Trajectories of the Jaws.

By

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CHAPTER 1.

History.

One of the earliest workers dealing with the architecture of bone was CLOPTON HAVERS. In his "Osteologia Nova" of 1692 he describes among other things the "bony strings" of the long bones, later to be named the Haversian systems. The difficulty of observing the structures concerned, which neither belong to the macro- nor microscopic field but rather to the region between them, is clearly stated by HAVERS as he says upon the occasion of demonstrating the bone-elements (Osteologia Nova: p. 43):

"And that I may not be thought to pretend to the discovery of what no other men's eyes can discern, because they (= the pores) are generally very difficult to be observed . . . I have the pieces of two bones, which I have brought along with me; in one of which the transverse, in the other the longitudinal pores are very well visible with the help of an ordinary magnifying glass."

In the 19th century the growth and development of bone was extensively studied by many investigators like DUHAMEL, JOHN HUNTER, FICK and VIRCHOW. A special interest in the architecture of bone arose with the work of v. MEYER and CULMANN 1867. Their graphic analysis of the texture of the femur neck gave the foundation for a series of functional interpretations of bone-architecture that now followed.

The ideas expressed in ROUX's theories of the functional adaptation of the organisms (1881, 1895) and in WOLFF's law of bone transformation (1892) were applied to the jaws by WALKHOFF (1900, 1902), who studied the morphology of the jaws and the bones of the facial region in relation to the teeth. His interpretations of the spongious trabeculation in the mandible followed "functional" lines, with attempts at a mathematical and mechanical interpretation of the structural conditions. WALKHOFF tried to coordinate the trajectorial structures of the mandible with functional influences. He applied X-ray examination of the bone. — According to WALKHOFF the inner architecture and the outer form are the results of function.

WALKHOFF stated that the skeletal reinforcements, visible in the outer form as well as in the interior architecture, are found at the places where the largest forces are exerted. Trajectories of the mandible are claimed to exist already in the foetus. The development of the teeth goes on with destruction of trajectories and reorganisation after eruption of the teeth. In senil atrophy on account of loss of teeth and function the trajectorial architecture of the alveolar bone is more or less destroyed.

GEBHARDT 1911 made a great contribution to the knowledge of the minute structural conditions of the bone. He analysed the elements that make up the internal architecture and distinguished the following forms:

"*Tubulus osseus*" (completus or incompletus) also called the haversian system, which he considered the most important of the architectural elements. These tubules consist of concentric layers of lamellae, in which the collagenous fibrils form a spiral course, crossing like plywood in the different layers of the tubule. GEBHARDT interpreted the different arrangement of the fibrils as associated with the mechanical properties of the tubules.

"*Pila ossea*", flat or shellformed lamella-systems.

"*Lamella statica*", for the purpose of resistance in a certain plane.

Subdivisions: a) Lamellae tenuae, thin, bandlike plates
b) " latae, broad, sheathlike plates.

"*Trabecula ossea*" for resistance in certain directions (axial to the trabecule).

Transitional forms between these different elements.

GEBHARDT considered the internal architecture as being worked out under functional influences within the limits of the gross bone form that was hereditarily determined. ROUX 1895 had more freely related both internal architecture and gross outer form to functional stimulation and adaptation.

This new knowledge of the minute elements that make up the internal architecture of the bone was not utilized to any considerable extent by the dental investigators who during the following decades studied the functional conditions of the jaws and the face skeleton. Instead of a careful comparative dissection of the bone they usually limited themselves to more or less superficial observations, either macroscopic or by X-ray examination of the visible spongious trabeculation.

GOERKE 1904 pointed out the functional importance of the canine crest, the alveolo-zygomatic crest and other reinforcements of the maxillary bone like the crests in the floor of the maxillary sinus that could be observed without special methods of preparation.

LEVIN 1913 published an analysis of the internal structural arrangement of the mandible, applying the laws of physics to the structural elements of this bone.

DAVIDA 1915 added to the knowledge of the architecture of the mandible by an examination of the canal systems in the undecalcified bone. It is a meticulous work with saw-sections and grind-cuts. However, DAVIDA like several investigators both before and after him seems to interpret trajectorial structures too mechanically just as if the jaws and facial bones were built in one plane, not considering the multiplicity of forces working in different directions upon the same structure. There is a lack of three-dimensional analysis and a too strict adherence to "lines of stress".

M. BARTH 1919 made a valuable contribution to the architecture of the face skeleton by X-ray investigation on skulls of a considerable material of New World monkeys. However, the X-ray method, although giving a good composite picture, does not permit any finer analysis of compact bone architecture, and therefore leaves place for criticism and further work.

WINKLER 1921 more than any previous worker in the dental field realized the importance of the cortical bone in the consideration of bone architecture. Lack of an adequate method, however, prevented him from making further advance in this question, although he tried by way of saw-sections to reconstruct the arrangement of the haversian canals in the mandible.

KOCH 1917 made a careful mechanical analysis of the compressive and tensile forces working in the femur, and defined his "laws of bone architecture" founded on the earlier works of ROUX and WOLFF.

Until yet the biologic side of the architecture in the facial region had been rather neglected, *i. e.* there was more interest in the mechanical mapping out of trajectorial schemes than in a coordination of the interplay of forces in soft and hard tissues and the structural reactions to functional influences. BLUNTSCHLI (1926, 1929) has contributed to this latter point of view although his reasoning is rather hypothetical and deductive. He encouraged several pupils to practical investigative work upon the functional anatomy of the face region. He stressed the hypothetical character of the trajectories although at the same time he encourages a rather mechanical interpretation of the bony ridges and structural conformations of the skeleton. BLUNTSCHLI grossly expresses the functional anatomy of the face-skeleton by the basal arches of the jaws and the three maxillary pressure pillars anchoring the face skeleton to the neurocranium and transmitting the main forces from the denture to the solid bone of the neurocranium. BLUNTSCHLI points out the extreme responsiveness of the bony structures to the varying dental conditions, not only considering the alveolar process but also the larger systemic connections in surrounding bones. A suggestion of the closed functional systems within this region, which will be further elaborated in this work, is also made by BLUNTSCHLI. WETZEL (1922) has experimentally and with more evidence arrived at the same concept.

In 1925 this field was enriched by the introduction of the "Spaltlinie"-method of BENNINGHOFF, which has proved very valuable in the clearing of compact bone architecture. This method was used by BENNINGHOFF and later by HENKEL 1931, DOWGJALLO 1932 and SEIPEL 1934 for the study of architectural arrangement in the jaws of man and higher animals.

Regarding the human face-skeleton and the architecture of the jaws, quite divergent results were obtained by different investigators. No attempts were made to differentiate the structures that make up the architectural frame, and to trace qualitative differences induced by different physiologic or pathologic conditions. The architecture was rather considered as a pure mechanical problem that was solved once it was shown to be present in a certain arrangement in a certain number of skulls. The functional variation was considered by DOWGJALLO 1932 in his investigation on the architecture of the jaws in different age conditions. DOWGJALLO is using the method of BENNINGHOFF with the isolated spot injection technique, with no subsequent dissection or histologic test. His composite drawings give a superficial picture of the alveolar process and the inside of the mandible, but according to the limitation to the superficial layers it might be subjected to changes in several respects, especially in the external compact layers of the mandible.

The inherent properties of bone to form a supporting structure with a definite architecture providing increased resistance in certain directions was analysed by anatomists like PETERSEN 1927 and BENNINGHOFF 1927, 1933, 1934, 1935, who further elaborated the earlier viewpoints of HUNTER and GEBHARDT. By histological study of fresh material PETERSEN confirmed the constant processes of building and rebuilding going on in the bone. The seat and object of these processes are the different building-systems of GEBHARDT, referred to above.

It has been suggested by several investigators (PETERSEN, BENNINGHOFF), that the bone in order to exhibit relatively constant mechanical properties must be a homogeneous substance, thus showing relative homogeneity in such a way that a *certain level of resistance* is maintained through proper balance between resorptive and appositional processes. It is obvious from GEBHARDT's statements of the interior arrangement that the bone is no really homogeneous substance. The bone homogeneity was worked out under the concept that a substance could show no definite trajectories or substantiated lines of stress if it was not homogeneous. However, the organic trajectories are different from fixed lines of stress in an inorganic material, in that they represent only temporarily increased resistance in a certain direction. As experience from the general pathology has shown, the vascular conditions and the fluid content must also be considered as important factors for the mechanical resistance of an organ and the hydraulic pressure mechanism plays a rôle in making the tissue homogeneous: any dense vascular tissue will show an abrupt fall in its mechanical resistance if the blood-supply is shut off.

It seems obvious that in a study of the architecture of a tissue, and especially in the mechanical and functional interpretation of this architecture, *extreme caution has to be exerted in the application of mechanical laws*. The tracing of a single abstracted force or external stimulus in a definite structural arrangement is seldom to be made. The multiplicity of reactions as well as the differences in the individual response to the same stimulus make the problem a complex one.

KÜNTSCHER 1935 has studied the mechanical properties of bone,

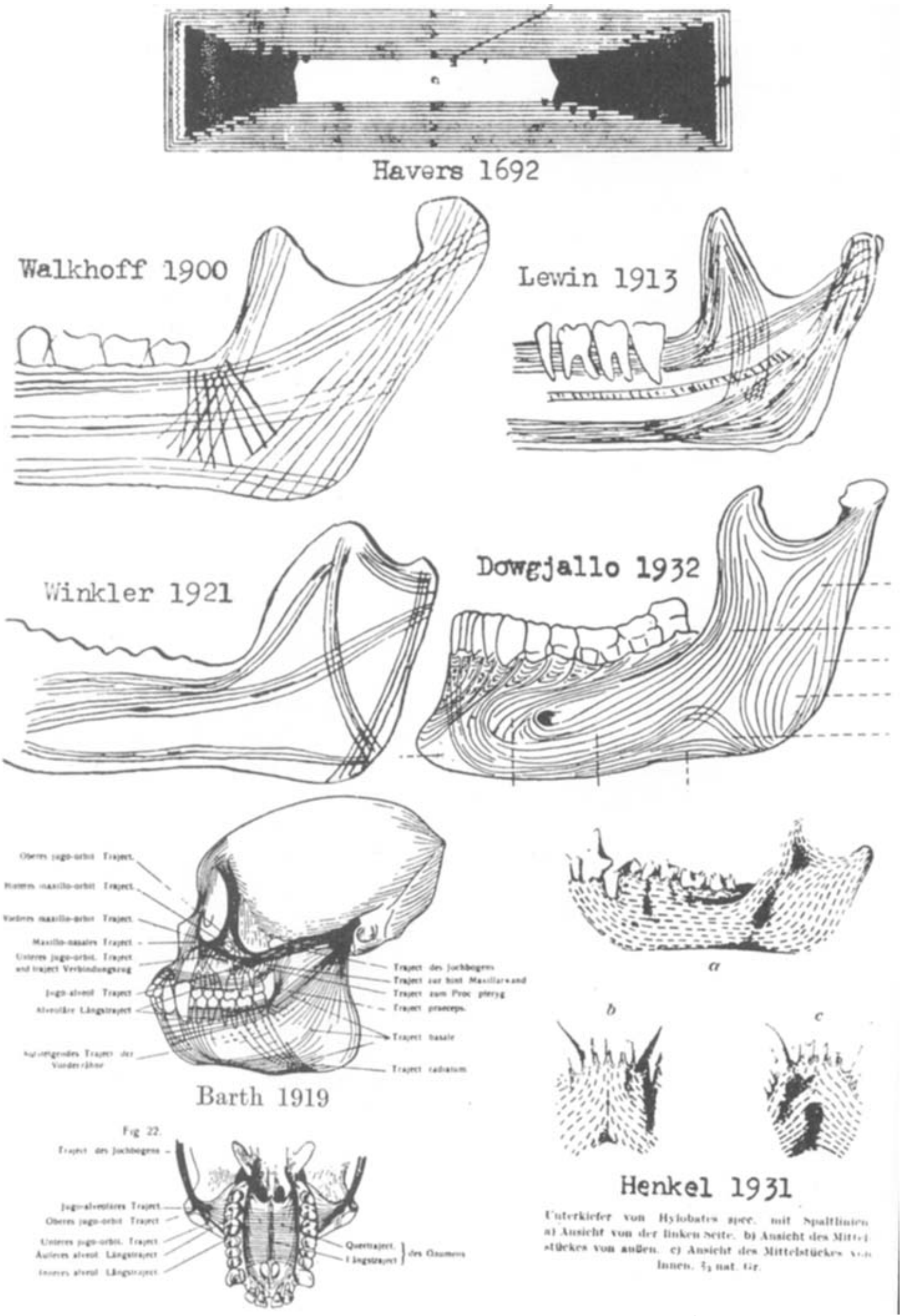


Fig. 1. From the history of bone and jaw architecture: **Havers** 1692 architecture of long bone. **Walkhoff** 1900 and **Lewin** 1913 trajectories of the mandible mainly referred to the spongious trabeculation. **Barth** 1919 (below left) constructed trajectories from X-ray pictures, note transverse trajectories of the palate. **Winkler** 1921 and **Dowgjallo** 1932 studies of the compact bone architecture of the mandible, the former through saw-sections and the latter through **Benninghoff's** "Spaltlinie"-method, which is illustrated in the pictures of **Henkel** 1931.

by way of measuring the degree of deformation occurring in the femur relative to certain known forces. He has mapped out areas of increased resistance (Spannungsspitzen) and determined the relative resistance in different directions from the same point or place of measurement (zweiachsiger Spannungszustand des Knochens). Wolff's law of bone transformation is questioned by KÜNTSCHER, as it has also been modified by several other workers in later years. That the bone formation is by no means determined by function alone is clearly shown by experimental evidence of American investigators; so f. i. BAUER, AUB and ALBRIGHT 1929 showed that the cancellous trabeculation in the long bones can be made to disappear entirely and to reappear again with variations in the calcium intake of the diet.

Practical orthopedic experience (v. BRÜCKE 1935) stresses the mechanical importance of the bone architecture for resistance to injuries. Fractures localize in a different way in younger and older bone, the latter reacting more as homogeneous plaster. Animal experiments carried out by several American investigators (McKEOWN, DOWNS, HARVEY, LINDSEY 1932 and CLARKE et al. 1935) in order to show the dietary influences upon the breaking strength and the fracture healing processes in bone, also tends to stress the importance of the organic matrix. The calcium-content, as revealed by X-ray density, according to those investigators played a less significant rôle, at least for the breaking strength. In low calcium and mineral salt diet the animals seemed to substitute for the lack of mineral salts in the bone by a different organization of the organic matrix. After realimentation with inorganic salts had been allowed to take place, this bone showed a considerably higher breaking strength than normal. As the organic matrix of the bone is largely formed by collagen the question of collagen formation and influencing biochemical factors must also be tied up with the physical properties of bone (cf. WOLBACH and HOWE 1926, WOLBACH 1933 and others).

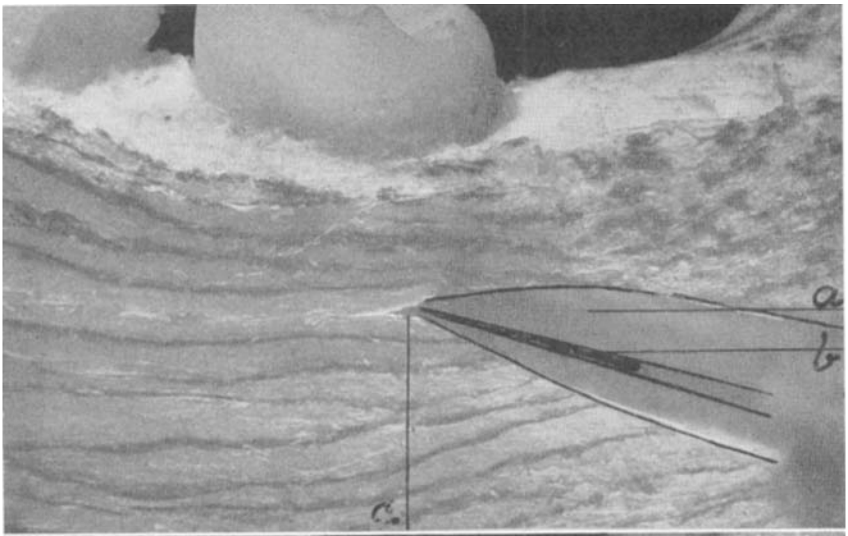
As far as the jaws are concerned there are essential questions of clinical importance for paradentosis and malocclusion of the teeth connected with the functional qualities of the bone. The trajectories of the jaws, which means the structural arrangement and the supporting ability of the skeletal parts carrying the dentition, are taken up in this work as an anatomical study of the organic pattern and its architectural arrangement mainly of the compact bone. This anatomical study of the supporting structures of the dentition seems to be required as a basis for further analysis of etiology and therapy in deformities of the jaws and malocclusion of the teeth.

CHAPTER 2.

Method.

Special methods have to be applied for an investigation on the trajectorial conditions of the compact bone. The architecture of both organic and inorganic constituents of the bone might be studied and separated one from the other. If a bone is heated, the organic framework is burned and only the inorganic components remain. A bone so treated is very brittle, but retains its external form and, to a certain extent, its microscopic structure. If on the other hand the bone is treated with weak acid, the inorganic salts are removed and the organic framework remains. The bone becomes soft and flexible and slightly translucent, and it retains its original appearance and microscopic structure. The organic framework forms 30 to 40 % of the interstitial substance and is apparently identical with the collagen of the ordinary connective tissue (MAXIMOW 1938). The collagenous fibrils are the main building material in the lamella-systems that compose the organic architecture. Now, histologic sections alone give only a limited view of the architecture in a larger bone, and are bound to thin sections in one direction only, whereas the architecture is often following irregular surface-reliefs and winding contours. Therefore in order to give composite pictures of the whole jaws and facial bones, a modification of the "Spaltlinienmethode" of BENNINGHOFF has been used.

The "Spaltlinienmethode" or crevice-line coloring method was applied by BENNINGHOFF in 1925 for the study of the architecture of decalcified compact bone. It consists of a mechanical test, a crack-line production by way of stitching with a round needle or similar instrument, and the application of a coloring fluid in the resulting crevices or cracks. The method depends upon the fact that the organic matrix of the bone after appropriate treatment with decalcification and desiccation is most easily splitting up in the direction of its lamella-systems. This method depends to a certain extent upon a *breaking of the continuity* of the organic



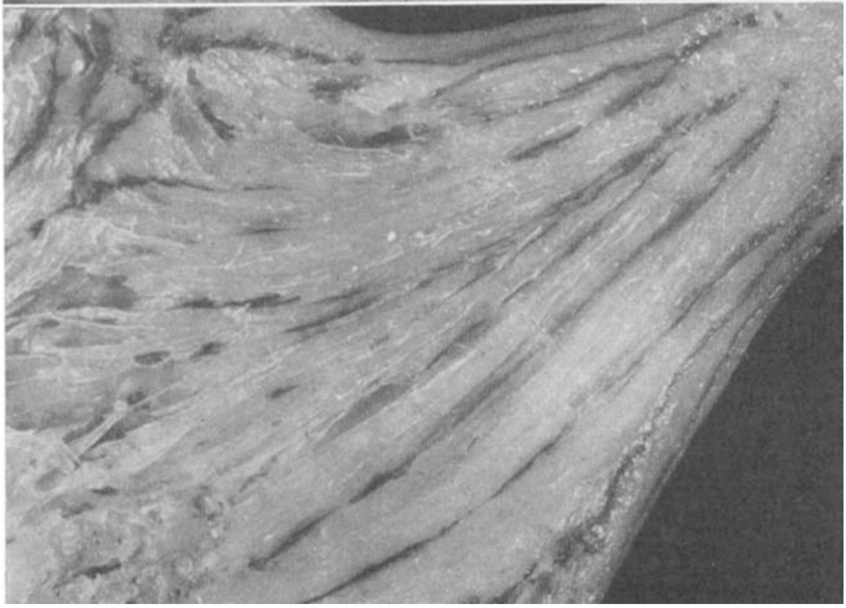


Fig. 2. The crevice-line method: india-ink (b) injected with a pair of tweezers (a), c = crevice produced by tweezers.

Fig. 3. Micro-dissection of trajectorial structures in the ramus of mandible (young chimpanzee).

matrix in the easiest direction and thereby *indicating the pattern* of fibrillar arrangement. The question is open how much the mineral-fixation changes the adherence of the lamella-systems and the mechanical properties of resistance in different directions.

A similar method was used to study the mechanical structures of the joint-cartilages by HULTCRANTZ, Upsala, in 1898. Also (in a more primitive form) still earlier in 1862 by LANGER for the study of the architecture of the epidermis.

The method includes a mechanical test to the bone as the crevice is produced by force. If the needle is inserted in an area with well-defined structural arrangement, there is a definite line or crack produced whereas in an area with less well-defined lamella-systems, either more irregularly fibrous (geflechtartiger Knochen) or more amorphous bone-matrix, there is only a round spot or a diffuse crushing of the material with no linear floating out of the coloring matter.

Black india ink is most advantageously used for the coloring. Whether it floats out in the haversian canals, or between the haversian systems, between the piled up lamella-systems or in the blood-vessels, is a matter of less importance, because the method is mainly used as an *indicator of structural arrangement.* The bone cracks in the direction where it is definitely organized. If there is a netlike arrangement to withstand multiple forces, the crevice formation is in the direction of the resultant of the different forces, *i. e.* in the direction of the longest diameter of the net-meshes, either these are made up of long regular haversian systems (osteons) or they consist of more or less shell-like lamellae or rudiments of lamellae that pile up in a certain direction. The connection to the blood-vessels of the bone is given by the lamella-systems being built up around the blood-vessels. As the human bone consists to a large extent of osteon- or haversian systems, it is easily seen that the crevice-line method is at the same time an indicator of the structural architecture and of the direction of the blood-supply. An injection of the vascular canals of the bone could be used for the same purpose but would not give as conclusive pictures of the mechanical properties as the crevice-line method.

The method is practically useful only on definitely organized dense, compact bone. In growing bone or cartilaginous tissue (except for joint cartilages) it would not be useful in demonstrating any architecture, because these tissues are too loose in their fibrous arrangement to produce definite crevices. The coloring matter would float out diffusely without giving any definite lines. The method is likewise unsuitable for bone in early stages of ossification, even if there are microscopically very definite pillars and strands of osseous tissue. As the bone matures, especially in areas where it gets dense and well-organized, with clear lamellar and osteon arrangement, the applicability of the "crevice-line" method increases.

If the bone consisted just of haversian system bone, it would be very easy and conclusive to prepare the complete architecture by this method. But as many parts of the bone have another arrangement, the method has to be used with a certain caution. The superficial parts of the bone are often composed of subperiosteal layers and thin surface lamellae. In such case the method is less conclusive and sometimes not to be used at all. If such an area is combined with a muscular insertion, with inserting fibrils of Sharpey still more complicating the surface architecture, the crevice-line method cannot be used in the superficial layers, but instead a microdissection has to be employed.

The architectural pictures brought out with the crevice-line method represent at the same time a simplification and an overemphasis of the existing bone-organization. A simplification while a multiplicity of lamella-systems and bone elements are represented by a few coloring-lines in the crevices produced. An exaggeration because the rather heavy injection-lines are signifying the directional arrangement of the minute structural elements which form the interior architecture. The coloring lines are by no means trajectories (meaning structural lines of stress), only *indicators of the main flow of lamellar and fibrous organization in the bone.*

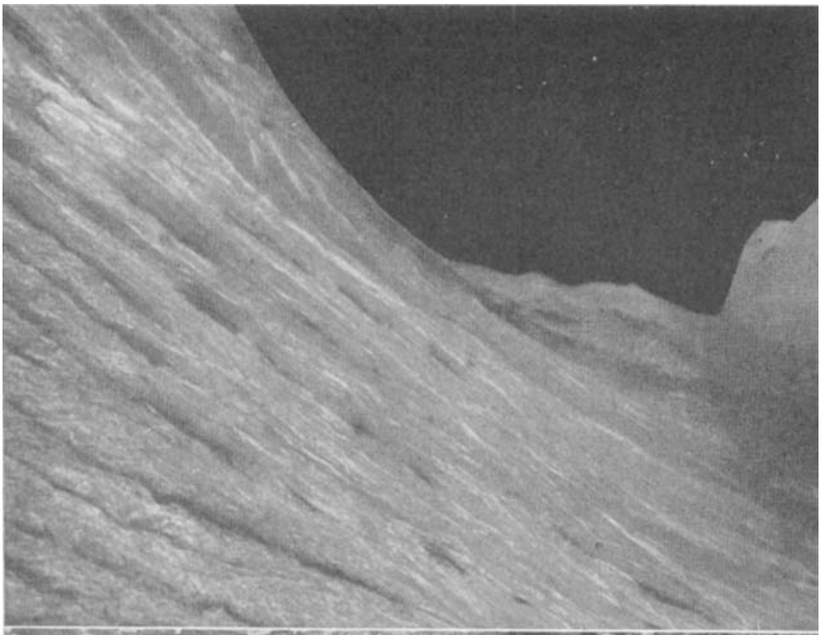
In the procedure of crevice-line preparation there might occur what could be called the "ploughing effect", that is when a previous crack or crevice predisposes the surrounding tissues to crack in the same direction. In a fairly homogeneous, more or less "hyaline" material this thing seems to occur and sometimes is responsible for an extreme parallelism of lines. However, it might also easily be avoided by starting the injections at a sufficient distance from each other, and by avoiding as much as possible the continuous preparation of adjacent lines and instead start at varying points and gradually let the injections fill out the space in between.

The complete treatment of the material is as follows:

1) Collection of the material in the freshest possible condition and fixation in 10 % formalin for at least one week.
2) Decalcification in 5 % nitric acid, the acid being stirred up by a rotator during the whole process of decalcification. Acid changed every day. Usual time for decalcification 3 days, followed by washing for 1—2 days.
3) Bleaching in 3 % H_2O_2 for at least one day in order to facilitate later photography.
4) Desiccation in alcohol 60, 70 and 80 %. Specimen preserved in 80 % alcohol during time of preparation. A proper desiccation is important as it facilitates the staining. On the other hand the specimens have to be kept wet (alcohol) even during time of preparation in order to prevent the material from getting tough and shrink by air drying, in which case it will be hard to stain.
5) Preparation of the material with a modification of the crevice-line method or "Spaltlinien-Methode" of BENNINGHOFF to visualize the structural arrangement. A modification of the original method has been used, with a continuous-line coloring, effected by a close follow up of crevices between the connecting structures and a following anatomical dissection under low magnification with tweezers as a test on the crevice-line injections.

Anatomical preparation and dissection of the decalcified bone under low magnification is a most valuable complement to the crevice-line method for a clearing of the architectural conditions of the bone. However, the value in this procedure is mostly that of a check-up on the coloring because the dissection itself breaks the continuity of the trajectorial systems and therefore does not add any advantages to the picturing of the gross trajectorial connections. The value of the dissection is definitely that of a test and a clearing of the minute structural connections in local areas.

For the purpose of studying the relationship between the crevice-lines and the microscopic conditions of the bone, histologic sections with different staining methods have been used. Haematoxylin-eosin was first used for a study of the cellular conditions, but as this stain is insufficient for a differentiation of the lamella-systems and the fibrillary structures, connective tissue stains were later used in addition. The Foot-modification of the



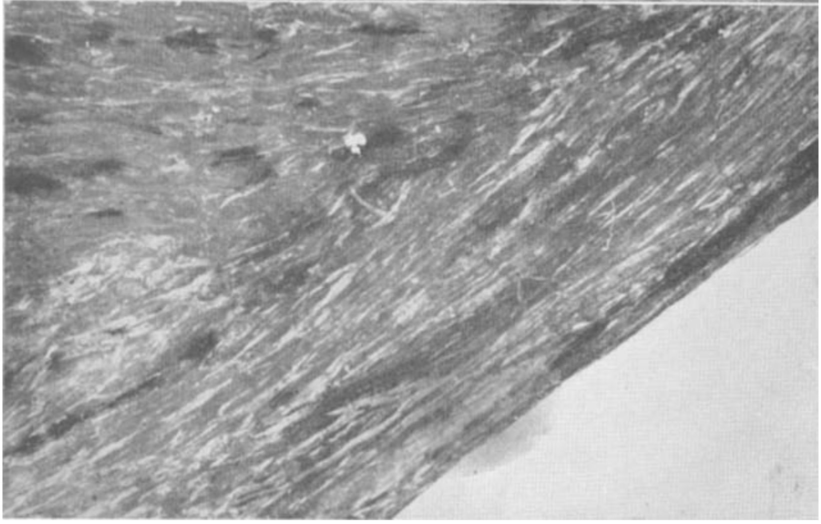


Fig. 4 (above). Chimpanzee 9 yrs (Y 5), external oblique tract of the mandible with clear trajectorial organization.

Fig. 5 (below). Posterior part of ramus mandibulae showing lamellar and osteon structures of deeper layers.

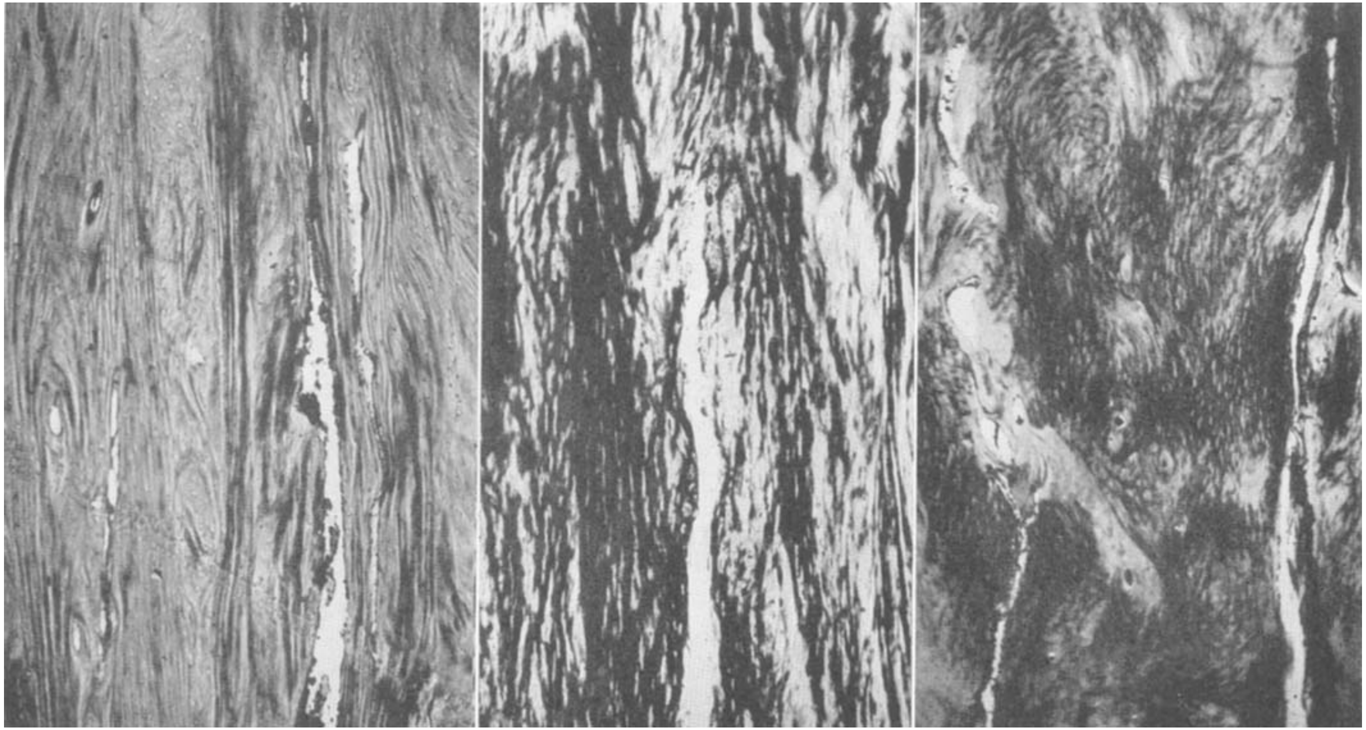
Masson-technique was used for a demonstration of the interior organization of the bone-matrix. VAN GIESON stain has also been used in some cases.

