THE CEREBELLM OF REPTILES: LIZARDS AND SNAKE

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TWENTY-FOUR FIGURES

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INTRODUCTION

The different groups of reptiles show a wide divergence in the structure and degree of development of the cerebellum. This appears to be correlated with the habits and activities of the various types, and these activities, in turn, are closely related to differences of bodily structure, with especial reference to the degree of development of the legs and to the use of the trunk in locomotion. In the single order of the Lacertilia there is present a variety of types. In the family Iguanidae, for example, there are many quick and active forms, with well-developed legs which support the entire weight of the body and lift it from the ground. In some genera, as Sceloporus, the tail also is relatively short, and in Phryno-
soma the tail is very short. Among the Anguidae there are various degrees of development of the legs, with less activity of these lizards, as a rule, than among the previous group. In the Euchirotidae, Amphisbaenidae, and Anniellidae we find subterranean forms in which the limbs have completed their degeneration, save in the Euchirotidae, in which the fore legs still remain.

A comparison of the cerebellum of the various members of these groups reveals striking differences of structure. When this comparison is carried further so as to include the active but limbless snakes, on the one hand, and the relatively sluggish but heavy-bodied turtles, on the other hand, many features are encountered which are of great interest to the general problem of the cerebellum. The present study has been conducted with the comparative point of view primarily in mind. The variations in the relatively simple cerebella of these reptiles are believed, in the light of the observations to be here recorded, to be significant when considered from the viewpoint of the mode of locomotion and degree of activity of the various species available for study. The present paper will be confined to the lizards and garter snake, with occasional reference to the turtle and alligator, of which only a preliminary study has been made by the present writer.

**MATERIAL AND METHODS**

Representatives of two orders of reptiles were used in this study, namely, lizards and snakes. For the snake group I utilized the common western garter snakes abundant in western Oregon, of which Thamnophis sirtalis concinna (Hal.) and Thamnophis leptocephala (B. and G.) constitute the most common species. The basis for the study of the lizard cerebellum was supplied by three families of this group, namely, the Anniellidae, the Iguanidae, and the Anguidae, as represented by Anniella nigra, Gerrhonotus principis, and Sceloporus biseriatus, Sceloporus graciosus, and Phrynosoma douglasii, respectively. In addition to adult animals, a number of embryos of Gerrhonotus and Thamnophis were also
available, but unfortunately in not sufficiently closely graded series to give a complete story of the development of the cerebellum in any one of these forms. The embryonic material has been of great value, however, in helping to resolve some points of difficulty with the adult cerebellum. For the three heads of Anniella nigra upon which is based the description of the cerebellum of this interesting species, I am indebted to Dr. W. F. Allen.

The brains of the adult snakes and lizards were removed and fixed by various standard methods. Some were studied by dissection with the aid of the stereoscopic binocular microscope, others were embedded in paraffin, cut in serial sections at a thickness of 15 to 20 μ in the three conventional planes, and stained by standard methods. The principle staining methods employed were Heidenhain’s iron-hematoxylin, the Pal-Weigert method, hematoxylin and eosin, and the method of Ramón y Cajal. The younger embryos of Gerrhonotus were embedded whole and sectioned, while with the older stages of the lizard, as well as all of the stages of the garter snake, the head was removed, embedded entire, and then sectioned.

Models were reconstructed by the wax-plate method of the cerebellar region, including part of the midbrain and part of the medulla oblongata, of the adult brains of Anniella, Gerrhonotus, and Thamnophis. With the exception of Anniella, these models were checked with dissected brains of specimens of the corresponding species under the binocular microscope.

**DESCRIPTIVE**

*General morphology*

Anniella. Because of its simplicity, the cerebellum of this legless lizard will be described first. It must be borne in mind that this cerebellum represents not so much a primitive condition as it does the organ of a degenerated type of lizard, so far as leg development and muscular activity are concerned. Anniella is a burrowing form, making its habitat in
the sand. Regarding its mode of progression in this medium but little is known. Like the lampreys and mud-puppies, which forms it resembles in the small size of its cerebellum, this lizard is capable of quick and violent jerking movements when captured.

The cerebellum of Anniella is small, both in actual size and in proportion to the size of the rest of the brain. It lies in a depression formed by the midbrain in front, the VII and VIII nerve roots laterally, and the swelling of the medulla oblongata caudally, so as to be almost hidden from view

ABBREVIATIONS FOR ALL FIGURES

aq.S., aqueduct of Sylvius
brconj., brachium conjunctivum
cb., cerebellum
c.c., central canal
cer.h., cerebral hemisphere
cocb., cerebellar commissure
c.t., caudal tongue of pars interpositaﬂ.arc.d., dorsal arcuate fibers
f.arc.int., internal arcuate fibers
f.l.m., median longitudinal fasciculus
gn.VII, ganglion of VII nerve
gn.VIII ac., acustic ganglion of VIII nerve
hyp., hypophysis
l.aur., auricular lobe
lm., lemniscus
l.olf., olfactory lobe
l.vest., vestibular lobe
med.obl., medulla oblongata
mes., midbrain
n.IV, trochlear nerve
n.V, trigeminal nerve
n.VII, facial nerve
n.VIII, acoustic nerve
nuc.cb.l., lateral cerebellar nucleus
nuc.cb.m., medial cerebellar nucleus
nuc.vest., vestibular nucleus
nuc.vest.l., lateral vestibular nucleus
nuc.vest.sup., superior vestibular nucleus

