ASYMMETRY IN THE SKULLS OF MAMMALS

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Reference to moderate asymmetry in human skulls is not infrequent throughout medical literature, but marked asymmetry in the crania of the other mammals (save the toothed whales, in which this state is the normal one) must be considered as a very rare condition. Careful examination of the material in any large collection would doubtless result in the discovery of a number of specimens showing some disparity between the development of the two sides of the skull; but it is exceedingly seldom that one occurs in which such condition is readily to be noted. Application to those in charge of some of the larger mammal collections of North America have produced but four specimens, two of which exhibit more emphatic distortion than seems ever to have been recorded.

Asymmetry in a skull may be brought about by a change in the size or relationship, through accident or disease, of the individual bones of one side of the head, an alteration, through the same agency, to one or more of the large muscles upon a single side, or a combination of these two factors. A further analysis of these reasons will suggest, as fundamental causes, a more or less permanently painful condition of some part of the head, as a sore tooth, a diseased mandibular condyle, or other such state causing the animal to chew entirely upon the teeth of one side, or otherwise to use the muscles in an uneven manner so as to ease the pain of the offending part as much as possible. This at first is voluntary, although it may later become entirely involuntary, and it implies a long-continued period of painfulness of the part originally affected. Again there may be a definite alteration in the shape of a bone, through fracture and later healing in a twisted position, changing the interrelationship of other parts of the skull, as the mandible. Accidental severance of certain nerves may also be productive of similar results. In all such cases of asymmetry in the skull, initial injury at a comparatively early age is a necessity—the earlier the injury the more pronounced will be its effects, other things being equal.

The pathological conditions resulting from the healing of a severe injury to the bone after the animal has attained full growth does not

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here concern us, for any resulting asymmetry will be purely mechanical, affecting only the immediate portion injured, and probably having no appreciable effect whatever upon other portions of the skull. That this premise is founded on fact is shown by a skull of *Ursus eltonclarki* (No. 232382, Biological Survey collection) from Chichagof Island, Alaska. This is of an adult whose entire right coronoid process is missing. The bone healed well, proving that the injury antedated the death of the animal by a considerable period. Had this happened during the youth of the animal, the practical destruction of function of the right temporal muscle would have resulted in profound cranial changes, but there is now not the slightest asymmetry.

Attention should here be called to the study by Hollister[1] of the skulls of captive lions. In this it is argued that certain conditions—notably massiveness—to be met with in the skulls of lions raised in captivity are the result of myological stimuli, the muscles being effected by conditions brought to bear during captivity. If this be the case, then the criteria usually employed for judging the strength of a skull and its musculature must be altered. A thorough examination of Hollister's material[2] by the present writer, however, has produced new evidence and led him to the conclusion that the conditions obtaining in the skulls of these captives are pathological rather than myological.

Published references to asymmetrical skulls of mammals other than man include an experiment conducted by Anthony,[3] in the course of which he cut the left temporal muscle of a puppy upon the day of its birth. The dog, killed by accident when something less than one year old, showed marked atrophy of one temporal muscle, even in life; but the only really definite asymmetry to be noted in the skull is the absence upon the left side of the ridge which normally marks the medial boundary of the origin of the temporal muscle. The left, or "abnormal," zygomatic arch, as compared to the right, is less than 1 mm. deeper, less than 3 closer to the cranium, and is practically the same in length. The latter points are of interest as showing the trend of the abnormal side, but the differences are too slight to be of much significance in the present study.

The same investigator, as senior author,[4] experimented upon two more dogs at a later date, with results that duplicated his first efforts.

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[1] Hollister, N., Some effects of environment and habit on captive lions, Proc. U. S. Nat. Mus., vol. 53, 1917, pp. 177–193.

[2] Howell, A. B., Pathologic skulls of captive lions, Journ. Mamm., vol. 6, 1925, pp. 163–168.

[3] Anthony, M. R., Introduction a l'étude expérimentale de la morphogénie, Bull. et Mems. Soc. Anthr. Paris, 1903, no. 2, pp. 119–145.

[4] Anthony, M. R., et Pietkiewicz, W. B., Nouvelles expériences sur le rôle du muscle crotophyte dans la constitution morphologique du crâne de la face, Compt. Rend. Acad. Sci., vol. 149, 1909, p. 870.

There is described and figured by Paravicius[5] the skull of a dog exhibiting a marked dextral twist to the rostral region. Unfortunately, this specimen lacked the lower jaw, for the characters strongly indicate that the reason for the asymmetrical condition was the subnormal development of the right ramus of the mandible, due to a fracture during puppyhood. There is no appreciable asymmetry of the temporal fossæ.

Toldt[6] discusses the asymmetrical skull of a fox in the Vienna Museum. On account of a diseased condition of the left, lower, fourth, premolar the animal had used the temporal muscle of the right side as exclusively as possible. The myological condition resulting was a slight increase in the size of the right temporal, shifting its ridge a bit entad. Atrophy, or rather nondevelopment, of the left temporal was marked, its ridge developing considerably laterad of the normal position, and there is practically no lambdoidal crest upon that side. The left supraorbital process and the portion of the temporal fossa immediately caudad thereto, however, are shown in the illustration to be better developed upon the left side. A somewhat puzzling circumstance is the fact that in the drawing, the left zygomatic arch is shown to be about 2 mm. farther from the cranium than the right, while the text also mentions that the disparity is slight. This state of the left zygoma is at variance with what one would naturally expect to accompany a reduced temporal muscle. I imagine, however, that there was some special disparity between the masseter muscles to account for it—an hypothesis which can hardly now be proven.

An instance is mentioned by Leisewitz[7] of slight asymmetry in the skull of a monkey of the genius *Lagothrix*. The bilateral disparity is very poorly defined, however, and the author is mainly concerned with consequent slight differences in tooth wear.

The skulls at hand exhibiting definite asymmetry number four. Two of them are of primates, whose musculature of mastication is adapted to the absence of true glenoid fossæ, and hence, to a considerable movement of the mandible in all directions. The remaining two skulls belong to a single species of pinniped—a carnivore having true glenoid fossæ, which permits practically no lateral nor propalinal motion of the mandible.