Histologic study was applied to the regions where the crevice-line method gave a negative result, which accordingly might be attributed to different reasons: dense trajectorial crossings or insertions, loose bundle-bone, infiltrative resorption areas, special net-trajectories or spongy bone, non-laminated bone etc. As a complement to the crevice-line method the histologic sectioning therefore is of deciding value.

In the testing of the crevice-lines the lamellar and fibrillary arrangement, the fibrillary bundles, the direction of the nutritional canals and the position and appearance of the lacunae of the bone-corpuscles have been judged. Thus the criterium of reliability on the crevice-line method would be:

1. crevices parallel to lamella-systems
2. " " " fibrillary bundles
3. " " " long. diam. of bone-lacunae
4. " " " main canals (not perforating canals)
5. parallelism occurring in succeeding layers of serial sections.

Microscopic sections taken from the specimens prepared with the crevice-line method show the laminated or lamellar type of bone to be the dominating in all areas where a definite architectural arrangement is shown by the gross preparation. Where there are clear lamella-systems the crevices follow parallel to them, splitting up the tissue in the main direction of the architectural elements. In bundle-bone with a longitudinal architecture the method also gives a good picture, as the crevices follow the direction of the bundles and split up the tissue in this direction. However, in areas of a loose and irregular arrangement, and where dedifferentiation of lamella-systems and resorption of the bone is going on, the crevice-line method gives no definite picture. The injection stitches leave only rounded holes or a diffuse crushing of the tissue with no definite crack or crevice and consequently no color lines. The method requires a certain density and elasticity of the tissue, beside the organization in a definite direction of lamella-systems or fibre-bundles. On account of the depth of the injection-stitches, varying from 1—5 mm, usually around 3 mm, the crevice gives the resultant direction of a series of layers or possibly the whole compact wall. Microscopic serial sections as



a b c

Fig. 6. Crevice-lines in compact bone of different organization, cf. relationship to lamella- and canal-systems, to fibrillary bundles and arrangement of corpuscular lacunae. a) homo, external oblique tract of mandible, b) and c) chimpanzee (Y 5), c = internal obl. tract close to erupting lower molar.

well as micro-dissection show that where an architecture of lamella-systems is present, the arrangement is usually prevailing through the whole compact wall. The superficial subperiosteal layers of the external general lamellae give a somewhat irregular or netlike arrangement, with inserting periosteal fibres deflecting the picture. The following compact-bone layers usually give a good picture of lamellar or osteon systems, which in the deeper layers show a gradual weakening and give way to a transitional form of compact bone with incomplete and irregular lamella-systems as the spongious bone approaches.

Material.

Homo newborn male (Y 7)
” ” ” (Y 11)
” 12 yrs sex unknown, mandible (Y 2)
” 20 ” male (Y 10)
” 22 ” ” (Y 8)
” adult 2 skulls (Y 3 and K 9)
” ” mandible, healed fracture (K 8)
” ” 6 mandibles (K 2—K 7).

Chimpanzee $2^1/_2$ yrs, female (Y 4)
” 3 ” male (Y 6)
” $4^1/_2$ ” ” (Y 9)
” 9 ” ” (Y 5)
” adult, female, mandible (Y 1)
Spider-monkey, adult, mandible, osteomalacia (Y 12).

CHAPTER 3.

Upper Jaw.

The maxilla is an intramembranous bone, embryologically proceeded by a connective tissue membrane, which later forms the periosteum. The formation of this bone to a considerable extent occurs in subperiosteal layers, with surface-parallel lamellae as a consequence. This mode of formation is influencing the architecture. Clear tracts of tubular-systems are less dominating in the compact bone of the maxilla than in the mandible. Osteon systems appear in certain parts where there is a denser compact bone, like the alveolar, nasal and zygomatic processes of the maxilla. But in the thin-walled parts an interwoven, net-like texture of flat lamellae appears, in some areas giving a relatively clear architectural picture, in others giving the impression of a loose fibrillary net-work.

In a trajectorial analysis it has to be considered that the mechanics of the maxillary bone might not be expressed only in the clear architecture of linear trajectorial structures, visible in the X-ray picture (cf. BARTH 1919), but also in surface-trajectories anatomically represented by flat lamella-systems. The thin-walled areas might have a mechanical importance as resistance in a certain plane, they might represent neutral areas, or they might be external general lamellae, the function of which is comparable to that of a protecting and binding cortex. A differentiation of the texture is usually possible through the method applied in the present study: namely crevice-line preparation, micro-dissection, and examination of the whole compact wall, to correlate the different layers. The architecture of the thin-walled areas is relatively hard to trace with the crevice-line method compared to the denser parts of laminated cortical bone. On the whole, and possibly to some extent depending upon technical difficulties of preparation, the maxillary bone does not give as clear pictures as that of the mandible, and the interwoven net-like texture is definitely more pronounced. Yet the architecture of most of the specimens prepared in the present study is sufficiently clear to support a trajectorial scheme, which seems more complete than the one of BARTH 1919.

As mentioned above (Chapt. 2) the architectural pictures brought out in the present study only indicate the main flow of lamellar organization in the bone, and can only within certain limits evaluate the complicated interior structural arrangement. Upon anatomical dissection of the decalcified bone it comes out quite clearly that only in rare instances do we have clear isolated trajectorial structures. Mostly the lamellae and fibrillary structures form a reticulation or net-work, wherein a main direction of lamella-systems and canals is more or less apparent. This is especially true of the maxillary bone. The crevice-line method gives a fairly simple picture of the maxillary texture, while at the same time there is an interlacement of the interior structural organization that does not come out in the picture, although it might have a vital mechanical importance. The crevice-line method, without the support of dissection, cannot give the qualitative differences of bone-organization. So f. i. the molar area, which upon anatomical dissection is shown to be an important meating point of trajectories, in many cases gives no clear crevice-line picture. On the other hand a similar diffuse picture is exhibited by the infraorbital area, which is relatively neutral in mechanical and architectural respects. Of course the crevice-line method in such cases has to be completed with micro-dissection and histological examination.

Barth (1919) introduced a system of vertical, longitudinal and transverse trajectories of the upper jaw from X-ray investigations on skulls of Cebus macrocephalus. Barth concludes that the roentgenologically demonstrable crests and processes of the maxilla are covering an interior architecture of trajectories that are mostly traced back to the surroundings of the teeth. The trajectorial system is as follows:

I. Vertical trajectories
    A. The trajectorial system of the canine crest
        1. the maxillo-nasal traj.
        2. the anterior maxillo-orbital traj.
    B. The trajectorial system of the zygomatic region
        1. the posterior maxillo-orbital traj.
        2. the jugo-alveolar traj.
        3. the inferior jugo-orbital traj.
        4. the superior jugo-orbital traj.

II. Longitudinal trajectories
    A. The longitudinal alveolar trajectories
        1. the lingual communicating traj. to pterygoid bone
        2. the labial communicating traj. to post-maxillary region
    B. The longitudinal trajectories of the hard palate.

III. Transverse trajectories
    The transverse alveolo-palatine trajectories.

The present method has given divergent results from Barth in several respects. Some might be attributable to species differences, others to the different methods of investigation. As I have shown earlier (Seipel 1934, p. 13) the X-ray method does not always give reliable pictures of the interior architecture of the bone compared to the direct examination by micro-dissection, which was used as a test method.

Before entering upon a description of the architectural and trajectorial structures of the bone a few words might be devoted to the fixation of the teeth by way of the peridental membrane, which in a way belongs to the trajectorial structures. WETZEL (1914, 1922 cit. SCHMIDT) gives the following system of fibrils connecting the teeth with the alveolar bone:

1. the gingivo-dental
2. " circular gingival
3. " interdental
4. " superior oblique alveolo-dental
5. " transverse alveolo-dental
6. " inferior oblique alveolo-dental
7. " apical.

C. SCHMIDT (1932) remarks that the peridental fibrils are most strongly developed towards the interdental septa. He also stresses the fact that unlike the ordinary collagenous fibrils of tendons the peridental fibrils do not form parallel tracts, but are constantly crossing and interlacing in bundles to form a dense interwoven fibrous membrane. The teeth are suspended in the osseous alveolar baskets by way of the oblique and transverse alveolo-dental fibrils. One would expect the trajectorial structures of the alveolar bone to have their origin in those parts of the alveolus that receive the fibrils, and especially in the interdental septa, which also seems to be the case in the following study.

Architecture of the Maxillary Bone.

The *alveolar process* under normal conditions in young specimens shows a system of border parallel and circular fibres around the necks of the teeth. This texture is usually rather clear both on the buccal and on the lingual side, inserting into the more porous and somewhat amorphous bone of the interdental septa, or continuing interdentally to form more or less complete circular architecture around the teeth. This architecture of the alveolar limbus appears in all parts of the dental arches. It is limited to the uppermost part of the alveolar bone although in the molar and premolar regions it is running parallel to and is rather intermixed with the longitudinal alveolar architecture. Yet the former is limited to the single teeth, while the latter is continuous from one tooth to another, overbridging the interdental septa. In the upper jaw this longitudinal alveolar architecture is forming clear tracts from the premolar region backwards on the buccal side (Fig. 7), spreading out over the tuber maxillae, and in adult stage with the wisdom-teeth in place also showing connections to the pterygoid process running out in the lower part of the lateral lamina. On the lingual side this longitudinal alveolar architecture is pronounced already in the canine and incisor regions continuing backwards along the premolar and molar regions to insert into the pterygoid bone or continue in its architecture (Fig. 13).

Above these circular and longitudinal alveolar architecture the crevice lines on the buccal side of the maxilla show a definite root-parallel arrangement, indicating an *ascending alveolar* texture. The trajectorial structures are usually stronger developed in the interdental regions, and in this way there is a tendency towards arcade formation at the apices of the teeth. The bone covering the roots is usually thinner, with a less definite ascending architecture, in the anterior regions. It consists of flat lamella-systems with a reticular ascending texture. Sometimes this reticulated architecture of the alveolar walls appears as arcade formation between the ascending interdental pillars, flat arches near the alveolar border and more gothic towards the apical region. However, this arrangement is less pronounced in the upper jaw than in the lower, where it is rather constant in the incisor region.

From the medial incisor region the architectural tracts turn laterally to follow the apertura piriformis and the lateral nasal wall into the naso-frontal process of the maxillary bone. There is a definite bilateral arrangement of the compact bone architecture, with few crossing connections between the two sides. In younger age stages, the newborn homo and the younger chimpanzee cases, the midline connections seem to be maintained largely by fibrous connective tissue. In adult stage with complete bony fusion of the two sides there is usually a clear ascending architecture even of the midline interdental septum, the crevice lines of the two sides deviating laterally below the nasal spine and to some extent also fusing in the nasal spine and at the subnasal border.

The lateral deviation from the incisor region leads to a concentration of the alveolar architecture to the so called canine crest. This trajectorial pillar around and above the canine is by

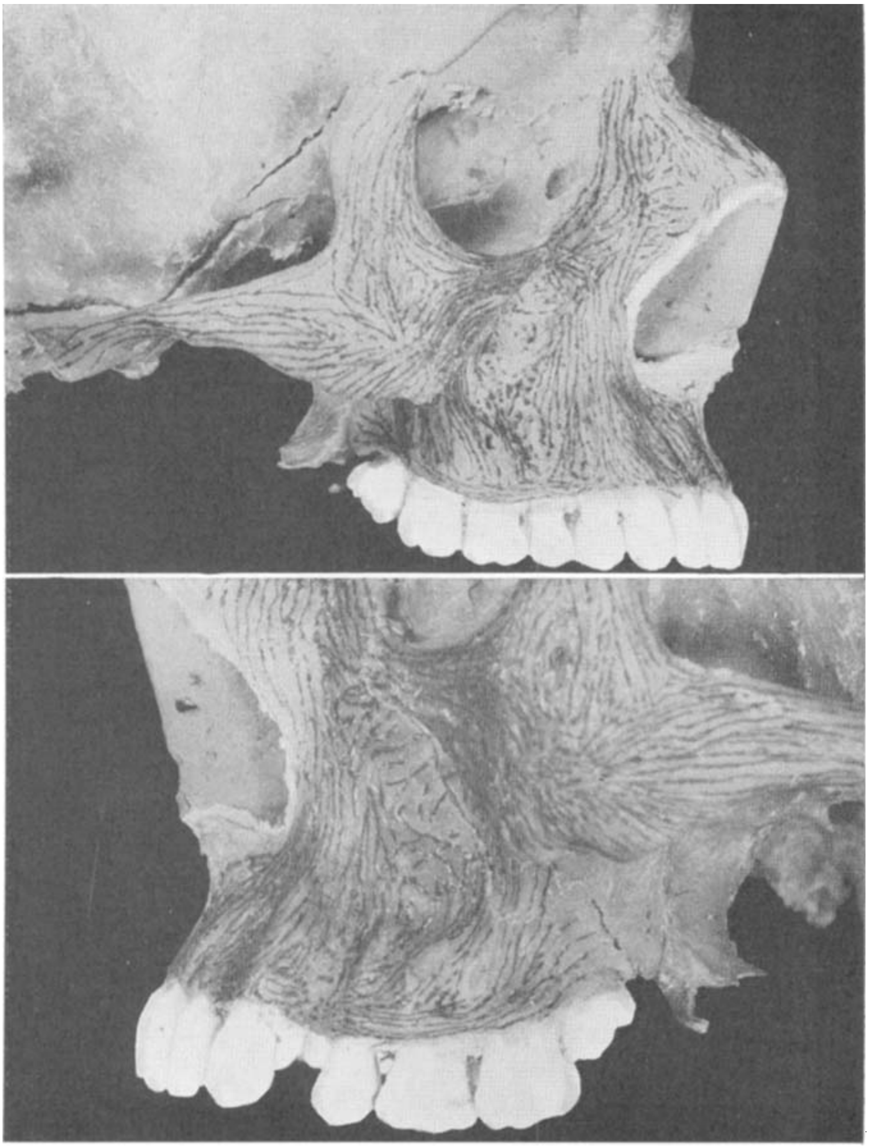


Fig. 7. (Y 8) man 22 yrs, cause of death accident. Healthy subject with well-developed trajectorial structures of the facial bones.

far not as dominating in man as in higher primates, where there is a larger functional importance of the canine tooth. In man the canine does hardly give this region the importance of an outstanding trajectorial system. It is rather the concentration of the ascending architecture from the incisor, the canine, and the anterior premolar regions that leads to the formation of the maxillo-frontal trajectorial system. The lower part of this system is marked by a sometimes well-developed — in other cases inconceivable — canine crest. In younger age stages it is less conspicuous, even in antropoid forms, than in the adult. It seems logical to name this important anterior trajectorial system of the maxilla from its origin and insertion as the *maxillo-frontal* trajectorial system including the variable canine crest. The maxillo-frontal trajectorial system thus comprises the anterior part of the maxillary bone and includes the ascending trajectorial structures of the external maxillary wall from the incisor, canine, and premolar regions as well as those of the lateral nasal wall from the incisor region and finally also contributaries from the infraorbital area.

There is no strict division of trajectories from the premolar area even if the majority of the architectural fibres from the first premolar turn towards the canine crest and from the second premolar towards the alveolo-zygomatic crest which is a corresponding landmark in the molar region. The ascending architecture of this area is marked by a reticulated texture, especially towards the supra-apical field of the premolars, where the relatively amorphous infraorbital texture makes the trajectorial picture unclear. But there are also clear tracts from the premolars turning laterally to each side of the neutral infraorbital area.

The molar region is marked by an increasing amount of longitudinal trajectories along the alveolar margin (Fig. 7). Its importance as a possible anchorage to the pterygoid process will be discussed further on. Above this horisontal texture and possibly also interwoven with it is an ascending architecture, which usually is well-defined at the first molar, but less developed at the second and third molars. Where molars are still in eruption the bone of the posterior molar area is rather porous and does not give any clear architecture with the crevice-line method. Even in adult stage I have never been able to find a correspondingly clear ascending architecture of this area as in the rest of the alveolar process. There is no clear demarcation but the well-defined ascen-

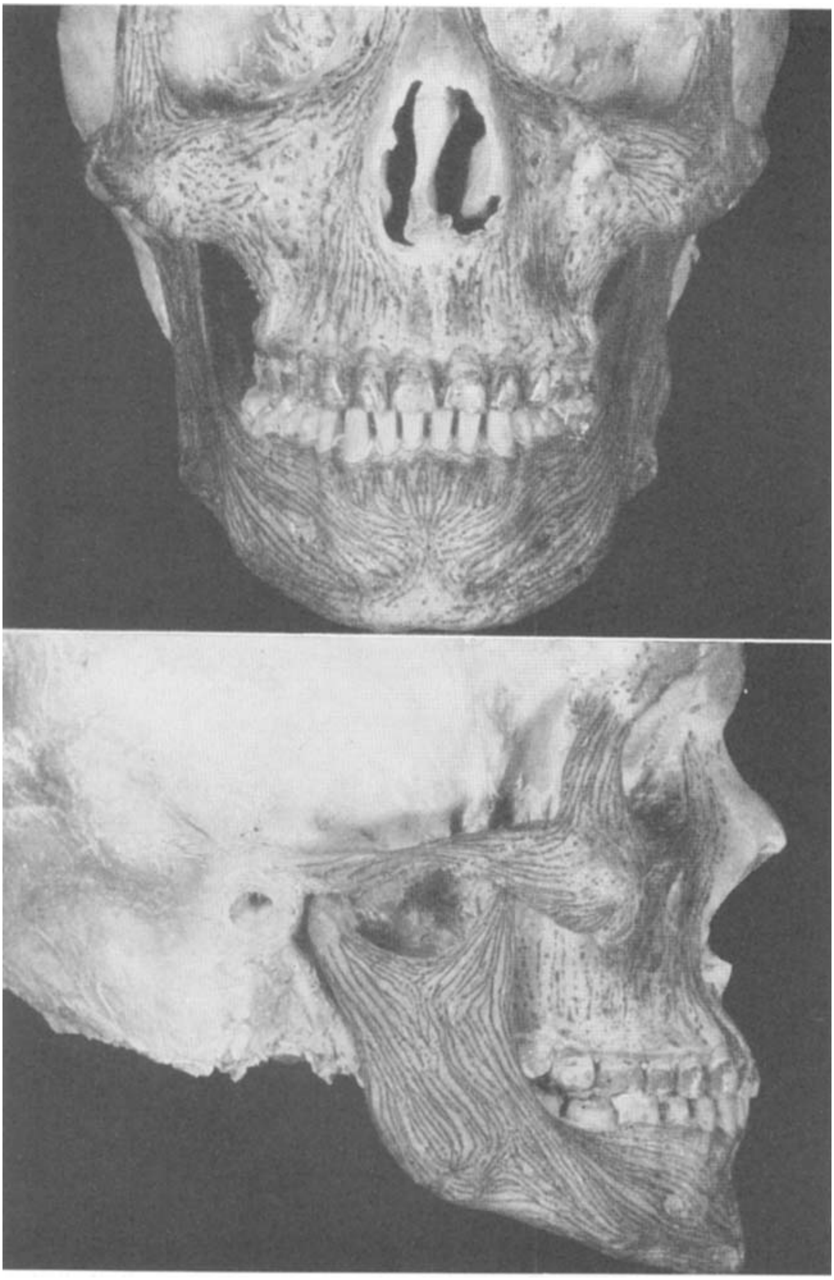


Fig. 8. Man 20 yrs (Y 10), cause of death pulmonary tuberculosis, emaciation. Weaker trajectorial arrangement, especially of the upper jaw, in comparison to the healthy subject of fig. 7.

ding architecture of the first molar gradually gives way to the netlike texture of the tuber area.

The ascending architecture of the anterior molar region is concentrated into the alveolo-zygomatic crest, which also receives contributions from the premolar region. This crest seems to have a definite functional importance in relation to the dentition, which migrates in the course of development. In the deciduous dentition the crest is placed above the second deciduous molar and in the adult permanent dentition taking the place above the first or between the first and second molars. Where the molars and premolars are lost in adult stage I have observed the arrangement of oblique trajectorial fibres from the canine region backwards to the zygomatic insertion, the functional importance of these alveolo-zygomatic trajectories being rather clear.

The alveolo-zygomatic crest has been claimed by several authors as a landmark for the dentition (KLAATSCH 1909, ZSIGMONDY 1911, PFAFF 1923, OPPENHEIM 1927). The first molar has been judged as being in a normal position when placed under the key-ridge of the alveolo-zygomatic crest (ANGLE 1906). Now in the trajectorial dissection this bony crest is dissolved into a more or less widespread alveolo-zygomatic tract of lamella-systems. The crest is less marked in the massively built chimpanzee than in the more gracile jaws of homo, and even here it is not sharply marked in the present material (cf. Figs. 7, 8 and 35). As we have to do with functional structures it is clear that their presence is not a sign of a normal position of a certain tooth (as in the determination of the key-ridge and the mesial root of the six-year molar) but of the functional importance of the structures in question. The tooth position might be abnormal from the point of view of occlusion, teeth might even be extracted, but the remaining alveolar trajectories still turn towards their insertion region in the zygomatic bone. Thus we might see the structures from a functional point of view, and not as stiff morphologic landmarks of normalcy.

Behind the alveolo-zygomatic crest there are some ascending trajectories from the posterior molar region, turning towards the inner posterior wall of the zygomatic process and by way of the postzygomatic fossa reaching the zygomatico-temporal region. Otherwise the posterior molar region and the tuber maxillae only rarely exhibit a definite architectural arrangement when tested with the crevice-line method. The bone shows a diffuse architecture and a spongy appearance. In younger age with developing molars this condition is still more pronounced and involves most of the molar region, then gradually with advancing age giving way to an ascending architecture and the longitudinal fibres of the alveolar border. In the adult stage the lower buccal as well as the palatine marginal fibres are passing through to the pterygoid region. The upper posterior part of the tuber area shows architectural connections with the pterygoid process as well, while the central area has the above-mentioned spongy texture.

Upon microscopic examination the bone of the *tuber maxillae* appears as a porous but fairly dense network of collagenous fibrils and lamella-systems. The pores do not show the appearance of resorption lacunae and there does not seem to be any pathology of the fibrillary systems. Therefore this reticulated texture of the tuber area appears to be the natural physiologic condition. This dense network might have a definite trajectorial importance in spite of the fact that there are no linear trajectories. This supposition is supported by the fact that the fibrillae and lamellae are rather clear and well-defined, not irregular and amorphous as in some other regions where the crevice-line method gives a diffuse picture. The tuber maxillae is embedded in soft tissues, and the question arises whether the net-like, spongy architecture is dependent upon hydraulic pressure conditions in the vascular living tissue: a *biologic trajectorial system* for pressure absorption. In a study of the dead architecture we must not overlook the possibility that the vascular living tissue might well exhibit other physical properties and possess trajectorial potentialities that cannot be studied in the frame that is left after the processes of dissection, decalcification and desiccation, when the tissue is robbed of its natural environment and much of its constituent parts. We might speak of biologic trajectories of the living tissue and include not only the organic and inorganic constituents of the bone, but also the vascular and fluid elements. The importance of surrounding soft tissues must also be considered.

If an area like that of the tuber maxillae gives a diffuse picture upon gross preparation and with the crevice-line method, but on the other hand upon microscopic examination appears as a regular network, with pores and lacunae of about equal size and regular borders, and with a well-defined fibrillary arrangement in the bone trabeculae, it can hardly be judged as a dedifferentiation in relation to the clear trajectorial tracts of other regions. It would rather

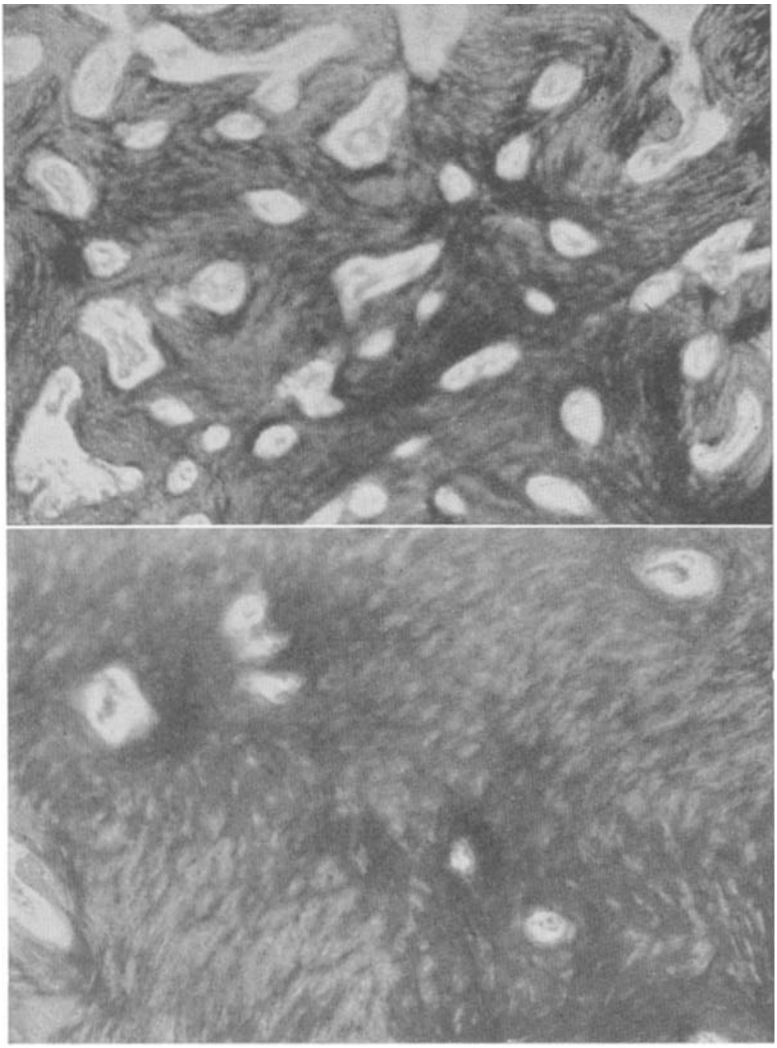


Fig. 9. × 50. Chimpanzee Y 9, Tuber maxillae. Above: transitional form of compact bone with net-like fibrous architecture enclosing rounded lacunae and canals with regular borders (no resorption area). Below: dense fibrous net-work in external cortical layers of alveolar wall.

merit the name of a special trajectorial arrangement, a net-trajectory or possibly a hydraulic pressure trajectory. This special arrangement might also be the characteristic of a growth-region.

The architecture of the maxillary bone might be separated into the following groups:

1. anterior maxillary trajectories:
from the incisor, canine and anterior premolar regions as well as from the palatine side by way of the lateral nasal trajectories, forming the maxillo-frontal trajectorial system, inserting into the frontal bone.

2. lateral maxillary trajectories:
from the premolar and molar regions forming the alveolo-zygomatic and connected trajectories — inserting into the zygomatic bone.

3. posterior maxillary trajectories:
from the posterior molar and the tuber maxillary regions, forming the longitudinal alveolar trajectories and the ascending posterior maxillary trajectories inserting into the pterygoid process.

These maxillary trajectories are thus largely following the three pressure pillars of the upper jaw, and the trajectorial study largely confirms the earlier opinions of the mechanics of the maxillary bone. The important facts about the trajectorial arrangement are related to the qualitative work-out of the structures and the trajectorial behaviour at the muscular insertions, which will be described below.

The *anterior maxillary* or maxillo-frontal trajectorial system runs as a rather well-defined architectural tract to the naso-frontal insertion where it usually disappears in the dense frontal bone. This is built for multiple protection of the brain-case and does not show any comparable trajectorial specialization as the jaws and facial bones. To some extent it is possible to trace an allied architecture of the frontal bone, but it is not always clear and seems to be of an accessory nature. Following the supraorbital crest there is a supraorbital architecture deviating laterally towards the temporal line. In younger chimpanzees this is rather clear, in older specimens it is obscured by the massive development of the supraorbital crest. In some cases a continuation of the maxillo-frontal architecture in the interior of the frontal bone is traceable, reaching the internal cortical membrane in the region above the gallic crest. As shown by BENNINGHOFF 1934 there is an interior architecture of the skull which from the lower interior part of the frontal bone (gallic crest) turns towards the temporal region. Thus

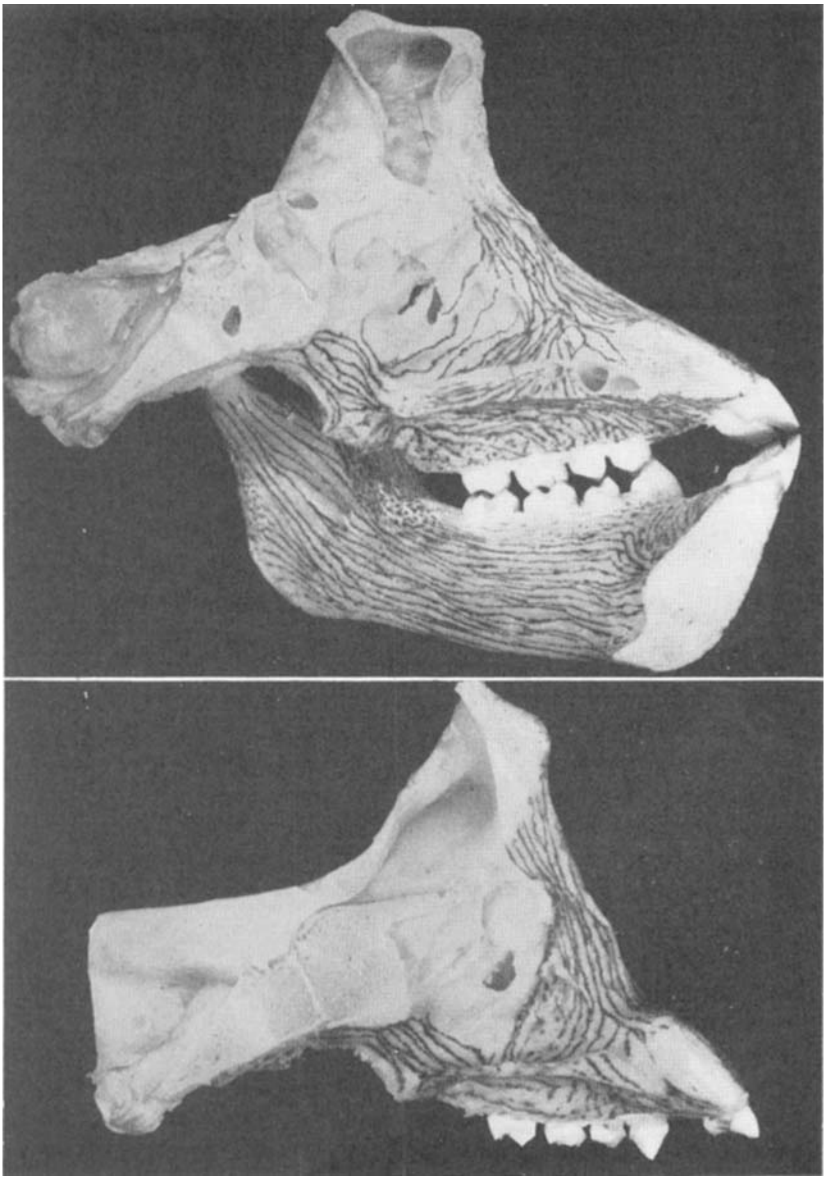


Fig. 10. Chimpanzees, above 9 yrs, below 3 yrs, Mid-sagittal sections, without vomer. The trajectories of the nasal wall joining the naso-frontal and pterygoid systems. Longitudinal palatine trajectories inserting in pterygoid process. Muscular insertion trajectories in lower part of pterygoid process, ascending pterygoid trajectories to sphenoid base. Stronger development of the longitudinal palatine trajectories with the larger prognatism at 9 yrs.

another indication of trajectorial connections between the maxillo-frontal trajectories and the temporal region.

