977), *The Vertebrate Body*.

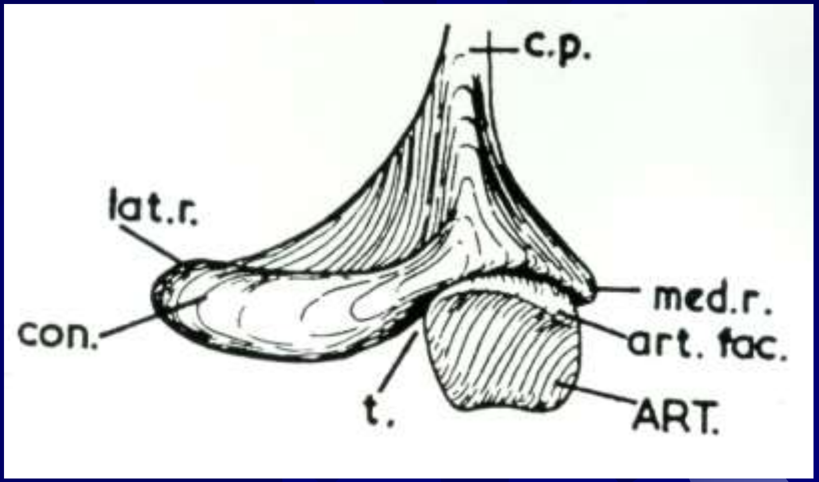
Fate of the mandibular and hyoid arch cartilages



- Fish 'hear' through their lateral line organs by sensing the movement of water produced by sound waves. Since air is too thin to permit hearing by this method, terrestrial vertebrates had to evolve a new mode of hearing.
- In osteichthyans both first ach cartilages became ossified at the articulation between the upper and lower jaws to form the articular and quadrate bones.
- With the development of the mammalian dentary–squamosal joint they no longer served an articular function, becoming the malleus and incus. The stapes is derived from the hyoid or 2nd branchial arch. A, primitive tetrapod; B, modern reptile; C, mammal.
- From Goodrich (1930). *Studies on the Structure and Development of Vertebrates.*

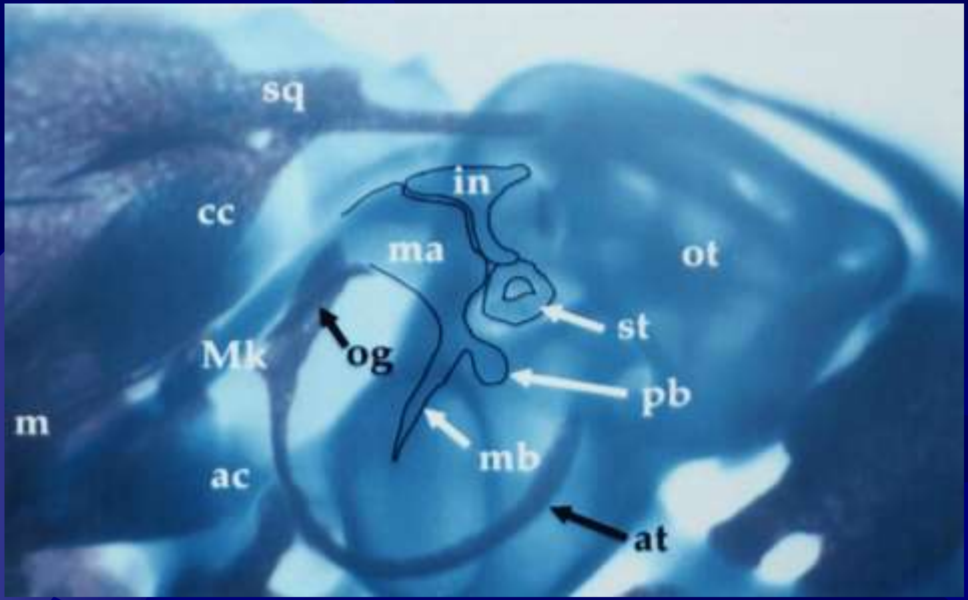
Double jaw articulation





- The theoretical basis for the homologous relationship between the reptilian articular and quadrate bones and the mammalian malleus and incus was provided by Meckel (1820) and Reichert (1837) and became known as Reichert's theory. The left figure is from Reichert's 1837 paper. Meckel's cartilage (e); alveolar bone (a).
- The prediction that during mammalian evolution animals with paired articular–quadrate and dentary–squamosal joints must have existed was confirmed by the fossil record. The first to be discovered was a small Triassic mammal-like reptile discovered in South Africa in 1924 and 1926 and named *Diathrognathus broomi.* ART, articular bone; con, condyle from Crompton and Parkyn (1963). *Proceedings of the Zoological Society of London* **140,** 697–749.

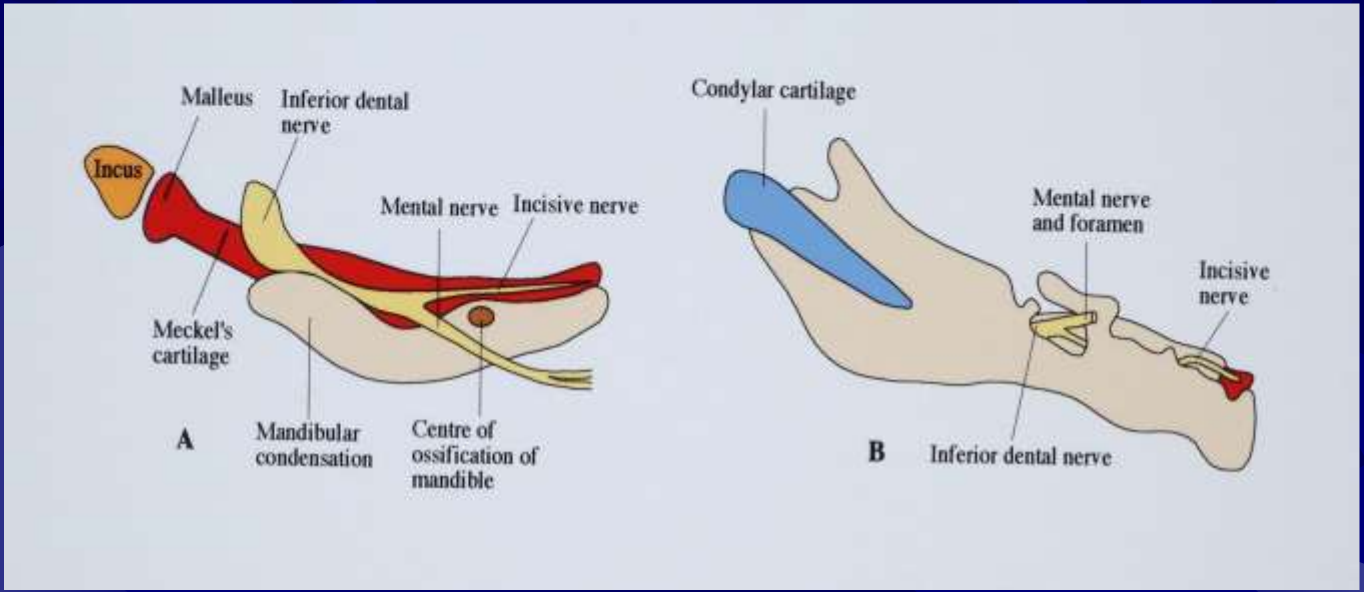
Development of the CMJ



Whole mount preparation E19.5 mouse stained with alcian blue and alizarin red. Courtesy of A AbdelFattah.

- In this figure a double joint can be observed.
- The CMJ between the condyle (cc) and squamosal bone (sq)
- The proximal end of Meckel's cartilage (Mk), the malleus (ma) articulates with the incus (in) which in turn articulates with the stapes (st)
- Processus brevis (pb); manubrium (mb); angular cartilage (ac); otic capsule (ot); os gonial (og); tympanic ring or annulus tympanicus (at) which is a bone of dermal origin homologous to the angular bone of the reptilian lower jaw.

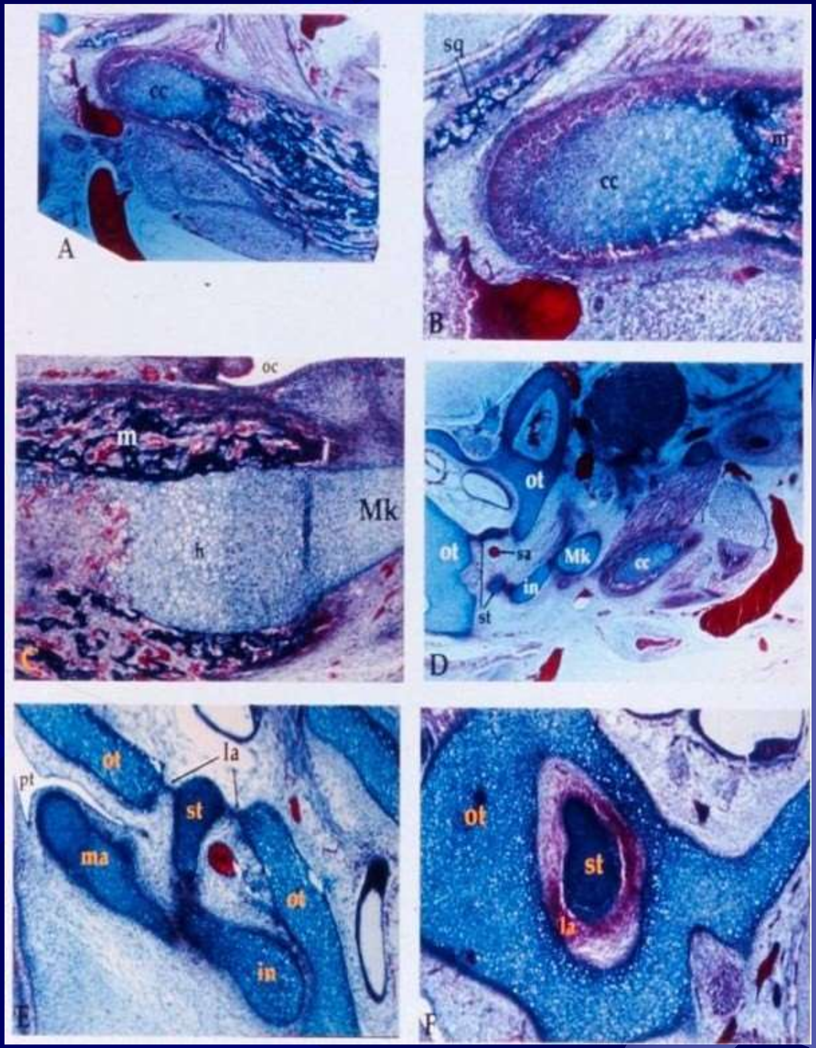
Development of the mandible



- Right side of the human mandible at the 19 mm C–R stage. An ossification centre has appeared at the bifurcation of the inferior dental nerve into its mental and incisive branches.
- Human mandible at the 55 mm C–R stage. The condylar cartilage has appeared; the coronoid cartilages appear at the 80 mm stage and the symphyseal cartilage at the 100 mm stage to unite the two halves of the mandible.
- Redrawn from Fawcett (1924). *The Growth of the Jaws, Normal and Abnormal in Health and Disease.* Dental Board of the United Kingdom.