ASYMMETRICAL SKULLS OF PRIMATES

The writer is indebted to Mr. G. S. Miller, jr. for permission to study the skull of a form of gorilla in the National Museum collection (see pls. 3, 4, 5, and 6). This bears the data "No.239883, male,

[5] Paravicius, G., Asimmetrie cranio fasciali in un cane, Atti Soc. Ital. scienze nat., 1902, pp, 349–352.

[6] Toldt, Von K., Asymmetrische Ausbildung der Schläfenmuskeln bei einen Fuchs infolge einseitiger Kautätigkeit, Zool. Anz , vol. 39, 1905, pp. 176–191.

[7] Leisewitz, W., Ein Beitrag zur Kenntnis der bilateralen Asymmetrie des Säugetierschädels, Sitzungsberichten der Gesells. für Morph. und Phys. in München, 1906, pp. 1–15.

Africa, Belgium Congo, Rec'd. 1923, Benj. Burbridge." It is the skull of a large adult and is in good condition. The specimen is definitely asymmetrical, though not to a startling degree. The cause of this was due either to an injury to, or a diseased condition of, the right side of the head at a sufficiently early age so that the bones were still plastic. It may be mentioned that a slight, chalky deposit upon some parts of its surface is probably attributable to the method of cleaning rather than to a pathological condition of the bone. Direct indications of abnormality are as follows:

(*a*) A scarred condition and marked lateral shortening of the right mastoid, as well as of the neighboring exoccipital (measurements, foramen magnum to lateral extremity of mastoid; left, 72.2; right, 59.5 mm.)

(*b*) A malformation, encircling the right jugular foramen, of the petrous portion of the temporal and adjacent portions of the basioccipital.

(*c*) A marked deformity of the inferior wall of the right auditory meatus, including some change in the part of the squamosal immediately above, resulting in an enlargement of this passage and a lateral shortening of its inferior wall.

(*d*) An alteration in the condition of the right glenoid fossa, damage to, and partial restoration through healing of, the postglenoid process, and a pitted condition of the surface immediately craniad of the fossa.

(*e*) A shortening of the right condyloid neck of the mandible, with alteration in the shape, and pitting of the articular surface, of the condyle.

(*f*) The absence of the lower left canine, with complete healing and filling in with bony tissue of its alveolus.

(*g*) A recession of the alveolar margins and septa between some of the teeth.

The possible causes of these results should first be considered. Healing of all malformed parts has been complete. There are now no signs of old fractures and there is little evidence from which to decide whether the conditions are the result of disease or of an accident. If they be due to disease, then this is most probably the result either of a severe abscess, an infection of a local wound originally slight, or improbably to some true disease of the bone. If the original injury were due to an accident, then this was caused either by a bullet, which I am inclined to doubt, by a native arrow or spear, or the piercing of the fleshy parts by a sharp stick or stone during a fall from a considerable height. Even though the theory of an accident be accepted, then severe, local infection most probably followed.

Inquiring more fully into the pathological situations present it is found that—

(*a*) The right mastoid is unusual only in being shortened laterally and in having a marked process inferiorly. The lateral shortening of the whole right side of the occipital is probably because of injury to, and subsequent abnormal development of, the muscles originating upon the infero-lateral part of its surface.

(*b*) The deformity of the petrous portion of the temporal is not marked, aside from its misplacement. Its chief point of interest lies in the fact that there is almost complete closure of the jugular foramen and obliteration of its fossa, probably through the healing of a small, diseased portion of both the petrous and occipital margins of the foramen. The occipital was, perhaps, chiefly instrumental, for its border has extended farther forward than normal, and the petrous is correspondingly displaced. It is, of course, impossible that the jugular vein was suddenly severed, else the animal had died at once. Rather was its gradual atrophy brought about, enabling other veins to care for the venous blood that is normally carried by the right jugular. The functional alteration has not, however, resulted in any increase in the size of the left jugular foramen, for the latter is, in fact, smaller than seems to be usual in this genus.

(*c*) The condition of the right auditory meatus indicates much damage to the inner ear, very possibly causing complete deafness upon that side, induced by severe suppuration of the parts. The passage is greatly enlarged, both superiorly and inferiorly, being about 13 mm. in diameter, as against 7 for this measurement of the left passage. The lateral length of the inferior border of the meatus, measured from the carotid foramen, is about 18 mm. shorter upon the right than the left side. This was evidently brought about by suppuration and partial absorption of the bony lining of the meatus, with subsequent healing and growth of new bony tissue only upon its outer or inferior face.

(*d*) The right glenoid fossa proper is not greatly altered, but the eminentia articularis, anteriorly adjoining, is flattened and much pitted. The same condition of pitting obtains upon the squamous eminence adjoining the process of the tensor palati. The conditions to be observed in the glenoid region are naturally correlated with the following:

(*e*) The right articular surface of the mandibular condyle is flattened, broadened in an antero-posterior direction, and much pitted and roughened, and the neck, as measured from the base of the coronoid process, shortened by about 7 mm. It is very likely that the functions of the abnormal side of the jaw were even more severely interfered with than can now be told from an examination of the skull, through destruction of part of the condyloid ligaments.

(*f*) There is no possibility that the left lower canine was congenitally absent, for the tissue now occupying the position of the normal alveolus is, in texture, different from the surrounding bone. This scar seems to be slightly smaller than the alveolus of the right canine, indicating that the left was lost some time during the youth of the individual. Another indication that the tooth was not lost in later life is that the healing of the alveolus would then hardly have been as perfect. The surrounding bone is smooth and healthy, and the prominence upon the chin formed by the root of the normal canine is absent upon the left side. There is no indication of how or why this tooth was lost.

(*g*) Many of the alveoli are markedly pathologic. This condition takes the form of excessive shrinkage, or lowering of the bony border, and is most marked in the septa between the tooth rows, especially between the second and third molars of both sides and the first and second of the left side, of the lower series; and between the second and third molars of both sides of the upper series. The majority of the remaining molariform teeth of the upper series are also affected, but in lesser degree. The bone involved is smooth, however, showing no sign of scars or injury, and the abnormality was not caused by suppuration.

