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THE BRAIN OF THE EMU (*DROMAEUS* *NOVAEHOLLANDIAE*, LATH)¹

I. GROSS ANATOMY OF THE BRAIN AND PINEAL BODY²

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and

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The histology of the cerebral hemisphere of the emu has been extensively studied by Craigie (1935a, 1935b, 1940) and three diagrams of the hemisphere have been published. Drawings of the whole brain have also appeared in the literature (Strong, 1911; Küenzi, 1918), and a photograph was published by Anthony (1928). No description of the whole brain, however, is to be found. Since the emu is, next to the ostrich, our largest living bird, and since it belongs to a taxonomically controversial group, it seems of value to describe the brain and compare it with the brains of other birds. Moreover, the emu is considered, by Pyecraft (1900) and many others, to be one of the most primitive of birds. The concept of "primitiveness" will be considered in the discussion at the end of this paper.

MATERIAL

Three specimens of *Dromaeus novae-hollandiae* were collected by S. J. J. Davies in November 1960 in Western Australia for Professor Ernst Mayr, Director of the Harvard Museum of Comparative Zoology. Two of them were kindly given to us by Professor Mayr for neurological study. The heads had been cut off

¹ This spelling of *Dromaeus* is not the one accepted by some newer checklists, but because *Dromiceius* (an alternative spelling) is the perpetuation of a graphological error (Newton, 1896) and because *Dromaius* is a less proper Latinization, it seems better to use the older form.

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and skinned, the eyes had been removed, and the specimens had been fixed in 10 per cent formalin solution in the field. After about two months the heads were packed in moist condition and shipped in cellophane bags to the United States. Here the brains were removed from the skulls after making photographs of various stages of the dissections. The brains were then fixed in fresh neutral formalin solution (10 per cent) for a month. One brain (that of Emu #85) was divided into its component parts for weighing and special histological studies. The other brain (Emu #104) was removed, photographed, fixed for a month in 10 per cent formalin as above, and embedded whole in celloidin for serial sectioning. Both are brains of adult males. The first (#85) appears somewhat larger and weighed 27.7 grams; the second (#104) weighed 25.1 grams.

DESCRIPTION

The position of an avian brain within the skull is determined by many developmental factors. The most obvious are the shape of the bill, the size and position of the eyes, the habitual posture of the bird, and the size and shape of the brain itself. Starck (1955) has given an excellent discussion of these relationships and emphasizes the importance of the size of the eye and the position of the orbit. One way of describing the position of the brain is to measure the angle between the cerebral axis and the axis of the bill (Cobb, 1959). In the emu this angle is about 27° (see Fig. 1), an angle somewhat smaller than that of the gull (*Larus argentatus*: 34°) and the grouse (*Bonasa umbellus*: 36°), but distinctly greater than that of the cormorant (*Phalacrocorax auritus*: 15°) which has the straightest (most extended) type of skull and an exceptionally small brain-bill angle.

Besides showing the relation of the brain to the skull, Figure 1 shows the olfactory bulb and membranous sac of the olfactory nasal chamber; the bulb seems to be in direct contact with the chamber, but closer scrutiny shows that there is a space bridged by the short olfactory nerves. When the light, diploic bone of the bill is removed, the sac which forms the lining of the olfactory chamber is revealed. It is a fairly tough structure containing blood vessels and many nerve fibers. It is crossed anteriorly by a branch of the first division of the trigeminal nerve. The main nerve trunk of this division is seen passing through the orbit, close to the optic nerve and up to a point just below the olfactory bulb.

This is the main sensory nerve from the bill, innervating the skin and vibrissae. Its large size suggests that tactile sense in the bill is acute and important.

On opening the olfactory chamber, the most posterior of the three nasal chambers, a well-developed turbinal mound (superior or olfactory concha) is seen on the lateral wall. It is covered with a soft, yellowish epithelium, which becomes thinner and less yellow as it spreads out over the dorsal and mesial aspects of the chamber. A vertical section through the nasal chambers of the bill at this level (Fig. 3) reveals that the concha is raised to a height of about 5 mm. and is slightly constricted at its base, but is not folded into a spiral like the conchae of some vultures and albatrosses (Bang, 1960). A specimen for microscopic examination was taken from the dorsal surface of the olfactory chamber; it shows cells and cilia typical of olfactory epithelium. About 5 cm. anterior to the olfactory concha there is a large nostril (Fig. 1), which is the external opening of the anterior nasal chamber.

The emu has large eyes and the orbits are spacious. As one sees in Figure 1 the brain lies mostly behind the orbit with the olfactory chambers in the bony structures just in front. The optic nerve enters the chiasm and passes directly to the optic lobe of the opposite side of the midbrain (Fig. 2C). The large fascicles of nerve fibers can be seen as they cross. The optic lobe is a large and conspicuous structure (Figs. 1, 2B and 2C). In the lateral view only about one-fifth of it is covered by the overlying hemisphere. In Figure 2B (in which the parts of the brain are slightly separated) the relation of the optic lobe to hindbrain and forebrain is emphasized. It is clearly a part of the midbrain. In fact, the optic lobes are homologues of the corpora bigemina of reptiles, and of the anterior corpora quadrigemina of mammals. They have taken a ventrolateral position in birds, perhaps because it was easier there to make room for the extraordinary tectal development in this class of vertebrates.

