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ORIGINAL PAPER

# Sven Ingvar (1889–1947) of Lund University and the Centennial of His Landmark Dissertation on Cerebellar Phylo-Ontogeny

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## Abstract

In January 1919, Sven Ingvar (1889–1947) defended his doctoral dissertation (required for the M.D. degree) on cerebellar phylogeny, development, and function at Lund University, Sweden. The work was supervised by Cornelius U. Ariëns Kappers (1877–1946) in Amsterdam and by Karl Petrén (1868–1927) in Lund. A physician of many interests, Ingvar became professor of Practical Medicine in his alma mater. His cerebellar papers, spanning over a decade, are the contributions that gained him international recognition in the neurological sciences. A key discovery was the demonstration, with the Marchi method, of the primary vestibulocerebellar afferent fibers. The merits of his work rest with the use of connections to compare lobes and lobules in different species, and the introduction of the idea of vestibular, spinal, and corticopontine storeys; on the other hand, based on current knowledge, one might take a more critical stance toward the proposition of a posterior lobe as a phylogenetically old structure, and the homolog of the human tonsil. Nonetheless, Ingvar was an early pioneer of the "evo-devo" synthesis (or the field of Evolutionary Developmental Biology, which aims at understanding how developmental processes evolve across species). He studied the comparative anatomy of the cerebellum in over 50 species of reptiles, birds, and mammals and theorized about the spatial relations of phylogenetically older and more recent acquisitions in both the cerebellar and the thalamocortical systems.

**Keywords** Sven Ingvar · Cerebellum · Evolution · Development · History of neuroscience

Sven Ingvar (Fig. 1a) is rarely remembered today outside Scandinavia, despite the remark before the Swedish Medical Association by Nils Antoni (1887–1968), professor of Neurology at Karolinska Institute and a member and chair of the Nobel Committee, that Ingvar was "the most brilliant scientist in Neurology that the Nordic countries produced, his celebrated father-in-law Salomon Henschen not excluded" [1].

The only readily available sources of information on his life are a biographical entry in Swedish [1] and a memorial tribute in English [2] by his pupil, the neuroanatomist Erik Ask-Upmark (1901–1985). The present article briefly reviews his medical career and contribution to cerebellar neurobiology.

Born on 15 December 1889 in Gevninge on the Danish island of Sjælland, Ingvar became the son-in-law of neurologist Salomon Eberhard Henschen (1847–1930), professor of Internal Medicine at Karolinska Institute, and the father of David H. Ingvar (1924–2000), professor of Clinical Neurophysiology at Lund University.

Sven Ingvar studied medicine in Lund and graduated in 1919. Karl Petrén (Fig. 1b, c), professor of Internal Medicine, encouraged Ingvar's research interest in neurology since the latter's student years. Petrén had studied with Joseph-Jules Déjèrine (1849–1917) in Paris and became internationally known for his contributions to neurology, diabetes, tuberculosis, and epidemic encephalitis.

During the flu epidemic of the First World War, Ingvar became engaged in aspects of prophylaxis and therapy [3]. Subsequently, he was appointed *Docent* (comparable to *Reader* in many Commonwealth countries) in Neurology at the University Clinic of Internal Medicine headed by Petrén, and in November 1929, he succeeded his mentor as professor of Practical Medicine, a position that he kept until his death, on 21 April 1947, at the age of 57 years [2].

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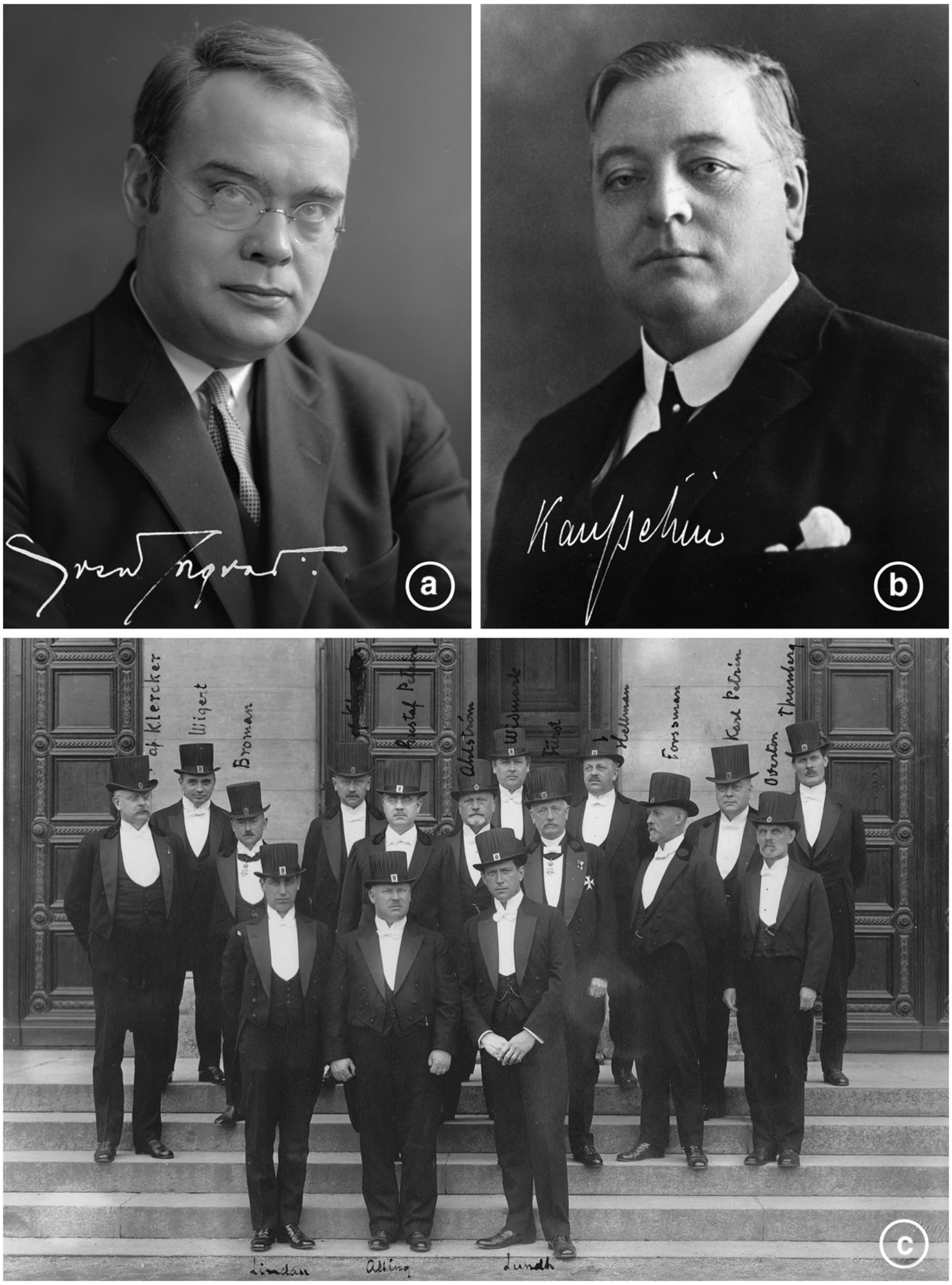