nuc.vest.v., ventral vestibular nucleus
nuc.III, nucleus of III nerve
nuc.IV, nucleus of IV nerve
nuc.V m., motor nucleus of V nerve
p.int.cb., pars interposita cerebelli
p.lat.cb., pars lateralis cerebelli
pl.ch., choroidal plexus
r.III, roots of III nerve
r.IV, roots of IV nerve
r.V, roots of V nerve
r.V m., motor V roots
r.V sp., spinal V roots
r.VII, roots of VII nerve
r.VII m., motor VII roots
r.VIII, roots of VIII nerve
r.VIII d., cochlear nerve
r.VIII v., vestibular nerve
s.a., anterior sulcus of cerebellum
s.p., posterior sulcus of cerebellum
s.gr., granular layer
s.mol., molecular layer
s.Pur.c., layer of Purkinje cells
t.ch., tela chorioidea
tr.mes.V, mesencephalic V tract
tr.sp.cb.d., dorsal spinocerebellar tract
tr.sp.cb.v., ventral spinocerebellar tract
tr.sp.t., spinotectal tract
tr.vest.aur., vestibulo-auricular tract
tr.vest.cb., vestibulocerebellar tract
tr.vest.d., direct vestibulocerebellar tract
vent.III, third ventricle
vent.IV, fourth ventricle
v.m.a., anterior medullary velum
The midbrain rises as a nearly vertical wall which is somewhat rounded caudally, directly in front of the cerebellum. The lateral margins of the organ are separated from the VII and VIII roots by a narrow furrow. The VIII nuclei are enlarged to such an extent at the caudal level of the VIII roots as to cover about half of the cerebellum, as this organ is viewed from behind. These nuclei of the VIII nerve also approach each other medially (fig. 1) so as to come nearly into contact at the midplane. They thus cover the rhomboid fossa, except for a narrow vertical slit between them. The lobes produced by the enlargement of these nuclei extend rostrally beneath the cerebellum (fig. 2) to such an extent that the floor of the fossa is rendered invisible when the brain is viewed from above.

Caudolaterally the cerebellum is continuous (fig. 4) with the lobe-like masses produced by the VIII nuclei. There is no sign of an auricular lobe, but laterally the cerebellum merges with the oblongata at the base of the VII and VIII nerve roots, with only a narrow depression between the two structures (fig. 4).

Although of small size, the cerebellum of Anniella is unlike that of lower urodeles and the early stages of the frog tadpole in the fact that it is massive throughout. At the midplane
there is a slight notching on the caudal border, but this merely marks the bilateral symmetry of the organ. There is a swelling on either side of the midplane which forms the corpus cerebelli. Across the midplane the massive structure of the cerebellar bodies continues unchanged, save for a slight reduction in size, as seen in sagittal section (figs. 2 and 3). In the further description this region between the corpora cerebelli will be referred to as the pars interposita, and the lateral region on either side as the pars lateralis, excluding the auricular lobe when that is present. The reasons for this terminology will be discussed in the final section of this paper.

Ventrally, the lateral recess of the fossa rhomboidea extends under the cerebellum on either side, forming a narrow, oblique cleft of separation between this organ and the lobe of the VIII nuclei. The main axis of the pars interposita is nearly vertical to the horizontal axis of the brain stem, but laterally the cerebellar axis assumes a position nearly parallel to the brain-stem axis.

The three typical cerebellar layers are present in Anniella in simple arrangement. The layer of granule cells faces caudally and ventrally, as in amphibians. The Purkinje cells form a single layer and are of small size. The molecular layer (fig. 4) faces rostrally and upward. The details of internal structure could not be satisfactorily studied in the iron-hematoxylin material, which only was available for Anniella, but without doubt the pattern of structure is very simple.

*Sceloporus and Phrynosoma.* The cerebella of these two lizards are relatively simple in structure and are very similar to each other in most respects. They have many points of general resemblance also to the organ in the frog, but they appear to represent an extreme specialization of this simple type of cerebellum. In both Sceloporus and Phrynosoma the cerebellum consists of a concavoconvex plate (fig. 5) which projects upward from the rostral end of the medulla oblongata, from which it has its genesis in the embryo. The lower part extends dorsally and slightly caudad, but about midway from the oblongata to the upper free margin it bends
rostrad and arches over the caudal part of the midbrain. The concave surface of the cerebellum is thus directed forward, and the convex surface, which represents the external surface of the stratum granulare, faces caudally and upward, in the dorsal part of the organ, and caudally and downward in the ventral part. These relations may be understood at a glance from the parasagittal section figured (fig. 5), in which

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**Fig. 3** Parasagittal section of brain of Anniella nigra. Iron-hematoxylin stain. Edinger-Leitz projection apparatus. × 12.

**Fig. 4** Transverse section at caudal level of cerebellum and level of entrance of VIII roots. Anniella nigra. Iron-hematoxylin stain. Camera lucida. × 43.

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the entire cerebellum appears sickle-shaped. In transverse sections (fig. 6) the granular layer forms the external surface all the way around the cerebellum. In cross-sections of the rostral portion a central space appears, but this has no relation to the cerebellar ventricle of turtles and some other reptiles. It is, instead, part of the cleft between the midbrain and the cerebellum, and is due to the great concavity of the
rostral aspect of the thin disc of the latter organ. The dorsal part of the cerebellum is not so large, relatively, as in Varanus, and does not show the dorsal notch (b, fig. 3, de Lange, '17) of the latter form. In other respects it is quite similar to Varanus. It is very unlike the cerebellum of Gerrhonotus, however, except laterally, where the two correspond in that both have the lacertilian feature of projecting upward and of exversion, as will be seen beyond.

Laterally, the cerebellum in both the swift and the horned lizard is continuous with the oblongata and with the vestibular lobes (fig. 6). These lobes are large, as in Anniella and other lizards, and extend medially in such a manner as to make of the rhomboid fossa a narrow slit, which is divided laterally into a dorsal and a ventral part.

The pars interposita of these two members of the Iguanidae is very similar to the pars lateralis. There is a caudal bulging of the entire region, but no trace of the tongue-like prolongation to be described in Gerrhonotus. The pars interposita projects first caudodorsally and then arches upward and forward so as to bring the stratum granulare to the dorsal surface of the organ, as previously described, and in contrast to the condition in the snake and the alligator lizard, Gerrhonotus. In transverse section of the cerebellum of Sceloporus and Phrynosoma, the stratum granulare is external and the stratum moleculare is internal because of this extreme exversion.