The emu brain when viewed from above (Figs. 1A and 2A) impresses one by its triangular shape, with cerebral hemispheres broad posteriorly and narrow anteriorly. The olfactory bulbs protrude, forming the anterior pole of the hemisphere. On the vertex the two sagittal elevations of hyperstriatum stand out conspicuously and are separated from the lateral parts of the hemispheres by a distinct sulcus, the vallecule (Portmann and Stingelin, 1961).

The cerebellum is larger in comparison to the forebrain than in passerine birds. It has a greater diameter dorsoventrally than laterally (Figs. 1 and 2) although the auricles protrude laterally on each side. These lobes, composed of flocculus and nodule, are the only ones that complicate the simple conformation of the cerebellum, the corpus cerebelli being largely a mid-line organ corresponding to the vermis of mammals. Between the anterior surface of the cerebellum (culmen and declive) and the posterior poles of the cerebral hemispheres there is ample space for the pineal stalk and gland.

The lateral view of the brain (Fig. 2B) shows the relative sizes of the main subdivisions. For this photograph the forebrain, midbrain, and hindbrain were slightly pulled apart. The hemispheres of the forebrain are well developed and extend backwards covering parts of the optic lobe and of the cerebellum. The greatest diameter of the hemisphere is 36 mm. and the greatest diameter of the olfactory bulb is 9 mm., giving a ratio of 4 to 1 or 25 per cent. This places the emu among those birds that have large olfactory bulbs (the Gruiformes, Caprimulgiformes, Procellariiformes, Podicepidiformes, and Apterygiformes). In a list of 47 different species of birds, arranged according to the relative size of the olfactory bulb, the largest at the top, the kiwi would come first and the emu seventh (Cobb, 1960). The anterior end of the hyperstriatum accessorium (sagittal elevation or Wulst) is close to the olfactory bulb, and the posterior end shades off into the neostriatum before reaching the occipital pole of the hemisphere. Thus the emu has a large Wulst that reaches well back towards the occipital pole (Figs. 1 and 2) and well forward to a point close to the olfactory bulb.

A comparison of the external configuration of the brain of the emu with that of other birds shows that it resembles most some herons and ducks. In comparing it with Stingelin's (1958) photographs, it is seen to be strikingly similar to the brain of *Ixobrychus minutus* (see his fig. 21 "Zwergreiher").

Seen from below (Fig. 2C) the conspicuous characteristics of the emu brain are: (1) the large, separated olfactory bulbs, forming the anterior pole; (2) the flatness of the ventral aspects of the lateral parts of the two cerebral hemispheres; and (3) the pair of big optic lobes shaped like flasks with their necks joined in the optic chiasm. The cerebellum is so narrow that it is almost hidden by the medulla oblongata, only the flocculi showing on each side. The roots of the third, seventh, eighth, ninth, and tenth cranial nerves show in this view.

The brain of emu #85 (after formalin fixation) weighed 27.7 grams; his body weight was 34 kg. The brain of emu #104 weighed 25.1 grams (also after formalin fixation); body weight 31 kg. This gives a ratio of brain weight to body weight in emu #85 of 1/1227 and in emu #104 a ratio of 1/1235. Little significance, however, should be given to these ratios because it is known that a living emu may vary 30 to 40 per cent in weight during a year due to conditions of food, climate and water supply. The first brain was separated into 8 pieces, for weighing, as follows:

Olfactory bulb (right)	(injured)
Olfactory bulb (left)	0.12 grams
Cerebral hemisphere (right)	8.85 grams
Cerebral hemisphere (left)	8.8 grams
Optic lobe (right)	7.3 grams
Optic lobe (left)	7.3 grams
Cerebellum	4.6 grams
Brainstem	3.9 grams

The brainstem (defined by Portmann, 1946, and named "Stammrest") is the basal mass of nerve tissue made up of thalamus, midbrain (with optic lobes removed) and hindbrain (with cerebellum removed). Portmann's purpose was to choose as his common denominator that part of the brain which varies least in its size relative to the size of the whole bird. That part is obviously the brainstem. He then compares its size to other parts of the brain and, by dividing the weight or volume of the stem into the corresponding value for another part, he obtains his index. This "index of cerebralization" he finds for an emu to be 4.18, obtained by dividing the weight of the "Stammrest" into the combined weight of the two hemispheres. In our emu #85 this index is $17.6/3.9 = 4.5$. According to Portmann's list the figures 4.18 and 4.5 both place the emu far below parrots and ravens, but above loons, grebes, and quail. He believes that this quotient gives an expression of the "level of integration" of the brain for each species.

