A STUDY OF THE ENDOCRANIAL CASTS OF OCAPIA, GIRAFFA AND SAMOTHERIUM, WITH SPECIAL REFERENCE TO THE CONVOLUTIONAL PATTERN IN THE FAMILY OF GIRAFFIDAE

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TWENTY-FIVE FIGURES

Introduction.....	329
Description of specimens.....	331
(a) <i>Giraffa camelopardalis</i>	331
(b) <i>Ocapia johnstoni</i>	336
(c) <i>Samotherium</i>	341
Types of fissural pattern on the lateral surface of the cerebrum in ungulates..	346
Discussion.....	352
Conclusion.....	355
Literature cited.....	356

INTRODUCTION

While the skeletal parts and especially the skulls of the okapi and giraffe have been carefully examined and compared in detail in the effort to determine the relationship of these living forms to one another and to the fossil Giraffidae, no attempt has been made to utilize such evidence as may be gleaned from a study of the endocranial casts.

In the present paper an effort has been made to place such data upon record in a more detailed fashion than was possible in the preliminary notes published as an abstract in the Proceedings of the American Association of Anatomists, December, 1914 (3).

The superficial convolutional pattern of the convex surface of the cerebrum in many of the lower gyrencephalous Mammalia is quite accurately reproduced by the corresponding irregularities upon the internal surface of the skull. This is especially the case,

for example, among the ungulates which I have studied in the preparation of this paper.

It is of interest to note in this connection that, in the skulls of gyrencephalous mammals of the sub-order Anthropoidea, the *juga cerebralia* and *impressiones digitatae* are much less evident than in the forms about to be described, while in man the value of endocranial markings in the determination of convolitional pattern has recently been seriously questioned (28).

Various factors must contribute to produce these different types of skull growth which are characteristic of different mammalian orders, and it would be irrelevant here to discuss this interesting question in any detail. However, as I have elsewhere mentioned, there can be no doubt that among the factors which combine to cause the condition obtaining in ungulates, the following, more especially the second, are most important: (a) the habitual position of the head in relation to the action of gravity and (b), the early maturation of growth processes in the encephalic portion of the skull.

With regard to my material, I wish to make again the following acknowledgments.

One endocranial cast of an adult okapi and one of an adult giraffe were obtained in Manchester through the courtesy of Prof. G. Elliot Smith, upon whose advice this study was undertaken. The second specimen from an adult okapi together with that from *Samotherium* was obtained through the courtesy of Dr. Smith Woodward from the Museum of Natural History at South Kensington, London. I am indebted also to Prof. Arthur Keith for the opportunity of studying the giraffe brains in the Museum of the Royal College of Surgeons, and to Dr. C. U. Ariëns Kappers for the like privilege of studying the ungulate and other material in the collection of the Central Dutch Institute for Brain Research in Amsterdam.

To Prof. Elliot Smith and Dr. Ariëns Kappers, I am further indebted for the helpful criticism of my earlier report.

DESCRIPTION OF SPECIMENS

(a) *Giraffa camelopardalis* (figures 1 to 3 and 17 to 19)

As the morphology of the giraffe brain is well known through the work of Krueg (22), Elliot Smith (9) and others, and the osteology of the skull has received special attention in the memoirs of Sir Ray Lankester (23 and 24) and Julien Fraipont (17), this cast affords excellent material upon which to begin the present study.

Only a few accurate observations upon the weight of the brain and the total body weight of the giraffe have been recorded. I quote the following figures from Max Weber (29).

	<i>Body Weight</i>	<i>Brain Weight</i>	<i>Ratio</i>
(1) Male, two months old....	150,000 grams	389 grams	1: 392
(2) Male, young adult.....	300,000 grams	420 grams	1: 761
(3) Male, adult.....	529,000 grams	680 grams	1: 777

The volume of the cast described here is 650 cc., but no record as to the total body weight of this specimen could be obtained. Taking it for granted that the specific gravity of nervous tissue in the giraffe is but little different from that in man, the approximate calculated weight of this brain would be 575 grams.

A study of the data recorded by Weber for the giraffe and of the ratios which obtain between the brain and body weight in the horse as cited by Flatau and Jacobson (12¹), makes it evident that, in these two species the relationship of brain weight to body weight is approximately the same in adult animals of equal bulk.

The transverse diameter of the cast is greatest in the parietal region, where it measures 116 mm. across. From the basi-

¹ The further statement of these authors (l.c., p. 527) that the volume of the brain compared with that of the skull is lower among ungulates than in any other group of mammals is of interest. In this heterogeneous group the ratio varies from 1:7 in the horse up to 1:10 in the elephant. This phenomenon may be correlated to some extent with the presence in certain members of the group of heavy defensive head appendages. However, it is much more probably the direct result of the herbivorous habit common to all these animals, which has given rise to the acquisition of a complicated dental mechanism and *pari passu* along with this, a facial development for its accommodation.

occipital or pontine surface to the highest point over the vermis the measurement is 70 mm. From the frontal to the occipital pole of the cerebrum the maximum length is 120 mm. The greatest diameter between the floccular areas of the cerebellum is 57 mm.