Gerrhonotus. The cerebellum of this lizard (figs. 7 and 8) presents a peculiar combination of features which relate it in one direction to Sceloporus and the common lizard type of cerebellum as represented by the exverted organ in this and related species; in another direction it is related to the snake type of cerebellum as shown in Thamnophis; and in a third direction it has many features which resemble the cerebellum of the crocodilian type. It appears, therefore, to be a generalized cerebellum among the reptiles which will throw light on the structure of the others named. Although generalized, it should not be regarded as the most primitive. In
Fig. 5 Cerebellar region from sagittal series of Sceloporus biseriatus. Method of Ramón y Cajal. Edinger-Leitz projection apparatus. × 25.

Fig. 6 Transverse section through cerebellar region of Sceloporus biseriatus. Iron-hematoxylin stain. Edinger-Leitz projection apparatus. × 25.
its development it resembles in early stages the iguanid type (fig. 9) and the caudal tongue of the pars interposita appears later in the development of the embryo (fig. 10). As compared with the developing human cerebellum, the exverted organ of the Sceloporus type corresponds more closely to that of the 11-mm. human embryo, as de Lange (’17) has pointed out for

Varanus. The cerebellum of Gerrhonotus, on the other hand, resembles that of the 90-mm. human embryo even more closely than does the alligator cerebellum, both as observed in median section and as seen from above. The Sceloporus type accordingly approaches more closely to the more primitive amphibian cerebellum and the early developmental stages of
the human cerebellum. However, the extreme exversion which accompanies the pronounced forward bending of the upper part of the organ in Varanus (Edinger, '08; de Lange, '17), which is also shown in Sceloporus and Phrynosoma, as

![Diagram of cerebellum](image)

*Fig. 9* Parasagittal section close to median plane of embryo of Gerrhonotus primipis of 9 mm. greatest length. Hematoxylin-eosin stain. Edinger-Leitz projection apparatus. X 17.

*Fig. 10* Parasagittal section near median plane of embryo of Gerrhonotus primipis in coiled stage of 12 mm. greatest length. Hematoxylin-eosin stain. Edinger-Leitz projection apparatus. X 32.

already described, appears to me to be an extreme specialization of a primitive type of cerebellum in these reptiles.

In Gerrhonotus, of the family Anguidae, the cerebellum is unlike that of the iguanid lizards, and of Varanus as described by Edinger and de Lange, in that it is not exverted except to a limited extent in the pars lateralis. Also, it does
not project upward and forward, save again to a limited extent laterally. The organ as a whole, viewed from above, is roughly triangular, made so by the caudally projecting median tongue of the pars interposita. This tongue is a continuation from the main mass of the middle portion of the cerebellum. A ridge, which is continuous with the lateral portions of the organ, extends over the median mass, but sections (figs. 11 and 12) show that the ridge is merely a swelling of the molecular layer. Two shallow furrows are present (figs. 8 and 11), one on the rostral surface and the other on the dorsal surface of the organ, which suggest the sulcus cerebellaris anterior and the sulcus cerebellaris posterior, respectively, of the alligator’s cerebellum, to which de Lange (’17) and Ingvar (’18) have called attention. As viewed in midsagittal section, the resemblance is even more striking, and one would appear justified in dividing the cerebellum of Gerrhonotus into three lobes—lobus anterior, lobus medius, and lobus posterior—as was done by Ingvar in the alligator, with the above-described furrows as the boundary lines. Kappers (’21) has pointed out that the sulcus anterior of the alligator is probably to be homologized with Elliot Smith’s sulcus primarius of mammals, and the sulcus posterior of the alligator with the sulcus secundus of Elliot Smith. This view appears to me to be correct and to be applicable to Gerrhonotus for reasons which will be more fully presented below.

The pars lateralis of the cerebellum of Gerrhonotus (figs. 7 and 8) is exverted like the entire organ of Varanus, Sceloporus, and many other lizards which it closely resembles except in the degree of forward bending of the dorsal portion. It is continuous ventrolaterally with the medulla oblongata, and extends medially with a nearly vertical axis, to become continuous with the pars interposita, as shown in the figure. The granular layer constitutes the caudal portion of the pars lateralis.

The pars interposita (figs. 7 and 8), on the other hand, is elongated caudally, and its granular layer, as seen in section,
looks downward (figs. 11 and 12) as in the snakes. The stratum granulare, therefore, forms the roof of the rhomboid fossa, and in transverse section, unlike Sceloporus, the molecular layer forms the dorsalmost and external layer, instead of being surrounded by a zone of the granular layer, as in the extremely exverted type of cerebellum (compare

Fig. 11 Section very close to midplane (fig. 7A) from sagittal series of Gerrhonotus principis. Iron-hematoxylin and orange-G stain. Edinger-Leitz projection apparatus. × 24.

(For plane of section of figures 11, 12, 13, and 14, see fig. 7A.)

Fig. 12 Section showing beginning of transition zone, described in text. From same series as figure 11. × 24.
The pars interposita includes the main mass of the cerebellum of Gerrhonotus and the tongue-like caudal projection above described.

The relations of the pars interposita and pars lateralis can be most readily understood by reference to the sagittal sections illustrated in figures 11 to 14. Near the midplane (fig. 11) the cerebellum is massive, with a thick molecular layer, and it extends caudally from the anterior medullary velum so that its major axis makes but a slight angle with the axis of the brain stem. Comparison with figure 16 will show the general similarity to the median portion of the snake's cerebellum. Somewhat more laterally (fig. 12) begins the transition which results in the disappearance laterally of the tongue-like caudal projection of the pars interposita and a rearrangement of the major axis, so that this, in the pars lateralis, becomes vertical to the brain stem. A parasagittal section taken from the lateral third of the cerebellum shows a typical lacertilian cerebellum (fig. 14) resembling that of Varanus, Sceloporus, and similar active forms. In the transition zone (figs. 12 and 13) it will be noted that the more medial of the two sections (fig. 12) shows chiefly ophidian characters, while the more lateral (fig. 13) shows lacertilian characters quite completely, save for the caudal extension of the granular layer. This feature of the stratum granulare becomes clear when it is recalled that the layer of granule cells forms the general ventral and caudal facies of the entire cerebellum. In the more lateral portion of the pars interposita this layer faces laterally, and a parasagittal section through this region of the pars interposita passes through the granulare, as shown in the figure. Somewhat more medially (fig. 12), the molecular layer also extends into the caudal tongue, but the granule layer arches dorsally and medially in such a manner as to form an island of gray above the caudal molecular zone, as seen in sagittal section.