THE PINEAL BODY

In the dissection of emu #104, a large part of the post-central area of the calvarium was left intact and carefully lifted off the brain. The pineal stalk was thus torn away at its attachment to the diencephalon. It is 10 mm. in length and remained attached

to the pineal body (Fig. 4). The body itself is embedded in the dura and lies in a depression of the cranial roof between the anterior and posterior fossae. The dorsal position of the epiphysis is thus clearly demonstrated; it lies between cerebrum and cerebellum at the level of their dorsal surfaces. The stalk leaves the brain at a point just rostral to where forebrain joins midbrain. The pineal body is round and firm, slightly flattened dorso-ventrally. It is yellowish in contrast to the white skull. The fibrous envelope is continuous with dura which has strong bands spreading laterally and anteriorly. Removed from the membranes, the pineal body is roughly triangular, 7 mm. long on each side. With stalk attached, it weighs 0.1 gm. after formalin fixation.

DISCUSSION

The description of the gross anatomy of the brain of the emu brings up five points for discussion: 1) the size of the brain, 2) the question of primitiveness, 3) the general shape of the brain in relation to the base of the skull, 4) the size and position of the Wulst, and 5) the topographic relations of the pineal body.

The size of the brain in relation to body size and "intelligence" has been the subject of much study and many pronouncements. Suffice it to say here that in our opinion the relation of brain weight to body weight (so called cephalization) is a ratio too simple to give information of much significance. Portmann's (1952) pioneer work in describing an index of encephalization is an advance in the right direction. Body weight in birds is too grossly variable to be used in comparison to the much more stable brain weight. Small birds may show rapid and marked change in weight. There is good evidence that some birds may lose from 30 to 50 per cent of their body weight in 24 hours during a migratory flight (Odum et al., 1961; Helms and Drury, 1960). The emu, being flightless, lives in a fairly uniform environment and does not go through the prolonged exertion of migratory flights. Its ratio of brain weight to body weight might, therefore, be relatively stable. Actually, in *Dromaeus novaehollandiae* this ratio is approximately 1/1230 (see p. 5). From the weights given by Crile and Quiring (1940) we deduce that the ratio for an ostrich (*Struthio camelus massaicus*) is 1/2929; for a sparrow (*Passer domesticus*) it is 1/23; and for a hummingbird (*Amazilia tzacatl*) it is 1/24. This does not mean that the hummingbird has a "better" brain than the emu. It merely indicates that the

body controlled by the brain of the hummingbird is just as complex as the body of the emu, though much smaller. The question as to which brain is "better," or more highly evolved, is meaningless unless one asks, "Better for what?" Obviously, the hummingbird's brain is better for flight and the emu's better for running.

Another factor relative to brain size must be considered. It has been pointed out by Sholl (1956) that small brains are in general more closely packed with nerve cell bodies than large brains which have more glial structures between neurons. Man has 10.5 nerve cell bodies per cubic micron; a mouse has 142.5.

In short, the need is to learn what parts of the brain, controlling what organs, are larger or smaller in each family of birds. With more investigation into the quantitative anatomy of the brain, some of these questions may be answered. Fritz (1949) has estimated the volume of four parts of the striatum in four different species of birds; he found significant differences, but no correlation with Portmann's cerebral index.

Many authors have spoken of the emu, and in fact all ratite birds, as primitive, but their concept of primitiveness is not clear. Some seem to call these birds primitive because they are flightless and have no keel on the sternum (Leach, 1923), others because they have a straight type of skull base (Streckschädel) (Marinelli, 1928, p. 156). Stingelin (1958) considers those birds, with a small Wulst which lies neither far forward nor far back, to be the less evolved type. The point would seem to be that one must not apply the term primitive in a general way to the emu (or probably any other bird). One should specify in what respect a given type or family is less evolved ("primitive") and in what respect it is more evolved (specialized). Even then, the gaps in our phylogenetic knowledge do not allow us to say whether the ratite sternum is due to a devolution from carinate ancestors or an evolution from cursorial reptiles. The presence of feathers and the avian type of brain suggest strongly a descent from flying ancestors. In respect to running and adaptation to life in open plains one feels confident in saying that the emu is highly evolved.

Much work has been done on the development of the avian skull. Pertinent to an understanding of the shape of the emu's brain are three recent lines of investigation. Duym (1951) described the bending of the base of the skull in different birds and specified four types — the stretched or extended type of

skull and three degrees of bending. Dullemeijer (1960) has related the shape and size of the principal parts of the brain to the amount of bending of the cerebral axis and has described four classes on this basis: 1) stretched skulls with little bending, 2) bending of 20 degrees, 3) bending of about 70 degrees, 4) bending of about 120 degrees. Starek (1955) has shown the great importance of the size of the eye and orbit in determining the shape of the brain and skull.

In the emu one finds a rather extended type of skull and a very large eye and orbit. Our measurements show that there is an angle of about 27 degrees between cerebral axis and bill axis, and a bending of the cerebral axis of about 13 degrees. Thus the emu falls into class "1" in Dullemeijer's grouping. We agree with him in emphasizing that "the position and shape of the brain parts is influenced by the position of the bill and the position and size of the eye." The development of the bill in birds has been remarkably variable, and with these special developments come variations in the bones of the skull and in the conformation of the brain.

