

ecology of alkaline lakes during the Percy Sladen Expedition to the Rift Valley Lakes in Kenya she was able to watch two species of flamingo feeding, and established that one of them, *Phoeniconaias minor*, feeds exclusively on minute blue-green algae and diatoms. An extremely fine filter is necessary to separate such minute organisms from the water, and further examination showed that the mesh of the filter mechanism in this species is of the order of only 0.01 mm. across. In the other species, *Phoenicopterus antiquorum*, the filter is much coarser with a mesh of about 0.5 mm. \times 1.0 mm., and the food consists of such comparatively large organisms as chironomid larvæ, small molluscs and crustaceans and seeds of lacustrine plants. The two species can therefore feed in the same lake without competing for food.

A transverse section of the bill of a flamingo shows a median ridge in the roof of the mouth that causes the palate to be V-shaped in section, with each limb of the V opposing the corresponding inner surface of the mandible. In some species, the "shallow keeled" forms, the angle of the V is obtuse; in others, the "deep keeled" forms, it is acute and the opposing surfaces are comparatively much larger. Beneath the apex of the V the tongue, more or less circular in section, fills a corresponding groove between the rami of the mandible. Two rows of recurved hooks on its dorsal surface fit into the spaces on each side between maxilla and mandible. The opposing surfaces of the jaws are beset with rows of lamellæ broken up into small platlets, which in some species have fringed edges so that they show a remarkable resemblance to the baleen of whalebone whales on a minute scale. At the margins of the jaws there is a series of much larger lamellæ or hooks, "the excluders", each corresponding to several rows of the finer lamellæ.

All species of flamingo wade or swim in the water and depress the head into such a position that the upper surface of the upper jaw is directed downwards, a posture which is facilitated by the downward curvature of the distal part of the bill. The head is swept from side to side in wide curves either at the surface or below it according to the species and the type of food sought. At the same time the fleshy tongue is moved to and fro in its groove like a piston so that water is pumped in and out of the mouth. On the suction stroke the jaws are slightly separated to break the filter and allow particles of a size that can pass the excluders to enter the mouth with the water. On the exhaust stroke the jaws are approximated so that the particles are retained on the filter as the water is expelled through it. On the following suction stroke the particles are removed from the filter and passed backwards towards the oesophagus by the recurved spines on the surface of the tongue. The movement of the bill produces an action analogous to that of woolcarders, so that the enmeshed particles are gathered together and presented to the hooks on the tongue.

Flamingoes are not, as has been claimed, monophagous. They eat any organisms that pass the excluders and are retained by the filters, and if the diet is limited to one species that is an ecological accident. When as a result of 'over fishing' or of climatic factors all the organisms that can be collected have disappeared, the flamingoes move to new feeding grounds—they are notoriously erratic in their appearances and breeding sites. But if the normal food supply runs short when they cannot depart because they are tied to a particular area where they are nesting they resort to feeding upon mud, and

obtain their nourishment from the organic matter, diatoms and debris, included in it.

Miss Jenkins emphasizes the importance of filter feeding to flamingoes feeding in lakes where the waters differ osmotically and in ionic balance from the body fluids of the birds. By concentrating the food organisms a minimum of the physiologically unsuitable medium is ingested, with a consequent easing of the burden placed upon the kidneys. Filter feeding, in addition to its use in obtaining nourishment, appears to have an equally important function in preventing excess salts from passing beyond the bill into the alimentary canal. In support of this conclusion the author adduces the well-known fact that flamingoes periodically leave their feeding grounds to drink at fresh-water sources.

Finally, Miss Jenkin discusses the affinities and evolution of the flamingoes, and concludes that they are descended from early anseriform ancestors and that they occupy an intermediate position between the Anseriiformes and the Ciconiiformes.

The author is to be congratulated upon a most interesting and important series of researches which have occupied her attention for a considerable time. As ever in original investigation, her results, while recording numerous hitherto unknown facts, raise a considerable number of new problems which, it is to be hoped, she or her pupils will have the opportunity of resolving.

L. HARRISON MATTHEWS

THE SITE OF THE NEUROHYPOPHYSIAL OSMORECEPTORS

THROUGH the classical work of Verney in the 1940's, presented so elegantly in his Croonian lecture (*Proc. Roy. Soc.*, B, 135, 25; 1947), a physiological mechanism was elucidated by which the organism is able to regulate its water loss with the urine. A series of elegant experiments accomplished under fully physiological conditions in the dog led Verney to the conception of osmoreceptors situated in the brain, within the distribution area of the internal carotid artery. These receptors, when activated by a normal or raised osmotic pressure of the blood, send impulses to the neurohypophysis to release the anti-diuretic hormone.

Recently, P. A. Jewell and Prof. E. B. Verney, in an extensive paper*, have summarized ten years continued work in this field. In a long series of laborious experiments, performed with the utmost carefulness, skill and inventiveness, they have been able to show that neurohypophysial osmoreceptors are localized within the anterior hypothalamus and, perhaps, also within adjacent parts of the pre-optic area. What makes this work so valuable and decisive is the fact that here as in Verney's earlier experiments they have exclusively used blood-borne, physiological stimuli on unanesthetized animals.

It is not possible to do justice to this work within the limits of a short review, but some of the main points may be mentioned.

To trace the arterial blood, which in the different experiments had carried the osmotic stimuli, it was first necessary to make a careful anatomical study of

* *Phil. Trans. Roy. Soc.*, B, No. 672, 240, 197 (1957): An Experimental Attempt to Determine the Site of the Neurohypophysial Osmoreceptors in the Dog. By P. A. Jewell and Prof. E. B. Verney. (London: Royal Society, 1957.) 52s. 6d.

the arterial connexions of the circle of Willis and of the detailed vascular architecture of the diencephalon and the hypophysis in the dog, and further, with the help of suitable coloured substances, to study the distribution of vertebral and carotid blood in the brain. These careful studies of the vascular supply of the dog's brain will certainly be of the greatest value to anyone who, in the future, traces the distribution of arterially injected substances in the brain of the dog.

