

ON THE ANGLE OF THE CEREBRAL AXIS  
IN THE AMERICAN WOODCOCK

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One of the conspicuous things about birds is the evolutionary development of forms suited to very special environmental conditions. Examples are easy to pick out, from hummingbird to ostrich, but perhaps one of the most interesting is that caricature of the Charadriiformes, the American Woodcock (*Philohela minor*). Evolutionary development has caused marked changes in the skull of the woodcock, especially the relation of the bones of the skull to the orbit, and to the *foramen magnum*. The unique osteology has been described by Shufeldt (1903).

Hofer (1952, 1954) has recently made careful studies of the skulls of various birds and describes two main types, the extended and the bent. He uses three axes: the axis of the bill, that of the base of the skull, and that of the brain. In the extended type of skull, these three are nearly parallel, and close together. In the bent type of skull they may make marked angles with each other. The cormorant is an example of the former; most birds are of the bent type; Hofer gives examples in his figures of parrot, hawk, pigeon and four of the snipe family, including *Scolopax*, which is the extreme of the bent type. No measurements of the angles are recorded.

The extraordinary position of the woodcock's brain within the skull, and its relation to eye and bill was brought forcibly to my attention the first time I removed the brain. It seemed to be almost upside-down with the cerebellum in a ventral position and the *medulla oblongata* leaving the cranial cavity through a ventrally placed *foramen magnum* with a slightly frontal slant (see Fig. 1).

## MATERIAL AND METHOD

In order to follow through on this preliminary observation, two more woodcock, a Short-billed Dowitcher, a Semipalmated Sandpiper, a Semipalmated Plover, and three Herring Gulls were collected. Dissections were made of formalin fixed specimens.

It was found that good fixation of the brain *in situ* could be obtained by skinning the head and neck immediately after death, removing the eyes, and then placing the whole head in 20% formalin for 10 days. After a thorough washing the dissection could be carried out using "magnifocuser" eye-glasses and small surgical rongeurs.

The skull was removed piece by piece starting at the cerebellar area where the bone is thick. The removal was carried forward, great care being taken to leave the rim of the orbit intact, to show the relationship of brain to eye. A lateral photograph was then made, showing the exposed brain, seated on the