Brain stem, cerebellum and basis cranii. In a ventral view (figs. 1 and 17), the relation of the large sessile olfactory bulb (*B.O.*) to the tractus olfactorius (*Tr.O.*), is well shown. Between the diverging lateral and mesial olfactory tracts, which in the recent state occupy special bony grooves, a small prominence represents a depressed area in the skull floor for the lodgment

ABBREVIATIONS

<i>Ar.Floc.</i> , floccular area	<i>R. ant. ectosylv.</i> , ramus anterior ectosylvii
<i>Ar.Lat.</i> , lateral area of interfloccular mass	<i>R. desc. ss.</i> , descending ramus of the sulcus suprasylvii
<i>Ar.Pyr.</i> , pyriform area	<i>R. post. ectosylv.</i> , ramus posterior ectosylvii
<i>B.O.</i> , protuberance corresponding to fossa for lodgment of bulbus olfactorius	<i>R. post. ss.</i> , posterior ramus of the sulcus suprasylvii
<i>For. Condyl.</i> , protuberance corresponding to condylar foramen	<i>S. ans.</i> , sulcus ansatus
<i>For. Lac.</i> , irregularities marking site of foramen lacerum basis cranii	<i>S. arc.</i> , arcuate constellation
<i>M.A.I.</i> , elevation indicating position of internal auditory meatus	<i>S. cor.</i> , coronal sulcus
<i>Md. V.</i> , protuberance corresponding to foramen ovale transmitting the mandibular division of the trigeminal nerve	<i>S. diag.</i> , diagonal sulcus
<i>Mx. V.</i> , protuberance which apparently corresponds to the foramen rotundum for the passage of the maxillary division of the trigeminal	<i>S. ent. lat.</i> , entolateral sulcus
<i>Oph. V.</i> , protuberance corresponding to foramen lacerum orbitale	<i>S. lat.</i> , lateral sulcus.
<i>Oph. & Mx. V.</i> , protuberance corresponding to skull groove lodging the first two divisions of the trigeminal nerve in their passage to a common exit at the foramen lacerum orbitale	<i>S. obl.</i> , oblique sulcus (of Holl)
<i>Post. Rh. Fiss.</i> , posterior rhinal fissure	<i>S. presylv.</i> , presylvian sulcus
	<i>S. Ps.</i> , pseudosylvian fossa—processus acuminis
	<i>S. suprasylv.</i> , suprasylvian sulcus
	<i>S. trirad. post.</i> , triradiata posterior of Kappers
	<i>T.O.</i> , elevation corresponding to fossa lodging tuberculum olfactorium
	<i>Tr.O.</i> , ridge indicating skull groove for lodgment of the tractus olfactorius
	<i>Vermis</i> , median area of interfloccular mass
	<i>II.</i> , tubercle corresponding to the position of the optic foramen

of the tuberculum olfactorium (*T.O.*). Behind this area a transverse groove caused by the posterior margin of the lesser sphenoidal wing marks the caudal limit of the anterior cranial fossa. The position of the optic foramina (*II.*) is indicated on each side of the cast by two dorso-ventrally compressed prominences, behind the trigonum olfactorium.

In the giraffe, as in the sheep and cow, the foramen lacerum orbitale and foramen rotundum form one large opening into

Figs. 1, 2 and 3 Outline drawings of endocranial cast of *Giraffa camelopardalis*, ventral, dorsal and right lateral views respectively. For lettering see list of abbreviations page 332. For the photographs from which these outlines were taken, see figures 17 to 19. About $\frac{1}{2}$ natural size.

which pass the ophthalmic and maxillary divisions of the fifth nerve together with the oculomotor, trochlear and abducent nerves. The prominence labeled *Oph. & Mx.V* represents a deep skull groove, the floor of which is occupied in the recent state from the medial to the lateral side respectively, by the ophthalmic and maxillary divisions of the trigeminus. The rostral limit of this prominence corresponds to the position of the anterior lacerated foramen. The site of the foramen ovale transmitting the mandibular division of the trigeminus and the slight groove occupied by this root, is indicated in the figures by the legend, *Md.V*. From the base of this "mandibular" elevation a ridge is evident in figures 3 and 19, passing dorso-caudally, which represents a skull groove along the attached border of the tentorium. This groove leads into the parieto-temporal canal (meatus temporalis) and in the recent state is occupied by the vena cerebialis dorsalis, which is in turn continuous with the transverse sinus.

The internal auditory meatus for the passage of nerves VII and VIII is indicated by a circumscribed elevation capped by two bosses and situated about 10 mm. behind the base of the tentorial ridge. The VII and VIII eminence is placed in the middle of a somewhat depressed area which is moulded by the periotic bone. Inferiorly, this area terminates at the foramen lacerum basis cranii. Through this foramen in the recent state pass the internal carotid artery, the middle meningeal artery, the IX, X and XI nerves and the inferior cerebral vein. The position occupied by this foramen is indicated in the cast by the irregular ridges on each side of the basi-occipital or pontine region.

No indication as to the relative development of the pons and corpus trapezoides can be obtained from the cast. These structures are apparently separated from the floor of the bony cranium as in the cow, by a bridge of dura beneath which is lodged the plexus of the basilar sinus.

The position of the condylar foramen is evidenced by a slight elevation on the lateral, caudo-ventral surface of the cast.

This cast gives but little information as to the morphology of the cerebellum save to indicate the presence of cake-like flocculi.

cular lobes common in ungulates. The large interfloccular mass exposed between the caudally diverging cerebral hemispheres shows no evidence of division into medial and lateral areas.

Cerebral hemispheres. Upon the convex cerebral surface of the cast, the marks left by the cerebral ridges and digital impressions are so distinct, that the convolutional pattern may be interpreted clearly.