Early craniomandibular joint and middle ear development

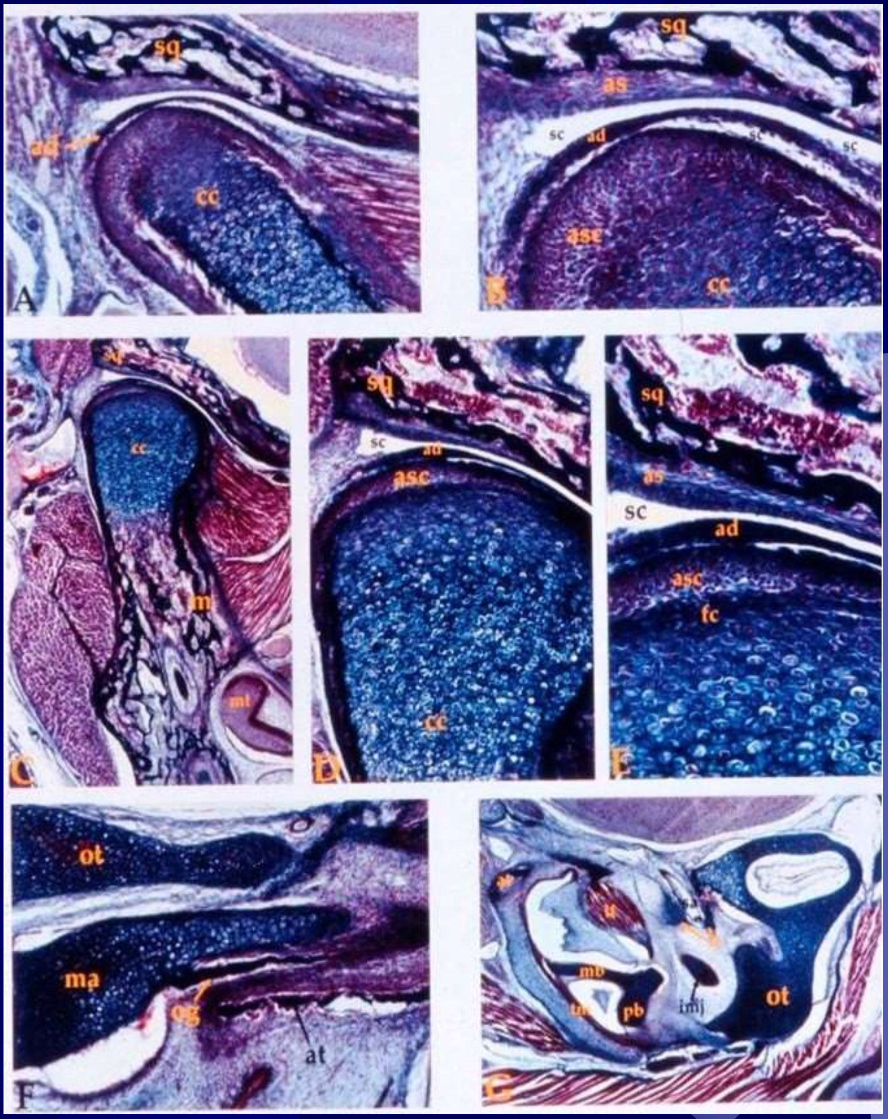
- A,B. E16.5 mouse; articulation between the condylar cartilage (cc) and squamosal bone (sq)
- C. Meckel's cartilage (Mk) is ensheathed by bone (m).
- D. Transverse section through the middle ear.
- E. Coronal section of middle ear; the stapes (st) is held in the oval window of the otic capsule (ot) by the annular ligament (la); stapedial artery (sa).
- F. Parasagittal section of the otic capsule (ot). The footplate of the stapes (st) is held in place by the annular ligament (la). Otic capsule (ot).



Courtesy of A AbdelFattah.

Later craniomandibular joint and middle ear development

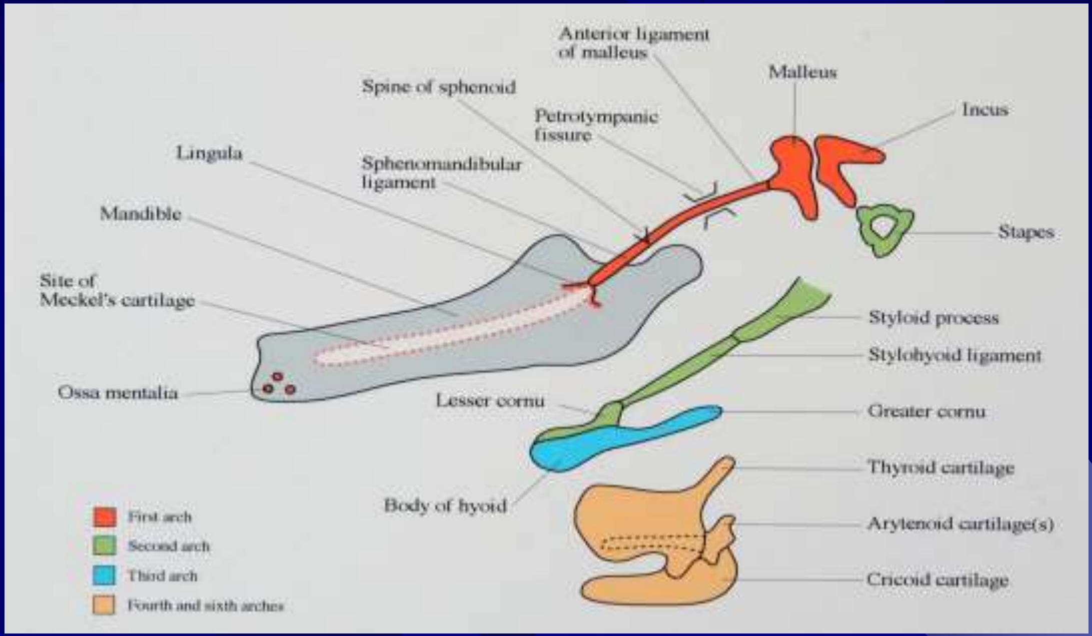
- A, B. Sagittal sections E18.5 mouse; articular disc (ad); squamosal bone (sq); condylar cartilage (cc); synovial cavity (sc).
- C-E. The morphology of the condyle is now well defined.
- F. Transverse section of malleus showing first signs of ossification of the malleus. Os goniale (og); malleus (ma); tympanic ring (at) and otic capsule (ot).
- G. Transverse section of middle ear P0. Manubrium (mb); processus brevis (pb); tensor tympani (tt) which inserts into the malleus; tympanic (at); tympanic membrane (tm).



Courtesy of A AbdelFattah.

Fate of Meckel's cartilage

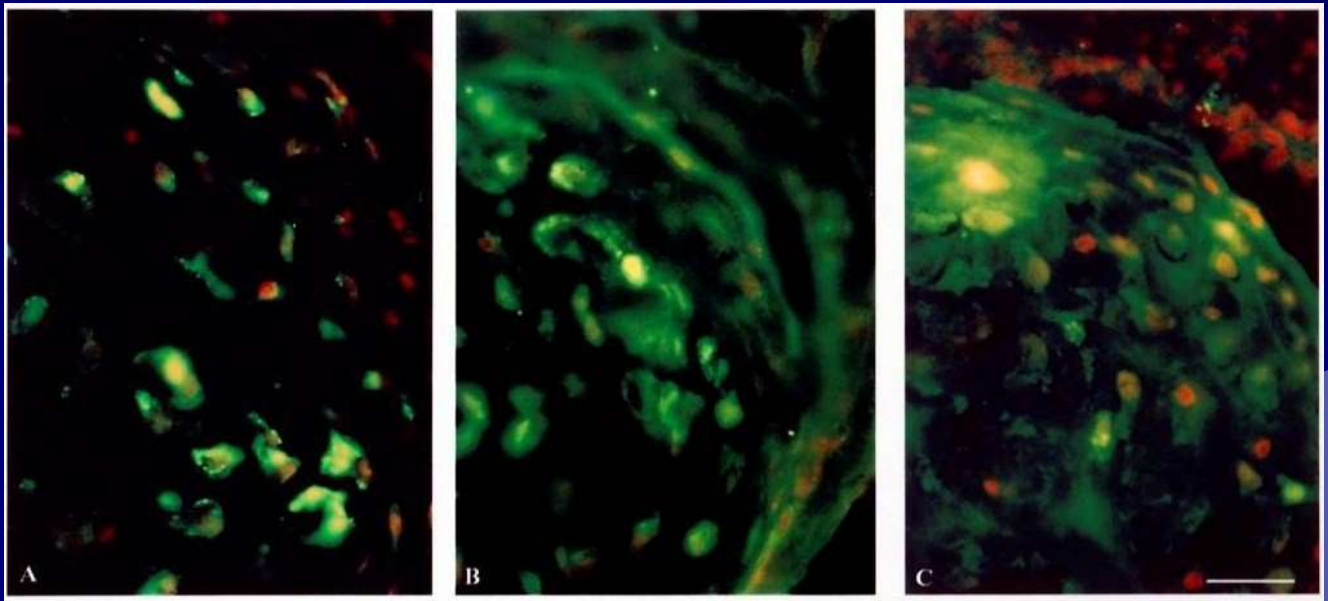
Redrawn from Wendell Smith *et al.* (1984), Basic Human Embryology.



- Meckel's cartilage serves as a morphological template for the embryonic mandible and disappears about the 24th week *in utero* except for ….
- (1) one or two remnants of cartilage (ossa mentalia) in the region of the symphysis which persist until birth; (2) lingula at the medial edge of the inferior dental foramen to which the sphenomandibular ligament is attached; (3) the perichondrium persists as the sphenomandibular ligament and anterior ligament of the malleus; (4) the dorsal end ossifies to become the malleus.

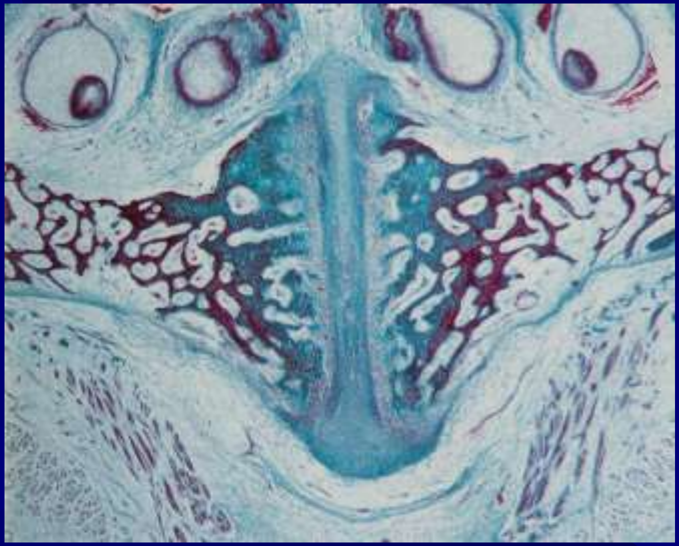
MMP-mediated degradation of Meckel's cartilage

Courtesy of J J W Breckon.



- There is evidence to suggest that MMP–mediated matrix degradation may be involved in the involution of Meckel's cartilage.
- Immunofluorescent detection of TIMP-1 (A), gelatinase-A (B) and collagenase (C) in Meckel's cartilage from 24-26 day *pc* rabbit embryos. TIMP-1 shows intracellular staining within chondrocytes. Cartilage matrix adjacent to positive chondrocytes shows intense staining for gelatinase-A and collagenase. Bar measures 20 µm.