**Fig. 1** Professors **a** Sven Olsson Ingvar (1889–1947) and **b** Karl Anders Petrén (1868–1927) of the Internal Medicine Clinic in Lund. **c** The renowned members of "The Great medical faculty" ("Den Stora medicinska fakulteten") of Lund University, photographed in May 1926. Credit: ALVIN Platform for Digital Collections and Digitized Cultural Heritage (www.alvin-portal.org) and Bildarkiv, Sydsvenska Medicinhistoriska Sällskapet (www.medicinhistoriskasyd.se)

Ingvar was fluent in Swedish, Dutch, French, German, English, and Russian. His research endeavors took him to Holland, England, and the USA. He visited the laboratory of Ross G. Harrison (1870–1959) at Yale University, where he carried out in vitro studies on the effects of electricity on the polarity of nervous tissue growth, and published a report on the orientation of nerve cell processes along the direction of force in a galvanic field [4]. Ingvar obtained polar directive effects by studying the influence of weak constant currents on the growth cones of embryonic neurons. Thus, Ingvar was the first investigator who reported and experimentally confirmed the phenomenon of *galvanotaxis* in tissue culture; his discovery was revived in the 1980s by several research groups working independently [5]. A similar term is *kataphoresis*, defined as the process whereby substances consisting of, resembling, or containing albumin show a shift under the influence of galvanic current.

In a couple of studies co-authored with histologist Erik Gottlieb Müller (1866–1923) of Karolinska Institute, the authors provided experimental proof in frogs and chicken on the origin of the sympathetic nervous system in the ectoderm [6, 7]. Having attained international renown, Ingvar was invited to give the Hunterian Lecture in England. With support from the Rockefeller Foundation, he established a Neurological Laboratory at the Clinic of Internal Medicine in Lund [2].

Some of his publications between 1923 and 1937 dealt with leakage of cerebrospinal fluid after lumbar puncture; anarthria in meningoencephalitis (co-authored with Petrén); cases of syphilis and tabes; Herpes zoster infection; hypothalamic and pituitary disturbances; subdural hematoma (co-authored with Ask-Upmark); and obituaries for his father-in-law, Salomon Eberhard Henschen, as well as Hans Christian Jacobaeus (1879–1937), professor of Medicine at the Karolinska Institute and chairman of the Nobel Committee from 1925 through 1937.

Later on, Ingvar was instrumental in establishing the first independent Rheumatology Unit in a university hospital in Sweden. He also presided over the Fifth International Congress of Rheumatology in Lund in 1936, where he lectured on myalgia and on neurovascular disturbances in sciatica [8]. Some further interests included the effects of chronic alcoholism on the nervous system, and the importance of sleep in therapy and social medicine [9]. In 1933–1936, he was president of the Lund-Malmö Medical Association (*Medicinska Föreningen*). During the Second World War, Ingvar was one of ten professors of Lund University who published a collection of essays [10] in which they defended democracy and took a clear stand against National Socialism.