These features of structures point to the interpretation that the pars interposita of the cerebellum of Gerrhonotus corresponds to the major part of the organ as it occurs in the
snakes, while the pars lateralis of Gerrhonotus is more strictly lacertilian. The cerebellum of the Iguanidae and of Varanus is to be regarded as an overdevelopment of the lateral por-

![Diagram 13](image13.png)

Fig. 13 Section showing lateral part of transition zone, described in text. From same series as figures 11 and 12. × 24.

![Diagram 14](image14.png)

Fig. 14 Section through lateral part of cerebellar region. Same series as figures 11, 12, and 13. × 24.

tion (pars lateralis), accompanied by a relative lack of development of the medial region (pars interposita). A specialization of the pars lateralis in these lizards, similar to that of the lobus auricularis in fishes and amphibians and of
different regions of the medulla oblongata in various fishes, appears to have taken place. In Gerrhonotus, and in the snakes especially, it is the medial region of the cerebellum (pars interposita) which has undergone hypertrophy concomitant with the development of methods of progression which bring into use other sets of muscles than are principally employed by the Iguanidae and their allies. This interpretation appears to be substantiated by observations on the movements of Gerrhonotus as compared with those of Sceloporus, Phrynosoma, and Thamnophis.

The quick, darting movements of Sceloporus are almost too rapid for accurate observation, but they are obviously due to leg activity. The tail does not appear to drag, and certainly plays no part in progression. In the snake the sinuous motions of the trunk and tail are entirely responsible for progression. Gerrhonotus uses both trunk and limbs, as well as the tail, in propelling itself along.

Regarding the Anguidae as a group, Ditmars ('10) states: "We find a curious mix-up in the phases of structure from creatures which run speedily on strong limbs to utterly limbless forms gliding like serpents and employing a black tongue to investigate their way in truly snake-like fashion." With especial reference to the genus Gerrhonotus the same author ('15) describes its movements as follows:

These lizards are less agile in their movements than other lizards of their size—such as the swifts and skinks—though they are by no means sluggish. However they are more easily captured than the majority of their kind. While progressing leisurely over rough places they are often snake-like in actions, the slender body and long tail following the outlines of the declivities and, although the small limbs are constantly in use, the effect resembles a gliding movement. Such actions demonstrate the close relationships of these lizards to the serpent-like, limbless forms.

My personal observations of the manner of progression of Gerrhonotus on tables and on the cement floor of the laboratory confirm the above description. The tail drags on the floor or table, and when the lizard attempts to move rapidly
to avoid capture, the tail frequently aids by side-to-side movements and pushes against the surface on which the creature is placed in such a manner as to propel the body forward. When the body is held between thumb and finger, just behind the fore limbs so as to leave the tail entirely free, the latter twines about the finger spirally and exerts a considerable push so directed as to move the body forward. When the lizard walks rapidly on the floor, the lumbar region of the trunk aids very materially by side-to-side movements which are coordinated with the movements of the hind limbs and make possible longer strides than the short legs could otherwise accomplish. It is very evident that the trunk and tail have a much more important part in the locomotion of Gerrhonotus than appears to be the case in the two species of Sceloporus, or in Phrynosoma, the only other lizards on which I have made personal observations with this point in mind. In Gerrhonotus there is an approach to the gliding movements of the serpents, to which Ditmars makes reference.

In writing of Sceloporus, on the other hand, Ditmars ('15) states: "It skims over the desert soil if pursued, and if deciding to stop for a moment to reconnoiter will actually slide a few inches from the great momentum of its scampering pace." This was written in description of Sceloporus clarkii of the Arizona desert, but is applicable to the two Oregon species captured for this study, and particularly to Sceloporus biseriatus. In fact, so rapid are the movements of this latter species that we found it necessary to shoot with a rifle nearly all the specimens captured. The horned lizards also, which, with the swifts, belong to the family of Iguanidae, are capable of very rapid movements. They "dart here and there with wonderful rapidity" (Ditmars), and one when frightened "darts away with the speed of a startled mouse."

Comparing the cerebellum of Thamnophis, Gerrhonotus, Sceloporus, and Phrynosoma from the point of view established by this description of the movements of these species, it is to be noted that among the swifts, as also in Varanus, there is present an exverted cerebellum which is nearly cres-
centic in parasagittal section, and which is relatively well
developed laterally, but in the median region retains the
characteristics of the pars lateralis. There is no caudal ex-
tension as in Gerrhonotus. In the horned lizard, Phrynosoma,
the same is true, save that the lateral portion of the cere-
bellum is somewhat larger than in Sceloporus. The alligator
lizard, Gerrhonotus, on the other hand, has a much less de-
veloped pars lateralis, but a well-developed pars interposita,
with a tongue-like caudal extension to which reference has
been made. It appears likely, in view of the differences of

locomotion and the correlated differences in cerebellar struc-
ture, that the pars interposita has to do with the musculature
of the trunk and possibly the tail, while the pars lateralis
appears to be more closely related, functionally, to the limb
muscles. The auricular lobe is so reduced in size as to be
virtually absent, both in lizards and in snakes, but it has con-
nections with the vestibular nuclei, to be described, thus cor-
responding with the amphibian lobus auricularis.

*Thamnophis.* In the garter snake the cerebellum is a simple
arch over the rhomboid fossa (fig. 15). It tapers laterally
and caudally toward the free margin of the organ. It is inclined as a whole caudally, and the dorsalmost portion is so rounded as to make it appear in sagittal section that the degree of inclination is greater than is actually true, as measured by the main axis of the cerebellum (fig. 16). The midbrain in front and the upward arching of the oblongata caudally form a hollow in which the cerebellum is nearly hidden from view, as in Anniella.