Secondary cartilages

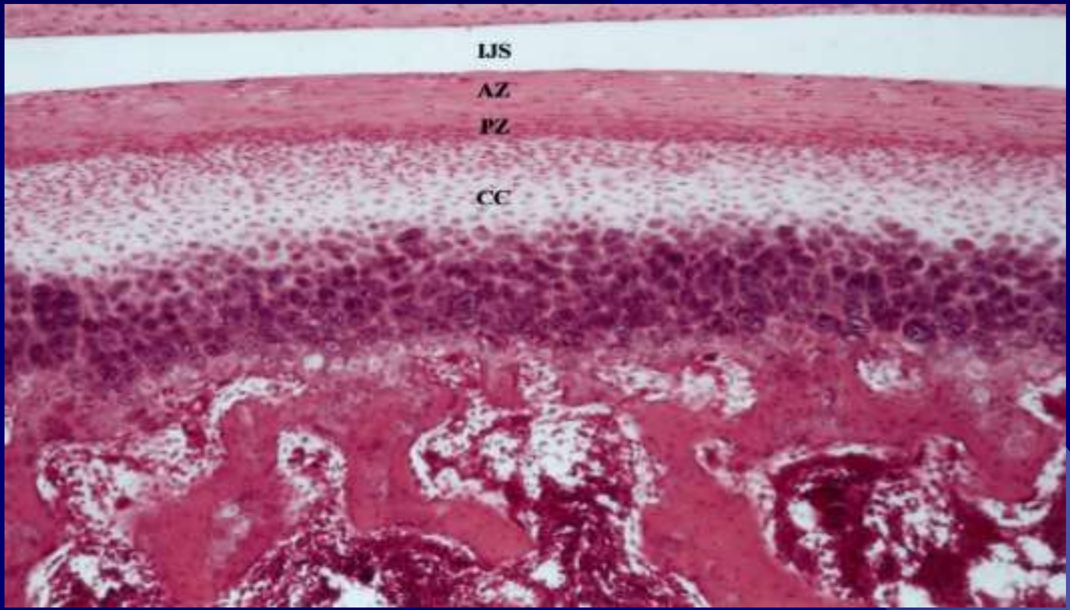


From Meikle (2002), *Craniofacial Development, Growth and Evolution*.

- The mandible is a dermal bone but its growth is modified by the development of secondary (accessory) cartilages. The condylar cartilage (right) appears during the 12th week (50 mm C–R stage). By the 5th month much of the original cartilage has ossified apart from a narrow cap beneath the articular surface.
- At the 80 mm stage the coronoid cartilage forms a strip along the anterior border of the coronoid process, but disappears before birth. The symphyseal cartilage (left) appears at the 100 mm stage; bone formation at this site ceases during the first year after birth.

Structure of the mandibular condyle

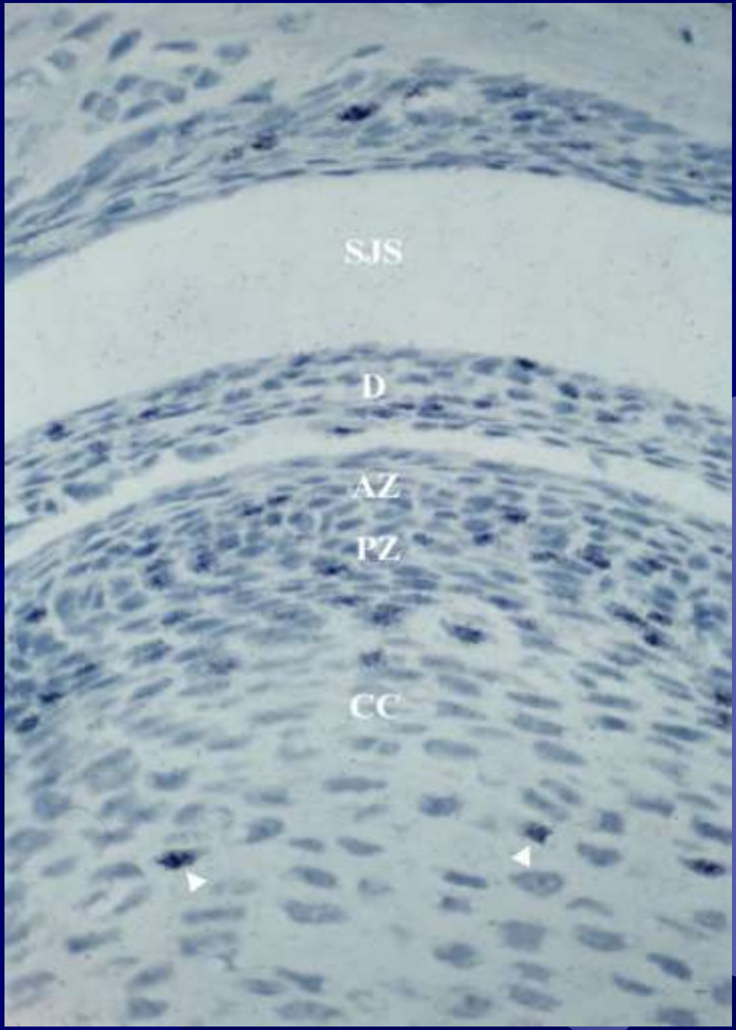
Sagittal section through the head of the condyle; human aged 10-12. Original magnification x20.



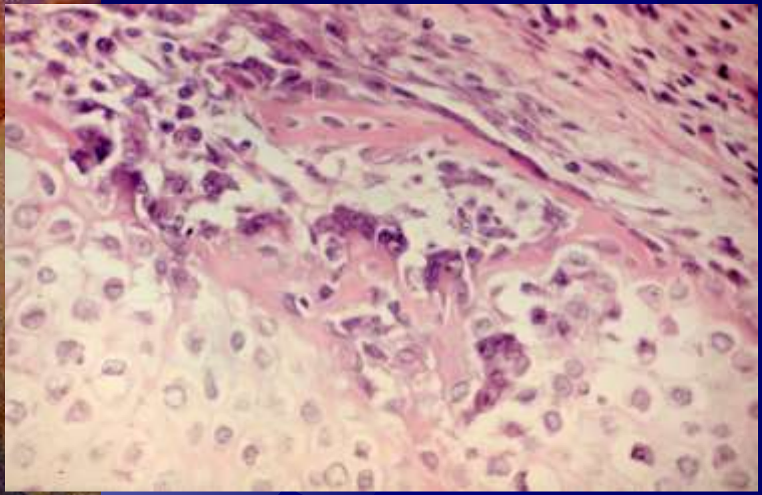
- Three distinct layers can be distinguished in the mandibular condyle.
- (1) An articular zone (AZ) composed of fibrous connective tissue; in response to mechanical loading some cells differentiate into chondrocytes so that in time the layer becomes fibrocartilaginous. IJS, inferior joint space.
- (2) A proliferative zone (PZ) of undifferentiated mesenchymal cells; and (3) a zone of cartilage (CC) composed of chondrocytes synthesizing a matrix of type II collagen and proteoglycans. The cartilage becomes progressively replaced by bone through endochondral ossification.

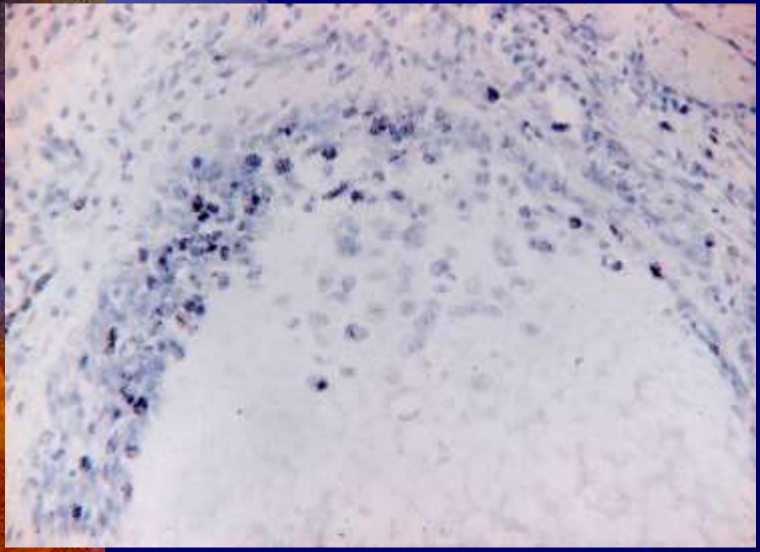
Chondrogenesis at the condyle

- Autoradiographic studies have shown that the cells of the proliferative zone give rise to the chondroblasts of the condylar cartilage. Once these cells have differentiated into chondroblasts they do not divide. SJS, superior joint space; d, disc; AZ, articular zone; PZ, proliferative zone; CC, condylar cartilage. ^{3}H-thymidine autoradiograph. X350.
- The majority of labelled cells are located within the PZ. Arrowheads indicate labelled cartilage cells.
- Unlike interstitial cartilage growth at the epiphyseal plate of a long bone, chondrogenesis at the condyle is appositional and the cells are not arranged into parallel columns.



Condylar cartilage is the product of periosteal chondrogenesis

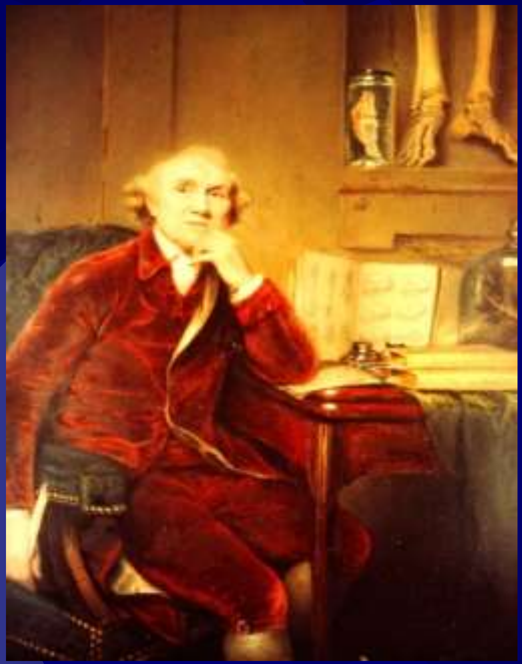


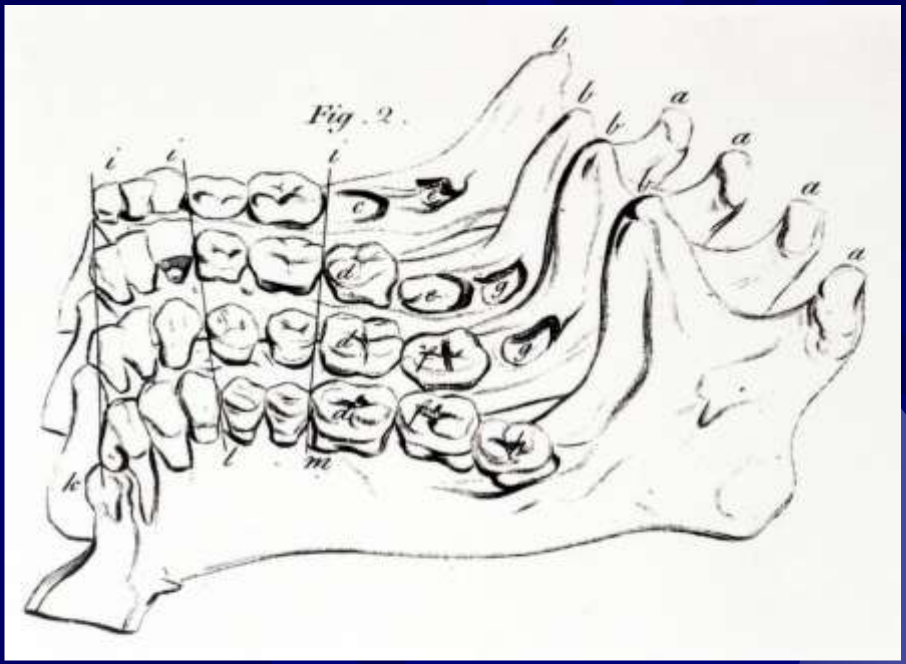


- If the rat CMJ is transferred into a non-functional environment chondrogenesis ceases and the cells of the PZ differentiate into osteoblasts.
- The AZ and PZ of the condyle are derived from the fibrous and cellular layers of the periosteum.
- The change from the normal osteogenic function to chondrogenesis has resulted from the development of a condylar process, and the altered functional demands placed on the periosteum covering the articular surfaces.