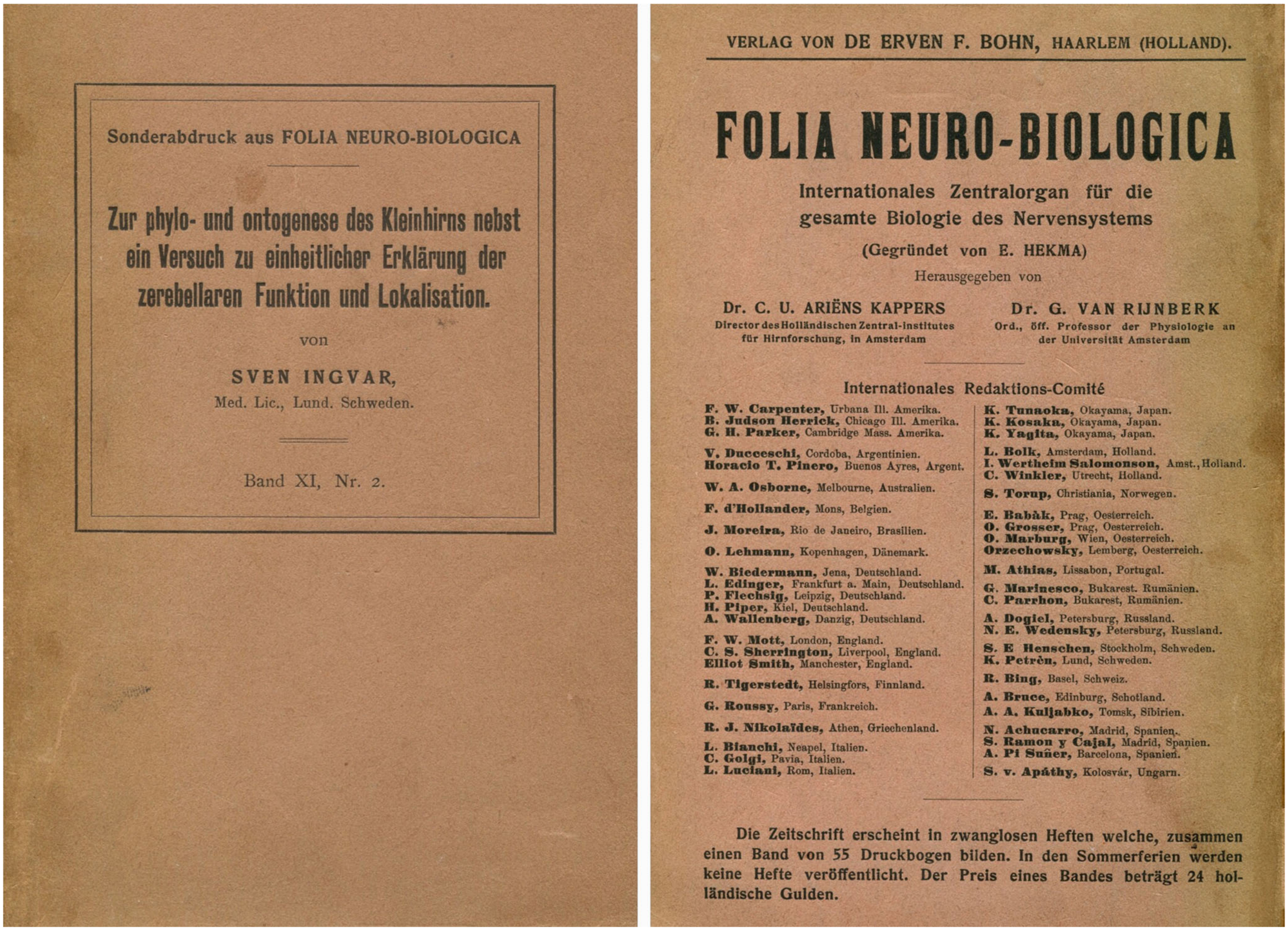
Sven Ingvar's interest in the cerebellum was prompted by studying its relation to speech in four patients who had been operated for tumors by Jakob Ludvig Borelius (1859–1921), professor of Surgery in Lund [11, 12]. Petrén suggested that Ingvar visit Cornelius U. Ariëns Kappers (1877–1946) at the Netherlands Central Institute for Brain Research in Amsterdam. This is where Ingvar began in 1917 the work for his Doctor of Medicine dissertation, supported by a Wallenberg stipend from the Swedish Society for the Advancement of Medical Research. He combined comparative anatomy, embryology, experimental lesions in animals, and neuropathological material from cerebellar patients, in an effort to decipher problems of cerebellar evolution, development, and functional localization. The resulting thesis, "On the Phylogeny and Ontogeny of the Cerebellum, with an Attempt at a Unified Explanation of Cerebellar Function and Localization" [13], written in German, is considered a landmark monograph and his magnum opus. It was published in Folia Neurobiologica [14] (Fig. 2) and "was to become known all over the globe" [2]. The defense took place in Lund in a morning of January 1919 amid "the glittering snow and shining sun" [2].

After a brief historical introduction, crediting Aristotle of Stageira (384–322 BC), Galen of Pergamon (129–216 AD), Thomas Willis (1621–1675), Vincenzo Malacarne (1744–1816), Félix Vicq d'Azyr (1748–1794), and Johann Christian Reil (1759–1813) for the early descriptions of the cerebellum, Ingvar places special emphasis on the work of Sir Grafton Elliot Smith (1871–1937) and Lodewijk Bolk (1866–1930) (Chaps. 1 and 2). The first part of the thesis deals with the phylogenetic evolution of the cerebellum, from fishes and amphibians (Chap. 3) to reptiles, birds, and mammals (Chaps. 4–7), on to the human cerebellum, its development and organization (Chap. 8). Next, he provides an overview of cerebellar forms in vertebrates (Chap. 9), the termination of direct vestibulocerebellar afferent fiber systems (Chap. 10), the comparative study of the termination of spinocerebellar pathways in birds and mammals (Chap. 11), and three cases of congenital cerebellar atrophy in cats (Chap. 12). The second part of the thesis deals with cerebellar function, specifically, experimental studies on the localization of function in the anterior and posterior lobes, experiments in rabbits (Chap. 13), the physiology of the cerebellum (Chap. 14), and the clinical cerebellar syndromes in light of the theories discussed (Chap. 15).

The American neurologist Smith Ely Jelliffe (1866–1945) offered an English synopsis [15] of Ingvar's 290-page thesis. I paraphrase Jelliffe's main points in the next paragraph.

> "The author presents the results of an extensive study on the evolution of the cerebellum. In the first part, he shows that the morphological development of the cerebellum follows the same general lines in all higher vertebrates; the homology between the cerebellum of reptiles, birds and mammals extends into the minutest details. In the second part, experiments are described which confirm a theoretical conception of the cerebellum as an organ of equilibrium; this theory is elaborated by the analysis of the clinical effects of injuries. Thus, the function of the cerebellum serves the unconscious sense of 'mass.' It operates to oppose and overcome gravity and inertia of the mass of the body to preserve its equilibrium. The author emphasizes the unity of function of the cerebellum. In contrast to the cerebral cortex, the cerebellar cortex does not consist of different cytoarchitectonic areas. Afferent stimuli to all parts of the cerebellar cortex are always of essentially the same nature, as are also the efferent innervations that project from the cerebellum to the various regions of the body, whether to the locomotor musculature or to the speech apparatus. Nevertheless, there is a precise localization according to the synergies of the muscles necessary for equilibrium, i.e., according to the directions of falling and body motion. Thus, the question of how is it possible that humans preserve the same 'primitive' cerebellum as lower animals is answered by the idea that it is the same force that holds all creatures to the earth. Reptiles have the same main parts in their brain as humans, and Purkinje cells are nearly as delicately elaborated in the amphibian brain as in the human brain" [15].

Fulton and Dow [16] acknowledged that Ingvar, alongside John B. Johnston (1868–1939), Ariëns Kappers, C. Judson Herrick (1868–1960), and Olof Larsell (1886–1964), with their comparative morphological work, suggested a new kind of



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Die Zeitschrift erscheint in zwanglosen Heften welche, zusammen einen Band von 55 Druckbogen bilden. In den Sommerferien werden keine Hefte veröffentlicht. Der Preis eines Bandes beträgt 24 holländische Gulden.

**Fig. 2** Ingvar's thesis on cerebellar phylo-ontogeny printed as a separatum from *Folia Neurobiologica* [14]. Obverse, left, and reverse, right, showing the distinguished international editorial board of the Dutch journal. Private collection

functional localization in the cerebellum and a rational basis for subdividing it based on phylogeny. We currently understand that the morphological development follows the same lines in all vertebrates, and the homology among the cerebella of reptiles, birds, and mammals extends to the minutest details.