It might be concluded that the maxillo-frontal trajectories to a major extent are absorbed in the frontal bone, and to a minor extent is it possible to trace an architectural continuation laterally towards the temporal region.

The lateral maxillary architecture as the alveolo-zygomatic trajectories largely insert into the zygomatic architecture and do only secondarily by way of the zygomatico-temporal structures reach the neurocranium.

The *zygomatic region* is interesting from an architectural point of view. It is the meeting point of trajectories from the dentition, from the infraorbital, temporal and auricular regions and at the same time the insertion area for the masseter muscle. As a consequence the molar area shows a dense texture wherein the separate trajectorial elements fuse and are hard to trace. But radiating from this concentrated centre there are quite clear osteon tracts in different directions: the anterior zygomatico-temporal towards the fronto-temporal region, the posterior zygomatico-temporal following the zygomatic arch towards its posterior insertion, the zygomatico-masseteric downwards in the direction of the masseter muscle, and the transverse infraorbital connecting with the maxillo-frontal system. The ascending maxillary architecture does not directly reach the zygomatic centre but is inserting into the infraorbital, the zygomatico-masseteric, and the posterior zygomatico-temporal. To a minor extent do the posterior maxillary trajectories also pass the post-zygomatic fossa towards the anterior zygomatico-temporal system.

Dominating the lower lateral part of the zygomatic region are strong trajectories that float out in the direction of the masseter muscle (Fig. 11). These zygomatico-masseteric trajectories have their origin in the zygomatic centre and also receive contributions from the transverse infraorbital and from the posterior zygomatico-temporal trajectories, while at the same time they serve as insertions for the alveolo-zygomatic trajectories from below. By way of the zygomatic centre they are furthermore connected with the anterior and posterior zygomatico-temporal trajectories.

The zygomatico-masseteric architecture apparently has the function of muscular insertion trajectories. These are not previously considered in the trajectorial scheme of BARTH or in any other of the cited literature on this subject. They are not possible to

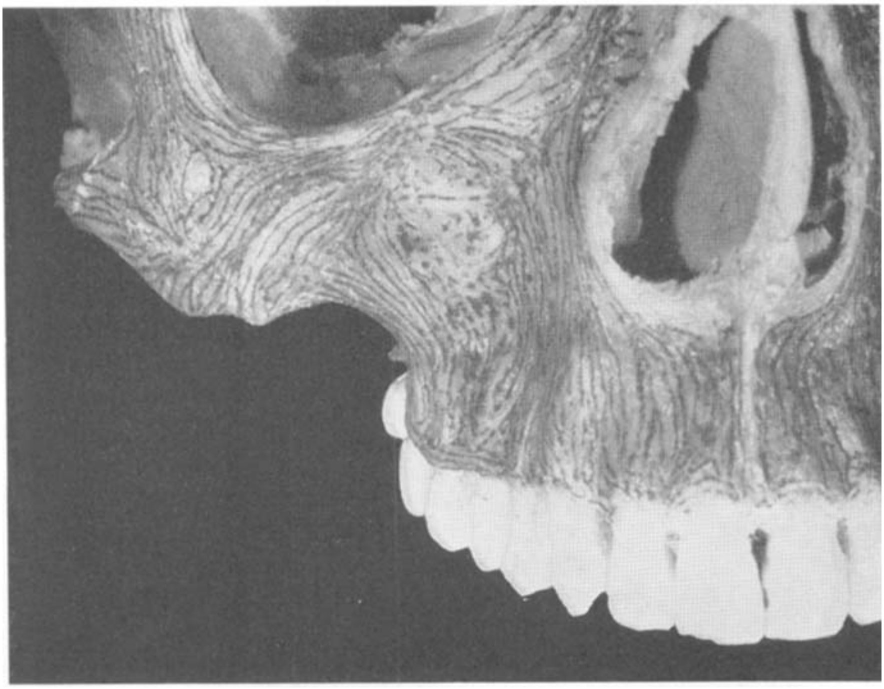


Fig. 11. Homo 22 yrs (Y 8). Ascending alveolar trajectories with neutral field in infraorbital region. Trajectorial insertion of zygomatic region, with masseter insertion trajectories, connecting with the alveolo-zygomatic, the infraorbital, and the anterior and posterior zygomatico-temporal trajectories.

demonstrate with the X-ray method, while an anatomical dissection of the decalcified bone brings them easily into sight. BARTH describes the trajectories of the zygomatic process as directly and completely absorbed into the architecture of the zygomatic arch with no mentioning of any muscular insertion trajectories. The dominating influence of the masseter muscle upon the trajectorial picture of the zygomatic region differs somewhat from the usual arrangement of skeletal muscles in other regions like the long bones, where they do generally not to any considerable extent influence the architecture of their insertion regions. In the long bones the muscular insertions are usually only marked by superficial tuberosities, with no special insertion trajectories. The fibres of Sharpey insert between and through the lamella-systems without notably disturbing the through-going architecture. However, in the zygomatic region the masseter muscle unclear in man and between the longitudinal alveolar and the central longitudinal architecture there is usually an area of diffuse and irregular texture. In the chimpanzee on the other hand where the longitudinal palatine architecture is well developed the ascending alveolar lines turn dorsally to join the longitudinal tracts of the palate (Fig. 10 and 12). In man the horisontal plate of the palatine bone forming the dorsal part of the hard palate is marked by a transverse texture from the centre towards the insertion of the pterygoid process. In front of these transverse trajectories is a thin-walled neutral field, limited anteriorly by the converging structures from the alveolar process towards the central palatine area. The posterior transverse palatine trajectories are clear even in the chimpanzee, although due to the different shape of the palate they have a lateral-dorsal direction, converging to join the longitudinal palatine trajectories and insert into the pterygoid bone.

On the whole the palatine region in man is rather diffuse in its trajectorial arrangement, showing only weak structural organization, which is hard to prepare and make visible on account of the surface relief and rugae that obscure much of the cortical bone architecture. Still it might be concluded that there is no dominating transverse trajectorial arrangement of the hard palate, as claimed by BARTH. In the chimpanzees the palatine architecture is definitely of a longitudinal direction, even the posterior transverse connections turning obliquely backwards. This lacking importance of the transverse palatine trajectories is also supported by the anatomical conditions of the hard palate in man. It is a structure formed by two secondary appendages from the maxilla. The central seam between the two bone-plates sometimes lies in a plane above that of the horizontal cortical plates, at the foot of the vomer. With the seam lying above, the line of direct mechanical connection is broken, and although transverse trajectories could be maintained to deflect and join upwards, the support for a transverse pressure trajectory is not clear. An important transverse pressure component of the masticatory forces as claimed f. i. by BLUNTSCHLI and BARTH is also unsupported by palatine pathology as f. i. the longitudinal palatine clefts are not known to close by functional influences from any transverse pressure components.

The nasal floor does to some extent show a parallel architecture to the hard palate. Although rather weak in development there

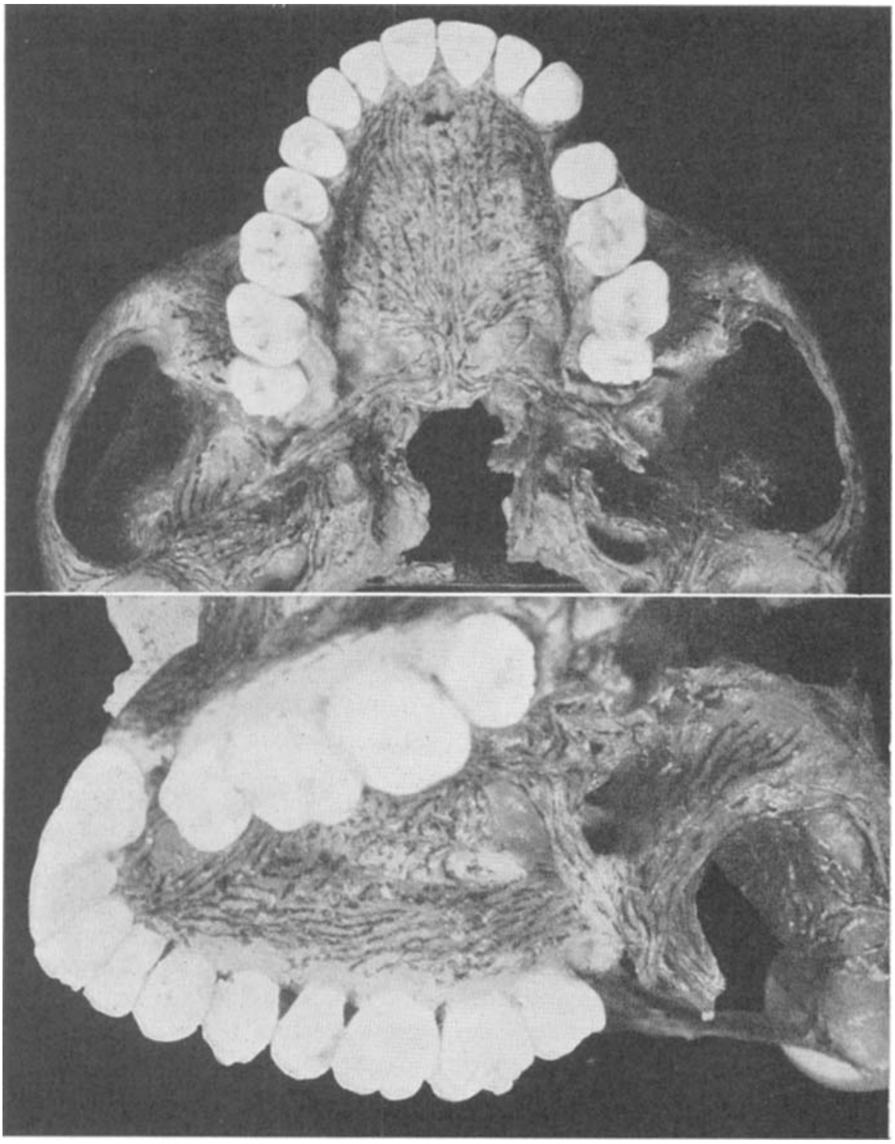


Fig. 13. Man 22 yrs (Y 8). Palatine structures, longitudinal alveolar architecture fairly well-developed.

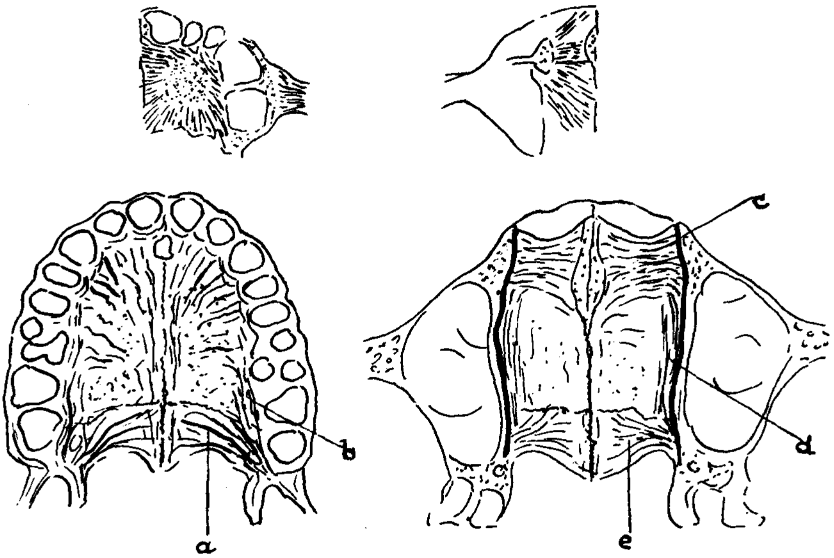


Fig. 14. Architecture of the palate and inferior nasal wall in adult man, compared to the growth-structure of the human new-born (above). a) Post. transv. palatine traj. b) Internal long. alveolar traj. c) anterior transv. nasal, d) lateral long. nasal and e) posterior transv. nasal trajectories.

are lateral as well as central longitudinal tracts connected by anterior and posterior transverse architecture. The anterior transverse texture has no direct parallel in the palate, being formed partly by the border parallel fibres of the nasal aperture.

The trajectorial connections between the upper jaw and the *pterygoid processes* is formed by the following tracts:

from the external maxillary wall:
buccal longitudinal alveolar traj.
posterior maxillary "
from the palate:
lingual longitudinal alveolar traj.
longitudinal palatine "
posterior transverse palatine "
from the nasal wall:
longitudinal nasal traj.
posterior ascending nasal traj.

The buccal trajectorial connections to the pterygoid process are relatively weak, the strongest connecting architecture being that of the palatine and posterior nasal trajectories.

The pterygoid processes show an architecture from the sphenoid base through the length of the processes and to a considerable extent ending freely in the distal lamellar parts of the bones. Into this pterygoid architecture the maxillary and palatine tracts are inserting in such a way that they to some extent are joining the free-ending distal trajectories of the medial and lateral pterygoid laminae. But to a considerable extent they are also inserting into and forming direct trajectorial connections with the ascending pterygoid architecture towards the sphenoid base. The posterior maxillary and posterior nasal trajectories are also entering into this latter system. The architecture of the pterygoid region might be separated into the ascending pterygoid and the pterygoid proper, the latter being the free-ending trajectories. The former includes the palato-pterygoid, the medial and lateral pterygoid, and the pterygo-temporal trajectories. The posterior nasal trajectories are forming a continuous tract with the palato-pterygoid and the medial pterygoid trajectories.

The ascending pterygoid trajectories insert into the sphenoid base spreading out over this region and to some extent forming continuous tracts as the pterygo-temporal, over the infratemporal region connecting with the temporal architecture.

The free-ending pterygoid trajectories fill up the lower and distal parts of both pterygoid laminae. In the lower part they form direct connections with the palatine trajectories. They largely follow the direction of the pterygoid muscles as they insert upwards in the ascending pterygoid structure. Their functional importance is undoubtedly parallel to that of the zygomatico-masseteric trajectories, namely as muscular insertion trajectories.

Compared to the maxillo-frontal and the zygomatic trajectorial systems the architecture of the pterygoid region is considerably weaker and less well-defined. The sphenoid base, where the ascending pterygoid trajectories insert, shows relatively little of special architecture in its external cortical bone. The dense cortical membrane seems to have a flat lamellar texture with few osteon systems. Only on the lateral side is there a clear formation of crevice-lines from the pterygoid process towards the temporomandibular joint area, and the above mentioned pterygo-temporal trajectories.

The architecture and trajectorial systems of the upper jaw have their origin in the alveolar process of the maxillary bone.

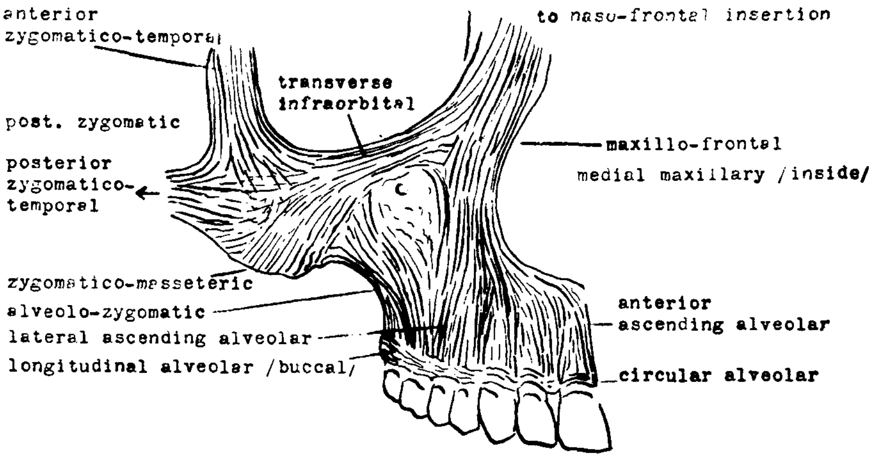


Fig. 15. Trajectories of the upper jaw.

From there on the bone texture forms more or less clear tracts towards the insertion areas of the muscles of mastication and towards the neurocranium. The trajectories of the facial bones insert in the dense cranial bones, or form trajectorial connections with the architecture of the muscular insertion areas, or they form direct insertion trajectories for the muscles of mastication. The architecture has a definite bilateral arrangement. There are some transverse trajectorial systems connecting the two sides or forming communications between different trajectorial systems.

A systematization of the architecture of the upper jaw might be done in relation to the muscles of mastication, although it is apparent that the muscular groups have no isolated trajectorial systems, but these are interrelated to a large extent. So f. i. the masseter and the temporal muscles have a large part of the zygomatic system of trajectories in common. The temporal system is superposed upon the masseter system. Likewise there are connections between the pterygoid and the temporal systems. The close connection between muscular and osseous structures seems to justify a systematization of this kind. At least it is more apt to bring out the functional conditions and the physiological coordination of structures than a system like that of Barth which separates the trajectories into vertical, longitudinal, and transverse systems (Fig. 1).

Trajectories of the upper jaw.

	Origin		Insertion
Temporal system	anterior ascending alveolar masseter system	maxillo-frontal ant. zygomat.temporal post. ” ” pterygo-temporal	circular temporal radiating temporal
Masseter system	lateral ascending alveolar	alveolo-zygomatic transverse infraorbital	zygmatico-masseteric post. zygomat. temporal
Pterygoid system	posterior ascending alveolar long. alveolar ” palatine ” nasal	posterior nasal ” transv. nasal ” transv. palatine palato-pterygoid	pterygoid proper ascending pterygoid

In the above scheme the maxillo-frontal trajectorial system is coordinated with the temporal muscle in spite of the fact that there are few direct structural connections between them, namely from the reason that they both insert into the anterior part of the dense frontal bone, the maxillo-frontal trajectories in its centre from below, the circular temporal trajectories in its lateral part from above, whereby a mechanical relationship is given.

CHAPTER 4.

Lower Jaw.

The architectural conditions of the mandible has attracted a special interest. The route of development goes from the more primitive studies of the spongious trabeculation (Walkhoff 1900), over the introduction of X-ray and following composite pictures of the bone architecture (Walkhoff 1900—1902, Barth 1919, Grunewald 1920) to the studies of the compact bone by way of specific methods, as for instance: studies of the canal systems of

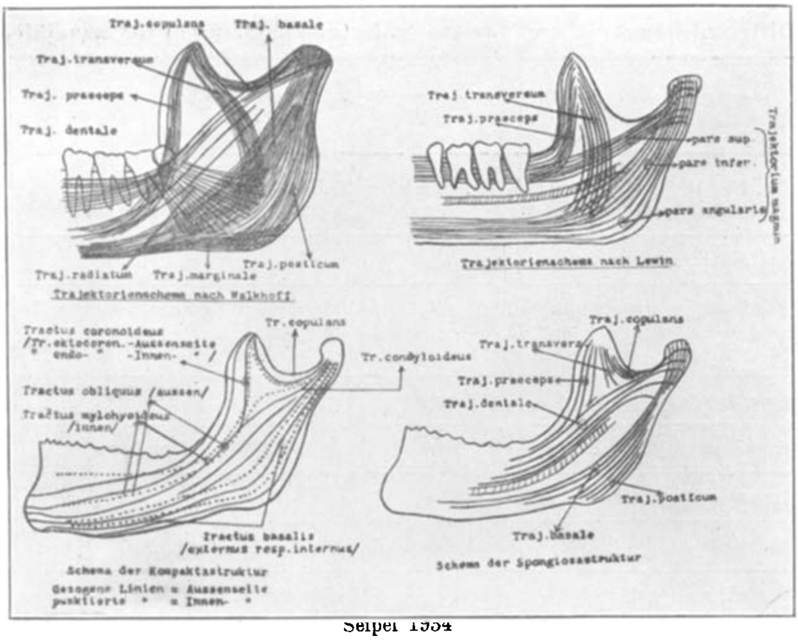


Fig. 16. Trajectories of the lower jaw: arrangement and nomenclature according to different investigators.

the compact bone by DAVIDA 1915 and WINKLER 1921, the use of the Spalteholz method on foetal mandibles by WISSMER 1927, the "Spaltlinienmethode" of BENNINGHOFF 1925 which was used by DOWGJALLO 1932, BENNINGHOFF 1934, SEIPEL 1934. With this last named method the way was opened for a more dissective anatomical treatment of the bone architecture, which has been used in the present study.

The earlier findings of the bone architecture are comprised into a series of trajectorial schemes, some of which are presented on fig. 1 and 16. The one by WALKHOFF 1900 was modified by LEWIN 1913 giving a better concept of especially the angular and the condyle regions, but otherwise (like WALKHOFF) limited to the lateral part of the mandible. BARTH considerably modified these schemes, but her findings, which were founded on X-ray pictures of Cebus macrocephalus, seem to diverge in several respects from the conditions in homo both as found by previous investigators and in the present study as well.

Different nomenclatures for the trajectorial systems of the mandible.

Walkhoff 1900	Lewin 1913	Barth 1919	Seipel 1934	Present study
Tr. basale	Tr. magnum, pars inferior	Tr. basale	Tr.basale	Basal tr. inferior portion
marginale	magnum	”	”	”
posticum	magnum, pars angularis	”	basale, pars angularis	basal, angular dispersion
praeceps	praeceps	praeceps	coronoideus	temporal
copulans	—	—	copulans	connecting
transversum	transversum	—	—	—
radiatum	—	radiatum	—	—
dentale	dentale + magnum, pars superior	long. alveolare	obliquus ext. ” int.	basal ext. oblique tr. int. ” ”
—	—	ascend. ant.	alveolare	alveolar catenary system
—	—	—	angulare transv.	transv. angular access. masseteric ” pterygoid
—	—	—	spongios. transv. mand.	transverse mandibular spongious
—	spongios. condyloid.	—	spongios. condyloid.	condylar spongious crossing

The main changes from the earlier systems are the consideration of the architecture for the whole bone, including the alveolar process and the elimination of some older trajectories that could not be confirmed. The transverse trajectory of Walkhoff and Lewin could not be found on anatomical preparation, but was considered as due to a contamination of two separate structural phenomena, namely the X-ray shadows of the lower ramus area (muscular insertion tuberosities) and the descending trajectories of the coronoid process, which partly insert into the oblique basal tracts in the middle of the ramus. There were also reasons to eliminate the traj. radiatum, earlier denied to exist by LEWIN 1913 and KATZ 1931.

The spongious bone architecture was found to have special importance in some respects, namely:

In the condyle head as an elastic pressure system and trajectorial meeting-point. In the alveolar region as a support of the alveolar baskets between the cortical bone plates, between the external and internal cortical walls as reinforcements and transverse mandibular trajectories.

Before entering upon a description of the architecture of the mandible we might consider the development and early architectural conditions which partly explains the architecture of the adult bone.

The mandible is ossified in the fibrous membrane covering the outer surfaces of Meckel's cartilage (LOW and FAWSETT, cit. from GRAY). The early cartilaginous bar of the mandible is formed by two parts joined to one another in the symphysis by mesodermal tissue. At birth the bone still consists of two parts, united by a fibrous symphysis, in which ossification takes place during the first year. WISSMER 1927 studied the interior architecture of the foetal human mandible by way of the Spalteholz method and has shown the basal architecture at this stage of development. Except the still undeveloped symphysical connection the fairly simple texture of a long tubular bone is dominating with the additions of some less welldefined architecture of the angular, coronoid and alveolar processes, all feebly developed at this stage. The jaws of a human newborn prepared with the crevice-line method (Fig. 17) gives an architectural picture coinciding with that found by WISSMER. A basal tract from condyle to condyle with fibrous connections at the symphysis is dominating. The coronoid and angular processes seem to represent only a dispersion of the basal trajectorial lines. The alveolar process has the architectural picture of radiating arcades, from the mandibular base upwards, this texture possibly being referable to growth conditions. In the symphyseal region the architectural lines spread out and disappear in the fibrous connective tissue. With advancing age the symphyseal organization goes on, until in the adult stage the trajectorial elements are quite clear and unbroken even in this region, the architecture then being continuous from condyle to condyle, like it is in the long tubular bones between the joint surfaces.

There is little anatomical background for the *basal arch* of the upper jaw as presented by BLUNTSCHLI 1926. But in the lower jaw the architectural conditions of the compact bone, as brought out by the present method, show a functionally important basal arch upon which the dentition and the muscular appendages are built. It seems appropriate from structural points of view, to consider the mandible as a long tubular bone when it comes to an analysis of its architecture. The separation into corpus and ramus mandibulae is in this respect thoroughly unsatisfactory, especially if it leads to a similar separation of trajectories belonging to one part or the other. Earlier investigators who have produced more or less complicated trajectorial systems in the mandible seem to have been less aware of the systemic connections of the tissues in the facial region. The all-too strong adherence to anatomical parts, like f. i. the ramus mandibulae, seems to explain a desire to satisfy every part with its own trajectories, more or less independent of larger systemic connections.

The basal trajectorial systems of the mandible.

The basal trajectorial systems of the mandible are most easily studied in younger age stages and in certain antropoid stages, before a higher specialization and functional development sets in and somewhat obscures the basal architecture. In the mandible of the human newborn (Fig. 17) the simple architecture of a long tubular bone is dominating. The similarity to that of younger chimpanzee specimens is striking. With advancing development of the coronoid, angular and alveolar processes as well as the chin, the simple basal architecture undergoes certain modifications, presumably determined by specialization of function and increasing strength of development.

The crevice-line preparation of the adult human mandible (Fig. 18) gives a dominating amount of clear trajectorial connections from the condyle to the lower chin region, in most cases also passing clear through the chin and connecting with corresponding trajectories of the other side. This structural arrangement of the compact bone I term the *basal trajectorial system* (Figs. 24, 25). It appears both in the outer and inner bone plate of the mandible. Appearing at the condyle it apparently has its

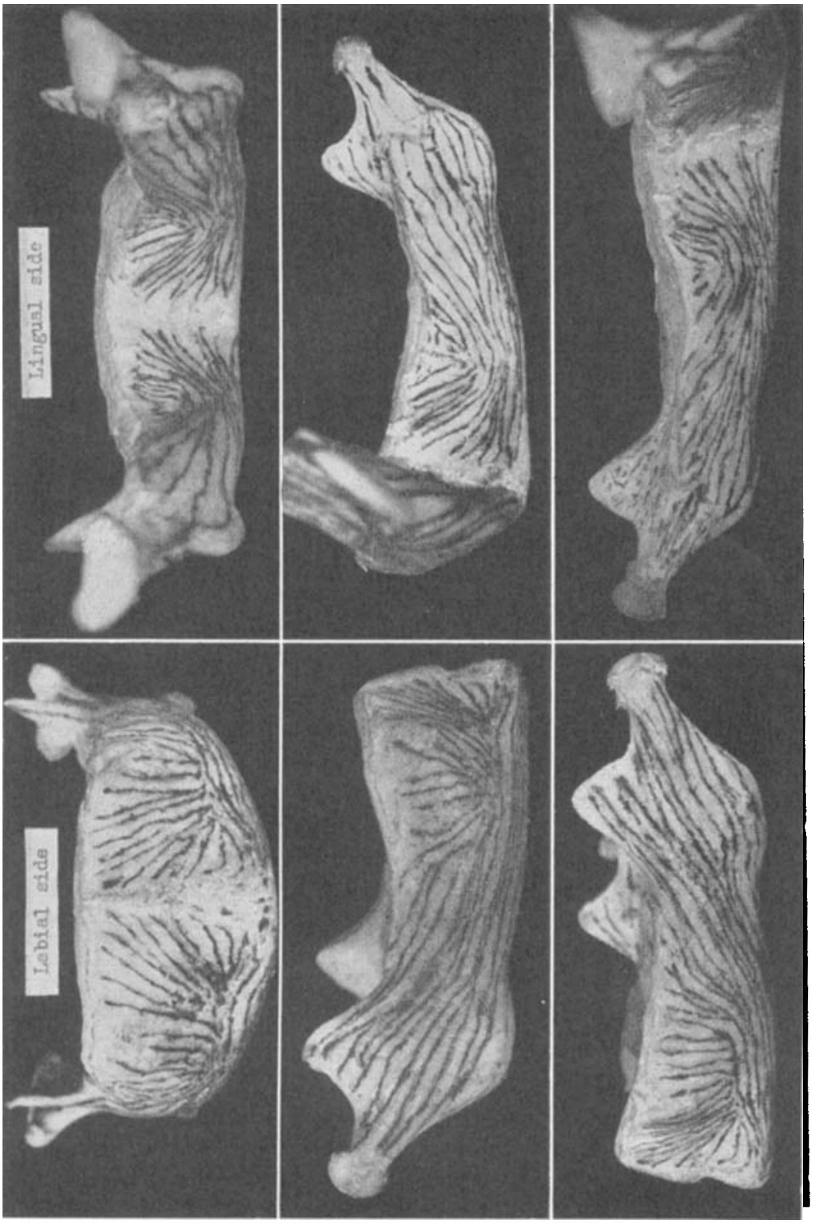


Fig. 17. Homo, newborn (Y 7). Crevice-line preparation showing trajectorial arrangement of the mandible.

origin in the heavy sub-cortical spongiosa, as the compact bone covering of the condyle-head is only made up of a rather thin cortical layer. From the neck of the condyle the compact bone fibres spread over the ramus; a minor bundle passes as a communicating system to the coronoid process following the border of the incisura semilunaris. These trajectorial connections are termed traj. copulans by WALKHOFF 1900. Providing it would be necessary to give a certain name to this superior part of the connections between basal and temporal trajectories, it seems more appropriate with the name traj. communicans, or connecting trajectory, following the usual terminology for a constant anatomical connection. A massive portion of the basal trajectories pass downwards in the posterior part of the ramus, spread over the angular region, in the interior undergoing a partial dispersion and transformation into spongious tracts following the same general direction. Some specific modifications of the superficial layers due to muscular insertions as well as the occurrence of a transverse angular trajectory are taken up under a special description of the angular process. Towards the incisura prae-angularis the dispersed trajectorial lines as well as most of the spongious trabeculae are condensed again into a heavy tract following the corpus and base of the mandible forwards. They undergo some superficial modifications and deflections at the tubercula mentalia, in the fossae digastricae and at the mental spine of the inside, but yet in the main part establishing clear connections with the trajectories of the opposite side.