Top figure shows a condyle 5 days post-transplantation; lower, autoradiograph from host labelled with ^{3}H-thymidine.

Postnatal growth and remodelling

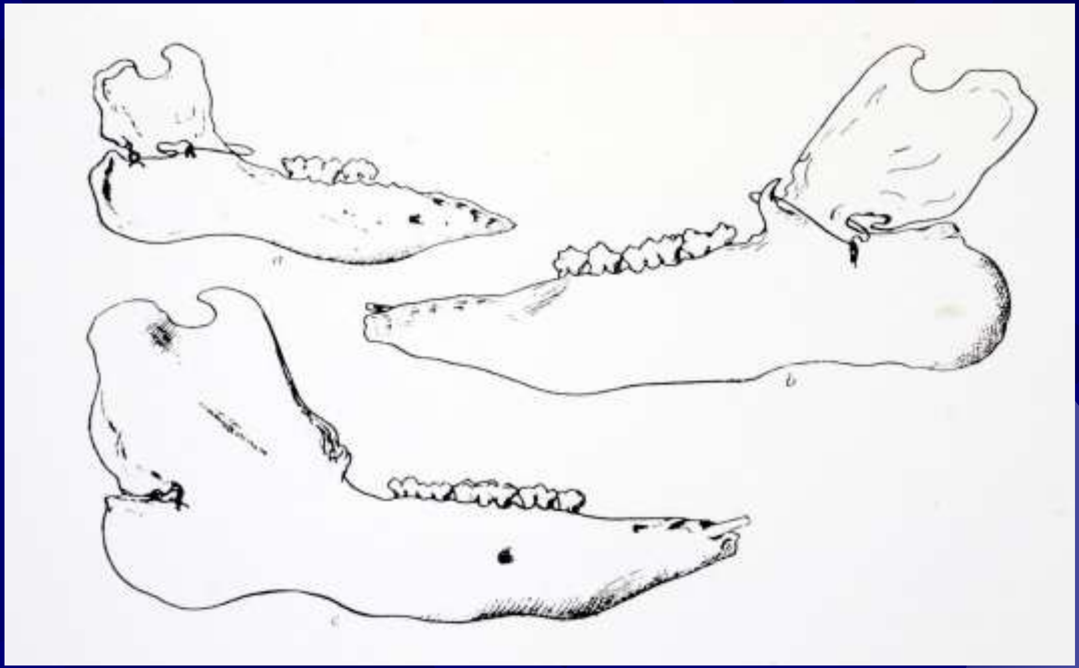




- This famous illustration from *The Natural History of the Human Teeth* (1778), was used by John Hunter to show that the jaws lengthen only at their posterior ends, and that the distance between the symphysis and the sixth tooth (first molar) does not increase in length. Considering the data are cross-sectional his observations turned out to be remarkably accurate.
- Hunter (painted here by Sir Joshua Reynolds) was also the first to realise that bone growth involved resorption as well as deposition, if the shape and proportions of a bone were to be maintained as it increased in size.

On the growth of the jaws

From Humphry (1866), *Transactions of the Cambridge Philosophical Society.*

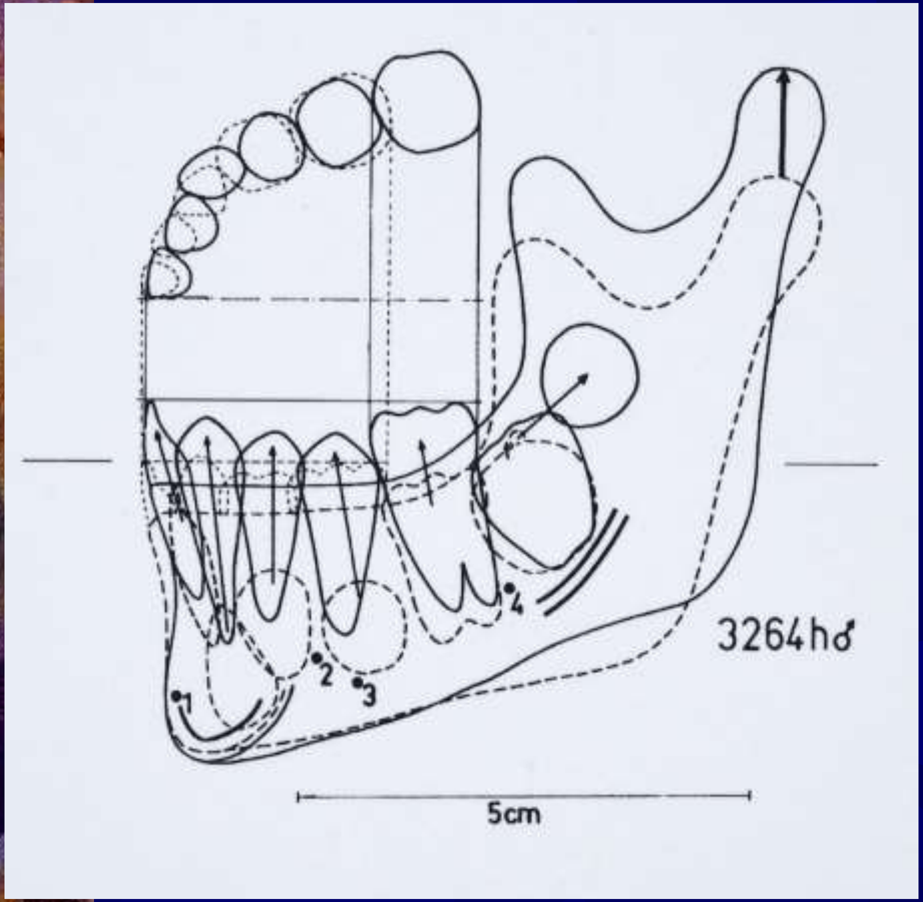


- Illustration from Sir George Humphry's paper 'On the growth of the jaws' confirming Hunter's observation that bone growth involved two processes: deposition and resorption.
- Wires were inserted into the mandibles of young pigs to encircle the anterior and posterior borders of the vertical rami. On sacrifice the anterior rings were either projecting beyond the anterior border or lying free from resorptive remodelling, while the posterior rings had become firmly embedded in bone.

Remodelling the human mandible

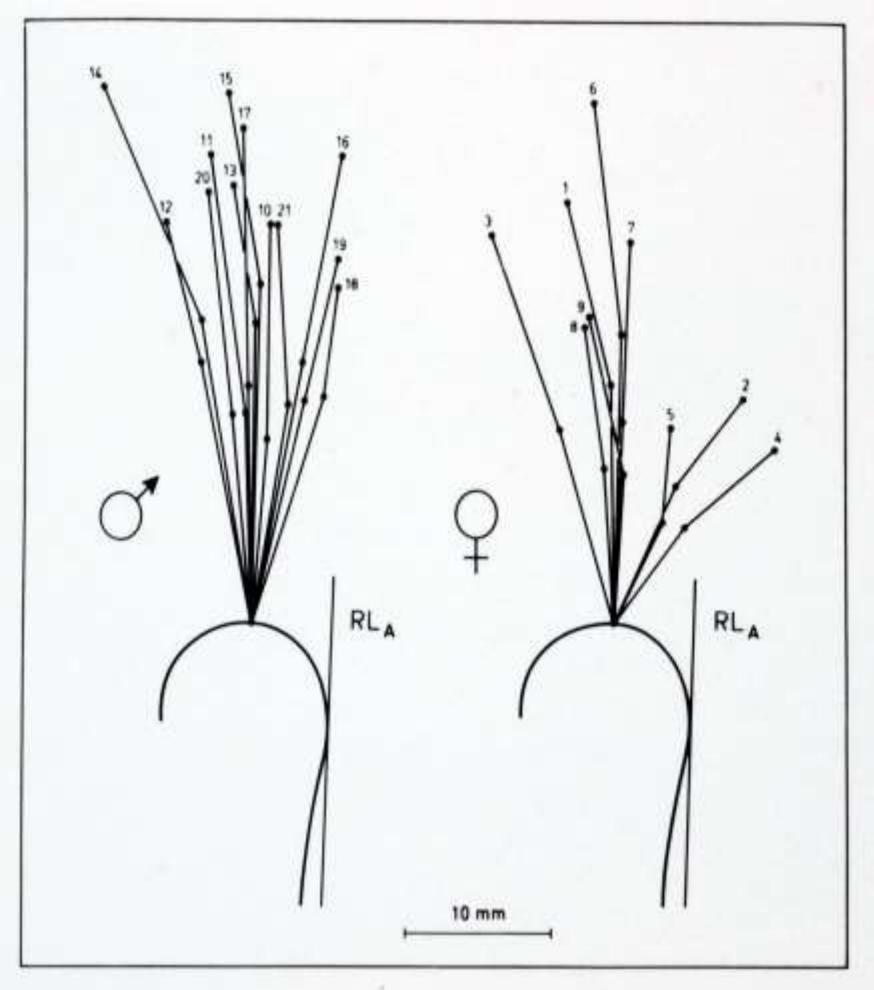
- Our current knowledge of the complex patterns of surface remodelling at the histological level is largely due to the work of Enlow, who serially sectioned human mandibles in the primary and mixed dentition (from 4 to about 12 years).
- This master diagram is a composite of all the various regional growth and remodelling movements occurring during postnatal growth. Directions of growth are indicated by arrows.
- From Enlow and Harris (1964). *American Journal of Orthodontics* **50**, 25–50.