Based on his phylogenetic, developmental, and lesion analyses, Ingvar concluded that the cerebellum plays a major role in adapting the parts of the body to the effects of gravity and inertia. He emphasized that each bodily movement involves a certain amount of inertia, i.e., every movement tends to continue if it were not counteracted at a determined moment. Ingvar conceived of the cerebellum as regulating muscular tension in the body masses in all motor activities, particularly in abolishing and neutralizing the forces of gravity and inertia that act on the different parts of the body masses in a physical sense, and advocated that the action of the cerebellum is synergic and concerned with the maintenance of equilibrium, static, and kinetic [17, 18]. Of equal importance to all vertebrates, the cerebellum would thus regulate the static and postural tone and maintain equilibrium in the wider sense of the term.

He also described the "past-pointing" sign [18], which he attributed to spinal mechanisms: when a normal individual directs one's finger toward a fixed point with the eyes closed, one succeeds perfectly; if the opposite arm is abducted to the horizontal plane, then the pointing arm deviates laterally from the fixed point. Such a sign is highly exaggerated in patients with cerebellar lesions.

Ingvar theorized that, in evolutionary terms, new acquisitions, such as the cerebellar cortical areas around the posterior pole, are located centrally, while phylogenetically older elements are arranged in a peripheral margin around the newer central acquisitions. (We now know that the anterior lobe, the pyramis, uvula and nodulus are considered as the phylogenetically older structures.) Ingvar extended that idea as a general principle and applied it to the entire brain. He tried to conceive the cerebral cortex as spread out into one plane, with the phylogenetically older structures, such as the rhinencephalon (serving the ancient sense of olfaction), at the periphery, and the structures subserving more recently acquired cognitive abilities, including stereognosis of the hand, speech and binocular stereoscopic vision, corresponding to central localities of the cortical surface [2]. In an attempt to understand the morphological basis of functional compartmentalization in the thalamus, he studied comparative anatomical homologies between birds and mammals. He arrived at the conclusion that, in phylogeny, the medial and ventral thalamic nuclei are the oldest, with the lateral nucleus and the pulvinar being the "neothalamic" regions which form later in evolution; reciprocal corticothalamic projections become more intricate and extensive in the phylogenetically newer nuclei [19].

He presented those ideas at the 14th annual meeting of the Society of German Neurologists, held in Innsbruck on 24–26 September 1924, in a lecture entitled "On the phylogenesis of the diencephalon, especially of the optic thalamus" [20].

On 3–4 November 1928, Ingvar delivered, by invitation, two Herter Lectures at the Medical School of Johns Hopkins University in Baltimore, where he gave an update of his theories on cerebral and particularly cerebellar ontophylogeny in relation to functional localization [21, 22]. Having studied 50 different species of birds, he underlined the homologies between the mammalian and the avian cerebellum, and emphasized the value of establishing the phylogenetic continuity of the central nervous system in the biological sciences and clinical neurology.

Chronologically, the cerebellar studies of Ingvar fall between Ramón y Cajal's 1888 discovery of the cerebellar circuitry and Larsell's 1937 identification of the cerebellar lobules I–X [23, 24]. More specifically, Larsell's work on the cerebellum focused on the sequential ontogeny of folia (he developed his observations and concepts based on research over the period of time of about 1920–1954), and pointed out that the appearance of folia divided the cerebellum into a flocculonodular lobe and a corpus cerebelli (separated by the posterolateral fissure), and the appearance of the primary fissure, which divided the corpus cerebelli in posterior and anterior lobes. The subsequent appearance of additional fissures divided the anterior lobe into lobules I–V, the posterior lobe into lobules IV–IX, and the flocculonodular lobe was designated lobule X. The designation HII to HX was assigned to the hemisphere portions of lobules II–X; there is not a hemisphere to lobule I. This became the standard terminology; the concept of a median lobe completely disappeared, and is not in use in contemporary terminology.

Ingvar's work was frequently cited in classic works, such as those of Ariëns Kappers [25, 26] and Larsell and Jansen [27, 28].

In the macroscopic subdivision of the cerebellum, Bolk [29–33] had described two lobes, anterior and posterior, separated by the primary fissure. Ingvar [14, 34] further divided Bolk's posterior lobe into two lobes, i.e., Ingvar's posterior lobe and lobus medius (Figs. 3 and 4), caudally delimited by the prepyramidal fissure that laterally extends in the ansoparamedian fissure. Ingvar's division was adopted by several authors, including Johann Paul Karplus (1866–1936) and Otto Marburg (1874–1948) in Vienna [35, 36]. The macroscopic division of the cerebellum in terms of lobes, lobules, sublobules and folia was based on fissure patterns, regional differences in histogenesis, and comparative morphology; Ingvar [14] defined the middle lobe as demarcated by the prepyramidal fissure (extending into the ansoparamedian fissure) and the fissura prima [37, 38].

Ingvar studied the homology of the mammalian paraflocculus and the human tonsil. Bolk's term "pars tonsillaris" for the paraflocculus and the homology of the (dorsal) paraflocculus are correct, whereas Ingvar's interpretation is incorrect. In the first place, the figures of Bolk on the subject illustrate several intermediate stages and are superior to the rather vague illustrations of Ingvar. The principal argument pertains to the zonal composition of the flocculus and the distribution of the pontocerebellar mossy fiber projection. The latter has been studied by Voogd [39, 40] and his group [41].

According to Ingvar [14], in crocodilians, the anterior and posterior sulci divide the cerebellum into three lobes, i.e., anterior, medius, and posterior (Fig. 3a(1, 2)). The anterior sulcus was considered homologous to the fissura prima of mammals [42]. However, Ingvar does not provide definitive evidence for the homology of these fissures in crocodiles, and thus his homology is questionable. He mentions that spinocerebellar afferents would terminate rostral to the anterior fissure, i.e. in the anterior lobe: "The two posterior lobules in the crocodile are innervated, mainly or exclusively, by the vestibular fibers" [14], i.e., the median and posterior lobes. A vestibular input is not in accordance with the homology of the median lobe in birds and mammals. The statements of Ingvar about afferent connections in crocodiles are not supported by actual experiments, and the Weigert specimens he published cannot be considered as such.

In evolution, Ingvar held the opinion that the cerebellar nuclei shifted from a subcerebellar position into the cerebellum, which occurred at the reptilian level; later comparative studies, however, showed that the cerebellar nuclei derive from the cerebellar anlage in all vertebrates [42].