From the anterior part of the condyle-neck there pass, beside the systems forming the traj. communicans, a well-developed bundle of fibres in a diagonal direction down the ramus. In the upper part, especially at the junction with the coronoid process, the crevice-line method gives a somewhat unclear picture. Upon anatomical preparation there appears in this region an interlacing of fibres from the condyloid and coronoid processes. Some osteons join in groups by direct crossing. Others form broader lamellae or lamella-systems, which receive a triangular shape from two systems joining at an angle and continuing downwards in a single plate or fibre. The trajectorial elements of the coronoid process, the *temporal trajectories*, in their posterior and middle portions thus join the basic systems of the ramus. Towards the anterior part of the ramus these trajectorial junctions gradually disappear and give way for direct continuous trajectories from the coronoid

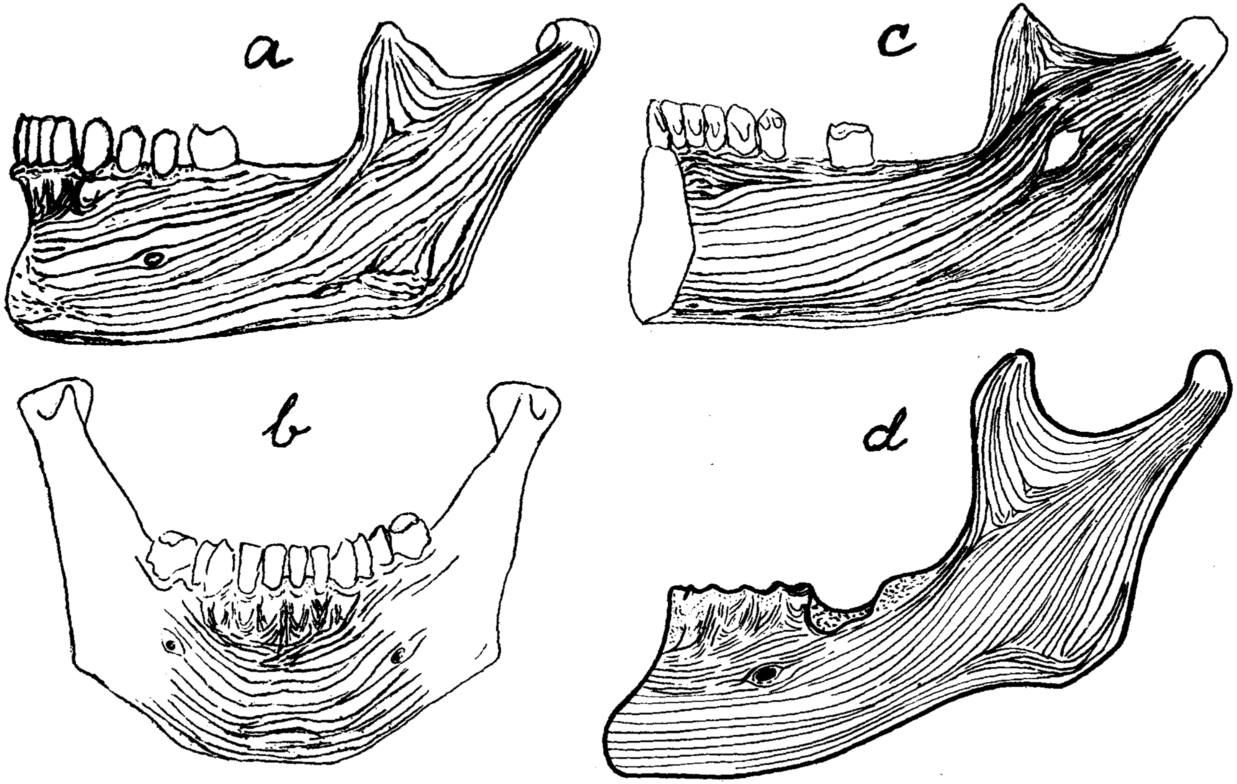
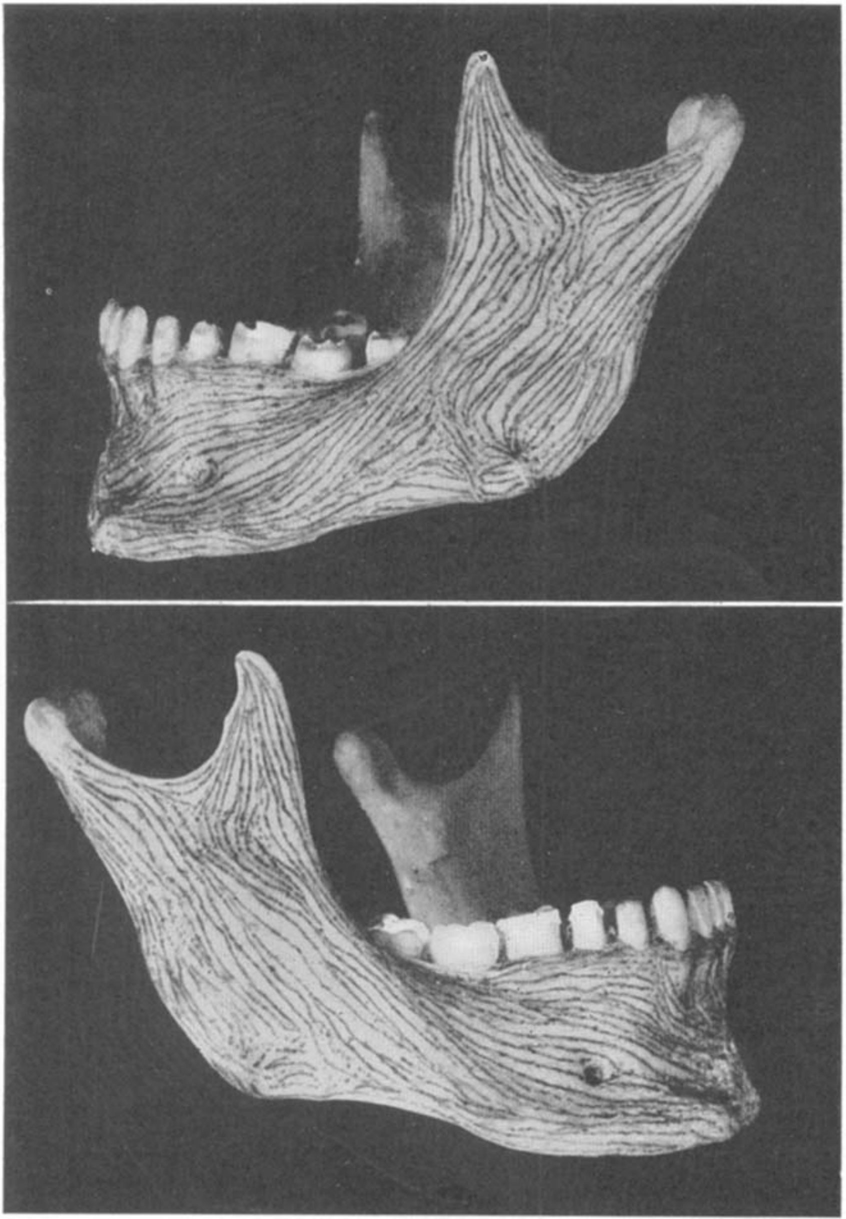


Fig. 19 a, b, c. Homo about 12 yrs. a) architecture of superficial layers of labial side, b) deeper layers of anterior region, alveolar catenary system above clear symphyseal connections, c) lingual side with typical longitudinal architecture and angular dispersion. d) Mandible of adult homo with atrophic changes of the alveolar bone, but clear trajectorial structures of the basal parts.



surface architecture. The transverse incremental lines of the angular region differ from the simpler basal architecture of the chimpanzee mandible (cf. fig. 21).

process downwards. Together these independent coronoid (temporal) trajectories and the diagonal fibres of the ramus form the massive *oblique fibre tracts* of the mandible, which are an important part of the basal trajectorial system. The *external oblique tract* dominates the lateral wall running along the external oblique line downwards and disappearing in the basal trajectories of the anterior molar and the premolar regions. The oblique trajectorial system of the inside has a somewhat different arrangement than that of the outside. It starts higher up, already at the neck of the condyle, runs obliquely downwards, receiving contributions from the coronoid process to form a broader oblique tract, the upper portion of which spreads out in the sub-molar region, and the lower portion continues as a definite tract along the mylohyoid line to the region of the mental spine. The lingual aspect of the mandible is characterized by a rather parallel distribution of trajectorial lines from the ramus forwards to the whole height of the symphyseal region. This is different from the buccal aspect which has a condensation of the basal trajectories to the lower third of the chin (Fig. 18).

It might be remarked at this place that the trajectories of the basal system are not always represented by osteon-systems of a thready texture. In certain regions like the mandibular base and the centre and lower part of the external oblique fibre tracts we often find surface layers of broad, thick lamellae instead of the thready texture that is otherwise usual in trajectorial systems of the lower jaw. These might be explained anatomically as subperiosteal layers and mechanically as lamellar reinforcements against forces working in a certain plane.

Angular region.

In the human newborn the basal trajectorial system of the mandible is passing through the angular region without interruption. There is a dispersion of the compact bone-wall as well as of the basal trajectories in this place but no interruption or deviation. The same is usually the case in the mandibles of younger chimpanzees, and the mechanism of the angular region as a dispersion and flattening of the usual basal trajectories is quite clear. In older chimpanzees the condition is somewhat obscured by the important muscular attachments, but in deeper layers of the compact bone the condition is exactly the same as described

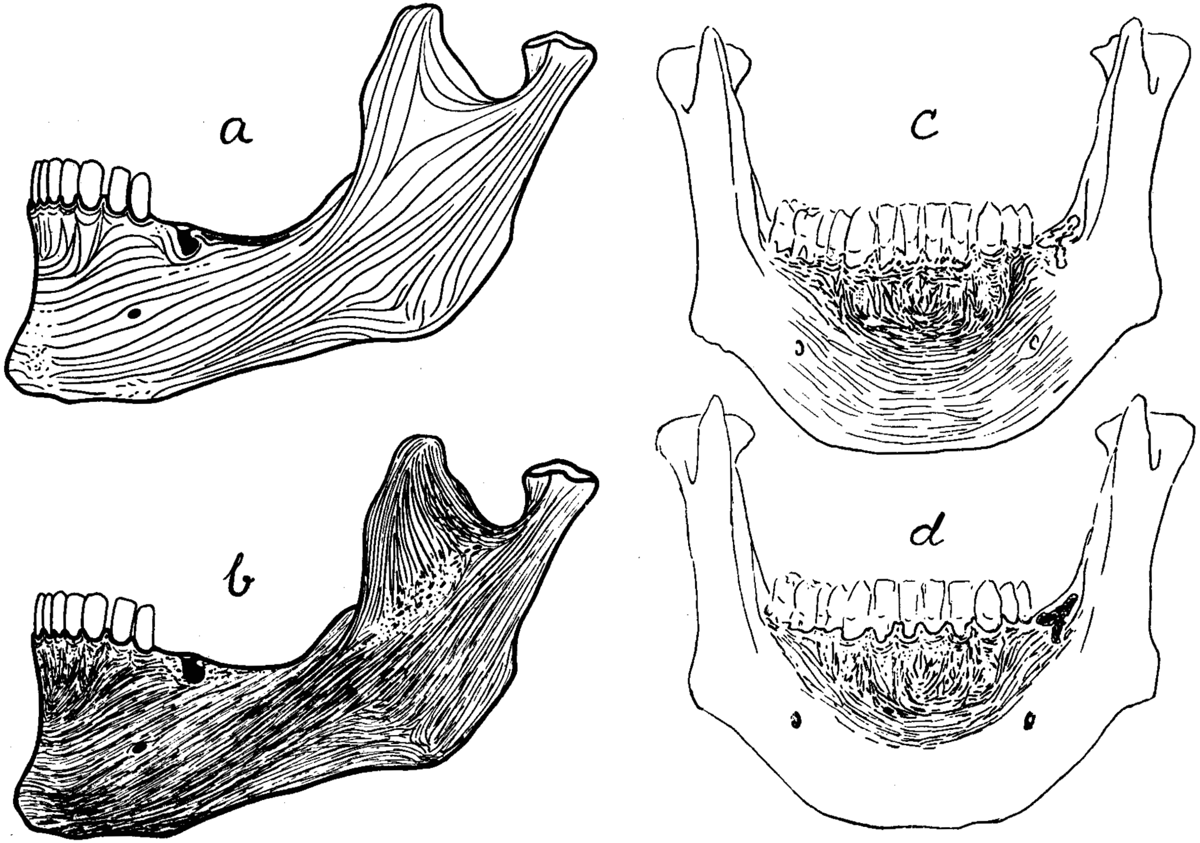


Fig. 20. Adult human mandible with well-developed trajectorial structures. Schematic drawings of mandibular architecture: a) crevice-lines of surface layers, this specimen showing accessory mental tubercles. b) fibrous osteon-texture of deeper layers of the compact bone, dedifferentiation around molar extractions space. c) and d) preparation of alveolar structures in deeper layers of the labial wall. The vertical interdental arcuate structures are closely connecting over the thin alveolar walls, especially in the apical region. There is a circular alveolar architecture below the more amorphous alveolar margin.

above, *i. e.* there are clear through-going trajectories from the condyle to the base of the mandible with a flattening and dispersion in the angular region. In adult human specimens the conditions are somewhat different. First the jaw angle is less obtuse than in young human and in the chimpanzee, approximating to a right angle from the slight bend in younger stages. This increased angulation between the base and the ramus seems to occur through a still larger spread and flattening of the angular region; a condition which can easily be traced in the trajectorial systems both of the compact and of the spongious bone.

As I have described on an earlier occasion (SEIPEL 1934), there are in adult human specimens to be found in the angular region, mostly on the external side, reinforcement lines or angular seams in the basal trajectories (Fig. 19 a, 20 b). These seams are mostly following the masseter and pterygoid tuberosities, being of a more or less superficial character. The strongest and most constant reinforcement line appears on the lateral surface, running from the middle of the angulus in a direction forwards and upwards, towards the central part of the mandible but never crossing the whole surface of the mandible. Microscopically this line is formed by a fusion of the osteon systems, by triangular plates formed through lamellae or osteons from above and below uniting with crossing trabecular elements. We also find fairly dense, whirl-shaped irregularities interrupting the straight thorough-going trajectories and making them deviate in an upwards direction.

These trajectorial fusions and whirl-shaped irregularities together form a fairly strong *transverse trajectory* from the posterior mid-angular border in a direction forwards-upwards, against the diagonal trajectories of the ramus, or disappearing in the more or less neutral field below the external oblique tract.

It lies close at hand to consider this trajectorial crossing simply as a mechanical reinforcement of the dispersed trajectorial systems of the angulus, serving to strengthen the flattened angular region against muscular pull of the masseter and pterygoid muscles. The fact that the usual muscular attachments, tuberosities and waves of the surface relief do only to a very limited extent deflect the underlying trajectorial systems indicates, however, that this relatively constant transverse angular trajectory of the human specimens has another meaning than that of a pure mechanical reinforcement. There are reasons to believe that its importance is also that of an incremental line, due to growth conditions. This

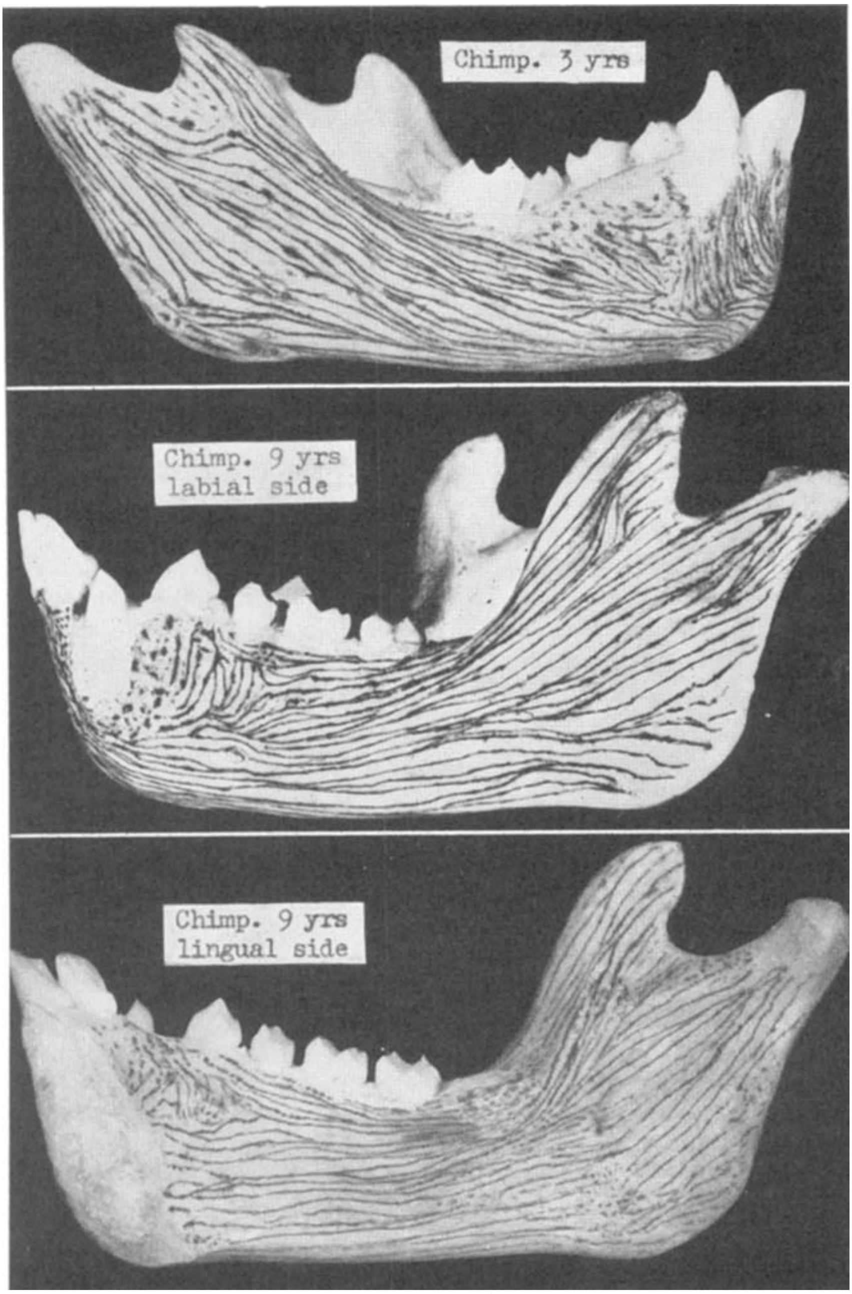


Fig. 21. Mandibles of chimpanzees showing the longitudinal basal architecture, in the older specimen somewhat deflected by the heavy muscular insertions of the angular region. There is an irregular architecture (dedifferentiation) of the alveolar bone in regions of lost temporary molars (above) of erupting permanent canine (middle) and beginning eruption of third molar (below).

is supported first by the similarity with the trajectorial phenomena of the tuberositas mentalia and the symphysis of the mandible, secondly by the constancy of its position, relatively independent of other irregular muscular tuberosities of the ramus mandibulae. Consequently this lower transverse angular trajectory is considered as an incremental line that fulfills the purpose of a mechanical reinforcement and muscular insertion trajectory (M. masseter).

The chin region.

The chin (Fig. 20, 22) of the adult human mandible is characterized through a fairly clear trajectorial arrangement of longitudinal fibres and lamella-systems connecting the basic trajectories of the two sides. However, this trajectorial connection must be considered as being of a secondary character. At birth the two osseous halves of the mandible are united only by way of fibrous connective tissue, and the trajectories in a crevice-line preparation at this age-stage spread out and disappear in the loose tissues of the symphyseal region. In a human specimen with erupting permanent canines (Fig. 22 c) the ossification of the symphysis is complete and there are clear trajectorial systems going through the basic part of the chin. In a chimpanzee with deciduous dentition and first permanent molars in place (about $4^1/_2$ years) the symphyseal architecture is about the same as in the adult specimen, although of a weaker texture. On the labial side the trajectorial systems are going clear through the symphysis. Consequently one must suppose the interior architecture of this region to develop parallel with the advancing ossification during the first years of life, and to undergo a successive strengthening with increasing functional requirements up to adult stage.

The importance of the tubercula mentalia might be considered in connection with the questions of the development of the architecture of the chin-region. In the newborn the basal trajectories disappear in the lower, broader part of the mental trigonum, and it is not possible at this stage to trace any functional importance to the mental tubercles by the crevice-line method.

In adult man the protuberantia mentalia, which are supposed to represent the development of the tubercula mentalia, stand out — in specimens where they are well developed — as a definite break in the longitudinal trajectorial systems. In such case the superficial layers of the whole mental trigonum is rather amor-

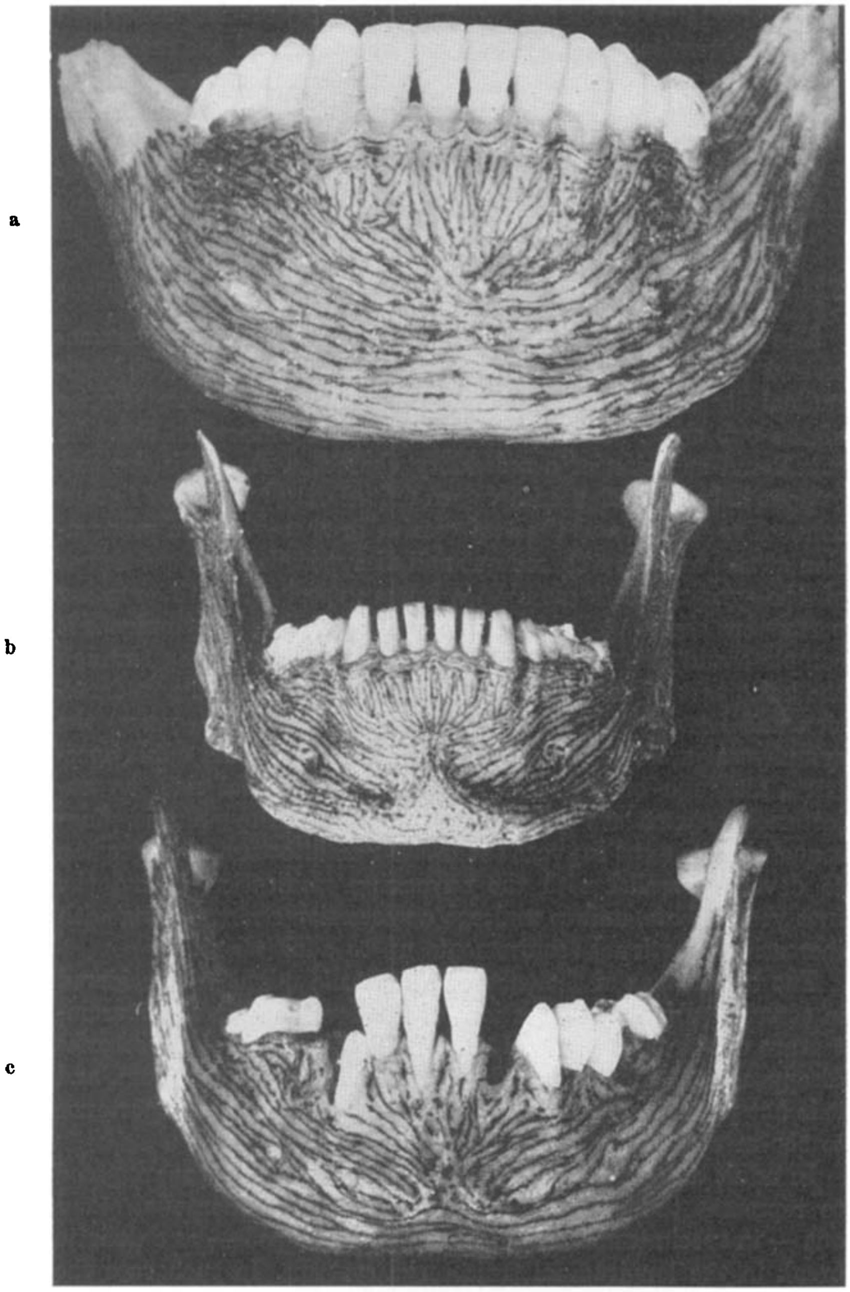


Fig. 22. Crevice-line preparations of human mandibles, lower 12 yrs, middle 20 yrs, upper 22 yrs. Basal trajectorial systems of the mandibular body meating in chin region. The symphyseal connections are somewhat deflected by different surface reliefs of the mental trigonum, but in deeper layers going clear through the lower anterior region. The alveolar catenary systems are superposed upon the basal systems of trajectories.

phous, giving no definite crevice-lines. The incoming trajectorial systems unite into larger lamellae or turn into whirl-shaped irregularities, or simply seem to disappear into the amorphous surface layers in this region. If they are prepared away, the deeper layers of the bone exhibit an increasing degree of trajectorial organization, giving clear through-going trajectories below the amorphous arrangements of the surface. In jaws with less outstanding mental trigonum, with an even surface relief lacking of protuberantia mentalia the trajectorial systems are continuing through the chin-region with little or no irregularities or disturbances of the longitudinal trajectories.

A possible functional importance might be attributed to the mental tubercles or the irregularities of the mental region by the fact that trajectorial elements from the external oblique fibre-tract and from the basic systems following the mandibular base seem to meet and cross in this region, thus suggesting the possibility of insertions or crossing points between trajectories of different importance (Fig. 24, 25). There are reasons that the external oblique tract is of importance as a tensile trajectorial system and the lower basal trajectories as a compressive system. A crossing between tensile and compressive systems would naturally occur under the formation of a trajectiorial condensation or knot-like irregularities. The crevice-line preparation would give a diffuse picture with crevices in different directions or round injection spots. Amorphous surface layers, with perforating canals as often appear in the mental trigonum, would have their anatomical explanation from the bony reinforcement and nutritional conditions in such a trajectorial knot.

In this discussion might be mentioned that in one specimen with excessively developed lower jaw I have observed accessory tubercula in the lower lateral part of the corpus mandibulae about 2 cm behind the regular mental tubercles of the chin. These two lateral tubercles were clear meeting points between an unusually low inserting portion of the external oblique fibre-tract and the lower basal trajectories (Fig. 20 a).

The human chin offers an example of the relationship between gross anatomical form, hereditarily given or otherwise conditioned, and interior organization through functional influences. The development of the individual chin seems to go on independently while the interior architecture attains its individual degree of strength and clearness. But on the other hand form and function can never be separated (cf. BENNINGHOFF 1935). The outer form sets the boundaries for and determines the lay-out of the interior architecture. In the bone as in the muscle the functional organization also to some extent influences the gross form of the organ as in the production of accessory tubercula mentalia in the above mentioned human mandible of excessively strong interior structural organization (Fig. 20 a).

Alveolar process of the mandible.

The trajectorial arrangement of the alveolar process of the lower jaw is somewhat different from that of the maxilla and therefore merits its own description. As a matter of fact the general mechanical principles are the same, but some differences arise from the lower arch of teeth being suspended in a free bone, the attachment of which, by way of ligaments and muscles, occurs largely behind the dental arch.

Border parallel and circular fibres occur as in the upper jaw (Fig. 22), interdental pressure pillars likewise, although their importance seems to be limited to the front and anterior lateral region. The buccal alveolar shields covering the roots of the incisors and canines show a somewhat weaker structural arrangement than in the upper jaw, while on the other hand the roots of the lower molars have a definitely stronger trajectorial covering than those of the upper jaw. Below the borderline-fibres there is in the lower anterior region an indication of arcade formation of the relatively weak fibres appearing in the buccal lamellae. These arcades connect the interdental pressure pillars and gradually assume a more V-shaped arrangement downwards (Figs. 19 b, 20 c, d, 22 and 23).

The interdental trajectories join in the apical region in a definite arcade formation. The apical continuations of the arcades converge towards the midline in the canine and premolar regions following more and more parallel to the basic trajectories of the mandibular body (Figs. 20, 22, 23). In the premolar region this arrangement gradually gives way for a flattening of the arcades and a more horizontal arrangement of the trajectories, the interdental pillars still existing as a definite interdental seam or fusion of the flat arcades or longitudinal osteon systems. In the molar region the horizontal longitudinal systems are dominating the whole buccal surface. The slightly inclined arrangement of the

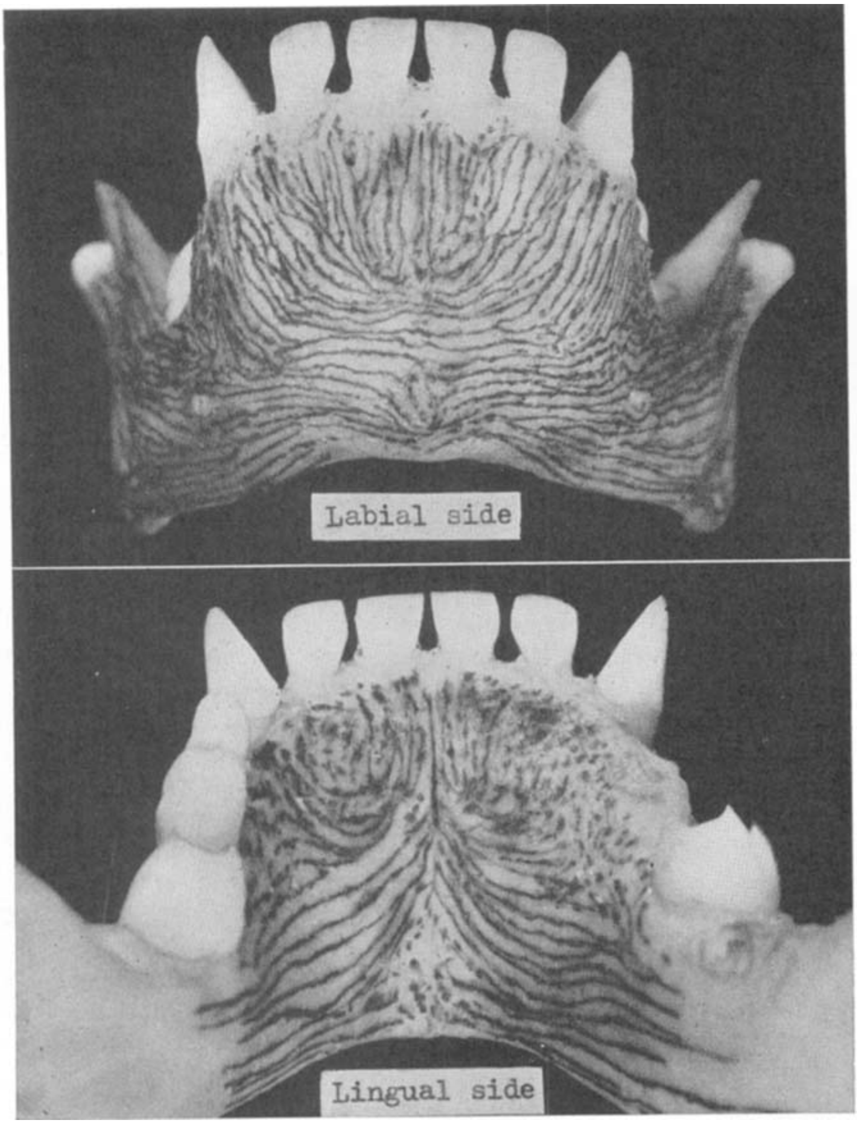


Fig. 23. Chimpanzee, 3 yrs (Y 6). Above: labial alveolar arcade system upon the basal trajectorial systems, which go clear through the symphyseal region. Below: irregular arch formation on lingual side of alveolar process (cf. permanent teeth in pre-eruptive positions on lingual side). There is also a diffuse picture in alveolar process below the lost temporary molars of the right side. There are few straight symphyseal connections on the lingual side, which might be compared to the different behaviour of the labial and lingual trajectorial systems in fracture healing in fig. 26.

premolar trajectories with a direction down-forwards from their origins in the alveolar walls, subsides for a border-parallel arrangement. The trajectorial fibres form a longitudinal dental trajectorial system, which is superposed on the oblique basal fibre tracts and backwards joins this system, or over the retrodental space continues into the temporal trajectories of the coronoid process.