Björk and the implant method



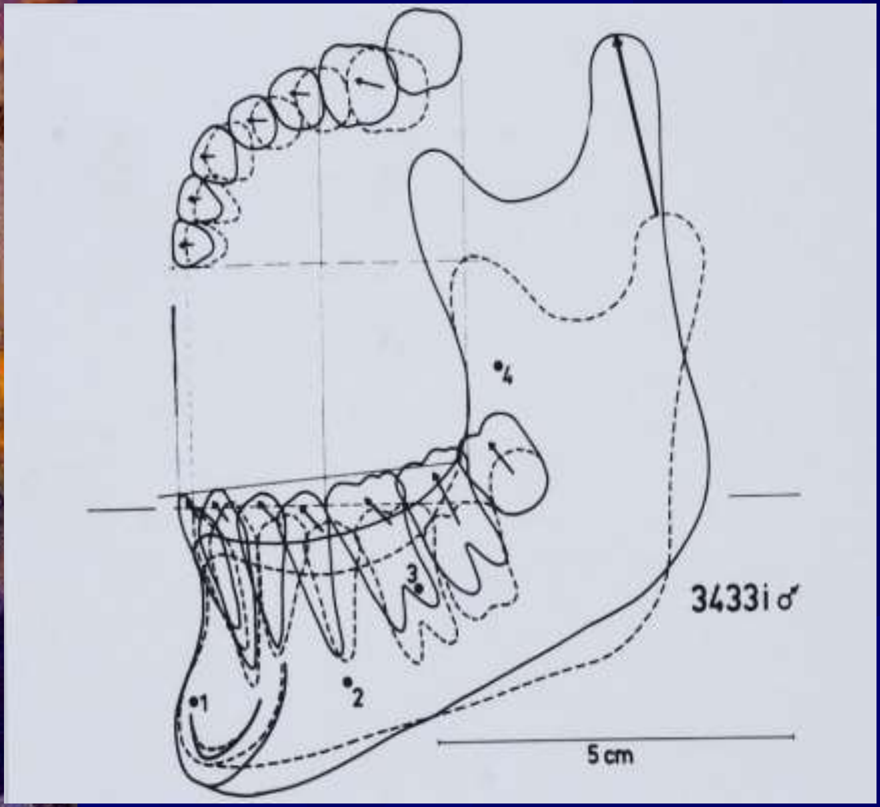
- Björk pioneered a technique at the Royal Dental College, Copenhagen in 1951 for inserting tantalum implants subperiosteally into the maxilla and mandible at sites where they were unlikely to be dislodged by resorptive bone remodelling.
- These were used to provide stable reference points on which to superimpose tracings of cephalometric radiographs from the subjects that formed the longitudinal Copenhagen growth study.
- From Björk (1963). *Journal of Dental Research* **42**, 400–411.

Variability in condylar growth direction



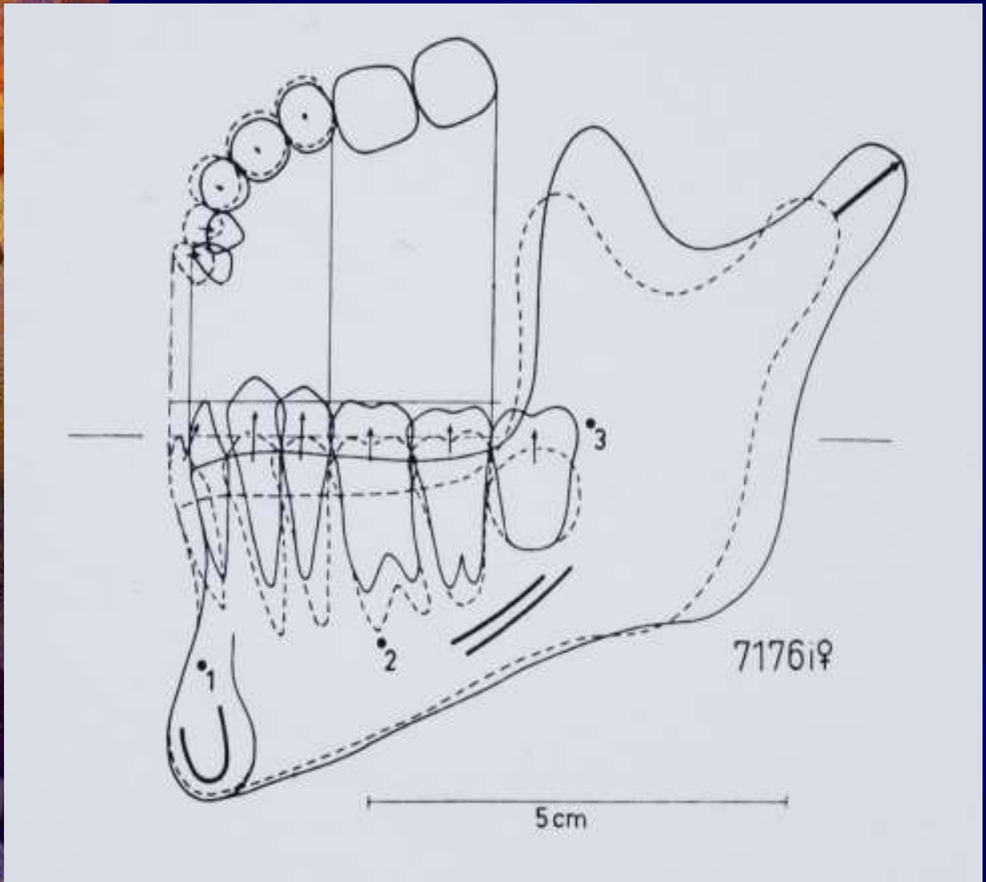
- Illustration of the wide variability in condylar growth direction (as revealed by cephalometric tracings superimposed on implants at 3-year intervals) over a 6-year period in relation to the ramus line (RL).
- The direction of growth in most cases followed a path that curved forwards and was strongly correlated with rotation of the mandible; in case 4, however, there was a backward curvature of 13^0 and in case 2 of 15^0.
- From Björk and Skieller (1972). *American Journal of Orthodontics* **62**, 339–393.

Forward growth rotation



- A case from the Copenhagen growth study superimposed on mandibular implants illustrating the extreme direction of vertical growth at the condyles in the male sample. The clinical outcome is a mandibular forward growth rotation.
- Broken line, 11 years 7 months; solid line, 17 years 7 months.
- In convential cephalometry without the aid of implants, rotary movements of the mandible are masked by compensatory surface remodelling at the posterior and lower borders.
- From Björk (1963). *Journal of Dental Research* **42**, 400–411.

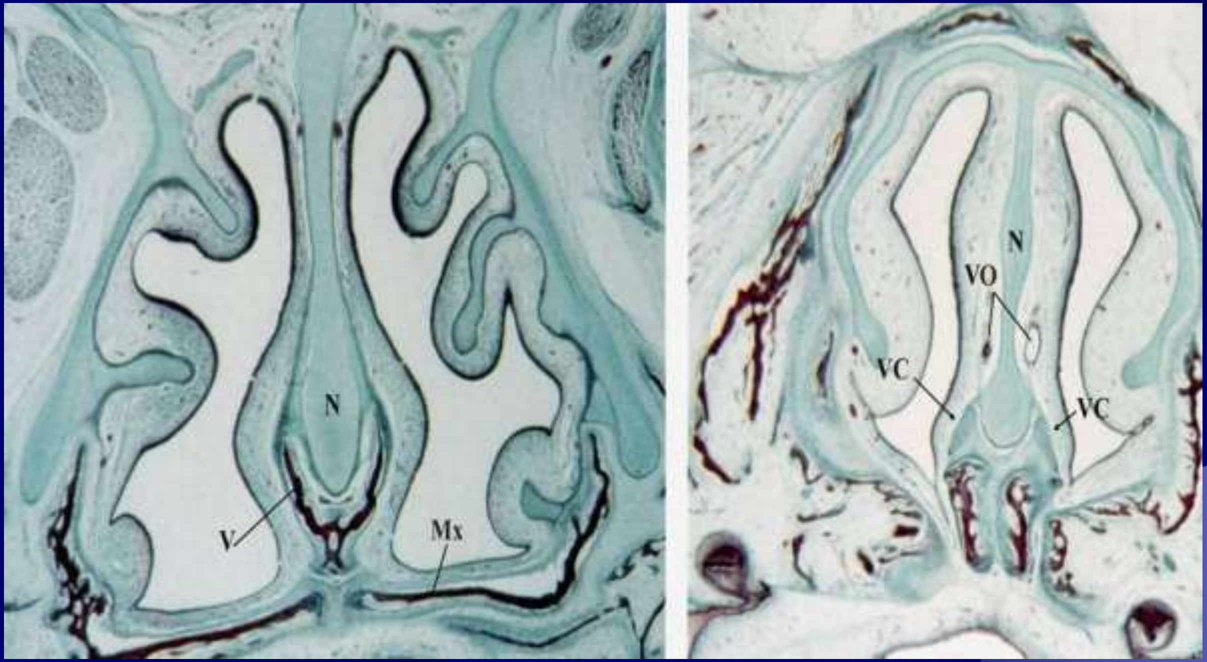
Backward growth rotation



- Case illustrating the extreme direction of sagittal growth in the female sample. The clinical outcome is a mandibular backward growth rotation.
- Broken line ,10 years 6 months; solid line, 15 years 6 months.
- This diagram also shows that in the absence of implants, three internal structures (1) the outline of the inner cortical plate at the symphysis, (2) the mandibular canal and (3) the lower contour of the third molar tooth germ can be used to superimpose mandibular tracings. These are usually referred to as Björk's structures.
- From Björk (1963). *Journal of Dental Research* **42**, 400–411.

Development of the nasomaxillary complex

From Meikle (2002). *Craniofacial Development, Growth and Evolution*.

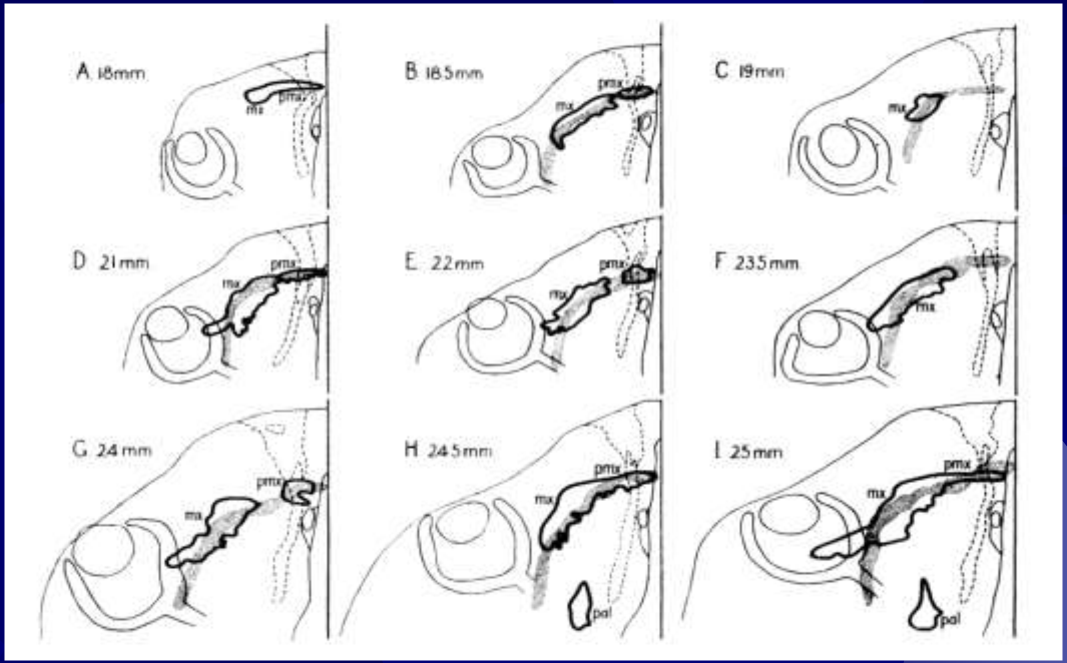


- Following fusion of the palatal shelves, further development of the medial nasal, lateral nasal and maxillary processes forms the cartilages and bones of the nasomaxillary complex.
- These figures are from a human fetus of 8 mm C-R length. x20. The vomer (V) and maxilla (Mx) have started to ossify. Right is a section through the anterior part of the nasal cavity from the same specimen.

  N, nasal septal cartilage. VO, vomeronasal organ; VC, vomeronasal cartilages.

Formation of the maxillary complex

From Chase (1942). *Journal of the American Dental Association* **29**, 1991–2001.