As mentioned on page 4, the general shape of the brain of the emu resembles that of *Ixobrychus* but shape in itself is not very significant phylogenetically or physiologically in comparing birds' brains. One feature, however, may be of interest: the size and position of the Wulst, because this ganglion is conspicuous on the surface of the cerebral hemisphere and because its size in relation to that of the hemisphere appears to vary. Unfortunately, however, there are not enough quantitative data concerning the size of the Wulst in various types of birds to make any statements about its significance.

In the lateral and dorsal views of the emu's brain the Wulst is conspicuous (Figs. 1 and 2). Its anterior end is almost in contact with the olfactory bulb. The posterior end reaches back to within 4 mm. of the occipital pole of the hemisphere. This rounded ridge is long and lies parallel to the interhemispheric fissure — hence, the name used by L. Edinger et al. (1903) "Sagittalwulst," translated as "sagittal elevation" by Portmann and Stingelin (1961). Its position in the emu is like that in the pigeon, a bird whose brain resembles Stingelin's (1958) "Grundtypus." But the Wulst of the emu in relation to the rest of the hemisphere is both longer and broader than that of the pigeon.

Stingelin emphasizes the importance of the position of the Wulst. In his chapter entitled "Comparison and extent of striatal fields" there is a comparative description of the striatal

ganglia in 18 species, with clear diagrams of each. He believes that in the "highly evolved" ("hochevolutiert," p. 38) species there is a tendency to marked frontal enlargement of the hemisphere. This is achieved in two ways. In developmental line A the frontal pole is largely Wulst, the rostral end of which is in contact with the olfactory bulb. In developmental line B the frontal pole is made from the neostriatum and ventral hyperstriatum, the Wulst having receded to a position on the vertex by successive caudal shifts. From these observations Stingelin deduces a morphological rank ("Formwert") in relation to the basic type ("Grundtypus"). In developmental line A, crows and owls are considered the more highly developed groups; in line B, the higher ones are snipe, spoonbill (*Platalea*) and parrot, with a plover considered as "lower" and the lapwing as "middle." This rank order seems to be entirely based on cerebral anatomy. Reference is made neither to fossils nor to other characteristics such as brain axis or anatomy of skull.

As descriptions of the different relationships of one ganglion of the brain to another, the figures and exposition of Stingelin have great value, but taken as indicating evolutionary levels they may be misleading. Until one knows the lines of descent from reptilian and avian ancestors, descriptions of such "Entwicklungsrichtungen" and levels of evolution with "hoher" and "niederer Formwert" are not justified because evolution is the process of phylogenetic transformation, a phenomenon that cannot be observed except in consecutive phases of an ancestral line.

The "Horizontalmodifikationen" (Stingelin's fig. 32) are certainly of interest as showing differences between the brains of living families of birds, but these modifications are not a basis for conclusions concerning evolutionary ancestry. In short, we doubt if any living bird has a conformation of the brain that we are justified in calling *primitive*. The data for making such a judgment are inadequate. On the other hand, research into the relative size of various parts of the brain, such as Fritz (1949) has done in Portmann's laboratory, may give us important leads as to the degree of cerebral developments. Such investigations would be especially useful if correlated with behavior.

We wish to emphasize the possibility of drawing erroneous conclusions when the anatomy of living forms is used as evidence for describing an evolutionary process, disregarding the evidence from fossils. We welcome the opportunity to point to one feature of the emu brain as a graphic argument against a persistent, but erroneous theory. This feature is the position of the pineal body,

so obvious when one looks at the dorsal surface of the brain. The theory is that absence in birds and mammals of a second epithalamic appendage in the pineal area, the "parietal eye" of reptiles, is due to enlargement of cerebrum and cerebellum in the two descendant classes. That concept supposes that the covering over of the diencephalon and mesencephalon by the cerebrum and cerebellum in Aves and Mammalia obstructed the access of epithalamic appendages to the brain surface. This process is believed to have caused devolution and loss of the predominantly sensory, stalked, second organ in the pineal complex which survives only in lizards and the tuatara, the parietal eye.

Actually, among birds, a pineal organ reaching to the level of the cerebral and cerebellar vaults, attached to the skull roof, is not an exceptional occurrence. This is found in our *Dromaeus* and has been previously reported in brains of other ratites (*Struthio*, *Rhea*, *Apteryx*) and, as a button-shaped convexity, on the endocranial cast of the extinct *Dinornis* (Starck, 1955). The difference between these recently and carefully prepared specimens and those figured in the literature is not a real difference, but a matter of preparation.