A study of the above situation and a consideration of all possible solutions points with probability to an intensely interesting explanation. At the age when this individual had just cut the front teeth of the permanent set, he suffered an injury, most likely followed by inflammation of the muscles of the right side of the head and neck. For an indeterminate interval thereafter the act of chewing food, and very likely that of swallowing as well, was so painful that the animal brought itself to the verge of starvation. From this cause, a state of malnutrition followed, reaching its maximum severity at a time during or immediately subsequent to the cutting of most of the rear molars, which occurs some time after the appearance of the anterior teeth of the permanent set. Any deficiency in the diet having an osteological effect at the time that tooth change is occurring would manifest itself at just this point, where the process of absorption of old, and formation of new, bony tissue renders this part most subject to any adverse influences. It is likely that the permanent cheek teeth were rather well formed when the condition of malnutrition was most acute, however, else their emplacement would show some abnormal irregularity, which is not the case. The state of the posterior borders of the alveoli of the third molars or "wisdom" teeth points to the conclusion that before the appearance of the latter, the animal had ceased to suffer pain, had resumed a normal diet, and had thus terminated the period of malnutrition.

An alternative hypothesis, in no wise dependent upon the original injury to the skull, was suggested by Capt. R. W. Leigh (MS), of the Army Medical Museum, to account for the alveolar condition. This is to the effect that the molariform teeth grew into position with abnormally large spaces between them, into which became more or less permanently wedged particles of fibrous foods, this finally forcing the recession of the alveolar borders. I have occasionally noted just this state of affairs between two or three teeth of ungulates and rodents, and I deem it very likely that the same situation operated to aggravate the abnormal condition in the gorilla; but that this was the original and sole cause for the recession of the bony borders I strongly doubt.

An examination of the skull impresses one with the probability that certain muscles suffered considerable violence, either directly or in consequence of severe infection after injury. The evidence indicates that the muscles thus involved were chiefly the digastric, trachelo-mastoid, sterno and cleido-mastoids, splenius, rectus capitis lateralis, and the levator and tensor palatis. It is not improbable that the obliquus superior was also affected. There is no satisfactory evidence that any other muscle suffered directly except in so far as the pathological condition of the articulation of the right side of the jaw means previous infection, to some extent, of the muscles surrounding it.

The direct results of injury, reflected in the stresses exerted by other muscles of the head, were of a more profound and lasting character. Injury to and subsequent healing of a muscle causes, under certain conditions, shrinkage of its length, and other strains may develop. It should here be understood that the term "pull" of a lesioned muscle, "shrinkage," etc., is merely relative and not actual. Shrinkage is very seldom sufficient for a muscle so affected to exert true tension upon a part; but a muscle of this character not only resists full relaxation, but by the same token resists normal growth. Hence, for all practical purposes, it does not matter, when speaking of a case where asymmetry of a bone is due to difference in the development of either of a pair of muscles, whether one conceive that the abnormal side of a bone has been pulled around by contraction (*i. e.*, resistance to normal growth), or that the growth of the normal side has pushed the other out of line.

With respect to the long axis of the skull, the foramen magnum is displaced toward the right in such a manner as to suggest that the articulation of the condyle with the atlas was forced in that direction, logically, by the pull of the lesioned obliquus superior and rectus capitus lateralis, and perhaps other, muscles upon that side. The basioccipital naturally is obliged to follow this tendency, and it

is similarly displaced, but the other sutures of the occipital are not traceable. Because of the fact that so few of the individual bones of the cranium can be defined, it is impossible to tell whether the lateral shortness of the right mastoid and exoccipital, which also means the lambdoidal crest upon this side, is due entirely to the effect of the cervical muscles involved, or also to that of the temporal. In all probability both have contributed to the existing state of affairs. It also seems likely that the right cervical musles previously enumerated were relatively weak.

The medial portion of the right petrous temporal has been advanced several millimeters, with corresponding displacement of the origins of the palati muscles. The origin of the right internal pterygoid is larger than the left, but the difference is not of greater degree than occurs in symmetrical skulls. The right curve of the palatal shelf extends slightly farther craniad than the left, indicating a corresponding disparity between the insertions of the two tensor palati muscles.

An examination of the superior aspect of the skull at once discloses the fact that the right temporal fossa as a whole is considerably smaller than the left. It is not less deep, to any appreciable extent, but the sagittal crest is displaced toward the right and the right lambdoidal crest is shorter. The fact is disclosed, however, that the anterior part of the right temporal was of greater mass than upon the left. This resulted in the displacement, in both anterior and lateral directions, of the right frontal, now best shown by the position of the supraorbital ridging. The origin of this part of the muscle is thus more extensive upon the right side, and it may well have been thicker also.

For certain work the right side of the jaw must have been favored to a marked degree. The right condylar articulation was either permanently painful when stressed, which I am inclined to doubt, or what is more likely, there was some mechanical handicap to its use, such as lesions of the ligaments or condylar capsule, causing the animal to rely largely upon the left side of the jaw. It seems certain that this is the proper explanation for the fact that the posterior part of the right temporal muscle was smaller than the left. The fact that the anterior part of the right temporal was larger than the corresponding portion of the left is somewhat unexpected. It would be entirely logical were the temporal muscle divisible into an anterior and a posterior part, but according to Sonntag [8] the division is rather into a superficial and a deep portion. The vacuity of the temporal fossa, inclosed by the zygomatic arch, is shorter and broader (transversely) upon the right side, and as the two zygomatic arches

[8] Sonntag, C. F., The morphology and evolution of the apes and man, London, 1924, pp. 1-364.

are otherwise of equal development, it is impossible now to be sure whether the muscles passing beneath (within) the arch were of greater bulk upon one side than the other, or whether the masseter of one differed somewhat in development from its fellow.

The right coronoid process is about 5 mm. longer than the left, but this is due to the fact that the mandibular notch is correspondingly lower upon that side, and not to differences in the lower-border-to-coronoid measurement. The reasons for this state of affairs are too obscure and complicated for satisfactory interpretation.