Dorsally (figs. 2 and 18) the relation of the lateral sulci to the suprasylvian arc is well shown. The coronal is caudally connected with the ansate sulcus, a common ungulate condition. This ansate sulcus is in no way to be compared with the somewhat similarly placed cruciate sulcus peculiar to carnivores.

The posterior rhinal fissure (figs. 1 and 3) limiting the pyriform area laterally, is well marked. Rostrally the anterior rhinal fissure is not so clearly indicated but may be made out as the ventral limit of a depressed area from whose dorsal boundary the ramus anterior ectosylvii emerges.

The presylvian sulcus, rostral to the ramus anterior ectosylvii may readily be identified but its continuity with the anterior rhinal fissure is not evident.

In my preliminary report (l. c.) I used Campbell's term "orbital sulcus" together with the term "paraorbital sulcus" to designate the "presylvian sulcus" and the "ramus anterior ectosylvii" respectively. The latter terms are more desirable, as both Kappers and Elliot Smith have shown that the so-called "orbital sulcus" of carnivores and ungulates is not in any way homologous to the sulcus bearing this name in primates. Furthermore Kappers has pointed out (21, p. 348) that the sulcus termed presylvian nearly always represents the caudal boundary of the area granularis frontalis and forms a line of demarcation between this area and the area giganto-pyramidalis or agranularis frontalis. If the term 'orbital sulcus' be discarded, it is obvious that the term 'paraorbital' has also lost its original descriptive significance, while the term 'ramus anterior ectosylvii' indicates at once the true relations of this sulcus.

The diagonal sulcus which is well marked on both sides shows no connection with the suprasylvian.

The whole course of the suprasylvian sulcus may be seen in a lateral view of the cast. In addition to the posterior horizontal limb common in ungulates, a long descending ramus of the suprasylvian sulcus is to be noted. This sulcus is probably not homologous with the postsylvian sulcus of carnivores, in which forms this sulcus is only separated from the lateral group of sulci by a comparatively small area.

The area ventral to the horizontal limb of the suprasylvian sulcus in the giraffe, as in the other ungulates, is of considerable extent, and is marked by two fairly constant sulci; the oblique sulcus of Holl and the constellation termed by Kappers the *tri-radiata posterior* (l.c., p. 309).

The pseudosylvian fossa is clearly indicated by a Δ -shaped, depressed area, the apical prolongation of which has been termed the *processus acuminis*. The caudal operculated lip of this fossa is notched by two or three slight compensating sulci and terminates in a well marked *ramus posterior ectosylvii*.

Between the *processus acuminis* of the pseudosylvian fossa and the suprasylvian sulcus, a well marked arcuate fissure is situated. This constellation is present on both sides of the cast and is indeed one of the characteristic features of the giraffe brain. It will subsequently be shown that this arcuate constellation is of distinct diagnostic importance when present together with the form of *ramus descendens suprasylvii* here described.

(b) *Ocapia johnstoni* (figures 4 to 6 and 20 to 22)

This member of the family Giraffidae was first discovered in the Belgian Congo in 1899. No material other than the skin and skeleton has as yet been available for scientific study. The facts relating to the discovery of this animal, together with notes upon its mode of life and detailed descriptions of its skeletal parts, may be had in the memoirs of Ray Lankester and Fraipont (l.c.).

In my preliminary report (l.c.) this animal was referred to as a 'hornless' form, and indeed the description in Beddard's text

(2, p. 305) states that 'there are no external horns.' This however is quite incorrect, for paired horns are present in the male though only represented by hair tufts in the female (18).

The volume of the endocranial cast is 450 cc.

As in the giraffe the greatest transverse diameter of the cast is in the parietal region, where it measures 100 mm. across. From the pontine surface to the highest point over the vermis the cast

Figs. 4, 5 and 6 Outline drawings of endocranial cast of *Ocapia johnstoni*, ventral, dorsal and right lateral views respectively. Abbreviations, see page 332. For photographs from which the outlines were taken, see figures 20 to 22. About $\frac{1}{2}$ natural size.

measures 67 mm., which is but little less than the corresponding distance in the giraffe. From the frontal to the occipital pole of the cerebrum, the maximum length is 106 mm. The greatest interfloccular diameter is 55 mm.

Brain stem, cerebellum and basis cranii. The appearance of the cerebellar portion of the cast is of interest for, in contrast to the giraffe, its configuration is such as to yield some accurate information concerning the morphology of the interfloccular mass.

The two endocranial casts of this animal in my possession differ from each another considerably in the clearness with which the so-called vermis area is demarcated. Thus there is an individual variation in this region in the okapi. This, however, may be accounted for readily when the condition which obtains in this region of the skull among other ungulates is considered.

Le Double (25, p. 45) has pointed out that the inner surface of the skull in mammals in general is often moulded in its caudal part by the cerebellum to form three fossae: a median one for the lodgement of the median lobe ('fossette cerebelleuse moyenne'), and two lateral ones for the lateral cerebellar lobes. This median fossa is present in many ungulates. In these forms this author further notes (p. 49) that caudally the falx cerebri may ossify at its junction with the tentorium and give rise to a projection, the inferior surface of which is concave and continuous with the median cerebellar fossa. This projection overlaps the vermis to such an extent among the Equidae that it has been described by Albrecht (1) as the 'operculum of the vermis.'

Ossification of the tentorium, though common in adult Carnivora, is rare in ungulates, especially in artiodactyles. In the latter group no indication of Albrecht's operculum was observed in the skulls collected in the anatomical museum of this department except among the Cervidae, in which it was only indicated in the skulls of old animals (*Cervus canadensis*).

