THE BRAIN OF COENOLESTES OBSCURUS

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Coenolestes is a small ratlike Americal marsupial about five inches in length from tip of snout to root of the slender tail. It is a native of the high Andean forests and has been known to science since 1860, so far by rare and usually incomplete specimens from Colombia, Ecuador and Peru. Dr. Wilfred H. Osgood of the Field Museum recently collected eleven specimens, which he made the basis of an extensive monograph published in 1921. The brain of one specimen was sufficiently preserved for study, and Dr. C. Judson Herrick described and figured its dorsal, lateral and ventral surfaces in an appendix to the monograph. Cut into serial sections and stained by the iron-haematoxylin method to show both cells and fibres, it forms the basis of the present study.

The brain of this creature is especially interesting for two reasons. First, because it is one of the simplest and most generalized of mammalian brains, since both the monotreme brains are rather highly specialized. Second, because the classification of Coenolestes in one or the other of the two marsupial suborders, Polyprotodontia and Diprotodontia, has given rise to a long and lively controversy.

In his account of the external features of this brain Dr. Herrick drew attention to its extreme simplicity, as evidenced both by the enormous development of the visible olfactory regions (olfactory bulbs, olfactory tubercles, lateral olfactory cortex) and by its small and smooth cerebral cortex, which he thought to be probably the least extensive, relative to the total weight of the brain, in the whole mammalian series, as so far described. He noted also that in external conformation the brain of Coenolestes resembled much more closely those of two Australian polyprotodont forms, the bandicoot Perameles and the marsupial mole Notoryctes, than it did that of the American opossum.

The lateral olfactory cortex, the cortex of the pyriform lobe (lob. p.), occupies more than half the lateral surface of the brain (Fig. 1). Both anteriorly and posteriorly it is in continuity with the median olfactory cortex or hippocampus (hip.). Dorsally (Fig. 2) the two are split apart by the wedgelike neopallium, which occupies the dorsal surface of the hemisphere. Its lines of contact with the two olfactory cortices are marked by two

Fig. 1

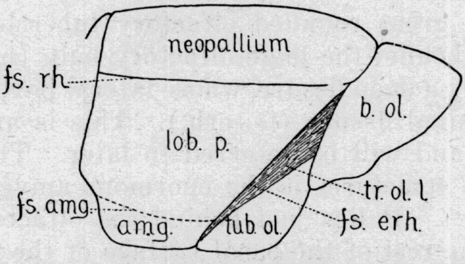

FIG. 1. Lateral view of the cerebral hemisphere of Coenolestes obscurus, as reconstructed from serial sections.

Reference letters: *amg.*, amygdaloid complex; *b. ol.*, olfactory bulb; *fs. amg.*, amygdaloid fissure; *fs. erh.*, endorhinal fissure; *fs. rh.*, rhinal fissure; *lob. p.*, pyriform lobe; *tr. ol. l.*, lateral olfactory tract; *tub. ol.*, olfactory tubercle.

Fig. 2

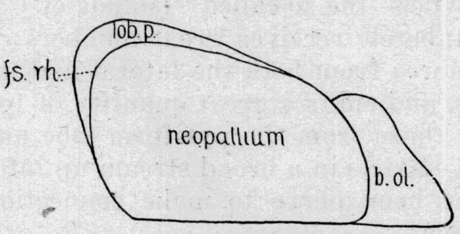

FIG. 2. Dorsal view of the cerebral hemisphere of Coenolestes obscurus, as reconstructed from serial sections.

Reference letters: *b. ol.*, olfactory bulb; *fs. rh.*, rhinal fissure; *lob. p.*, pyriform lobe.

Fig. 3

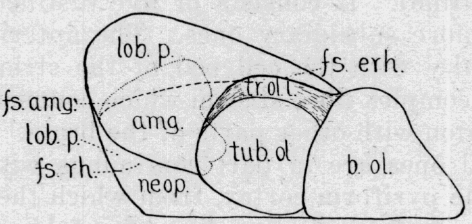

FIG. 3. Ventral surface of the cerebral hemisphere of Coenolestes obscurus, as reconstructed from serial sections.

Reference letters: *amg.*, amygdaloid complex—dotted outline indicates internal extent; *b. ol.*, olfactory bulb; *fs. amg.*, amygdaloid fissure; *fs. erh.*, endorhinal fissure; *fs. rh.*, rhinal fissure; *lob. p.*, pyriform lobe; *neop.*, neopallium; *tr. ol. l.*, lateral olfactory tract; *tub. ol.*, olfactory tubercle.

fissures—the hippocampus fissure (fs. hip.), where it meets the hippocampus, and the rhinal fissure (fs. rh.) where it meets the pyriform cortex (lob. p.)