The avian cerebellum is more massive compared to the reptilian and has a more complex pattern of transverse fissures (Fig. 3a(3)). The degeneration studies of Ingvar showed that the spinocerebellar afferent system of birds is very similar to its mammalian homolog (Fig. 3a(4), b). Ingvar described three grooves (fissures *x*, *y*, and *z*) in the chick cerebellum, which develop very early, as homologous to the fissura prima, fissura prepyramidalis, and fissura secunda of mammals. Moreover, he showed that the avian cerebellum develops from two bilateral thickenings of the alar plates (Fig. 4a, b) that later fuse in the median plane to form a single cerebellar plate [42].

Ingvar admitted that, "In making his subdivision, a morphologist only gives expression to his personal phantasy, and will never get rid of his subjectiveness in viewing the matter, any subdivision therefore being really quite arbitrary" [21].

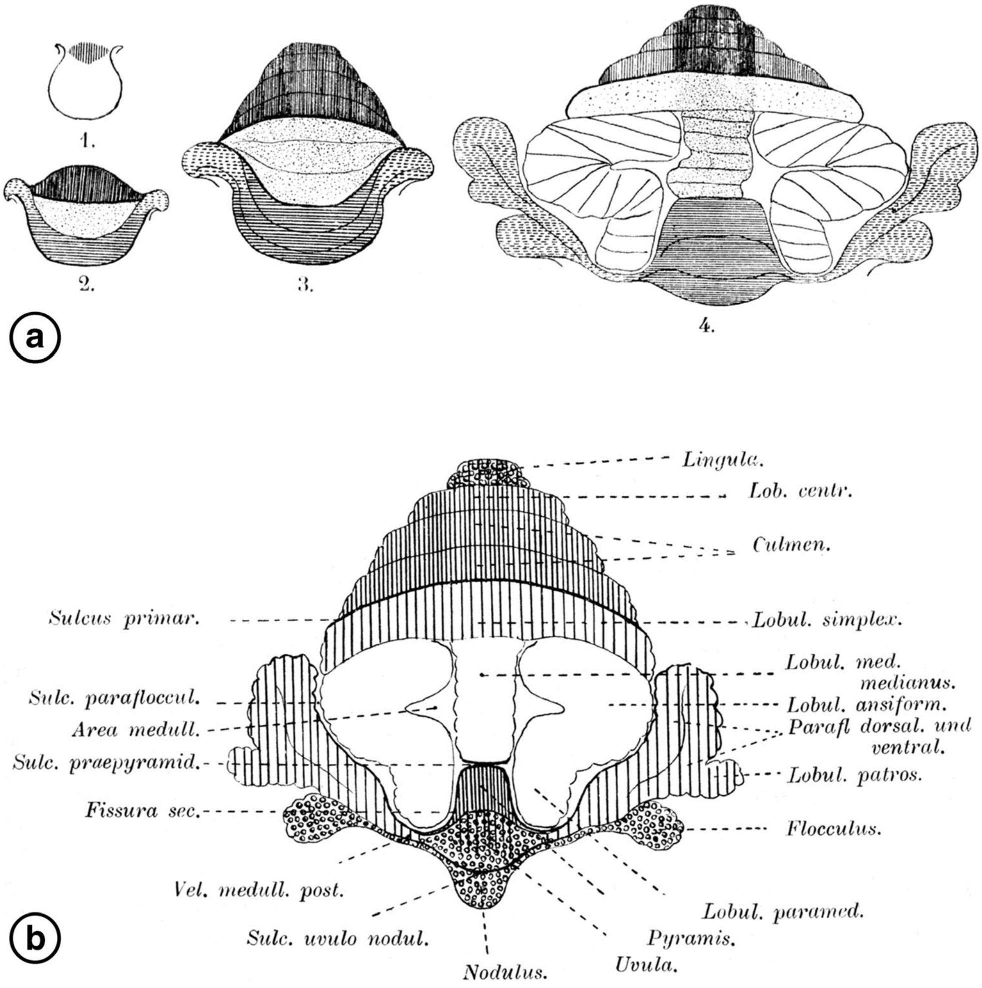

**Fig. 3** **a** Schematic drawings of the lizard (1), crocodile (2), avian (3), and mammalian (4) cerebellum, with Ingvar's designations. Vertical lines, anterior lobe; horizontal lines, posterior lobe (with the pars auricularis, broken lines, shown only in part); dotted, lobus medius; white, lobus ansoparamedianus. **b** The distribution of the direct vestibulocerebellar (small circles) and spinocerebellar projection systems (vertical lines) in the mammalian cerebellum. The cerebellar cortex is shown spread in one plane; the periphery of the drawing corresponds to the base of the cerebellum, i.e., the parts situated in the immediate vicinity of the fourth ventricle and the vestibular nuclei. Figures 73 and 82 from Ingvar [14]

Although he repeatedly pointed out the laminar uniformity of the cerebellar cortex, as opposed to the cerebral cortex, he noted certain regional differences regarding the number of Purkinje cells as well as myeloarchitectonic variations [22]. However, it was four decades later that Voogd, using the Häggqvist method of myelin staining, demonstrated in ferrets the division of the cerebellar white matter into seven longitudinal compartments corresponding to Purkinje cell axon cohorts, which set the stage for our current understanding of the zonal pattern in the *Bauplan* of cerebellar histophysiology [43, 44]. Following systematic studies in several species, including the cat, prosimian primate, tree shrew, squirrel monkey, opossum, and rat, the zonal pattern was since extended to include olivocerebellar fibers and the congruent corticonuclear axons of Purkinje cells [45–48]. Voogd [44] noted that Haines [46] was first to provide experimental evidence that rostrocaudally oriented zones existed as Voogd [43] had hypothesized; the wide variety of animals studied proved that such a zonal pattern was not likely species-specific. Based on their ontogenetic and molecular signatures, Purkinje cells were also found to be parcellated into heterogeneous subpopulations, which are congruent with the olivocerebellar and spinocerebellar maps [49, 50].