From this it is reasonable to infer that the difference in the appearance of the vermis region in the two okapi casts in my possession is one due to age.

The prominent asymmetrical boss formed in the mesial plane by the median lobe of the interfloccular mass is distinctly outlined and is separated by a well marked furrow from the less prominent lateral areas of this mass. Rostrally the median protuberance ends abruptly in a depression occupied in the recent state by the junction of the falx cerebri and the tentorium cerebelli. The lateral cerebellar swellings apparently correspond to those portions described by Elliot Smith (10) as Area B of the interfloccular mass (=Crus I of Bolk, 4). These lateral areas are placed dorso-caudal to the floccular region, from which they are only separated by an indistinct groove. On the whole it may be said that, in its general morphology, the cerebellar portion of this cast recalls the condition obtaining among the Cervidae.

Unlike the condition found in the giraffe, the olfactory bulbs in okapi are pedunculated and project a considerable distance beyond the frontal poles of the cerebrum. The fossae lodging the olfactory tracts are well developed.

It should be noted here that the asymmetry of the portion of the cast representing the olfactory bulbs and tracts and optic nerves is due to the defective restoration of these parts after they had been damaged on the left side.

As the remaining structures represented in the basal portion of the cast differ in no important detail in their general relations from those already described in the giraffe, further description of this region may be dispensed with.

Cerebral hemispheres. The arrangement of the sulci appearing upon the dorso-lateral surface of this cast gives evidence of a close relationship between the okapi and the giraffe. The arcuate constellation and the arrangement of the lateral group of sulci in the okapi are essentially similar in their relations to the corresponding furrows already noted in the giraffe. There are, however, not a few significant differences, to which attention will be drawn in the following description.

Dorsally (figs. 5 and 21) the relations of the lateral sulci to the coronal and suprasylvian are evident and present no unusual feature. However, the changed relations of the coronal, ansate

and suprasylvian sulci, together with the diagonal, are worthy of note. In the okapi, as is usually the case in the Cervidae and often in other ungulates, the ansate sulcus joins the coronal to the suprasylvian.

The suprasylvian is also continuous with the diagonal on the right side (fig. 6), though this is not the case on the left.

The continuity of the suprasylvian and the diagonal sulci is a common phenomenon among ungulates, appearing in both the Perisodactyla and Artiodactyla (figs. 10 to 16) and also among carnivores (11). This is regarded by Kappers as evidence that the diagonal sulcus is originally an anterior branch of the suprasylvian.

Thus the continuity of the suprasylvian and diagonal, which occurs on the right side, and the junction of the coronal and suprasylvian by the ansate, which occurs on both sides, represent, in the okapi, generalized ungulate characteristics which have been retained.

Laterally, the posterior rhinal fissure and the pyriform area lying below it may be clearly seen, but the anterior rhinal fissure cannot be definitely distinguished.

The pseudosylvian fossa is represented on the surface by a short vertical fissure and, as the frontal operculum is well developed, only a very small part of the anterior ectosylvian sulcus is visible.

The presylvian sulcus is large and extends frontad till it almost reaches the coronal, from which it is only separated by a narrow space.

The broad area between the short processus acuminis of the pseudosylvian fossa and the quite dorsally placed suprasylvian sulcus, is marked by a well developed arcuate constellation.

The descending ramus of the suprasylvian sulcus is well developed and differs from the sulcus bearing this name in the giraffe by being more caudally placed and by cutting the rhinal fissure. This communication with the rhinal fissure is apparently brought about by a junction of the descending ramus with the upturned ramus posterior ectosylvii, behind the caudal pseudosylvian operculum.

In the Cervidae and in other forms where the descending ramus of the suprasylvian is usually small, the oblique sulcus is large, and passes forward into the region which is occupied in the giraffe by the large descending ramus suprasylvii (figs. 10 and 12). Also in Cervidae, this oblique sulcus often cuts the posterior rhinal fissure, either independently or by joining the ramus posterior ectosylvii.

I have already (3) mentioned the possibility of the oblique sulcus in Cervidae (fissura postica of Krueg, fissura suprasylvia posterior of Flatau and Jacobson) being the homologue of the prolonged descending ramus of the suprasylvian in okapi. I am, however, inclined to modify this view somewhat on further study of the relations of the sulci in this region.

In the giraffe (fig. 3) the descending ramus of the suprasylvian, the oblique and the ramus posterior ectosylvii, are each to be distinguished as separate sulci. In the okapi, however (fig. 6), the sulcus termed ramus descendens suprasylvii is much more caudally placed and cuts the rhinal fissure (see also *Samotherium*, fig. 9). Thus, the arrangement of this constellation in the okapi is such as to suggest at least the possibility of its representing, not the oblique sulcus only, but rather a complex of three sulci, viz., the ramus descendens suprasylvii, the oblique and the caudal end of the ramus posterior ectosylvii.

The possibility of this is increased when it is remembered that such combinations of sulci are not rare, and that in this same cast other examples of such a phenomenon have been noted (corono-ansate-suprasylvian and also suprasylvian-diagonal).

The irregular sulci marking the caudo-lateral surface of the cast are thus to be considered as representing the triradiata posterior of Kappers.

(c) *Samotherium* (figures 7 to 9 and 23 to 25)

This primitive ruminant, resembling the modern okapi, was discovered in upper Miocene deposits in the island of Samos (Forsyth Major, 15, 16). Like the okapi, horns were present only in the male and were situated upon the frontal bones.