Fig. 17 Transverse section through cerebellar region of Thamnophis (leptcephala?). Pal-Weigert stain. Camera lucida. × 36.

As represented in the snake, the cerebellum is well developed in the midregion, but with slight development of the lateral part and the auricular lobe, as may be seen from figures 15 and 17. In the earliest snake embryos available, which, however, were already in the coiled stage, the cerebellum has little resemblance to the iguanid type (fig. 18), while in the adult there is no suggestion, in any part, of the exverted condition which is so striking a feature of the cerebellum in most lizards. Because of this, the stratum ganulare in the snake occupies a ventral position, as seen in cross-
section of the brain stem (fig. 17). The organ as a whole is elongated and narrow, with a pronounced caudal tapering. It corresponds to the median portion or pars interposita, including the caudal tongue, of the cerebellum of Gerrhonotus. The pars lateralis is very rudimentary in the snake.

**Histological**

The three typical cerebellar layers are present in all the species studied. The granular layer in Gerrhonotus has already been referred to in the previous section. The granule cells are small, and fibers from the various afferent cerebellar tracts are scattered among them in the typical manner. Without Golgi preparations details of structural variation, as compared with other forms, could not be ascertained.

The granule layer in Gerrhonotus forms the roof of the rhomboid fossa (figs. 11 and 13), and everywhere except in the pars lateralis it is thinner than the molecular layer. Rostrally, it becomes still more attenuated and disappears at the level of the cerebellar commissure (fig. 11). The lateral as well as the ventral surfaces of the caudal projection of the pars interposita are formed by the granulare (figs. 12 and 13), and in the transition zone from pars interposita to pars lateralis this layer becomes rearranged from a ventrally facing stratum to one which faces both ventrally and caudally, as illustrated in figures 12 to 14.

In Sceloporus and Phrynosoma the granular layer completely covers the stratum moleculare on all sides as observed in transverse section. Sagittal sections (fig. 5), however, reveal that this appearance is due to the marked exversion of the cerebellum and that the two layers have their normal morphological relations.

The granular layer of the snake faces ventrally and is uncomplicated in its relationships. A slight lateral and dorsal extension of the granulare (fig. 17) at the transition zone between the cerebellum and the bulb, together with its covering of molecular layer, is interpreted as a vestige of the auricular lobe. The granular layer is relatively thick in
cross-section in the snake, but the molecular layer compensates by its greater spread in arching over the entire cerebellum externally.

The zone of Purkinje cells is three to four cell layers in thickness, but is reduced to one or two layers caudally in the pars interposita of Gerrhonotus (figs. 11 and 12) and also dorsally in the pars lateralis (figs. 13 and 14). Cajal series indicate that the dendritic branches of the Purkinje cells extend into the molecular zone in the typical manner. In

Sceloporus the Purkinje cells also constitute several layers (figs. 5 and 6) except at the margins of the cerebellum, and this is also true of Thamnophis.

The stratum moleculare is very thick in the midregion in the alligator lizard (fig. 11) where it faces both rostrally and dorsally. This marked thickness is due in part to a ridge which crosses from side to side as a continuation of the molecular zone of the pars lateralis, to which reference has already been made. In the transition zone between pars interposita and pars lateralis a thin tongue of molecular substance

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**Fig. 18** Parasagittal section through cerebellar region of embryo of Thamnophis (leptocephala?) in coiled stage of 13 mm. greatest diameter. Iron-hematoxylin stain. Edinger-Leitz projection apparatus. × 17.

**Fig. 19** Transverse section through cerebellar region of Anniella nigra. Iron-hematoxylin stain. Camera lucida. × 43.
extends laterally and caudally (fig. 12) between the main part of the granular layer ventrally and the lateral mass, which in section appears as an island of the granulare above the extension of the molecular layer. This island is, however, continuous with the main mass of the granulare. The latter merely arches around and above the molecular layer in the lateral portion of the pars interposita and extends medially a short distance. Hence the stratified appearance when the lateral region of the pars interposita is cut in the parasagittal plane (fig. 12). Laterally, this island is continuous with the granular layer of the pars lateralis.

The molecular layer in the cerebellum of Sceloporus and Phrynosoma faces in general rostrad, due to the dorsal direction of the axis of the cerebellum in these lizards. In the dorsalmost part of the organ, which part arches over the midbrain, it faces ventrorostrally instead of dorsally or dorso-rostrally, as in other reptiles and in amphibians.

Thamnophis shows the least complicated arrangement of the molecular layer. Here it forms the dorsalmost part of the cerebellum throughout the extent of the organ. It forms an arching cover (fig. 17) of the other two layers, extending completely from side to side. A slight projection, to which attention has already been directed in connection with the granular layer of the snake, extends laterally, and evidently represents the molecular covering of the auricular lobe.

Cerebellar nuclei

The deep nuclei of the cerebellum are present in Anniella as two masses, a medial and a lateral. They are not sharply separated, but the lateral portion, which is continuous with the tegmentum (figs. 19 and 20), is larger and will be designated the nucleus lateralis. The attenuated medial division (fig. 19) extends nearly to the midline of the cerebellum in the border zone between the corpus cerebelli and the anterior medullary velum, and is designated the nucleus cerebelli medialis. The two masses appear to correspond with the nuclei of the same designation in the cerebellum in larger
reptiles, as described by van Hoëvell ('16). There is sufficient differentiation from the single mass of cells of the nucleus cerebelli as seen in amphibians (Larsell, '20, '23, '25) to justify the division into lateral and medial cerebellar nuclei as given. In Anniella the nuclei are quite small as compared with the alligator and other reptiles studied in this connection by van Hoëvell, and the distinction is not so evident as in the larger and better-developed cerebella of the larger reptiles.