Since the cerebellar cortex has the same basic cellular organization throughout, the attempt to understand functional localization was based on phylo-ontogenetic criteria, the distribution of afferent and efferent axons, and somatotopy, rather than on cytoarchitectonics [13, 14, 51]. Ingvar [14] demonstrated a rough somatotopic organization of the terminations of spinocerebellar fibers in the cerebellar cortex (Fig. 5a–c); caudal segments project to the most rostral folia of the anterior lobe, while rostral segments project more caudally [52]. Moreover, it was later found that the somatotopic organization in the vermis is mediolateral rather than rostrocaudal [53].

As Llinás and Simpson [51] explain, Ludwig Edinger (1855–1918) had divided the cerebellum into a paleocerebellar part, comprising the vermis and flocculus, and a neocerebellar part, comprising the intermediate and lateral zones of the hemispheres [54]. A decade later, Ingvar [14, 34] proposed a division of the cerebellum into three parts, namely, a vestibular, a spinal, and a corticopontine cerebellum; he based such a division on the consideration that the afferent pathways respectively emanating from the vestibular nucleus, the spinal cord, and the pons were the most prominent. Ingvar allocated the paraflocculus to the spinocerebellum, and the middle part of the vermis (his

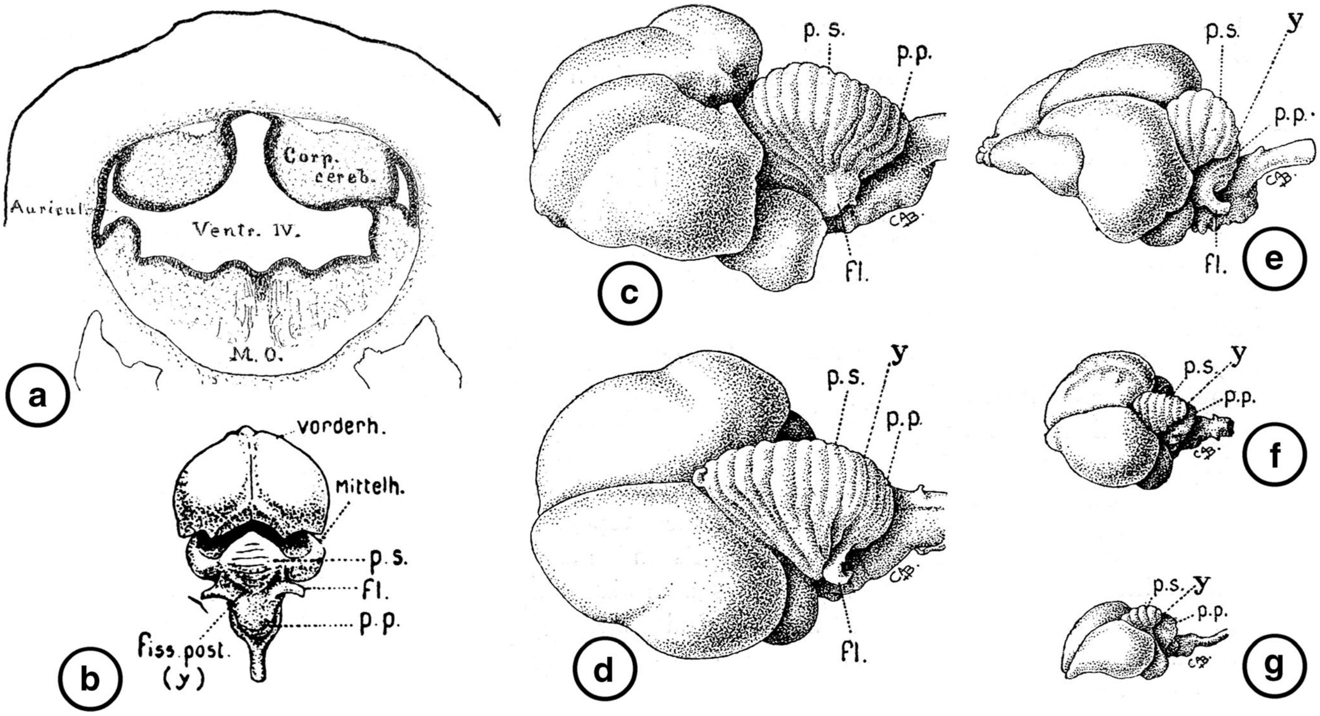

**Fig. 4** **a** Section of the cerebellar anlage in a 5-day-old chick embryo. **b** Rear view of the brain of an ostrich embryo just before hatching; note the fissure *y* (fiss.post.) cutting off the part of the cerebellum caudal to it. **c** Cerebellum of *Dromaius novaehollandiae* (emu). **d** Cerebellum of *Morus bassanus* (northern gannet). The cerebellar of **e** *Anser indicus* (bar-headed goose), **f** *Nucifraga caryocatactes* (nutcracker), and **g** *Ottocampsa leucotis* (sparrow); note the sharpness of fissure *y* in the smaller animals. Abbreviations: Vorderh., forebrain; Mittelh., midbrain; p.p., posterior lobe; p.s., lobus medius; fl., flocculus. Figures 13, 24, and 44 from Ingvar [14]

lobulus medius medianus or sublobulus C2 of Bolk or lobule VII of Larsell) to the pontocerebellum [51].

In experimental studies with the Marchi method in cats, Ingvar [14] traced degenerating primary vestibular fibers to the ipsilateral flocculus and nodulus, the uvula, lingula, and fastigial nucleus as well (Fig. 5d) [21, 55]; such projections were subsequently confirmed and expanded by other investigators [51]. In the uvula and lingula, vestibular root fibers are mixed with spinocerebellar fibers [14, 16]. The finding by Ingvar [14] of primary vestibular fibers crossing the midline was based on experiments where, presumably, inadvertent damage was caused to the vestibular nuclei; thus, there is no convincing evidence that primary vestibular afferents pass to the contralateral side [56, 57]. Another argument for the vestibular nuclei sustaining lesions is the presence of vestibular fibers in the flocculus. In the rabbit and monkey it was demonstrated that this projection does not exist for primary, but does exist for secondary vestibular fibers [58, 59].

Snider and Lowy [60] credit Ramón y Cajal [61], Ingvar [14], Larsell [62], and Dow [63] for the experiments that established the major vestibulocerebellar connections. Ingvar, in particular, showed that lobule I receives the projections of primary vestibular afferents [64]. The phylogenetically old flocculonodular lobe of Larsell has predominantly vestibular connections [14], whereas the younger part, the corpus cerebelli, receives spinocerebellar and pontine afferents [65]. Further, the older divisions within the corpus cerebelli, i.e., the lobus anterior and the pyramis and uvula, are the end stations of the spinocerebellar projections [14], whereas the younger parts of the corpus cerebelli, i.e., the lobulus medius medianus of Ingvar (lobule VII of Larsell) and the lobulus ansoparamedianus, which together form the neocerebellum, receive most if not all the pontocerebellar fibers [65].