Ventrally (Fig. 3) also these two olfactory cortices, lateral and medial, are separated by another wedgelike mass composed of two structures, one behind the other, both enormously developed in this brain. The anterior one is the great rounded olfactory tubercle (tub. ol.), lying just behind the huge olfactory bulb (b. ol.). It is encircled by a deep fissure, whose lateral portion is called the endorhinal fissure (fs. erh.). This is an important landmark and will be referred to later. The posterior of the two structures is the enormous amygdaloid complex (amg.). It lies just behind the olfactory tubercle and fills the rest of the basal surface of the brain.

Both these structures are complex as well as very large. In microscopic sections the olfactory tubercle presents a highly spectacular picture of convoluted and rolled cell masses or sheets, composed of cells of many sizes and types—the so-called ''islands of Calleja''. The olfactory tubercle receives great numbers of secondary olfactory fibres from both the lateral and median olfactory tracts, and emits a great quantity of tertiary fibres which join those from the pyriform lobe and sweep beneath the ventricle in a broad stream up into the median wall of the hemisphere to make connections with the hippocampus.

The amygdaloid complex (amg.), whose enormous superficial extent has already been emphasized, exceeds internally this area both in breadth and length (Fig. 3, dotted outline). It consists of five distinct nuclei and perhaps more subsidiary ones. The anterior ones are in continuity with the cell bed of the stria terminalis, the great complex fibre stream which connects the amygdaloid region with other parts of the brain. The posterior lateral ones are in part continuous with the lower edge of the pyriform cortex, from which they appear to have been derived along a line of infolding whose external manifestation Dr. Johnston has called the amygdaloid fissure. This fissure, externally very obscure but internally obvious, continues the endorhinal fissure (fs.

erh.) backward, and the two together mark the ventral border of pyriform cortex.

The median surface (Fig. 4), known only in reconstructions (since the brain was cut entire), strikingly conforms to the simplicity of the exposed surfaces. It is typically marsupial, but the dorsal or hippocampal commissure (com. d.), which assumes a more or less pronounced bilaminar form in marsupials, is here triangular, with only a hint of bilaminarity. In this respect it approaches nearer to the solid rounded monotreme form in Coenolestes than it does in the other marsupials.

Fig. 4

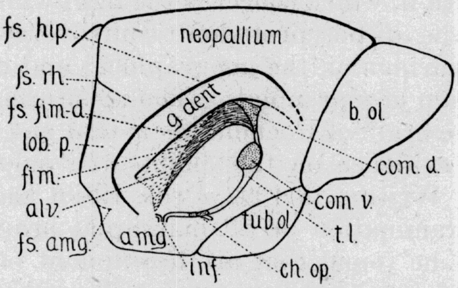

FIG. 4. Median section of the cerebral hemisphere of Coenolestes obscurus, as reconstructed from serial sections. The thalamus has been cut away. The gyrus dentatus appears on the exposed median surface between the hippocampal and fimbrio-dentate fissures (the latter of which is posteriorly really an alveo-dentate fissure in this case, since the extra-ventricular alveus covering the hippicampus inversus or upturned median flap of the ammon's horn, intervenes between this part of the fissure and the fimbria).

Reference letters: *alv.*, extraventricular alveus; *amg.*, amygdaloid complex; *b. ol.*, olfactory bulb; *ch. op.*, optic chiasma; *com. d.*, dorsal commissure; *com. v.*, ventral commissure; *fim.*, fimbria; *fs. amg.*, amygdaloid fissure; *fs. fim.-d.*, fimbrio-dentate fissure (alveo-dentate fissure posteriorly); *fs. rh.*, rhinal fissure; *g. dent.*, gyrus dentatus; *inf.*, infundibulum; *lob. p.*, pyriform lobe; *l. t.*, lamina terminalis; *tub. ol.*, olfactory tubercle.

Two great arched fissures mark the position of the hippocampus (hip.), which occupies a great part of the median wall of the hemisphere. Anteriorly the upper or hippocampal fissure (fs. hip.) extends very far forward, in the manner characteristic of this type of brain. Posteriorly it is considerably less developed than in the opossum, and apparently even less than in Notoryctes. No suitable figure of Perameles was available for comparison on this point. Internally this fissural situation is correlated with an extremely simple condition of the posterior or temporal end of the hippocampus. In this brain the temporal end of the hippocampus, which marks the morphological anterior end of the temporal lobe in higher mammals, lies very near the posterior pole of the hemisphere, a condition recalling that found in the reptiles. There is only a very slight forward curvature of the hippocampal formation in this region. The hippocampus is, as it were, caught in the very act of ''turning the corner''. The opossum hippocampus has already done so very neatly, by means of the formation of a forwardly directed pouch of cells.