Küenzi's (1918) diagrammatic figures of the brains of 36 different kinds of birds give the impression that no bird possesses an externally visible pineal organ, as do almost all macroscopic figures of avian brains in the literature, including Strong's (1911) figures which show *Dromaeus*. Küenzi, however, mentions in several places (pp. 28, 52, 89) that the pineal body is too firmly embedded in the meninges to be removed with the brain; he reports (pp. 70-71) that the pineal body in all birds studied occupies a median space between the posterior borders of the hemispheres and the front end of the cerebellum, its distal end reaching approximately to their dorsal level. Our observations on *Bubo*, *Corvus*, *Gallus*, *Columba*, and *Larus* agree with those of Küenzi; all have pineal bodies extending into the dura. A recent study on ten embryonic and three later developmental phases of *Larus* (Wetzig, 1961) also clearly testifies against the theory of mechanical suppression in birds of the second (the stalked) organ in the pineal complex of reptiles. The epiphysis extends to the level of the prospective skull roof in an early transitory phase, and again in the last phases of embryogeny. It is then, and remains in the adult, fitted into the space between cerebrum and cerebellum. It is club shaped, its apex coalesced with the dura in contact with the roof of the skull.

Thus, there is more space available than was assumed. The club shape (with the largest circumference distal) suggests that the form is governed by the space available. While we are well aware that the shape of a predominantly glandular organ (Stammer, 1961) has no great significance, we do wish to draw attention to the shape of the epiphysis of the emu. When, as in our emus, the distal expansion is abrupt, its connection with the corpus diencephali a mere stalk (Fig. 4), the avian pineal body strikingly resembles not the reptilian pineal organ, which is more or less sessile, but the reptilian parapineal vesicle with its nervous and vascular stalk — that is, the parietal eye. Krabbe (1961) observed this similarity in an embryo *Cygnus*. Many species of birds similarly demonstrate that there is no obstruction to the development of a parietal eye.

The reason for the absence of a parietal sense organ in birds is obviously not mechanical suppression; it is to be found in the fossil record, namely in pre-avian phylogeny. The presence of a parietal eye is reflected in a corresponding foramen of the roof of the skull. The fossil record of skulls plainly shows that the organ was first present and then lost in innumerable phyletic lines within the classes Pisces, Amphibia, and Reptilia. Birds are an offshoot of the great reptilian subclass Archosauria. Among the many hundreds of known skulls from its various orders, only two have the parietal foramen. Significantly, both the specimens showing that heritage from Palaeozoic ancestors belong to the earliest forms identifiable as archosaurian, each representing the beginning of a suborder of the order Thecodontia, “stem archosaurs” (*Mesorhinus*: Jaekel, 1910, and *Erythrosuchus*: Huene, 1911). These openings in the parietal bones of Archosauria occurred for the last time at the beginning of the Mesozoic era in the earliest Triassic times. It follows that parietal eyes were lost, not within the evolution of birds, but in remote reptilian ancestors some 80 million years before the first, late Jurassic, appearance of feathered animals, and presumably more than 100 million years before the modern type of avian brain was evolved.

In the Mammalia, likewise, both recent and fossil conditions plainly contradict the assumption that possession of a parietal photoreceptor became impossible because of progressive brain evolution. In various groups of mammals now living, much or all of the midbrain is dorsally exposed in a gap between cerebrum and cerebellum. Actually, it has long been known that in some bats, lagomorphs, and rodents the pineal gland extends into the

dura mater at the caudal end of the interhemispheric fissure, and this condition has now been found prevalent in studies of a large material from a great number of genera (Pilleri, 1960). The usual absence of a pineal organ in specimens of the rabbit brain is the result of its having been torn off with the tentorium during preparation. Furthermore, endocranial casts show that in most early Tertiary mammals there was a considerable gap between cerebrum and cerebellum. The parietal foramen was obliterated, i.e. the parietal eye had been lost in a pre-mammalian phase of evolution, in this case, in mammal-like Reptilia shortly before the emergence of the new class.

SUMMARY

A description of the gross anatomy of the brain of *Dromaeus novaehollandiae* is presented on the basis of two specimens from Western Australia. The brain is of the extended type. The olfactory bulbs and sagittal elevations of the forebrain, and the optic lobes of the midbrain are comparatively large. The index of encephalization is 4.5. The brains weighed 27.7 and 25.1 grams, respectively. The pineal body lies in a shallow fossa in the roof of the skull and weighed 0.1 gram. It is pointed out in discussion that there is no good reason for considering this brain to be primitive, and that phylogenetic relationships cannot justifiably be deduced from the anatomy of the brains of living birds.