At first thought it would appear that the displacement towards the right of the rostrum is attributable to the effect of the teeth of the mandible having been pulled in that direction by the action of the asymmetrical muscles attached to the latter. Although it seems that this hypothesis should be the logical one, a closer scrutiny of the existing state of affairs demonstrates that the rostrum (*i. e.*, the portion of the face craniad to the frontals and orbits) primarily has been deflected towards the right. The reason for this rostral movement is obscure. As there are no powerful muscles connected with this region, it can only be presumed that the displacement was in response to certain muscular forces operating asymmetrically upon the bones with which the rostrum articulates. It is clear that the mandible, through its condylar articulation, has resisted this dextral trend of the rostrum. The lower border of the mandible exhibits a tendency to remain in normal position, while the alveolar margin, in response to the force exerted by the teeth of the rostrum with its dextral twist, is also twisted towards the right.

Extremely grotesque is the skull of a monkey (pls. 1 and 2)—*Lasiopyga griseoviridis* (Desmarest)—for the loan of which I am indebted, through Dr. G. M. Allen, to the Museum of Comparative Zoology. This is a fully adult male (No. 15720, Mus. Comp. Zool.), bearing the data "Sudan, Blue Nile, Magangani, 29 Jan., 1913, Phillips Sudan Ex. 1913, Col. G. M. Allen, J. C. Phillips, orig. 84". Recent injuries, received by the skull at the time when the specimen was collected, consist of the breaking away of a part of the upper alveolar border, including the two left incisors, and injury to the right temporal, including mastoid, auditory and squamous portions. Old osseous scars comprise a fracture of the nasal bridge, which probably has had no effect upon the conformation of the skull, the absence of the right lateral, maxillary incisor, broken off at the root, and the absence of the entire posterior portion of the left ramus of the mandible, including angular process, the whole condyle, and all but the extreme anterior border of the coronoid process. There is no indication of disease, so it is likely that the mandibular fracture was due to an accident of some sort, such as a glancing rifle ball or a long fall. The portions of bones detached were either absorbed, or sloughed off

through an open wound. It is certain that this occurred when the animal was less than half grown, or probably very young.

The injury immediately caused a profound alteration in the mechanism of the lower jaw. As fully half of the bone upon the left side measuring from the last molar to the condyle, was lost, there was no articulation between the mandible and that side of the skull, and the only motion possible was a sort of rotation of the lower jaw. It is certain, of course, that the mouth could be opened sufficiently for the insertion of required food, but it is hardly likely that possible movement was sufficient to enable the animal to use its canines for any practical purpose. The lower canines to some extent, and the upper ones especially, are developed in length well beyond what is normal in this genus. The mandible is further characterized by a stunted or infantile condition of the left ramus, which results in an abnormal, crowded position of the third molar upon that side. The balance of the asymmetry exhibited by the mandible is due to the more normal growth of the right ramus and the twisting effect exerted, through the teeth, by the maxillary deformities.

In considering the form of the skull proper it must first be remembered that the insertions of the left pterygoid muscles have been totally destroyed, and those of the left temporal and masseter, largely so. To just this extent are the effects of these muscles upon the skull destroyed, except as there may have been fractional, aberrant functions through chance secondary attachments.

The supraorbital ridging and the relational position of the two orbits may be said to be the only symmetrical part of the skull The occipital plane also shows practical symmetry, although the basioccipital does not.

The growth of the right side of the skull has been as nearly normal as the limitations of the left side would permit. This has resulted in a disproportionately swollen appearance of the right side of the cranium, and in a sharp twisting of the face to the left. A somewhat fantastic, though expressive, way of describing the present effect is to imagine the juvenile skull as having been made of soft rubber, held rigid in the vicinity of the left zygomatic process of the maxilla, and the rest of the skull then inflated and expanded. This appearance, as previously mentioned, has been attained through nongrowth of the left side. All parts of this side have remained infantile, especially the length of the zygomatic arch, which has ensued upon the virtual destruction of functions of the muscles of mastication upon the left side.

One result of the infantilism of the maxillary border upon the left was the failure of the alveolar row to increase in length, with the consequence that insufficient room was provided for the normal emplacement of the permanent first molar. This has resulted in the

inward and upward growth of the roots of the tooth and the alteration of its shape.

Of significance is the practical nondevelopment of the outer pterygoid plate upon the left, following the destruction of function of the muscles normally attached to it. A more detailed description of the individual bones of the skull, although of interest, is hardly sufficiently instructive for presentation here.

ASYMMETRICAL SKULLS OF PINNIPEDS

It is through the kindness of Dr. J. Grinnell that the writer has been enabled to study the pathological skull of a sea lion from the collection of the Museum of Vertebrate Zoology (pls. 5, 6, and 7). This is a male specimen of *Eumetopias jubata* (Schreber), adult but not aged, and evidently somewhat stunted by its condition. It now bears the data "No. 4964, Museum of Vertebrate Zoology, July 2, 1907, Ana Nueva Id., California, John Rowley, 257." In asymmetry it is far more spectacular than the skull of the gorilla already discussed, but its condition is considerably easier of interpretation.

The specimen was probably shot, as evidenced by a hole in the right frontal and a larger one obliquely opposite within the orbit. In addition it seems that the skull has since been dropped upon a hard surface, for the cranium is badly fractured. John Rowley, the collector of the specimen, writes (MS) that it "was apparently as fat and husky as any of the others." The only evidence of old scars upon the skull is to be found in the posterior half of the left zygomatic arch, and upon the medial portion of the left glenoid fossa. It is possible that there was also partial fracture along the suture formed by the left jugal with the maxilla, for this is now obliterated, whereas it is strongly defined upon the opposite side.

Although no full tables of measurements of the four skulls herein discussed have been thought necessary, a number of the most significant ones of the abnormal sea lion, compared with a normal one which is somewhat larger, but probably of about the same age, are found to be of interest.

		Injured male	Normal male
		Mm.	*Mm.*
Total length		331	369
Rostral width		96	88
Exoccipital to anterior border of canine	right	295	313
	left	258	
Length of jugal	right	150	150
	left	127	
Total length mandibular ramus	right	267	278
	left	249	

It is clear that the original injury was received by the animal when the bones were extremely plastic. It is equally apparent that the injury was in the nature of a smart blow upon the side of the head, such as might have been received by a fall from a ledge upon a sharp rock some distance below.