As the result of considerable compression of the skull during fossilization, the endocranial cast is quite asymmetrical, and much detail in the ventral area has been obscured. Notwithstanding this unfavorable condition, it is possible to trace the course of the principal sulci with comparative ease.

The volume of the cast is 425 cc., which is but little less than that of the okapi. Indeed, if due allowance be made for the

Figs. 7, 8 and 9 Outline drawings of endocranial cast of *Samotherium*, ventral, dorsal and right lateral views respectively. For abbreviations see page 332. For photographs from which the outlines were taken, see figures 23 to 25. About $\frac{1}{2}$ natural size.

above mentioned distortion, the volume of this cast would at least equal if not exceed that of okapi.

On account of asymmetry the following measurements may be compared only approximately with the similar measurements recorded for the giraffe and okapi.

The greatest transverse diameter of the cerebral portion of the cast is 96 mm. From the pontine surface to the highest point over the vermis area the distance is 60 mm. From the frontal to the occipital pole of the cerebral portion, the maximum length is 110 mm. The greatest interfloccular diameter is 57 mm.

Brain stem, cerebellum and basis cranii. In its cerebellar portion this cast resembles that of okapi, and like the latter there is evidence here of ossification having occurred in the dura to some extent in the region of the junction of the falx and tentorium. The presence of a well marked "fossette cerebelleuse moyenne" is indicated by the prominence of the interfloccular mass in the median plane. There is but little trace of the definite furrows separating this median prominence from the lateral portions of the interfloccular mass so obvious in the okapi.

The olfactory bulbs are pedunculated as in the okapi, and project a considerable distance beyond the frontal pole of the cerebrum.

It has already been noted, that the configuration of the ventral area is altered to some extent, but most of the landmarks of this region may still be recognized.

In figures 7 and 23, the protuberance marking the site of the right optic foramen is quite evident. Caudad from this certain elevations indicate the position of the emerging divisions of the trigeminal nerve. Between the protuberances which correspond to the foramen lacerum orbitale and the foramen ovale respectively on the right side an irregular elevation occurs which suggests the presence of a foramen rotundum. Though not so evident on the left, this possibility at least may not be excluded, from an examination of the cast alone. The presence of two separate foramina in the great wing of the sphenoid however, in any of the modern Ungulata vera, if it ever occur, must be a somewhat rare condition as may be judged from the following.

In Hyrax these three foramina are normally present. In Artiodactyla, so far as I am aware, the foramen rotundum is not present as a separate opening, while a distinct foramen ovale in these forms is characteristic. Among the modern Perissodactyla, a foramen rotundum occurs not infrequently in the Equidae, separated by a thin plate of bone from the foramen lacerum orbitale. In these forms, however, the foramen ovale is confluent with the foramen lacerum basis cranii (13), though the primitive stem perissodactyls were characterized by the presence of all three foramina (19, p. 390). The condition in the Indian elephant is similar to that in Artiodactyla in so far as the foramen ovale is discrete while the foramen rotundum and lacerum orbitale are confluent.

The remaining structures in this region correspond in general to the plan already described in the giraffe.

Cerebral hemispheres. A most interesting variation in the arrangement of the sulci in the dorsal view is seen in this case (figs. 8 and 24). While the entolateral sulcus occupies its usual position, the lateral sulcus becomes joined to the coronal as well as to the suprasylvian by the intermediation of the ansate sulcus.

The continuity of the suprasylvian and coronal sulci by way of the ansate is a common ungulate condition, while in Carnivora the lateral and coronal sulci are similarly associated. In the latter group of animals the junction of the coronal to the suprasylvian by the ansate is practically never present (21, footnote, p. 299).

The direct continuity of the lateral and coronal sulci is a very primitive feature in ungulates, which is recorded only in the hippopotamus (9, p. 321).

The condition obtaining in the present instance, however, in which these sulci are united by the ansate is not so rare an occurrence, though it represents a primitive arrangement in so far as it combines features common to both ungulates and carnivores.

The coronal sulcus, which is placed far forward, is comparatively small as in Hyrax. The diagonal sulcus is not continuous

with the suprasylvian on either side though it is almost so on the right.

The presylvian sulcus becomes evident a slight distance above the anterior rhinal fissure. Although it is placed far forward on the cerebrum, it is still separated from the coronal by a considerable interval on account of the shortness of the latter sulcus.

A sulcus recalling the carnivor "cruciatu," but not to be homologized as such, appears emerging from the sagittal furrow and probably represents the upturned termination of the splenial.

The anterior rhinal fissure is poorly marked as the ventral limit of a depressed area, whose dorsal border is formed by the frontal operculum of the pseudosylvian fossa. The ramus anterior ectosylvii is probably represented by the small notch in this operculum some distance behind the origin of the presylvian sulcus.

The pseudosylvian fossa is indicated on the right side by two or three small vertical notches, while on the left side the condition more nearly resembles that which has been described in the giraffe.

The suprasylvian sulcus is very dorsally placed and has a well marked, long descending ramus. The area between the pseudosylvian region and the suprasylvian sulcus is furrowed on both sides by a well developed arcuate constellation, which is in every respect similar to the sulcus bearing the same name in the giraffe and the okapi.

The relations of the caudally placed descending ramus of the suprasylvian in this form are such as to support the hypothesis put forward in the description of the okapi, viz: that this sulcus may represent a complex corresponding to the ramus posterior ectosylvii, the ramus descendens suprasylvii and the oblique sulcus. The small sulcus occupying the area caudal to the descending suprasylvian ramus of this form would thus represent the triradiata posterior of Kappers.