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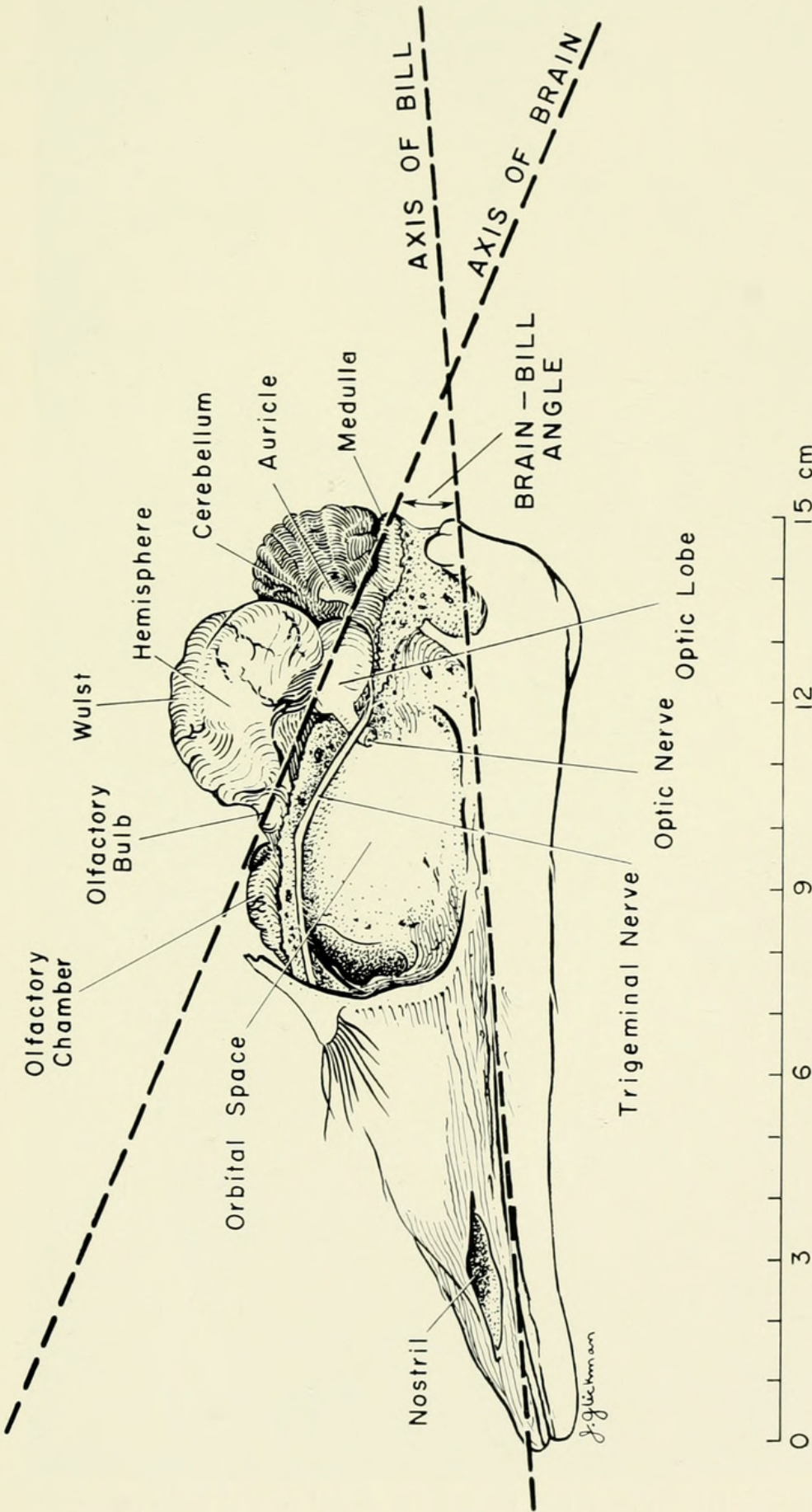


Figure 1A. Drawing of lateral view of brain of emu, in situ on base of skull. Brain-bill angle is 27° .