The inside of the alveolar process differs from this description in some respects. The cortical bone wall of the inside is notably thicker than that of the outside, at least in the anterior region. The basic trajectories show a more parallel distribution over the inside. (Fig. 19 c.) The internal oblique fibre tract runs further back on the ramus than the external tract, and consequently there is no such diagonal arrangement of trajectories as on the outside. The parallel architectural lines are distributed over the larger part of the alveolar wall with no sharp demarcation between alveolar and basic architecture. In the anterior region there is some indication of arcade formation. However, the arcades of the incisor region are rather flat, the structural reinforcement of the interdental pillars being noticeable, but giving no definite crevice-lines in a vertical direction. Flat arcades with stronger interdental seams or pillars appear even in the canine and premolar regions of the inside, but in the middle and lower apical thirds of this area as well as in the whole molar region of the alveolar process the architecture is definitely longitudinal, continuing backwards into the internal oblique tract and into the temporal system of the coronoid process.

Mechanical interpretation of the architecture of the mandible.

The architecture of the mandible is somewhat more complicated and less easy to bring into functional relation to the muscles of mastication than that of the maxilla. A simplified mechanical interpretation might enlighten an understanding of the architecture, but can only be of a hypothetical value for the following reasons:

Trajectory is a hypothetical structure, implying a simplification of the anatomical conditions. Furthermore the decalcified bone or organic matrix is not identical with the normal bone, because the mineral fixation changes the mechanical conditions, and maybe also the character of the trajectorial elements, to an unknown extent. The vascular conditions during life are also apt to play an important rôle for the physical properties of the bone, for breaking strength, pressure resistance etc. Therefore tests performed on dead bone cannot adequately reproduce the conditions during life.

From an anatomical point of view tensile and compressive elements of the bone are not clearly differentiated, as this tissue is built for multiple requirements. But mechanically, under the influence of known forces, we might separate regions where tensile and compressive forces can be supposed to work. KOCH 1917 thus separates tensile and compressive structures in the femur, and even claims a different macroscopic appearance.

As before mentioned the mandible might most readily be considered as a long tubular bone, which has been subjected to some modifications of form and muscular attachements (Fig. 24). The angular enlargement does not markedly change the relations of upper tensile and lower compressive systems. With the U-shaped form the compressive systems turn more to the inside and the tensile to the outside (Fig. 24 c). The simplified end-result (Fig. 24 d), with the specific loads of the mandible upon a modified long bone, is that of upper-anterior tensile and lower-posterior compressive systems, which coindices fairly well with the results found in the present study.

The teeth are set in an alveolar catenary system (Fig. 25), which in the superior lateral extremities of the dental arch is placed between tensile trajectorial systems ending in the temporal muscles. This tensile system itself is locked frontally, and partly also laterally, through insertions into the lower basal trajectorial system of compressive nature, which dominates the base and the inside of the mandible. In the upper posterior part the tensile and compressive systems are also connected both through the external and internal oblique tracts which pass diagonally over the ramus to join the basal systems, and secondly through communicating trajectories following the incisura semilunaris, as well as the inserting fibres of the coronoid process. The upper posterior portion of the internal oblique tract, representing a well-developed trajectorial system from the foot of the coronoid process spreading out over the anterior surface of the condyle neck, appears to have a specific importance. It has the place of an oblique support between the ascending tensile and the descending compressive systems of the ramus and might be compressive in nature. Its

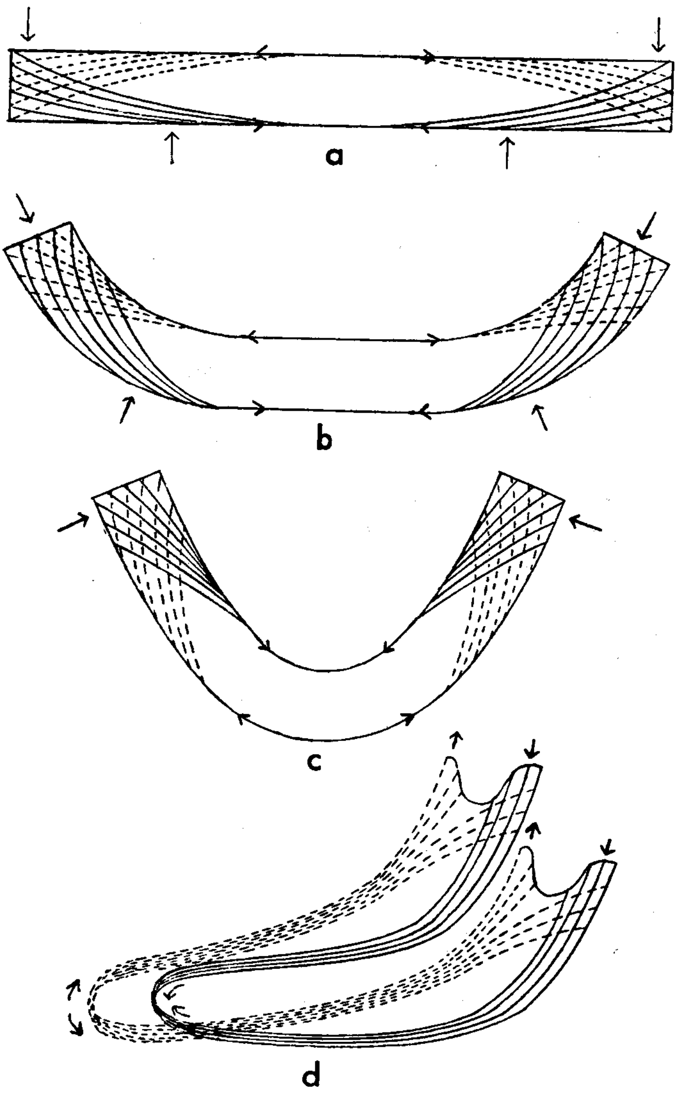
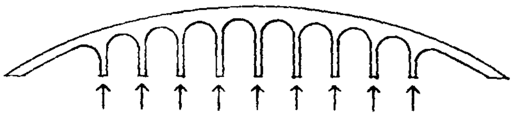


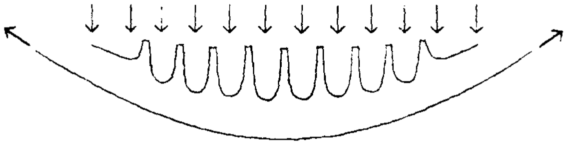
Fig. 24. The basal trajectories of the mandible in simplified mechanical interpretation:

a) architecture of a straight rod or long bone with upper tensile and lower compressive systems, at forces indicated by arrows.

b) angular bending and c) U-bending at the chin with migration of the tensile trajectories towards the outside and compressive towards the inside.

d) basal systems of the mandible with upper-anterior tensile and lower-posterior compressive trajectorial systems.





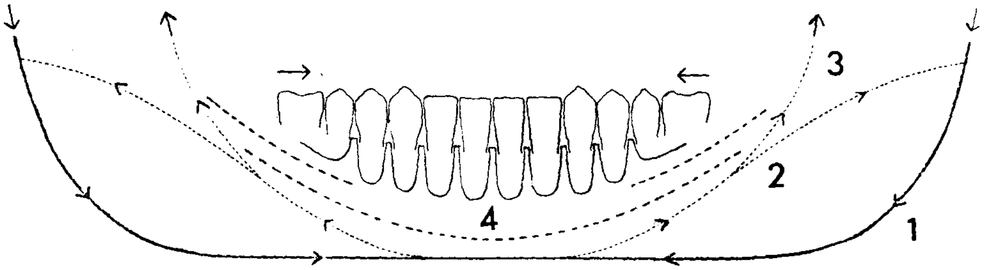


Fig. 25. The alveolar arcade system, comparable to an inversed bridge construction, supporting the teeth and carried by the sloping basal tracts of the mandible.

1) inferior basal trajectories (compressive).
2) oblique mandibular trajectories (tensile).
3) temporal trajectories (tensile).
4) alveolar arcade system.

insertion into the precondyloid fossa, the insertion area of the ext. pterygoid muscle, also supports this supposition.

The trajectories of the coronoid process, traj. temporale, seem to represent a direct connection of the temporal muscle, and the tensile nature is fairly obvious. Upon preparation the connections between osseous trajectorial elements and tendinous insertion fibres of the muscle are easily seen. The masseter and int. pterygoid muscles on the other hand, which insert transversely into the longitudinal basal trajectories, do only superficially deflect the basal systems. Only accessory superficial deflections in the tuberosities indicate the muscular insertions, while in deeper layers the trajectorial elements usually are going clear through this area transversely to the direction of the muscles. This latter condition is the rule in the skeletal muscles and their insertions especially in the long bones. The direct musculo-osseous connections on the other hand, as they appear both in the coronoid process and in the zygomatic region at the origin of the masseter muscle, are characteristics of the masticatory system.

The interpretation of the structural arrangement in the dense and solid compact bone as tensile and compressive trajectories is somewhat hard to realize unless we apply the view-point of the functional anatomy, exemplified f. i. by BENNINGHOFF. According to these theories a supporting tissue and a solid anatomical form like a bone does still represent function, a physiological happening of extreme slowness, an arrangement of active elements like that of a magnetic field, and in this way certain structures in a certain arrangement might be given a mechanical sense and interpretation. The cells build together into syncytial lamella-systems, these systems into trajectorial units, these latter forming an architecture within the gross bone-form, and thus the different parts and units obeying the organization and serving systemic purposes within the organism.

On the basis of the material herewith presented I give the following scheme of the gross trajectorial architecture of the human mandible:

I. Basal trajectorial system composed of
  1. Inferior basal tract, with angular dispersion
  2. external oblique tract
  3. internal " "

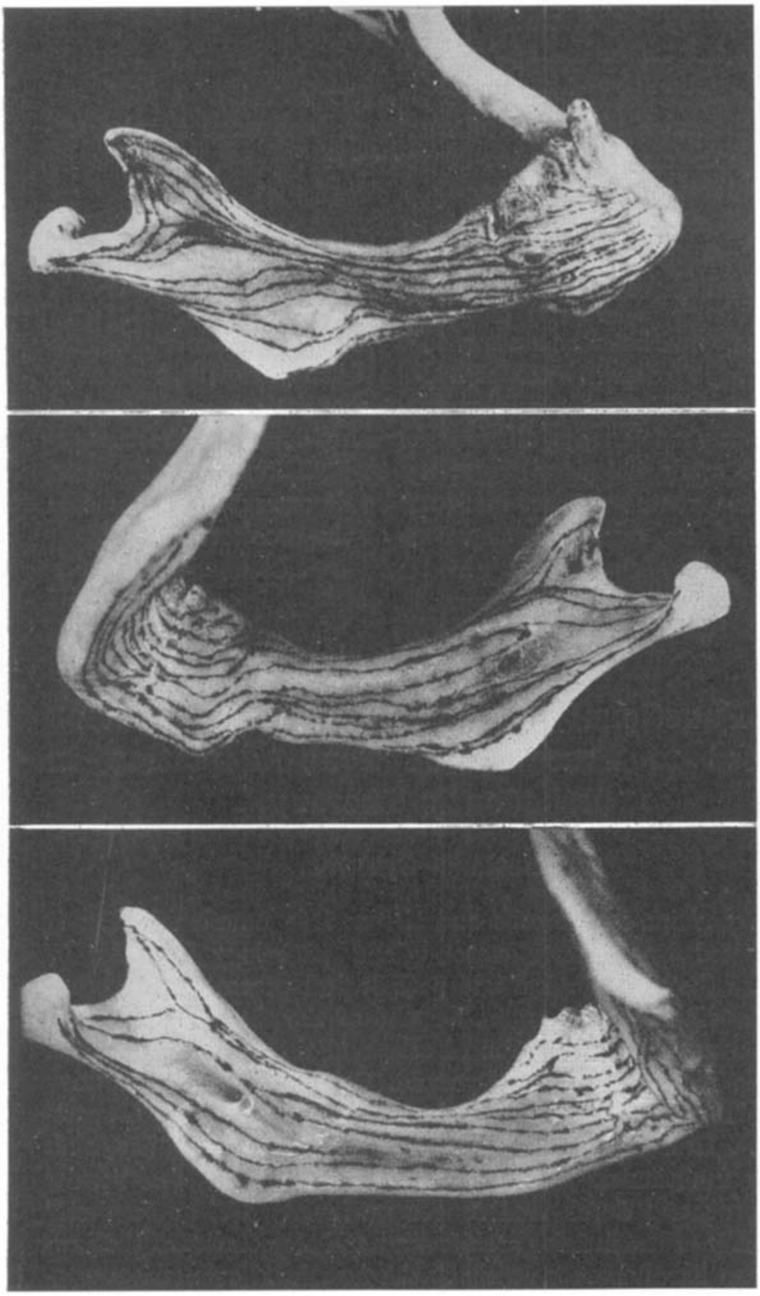


Fig. 26. Homo (K. 8) age over 50 yrs. Healed fracture in the anterior premolar region with about 1 cm dislocation between fracture ends. Crevice-line preparation showing trajectories going straight through the fracture line on the buccal side, but deviating on the lingual side to establish connections between broken trajectories: an indication of tensile forces working on the outside and compressive on the inside of the mandible. Below: normal side of same jaw showing straight longitudinal trajectories of inside.

II. Accessory trajectories

1. temporal trajectories
2. connecting (temporo-condyloid) trajectories
3. muscular insertion trajectories or transverse angular trajectories: a) masseter, b) pterygoid
4. alveolar catenary system
   a) ascending alveolar
   b) longitudinal alveolar
5. transverse mandibular spongious trajectories.

There could be some reasons to separate the trajectorial structures of the compact bone from those of the spongious, but on the other hand they are to a large extent manifestations of the same tissue, only representing different degrees of density in the arrangement. I apply the name trajectory to both kinds of structures, the name tractus or tract being used only accessorily to indicate a clear, dense, regular arrangement of the architecture.

CHAPTER 5.

The Functional Systems of the Face-Skeleton Related to Processes of Bone-Adaptation in Orthodontic Therapy.

Functional Systems.

The coordination of cells and tissues into functional units is emphasized by modern anatomy and pathology in order to visualize the physiological and pathological processes that occur in a certain region or organ. Instead of the single cell and the single tissue the *organization* of cells and tissues into functional units is placed in the fore-ground. Confer f. i. BENNINGHOFF 1933: "Funktionelle Systeme sind *Wirkungsgefüge im Organismus* . . . Es liegt im Sinne eines funktionellen Systems, das es als Ganzes funktioniert und als Ganzes auf geänderte, funktionelle Beanspruchung durch Änderungen im inneren Gefüge reagiert."

A study of the interior architecture and trajectories of the jawbone can hardly be done without the functional connections suggesting themselves. The function of the dentition is to a high degree mechanical. Consequently functional systems of a mechanical character (trajectories of the bone) and the relationship between muscle and bone must be of importance. BLUNTSCHLI 1929, who has extensively studied the functional conditions of the jaws and face, concludes that there is hardly an organ wherein changes in one place with such clearness affect the whole system and bring about changes in pertaining tissues.

WETZEL 1922 in experiments on decalcified skulls, stresses the important fact that muscles of mastication are contra-acting the bone-deformations which their own masticatory pressure is causing. So f. i. the internal pterygoid muscle is pulling the pterygoid process backwards-downwards, while the masticatory force, as shown by experiments, is pressing this bone forwards-upwards. A similar condition appears in the zygomatic bone, the upward deflection of which is contra-acted by the downward pull of the masseter. WETZEL 1922: "So entstehen natürlich geschlossene Kraftketten, die eine besondere Stabilität des ganzen Systems garantieren." These functional systems in the face region exhibit a mechanical balance of pressure and contra-pressure in the arrangement of muscle, bone, and dentition. The compact bone architecture of the jaws was previously not considered in this connection although the skeleto-muscular relations of other functional units in the body have been worked upon f. i. by CAREY 1929, MURRAY 1936.

In the "kinetic chain" of PAYR 1932, the nervous mechanism as well as the mechanically concerned tissues were included. Of course the nervous mechanism is of vital importance for the regulation and development of any functional system. But as long as we are concerned with the structural organization and the pure architectural conditions of the bone, the regulating mechanism might be left out of the picture.

WARREN points out the predominance of the muscles closing the jaw over those that open it. The balance between opponent muscles is more uneven than in any other part of the body, which f. i. accounts for the fact that the rigidity of tetanus first appears in this region. The special position of the muscles of mastication as more or less unopposed closing muscles does highly influence the architectural conditions of this region.

In the maxillary bone and the upper face skeleton the dominating influence of the muscles of mastication upon the trajectorial and architectural arrangement is quite clear. Excepting the maxillo-frontal trajectories, the major part of which are absorbed in the frontal bone, most of the architecture is traced directly to the insertion regions of the muscles of mastication, some ending directly as muscular insertion trajectories, others passing to the insertion area and spreading out diffusely in pertaining regions of the cranial bones.

The trajectorial extensions of the maxillo-frontal system towards the insertion area of the temporal muscle have been mentioned before. By way of the central insertion into the anterior part of the frontal bone the functional connections are largely bound to the neurocranium. The maxillo-frontal trajectories are tied up laterally with the masseter system through the transverse infraorbital connections (Fig. 11 and 15).

Contrary to the somewhat unclear and indirect muscular connections of the maxillo-frontal system, the zygomatico-temporal system of trajectories is on the other hand definitely tied up with the masseter and temporal muscles. This system is receiving contributions from the larger part of the maxilla. A most striking picture is offered by the muscular insertion trajectories of the masseter muscle (Fig. 11). As a direct architectural continuation of the muscle and tendon fibres they insert in the central area of the zygomatic bone, where trajectorial fibres from the infraorbital, the lateral orbital and temporal areas, and also from the infrazygomatic and posterior maxillary regions meet and join into a dense trajectorial crossing. The larger part of the ascending alveolo-zygomatic trajectories join the masseter trajectories at more or less right angles, which might be an expression of meeting tensile and compressive trajectories, the maxillary pressure being absorbed into the masseter tension-systems (Fig. 11).

The insertion area of the temporal muscle receives trajectorial contributions from the anterior and posterior zygomatico-temporal, the maxillo-frontal and the pterygo-temporal systems. The temporal system of trajectories is to a certain extent coordinated with and superposed upon the masseter system. The temporal area does not exhibit any similar free-ending muscular insertion trajectories as the zygomatic region. But the ascending trajectories like the tendon fibres disappear in the dense cortical bone of the temporal crest, which is showing a longtidudinal architecture (circular temporal trajectories), wherein the ascending fibres insert.

Finally the pterygoid muscles, as previously described, show a similar trajectorial absorption as that of the zygomatic region. The trajectorial contributions to the pterygoid process are not as strong as those of the masseter, consisting mainly of the longitudinal palatine and posterior maxillary trajectories. Part of the architecture is passing through the pterygoid processes to spread out over the base of the skull and the infratemporal fossa. However, the trajectories in the pterygoid processes are also undergoing a muscular absorption, thus forming a muscular insertion trajectory.

The architecture of the mandible does not show as much of direct muscular connections as the maxilla. The main muscular insertion trajectories are those of the coronoid process, where a direct continuation of muscular- and bone-architecture is seen. The masseter and pterygoid muscles on the other hand do only superficially deflect the basic trajectorial systems upon which they insert. This latter condition is rather conforming to the arrangements in the long bones, and is easily explained from the position of the mandible as a lever, taking its load at the dentition and upon the condyles, with muscular support attacking in the angular region, at right angles to the trajectories of the mandibular body.

The face skeleton is thus exhibiting an unusual influence of the muscles of mastication upon the interior architecture of the bones. Such a muscular dominance over the architecture is less apparent in other skeletal parts of the body like f. i. the extremities. Here the muscles are serving the purpose of wider, antagonized movements, somewhat different from the limited and unantagonized constriction in a closed musculo-osseous chain as appears in the jaws. The long bones have a fairly simple architecture between their two joint-surfaces, that are facing opposite directions. The face skeleton on the other hand has both its pressure absorbing surfaces, the teeth and the mandibular joint surfaces, facing the same direction and the muscles of mastication attaching between them. As a consequence the muscular influence should be different.

This study of the interior architecture and its connections with the muscles of mastication leads us a definite step beyond the usual concept of the mechanics of the face-skeleton — three main pressure pillars, the frontal, zygomatic and pterygoid, transmitting the pressure from the dentition to the dense bones of the skull (cf. SICHER-TANDLER 1928). The trajectorial arrangement

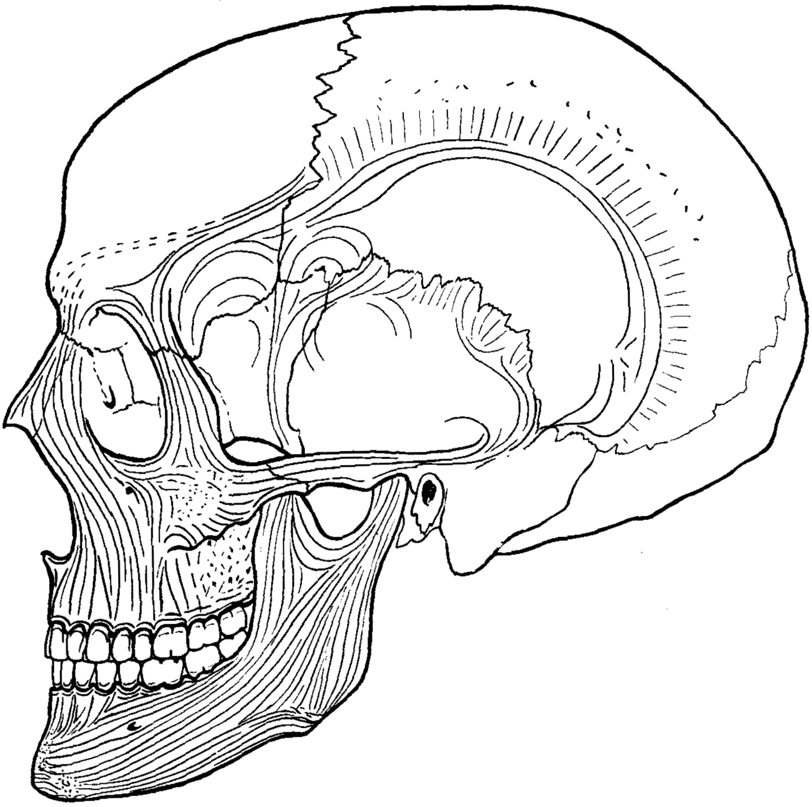


Fig. 27. Schematic drawing of the trajectorial arrangement in the jaws and facial bones of adult man. Compared to BENNINGHOFF 1934 there are modifications in the zygomatic, tubar maxillary, angular mandibular and alveolar regions. Parietal region according to BENNINGHOFF.

to the insertion regions of the face-skeleton, the existence of special muscular insertion trajectories connected with the trajectories of the jaws, indicates that the mechanics of this region is not one of simple pressure transmission to the neuro-cranium by way of the facial bones. Instead the forces of mastication are to a certain extent *structurally bound within the face-skeleton.* In a way this condition is comparable to the shortcut of the reflex arc in the nervous system. The ascending pressure in the maxillary bone is absorbed by the downward pull of the muscles, through a unit of ascending and descending structures, without severing the cranial connections. The masseter and pterygoid muscles are structurally shown to absorb ascending trajectories from the dentition. Furthermore they are balancing each others in a transverse direction, one of them inserting medially and the other one laterally to the main trajectories of the maxilla. The temporal muscle, with its broad insertion over the lateral part of the skull, does not show similar insertion trajectories, but the importance of the ascending and radiating temporal trajectories might well be the same as they spread out over the muscular insertion area.

The structural conditions of muscles and jaws in an encephalic anomaly (Homo, newborn, fig. 28) might throw some light on the independent character of the functional systems within the face-skeleton, the masseter and pterygoid systems being comparable to those of a normal newborn in spite of the reduction of the temporal area. On the other hand we cannot separate the face-skeleton from the neuro-cranium, either structurally or functionally. The firm atachment and the amount of structural pathways connecting the upper jaw and facial bones with the neurocranium clearly show that the closed functional systems of the face-skeleton are only of an accessory character, taking part of the load, the stabilization of the facial architecture being maintained by the denser bones of the neurocranium.

The suggested masticatory mechanism, based upon the architectural conditions of the jaws and facial bones, is thus as follows:

From the upper jaw the main trajectorial architecture is connected with the frontal, temporal and sphenoid-base regions. Some trajectorial portions form direct muscular connections in the zygomatic and pterygoid processes, indicating the existence of closed kinetic chains within the face-skeleton. To some extent the ascending trajectories to the temporal region also seem to undergo a muscular absorption, namely those ones running parallel to the inserting muscle and tendon fibres, and we might even in this region speak of a closed functional system. The compact bone architecture of the face-skeleton reaching the frontal, temporal and sphenoid regions naturally also serves the purposes of skeletal insertion and stabilization.

The functional systems of the facial bones would thus consist of the architecture that connects the dentition with the skull or with the insertion areas of the muscles. Together with the muscles of mastication and the dentition this architecture is forming certain closed functional chains, consisting of the ascending trajectories of the maxilla — the connecting muscle fibres —

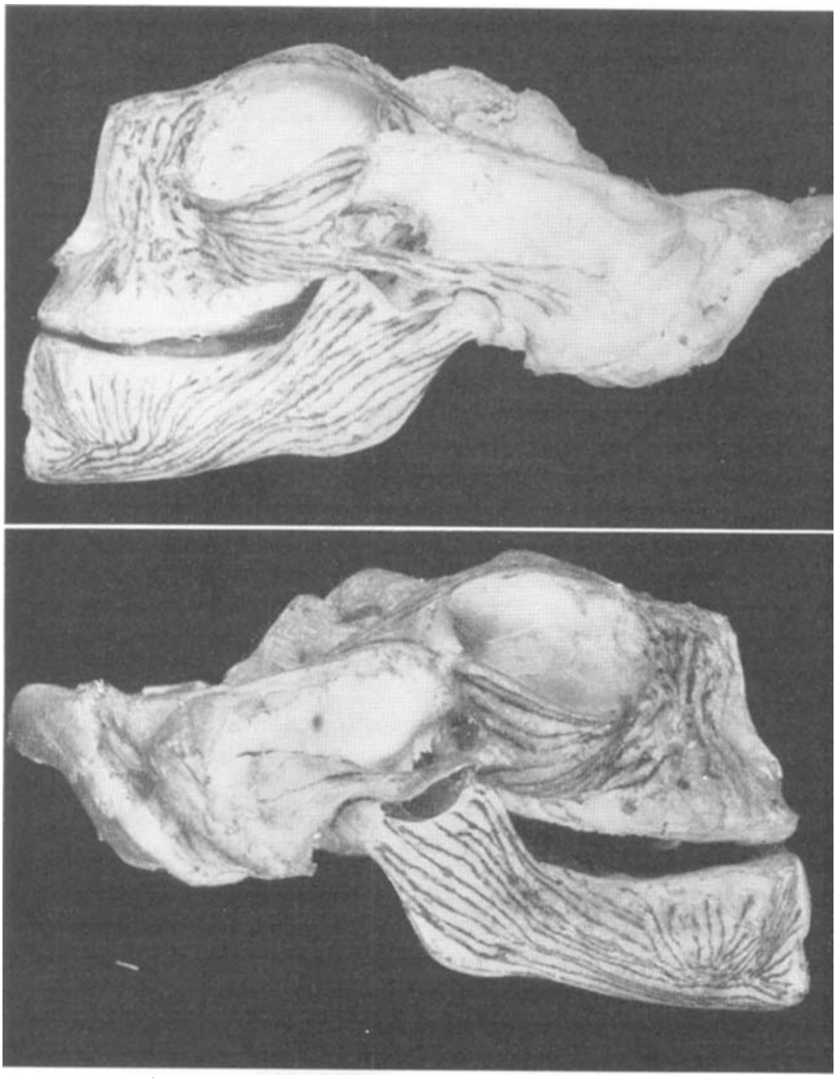


Fig. 28. Jaw structures of an encephalic anomaly (human newborn).

the basal systems of the mandible carrying the lower alveolar trajectories and completing the chain back to the dentition. The temporal muscle is connecting up directly with the trajectories of the mandible, the masseter and internal pterygoid muscles are inserting more or less transversely to the basal trajectories comparable to the support of a lever.

The functional character of the architecture and trajectorial arrangement of the facial bones has largely been taken for granted. According to Wolff's law of bone-transformation and Roux's theories of the functional adaptation of the organisms we would expect the work-out of the interior architecture to be in accordance with the physical and physiological requirements. Koch 1917 has experimentally tested the trajectories of the femur and found them to be in close relation to mathematical requirements. In the alveolar process a direct functional relation might be observed, whereas loss of teeth and the eruption of new teeth directly affect the trajectorial tissues of the alveolar bone (Figs. 21, 35, 37). And on the basis of the above theories we might conclude that a clear, well-arranged structural organization represents a good balance between physiological requirements and tissue adaptation. When with advancing age up to adult stage a gradually clearer work-out of the structural organization occurs (Fig. 34), we would also have reasons to suppose this architecture to be functional. This does not exclude other factors than function as exerting an influence upon the interior organization. An attempt to comprise the regulating mechanism of the interior architecture of the jaws would at least include the following factors:

1) function (cf. Roux, Wolff)
2) age (tissue vitality and time of functioning)
3) peripheral and central nervous regulation, muscle-tone, reflex-action etc.
4) bone-composition: a) nutrition, b) endocrine regulation
5) hereditary influences on the determination of gross bone-form and interior structure (compare man — chimpanzee)
6) conditioned mechanical influences of a non-functional character (orthodontic therapy, extractions).

Orthodontic bone changes.

Of practical importance is the question to what extent orthodontic changes in the position of the teeth might influence the interior architecture and trajectorial arrangement of the bone, and to what extent the interior balance might be disturbed and rearranged in changes of the dental arches. The laws of bone-adaptation imply that any kind of dentition, either normal or deformed, if it persists for a sufficient length of time, will attain its own balance between bone organization and functional requirements. But the bone adaptation cannot be utilized to such an extent that we could do any change of the dentition and just sit down and wait for the reorganization to take place. Clinical experience shows that orthodontic changes are rather limited in extent. First *the bone is just an inherent part of organs and systems that do not permit changes* at will, and secondly there seems to be a gradient of changeability varying from one tissue to another and even from one part of a tissue to another, corresponding to gradients of differentiation in development. So f. i. the alveolar process of the jaws is more subjected to and more apt to undergo changes in its interior architecture, as shown by several specimens of the present study. Reorganization would be more apt to take place following changes in the dental arches, but due to the systemic connections and the inherent qualities of functional systems, of which the alveolar architecture is a part, this changeability is limited.