Ingvar suggested naming the basal cerebellar regions, to which direct vestibular afferents arrive, the "vestibular storey or floor"; the regions above the vestibular floor, where the spinocerebellar afferents terminate, the "spinal storey"; and the remaining parts of the cerebellum, i.e., his lobus medius, including the cerebellar hemispheres, where the phylogenetically younger cerebropontocerebellar afferents run, the "top or cerebral floor" [21]. Those terms did not catch on, and do not appear in contemporary terminology. The modern terms that prevailed for these divisions are, respectively, the *vestibulocerebellum* (or *archicerebellum* on phylogenetic/evolutionary criteria, comprising the flocculonodular lobe and the immediately adjacent vermis), the *spinocerebellum* (or *paleocerebellum*, including the vermis and "paravermis" or intermediate parts of the cerebellar hemispheres), and the *cerebrocerebellum* (or *neocerebellum*, consisting of the lateral parts of the cerebellar hemispheres).

Ingvar appears not to have properly fathomed Elliot Smith's proposal of the copula pyramidis as the hemispheral

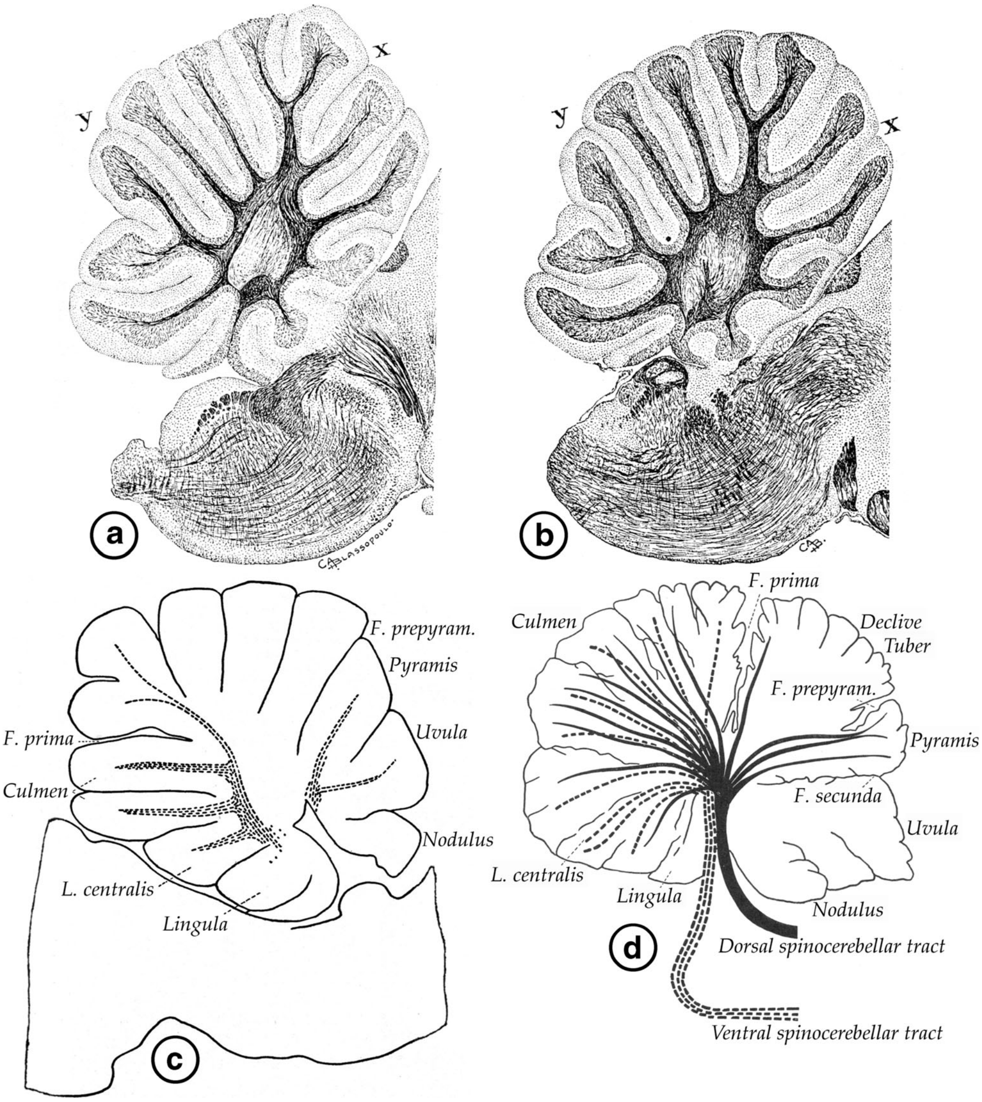

**Fig. 5** **a**, **b** Two sagittal sections though the cerebellum of the Eurasian blue tit (*Cyanistes caeruleus*). Pal-Weigert stain. **c** Termination of the spinocerebellar projection system in a midsagittal section of the dove cerebellum. Marchi method. **d** Termination of the spinocerebellar fiber systems in the cerebellar cortex of the cat vermis. Figures 27, 75, and 77 from Ingvar [14]

component of the pyramis, especially when Bolk's idea of the cerebellar hemisphere as a folial chain is accepted. The copula forms a single lobule in rodents, nowadays indicated as lobule HVIII, located between lobule HVIIB, the paramedian lobule, and the lobule HIX, the paraflocculus. In carnivores and primates it consists of several folia and is generally incorporated in the paramedian lobule as its caudal portion. The copula-paraflocculus transition also indicates the caudal pole of the C1, C3 and Y zones.

The pontocerebellar mossy fiber projection was not studied by Ingvar, which may explain some of his caveats. In cat and monkey [39, 41], its terminations were found in Larsell's lobule VII (folium and tuber) with the ansiform lobule and the rostral papamedian lobule, and in the rostral uvula with the paraflocculus. The flocculus receives its main pontine afferents from the nucleus reticularis tegmenti pontis [66]. The pontine afferents to the uvula intervene between the vestibular input to its caudal part and the spinal projection to the pyramis. It is at variance with Ingvar's idea about a phylogenetically ancient posterior lobe. Therefore, intermingling of vestibular and spinal afferents in the uvula cannot occur.