In Gerrhonotus they have the same general arrangement as in Anniella, but are larger. As shown in figure 21, a mass of cells continues dorsally and medially from the vestibular nuclei around the recessus lateralis. It occupies a position between the granule layer and the lateral recess. The mass may be divided into a smaller medial portion and a larger division placed more laterally. These two are regarded as the medial and lateral cerebellar nuclei, respectively, corresponding with those of Anniella. From the lateral nucleus the brachium conjunctivum takes its origin (fig. 22), as may be seen in sagittal series to best advantage. The iguanid lizards and the garter snake show essentially the same features with respect to the cerebellar nuclei as described for Gerrhonotus.

As compared with the single nucleus cerebelli of the frog and other amphibians, these nuclei in reptiles are definitely pushed upward into the cerebellum. They also extend medially to a marked degree—a feature which is lacking in the Amphibia. There is the added development of division into lateral and medial masses, as already noted.

**Fiber tracts**

The tractus spinocerebellaris ventralis is the largest tract connected with the cerebellum in all of the reptiles under consideration. It accompanies the spinotectal tract through the greater part of the bulb, as in amphibians, to the level of the trigeminal roots. It arches around these roots rostrally, to turn dorsalward and pass to the cerebellum, where it is distributed in the granular layer. The separation from the
spinotectal tract takes place ventral to the Vth roots. This description holds true in general for the various species studied. There are, however, certain differences of detail which may be noted. In Anniella the ventral spinocerebellar tract (fig. 19) constitutes the principal connection of the cerebellum with other parts of the nervous system, so far as one may judge from its size. It is closely associated with the cerebellar commissure in the anterior medullary velum in this legless lizard, but distributes its fibers in the stratum granulare, chiefly on the same side, but with some crossing of fibers to the opposite side.

In Gerrhonotus the ventral spinocerebellar tract (figs. 21 and 23) does not enter into the anterior velum, as in Anniella, and is relatively not so large, but in other respects is very similar. In Sceloporus (fig. 6) and in Phrynosoma it is somewhat larger than in the alligator lizard. In its distribution to the granular layer there is considerable decussation, not only through the ventral cerebellar commissure, but in the swift, through a dorsal commissure which is not evident in the alligator lizard.

Thamnophis has a large ventral spinocerebellar tract (fig. 17), which, as in Anniella, appears to constitute the principal connection of the cerebellum with other parts of the nervous system. In the snake there is evident a very large amount of decussation of this tract, so that the cerebellar commissure appears to be made up chiefly of decussating fibers of the ventral spinocerebellar tract.

The tractus spinocerebellaris dorsalis (or bulbocerebellaris) is also present in these reptiles. As represented in Anniella (fig. 20), it passes lateral to the vestibular nucleus and may be traced caudally as a distinct bundle through the greater portion of the bulb. In the caudal region of the oblongata, however, it becomes intermingled with other tracts to such an extent as to lose its identity. In Thamnophis it is also difficult to follow in the caudal part of the bulb, but it is large and distinct rostrally. This statement applies also to Sceloporus and Phrynosoma. The tract occupies a posi-
tion along the lateral margin of the oblongata just dorsal to the ventral spinocerebellar tract, after it has passed from the cerebellum through the Vth roots, to take its place in the lateral portion of the bulb. Cajal series of Gerrhonotus indicate somewhat more clearly that the tract in question does not

Fig. 20 Parasagittal section through cerebellar region of Anniella nigra. Iron-hematoxylin stain. Camera lucida. × 63.

Fig. 21 Transverse section through cerebellar region at rostral level of V roots. Gerrhonotus principis. Iron-hematoxylin stain. Camera lucida. × 38.
have its origin in the bulb, but none of the series of any of the reptiles which I have had opportunity to examine gives clear-cut evidence on this point. Without Golgi preparations or degeneration experiments it does not appear possible to determine with certainty whether it is spinal or bulbar in origin, although the evidence appears to favor the former.

**Tractus vestibulocerebellaris.** This tract has its chief origin in the superior vestibular nucleus, whence it arches around the lateral extremity of the recessus lateralis to pass into the stratum granulare (figs. 4, 17, and 23). There is little variation in this tract in the different species under observation. A direct vestibular tract (fig. 22) is also present as a continuation into the cerebellum from the vestibular root.

In Thamnophis a small tract from the lateral vestibular nucleus reaches to the auricular lobe (fig. 17), but I have been unable to find its counterpart in the lizards.

A *tractus olivocerebellaris* is present in Thamnophis, Sceloporus, and Gerrhonotus, but I have no clear evidence of its existence in Anniella. In this lizard, however, the inferior olivary nucleus is also somewhat uncertain. A group of small

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**Fig. 22** Parasagittal section through lateral part of cerebellar region of *Gerrhonotus principis*. Method of Ramón y Cajal. Edinger-Leitz projection apparatus. $\times 38$. 

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Fig. 23 Transverse section through cerebellar region at caudal level of V roots. Gerrhonotus principis. Iron-hematoxylin stain. Edinger-Leitz projection apparatus. × 38.

Fig. 24 Diagrams of cerebellum to show relations between pars interposita and pars lateralis of the present writer, and the relation of both of these to the lobus medianus of the alligator, as described by de Lange and Ingvar. A, Sceloporus biseriatus; B, Gerrhonotus principis. The areas marked by vertical lines represent pars interposita, those marked by oblique lines represent pars lateralis, and the horizontal lines in B represent the lobus medianus of other authors.
cells may be recognized in the region of the bulb corresponding to the location of the inferior olive, and fibers from this cell mass extend toward the cerebellum, but I have not been able to follow their course into this organ, if they reach it, in the available material of Anniella. Weigert series of Thamnophis, however, show that it is associated with the dorsal spinocerebellar (or bulbocerebellar) tract from the level of the inferior olive to the cerebellum. A similar arrangement is apparent in the several species of lizards studied except Anniella, but it is not so clear as in the snake. In Sceloporus, Phrynosoma, and Gerrhonotus the tract is quite small.

_Tractus tecto-cerebellaris._ Cajal series of both Sceloporus and Gerrhonotus show the presence of a small bundle of very fine fibers which enter the cerebellar commissure, on the one hand, and spread out into the tectum, on the other hand. No cell connections could be established, but it appears likely that this is the tectocerebellar tract, for its relations are quite similar to those in the frog for this tract. In the snake and legless lizard I have not been able to detect any evidence of this tract, probably due to lack of silver preparations of these forms.