Roentgenological evidence is presented by BRODIE, DOWNS, GOLDSTEIN and MYER 1938 that the changes in orthodontic therapy are rather exclusively limited to the alveolar process, as far as the remodelling of the outer bone-form is concerned. Changes in the basic parts of the jaws are small in extent as is previously shown by LUNDSTRÖM in 1923. The changeability decreases from the alveolar bone towards more proximal parts of the trajectorial systems.

As soon as a functional architecture of the alveolar bone and the jaws is shown to exist, movements of the teeth must be accompanied by reorganization of these structures, in accordance with the theories of the functional adaptation. Positional changes cannot be effected at will as if the jaw-bone consisted of an inert substance, wherein the teeth could be moved around and shifted to fit the taste of the spectator. But the movements are limited by the same factors that regulate the rebuilding and adaptation of the trajectorial tissues, and furthermore by the gross bone form and the topographic relations of the dentition.

The local changes of resorption and apposition that accompany the movement of teeth are just one limited phase of the tissue reactions in orthodontic therapy. The structural reorganization following the changes in tooth-position is a secondary effect that is of deciding importance for the outcome of the treatment.

Relapses are easily explained on the basis of disturbances in this interior reorganization.

BARTH, BLUNTSCHLI, OPPENHEIM and others have pointed out that the final outcome of orthodontic treatment is dependent upon the total structural changes and the growth of the bone in the connected regions. But such changes are mostly hypothetically claimed. Experimental evidence of remote bone changes induced from the dentition has been shown by BAKER in 1941. BREITNER 1940 in experiments with intermaxillary changes of the dentitions in monkeys showed the deposition of new bone in remote regions from the dentition, as the mandibular angle and the temporomandibular joint. However, no sufficiently sensitive method to show the reorganization of the trajectorial elements within the bone has been applied. (The Korneff method of lamellar differentiation could possibly be used for this purpose.)

The reorganization of the functional units of bone and musculature within the region of the face and skull are rather hard to show experimentally. After a new occlusion has been established through orthodontic treatment, these changes are supposed to take place gradually, and the degree of completeness to which a new balance is attained through growth and reorganization is responsible for the more or less permanent result of the treatment, or in other words for the tendency to relapses.

Orthodontic reactions.

The first phase of tissue reaction in orthodontic tooth-movement is the *paradental reaction:* resorption-apposition or *osteoclastic-osteogenic* reaction in the paradental tissues: peridental membrane, alveolar bone, cementum.

The second phase is the *trajectorial reaction,* the organizor reaction or the adaptation of those functional systems upon which the load of the dentition is placed.

The *paradental reaction* described by SANDSTEDT (1901) and later confirmed by a series of other investigators is presumably regulated by mechanical pressure and the vitality of the tissues concerned. The reaction is reversible: it goes as well in one direction as in the other. It does not lead to a reliable fixation of the tooth in the new position but is easily reverted if the pressure ceases, or resistance of some kind is met with. The reaction is cellular in nature and therefore seems to occur wherever releasing forces set in and the nutrition and tissue vitality are appropriate.

The *trajectorial reaction* on the other hand is of a different nature. It includes the re-organization and readjustment of the trajectorial tissues after the change in the mechanical position of the teeth. It depends upon the organizor-processes of functional systems, which are responsible for the interior architecture of the bone as expressed in the law of bone transformation. The trajectorial reaction is released by the mechanical change, or by the destruction of trajectorial tissues through the local reaction. It is highly conditioned first by mechanical possibilites of readjustment, and secondly by biological possibilities of the tissues of the pertaining functional system to readjust, rebuild and regenerate.

Orthodontic relapse tendency.

The variations of architectural arrangement in different parts of the alveolar process must be influencing the possibilities of moving the teeth. Lateral movement of the lower molars, which are set between heavy longitudinal and basal trajectories would f. i. have quite a different effect on the functional chains and the trajectorial support than a movement of the upper incisors with their individual vertical support and the less differentiated palatine structures. *The possibilities of movement of the teeth must be bound within certain limits through the supporting tissues and the different possibilities they offer of adaptation to a new static and functional balance.* Not every change in the position of teeth can be followed by a complete adaptation of the tissues involved; *the movements must be kept within the range of physiological possibilities of adaptation.* A direct scheme, or reliable measurements for the possible movements of teeth is at the present not possible to elicit on account of the manifold factors involved of a biologic and unmeasurable character. The question is largely left to the clinical experience. At this place it is only meant to point out the importance of the trajectorial tissues and the boundaries they raise for orthodontic therapy. For practical purposes the following statements could be made:

The trajectorial reaction is delayed or encumbered where tooth-movement is carried out cross-wise to trajectorial systems and where longitudinal systems are stretched or broken through the tooth-movement, as in the excessive lateral movement of single teeth (cf. Fig. 29).

The trajectorial reaction is simplified and facilitated where tooth-movement is going parallel to trajectorial systems, without stretching or breaking their continuity. The spontaneous migration

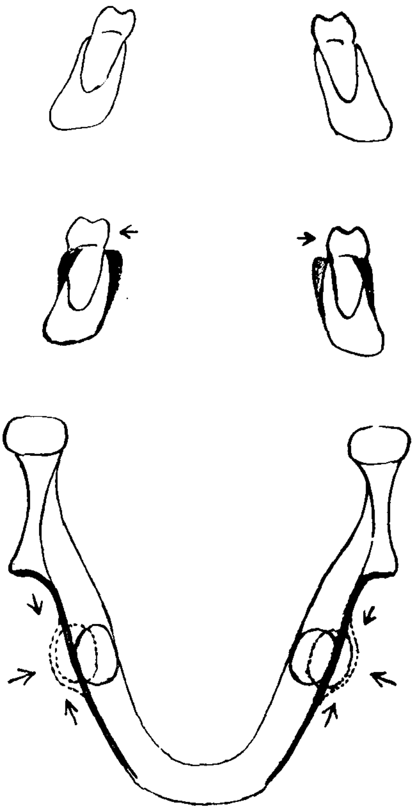


Fig. 29. The trajectorial reaction in orthodontic tooth movement: Natural movements of teeth occur parallel to trajectorial systems (f. i. lateral longitudinal systems) without change of basal support. Movements transversely to trajectorial systems break the continuity of the trajectorial support. Readjustment may follow through: 1. replacement of teeth = relapse, 2. growth and rebuilding of trajectorial systems, 3. combination of both = facilitated trajectorial adaptation (cf. over-expansion in treatment).

of teeth in extraction cases thus follows the least resistance of trajectorial pathways.

As to the possible changes one might differentiate the following degrees of trajectorial adaptation:

1) no trajectorial change, the movement being within the field of functional variations. The paradental reaction taking care of necessary tissue changes.
2) adaptation through re-positioning of the teeth into the previous place, healing and restitution with orthodontic relapse

of teeth. The easiest way of adaptation, requiring no complex tissue changes.

3) Trajectorial adaptation to the new positions of the teeth, being of a more or less complete character and possibly combining with partial restitution as above (2).

Determining for the processes ensuing is the *mechanical and physiological advantage* of the new position and the time admitted for adaptation (fixation, retention) in case of labile mechanical conditions after the movement.

Since the teeth are set in the free and adjustable end of the functional systems, with the jaws supposedly adapted for closure in lateral and protrusive contact as well as centric (width of masticatory field), it seems that certain adjustements of the teeth could be made without perceivable effect on the mechanics of the trajectorial and muscular systems, at least for certain groups of teeth that are not directly involved in basal or longitudinal architecture proximating the insertion regions. There are no compelling reasons that every change in the position of teeth should produce trajectorial reactions. Some adjustments of position, especially those effecting the regions of vertical and less differentiated architecture, might well be performed with the peridental reaction taking care of the adjustment (f. i. treatment of local inversion of incisors).

On the other hand where movements are performed that either destroy the existing trajectories or else definitely change the mechanical position of the teeth in relation to the dental arches, readjustments of the trajectorial systems must be supposed to take place. It is a practical question to what extent the law of bone-transformation and the theories of functional adaptation might be applied to these changes and adjustments. The therapeutical influences upon the apical base has been discussed by LUNDSTRÖM 1923, and concluded to be of no demonstrable effect. Now, the demonstration of an interior architecture or its changeability does not necessarily contradict this statement, because functional readjustments might well be going on in the interior of the bone, without the outer form being notably effected. How far the trajectorial changes reach is not shown for the jaws. But there is evidence from general bone studies that a local change of a skeleto-muscular unit will affect regions far beyond that, directly concerned in the alteration (cf. MURRAY 1936). According to the older teleologic reasoning of ROUX, WOLFF and even BENNING-

HOFF, any change of such a system would affect the whole pertaining region. But practical orthopedic experience shows the functional and therapeutic changes to have a more limited range.

In any discussion of bone transformation, of functional adaptation, or of therapeutic bone-changes, the time-factor is of deciding importance. Whether a functional or therapeutical stimulation will produce changes or not is more dependent upon its *duration* than its momentary intensity. A temporary influence of a diverse nature, like that of an orthodontic appliance, will act as a disturbance of the existing functional system. Unless the temporary movement of teeth produces a definite mechanical advantage in the interlocking of the dental arches, the tissue reactions will strive for a return to the previous condition and a healing of the disturbances produced. From the point of view of trajectorial readjustment a slow change or a permanent mechanical influence (retention) is indicated in order to call forth a tissue-adaptation and a change of the previous functional system. Where the border goes between relapse and adaptation is individually varying, like any organic reaction. Some of the possible determining factors have been mentioned, as age, vitality of tissues, gradient of tissue-adaptability. From anatomical side the changes in the interior architecture and those of the outer form are separated. GEBHARDT considers the former to be worked out under functional influences, whereas the latter is hereditarily determined. The theories of ROUX leave a greater room for functional changes even of the outer bone form, and WOLFF in his law of bone-transformation coordinates the interior architecture and the external conformation, to be mathematically dependent upon each other, as well as upon functional changes. With the introduction of "gradients of adaptability" these viewpoints might be united. If we suppose a gradually diminishing adaptability from the reacting cells upwards through the cellular systems to the external bone-form and the organ-systems, we get, as regards the orhodontic changes, at least the three following stages with a decreasing possibility of therapeutic regulation through orthodontic means:

1) *cellular reaction*, paradental resorption and apposition.
2) *trajectorial reaction*, readjustments of the interior architecture.
3) *morphologic reaction* or changes in the external conformation of the facial bones and pertaining tissues.

As regards point 2 and still more point 3 we must consider the systemic connections and the functional systems involved. The

Bone changes in orthodontic tooth-movement.

Reaction	Conditioning factor	Therapeutic regulation	Tissue involvement	Healing	Orthodontic result
Paradental	mechanical pressure or tension	yes	cellular reaction resorption-apposition of alveolar bone	a) complete	+
				b) incomplete	paradental injury or scarring
Trajectorial	tissue adaptability	no	a) restitution no trajectorial change	paradental readjustment	relapse
			b) adaptation of trajectorial tissues	a) complete	+
				b) incomplete	relapse tendency
Morphologic	growth and tissue adaptability	no	change of external bone-form, adjustment of muscles and dependant organs	growth and physiological adaptation a) complete	+
				b) incomplete	relapse tendency

place and position of the changing structures in that system are determining the possibilities of adaptation, considering the gradient decrease. We have observed a high adaptability of the architectural structures of the alveolar process. Bone changes in orthodontic therapy, as demonstrated by Brodie et al. 1938, are mostly involving the alveolar bone and only to a minor extent the surrounding regions. It thus seems that the adaptability is rapidly decreasing from the alveolar structures towards the basal architecture of the jaws and the systemic connections with muscular and cranial insertions. In other words this could be expressed so that the distal (more independent) parts are more apt to undergo changes than the central parts, which involve more dependent structures of vital tissues and organs.

CHAPTER 6.

Micro-Biology of Trajectorial Structures of the Jaws and Their Relationship to Malocclusion of the Teeth.

Composition of Trajectorial Structures.

One of the main structures to which a trajectorial character might be applied is the osteon or the Haversian system. It consists of a concentric layer of lamellae, varying in number from 4 to 20 or more, the thickness of each lamella being from 3—7 micra. With a width of the central canal of 22 to 110 micra the diameter of the whole haversian system might thus vary from about 40 to over 500 micra: the tubules usually being visible to the naked eye (cf. PETERSEN 1927, MAXIMOV 1938). The length of the osteon is utterly variable and it is hardly possible to give any figures in this respect as the lamella-systems are interrelated and fusing or they break up into irregularly shell-formed systems.

The lamellae of the osteon contain collagenous fibrils, which form a spiral course around the central canal, the spirals of each layer having an opposite direction to the previous one (GEBHARDT, PETERSEN). The elevation of the spirals is varying, presumably having some connection with the differences in physical properties of the lamella-systems. I quote BENNINGHOFF (1935) in this question: "Die Variabilität in der kollagenen Faserwickelung der einzelnen Osteonen ist nicht am Osteon selbst zu erklären sondern gewinnt seine Verständnis erst wenn man die Tatsache heranzieht, das der ganze Knochen in seiner Bau elastiche Homogenität ergeben muss und beim Bau und Umbau die einzelnen Osteonen so abgestimmt werden, dass die Summe der einzelnen Variationen immer die elastische Gesamthomogenität nachstrebt." GEBHARDT 1910 has suggested that the differentiation and arrangement of the collagenous fibrils is dependent upon the pulsation of the bone arteries and local trophic stimulation. TRIEPEL 1902 points out that the collagenous fibrils are not trajectorial in their arrangement in relation to the gross architecture of the bones. In the lamellar bone f. i. they have a circular course, whereas the trajectories go straight following the lamella-systems. In other conditions the collagenous fibrils have a direct trajectorial importance where they form bundles, strands, or network of a trajectorial character. One could therefore differentiate between primary and secondary fibrillar architecture. In the former the architectural strands being formed directly by fibrillae or bundles of fibrillae, whereas in the latter the collagenous fibrils have a secondary rôle as building material forming f. i. the spiral reinforcements of the lamella-systems.

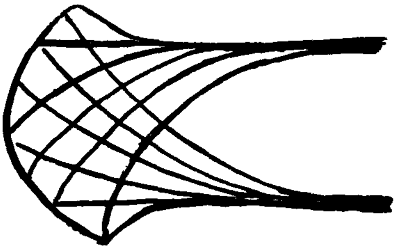
The composition of the haversian systems and other lamella-systems of the bone has attracted much anatomical interest (GEBHARDT, FOOT and others). Species differences have been claimed to exist in the interior lay-out of the bone (cf. FOOT 1928). In this study it is impossible to enter upon a comparative analysis of lamella-systems. We are only referring to them as an important component of the interior architecture.

The differentiation of the lamella-systems of the compact bone is highly varying. Only in rare instances do we find clear tracts of haversian systems. GEBHARDTS main forms of bone organization are referred to above p. 6. Now the bone might be composed of different lamella-systems in a fairly irregular arrangement, or one or the other form might prevail. Even if the lamellar bone is the one type that usually exhibits a definite architecture or trajectorial arrangement and gives a definite picture with the crevice-line method as applied in this study, the interior architecture is by no means limited to this form of bone only. Grossly we might differentiate between osteoid, bundle bone and lamellar bone. The former only exceptionally giving some kind of fibrillar architecture, whereas the bundle bone often shows a rather heavy texture of fibrillary strands or network.

The architectural structures referred to in this study are largely bound to the organic matrix of the bone. The organic framework represents only about 30—40 % of the tissue and is formed by collagen or ossein with small amounts of osseo-mucoid and osseo-albuminoid. The trajectorial and mechanical importance is intimately dependent upon the incorporation of inorganic salts. The relative amounts of ossein and the salts fluctuate, varying with age and with physiological and pathological conditions. For a mechanical concept of the bone, as applied in a trajectorial study, it is important to note that the architectural structures are intimately dependent upon the biochemical processes of the tissue. The calcification of the bone requires not only the proper concentration of inorganic salts but also certain physico-chemical

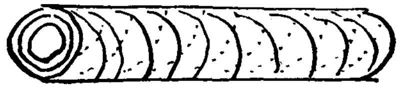
Development of the trajectorial concept.

I



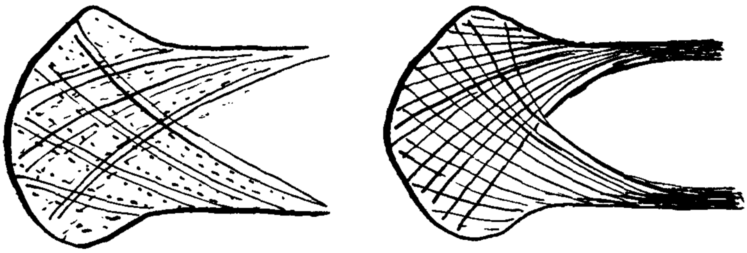
Mechanical construction of the bone, "lines of stress". Trabeculation of bone following mathematical requirements (v. MEYER and CULMANN 1867, WOLFF 1892).

II



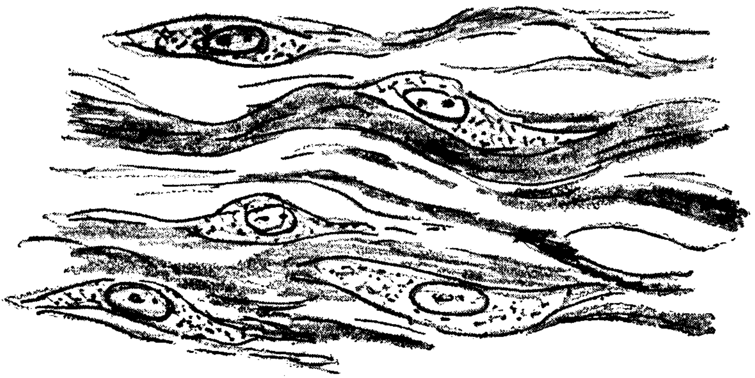
Micro-composition of trajectorial structures. Lamella-systems with alternating spiral course of collagenous fibrils (GEBHARDT 1911, PETERSEN 1927).

III



Biologic variations of trajectorial tissues. Interplay of organic and inorganic constituents for supporting requirements: fibrosis vs sclerosis (BAUER, AUB and ALBRIGHT 1929, LERICHE and POLICARD 1928, ROBISON, MACLEOD and ROSENHEIM 1930, McKEOWN et al. 1932).

IV



Cellular regulation and molecular organization. Organization of the supporting tissues under the influence of growth regulating factors, formation of collagen and reticulum, fibril formation parallel to cell membranes (WOLBACH 1933).

Fig. 30.

properties of the matrix as well as the presence of enzymes (Robinson, Macleod and Rosenheim 1930).

The different layers of the lamella-systems are by no means undergoing a simultaneous calcification. On the contrary they are formed successively, through the periodic differentiation of a fresh generation of osteogenic cells from the endosteum. Although showing rather sharp lines of demarcation the various types of laminated structures are firmly bound together in the calcified state (Cowdry 1932).

Bone Reactions of Trajectorial Importance.

Bone adaptation.

The time is passed when the interest was focussed on the "lines of stress" alone, and on the mechanical appearance of the bone-architecture. We have to widen the trajectorial study from the anatomical configuration of the bone trabeculae to include a consideration of the biologic reactions, as determining for the physical properties of the bone. Wolff's law of bone transformation was long used as a basic principle of bone reaction. It says that "every change in the form and the function of a bone, or of the function alone, is followed by certain definite changes in its internal architecture and equally definite secondary alterations of its external conformation, in accordance with mathematical laws". As this law is only dealing with the adjustments between form and function and is of a rather teleologic nature, not considering the physiologic and pathologic variability of bone, its biologic value might be questioned. For practical purposes and especially in the trajectorial study it is important to note that the bone as a supporting tissue possesses a certain degree of adaptability, which is conditioned by external mechanical influences as well as by internal physiological and pathological factors. The working mechanism of the interior architecture is the cell activity of the bone matrix, with the cells presumably acting as perceptors in the organization of the bone elements according to mechanical requirements. Function alone is by far not the only determinator of the bone architecture, as for instance the spongious trabeculation might disappear or hypertrophy under varying nutritional conditions (Bauer et al. 1929, 1931). A principle of bone adaptation should take care of the biologic side of bone reactions as well as the mechanical stimulation, and a setting like this could be suggested: *Changes in the form, function, elementary composition, or nutritional* *and vascular conditions of bone produce changes in its interior architecture and trajectorial qualities.*

Gradients of adaptation.

The ability of adaptation is not constant for all bone, but differs with individuals and age, with organs and different parts or organs. So f. i. in orthodontic therapy there is a different potency of transformation in the alveolar process, which is readily changed and adjusted to new conditions, and the basal parts of the jaws, which are rather resistant to orthodontic changes (cf. BRODIE et al. 1938). Accessory parts are more readily adapted than the main structures.

Minimum-law.

The inner architecture of normal bone is determined by mechanical requirements to produce a maximum of strength with a minimum of material (KOCH 1917). This minimum law might be accepted as a working hypothesis for the trajectorial adaptation, implying that, *within functional parts*, superfluous structures are eliminated and *useful structures are withheld* according to functional demands.

Trajectorial retardation.

There is a slowness of reactions in the trajectorial adaptation. According to ASCHOFF 1928 the internal bone changes of early rickets may be persistent for lifetime. Therefore the bone architecture may be expected to reproduce only persistent functional changes, or the accumulated effect of temporary mechanical influences. Orthodontic bone-changes require retention in order to undergo fixation through permanent trajectorial changes.

Structural reserve.

The compact bone in most parts of the body is built with a reserve or surplus of structure that allows a fairly wide margin of functional variations. Defensive parts like the skull have a larger structural reserve, whereas purely functional parts as the bones of the middle ear more closely obey the minimum-law. There is a reserve in the fact that compressive structures (cf. KOCH 1917) are resistant even to tensile forces and vice versa, due to the combination of matrix architecture and mineral fixation. On comparing skeletal bones like the mandible (17 specimens of the present study) there are variations in the work-out of corresponding structures (basal tracts, chin, jaw-angle etc.) which suggest a more or less complete organization and utilization of the structural reserve. The varying utilization is even more apparent in the alveolar supporting structures with functional variations of the dentition.

The minimum-law does not imply that bone is comparable to a finished static construction. Not all the bone cells complete their differentiation. Some always remain in reserve to provide by proliferative activity a fresh group of cells for additional differentiation and growth (cf. HAM in COWDRY 1932 p. 1008). Likewise the formation of collagen and fibrils for supporting requirements shows a varying utilization of the ground substance of the bone (cf. WOLBACH 1933).

Constant interior changes.

There is evidence available (BENNINGHOFF, PETERSEN, HAM and others) that the lamella-systems and the composite elements of the bone are constantly undergoing changes during life. This continuous remodelling of the interior texture seems to be a fundamental principle of mammalian bone (cf. CRAWFORD 1939), accounting for the adaptability of this tissue to functional demands. The vital processes of the bone also account for the fact that, when it comes to a study of the interior architecture, we do not find so much of clear lamella-systems representing specific trajectories, but a rather large amount of incomplete and irregular lamellae piling up in a more or less definite direction. Only in limited areas do we find clear tubular systems of a definite order. Thus on the whole it is not the specific trajectorial structure that is important but the *amount and direction of the trajectorial organization* of the bone. In the processes of differentiation and dedifferentiation of lamella-systems that are going on in the bone, it is the temporary result of these processes that is determining for the physical properties. The vital rebuilding of the bone seems to decline with age, and older specimens show more clear trajectorial pictures — before degenerative processes set in.

The reproductive activity of the structures that form the interior organization of the bone accounts for the functional changes and readjustments in orthontic tooth-movement, where changes are brought about by mechanical stimulation. In this connection it is of great importance to notice the limitations of the rebuilding activity. Firstly there is the outer form and the relations to other organs that limit the conditioned structural changes. Then there is a definite slowness of reactions in the interior bone-organization, appearing in the retainment of early pathologic changes. These conditions can only to a minor extent be overcome by mechanical stimulation, and — for the present — the trajectorial reactions cannot be influenced by therapeutical means.

Compensatory reactions between organic and inorganic constituents of the bone.

The balance between organic and inorganic components of the bone under normal conditions varies within certain limits with a ratio 40/60—30/70 %. With increasing age there is a shift towards the inorganic side, indicating a decreasing activity of the organic matrix. When deficiency disease or pathologic processes occur disturbing one or the other of the bone components, it seems that — to a certain extent — they are able to compensate for each other in an effort to withhold the mechanical properties of the tissue. Such compensatory processes have been traced experimentally f. i. by CLARKE, BASSIN and SMITH 1935 in dietary experiments on rats. Rapidly growing rats received a restricted ration extremely poor in salts. Although increase in body-weight ceased, the length and weight of the long bones (femur, humerus etc.) continued to increase slowly. During this period of salt restriction the moisture of the bone increased, the ash decreased, and a marked distortion of the ratio between ash and fat-free organic residue was established. Even after relatively long periods of re-alimentation with an adequate diet, the per cent of moisture and ash and the dimensions of the bones failed to attain values normal for the age. The breaking strength was tested and SMITH concludes that breaking strength of the long bones appears to be more closely correlated with organic pattern as reflected in the size of the bone than with the proportion of inorganic salts. There are no exact measurements as to the extent of compensatory exchanges, nor to their importance in relation to different mechanical tests as tension, pressure, torsion, and breaking.

The compensatory processes also apply rather well to the conditions in rickets. An early disturbance of mineralization induces a compensatory hyperplasia of the organic matrix, which in later re-alimentation and adequate mineralization gives a bone of

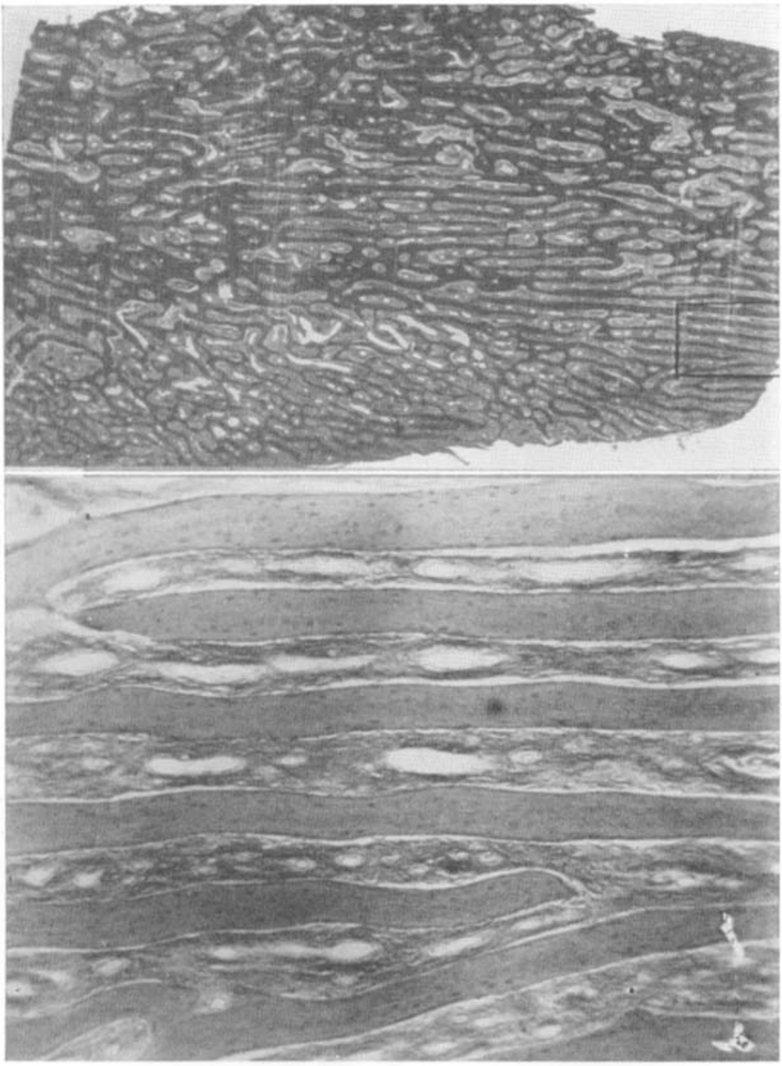


Fig. 31. (Y 12: 1). Spider-monkey with osteomalacia, bones flexible. External oblique tract of mandible, superficial layers of compact bone. Clear architectural strands in spite of extensive bone changes. Hyperplastic fibrous tissue between trabeculae of an osteoid appearance (below).

higher resistance than normal. Over-compensation of the supporting structures, appearing as increased size and strength, is shown in re-alimentation after mineral deficiency by Clarke et al. 1935, and after phosphorus deficiency by Becker and Neal 1930. In

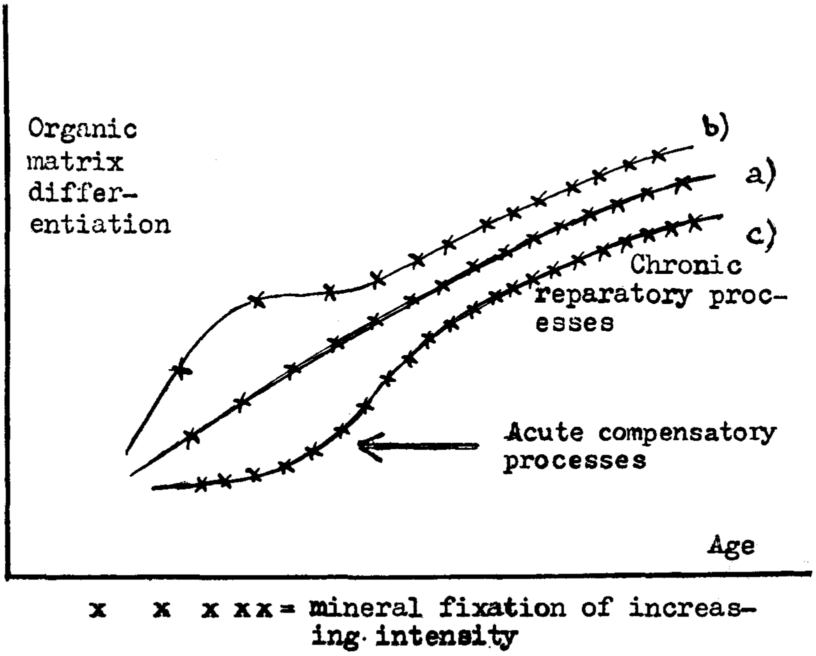


Fig. 32. Schematic representation of compensatory processes between organic matrix differentiation and mineral fixation of the bone.

a) normal matrix differentiation and mineral fixation.
b) early disturbance of mineralization compensated by organic matrix hyperplasia and later re-alimentation (cf. rickets). *Increased density of organic trajectorial structures.*
c) disturbance of organic matrix differentiation with compensatory (premature) mineral fixation: hypothetic occurrence possible in deficiency disease and growth retardation.

orthodontic therapy this condition is manifested in the increased resistance to tooth-movements in many cases of previous rickets.

In a spider monkey with a clinically manifest osteomalacia among the present material (Fig. 31) the organic matrix of the jaws showed a dense fibrous structure in the compact bone of the mandible, suggesting a compensatory process of the organic trajectorial tissues against the lacking mineral fixation of the osteoid bone. Ham 1934 explains the ostitis fibrosa as an attempt of the cells to compensate for the mineral loss caused by abnormal amounts of calcium in the circulation.