TYPES OF FISSURAL PATTERN ON THE LATERAL SURFACE OF THE CEREBRUM IN UNGULATES

Before discussing the possible significance of the data recorded in the preceding description, it will be well for the sake of comparison to consider briefly certain types of fissural pattern which obtain among ungulates other than the Giraffidae.

Only the sulci on the lateral surface of the cerebrum in forms belonging to the group Ungulata vera (Flower and Lydekker, 14) will be considered.

(1) *Bos taurus* (figure 10). The ectosylvian sulci are hidden in the ox for a large part of their extent by the frontal and caudal pseudosylvian opercula, which come together and form the large processus acuminis. The anterior and posterior rami of the ectosylvian may be seen as they diverge from the base of this sulcus. No doubt can remain as to the identity of these sulci since Holl's interpretation (vide infra, p. 352) has again been confirmed by the study of their ontogenetic development (Kappers, l. c., p. 289).

Below the diverging ectosylvian limbs is a somewhat depressed area limited ventrally by the rhinal fissure. From this fissure a Y-shaped notch extends upward as in the specimen figured by Elliot Smith (9, p. 343), and represents the homologue of the feline pseudosylvian sulcus. The presylvian arises from the anterior rhinal fissure. It is not connected with the ramus anterior ectosylvii as is the case in the specimen just cited, neither is it connected with the coronal as is often the case in Cervidae and other ungulates.

The diagonal is not connected with the suprasylvian, though the latter is linked to the coronal, as is frequently the case in the Bovidae and usually so in the Cervidae.

The suprasylvian sulcus is dorsally placed and gives off several secondary sulci. One of these, on account of its depth and its relation to the oblique, has been termed the ramus descendens suprasylvii in figure 10. A more characteristic arrangement obtains on the left side of this specimen, where the short descending ramus is closely related to a caudally placed upturned branch of the oblique. Behind the oblique sulcus an irregular

complex conforms to Kapper's description of the triradiata posterior (l. c., p. 309).

Posteriorly the suprasylvian sulcus ends in the characteristically ungulate fashion. There is no indication of an arcuate constellation as described in Giraffidae.

Fig. 10 Right lateral views of the cerebrum of a young specimen of *Bos taurus*. Abbreviations as before. $\times \frac{1}{2}$.

Fig. 11 Right lateral view of the cerebrum of *Ovis aries* (adult). Abbreviations as before. $\times \frac{1}{2}$.

(2) *Ovis aries* (figure 11). Compared with the ox, the posterior lip of the pseudosylvian fossa is in general somewhat further operculated in the sheep, so that all but the extreme caudal tip of the posterior ectosylvian sulcus remains hidden from the surface. Frontally also only a small part of the ramus anterior ectosylvii is exposed. The presylvian sulcus does not reach the rhinal fissure and is continuous frontally with the coronal.

The diagonal with its quite constant accessory sulcus (9, p. 340) is present on both sides. On the right the diagonalis proprius joins the suprasylvian.

The ansate joins the coronal sulcus but does not link the latter to the suprasylvian as in the ox. The long descending ramus of the latter sulcus is closely related to a simple linear oblique sulcus. The suprasylvian itself is prolonged caudad in

a characteristic ungulate fashion. There is no indication of an arcuate constellation between the long processus acuminis and the suprasylvian sulcus.

Variations in cortical pattern in the Bovidae

Although most members of this family conform more or less closely to one or other of the types of cortical pattern above exemplified, several exceptions are to be noted. Thus, the black-buck (*Antilope cervicapra*), the guib (*Tragelaphus scriptus*), the kudu (*Strepsiceros kudu*) and the eland (*Taurotragus oryx*) are each characterized by the shortness of the pseudosylvian processus acuminis and the development, between this sulcus and the dorsally placed suprasylvian, of a well marked compensating arcuate constellation (9, pp. 336 and 338).

(3) *Cervus virginianus* (figure 12). The operculation in the pseudosylvian region is rather more advanced in the deer than in the ox and sheep. The free extremities of the ectosylvian sulci are evident, however, as the ramus anterior and posterior respectively.

The presylvian is continuous with the coronal, while the latter sulcus is in turn joined to the suprasylvian by the arcuatus. The diagonal is independent of the suprasylvian.

The descending ramus of the suprasylvian may be represented by the slight notch labelled as such in figure 12, but among the Cervidae this sulcus is either absent or but poorly developed, as frequently is the case in the Bovidae. The caudal bifurcation of the suprasylvian is well marked. The oblique sulcus is large and irregular in this form as in most of the Cervidae. It is possible that certain inconstant sulci behind the oblique may represent the triradiata posterior.

The long processus acuminis almost meets the suprasylvian. This is a characteristic phenomenon in Cervidae and precludes the formation of an arcuate constellation.

(4) *Sus communis* (figure 13). The operculation in the pseudosylvian area has progressed so far in Suidae that as a rule

only a small portion of the floor of this fossa remains exposed, as is shown in the specimen figured.

The large suprasylvian sulcus is fused anteriorly with the diagonal and is joined by an offshoot to the splenial sulcus as is usual in pigs. The latter sulcus however in this specimen is not joined to the coronal, though such a junction is usual in these forms.

Fig. 12 Right lateral view of cerebrum of an adult specimen of *Cervus virginianus*. Abbreviations as before. $\times \frac{1}{2}$.

Fig. 13 Right lateral view of cerebrum of *Sus communis* (young adult). Abbreviations as before. $\times \frac{1}{2}$.