The _brachium conjunctivum_ is best seen in sagittal series (fig. 22). It forms a tract, which in Anniella is very small, composed of scattered fibers which pass rostromedially into the midbrain. Thamnophis shows it more distinctly as a tract which decussates in the midbrain and terminates, in part at least, in a group of large cells near the midplane, which evidently represent the large-celled element of the nucleus ruber.

A _tractus trigeminocerebellaris_ is doubtful in the species under consideration. Weigert and iron-hematoxylin series of the several forms give the appearance of fibers from the Vth roots to the cerebellum, but the intermingling of fibers of the ventral spinocerebellar tract with the rostral strands of the Vth root is largely, if not entirely, responsible for this. The fibers are similar in size and appearance, and no individual fiber from the trigeminal root has been traced indubitably into the cerebellum, while ventral spinocerebellar fibers
can be thus followed. A sagittal series of Gerrhonotus, by the Cajal method, in which the fibers and fiber tracts are unusually well differentiated, fails to reveal any fibers from the trigeminus to the cerebellum. De Lange ('17) believes that they are doubtful, although he states that in the crocodile there is an appearance of trigemino-cerebellar fibers, as I have found in the snakes and lizards. The apparent absence of such connections in reptiles is in contrast with the condition in the frog, where such fibers are clearly present (Larsell, '23, '25) as shown by Golgi sections.

The *tractus trigeminomesencephalicus* passes beneath the cerebellum in these reptiles, rather than through it as in amphibians, and need not be considered in this connection.

**DISCUSSION**

Attention has already been directed (p. 112) to the sulci of the alligator's cerebellum pointed out by de Lange ('17), and to the divisions of this cerebellum made by Ingvar ('18) into anterior, median, and posterior lobes, with the anterior and posterior sulci as the boundaries between the lobes. Ingvar (p. 380) has also differentiated the anterior cerebellar lobe in the lizards and chameleons on the basis of internal structure.

The cerebellum of Gerrhonotus shows lobes and sulci corresponding to those of the alligator, although the lobes are relatively smaller, and the sulci are shallow, superficial furrows. It appears to me, however, that in the lizard cerebellum may be recognized a more fundamental division than that indicated by the lobes in question, and that, indeed, these lobes are secondary to a more primitive arrangement. This arrangement has reference to the transverse axis of the cerebellum, rather than to the anteroposterior axis, and may also be recognized in the amphibian cerebellum, as a consideration of the development of the latter will indicate.

The cerebellum of Necturus (Herrick, '14) is composed of two lateral masses connected across the roof of the IV ventricle by membrane. In Amblystoma (Larsell, '20) this mem-
brane has given place to nervous tissue, so that a massive roof, albeit rather thin in the region of the midplane, is present. The frog recapitulates these conditions in its developmental stages (Larsell, '25), and in the adult frog the cerebellum is massive from side to side (Larsell, '23). In other words, there is formed between the two corpora cerebelli, which have a lateral position and which represent the most primitive part of the cerebellum proper, a new region, beginning with the urodeles just above the scale of Necturus. This median part reaches its culmination of development among the Amphibia in the adult frog.

The principal aspects of this process are repeated in the embryonic development of the higher vertebrates, including the human. In the series of lizards and the snake described in the present paper the variations of this median portion are so pronounced in the different species as to constitute the most striking feature of cerebellar structure in these forms. It is a consideration of these variations in reptiles and of the progressive development of the median region of the cerebellum which has led me to divide the organ into a pars lateralis on either side and a pars interposita between. The term 'lobus' or 'pars media' is preempted by Ingvar ('18) and Brouwer ('13) for a division which is based upon the appearance of the cerebellum in the higher reptiles and in birds. It should be pointed out, however, that the lobus medius of Ingvar and the pars interposita, as here defined, overlap to a considerable extent. The pars interposita is more inclusive anteroposteriorly, while the lobus medius is more inclusive laterally, as the diagram (fig. 24) indicates.

The pars interposita, as here defined, corresponds in general to the dorsal median body of fishes (Herrick, '24). It should not be confused with the 'cerebellum jugale' of Tilney ('23), for, as Herrick has pointed out, the latter includes the body of the cerebellum of Petromyzon, together with the lower cerebellar lip of elasmobranchs and teleosts. These parts are paired and functionally, as well as morphologically, belong to the lateral part of the cerebellum. They are very
different structures than the region between the two cerebellar bodies to which the term pars interposita is here applied. As here used, the pars interposita corresponds more closely to the ‘cerebellum mediale’ of Tilney. This author has recognized the similarity between this region of the cerebellum in the alligator and the fishes by applying the term ‘cerebellum mediale’ to both.

As regards the pars lateralis, the distinction must be carefully drawn to avoid confusion with Tilney’s ‘cerebellum laterale.’ Tilney applies this term to the flocculus of birds and considers this part of the cerebellum to be a new development in cerebellar organization. Leaving to one side the question as to whether or not this structure is concerned with coordinating the movements of the tail, it cannot be considered in any case as a new morphological development. A rudiment of the auricular lobe or flocculus is present in the snake and the lizards, as shown not only by the lateral outgrowths on either side, corresponding in position to this lobe in amphibians, but also by the fact that the fiber connections are similar to those of the flocculus of mammals in that they are vestibular. The lateral-line connections of urodeles and of the tadpole stage of the frog are, of course, entirely absent in the reptiles. This lobe is also present in the alligator, where it attains a considerable size. It would therefore be surprising to find it altogether absent in the birds or replaced by a new structure.

In the cerebellum of the frog and of the reptiles there is present, however, a structure which may be considered to be new, as distinguished from the ancient corpus cerebelli and the auricular lobes of lower amphibians and of the tadpole stages of the frog. This structure develops across the floor of the lateral recess, between the corpus cerebelli on either side and the auricular lobe of the same side so as to join these two bodies by a mass of nervous tissue. In the reptiles it has reached a sufficient degree of development to constitute an important feature of the cerebellum, overshadowing the auricular lobe with which it is continuous laterally.
It is this region particularly, together with the primitive corpus cerebelli, which I designate by the term pars lateralis, and which appears to be concerned primarily with coordination of leg movements.