The occipital bone is entirely symmetrical, but this, perhaps with the pterygoids, is the only portion of the skull of which this may be said.

Beginning at the point of original injury, it is seen that the jugal has been fractured in at least one and possibly two places. This, however, as well as the distal end of the zygomatic process of the squamosal, is now so distorted that but little can be told from it. That the injury took place during the very early life of the animal can be seen not alone by the general distortion, but from the fact that the left zygomatic arch is very much stunted; not that it is shortened, of course, but that it has failed to grow at anywhere near the normal rate. An examination of the glenoid fossa upon this side discloses the fact that the medial portion of its concavity is granular and distorted in form. There was assuredly further injury at this point, and some sort of fracture or derangement of the precise relationship between the bones immediately caudad, so that they failed to grow at the normal rate. This certainly seems to be the sole extent to which the skull was directly injured, all other details of asymmetry having been due to indirect influences.

An early and complete fusion of the adjacent sutures evidently followed the injury to the last-mentioned region, which resulted in a permanent stunting of this portion of the skull. The left auditory and petrous part of the temporal are especially affected, being small and misshapen. The resistance to growth may have been augmented by the pressure of the left mandibular ramus against its glenoid fossa, caused by increasing displacement of the rostrum, although this was not the primary factor in causing the condition. The distance between the left zygomatic process of the squamosal and the normal mastoid is but 4.5 mm., while the same distance upon the right side measures 18 mm. As the mastoids, occipital, and lambdoidal crests are entirely normal, or at least symmetrical, it is seen that there is a sharp bending of the cross axis of the skull, through the glenoid fossae, of four degrees. This, carried at right angles to the anteriormost point of the mandibular symphysis, would show a lateral deflection from the normal axis of the skull (as projected at right angles to the occipital plane) of about 20 mm., even were there no other asymmetrical forces operative. As a matter of fact, other conditions have contributed to increase this deflection so that it actually approximates 65 mm., as near as can be calculated.

The above theoretical deflection of the symphysis by 20 mm. is purely mechanical in character. All the remaining forces of asymmetry that have operated to alter the skull are either myological or developmental (growth of bone).

An examination of the superior aspect of the skull indicates that in comparison with normal crania the one under discussion seems to be unusually small, as well as can be judged from general criteria of age. Not only is it short, but the sagittal crest is more poorly developed. The cephalic musculature was therefore undoubtedly below normal, although one may presume that it was entirely adequate for the feeding needs of the animal.

The sagittal crest is displaced about 10 mm. toward the left, but with this exception there is no decided indication that the posterior portion of the right temporal muscle was more powerful than that upon the left. There is striking evidence to this effect, however, in the anterior part of the right temporal fossa. As clearly shown in the illustration, this portion of the right temporal was several times the larger, not only displacing the sagittal crest but extending well forward upon the frontal and modifying the shape and size of the right supraorbital process. The sinistral displacement of the rostrum is largely attributable to the disproportionately great development of this part of the muscle, coupled with the fact that the right zygomatic arch and masseter were free to accomplish anterior growth. On the other hand the stunting of the left zygomatic arch resisted normal growth of the left half of the skull, and necessarily limited the size of the mass of muscle that could pass within the zygomatic vacuity of the temporal fossa. These would seem to be the two causes that tended to limit the growth to the left temporal muscle, while the reduced length of the zygomatic arch upon that side prevented normal growth, and undoubtedly strength, of its attached masseter. Thus, during the development of the animal, the root or base of the left side of the rostrum was held back, while that of the right side was pushed forward, resulting in the great displacement toward the left exhibited by that part of the skull. Another consequence has been the disproportionate, dextral bowing of the mesethmoid, and undoubtedly of the cartilaginous septum, which resulted in a crowding of the right ethmoid and, therefore, expansion of the left nasal passage, from which the ethmoid is now missing. This whole process has naturally effected a disproportionate development of the individual bones of the rostrum which is of interest; but there is no necessity here for dwelling at greater length upon their individualities.

Returning to an examination of the mandible, one notes that there is no indication of asymmetry in its muscular insertions. It is clear, however, that the displacement of 20 mm., caused by the shifting

of the left glenoid fossa, has been much augmented by the rostral twist. In fact the latter is so great that the mandible has resisted it, through the interlocking of the teeth. Thus, the mandibular canines have been forced to incline toward the left, while the maxillary canines and lateral incisors have been pushed toward the right. The result is that although the rostrum as a whole turns strongly to the left, the anterior portion of its alveolar border exhibits a slightly dextral counter twist. The mandible reflects the varied stresses in a form difficult to describe with accuracy, but to attempt to do so is hardly necessary.

Another skull of *Eumetopias jubata* showing some asymmetry was also discovered. This is No. 131895 of the United States Biological Survey collection, and bears the data "♀, California, Santa Cruz Id., W. J. Hockmeier, 4386X." It is of an adult, though not aged individual (pl. 8). The original cause leading to present asymmetry was a pathological condition of the left auditory and petrous temporal, which are now misshapen, with rough surfaces, and a large perforation inferiorly. An abscess probably constituted the original cause. The result has been a stunting of the region involved, and the distance from craniad of the glenoid fossa to the paroccipital process is 7 mm. less upon this side than the right. The zygomatic arches are also involved, probably through lack of normal growth of this process of the left squamosal, for the left arch is about 6 mm. shorter than the other. This, in turn, has evidently been instrumental in limiting the growth of the anterior portion of the temporal muscle, as clearly shown by the differences in the development of the supraorbital processes and the ridging between them. The remainder of the temporal fossae do not show any appreciable disparity, however.

Very slight asymmetry exhibited by the posterior half of the rostrum is probably due to dissimilarity in the development of the two zygomatic arches and the temporals, while the decided sinistral twist of the rostral extremity is attributable, through the interlocking of the canines, to the displacement of the left glenoid fossa, and hence, the mandible.

An interesting point which can hardly be explained entirely by the foregoing conditions is asymmetry in the occipital region. This is precisely the opposite of what might be expected, for the distance between the foraminal margin of the occipital condyle and the paroccipital process is, upon the left, 61, and on the right, 54 mm. It is due to growth of the left paroccipital process and the exoccipital rather than to displacement of the foramen magnum. One might hazard the opinion that it is the result of a compensating development of the attached muscles, as the digastric, or to some pathological

condition of the cervical region; but all such hypotheses are pure speculation.