The presylvian sulcus is both well marked and separate from the coronal. On account of the extensive operculation already mentioned, the ramus anterior ectosylvii, which is small, appears to arise from the rhinal fissure.

Caudally one extremity of the bifurcated suprasylvian gives rise to a branch resembling the ramus descendens suprasylvii, but not to be homologized as such. Behind this sulcus lies the triradiata posterior.

The extensive upward prolongation of the ramus posterior ectosylvii is an unusual feature in the pig brain. In front of this is situated a linear sulcus which is curiously reminiscent of the sulcus E of Elliot Smith in the hippopotamus (9, p. 321) and it is possible that these sulci may both represent atypically

developed descending rami of the suprasylvian. There is no indication of an arcuate constellation.

(5) *Procamelus occidentalis* (figure 14). This figure has been inserted in the present series for purposes of comparison with the modern camel. The endocranial cast of this form has been described by Cope, from whose drawing (7) the outline in question has been taken.

The processus acuminis of the pseudosylvian fossa is seen to be well developed and only separated from the suprasylvian sulcus by a small space. The groove labelled descending ramus of the suprasylvian in figure 14, has precisely similar relations to the pseudosylvian fossa and upturned ramus posterior ectosylvii as the sulcus bearing the same name in the pig.

The long horizontal ramus of the suprasylvian, together with the lateral and entolateral sulci, is simple and linear, but without a re-examination of the cast their frontal relations are not clear.

(6) *Camelus dromedarius* (figure 15). The above figure has been taken from Flatau and Jacobson's text (12, p. 432). Their drawing has been enlarged in the present instance until the fronto-occipital diameter was equal to this dimension in an adult skull of *Camelus* in the Reserve Anatomical Museum collection. In this way some idea of relative size can be gained.

In the camel the suprasylvian sulcus is quite dorsally placed, while the processus acuminis of the pseudosylvian is short. There is thus a broad area between these two sulci, which is marked by certain compensating furrows similar in nature to the arcuate constellation of Giraffidae. It is evident, however, from the arrangement of the sulci in the ancestral *Procamelus* (26, p. 300) that the arcuate group of sulci has been recently acquired in the camel.

The sulcus which I have labelled *R. desc. ss.* is termed by Flatau and Jacobson the 'fissura postica' or 'fissura suprasylvia posterior.'

(7) *Equus caballus* (figure 16). Among Perissodactyla in general, the presence of an arcuate constellation similar to that described in the Giraffidae, is a characteristic feature. In the

Fig. 14 Left lateral view of cerebral part of endocranial cast of *Procamelus occidentalis*. From a drawing of the cast described by Cope (7, plate 1, fig. 1, p. 36). Lettering as before. $\times \frac{1}{2}$.

Fig. 15 Right lateral view of cerebrum of *Camelus dromedarius*. (Modified from Flatau and Jacobson after Krueg (12). Abbreviations as before. About $\frac{1}{2}$ natural size.

Fig. 16 Right lateral view of cerebrum of *Equus caballus* (adult). Abbreviations as before. $\times \frac{1}{2}$.

horse this constellation is so constant and well marked that it has frequently been wrongly described as the ectosylvian sulcus.

The suprasylvian, coronal and presylvian sulci in the horse are usually in continuity as in this specimen, a condition which begins early in foetal life (5). The presylvian area in the horse is marked by an irregular sulcus, which is quite constantly present and has been termed the intraorbital sulcus (5) and (21, p. 293).

Reference to figure 16 renders further description of the specimen unnecessary in the present connection.

DISCUSSION

Arcuate constellation

The first point which requires consideration is the relation of the furrow which has been described in the foregoing account as the 'arcuate constellation,' to the ectosylvian arc.

Several authors, among whom may be mentioned Flatau and Jacobson (12), Sisson (27) and Bradley (5), have noted this sulcus in such forms as it occurs and have termed it the ectosylvian. It may be added that this sulcus is figured by Ellenberger and Baum (8, p. 779) and by Chauveau (6, p. 787) in the horse, but in neither case has it been given a name.

The error in using the term 'ectosylvian' as applied to this 'arcuate constellation' becomes apparent, however, when the following facts are considered.

Holl (20), Elliot Smith (9, p. 309 and elsewhere) and Kappers (l.c., supra), have already demonstrated that the pseudosylvian sulcus in ungulates is not at all homologous to the sulcus bearing the same name in carnivores. In the former group this sulcus is the result of either the partial or the complete submergence of the first arcuate or ectosylvian gyrus. The ectosylvian sulci are thus incorporated in the formation of the ungulate pseudosylvian sulcus, and depending upon the degree of operculation, are more or less hidden for a considerable part of their extent (figs. 10 to 13).

Anteriorly, however, the frontal extremity of the ectosylvian sulcus usually forms the well marked fissure termed the ramus

anterior ectosylvii. If, however, the frontal operculum of the pseudosylvian fossa be well developed, this sulcus may appear to take its origin from the anterior rhinal fissure (compare figs. 10 and 13).

In many cases also the posterior extremity of the ectosylvian sulcus appears on the surface as the ramus posterior ectosylvii.

It is obvious therefore that this arcuate constellation present in certain ungulates between the processus acuminis of the pseudosylvian fossa and the suprasylvian sulcus, does not in any way represent the homologue of the similarly placed ectosylvian arch of Canidae. It is indeed peculiar to certain ungulates, and has no homologue among carnivores.