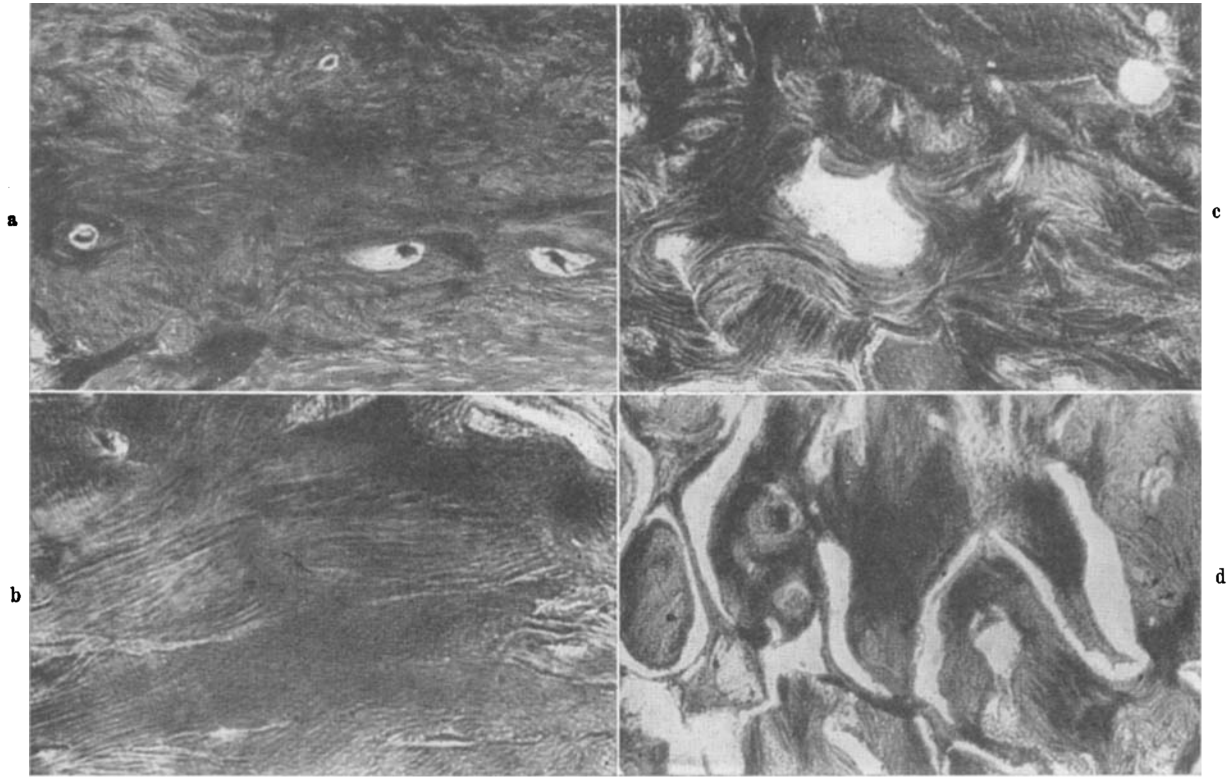


Fig. 33. Variations of bone organization, showing a structural reserve that is more or less utilized for functional organization. Transitional forms from compact to spongy bone, mandibular body, molar region (Y 9). a) subperiosteal layers, b) deeper layers of compact wall, c) sub-cortical layers, d) spongy layers.

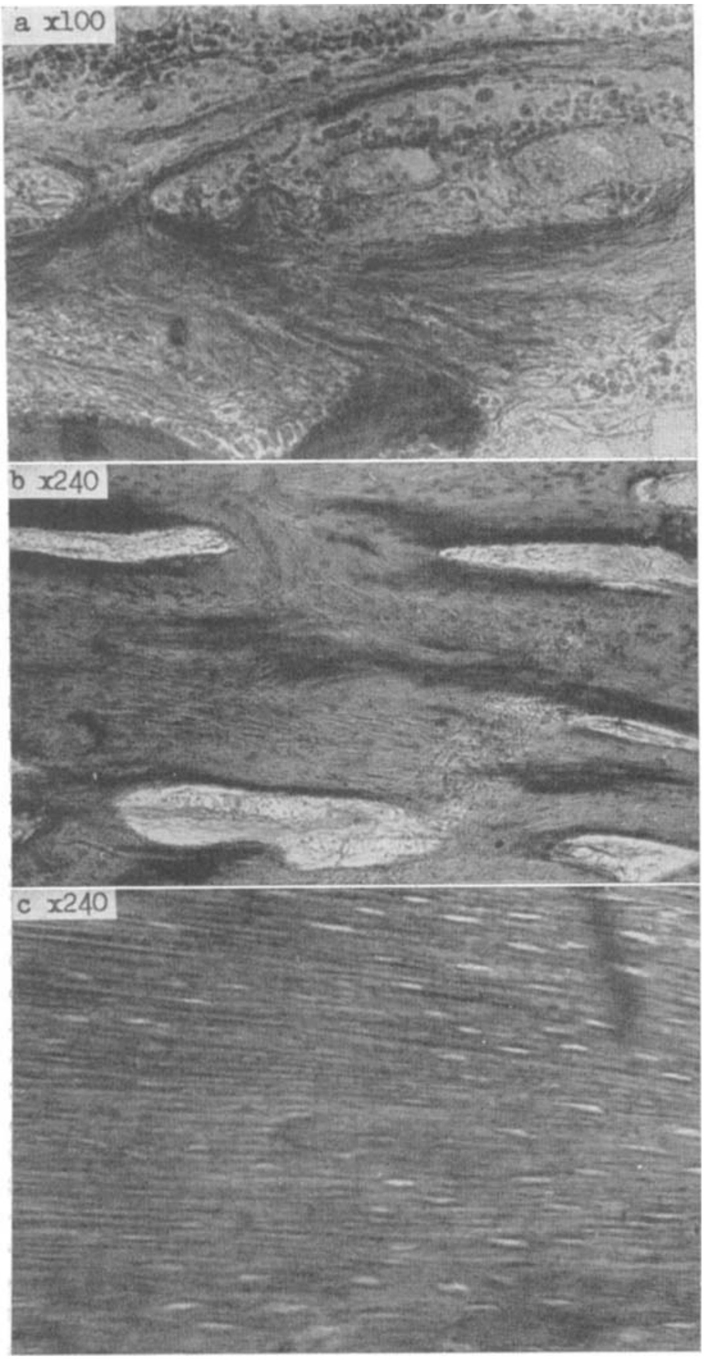


Fig. 34. Variations of bone organization. a) and b) homo, newborn (Y 11), posterior part of ramus mandibulae showing weak strands of organized bone. c) homo 22 yrs (Y 8) longitudinal section of external oblique tract of mandible showing well organized lamellar bone of strong healthy subject.

Variations of Trajectorial Structures.

The normal variations of the trajectorial structures of the jaws with an increasing strength of development from infancy to adolescence have been touched upon in the previous chapters (cf. Fig. 34). Furthermore there are individual variations (Fig. 7 and Fig. 8) and functional variations with changes of the dentition (Figs. 21, 36, 37). Although the material is small some functional and structural variations bearing upon the trajectorial tissues might be treated in the following.

Dedifferentiation in eruption areas.

In some of the specimens examined there are regions showing an architectural picture different from the usual one. Such is the case in a rather wide field around erupting canines (in Y 5), around erupting molars, in the alveolar process below lost or non-functioning teeth, and even above the upper permanent first molars of Y 6, and most strikingly in the alveolar processes and some pertaining regions in Y 9. These areas do not yield any architectural arrangement to the crevice-line method. The injections give only diffuse spots in a tissue that in certain cases appears loose and spongy, while in others (like Y 9) it is still fairly dense and resistant. Already upon macroscopical examination in the undecalcified state the bone of these areas appears different from the regular compact bone. It is more porous and shows a less smooth and even surface. Around the erupting permanent canines of Y 5 fig. 35 the alveolar bone in the immediate surroundings (about 3 mm circumscript area) of the tooth after decalcification has the appearance of loose connective tissue. Further out the bone is denser although not giving a clear picture, until at a distance of about 1 cm from the tooth there is a rather clear demarcation against the regular bone (Fig. 36). The microscopic picture shows a zone of demarcation in the bone, the tissues of each side taking stain (H & E) with different intensity. On the outside there is a dense, lamellar compact bone, possibly showing some more canalization than usual, while on the inside the bone is interspersed with resorption lacunae of varying size. In some parts the lamellation of the latter bone is still fairly clear although broken up by the large lacunae, in others the interstitial cells show an enlargement of their cellular spaces, the lacunae being rounded in-

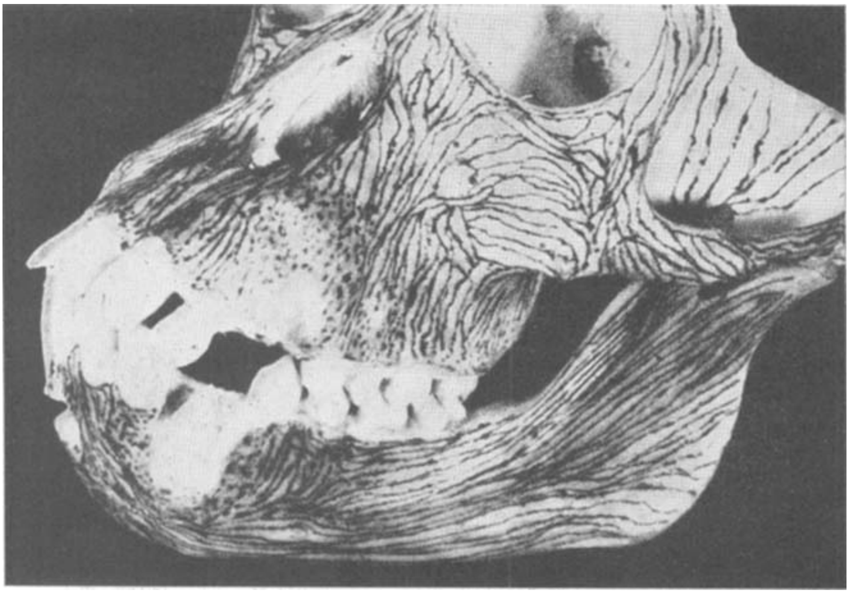


Fig. 35. Chimpanzee 9 yrs (Y 5) with permanent canines in eruption. Bone architecture disturbed in circumscribed area of about 1 cm around erupting canines, where the bone shows a halisteretic appearance (cf. fig. 36).

stead of flat. The interspaces and canals show irregular borders which is taken as an indication that active resorption is going on in the region. Closer to the tooth the lacunae float together into larger continuous canals and spaces. The disappearance of the architectural arrangement in this region thus has its natural explanation in the intense resorption going on, the consequent breaking up of the lamella-systems, and the following looseness of the bone. It seems apparent that the eruption of the massive, permanent canines of the chimpanzee should be accompanied by a regional destruction of the compact bone and its architecture through an osteoclastic mechanism. It seems to be an active resorption, the regulation of which is unknown but might be suggested as being of local dental origin judging from the demarcated and circumscript area of resorption.

The erupting lower right second molar of Y 5 also shows a corresponding area of architectural destruction, however, in this case limited to the lingual side involving the alveolar process and the upper part of the internal oblique trajectories. The microscopic picture of this field is of a different character from that

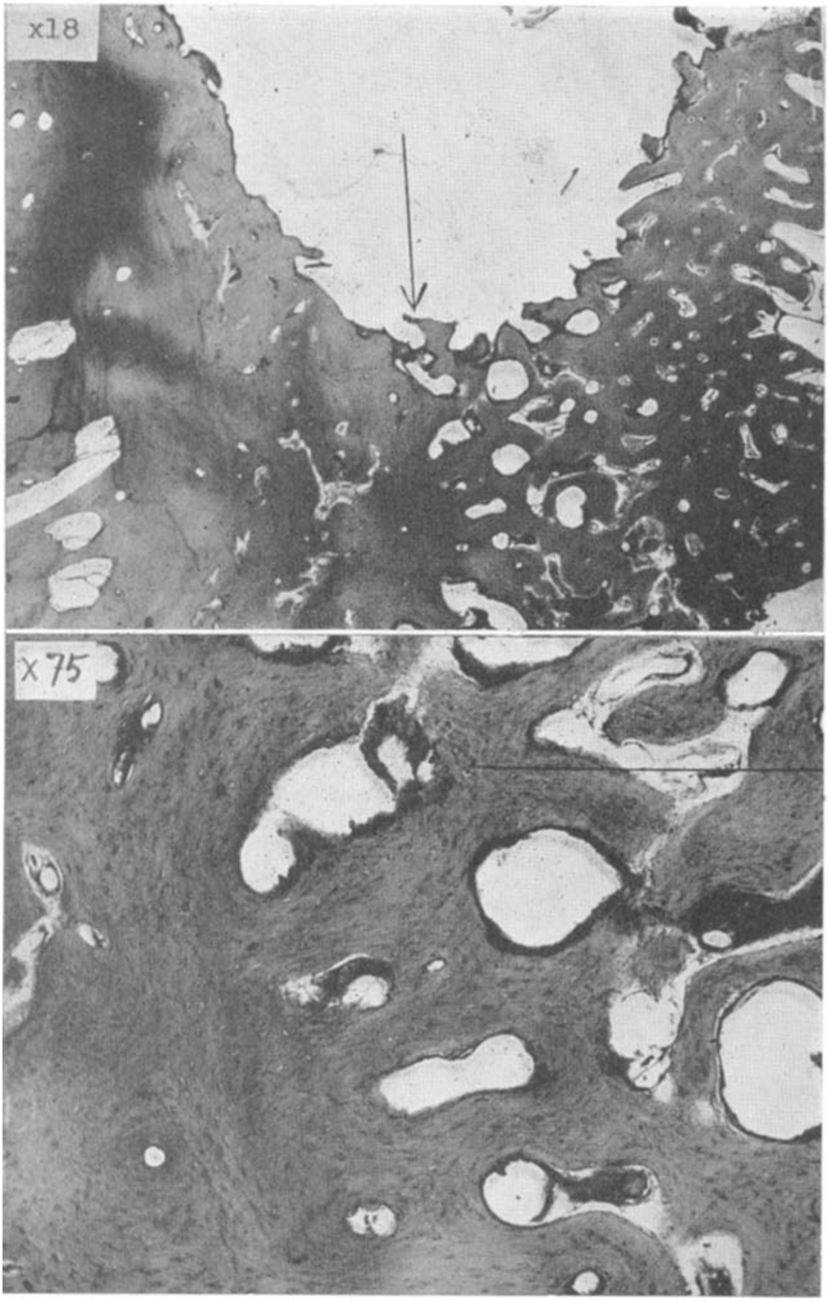


Fig. 36. Chimpanzee Y 5, region of erupting lower canine, labial wall of alveolar process. Extensive resorption and dedifferentiation of eruptional area against the dense organized bone of adjoining regions.

surrounding the canine. The resorption-lacunae are less frequent and at least in its central part it has the appearance of fibrous connective tissue with interspersed wide canals and larger resorption lacunae of irregular outline. There is a definite arrangement of the fibre bundles in a longitudinal direction, comparable to the architecture generally found in this area. The difference in microscopic character from the canine area might be dependent upon:

1) differences in pre-resorptional architecture, the molar area having a special longitudinal arrangement.
2) differences in mechanical importance, the molar area having through-going trajectories supporting a larger portion of the dentition, and the function of which has to be maintained even during the eruption of molars.
3) finally the possibility must also be mentioned that the two areas represent different stages of de- and redifferentiation occurring in the alveolar bone as an accompaniment to the eruption of teeth.

Trajectorial de-differentiation in non-functioning areas.

The above described processes, including a destruction of the architecture, later to be rebuilt again, and serving the purposes of facilitating the eruption and building in of new teeth in the dental arch, occurs through active resorption of trajectorial structures. On the other hand there occurs a de-differentiation more passive in character in those areas of the alveolar process where teeth are lost or where teeth stand without occlusal function. This condition occurs f. i. in Y 6 (Fig. 37) where some deciduous molars are prematurely lost and others stand without antagonists. The crevice-line preparation gives the same picture as in the resorption areas. The microscopic picture (Y 6: 9) in the bone of the alveolar process (mandible), especially the superior part, is as follows:

Lacunae of bone-corpuscles are to a large extent rounded in contour and highly varying in size, both facts contrary to the conditions in an area of regular lamella-systems. The bone is richly interspersed with rounded or beanshaped lacunae varying in size from somewhat supra-cellular up to large lacunated spaces, the major part of them being within the size of 1/20 to 1/10 mm in diameter. Partly irregular borders with apparent resorption processes going on are observed in many of the middle sized and larger lacunae. No texture of the intercellular substance is observed in

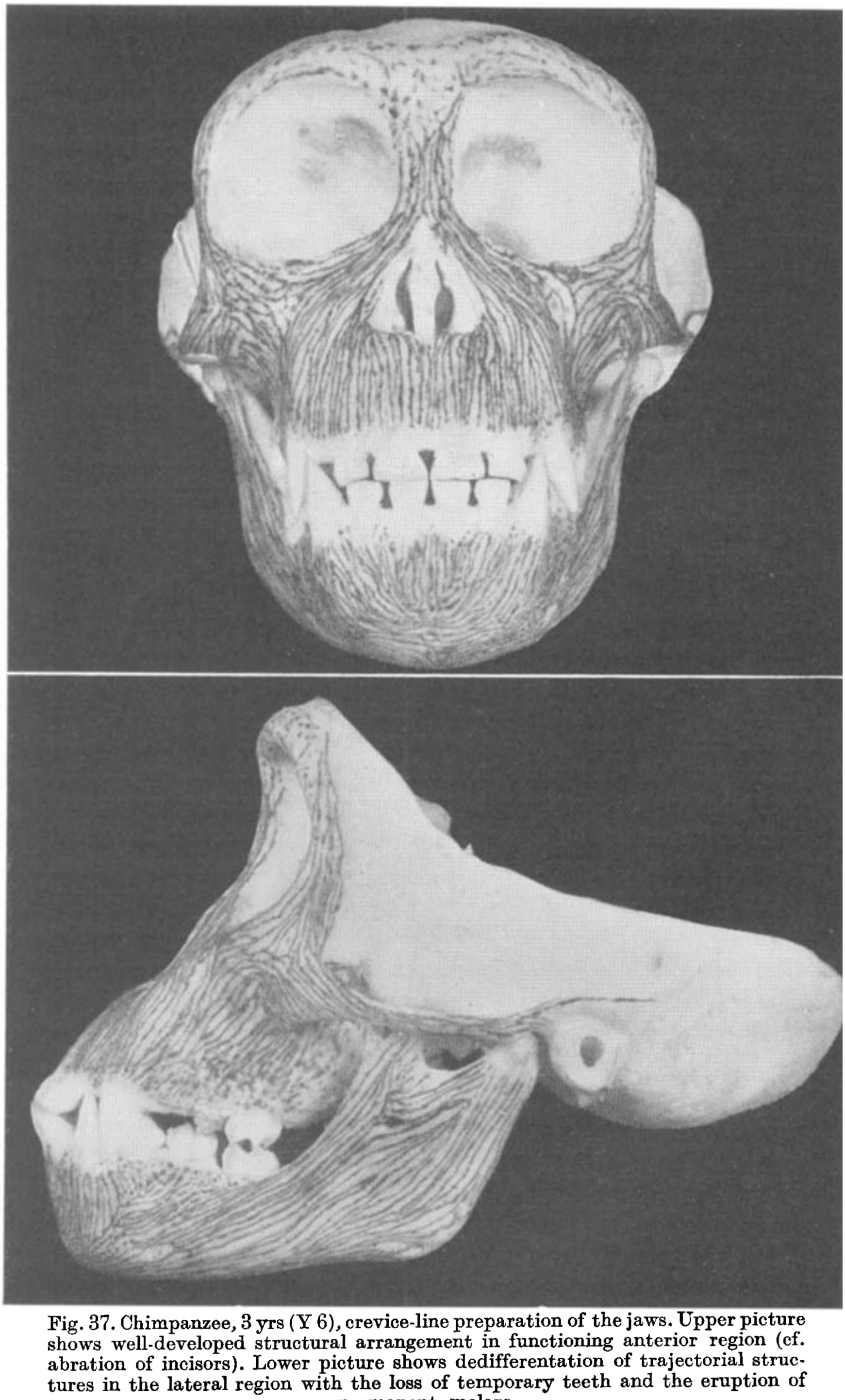


Fig. 37. Chimpanzee, 3 yrs (Y 6), crevice-line preparation of the jaws. Upper picture shows well-developed structural arrangement in functioning anterior region (cf. abration of incisors). Lower picture shows dedifferentation of trajectorial structures in the lateral region with the loss of temporary teeth and the eruption of permanent molars.

the superior part of the alveolar bone. In the richly lacunated areas the intercellular substance looks rather amorphous, only exceptional strands of fibrils and fibre-bundles are observed. Towards the lower part of the alveolar bone the lacunae are gradually diminishing in number, the size being about equal. At the same time the fibrillar strands are appearing more richly, forming more or less of a net-work. Instead of larger lacunae we find canals and canal-systems, the diameter of which varies around 1/20 mm. In the lower parts of the alveolar process, towards the apical end of the teeth we find rather regular parallel fibre- and lamella-systems. The cellular lacunae between the lamellae being flat, but the tissue also showing in certain areas rounded cellular spaces, arranged in clusters.

It is apparent that some resorption is going on even in this part of the alveolar bone. However, *the process is not as violent as that one around the erupting teeth.* Furthermore *the area of resorption is not demarcated, it is gradually disappearing downwards.* These facts point towards a process of dedifferentiation or desorganization of a different nature from that one occurring in local areas around erupting teeth. In the latter case the demarcation of the area indicates a regulating mechanism outside the bone-cells, possibly an enzymatic action from the growing pulp. In the former case the most striking fact is the gradual appearance of rounded cell contours and disappearance of matrix organization. Combined with the apparent non-functioning condition of the alveolar bone (loss of teeth) a cellular mechanism of architectural dedifferentiation suggests itself: loss of function — no mechanical influences on the bone — the cells assume a rounded contour from the flat appearance in the functional bone (*the bone-corpuscles acting as perceptive organs,* as indicators of function) — enlargement of corpuscular lacunae and resorption sets in with a dedifferentiation of the matrix architecture. This process as it occurs in the alveolar bone could be termed afunctional dedifferentiation.

Trajectorial changes of pathologic character.

Quite a different problem from the above regional variations is exhibited by Y 9 (Fig. 38), where the whole alveolar processes and some connecting regions of the jaws and facial bones are lacking the usual architecture and do not give any picture of definite architectural arrangement with the crevice-line method.

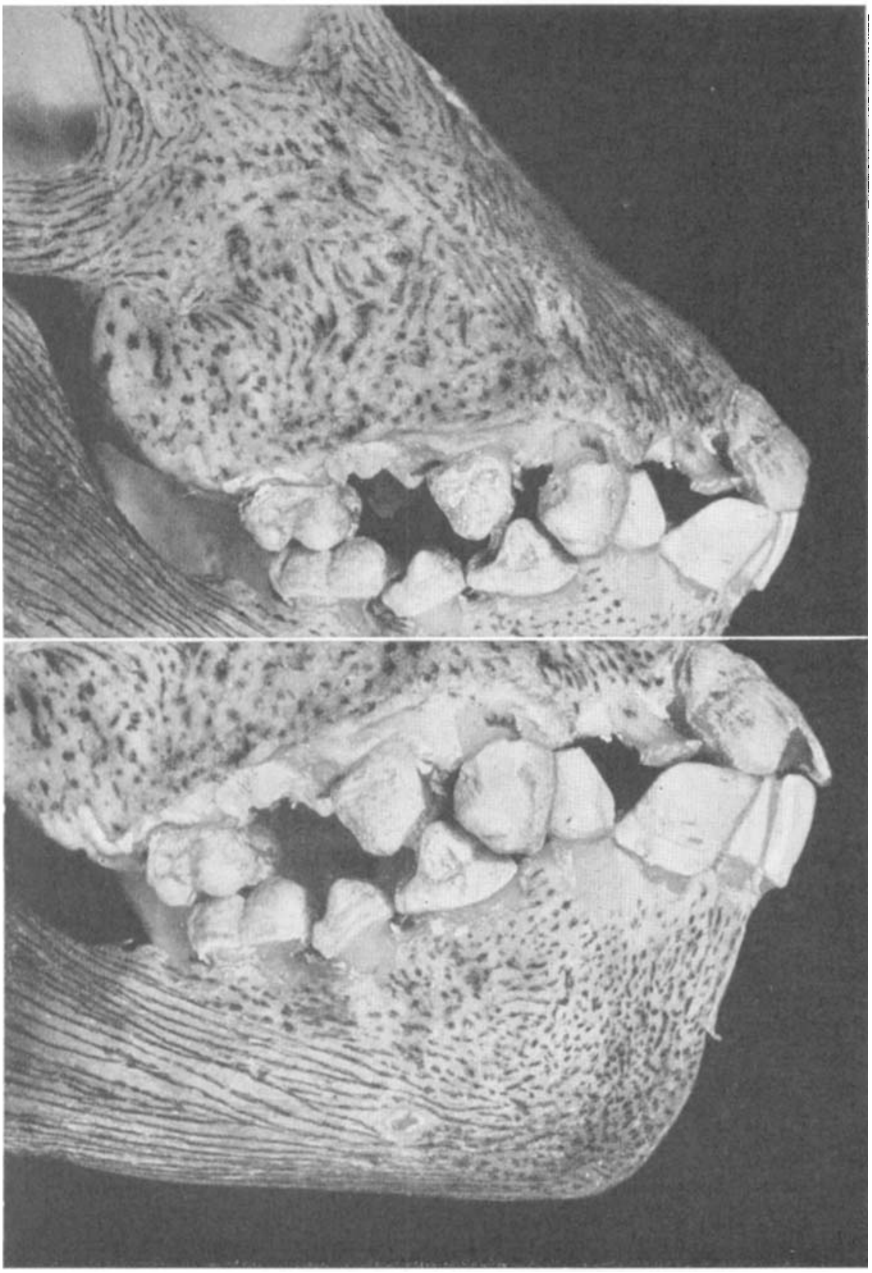


Fig. 38. Chimpanzee 5 yrs (Y 9). Pathology of structural organization combined with malocclusion of the teeth: crowling, premolar rotation and incisor inversion.

The following data are available about the specimen Y 9: Tommy, Chimpanzee, species: Pan satyrus, age 4—5 years.

Dentition: primary
Laboratory series: SEE Thamalus Tommy, Area 6 LXIA
Operations: Nov. 4. 1935: Ablation r. postcentral convolution (1—3—2)
Dec. 6. 1935: " l. areas 4 a. 6
Febr. 7. 1936: " r. parietal cortex (5+7)

Date of death: May 14. 1936, cause: sacrifice.

Y 9 has to be treated in some detail in connection with the variations of trajectorial structures for the following reasons:

1) It is the only specimen examined that exhibited a complete divergence in the architecture of the alveolar processes.
2) It is the only one among the human and chimpanzee specimens of the present material that showed definite signs of malocclusion of the teeth.

Dental status: $\dfrac{6\quad 4\ \mathrm{III}\ \mathrm{II}\ 1\quad 1\ 2\ \mathrm{III}\ 4\ \mathrm{V}\ 6}{6\ 5\ 4\ \mathrm{III}\quad 2\ 1\quad 1\ 2\ \mathrm{III}\ 4\ 5\ 6}$

Lower incisors show crowding and ectopic positions. Six months previous to death there was a definite labial inversion of 2—,—1 which later developed into an edge-to-edge bite.

Lower premolars show rotations and lack of space for full eruption. First molars are in normal occlusion.

The jaws and facial bones upon macroscopic examination appear thinner, more sharp-edged and hollow than those of the other chimpanzees examined, which have definitely more rounded contours and a bulkier appearance. This condition might, to some extent, be attributed to species and sex differences, as well as age.

The bone of the alveolar processes and surrounding regions appear less smooth and somewhat darker than the basal parts of the jaws, a difference which is usually not as apparent. In some parts there appears as scar-like grooves or constrictions in the alveolar bone. This is especially the case in the premolar region below 5 — and 4 —. The alveolar borders are thin and irregular, exhibiting none of the usually clear alveolar limbus.

The crevice-line method gives the following architectural picture:

Mandible: Basal tracts and muscular insertion trajectories rather clear. Above the oblique mandibular tracts the alveolar bone shows no clear architectural arrangement. This diffuse picture is spreading out in the anterior region almost to the base of the mandible.

Maxilla: The alveolar process is showing some strands of regular architecture in its middle and upper height, mostly in the incisor, canine and infrazygomatic regions. In other parts of the alveolar process a diffuse and irregular picture prevails. The lack of architectural arrangement is also apparent in the central infraorbital as well as in the medial and lateral infraorbital regions. Even the anterior zygomatic region is involved to some extent.

The lack of the usual architecture in the alveolar region might to a certain extent be dependent upon intermediary stages in the shedding and eruption of teeth (5 +, + 4, 5 —, — 5) in which case a desorganization of the matrix architecture would be expected. Such a condition would not necessarily require active resorption processes; the porous and lacunated appearance of the bone might be a post-resorptional stage of reorganization, or an intermediary stage in the processes accompanying the shedding of the temporary and the eruption of permanent teeth. But these processes would be localized to the immediate surroundings of the teeth and cannot explain the lack of matrix architecture in the whole alveolar process. Some other factors than the localized reorganization of eruption must be at work.

It is remarkable that the architectural changes of the bone are limited rather strictly to the alveolar processes and their immediate surroundings. The basal trajectorial systems of the face-skeleton are fairly unchanged.

The microscopic picture (Y 9: 9.).

Although the whole alveolar process is giving the same diffuse crevice-line picture the microscopic study shows rather large variations of different regions. The general impression is that of a *delayed organization.* There are fibrils, fibre-bundles, and lamellae of a marked clearness, but they do not form so massive or continuous trajectorial structures as observed in other specimens with a good-crevice-line picture. In the interdental regions of the front there are some vertical strands of lamella-systems, but in the lateral region below the premolars there are only short bundles of different directions, interlacing into a fibrous network. Porosities and lacunae are also occurring more richly in this latter region. There are no apparent resorption processes going on. The lacunae usually show clear borders with circular or semicircular depositions around the canals. There is some similarity to the appearance of the tuber maxillae, with its netlike trajectorial structures. The difference being that the fibrillary and lamellar organization is less clear in the former alveolar process, there being interspersed areas of completely amorphous texture. The condition could be termed a *pathology of organization.* On a comparison with other specimens the alveolar bone of Y 9 is definitely lacking in clearness, density and strength of trajectorial structures, which condition is most pronounced in the alveolar process.

This pathology of organization is presumably a secondary phenomenon, following upon a more or less remote disease process of the bone. The pathological disturbance seems to bring about a regression to more primitive fibrillar architecture instead of lamella-systems (cf. CRAWFORD 1939). It is comparable to the histopathologic changes in vitamin C deficiency, where there is a formation of pathologic dentin of an osteoid appearance instead of the regular tubular dentin.

The alveolar process seems more sensitive than the basal parts of the jaws, possibly due to its closer functional dependence upon the dentition. The variations of the dentition in the transitional period might also contribute to the extensive changes of its architecture, while the basal parts of the jaws do still possess a fairly clear structural arrangement.

It cannot be entirely excluded that the operation of the motor area involving the jaws (left precentral area 6) six months previous to death might have some influence upon the structural changes. But on the other hand the malocclusion was observed before the operation, and the extensive bilateral changes can hardly be explained on the basis of a unilateral motor disturbance. Although there are no exact clinical data available, the histologic picture points towards a nutritional disturbance (Vitamin C and D), which seems probable with the animal being taken into captivity at an early age.