A comparison of the cerebellum of different reptiles, especially those of Sceloporus and Thamnophis, with reference to the development of different parts of the organ in relation to the degree of development or degeneration of the locomotor appendages and with regard also to the method of locomotion, appears to demonstrate some important features. First of all, the cerebellum of Sceloporus, while the most primitive in type, has assumed a special form of this primitive condition, giving rise to the extremely exverted type usually considered characteristic of lizards, and the pars lateralis has become greatly developed. Kappers ('21, p. 680) accurately describes this form of cerebellum as "eine excessive Ausbildung des primitive Typus." De Lange ('17) has called attention to the similarity between the exverted type and the early human foetus, and of the alligator type with the three months' foetus, as already noted.

Thamnophis has also a very simple cerebellum, but this should not be considered primitive. It represents rather an overdevelopment of the pars interposita and a lack of development of the pars lateralis which has accompanied the degeneration of the extremities and the development of the special mode of locomotion characteristic of the serpents.

The cerebellum of Gerrhonotus, while obviously not so primitive as in Sceloporus, since it corresponds fairly closely to the development of this organ in the human foetus of about three months, as contrasted with the two months' stage to which Sceloporus corresponds, nevertheless represents a more generalized type than either of the others, in the sense that it has characteristics of the cerebellum of various reptilian groups. When considered in relation to the mode of locomotion, it appears clear that the pars interposita, because of its relatively large development in Gerrhonotus and Thamnophis, must have to do with the segmental musculature of
the trunk and, perhaps, to some extent, of the tail. The pars lateralis, practically absent in the snake, well developed in Sceloporus and its allies, and occupying a middle position between these two types in Gerrhonotus, appears to preside over the musculature of the paired appendages. This point could probably be subjected to further test, from a morphological point of view, by a study of the cerebellum of Euchirotes, in which lizard the forelegs alone are developed. Unfortunately, however, I have been unable to secure material of this rare lizard for such a study.

A comparison of the results of the present study with those of Bolk (’06), Bouwer (’13), and Ingvar (’18) on birds and mammals is of interest. Brief reference will also be made to the experimental results of van Rynberk (’08), although I have made no corresponding experiments on the reptilian cerebellum. According to the anatomical studies of Bolk, the lobulus ansiformis, which he subdivides into crus primum and crus secundum, represents the cerebellar centers for the extremities. The lobulus medianus posterior governs the segmental musculature of the trunk. Van Rynberk’s experimental results are in substantial agreement with the conclusions of Bolk.

In the reptiles which I have studied the pars interposita corresponds to the lobulus medianus, in part, both in position and apparently in function. It is the principal, almost the only part of the cerebellum in Thamnophis, and is well developed in Gerrhonotus. In Sceloporus and Phrynosoma it is not marked off from the rest of the cerebellum, and this also appears to be the case in Varanus, so far as I can judge from the figures of Edinger and de Lange.

The pars lateralis of the lizard cerebellum appears to represent the lobulus ansiformis of Bolk in a primitive condition. According to Bolk’s interpretation, confirmed by van Rynberk, the lobulus ansiformis has to do with the paired appendages. This part of the cerebellum is absent in the snake, highly developed in Sceloporus, and occupies an intermediate position in Gerrhonotus, corresponding to the degree
of development and activity of the paired appendages in these forms, respectively.

The auricular lobe is very small in the snakes as well as in the lizards and, as has been shown in the amphibians, corresponds to the flocculus of mammals. In the reptiles it no longer has the important lateral-line connections which characterize it in amphibians, and has not yet developed the vestibular connections to the degree found in the mammals.

Regarding the anterior part of the cerebellum in the reptiles, my material sheds little light on this region, unless the interpretation given above is correct, namely, that the transverse groove in Gerrhonotus is the primitive forerunner of the sulcus primarius. If this be true, the cerebellar portion rostral to this fissure corresponds to the lobus anterior of mammals, birds, and reptiles, according to Ingvar’s interpretation.

Since there are no other furrows in the reptilian cerebellum than the two described, it is not possible to compare with accuracy the lobulus simplex of mammals with any part of the lizard cerebellum. Possibly the long-necked lizards like Varanus show some hypertrophy in the region just caudal to the sulcus primarius, corresponding to the enlarged lobulus simplex of the giraffe (Bolk, ’06, p. 110). It would also be of great interest, as already suggested, to examine the pars lateralis of the two-footed lizard, Euchirotes, for possible differentiation of the crus primum of Bolk.

In general, the reptilian cerebellum, as represented by the lizards and the snake which I have studied, shows a differentiation of parts correlated with differences of bodily structure which corresponds in a primitive way to that found in the mammals by Bolk. Further studies on the more elaborate cerebellum of the larger reptiles, such as the turtles and the alligator, are in progress. The preliminary survey of the material indicates that the general plan of structure and cerebellar division in these forms is in keeping with the interpretation given for the lizards and snakes.
SUMMARY

The cerebellum of the lizards and the snake may be divided into a pars lateralis on either side and a pars interposita between. Comparative studies on the structure of these parts from the viewpoint of the methods of locomotion of the several species under consideration, point to the conclusion that the pars lateralis is primarily concerned with the movements of the paired appendages, while the pars interposita is concerned with the segmental muscles of the trunk and possibly the tail.

The cerebellum of Anniella is very simple and probably represents considerable degeneration, that of the iguanid lizards shows an extreme specialization of the primitive type of cerebellum, while the cerebellum of Gerrhonotus is a generalized type with affinities in the various groups of reptiles. The snake cerebellum is relatively simple, but appears to represent a great specialization of the pars interposita, accompanied by degeneration of the pars lateralis.

The deep cerebellar nuclei are present as a medial and a lateral group of cells. The afferent and efferent cerebellar fiber tracts, in general, are similar to those of mammals.

LITERATURE CITED