After an account of these preliminary studies, the authors describe experiments performed to localize the osmoreceptors. Having tested the antidiuretic response obtained from infusions of hypertonic saline into the common carotids in dogs supplied with carotid loops but otherwise intact, they started to study the effect of tying one or more of the carotid branches supplying the brain with blood. Tying of the branches of the internal carotid intradurally, especially, necessitated a very delicate operative technique. After killing the animals, the distribution areas of both carotids were traced with the help of coloured substances. In all cases where an antidiuretic response to infusions of hypertonic saline was obtained on the side of the brain where the distribution of carotid blood had been restricted, the anterior hypothalamus and adjacent parts of the pre-optic area had been reached by hypertonic blood. No other part of the brain was reached directly by the infusions. The authors thus have good reason to conclude that the neurohypophysial osmoreceptors are localized in the anterior hypothalamus and perhaps also parts of the pre-optic area.

The results of the last two experiments reported in the work might at first sight seem somewhat confusing. In these, all three main branches of the internal carotid had been tied intradurally on one side, leaving some smaller branches to supply the ipsilateral parts of the hypothalamus with arterial blood. The result in both cases was that the antidiuretic response seen before the operation, due to intracarotid infusions of hypertonic saline, vanished completely. The occlusion of these three branches of the internal carotid had, however, in one of the dogs, caused the formation of a cyst in the anterior hypothalamus, and a reduction in the number of cells in the remaining nuclei. In the other dog a large cyst was formed in the thalamus, and the greater part of the anterior hypothalamus had been supplied from the carotid of the opposite side. This seems in itself to be a possible explanation for the lack of response to the infusion of hypertonic saline on the side operated upon.

On the basis of these two experiments, and of other observations which cannot be mentioned here, the authors put forward the interesting hypothesis that the functioning of the hypothalamic osmoreceptors may be dependent upon the integrity of nervous connexions with the thalamic paraventricular nucleus. Further experiments to test the validity of this hypothesis are suggested at the end of the paper.

In short, this solid work of Jewell and Verney forms an extremely valuable complement to Verney's earlier pioneering research on the physiological regulation of the function of the neurohypophysis. Their results have meanwhile been fully supported by the work carried out at the Royal Veterinary College of Stockholm by B. Andersson and his collaborators, who have been able to elicit not only thirst, but also an inhibition of water diuresis in conscious goats, by electrical stimulation within the anterior hypothalamus.

YNGVE ZOTTERMAN

MOSAIC EVOLUTION IN HYDROIDS

IN many animals different organs are capable of undergoing independent evolution at different rates. The idea of 'mosaic evolution' is becoming familiar to systematists in a number of groups. It both enriches the story of phylogeny, and bedevils those classifications that have relied on a few 'good taxonomic characters'. In the hydroid cœlenterates, moreover, the two phases of the life-history—polype and medusa—have an almost independent existence, and it is peculiarly easy for them to evolve separately and each acquire new characters not apparent in the morphology of the other. In traditional classifications, the polype and medusa of the same species have often had different names, separate families and have been described by different workers. Realization of this was not wanting, even in 1864 with Allmann's lament that "the principles of classification that have been regarded as the only sound ones in other groups have been almost entirely ignored in our attempts at a systematic arrangement of the Hydroida".

With modern knowledge the need for dual classification is ending, and in a recent report* by Dr. W. J. Rees, proposing a new arrangement of the capitate hydroids, a large advance has been made. Dr. Rees has, for the first time, merged polypes and medusæ into a single phylogenetic classification; and in this he has had much careful work to draw upon, especially the studies of Russell, Kramp and himself. This must be an important paper for the hydroid specialist; and it is a stimulating one for the general zoologist who is fond of hydroids or teaches marine biology. The author gives a lucid account of the suborder Capitata, drawing his evidence widely from both polype and medusa, with particular attention to the relation of form and function in his own experience of living hydroids. The resulting classification is a 'liberal' and broad-based one.

Theories of alternation of generations (there seems no good reason to avoid this term) are reviewed. The older hydroid theory held the sexually propagating polype to be the primary form in Hydrozoa. The medusa arose from a later 'division of labour', though this hypothesis could never properly account for the Trachylina. Dr. Rees firmly supports Brooks's theory (now most widely accepted) of the ancestral role of the simple 'actinula', which gradually took advantage of attachment, and by vegetative proliferation gave rise to a polypoid phase. The earliest hydroid was probably a primitive medusa, comparable with a trachylinid, and the medusal theory and actinula theory are in fact complementary.

The body of the paper is a consideration of evolutionary trends and mosaic patterns developed in the polype and the medusa. Dr. Rees rejects Kramp's view that the colonial corynoids are the most primitive polypes: colonial forms—he holds—have arisen from solitary forms, and the existing lower Corymorphines come nearest to the ancestral form of the hydroid polype. Here we have types like *Hypolytus* and *Euphysa* with a feeble perisarc, no diaphragm and no well-developed stem canals. The oral tentacles are capitate or moniliform but the aboral circlet always moniliform, corresponding with the tentacles of the

* Bulletin of the British Museum (Natural History). Zoology, Vol. 4, No. 9: Evolutionary Trends in the Classification of Capitate Hydroids and Medusae. By Dr. William J. Rees. Pp. 453-534 + plates 12 and 13. (London: British Museum (Natural History), 1957.) 25s.