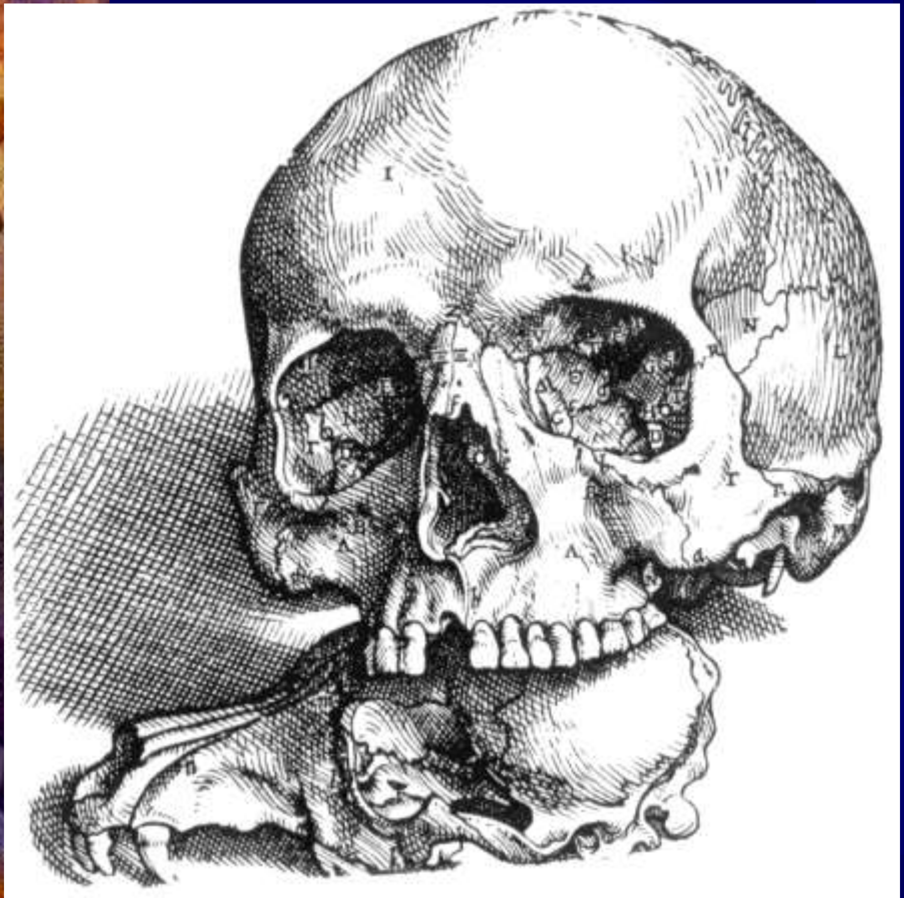


- Each maxillary bone develops from two ossification centres; the posterior gives rise to the maxilla proper and the anterior to the premaxilla. The main centre appears above the deciduous canine where the infraorbital nerve gives off the superior dental branch. Osteogenesis spreads from these centres in several directions.
- The maxilla is augmented by the palatine bone from behind and by the premaxilla in front.

The problem of the premaxilla

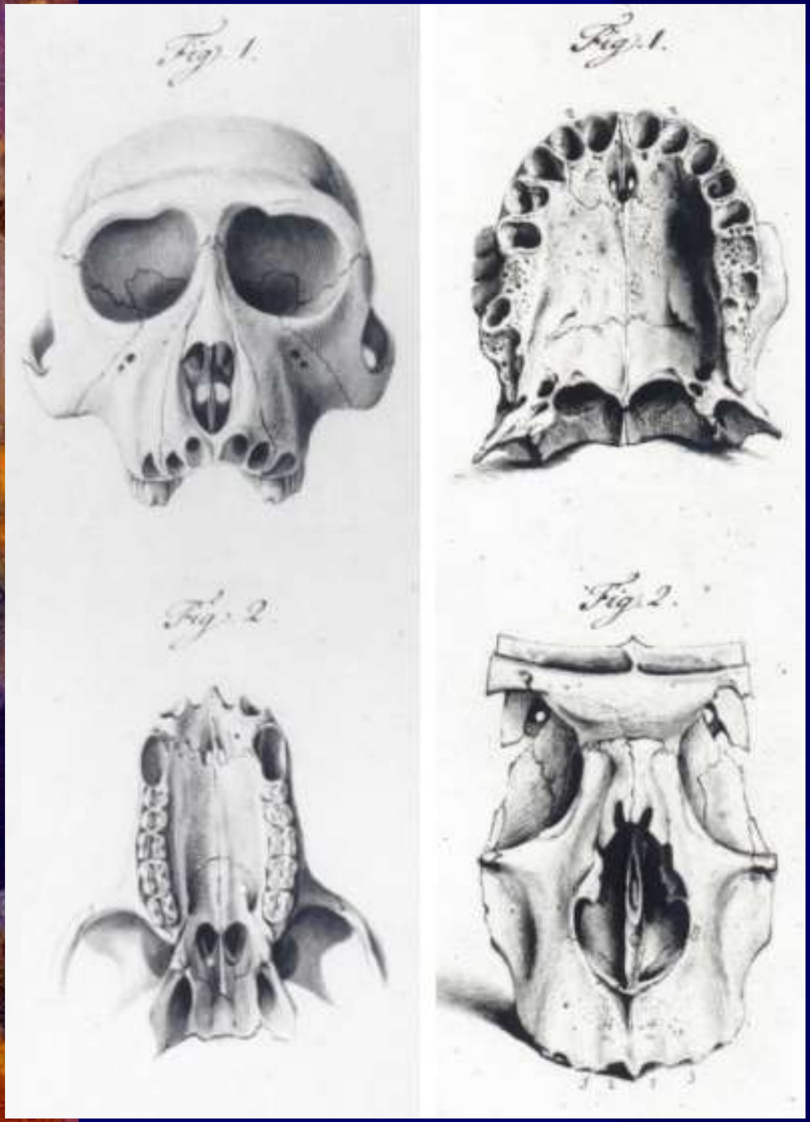
- The premaxilla (*os incisivum*) is customarily defined as the part of the upper jaw that carries the incisor teeth. In non-human primates as well as the hominid *Australopithecus africanus*, a clearly defined premaxillary–maxillary suture is evident on the facial surface.
- In *Homo sapiens* no such suture is evident and there has been controversy as to whether this bone exists ever since the publication of *De Humani Corporis Fabrica* in 1543 by Vesalius.
- The figure is the title page showing Vesalius giving a public anatomy demonstration.

Woodcut from the *liber primus*



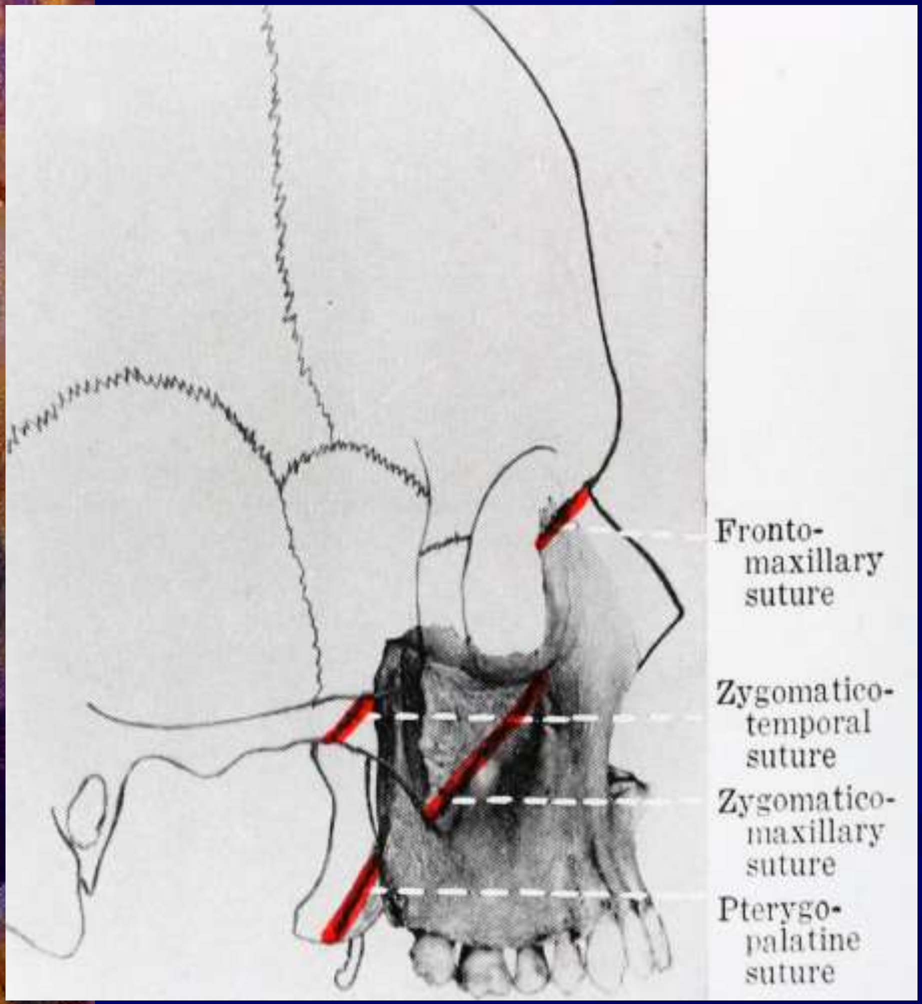
- Vesalius used this illustration twice as a chapter heading. The main purpose was to show that Galen had described the premaxillary bone and suture of the dog as though present in man, and therefore could not have been familiar with human anatomy.
- This discovery was one of the factors leading to the ultimate overthrow of Galenical anatomy, which had remained unquestioned for 1300 years.
- The teaching of ancient authorities was consequently undermined, which created a new atmosphere of enlightened enquiry based on personal observation and experience.

Goethe and the premaxilla



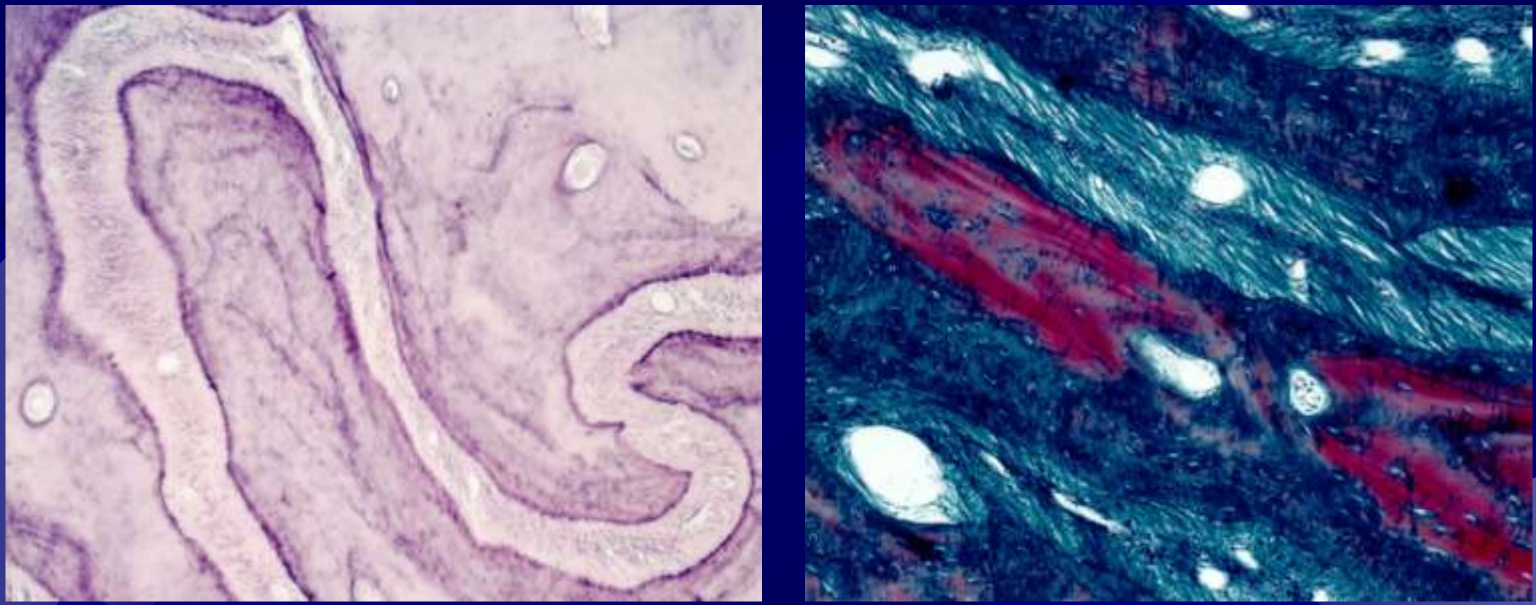
- In the late 18th, early 19th century the existence of the premaxilla was part of a wider debate as to what distinguished humans from the animal world.
- The premaxilla is a constant feature of nonhuman primates and its abrupt disappearance in man seems unlikely (an argument used by Goethe), since it is part of the archetype or standard form of all reptiles, birds and mammals.
- A premaxillary-maxillary suture is often visible on the palatal surface in humans and if the premaxilla does not exist how does one explain CL/P?
- Courtesy of Goethe- und Schiller-Archiv, Weimar, Germany.