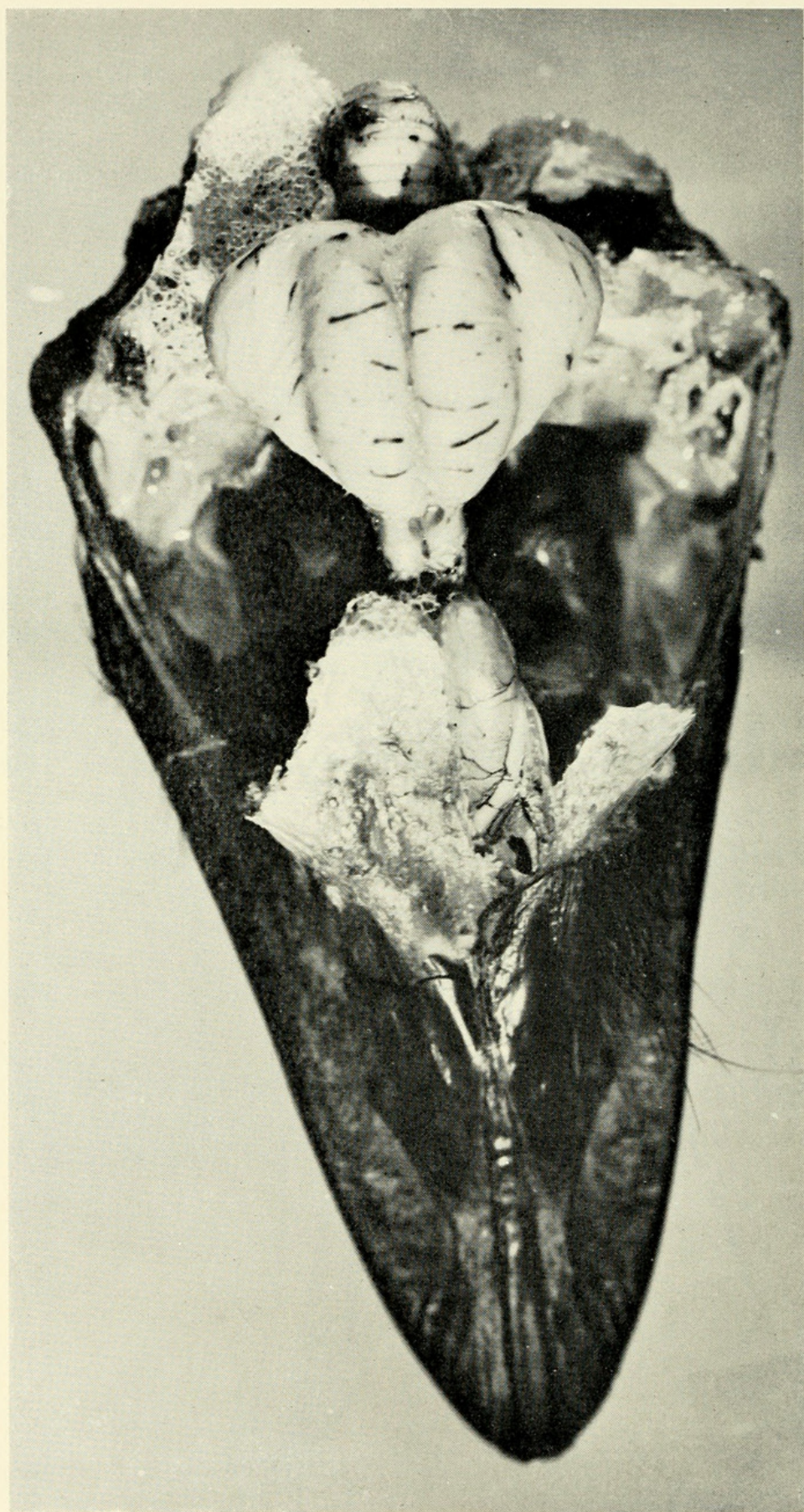


Figure 1B. Photograph, life size, of dorsal view of same dissection.

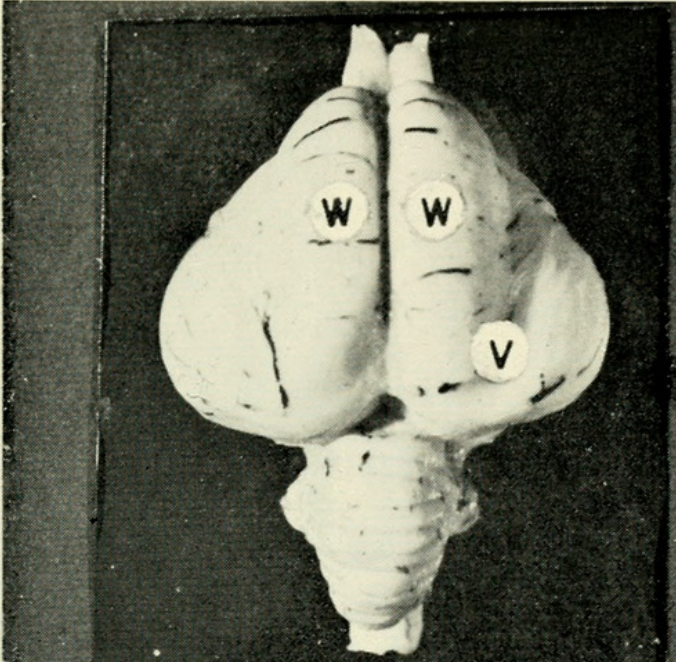
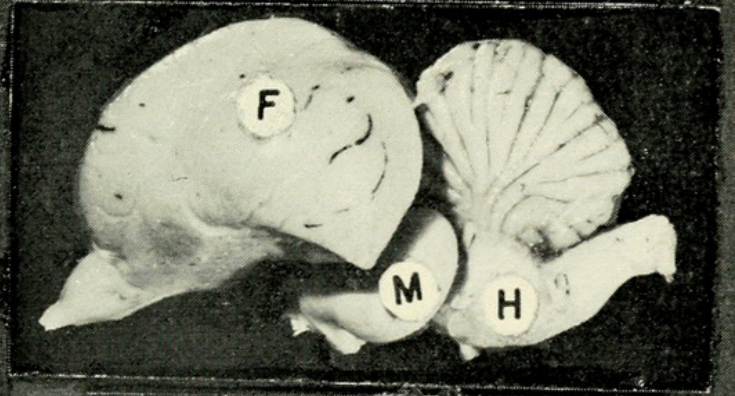
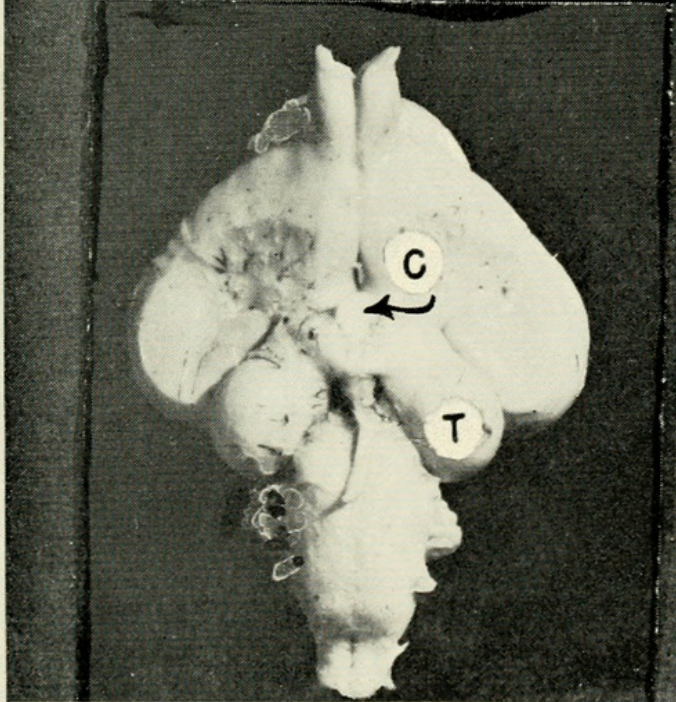
FIG 2^A DORSALFIG 2^B LATERALFIG 2^C VENTRAL