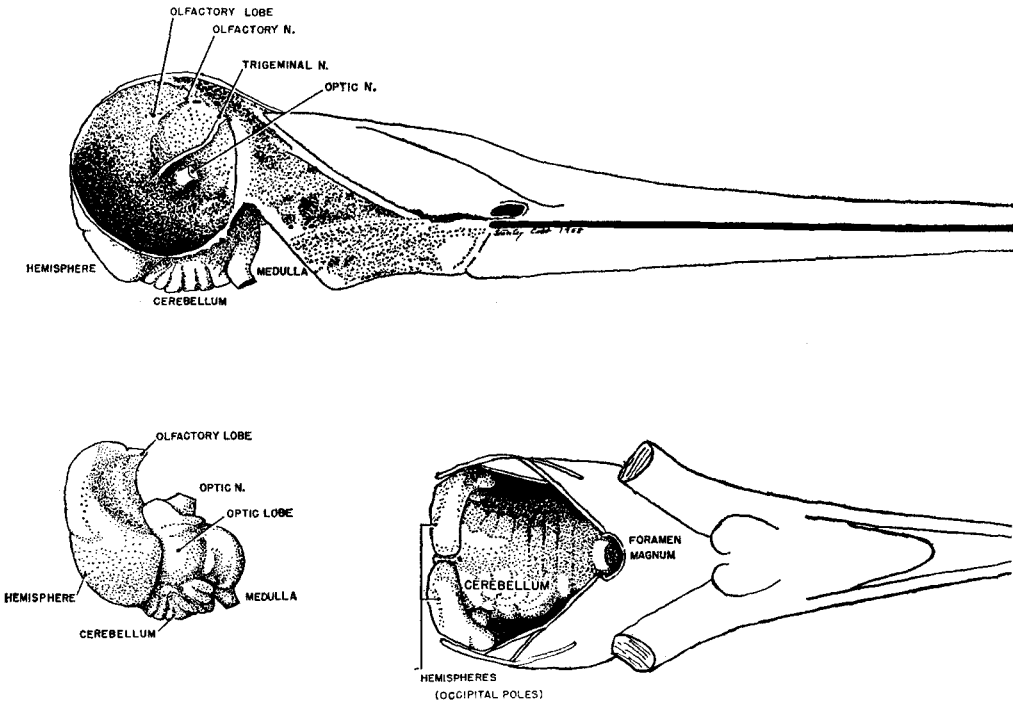


FIGURE 1. Lateral and ventral view of woodcock's brain *in situ*, and one lateral view of brain removed. The anterior part of the fore-brain and the olfactory bulb can be dimly seen through the thin bone of the orbit. The olfactory nerve going to the superior turbinal chamber of the bill can also be dimly seen. The cerebellum in the ventral view appears comparatively large because three large folia are exposed that are mostly hidden by the occipital pole of the cerebral hemisphere in the lateral views. (Dissections and drawings by the author.)

base of the skull, in its relation to orbit, nasal chambers and bill. It was difficult to make measurements directly from the specimen or even from a photograph, so tracings were made in which were emphasized the relative positions of brain, orbit, nasal chambers, nostril and bill.

On these tracings, an axis was plotted along the base of the brain, passing anteriorly through the middle of the olfactory lobe, and posteriorly through a point in the middle of the *medulla oblongata* just below the caudal tip of the cerebellum (see Fig. 2). This is called the cerebral axis. It meets a secondary imaginary line drawn the length of the bill between the mandibles and extending through the skull to the base of the brain. The angle formed by these lines is called the brain-bill angle. It seems to indicate the amount of rotation backwards of the brain from its more usual anterior position in birds that have smaller orbits and shorter bills. Taking the Semipalmated Plover as an example (Fig. 2), this angle can be measured as  $85^{\circ}$ . The error in measurement is rather large because the exact axis of the bill cannot be determined, the curve of the mandibles often not fitting any straight line. Nevertheless an average line can be chosen and the angle measured in degrees is accurate enough to permit meaningful comparisons.

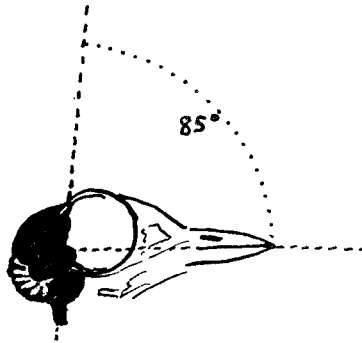


FIGURE 2. Tracing from photograph of brain and dissected skull of Semipalmated Plover, showing *cerebral axis*, *axis of bill*, and *brain-bill angle*.

#### OBSERVATIONS

Using this method, the brain-bill angles in 5 birds of the order Charadriiformes is found to be as follows:

Herring Gull ( <i>Larus argentatus</i> )	$34^{\circ}$
Semipalmated Sandpiper ( <i>Ereunetes pusillus</i> )	$60^{\circ}$
Short-billed Dowitcher ( <i>Limnodromus griseus</i> )	$78^{\circ}$
Semipalmated Plover ( <i>Charadrius semipalmatus</i> )	$85^{\circ}$
American Woodcock ( <i>Philohela minor</i> )	$117^{\circ}$

These angles between brain axis and bill are shown diagrammatically in Figures 2 and 3.

The Herring Gull is included for comparison, because of its inclusion in the order Charadriiformes (A.O.U., 1957) or Laro-Limicolae (Mayr and Amadon, 1951). It is used as an example of a member of this order that has not developed snipe-like modifications. The other three shown in Fig. 3 obviously are snipe-like, the woodcock being the extreme.