Postnatal growth and remodelling



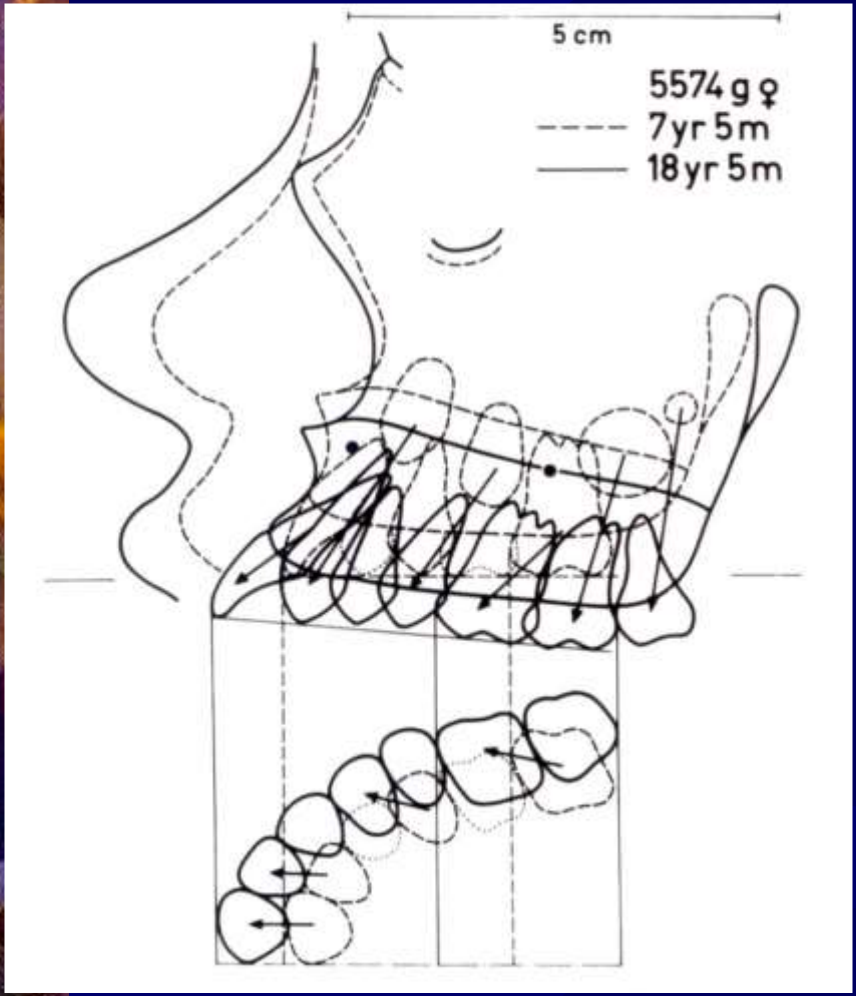
- The maxilla is a highly complex bone articulating by means of fibrous sutures with the nasal, frontal, lacrimal, ethmoid, zygomatic and vomer as well as the palatine bone and premaxilla.
- In contrast to calvarial sutures most of which have fused by the formation of osseus bridges by the third decade, with the exception of the midpalatal suture (30-35) some maxillary sutures can remain patent until the seventh decade.
- From Weinmann and Sicher (1947), *Bone and Bones: Fundamentals of Bone Biology*.

Structure of facial sutures



- Left. Numerous reversal lines are evidence of past remodelling activity; the absence of cellular activity is indicative of a quiescent suture. H&E stain, x75.
- Right. Complex patterns of remodelling with highly cellular new bone (blue) deposited on old bone (red) with a central zone of fibroblastic cells. Sutures consist of mainly type I collagen fibres and noncollagenous glycoproteins uniting adjacent bone surfaces. Mallory stain, x120.
- From Meikle (2002), *Craniofacial Development*, *Growth and Evolution*.

Growth of the maxillary complex

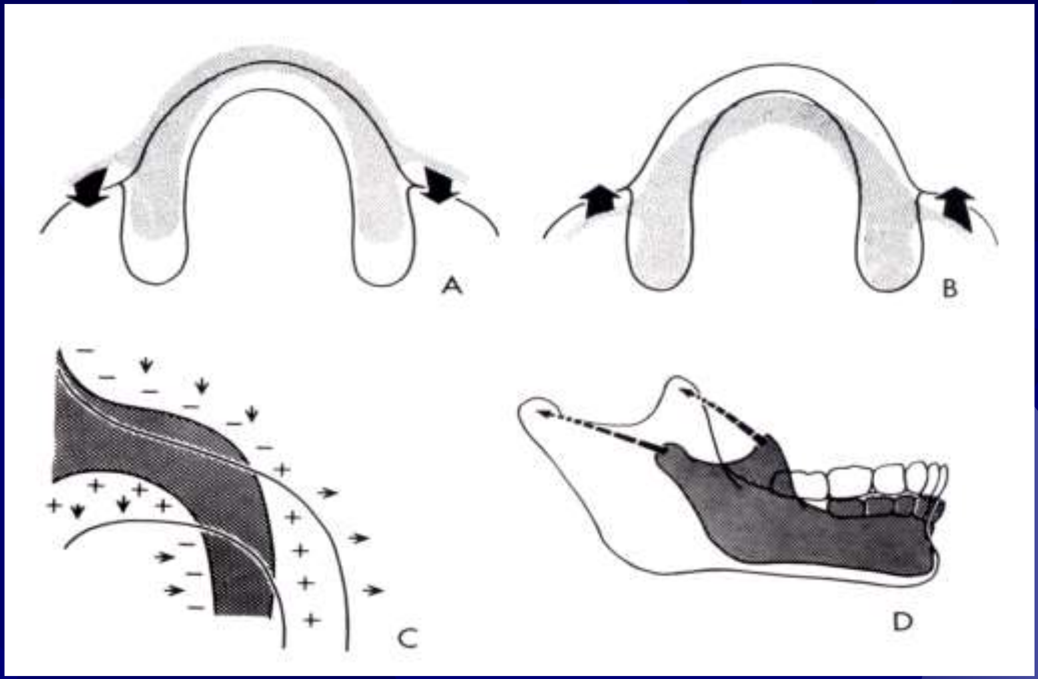


From Björk (1966). *Acta Odontologica Scandinavica* **24**, 109–127.

- Growth of the maxillary complex analyzed by the implant method. Growth in length is due to periosteal deposition at the maxillary tuberosity.
- Growth in height takes place at the frontonasal suture and by periosteal deposition at the alveolar process. The nasal floor is lowered by resorptive remodelling of the nasal surface of the palate, with concomitant deposition on the palatal surface.
- Also notable in this subject is the increased dentoalveolar prognathism and increase in arch width associated with eruption of the permanent teeth.

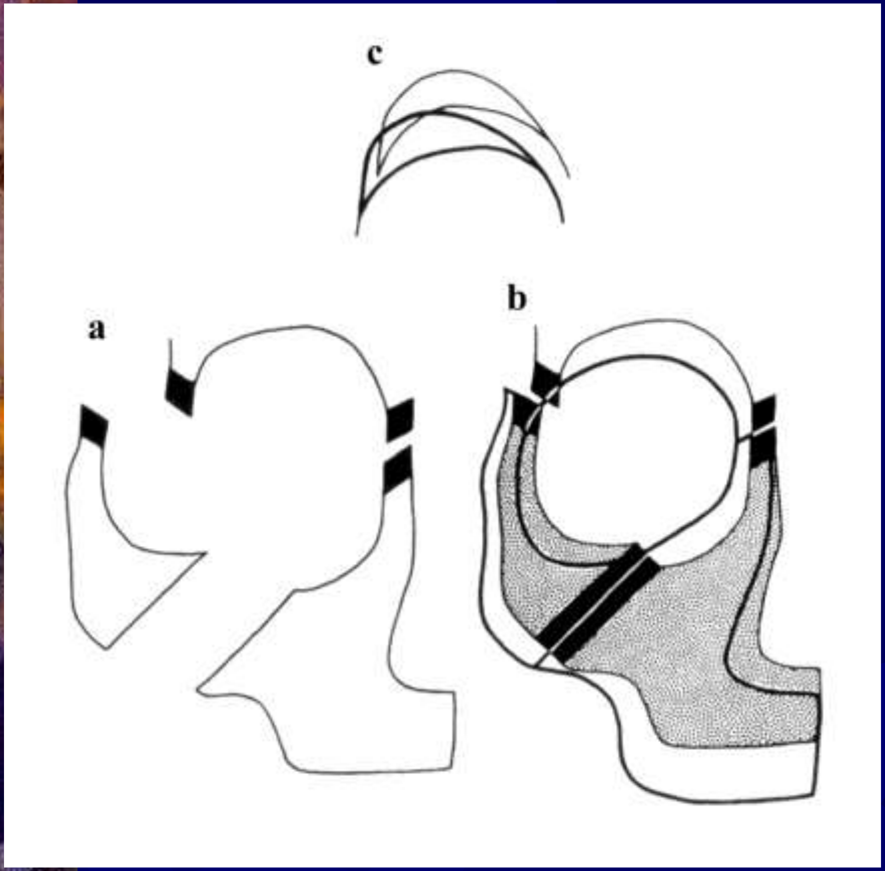
Surface remodelling of the maxilla

From Enlow and Bang (1965). *American Journal of Orthodontics* **51**. 446–464.