CONCLUSIONS

From the study of these four specimens it has been concluded that the primary cause inducing asymmetry in the skulls of mammals other than toothed cetaceans is probably, in most instances, by accident or disease, to the bones or muscles of a single side of the head at a comparatively early age, and that this must be of such a character as to result in a stunted or infantile condition of a crucial part of the bony framework, and a reduction in the rate of growth, or strength through lesions, of the muscles of a single side. Asymmetry usually is directly dependent upon unevenness in the strains developed upon the two sides of the head while an animal is eating.

Certain injury to the bones of the head causes a premature obliteration of the sutures, as already indicated. Published data respecting human crania have shown that such early obliteration of the sutures may also occur from obscure causes without violence having been suffered by the individual. It is doubtless fortuitous that no skulls of this character have been available in the present study. Conversely, it is known that retarded obliteration of certain sutures beyond the usual time for their disappearance results in the hypertrophy of the corresponding part of the skull. It is only a question of time before material illustrating the latter point in the mammalia other than man is brought to light.

One of the most conspicuous results of this investigation, and one that deserves to be stressed, is the conclusion that normal development of the bones of the skull is directly dependent upon the growth of the attached muscles. In other words, if for any reason the muscles of an animal remain infantile and fail properly to grow, the bones to which they are secured will remain proportionately undersized. This assertion can not be proven in the case of the masseter muscles until the myology of asymmetrical skulls can be more fully investigated. It is also apparent that the smaller the origin or fossa of a muscle the smaller must the muscle itself be.[9] The significance of these facts, when considered with reference to specific (and higher) variation of the skull, is profound.

It is apparent that asymmetrical development of a skull inclines to progress both forward and backward from a center that is rather uniform. In other words, it always appears as though a part of the skull were held stationary while the portions craniad and caudad

[9] Of interest in this connection is a paper by J. A. Howell (An experimental study of the effect of stress and strain on bone development, Anat. Rec., vol. 13, 1917, pp. 233–252) comparing the leg bones of a dog, the muscles upon one side of which had been transected when the animal was very young. The diameter of the bone was very greatly diminished thereby, but its length was but little below normal.

were both forced either to the right or to the left. This center is not precisely the anterior one of the three segments of the cranium proper, as has been claimed,[10] but the "dead center" may be considered as passing through the frontals above and palatals below. Either of these pairs of bones may vary somewhat in accordance with the portion of the skull either craniad or caudad thereto, according to whether the more powerful influence lies in one direction or the other. In the four skulls examined the original seat of injury has been in the neighborhood of one of the glenoid fossae.

It is difficult, if not impossible, to speculate with any degree of certainty upon the relative development of the temporals and masseters, considered as separate muscles, because of their extreme interdependence. The previous condition of the masseters can only be deduced from the configuration of the zygomatic arch. Reduction in the size of one temporal muscle is not necessarily followed by a smaller zygomatic arch, and therefore by inference, a smaller masseter upon that side; but reduction, for any reason, of the size of the arch does seem to result in a lessened volume of the adjacent temporal muscle.

The interrelationship of the anterior with the posterior portion of the temporal muscle is somewhat obscure, but fluctuations in the size of this muscle are not necessarily uniform for the two parts. The size of the anterior portion of the temporal fossa—lying immediately adjacent to the supraorbital processes in carnivores—may be very much larger, indeed, upon one side when the posterior portion—overlying the brain case proper—is but a trifle more extensive than upon the opposite side. The explanation of this fact is believed to be that the extreme cranial portion of the temporal muscle is the part that is used in contributing the ultimate contracting power of which the jaw muscles are capable. As this final force can hardly be applied upon the weaker side of the head, because of pain or mechanical disability, nondevelopment of the anterior part of the temporal muscle upon that side of the cranium results. Certain it is that a disparity in the development of the anterior, as compared with the posterior, part of an abnormal temporal fossa recurs sufficiently often to indicate a substantial difference in the precise functions of the two corresponding portions of the temporal muscle.

The pterygoid plates and fossae naturally reflect the development of the pterygoid muscles, and a smaller plate upon one side means that the muscles attached thereto were correspondingly weaker.

Asymmetrical development of the rear half of the skull—at least of the superior portion—is closely correlated with size and strength

[10] Howell, A. B., Individual and age variation in Microtus montanus yosemite, Journ. Agric. Research, vol. 28, 1924, pp. 977–1016.

of the temporals and masseters, but such a condition of the face,[11] when marked, can not be due primarily to myological stimuli. It may be attributable first to a setting out of plane, through nongrowth of one side, of the bones with which the rostrum articulates, as a house may be thrown out of plumb by the settling of one side of its foundation; or it may be due to the pull, through the interlocking of the canines, primarily exerted by a glenoid fossa, and hence the mandible, which has been displaced.

Asymmetry of the occipital plane may be ascribable in part to differences in the size of the lambdoidal crests induced either by the temporal muscles, or by variation in certain of the cervical muscles, or both. As only the insertions, and not the origins, of the latter are available for examination, interpretation of the few facts presented is difficult.

The form of an asymmetrical mandible is determined mostly by the positions of the glenoid fossae at one extreme, and by the force that may be exerted by the interlocking canines at the other. Variation in size between the mandibular processes of the two rami is not likely to be as great as are certain asymmetrical differences in the skull proper. In other words, the muscular origins seem to be more sensitive to asymmetrical influences than are their insertions. Asymmetry of the mandible, in fact, seems to be due chiefly to mechanical stimuli.

[11] For convenience the posterior portions of the zygomatic processes of the maxillæ are here considered as not belonging to the face proper.

EXPLANATION OF PLATES

Plate 1

Upper figure, dorsal view of mandible; and lower figure, ventral view of asymmetrical skull of monkey—*Lasiopyga griseoviridis* (No. 15720, Mus. Comp. Zoöl.).