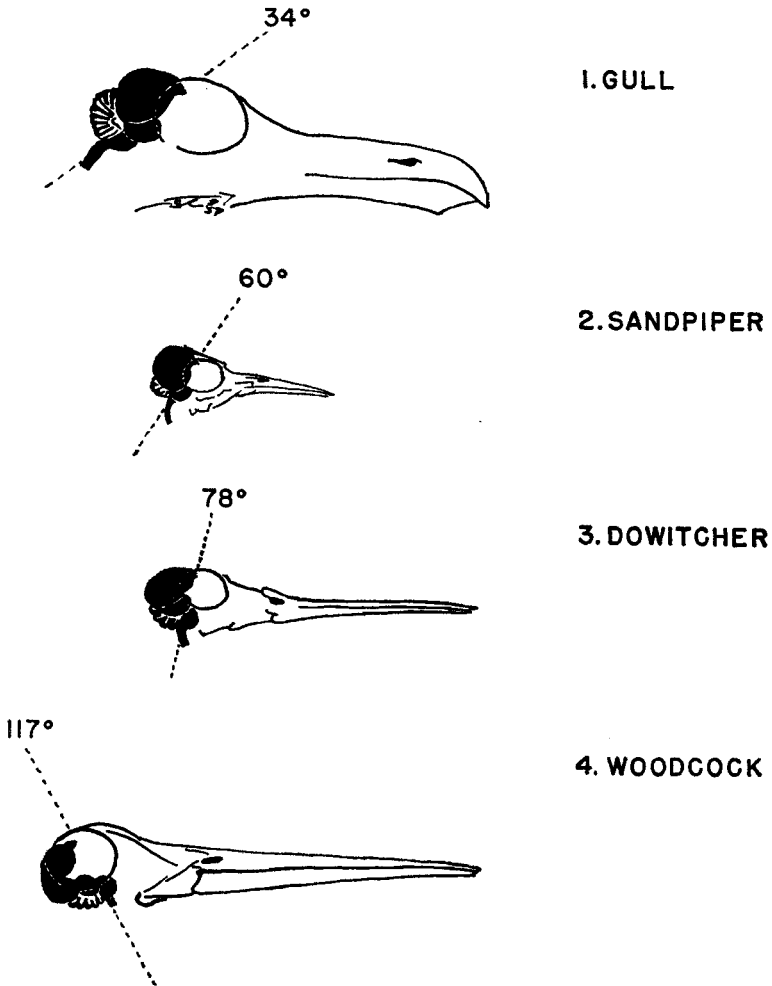


FIGURE 3. Diagrams of brains *in situ* in skulls of four Charadriiformes, showing cerebral axes (dotted lines) and brain-bill angles, measured in degrees. (From above down) *Larus argentatus*, *Ereunetes pusillus*, *Limnodromus griseus* and *Philohela minor*.

## DISCUSSION

The brain-bill angle seems to give a means of measuring a significant phylogenetic change occurring in those Charadriiformes which become progressively more specialized for probing for food with a long bill in wet ground. What actually occurred during the millions of years of evolution is not known, but one can speculate as to the series of events. The eye apparently moved backward as the bill lengthened and the nostril approached the base of the bill. As the eye developed its large size and posterior position, it gained space at the expense of the fore-brain, which was rotated backward, causing the mid-brain and hind-brain to push downward and even slightly forward. The woodcock feeds largely at night, and the eye is relatively enormous. It is also more posterior (occipital) in position. This would seem to have two advantages to the bird; when feeding he can see more above and behind, and the eye will be less likely to get in the mud.

Since the evolutionary change is evidently related to such an important function as food intake, it is reasonable to look on it as caused by natural selection. But it is remarkable that such a profound anatomical reconstruction could take place within a group of such closely related species. The brain-bill angle is merely a convenient and measurable indicator of the evolutionary development.

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