It is evident that the arcuate constellation is not confined in its occurrence to the Giraffidae. Indeed it becomes increasingly manifest that the formation of this arched furrow, or series of furrows, is dependent upon the inter-relationship of the pseudosylvian acuminis and the suprasylvian sulcus. In the Perissodactyla, and equally in the Artiodactyla, whenever the acuminis is short and separated from the dorsally placed suprasylvian by a considerable interval, there appears quite constantly this additional arched fold, compensatory in nature, about the pseudosylvian region.

In all modern Perissodactyla the processus acuminis is usually separated from the suprasylvian sulcus by a broad area, and in this group the appearance of an arcuate constellation is a constant phenomenon.

In the Artiodactyla the requisite conditions for the occurrence of this constellation have been present among the Giraffidae since Miocene times. In the Camelidae on the other hand, these relations are of modern acquisition.

The ancestral conditions among the Perissodactyla and in the Artiodactyla other than the Giraffidae and Camelidae, have not as yet been examined.

Since a typical arcuate constellation has been independently acquired late in phylogeny among the Camelidae, it becomes evident that the mere presence of a well developed arcuate constellation in both the Equidae and the Giraffidae is in no way

indicative of a close relationship between the two groups. This would appear to be but another example of resemblance due to convergent or analogous evolution (vide Gregory, 19, p. 400).

Distinctive characters of convolutional pattern in Giraffidae

The chief peculiarities of the convolutional pattern in the Giraffidae, as evidenced by the material at my disposal, may be enumerated as follows: (a) a well marked and caudally situated ramus descendens suprasylvii; (b) a dorsally placed suprasylvian sulcus separated from the pseudosylvian acuminis by a broad area in which is developed a very evident arcuate constellation; (c) a small presylvian area (rostral to presylvian sulcus).

TABLE 1

	(1) R. DESCENDENS SUPRASYLVI	(2) ARCUATE CONSTELLATION	(3) PRESYLVIAN AREA
Giraffidae.....	Well marked and caudally placed	Present	Small—no sulcus intraorbitalis
Cervidae.....		Absent	
Antilocapridae.....		Absent	
Bovidae.....		Absent	
Bovidae* (exceptions)	Variable and when present, not so caudally placed		Usually larger than in Giraffi- dae
Tragulidae		Absent	
Camelidae.....	Usually separat- ed from sup- rasylvian and not so caud- ally placed		Large—sulcus in- traorbitalis well developed
Hippopotamidae.....		Absent	
Suidae.....		Absent	
Equidae.....	Not caudally placed		Large—sulcus in- traorbitalis well developed
Tapiridae.....	Frequently sep- arate from suprasylvian		Similar to Equi- dae
Rhinocerotidae.....	Similar to Equi- dae		Similar to Equi- dae

* Vide supra, page 348.

So far as the brain is concerned, the foregoing characters, when present in combination with one another, appear to be distinctive of the Giraffidae among the various groups comprising the modern Ungulata vera, as may be seen from the accompanying brief comparative summary (vide table 1).

CONCLUSION

From a comparison of the endocranial casts of the Giraffidae considered in this paper it becomes evident that among these the cast of *Samotherium* shows undoubtedly the most primitive arrangement of sulci, presenting as it does certain features common both to the Carnivora and to the Ungulata. In other respects however, this brain shows evidence of considerable specialization. Thus it will be noted that this early form is already possessed of certain brain characters which still serve to distinguish the Giraffidae among modern ungulates.

This early specialization of the convolutional pattern in the Giraffidae presents a marked contrast to the condition obtaining in the Camelidae of the same epoch (upper Miocene) as evidenced by the endocranial cast of the American form *Procamelus occidentalis*. The latter cast shows but little if any indication of a distinctive cameloid arrangement of sulci (vide p. 351).

In both *Ocapia* and *Samotherium* the brain presents certain generalized characters in the arrangement of the cortical pattern which are common and peculiar to the Ungulata, such for example as the relations of the corono-ansate-suprasylvian complex. In this category also I am inclined to consider the sulcus described in *Ocapia* and *Samotherium* as the ramus descendens suprasylvii, in so far as it may represent in these forms three sulci which are no longer continuous in the giraffe (viz., the caudal part of the ramus ectosylvii posterior, the ramus descendens suprasylvii and the sulcus obliquus).

In the giraffe there appear certain specialized characters which serve to distinguish this form from both *Ocapia* and *Samotherium*; such for example as the complete separation of the corono-

ansate from the suprasylvian sulcus and also the presence of the three discrete sulci mentioned in the preceding paragraph which appear to be merged in a single complex in *Ocapia* and *Samotherium*.

The curious superficial resemblance of the giraffe brain to that of the horse must be considered as the result of analogous or convergent evolution. Further consideration of this interesting condition however is left to a later date, when it is hoped to extend these observations by the examination of an extensive series of endocranial casts from allied forms, both recent and extinct.

Finally, the present study emphasizes once more the value of endocranial configuration as an index to the morphology of the brain, the taxonomic importance of which has long been recognized (11).

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Figs. 17, 18, 19 Photographs of endocranial cast of *Giraffa camelopardalis*, ventral, dorsal and right lateral views respectively. About $\frac{1}{2}$ natural size.

Figs. 20, 21, 22 Photographs of endocranial case of *Ocapia johnstoni*, ventral, dorsal and right lateral views respectively, About $\frac{1}{2}$ natural size.

Figs. 23, 24, 25 Photographs of endocranial cast of *Samotherium*, ventral, dorsal and right lateral views respectively. About $\frac{1}{2}$ natural size.