Plate 2

Upper figure, frontal view; and lower figure, dorsal view, of asymmetrical skull of *Lasiopyga griseoviridis.*

Plate 3

Ventral view of asymmetrical skull of gorilla—*Gorilla beringei mikenensis* (No. 239883, U. S. Nat. Mus.).

Plate 4

Upper figure, right, lateral view of maxillary molars; and lower figure, dorsal view, of asymmetrical skull of gorilla.

Plate 5

Upper figure, frontal view of asymmetrical skull of gorilla. Lower figure, frontal view of asymmetrical skull of male sea lion—*Eumetopias jubata* (No. 4964, Mus. Vert. Zoöl.).

Plate 6

Upper figure, dorsal view of mandible of asymmetrical gorilla. Lower figure, dorsal view of asymmetrical mandible of male sea lion (No. 4964, Mus. Vert. Zoöl.).

Plate 7

Upper figure, dorsal view; and lower figure, ventral view, of asymmetrical skull of male sea lion (No. 4964, Mus. Vert. Zoöl.).

Plate 8

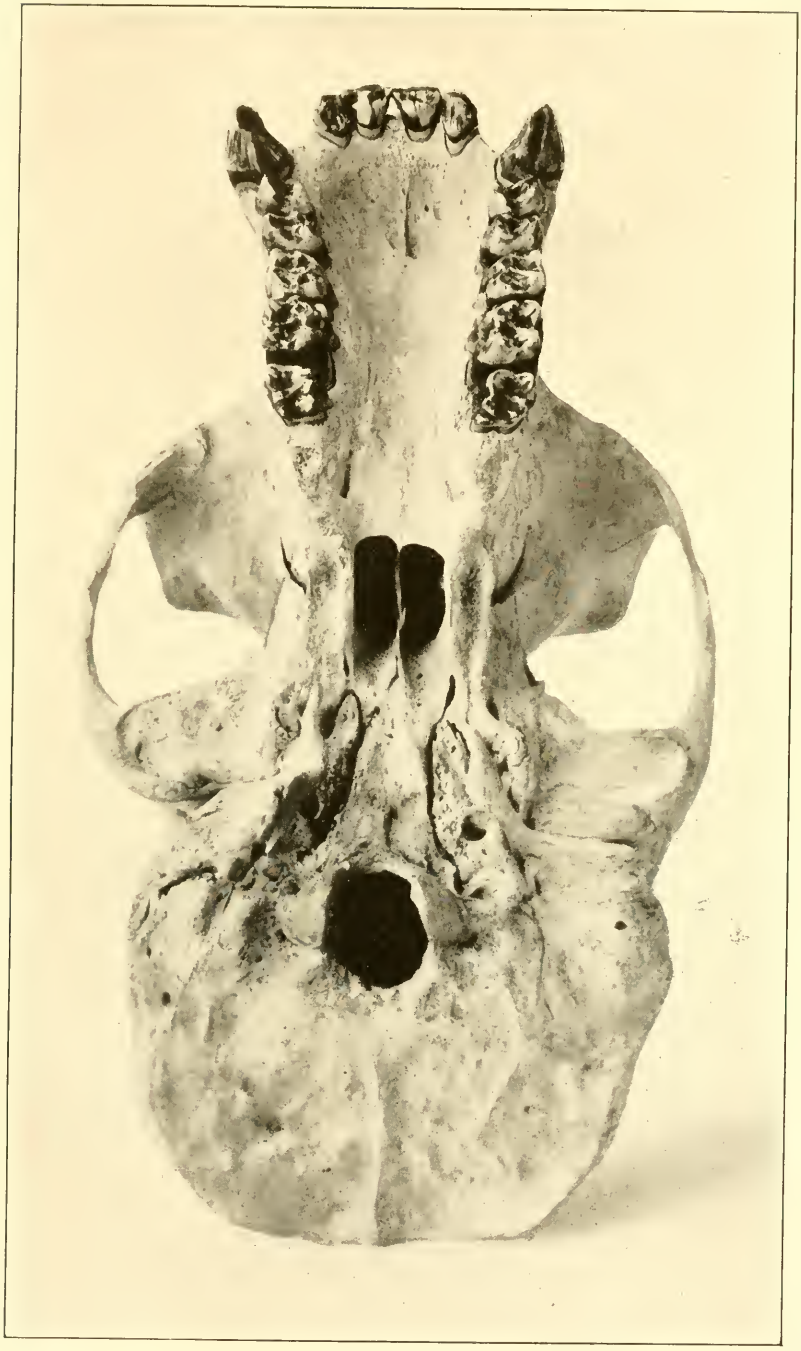
Upper figure, dorsal view; and lower figure, ventral view, of asymmetrical skull of female sea lion—*Eumetopias jubata* (No. 131895, Biol. Surv. coll.).