Figure 2. Three views of the brain of the emu (*Dromaeus novae-hollandiae*) #104. Life size. *F*, forebrain hemisphere, *H*, hindbrain, *M*, midbrain, showing optic lobe (*T*) and optic chiasm (*C*), *V*, vallecule, *W*, Wulst or hyperstriatum accessorium.

FIG 3

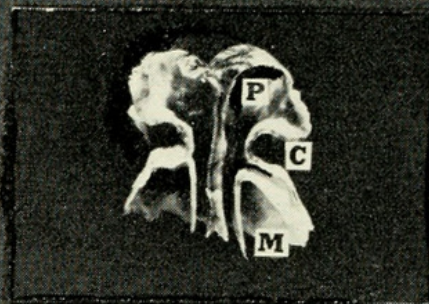
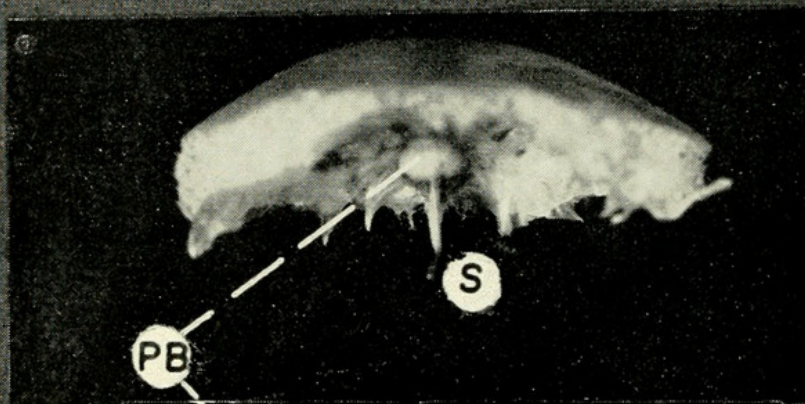
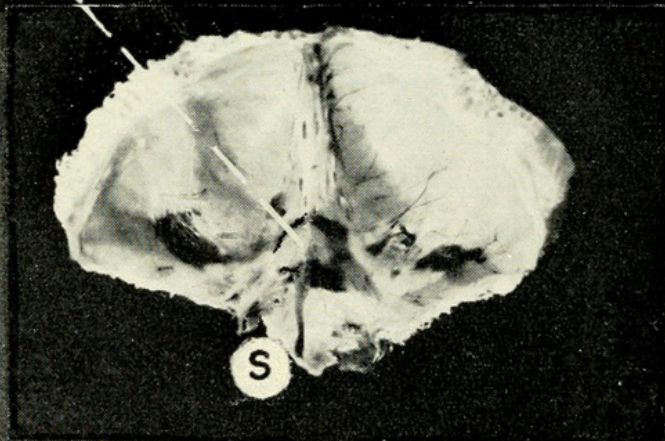
FIG 4^AFIG 4^B

Figure 3. Section through the nasal chambers cut in frontal vertical showing the olfactory (or posterior) chamber (*P*) into which protrudes the olfactory *concha* (*C*) covered with yellow olfactory epithelium. Below is seen part of the middle nasal chamber (*M*). The two chambers are divided by the *septum*. They connect anteriorly with the anterior chamber and the external nostril. Life size.

Figure 4A. Photograph, life size, of pineal body (*PB*) lying in shallow cavity of the calvarium, posteroanterior view. The stalk (*S*) protrudes downward.

Figure 4B. Ventral view, looking upwards at under surface of calvarium. The stalk (*S*) is bent backwards.



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