Turning now from a study of the general anatomy of this brain we may consider the second phase of interest connected with it, which concerns the light which it might shed upon the di-polyprotodont controversy, with its important bearings on the geographical and chronological distribution of marsupials. The most exciting single feature of the brain of Coenolestes is that one which constitutes the evidence on this point—the only evidence, apparently. Writing in 1902, Prof. Elliot Smith stated that upon examination of all marsupial brains (except Coenolestes) he found that all diprotodont brains without exception possessed an anatomical peculiarity which was not to be found in any polyprotodont brain or in any other mammalian brain, and which therefore constituted a true diagnostic character of diprotodont brains. This structure he named the 'aberrant bundle''. It is the upper part (Fig. 5, f. ab.) of the anterior or ventral commissure which splits away from the lower part to gain the corona radiata by way of the internal capsule (cap. i) instead of by the usual route in the external capsule (cap. e). It appears in every diprotodont brain regardless of size, from the giant kangaroo, five feet long from snout to root of tail and weighing 200 pounds, to the pygmy flying phalanger, two and a half inches long exclusive of the tail. It is absent in every polyprotodont, American or Australian, including the largest, the Tasmanian wolf, which it is said a number of dogs will hesitate to attack. I have not been able to detect it in Coenolestes. If it be accepted as a criterion of diprotodont brains, Coenolestes should be classified with the polyprotodonts. This reverses Dr. Osgood's conclusions, based on careful and exhaustive sifting of all lines of evidence save that from the nervous system. Thus America is left with only extinct diprotodonts, the internal anatomy of whose brains we can, unfortunately, never know. One might, of course, take the position that the "aberrant bundle" is a character of the Australian

Fig 5

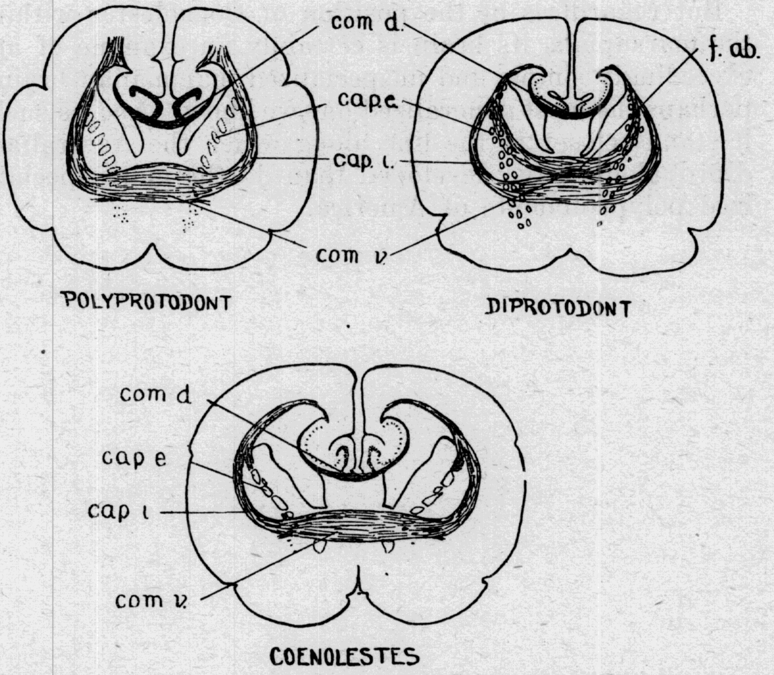

FIG. 5. The aberrant bundle. Corresponding sections through the brains of a polyprotodont and a diprotodont (from Elliot Smith), and Coenolestes.

Reference letters: *cap. e.*, external capsule; *cap. i.*, internal capsule; *com. d.*, dorsal commissure; *com. v.*, ventral commissure; *f. ab.*, aberrant bundle.

diprotodonts alone, developed after the diprotodont stem split in two, an Australian and an American. Dr. Osgood in the final paragraph of his monograph says that the classification of Coenolestes with the diprotodonts "does not emphasize its supposed phylogenetic relationship to the [polyprotodont] peramelids, but recognizes its advance beyond them to greater morphological similarity to the specialized diprotodonts. On the basis of present findings, the only logical alternative would be to remove the peramelids from the Polyprotodontia and unite them with the coenolestids in a group co-ordinate with (1) the Australian Diprotodontia and (2) the remaining Polyprotodontia. This, however, could not be done consistently without further division, especially of the polyprotodonts, which does not seem advisable in the present state of knowledge."

But regardless of the position of Coenolestes within the marsupials, its brain is certainly an example of an exceedingly simple and unspecialized mammalian brain, perhaps the most generalized one we know. And as such it stands closer to the line along which the Australian diprotodonts have developed than do the more specialized polyprotodonts of America.