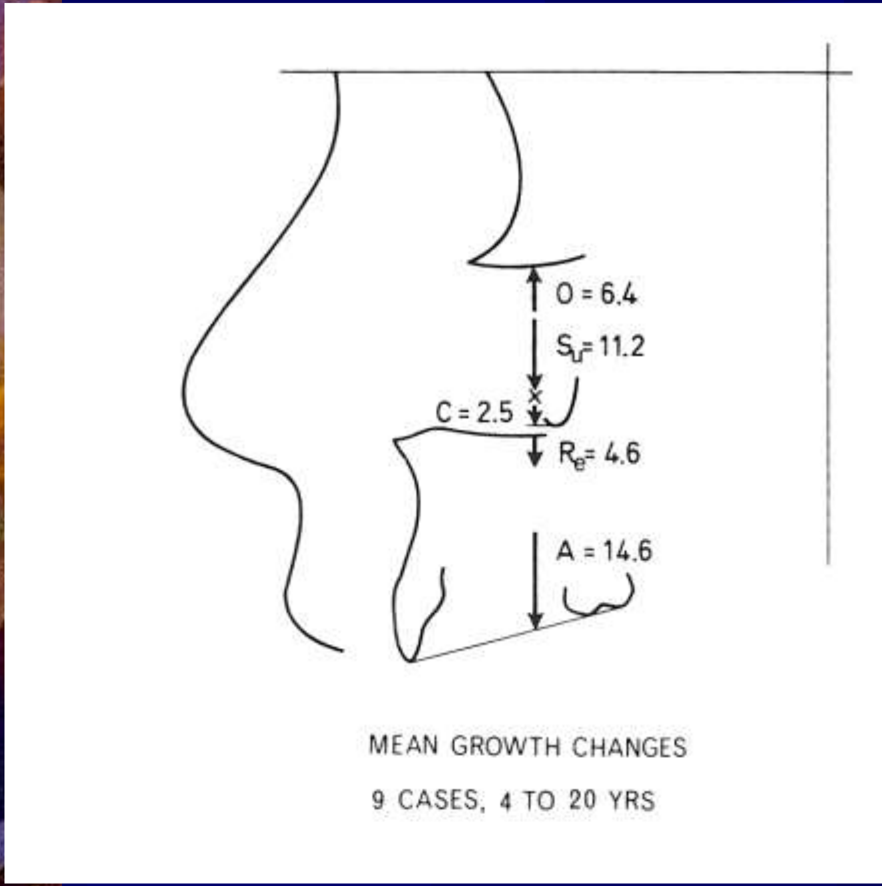
- Growth of the maxilla and zygomatic process based on the histological evidence. A. Bone is deposited along the posterior surfaces of the arch and at the tuberosity, as well as the posterior-facing surface of the zygoma.
- B. Shows the apparent direction of growth, resulting in forward movement of the maxillary complex. C. Complex patterns of resorption and deposition in remodelling the zygomatic process and arch. D. The generalized mode of maxillary growth closely parallels that of the mandible.

Sutural growth – histological evidence



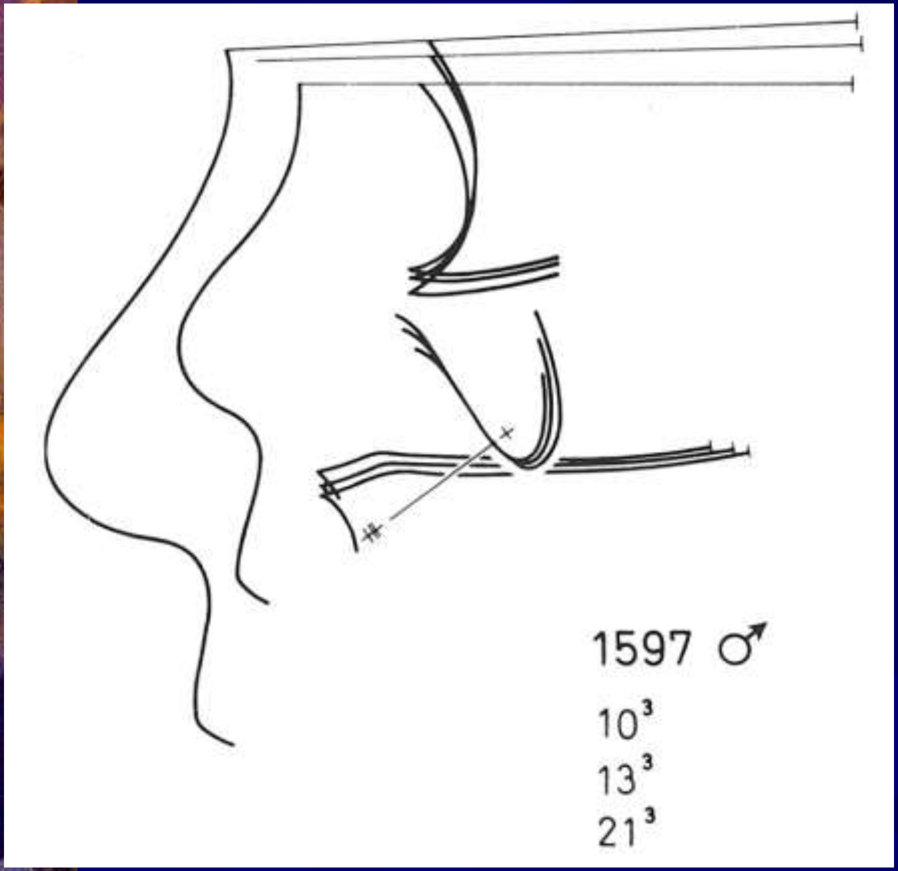
- The relative contributions of sutural and surface deposition to maxillary growth have been controversial. However, the studies of both Enlow and Björk emphasize the key role of sutural growth.
- In (a) the individual bones of the 6-year facial complex are separated to show new growth. In (b) the profile is superimposed over the 15-year face. In (c) the remodelling of the orbit relocates it in an upward and lateral direction.
- From Enlow and Hunter (1966). *American Journal of Orthodontics* **52**, 823–830.

Sutural growth – radiographic evidence



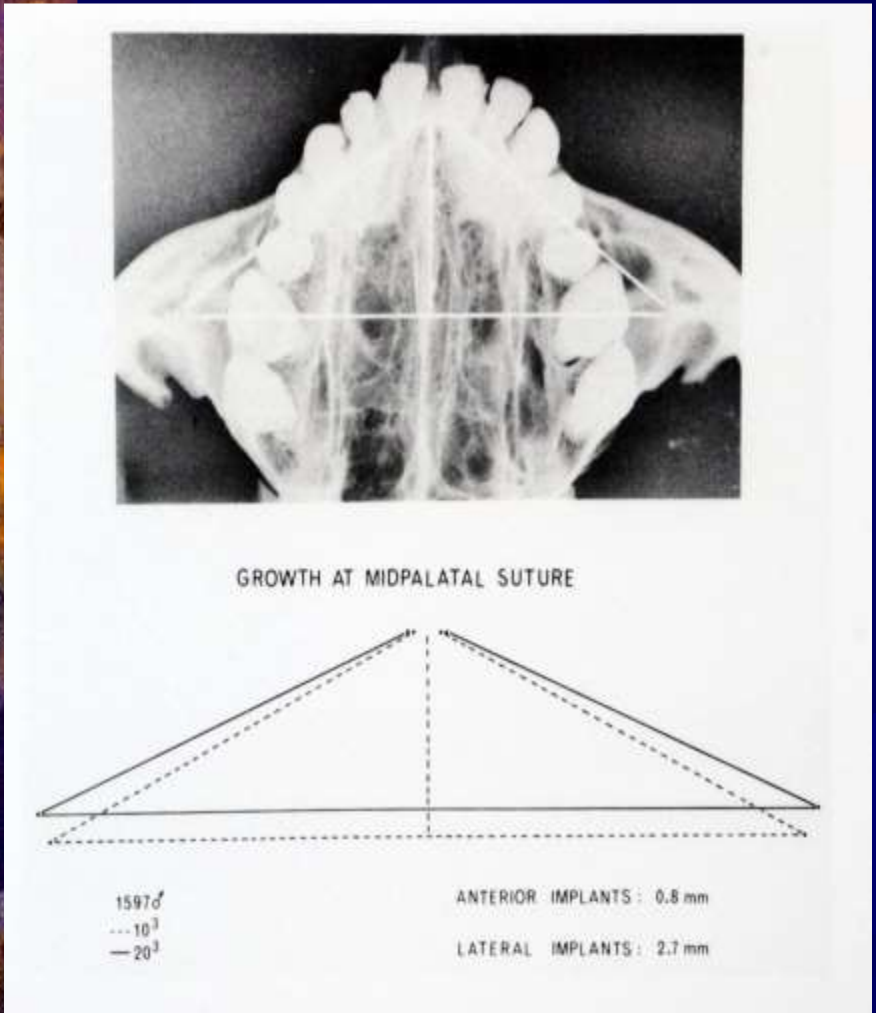
- Mean changes in vertical facial growth from 4 to 20 years of age in nine boys measured from implants (x) inserted into the zygomatic process of the maxilla.
- O, apposition on the floor of the orbit (6.4 mm); Su, sutural lowering of the maxilla (11.2 mm); resorptive lowering of the nasal floor (4.6 mm); A, appositional increase in the height of the alveolar process (14.6 mm); C, apposition at the infrazygomatic crest (2.5 mm).
- From Björk and Skieller (1977). *British Journal of Orthodontics* **4**, 53−64.

Maxillary growth rotation



- Björk was also able to show by superimposition on implants that as a result of the growth being greater posteriorly, there is a forward growth rotation of the maxilla as indicated by changes in S-N.
- Forward rotation of the maxilla in relation to the anterior cranial base in a male subject at 10, 13 and 21, is represented by the sella-nasion line.
- This figure also shows that the anterior contour of the zygomatic process appears stable while the posterior surface is appositional.
- From Björk and Skieller (1977). *British Journal of Orthodontics* **4**, 53−64.

Transverse rotation of the maxilla



From Björk and Skieller (1976). In: *Factors Affecting the Growth of the Midface.*

- Björk and Skieller (1976) concluded from their implant studies that growth of the midpalatal suture was the most important factor in growth in width of the maxilla.
- As a result of the growth being greater posteriorly than anteriorly, the two maxillae rotate slightly relative to each other in the horizontal plane.
- In this illustration increase in width of the lateral (posterior) implants was 3.5 times as great as anterior implants. Shortening of the dental arch in the mid-sagittal plane is related to the transverse rotational growth of the maxillae.

Summary

- In jawed vertebrates the palatoquadrate and Meckel's cartilages are generally regarded as being homologous with the first arch (mandibular) cartilages of agnathans.
- In more advanced vertebrates, there has been a trend for the number of dermal elements in the jaws to be reduced; in modern mammals the mandible is composed of the dentary alone.
- These evolutionary changes led to the development of a new craniomandibular articulation, known in humans as the temporomandibular joint.
- The articular and quadrate bones (which formed the original jaw articulation) became incorporated into the middle ear as the malleus and incus respectively, and with the stapes now form the auditory ossicles.

- The mandible is a membrane bone but during ontogeny its growth is modified by the development of three secondary cartilages, of which the condylar is the most important.
- Condylar cartilage is the product of periosteal chondrogenesis (not a remnant of the primary cartilaginous skeleton), and results from the altered functional demands placed upon the periosteum following the development of an articular condylar process.
- Although the condyle is a major postnatal growth site it does not control overall mandibular growth. However, a strong correlation exists between condylar growth direction and rotational movements of the mandible.
- Growth of the mandible results from a complex process of surface deposition and structural resorptive remodelling to maintain the shape and proportions of the bone as it increases in size.

- The maxilla is a complex bone which articulates with other facial bones by means of fibrous sutures. Growth occurs through both sutural and surface deposition, as well as structural surface remodelling. During growth the maxilla undergoes minor rotational movements in both the vertical and horizontal planes.

- The premaxilla is a constant feature of non-human primates and *Australopithecus*; its abrupt and complete disappearance in man seems unlikely.