Application of Bone Studies to Malocclusion of the Teeth.

The architectural pictures of the jaws in man and chimpanzee presented in this study show that the jaws and facial bones possess an interior architecture comparable to that of other organs, corresponding to the lobulation of the liver, the arrangement of the heart muscle bundles, the architecture formed by the renal tubules and so on. Furthermore this interior architecture of the jaws is functional, in a mechanical sense of the word, responding closely to the functional variations of the dentition. From an orthodontic point of view the question then arises if there might be any connection between malocclusion of the teeth and disturbances in this supporting interior architecture.

Malocclusion of the teeth and deformities of the jaws occur in over 50 % of modern civilized populations in their second decade of life. A certain amount of these anomalies is attributed to hereditary and congenital causes. A big group is usually referred to as developmental disturbances, implying that the deformity develops as the teeth erupt and a proper occlusion fails to establish itself due to lack of growth of the jaws. The acute production of a deformity from a previously normal dentition is rare. Yet it might appear in grave changes of the bone as in Pagets disease and acromegaly. In a high percentage of cases the malformations are unassociated with any other deformities or manifest diseases of the body, which might be taken as an indication that form-variations and genetic variability play an important rôle. The high incidence of malocclusion seems to contradict a relationship to structural pathology of the supporting tissues, or else the jaw-bone would be extremely sensitive to pathological changes.

As shown by Seipel 1946 the majority of anomalies of tooth position fall within the range of 0—6 mm of deficient space within the dental arch. These deviations are mostly non-specific for any causative factor and might well be explained on the basis of morphologic variations between tooth-material and jaw-size without any structural pathology being necessarily involved. But for larger deviations, and especially where (beside the dental malocclusion) there are associated symptoms connected with the skeletal development, as deformed alveolar processes, hypertrophied alveolar limbus, extensively delayed eruptions and so on, we are compelled to look for pathologic factors.

The fact that malocclusion of the teeth is not produced in acute disease is not disavowing the possibility of a structural pathology behind these kinds of malformations. But it is obvious that only certain types of malocclusion can be referred to a structural pathology of the bone, namely first developmental disturbances, and secondly anomalies of deformation, or those ones where an insufficient support of the teeth or insufficient fixation of the dental arches can be made responsible for the deformity. The productive mechanism in such forms of malocclusion would thus be either that 1) bone pathology inhibits the growth of the jaws with later eruptive crowding of the teeth, in such cases where the size and number of the teeth would predispose for malocclusion, 2) or else the bone pathology would condition derangement of the dentition through lacking support of trajectorial tissues to mechanical influences. A possible occurrence would also be a combination of both.

Concerning the first point the development of malocclusion is of a chronic nature, and an inhibition of growth would well influence the development of the dentition, which is drawn out over a long period of time from infancy to adolescence. The anomaly does not occur clinically until the teeth erupt or vainly try to find their place in the dental arch (Fig. 39). The processes in the bone that might be responsible for the malocclusion have then passed off years ago leaving no other trace than an underdevelopment or dwarfed condition of the skeletal parts. According to SEIPEL 1946 there is a definite correlation between crowding of the teeth and decreased skeletal dimensions.

Due to the specific conditions of the dentition as a secondary organ built up upon the bone-basis, a pathological process of the bone and a resulting dental malocclusion are by no means synchronous in their occurrence. There might be years or decades in between — a fact which makes investigation in this field rather problematic. The resultant dental malocclusion is also dependent upon the predisposing factors in the tooth-material — largely of a hereditary character — so that the same disease process might give quite divergent pictures in different dentitions. When an external factor of structural pathology turns up its effect will then be largely conditioned by individual form and size variations.

The complex mechanism of growth regulation through the anterior pituitary hormon is of such a finely balanced nature as to be termed hereditary, or its larger aberrances lie beyond the scope of therapy. In the possible causes of structural malocclusion we are mostly concerned with infectious diseases and nutritional disturbances. HARRIS 1926 showed a decrease of growth of the long bones following upon long-drawn diseases of childhood. Experiments by A. H. SMITH et al. 1935—36 showed that the long

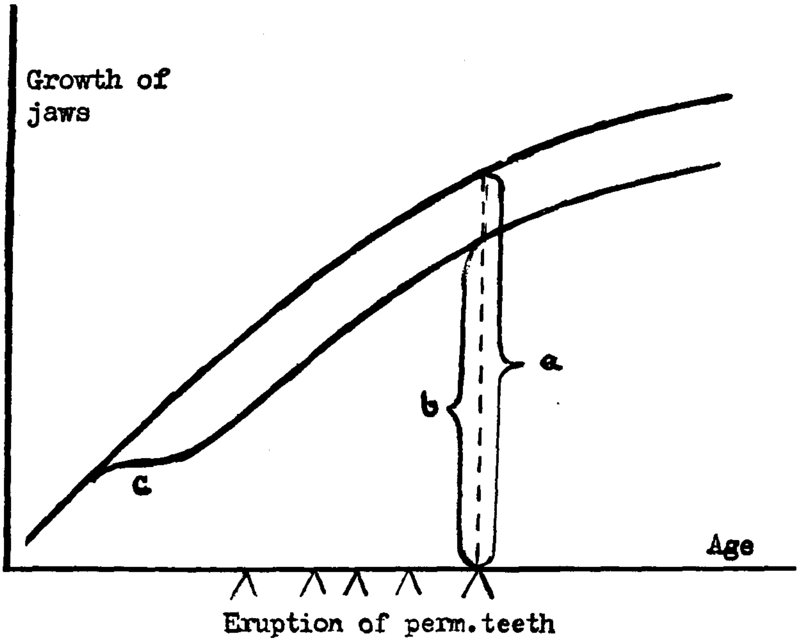


Fig. 39. Diagram of the hypothetic relationship between pathology of trajectorial structures and malocclusion of the teeth.

a) Normal place required for the accomodation of the teeth.
b) Insufficient place attained after growth retardation, crowding of the teeth as a result.
c) Early disease process with change in growth pattern, predisposing for malocclusion and crowding of the teeth. Malocclusion developing in conditions of reattained health years after predisposing disease and primary structural pathology have occurred.

bones of rats which were subjected to early dietary restrictions (Ca-deficiency), failed to reach their normal size (compared to control animals) even when re-alimentation with a complete diet had taken place. In an analogous manner we might expect restrictions in growth of the jaws, which will then secondarily lead to malocclusion due to lack of space as the teeth erupt (cf. SEIPEL 1946, chapt. 10). Growth inhibition of the jaws is shown by several investigators to follow upon nutritional disturbances (HOWE 1926, MELLANBY 1929). Thus the causation of growth inhibition through environmental factors is fairly clear, but due to the time-shift, the varying tooth-material and the usual non-specificity of positional deviations the etiological connections are still unclear.

Growth inhibition and dental malocclusion of a specific character may be found in congenital syphilis (B. G. ANDERSON 1939, JOHNSTONE et al. 1941). There is a shortening of the incisor region of the maxilla, little or no deformity of the dental arches. In such case the interior architecture might be changed, but the primary cause of the anomaly lies in the general pathology hitting certain parts of the bone in this disease. The congenital syphilis shows, among other characteristics, disturbances in the epiphyses and lines of ossification, the latter becoming wide, irregular and indefinite, the tissue showing a yellowish opacity due to degeneration. Such a process is likely to hit both the intermaxillary bone and the condylar growth of the mandible, the result being a tendency towards anterior open bite. Associated malocclusion of the teeth would thus be due to changes of bone form.

Now the question is to what extent the trajectorial structures might be involved in the bone disturbances. ASCHOFF 1928 claims that the changes in rickets are primarily concerned with the organic matrix of the bone, and thus with the trajectorial tissues. They are extensively changed in the formation of osteoid instead of lamellar bone. According to ASCHOFF the rachitic bone-changes will sometimes heal and dissolve completely, in other cases the interior changes of the bone, as well as the gross deformations of bone-form, will persist for life-time. In nutritional experiments ANDERSON et al. 1936 showed a deficient development of the jaw-bone with osteoid changes and lack of lamellar organization in animals on a low salt diet. ARNIM et al. 1936 also showed extensive interior changes of the alveolar bone as a consequence of dietary changes.

We might take rickets as an example of a disturbance involving the trajectorial structures and the position of the teeth. The older views on rickets (ASCHOFF, SCHMORL) were concerned with the severe forms with extensive histo-pathologic and skeletal changes, even involving the jaws. Modern bio-chemical and nutritional aspects, on the other hand, stress the retardation of the calcification process as the main point, as brought out by PARK in 1940. The subnormal concentration of calcium and phosphorus in the blood during early growth periods might then produce a change of bone structure and retardation of growth comparable to the conditions in low salt diet. Mild cases of rickets are still fairly frequent. ROSE 1940 counts 21 % of clinically diagnosed rickets in 1926 and 7.1 % in 1935 in Chicago pre-school children, but of these latter cases only one in 200 showed severe symptoms. There are no records of a simultaneous decrease in malocclusion. On the whole the question of rickets as a causative factor in malocclusion is open. Several investigators like HATFIELD 1919, FRANKE 1921, ANDERSON and HURME 1941 deny rickets as a prominent cause of malocclusion, while others like SCHRÖDER 1923 and KANTOROWICZ 1930 (p. 1385) show the etiologic effect of rickets. The divergent ideas might partly be explained by the above-mentioned different effect of a disposing factor upon the individual hereditary complex. There are also divergences as to the time of onset and severity of the disease.

In rickets as in osteomalacia and osteitis fibrosa there is a lacking mineral fixation of the organic matrix and deformities due to mechanical influences are likely to occur. The experimental low-salt diet likewise effects the ability to form adequate trajectorial structures. SCHRÖDER 1923 describes the well-known deformities of severe rickets, the maxillary contraction, the open bite, and the deformity of the mandible, the deflections being experimentally shown to occur in a weakening of the bone, comparable to the deficiency of trajectorial structures. Such extreme deformities are likely to occur only in severe, uncompensated rickets. When an adequate anti-rachitic therapy sets in, as in the above material of ANDERSON and HURME 1941, the bone-deformities and the dental malocclusion may be diminished or prevented. In the milder forms of rickets, which are rather frequent according to ROSE 1940, there may also be bone-changes with a trajectorial weakening and a consequent tendency to malocclusion, but these conditions are not sufficiently examined.

The importance of the structural pathology in malocclusion is clearly demonstrated on a comparison between the open bite in rickets and the common open bite of finger-sucking. In the latter the deformity disappears and the teeth grow down into occlusion, when the deforming pressure subsides. The rachitic open bite on the other hand does usually not show any tendency towards recovery once it is established. The interior bone-changes and the deformities of gross bone-form retain the malocclusion (cf. ASCHOFF 1928), and the tissues are rather resistant even to orthodontic movements of the teeth.

Considering the possible influence of structural variations and pathology upon the position of the teeth, we might thus separate the following conditions:

1. Disturbances of jaw-growth: where size-space relations of the individual case are predisposing, this may lead to crowding deviations, with the typical disturbance of crowding and retention of late-erupting teeth.
2. Pathologic bone-changes may hit certain parts of the jaws, leading to form variations, as the open bite in congenital lues or the mandibular deformation in severe rickets.
3. Deficiency of trajectorial structures may lead to resistance deviations as: transverse contraction of the dental arch, incisor protrusion, and posteruptive crowding of teeth.

The influence of the structural changes will act as a modification upon the individual hereditary complex, and the morphologic picture will vary with the form- and size-relations of the case in question.

From the above the following *theory of structural malocclusion* will be concluded: In nutritional and pathological disturbances during early growth periods there is a retardation in the formation of trajectorial structures and in the growth of size of bones which secondarily might lead to malocclusion through

1. Deficiency of jaw-size, with crowding deviations of tooth-position where size-space relations predispose.
2. Defects of bone form.
3. Deficiency of trajectorial resistance.

Efforts have been made in this chapter to elucidate in some way the composition, variations, and reactions of the basic structures upon which the dentition is built. Certain forms of malocclusion of the teeth might be associated with structural changes of the supporting tissues, occurring during the period of development. The organic matrix of the bone, consisting to a very large extent of collagenous fibrils, is the basis upon which pathological factors are supposed to work. The sensitiveness of this structure to disturbing influences being most pronounced during early developmental stages, before an increasing trajectorial development and Ca-fixation ensures and secures more stable conditions of the tissue. Malocclusion of the teeth does not belong to the primary pathologic picture, but appears as a secondary effect to the structural disturbances. These latter being by no means specific for malocclusion of the teeth, but being general bio-chemical or histo-pathological changes occurring in certain tissue elements (organic matrix, collagenous fibrils, Ca/org. tissue ratio). Only through their occurrence at a disposing age and in the proper sequence of events might they bring about disturbances in the dentition. The same conditions occurring at a later age, after a proper organization and fixation of the dentition and pertaining structures has taken place, might not bring about malocclusion, but rather different clinical manifestations, f. i. in case of collagen disturbances loosening of the teeth and periodontal disease being the most probable (cf. BURKET 1946 p. 402). Namely for the reason that the weakest point of attack at this stage is not a developing organic matrix of the bone —but the connecting tissue between tooth and bone, the peridental membrane, which ordinarily does not derive any benefit from an increased bone organization and Ca-fixation or sclerosis.

Thus it seems possible, by way of the supporting tissues, to relate certain forms of malocclusion and periodontal disease to common pathological factors —the age being determining for the occurrence of one or the other. The predisposing factors, deficiency disease, vitamin or endocrine disturbances or any disturbance hitting the collagenous tissues are identical, the histo-pathologic picture varies with the selective localization at different age, and the clinical picture is influenced by the functional conditions of the dentition.

Summary.

1. This is primarily a morphologic study of the structural arrangement in the jaws. But efforts have been made to develop the trajectorial study from the "lines of stress" of earlier investigators to include the composition, variations and reactions of the bone as well.
2. *Method:* By means of a refined crevice-line preparation as an indicator of structural arrangement, by means of micro-dissection and histologic sections the interior architecture of the compact bone has been elucidated in the jaws and facial bones of man and chimpanzee. This architecture is referred to the organic matrix and is formed by lamella-systems of different

order, or by a fibrillar arrangement in fibrous strands, in bundles or net-work. In the photographic pictures we must keep in mind that the crevice-line method shows only the main direction of lamellar organization. With a simplification of the existing conditions it is a test or an indicator of the tissue architecture.

3. *The trajectorial structures of the jaws:* The organic pattern of the jaw-bones has a fairly regular and constant occurrence, comparable to the interior organization of other organs (like the liver, the heart muscle etc.). The texture of the alveolar processes, based upon the maxillary ascending and the mandibular basal structures are elucidated. The architecture of the alveolar, zygomatic, posterior maxillary, and palatine structures are revised. Earlier trajectorial concepts are considerably changed and completed, both regarding the topography, the age-changes, and the structural variations.

   The relations of the jaw trajectories to the insertion regions of the muscles of mastication support the following trajectorial nomenclature:

	Temporal system	Masseter system	Pterygoid system
Upper jaw	Maxillo-frontal traj.	Alveolo-zygomatic tr.	Post. maxillary traj.
	infraorbital ,,		palatine ,,
	lateral orbital ,,		long. alveolar ,,
	ant. ascend. alveolar	lateral ascend. alveolar	post. ascend. alveolar
Lower jaw	Alveolar arcade system — longitudinal alveolar trajectories		
	external oblique tr.	basal mandibular tr. (lateral portion)	basal mandibular traj. (medial portion)
	internal ,, ,,		
	ascending temporal tr.	ext. transv. angular tr.	int. transv. angular ,,

4. *Variations of trajectorial structures:* In the organization of the jaw bone there are large variations as to the bulk and clearness of the trajectorial structures, varying with species, with age, and between individuals. In some specimens the trajectorial structures are less developed, even unclear or pathologically changed (Y 9), in others they are clear and strongly developed. These differences appear in the crevice-line preparation, but they are best studied by micro-dissection and on histologic sections. They are coordinated with functional conditions, as observed in the changes of the alveolar bone, with functional variations of the dentition (loss of teeth: Y 6, eruption of teeth: Y 5).

5. *The functional systems of the jaws* consist of the dentition, the muscles of mastication and the connecting trajectorial structures of the bone. Judging from the theories of functional adaptation (ROUX, WOLFF, BENNINGHOFF), from bone studies and from clinical orthopedic experience (CAREY, PAYR, v. BRÜCKE, MURRAY) these functional relations of the dentition must be of importance for orthodontic therapy. Where the positions of the teeth are changed in transverse or intermaxillary directions, so as to upset the physiological balance of the functional systems, we might suppose reorganization of the trajectorial and functional tissues to take place. This is most strikingly shown in the alveolar bone and its close relations to changes of the dentition.
6. *Trajectorial relations to orthodontic therapy:* The orthodontic tissue changes are subdivided into paradental, trajectorial and morphologic, with a decreasing adaptability the more structures are involved in the orthodontic changes.

   The following hypothesis of orthodontic bone changes is advanced: Orthodontic changes are facilitated where tooth-movements are going parallel to trajectorial structures within the alveolar bone, without breaking the continuity of the trajectorial pathways or stretching them. When the trajectorial systems are stretched or broken the trajectorial adjustment is encumbered and the orthodontic results are unsafe.
7. *Bone reactions of trajectorial and orthodontic importance:*
   a) In the alveolar bone the trajectorial structures are closely subjected to functional influences, where the bone-corpuscles give evidence of acting as perceptive organs. Following the loss of teeth there is a dedifferentiation of the corresponding part of the alveolar trajectories, accompanying a change of cell contours. In the eruption of teeth there is a lacunary resorption and breakdown of trajectorial structures in a demarcated area of the pertaining alveolar bone (Y 5).
   b) There is a structural reserve of the bone which might be more or less utilized for trajectorial organization. This allows a considerable margin of functional variations, and even positional changes as far as the teeth are concerned.
   c) Vital rebuilding is constantly going on in the bone (PETERSEN, BENNINGHOFF). This keeps the trajectorial structures in a state of flux, which might be utilized for therapeutical changes. Concerning orthodontic changes there is a gra-

dient of adaptability of the trajectorial structures, younger age stages and more distal parts (alveolar process more than basal parts of the jaws) responding more closely to functional and therapeutic changes. The functional changes appear in different stages of the eruption of teeth and loss of teeth in the present material.

d) In nutritional disturbances there are changes of bone growth and compensatory adjustments between organic and inorganic constituents of the bone (A. H. SMITH et al., MC KEOWN et al.). Such processes will influence the trajectorial structures of the jaws and their supporting abilities (Y 12), even bringing about pathologic forms of trajectorial organization and malocclusion of the teeth (Y 9).

8. *Structural pathology of the trajectorial tissues of the jaws:* In one case of malocclusion and crowding of the teeth (Y 9) there was observed a structural pathology of the trajectorial tissues of the jaws, appearing as an inability to form the usual architecture of the alveolar process. There was a considerable amount of bundle bone and amorphous structures substituting for the usual lamellar architecture of the alveolar bone. The production of malocclusion as a secondary phenomenon following upon a more or less remote disease process of the bone is discussed in this connection.

Literature.

ALBRIGHT, F., BAUER, W., and AUB, J. C., Studies of calcium and phosphorus metabolism: influence of thyroid gland and parathyroid hormone upon total acid-base balance. J. Clin. Invest. 1931: 10: 187—219.

ANDERSON, B. G., Dental defects in congenital syphilis. Am. J. Dis. Child. 1939: 57: 52.

ANDERSON, B. G. and HURME, V. O., Malocclusion in a group of postrachitic and non-rachitic adolescent children. Int. J. Orth. 1940: 26.

ANGLE, E. H., The upper first molar as a basis of diagnosis in orthodontia. Dent. Items of Interest 1906: 28.

ASCHOFF, A., Pathologische Anatomie. G. Fischer, Jena 1928, 7 Aufl.

BAKER, L. W., The influence of the formative dental organs on the growth of the bones of the face. A. J. Orth. 1941: 27: 489—506.

BARTH, M., Ueber die funktionelle Struktur des Oberkieferapparates bei Neuweltaffen. Anatomische Hefte I: 1919: Bd 56.

BAUER, W., AUB, J. C. and ALBRIGHT, F. Studies of calcium and phosphorus metabolism V: A study of the bone trabeculae as a readily available reserve supply of calcium. J. Exper. Med. 1929: 49: 145.

BECKER, R. B. and NEAL W. M., Proc. Am. Soc. Animal Prod. 1930: p. 81.

Benninghoff, A., Spaltlinien am Knochen, eine Methode zur Ermittlung der Architektur platter Knochen. Verh. Anat. Ges. 1925.

— Ueber die Anpassung der Knochenkompakta an geänderte Beanspruchung. Anat. Anz. 1927: Bd 63.

— Funktionelle Anpassung. Hdbuch d. Naturwissenschaften. Fischer, Jena 1933.

— Die Architektur der Kiefer and ihrer Weichteilbedeckungen, Paradentium 1934.

— Form und Funktion. Ztschrft f. d. ges. Naturwissenschaft 1935: H. 4—5, 1936: H. 3.

— Ueber Leitsysteme der Knochenkompakta. Beiträge z. Anatomie funktioneller Systeme 193: Bd 1.

Bluntschli, H., Rückwirkungen des Kieferapparates auf den Gesamtschädel. Ztschrft f. zahnärztliche Orthopädie 1926: 3.

— Die menschlichen Kieferwerkzeuge in verschiedenen Alterszuständen. Verh. Anat. Ges. 1926.

— Von den Kräften, welche den Kiefer bewegen und gestalten. Paradentium 1929: 3.

Breitner, C., Bone changes resulting from experimental orthodontic treatment. Am. J. Orth. 1940: 26: 521.

— Alterations of occlusal relations induced by experimental procedure. Am. J. Orth. 1943: 29: 277.

Brodie, A. G., Downs, W. B., Goldstein, A. and Myer, E., Cephalometric appraisal of orthodontic results. Angle Orthodontist 1938: 10: 261.

v. Brücke, H., Ueber Oberschenkelbrüche, Dtsche Ztschrft f. Chir. 1935: 244: 405.

Burket, L., Oral Medicine. Lippincott, Philadelphia 1946.

Carey, E. J., Studies in the dynamics of histogenesis. Radiology 1929: 13: 127.

Clarke, M. F., Bassin, A. L. and Smith, A. H., Skeletal changes in rat induced by a ration extremely poor in inorganic salts. Am. J. Physiol. 1935: 115: 556—563.

Cowdry, Special Cytology. New York 1932.

Crawford, G. N. C., The evolution of the haversian pattern in bone. J. of Anat. 1939: 74: 284.

Cushing, A. H., Acromegaly from a surgical standpoint. Brit. Med. Journ. 1927: 2: 48.

Davida, L. v., Die Struktur des Unterkiefers, Festschrift zum Prof. K. Lechner. Klausenburg 1915.

Duhamel cit. Ham.

Fick, L., Ueber die Architektur des Schädels. Müllers Archiv 1853.

Flourens cit. Ham.

Foot, J. S., Bone as a measure of development. Omaha Press 1928.

Franke, G., Ueber Wachstum und Verbildung des Kiefers und der Nasenscheidewand auf Grund vergleichender Kiefermessungen und experimenteller Untersuchungen über Knochenwachstum. Kabitzsch, Leipzig 1921.

GEBHARDT, W., Ueber die funktionelle Knochengestalt. Ztschrft f. orthopäd. Chir. 1910: 27.

— Ueber den Skelettbau mit dünnen Platten. Anat. Anz. 1911: Bd 38 Ergänz.

GOERKE, Beitrag zur funktionellen Gestaltung des Schädels bei den Anthropomorphen und dem Menschen durch Untersuchung mit Röntgenstrahlen. Arch. f. Anthropologie 1904: Bd 29 Nachf.

GRAY, H., Anatomy of the human body. 23rd ed. Lea & Febiger, Philadelphia 1936.

HAM, A., The last hundred years in the study of bone. J. A. D. A. 1934: 1: 3—12.

HARRIS, H. A., The growth of the long bones in childhood, with special reference to certain bony striations of the metaphysis and to the rôle of the vitamins. Arch. int. med. 1926: 38: 785.

— Bone growth in health and disease. Oxford Univ. Press, London 1933.

HAVERS, C., Osteologia Nova or some new observations of the bones, and the parts belonging to them; with the manner of their accretion and nutrition. W. Innys, London 1729 (2nd ed.).

HEMLEY, S., Fundamentals of occlusion. Saunders, Philadelphia 1944.

HENKEL, Vergleichend-anatomische Untersuchungen über die Struktur der Knochenkompakta nach der Spaltlinienmethode. Morph. Jahrbuch 1931: Bd 66.

HOWE, P. R., The influence of food on malocclusion. Proc. 1st Internat. Orth. Congr. 1926: 32.

HULTCRANTZ, W., Ueber die Spaltrichtungen der Gelenkknorpel. Verh. d. anat. Gesellsch. Jena 1898: 12: 248—256.

HUNTER, J., Natural History of the Human Teeth. London 1771.

JOHNSTONE, W. D., ANDERSON, B. G. and MCALENNEY, P. F., Effects of congenital syphilis on the teeth and associated structures in children. Am. J. Orth. 1941: 27: 667.

KATZ, A., Architektur des Unterkiefers im Zusammenhang mit der Lage der Wurzeln und der Widerstandsfähigkeit des Zahnbogens beim Erwachsenen. Vierteljschrft f. Zhkde 1931: 1, 2.

KLAATSCH, H., Kraniomorphologie und Kraniotrigonometrie. Arch. f. Anthropol. 1909: 8.

KÜNTSCHER, G., Ueber den Nachweis von Spannungsspitzen am menschlichen Knochengerüst. Gegenbaurs Morph. Jahrbuch 1935: 75: 444.

— Die Bedeutung der Darstellung des Kraftflusses im Knochen für die Chirurgie. Arch. f. Klin. Chir. 1935: 182: 489—551.

KOCH, J. C., The laws of bone architecture. Am. J. of Anat. 1917: 21.

LANGER, C., Lehrbuch der Systematischen und Topographischen Anatomie. Wien 1882 (p. 590—591).

LENHOSSÉK, M., Das innere Relief des Unterkieferastes. Arch. f. Anthropol. 1920: 49.

LERICHE, R. and POLICARD, A., The normal and pathological physiology of bone. Mosby, St. Louis 1928.

LEWIN, Die innere Struktur der Mandibula der Anthropinen und Anthropoiden in mechanischer Beleuchtung. Diss. Bonn 1913.

LUNDSTRÖM, AXEL, The apical base. Sv. Tandl. Tidskrift 1923.

MAXIMOW, A. and BLOM, W., Textbook of Histology 1938.

MCKEOWN, R. M., LINDSAY, M. K., HARVEY, S. C. and LUMSDEN, R. W., The breaking strength of healing fractured fibulae of rats. Arch. Surg. 1932: 24 and 25.

MELLANBY, M., Diet and the teeth. Med. Res. Council. Spec. Report nr 140, 1929.

MEYER, H., Die Architektur der Spongiosa. Arch. f. Anat. u. Physiol. 1867.

MURRAY, P. D. F., Bones, a study of the development and structure of the vertebrate skeleton. Univ. Press, Cambridge 1936.

OPPENHEIM, A., Die Prognathie vom anthropologischen und orthodontischen Gesichtspunkt. Ztschrft f. Stomat. 1927: 28.

— Biologic orthodontic therapy and reality. Angle Orthodontist 1935: 5: 157, 233.

PARK, E. A., The therapy of rickets. J. A. M. A. 1940: 115: 370.

PAYR, E., Die kinetische Kette — Tonuspathologie. Acta Chir. Scand. 1932: 72: 318.

PETERSEN, H., Ueber den Feinbau der menschlichen Skeletteile. Ztschrft f. wiss. Biol. D. 112: 1927.

PFAFF, C. L., Rassenkraniologische Untersuchungen über die Stellung des oberen M_1 im Kiefergerüst. Dtsche Zhkde 1923: 61.

ROBINSON, R., MACLEOD, M. and ROSENHEIM, A. H., Possible significance of hexosephosphoric esters in ossification; calcification in vitro. Biochem. J. 1930: 24: 1927—1941.

ROSE, M. S., Feeding the Family. 1940: 170.

ROUX, W., Der Kampf der Teile im Organismus. Leipzig 1881.

— Das Gesetz der Transformation der Knochen. Berliner Klin. Wochenschrift 1893: 509, 533, 557.

— Gesammelte Abhandlungen über die Entwicklungsmechanik der Organismen. Bd 1: Funktionelle Anpassung. Engelmann, Leipzig 1895.

SCHMIDT, C., Die Benennung der Befestigungsfasern des Zahnes und das Verhalten einiger wichtiger Fasergruppen beim Menschen. Ztschrft f. Anat. u. Entw. 1932: 97: 5: 563—587.

SCHRÖDER, B., Die Entwicklungsmechanische Erklärung des rachitischen Unterkiefers. Dtsche Mtschrft f. Zhkde 1923: 15: 449.

SCHMORL cit. SHERMAN.

SEIPEL, C. M., Ueber den strukturellen Bau des Unterkiefers beim Menschen. Diss. Bonn 1934.

— Variation of Tooth Position, Sv. Tandl. Tidskr. 1946: 39, Suppl.

SHERMAN, H. C., Essentials of Nutrition. Macmillan, New York 1940.

SICHER, H. and TANDLER, J., Anatomie für Zahnärzte. Springer, Wien und Berlin 1928.

SMITH, A. H. see CLARKE.

THOURÉN, G., Om underkäkens arkitektoniska byggnad hos adult homo. Odontolog. Tidskrift 1947: 4 o. 5.

Thourén, G., Om mellanansiktets arkitektoniska byggnad hos adult homo. Odontolog. Tidskrift 1947: 4 o. 5.

Triepel, H., Einführung in die physikalische Anatomie. Wiesbaden 1902.

Virchow, R., Knochenwachstum und Schädelformen. Virchows Archiv 1858: Bd 13.

Walkhoff, O., Der menschliche Unterkiefer im Lichte der Entwicklungsmechanik. Dtsche Mtschrft f. Zhkde 1900/01.

— Der Unterkiefer der Anthropomorphen und des Menschen in seiner funktionellen Entwicklung und Gestalt. Menschen-Affenstudien über Entwicklung und Schädelbau. Selenka, Wiesbaden 1902.

Warren, J., Handbook of Anatomy. Harvard Univ. Press. 1930.

Westin, G., Zahnveränderungen in Fällen von Skorbut bei Homo. Fahlcrantz, Stockholm 1928.

Wetzel, G., Studien zur Schädelstatik. Verh. Anat. Ges. Anat. Anz. 1922: 55, 58. Suppl.

Winkler, R., Ueber den funktionellen Bau des Unterkiefers. Ztschrft f. Stomat. 1921: 7.

Wissmer, A., Le developpement et l'organisation statique de la mandibule foetale chez l'homme. Arch. d'Anat., d'Histol. et d'Embryol. 1927: 7.

Wolbach, S. B. and Howe, P., Intercellular substances in experimental scorbutus. Arch. Path. and Lab. Med. 1926.

Wolbach, S. B., Controlled formation of collagen and reticulum. Am. J. Path. 1933: IX: Suppl. 689.

Wolff, J., Das Gesetz der Transformation der Knochen. Hirschwald, Berlin 1892.

— Ueber die normale und pathologische Architektur des Knochens. Arch. f. Anat. und Physiol. 1901: 239.

Zsigmondy, O., Ueber das Wachstum des Oberkiefers in sagittaler Richtung. Wien 1911.