SKULL OF MONKEY, LASIOPYGA GRISEOVIRIDIS

FOR EXPLANATION OF PLATE SEE PAGE 18

SKULL OF MONKEY, LASIOPYGA GRISEOVIRIDIS

FOR EXPLANATION OF PLATE SEE PAGE 18

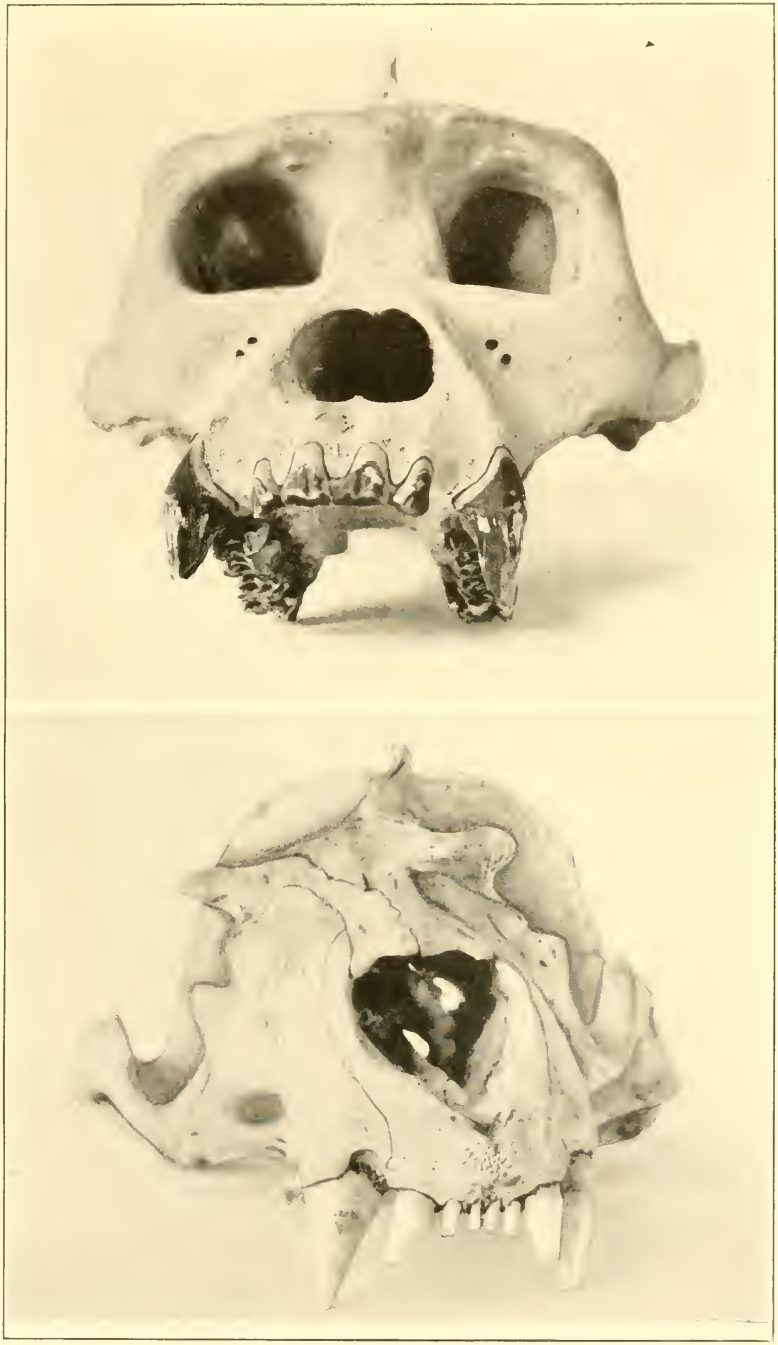


SKULL OF GORILLA

FOR EXPLANATION OF PLATE SEE PAGE 18

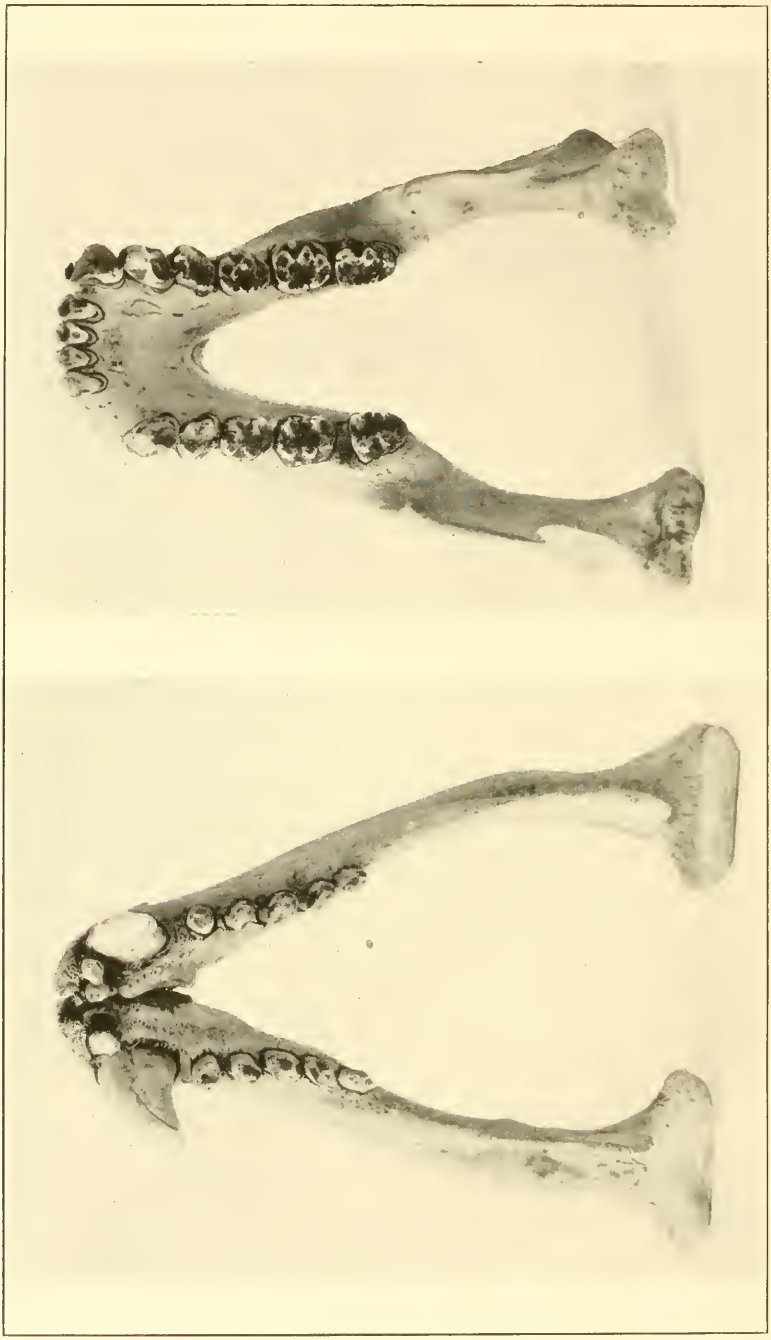
TEETH AND SKULL OF GORILLA

FOR EXPLANATION OF PLATE SEE PAGE 18



SKULLS OF GORILLA AND SEA LION

FOR EXPLANATION OF PLATE SEE PAGE 18



MANDIBLES OF GORILLA AND SEA LION

FOR EXPLANATION OF PLATE SEE PAGE 18

SKULL OF MALE SEA LION

FOR EXPLANATION OF PLATE SEE PAGE 18

SKULL OF FEMALE SEA LION

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