The border between the paraflocculus and the flocculus is the change in the zonal composition of these lobules. Three zones, the C2, D1, and D2 zones, typically extend into the paraflocculus; the C1, C3, and Y zones do not. The flocculus contains two interdigitating pairs of zones, projecting to the vestibular nuclei and an extension of the C2 zone. In all species, the floccular zones extend for some distance onto the ventral paraflocculus; in the monkey, they even occupy the entire ventral paraflocculus. The connection of the ventral paraflocculus with the (lobulus petrosus of) the dorsal paraflocculus consists of a narrow cortical bridge. This point, which separates the dorsal and ventral paraflocculus, can be identified as the breach in the cortex between the tonsil and the accessory paraflocculus in humans and the great apes. As a consequence, these two structures are the homologs of the dorsal and ventral paraflocculus, respectively [39, 66–69]. In humans and the great apes, a lobulus petrosus, located in the subarcuate folia of the petrosal bone, does not occur.

Ingvar [14] noted that the granule cell layer of amphibians differs from that of mammals, birds and some reptiles in that the myelinated afferents of the frog lie in the central region of the granular layer [70]. Moreover, the cerebellar cortical layering in the frog differs from that of mammals in that there is not a deep axis of white matter, and myelinated fibers are intermingled with granule cells at the central region of the granule cell layer [71]. In birds, Ingvar showed that spinocerebellar fibers arise over the entire length of the spinal cord, all the way down to the level of the last lumbar roots, in contrast to fishes, in which spinocerebellar fibers only originate from the cervical cord [25, 26]. The origin of the spinocerebellar projection in reptiles resembles the origin of the rostra1 and ventral spinocerebellar tracts in mammals [72].

Regarding development, Ingvar found the cerebellar anlage represented in the 5-day-old chick by two bilateral swellings, not as yet joined in the midline, but with the auricular or floccular portion separated from the corpus cerebelli on each side by a slight depression (Fig. 4a–g). In the 9.5-day-old chick, the eminences have increased in size and fused in the midline [14, 28]. Altman and Bayer [73] later showed that the midline fusion of the cerebellar plates in the rat begins on embryonic day l6, when the neuroepithelium bridges the midline in the caudal portion of the cerebellum and adjacent to the attachment of the tela choroidea. From that fused neuroepithelium derives the germinal trigone on embryonic day l7, which in turn produces the external germinal layer [73]. The vertical ventricular cleft which separates the two halves of the cerebellum virtually disappears by embryonic day 22 in mammals, but not in birds.

In the introduction of his thesis, Ingvar queried, “How can one begin a fruitful study of localization before agreeing on what to locate, the function itself!” [14]. Nonetheless, based on his animal experiments and human neuropathological studies, Ingvar [17, 34] supported the idea of functional localization in the cerebellum, correlating specific topographical regions or parts of the body to specific subdivisions of the cerebellum, and opposing the view of Holmes of a more holistic relation between parts of the cerebellum and the corresponding limb or portion thereof [74].

The first clear-cut evidence of functional localization in the cerebellar cortex became implicit toward the end of the nineteenth century through the physiological experiments of Max Löwenthal (1867–1960), Victor Horsley (1857–1916), and Sir Charles S. Sherrington (1857–1952), who showed that stimulation of a confined area of the cerebellum inhibited decerebrate rigidity [74]. Ingvar’s concept of three divisions of the cerebellum, based on vestibulocerebellar, spinocerebellar and corticopontocerebellar afferents [14, 34], helped to supplement the anatomical substrate of such localization of function [74].

After destroying the pyramis, uvula and nodulus in rabbits, Ingvar [14] reported opisthotonus and a tendency of the animals to fall over on their back. Those effects led him to regard the lobulus posterior medianus (lobule VIII–X of Larsell) as the center of muscular activity which prevents the animal from falling backwards [74]. Gino Simonelli [75] of the Physiological Institute in Florence, after performing similar operations in rabbits, cats, and dogs, criticized Ingvar’s conception. Simonelli did observe opisthotonus with extension of the forelimbs and a tendency of animals to fall backwards; however, he noticed that such effects depended on the tonic extension of the neck, and they could be prevented by a passive flexion of the head. Thus, he explained Ingvar’s findings [14, 34] as a consequence of the opisthotonus, which is produced by a release of tonic labyrinthine reflexes, and not directly related to the trunk or limb muscles. In subsequent experiments, Simonelli [76] realized that the collateral destruction of the fastigial and dentate nuclei, which relay impulses from the anterior cerebellar lobe, could explain the opisthotonus and forelimb hyperextension, as these are the most typical signs induced by anterior lobe damage [74].

Chambers and Sprague [77] introduced a concept of functional localization based on experiments in cats. They suggested the existence of two physiologically different, longitudinally organized corticonuclear zones, identical in extent to those which were previously defined anatomically. In their view, the *medial* zone comprises the vermal cortex and the fastigial nucleus, and is concerned with postural tone, equilibrium and locomotion of the entire body; its attributes fall into the category of motor function known as extrapyramidal. The *intermediate* zone comprises the paravermal cortex and the nucleus interpositus, and is involved in a discrete control of the use of only the ipsilateral limbs; that mechanism falls into the functional classification of the pyramidal motor activity. Actually, there are three zones, based on the observations of Brodal [78] and Jansen and Brodal [79] on the olivocerebellar and corticonuclear projections. It should be realized that each of these zones is an amalgam of two or more zones that were discovered more recently.

The morphofunctional organization of the cerebellum is complex and involves organizing principles different from those operating in the cerebral cortex. The cerebellar cortex is relatively uniform when studied histologically, and it does not appear to have well-defined cytoarchitectonic areas, in contrast to the parcellation of the cerebral cortex. There is histochemical heterogeneity in the cerebellar cortex in the form of parasagittal zones; further, a topographic organization of somatosensory regions has been mapped. The “fractured somatotopy” of the rodent and primate cerebellum into dorsomedial and ventromedial somatomotor maps differs substantially from the cerebral somatotopic maps [80].

The vestibular, spinal, and corticopontine divisions of the mammalian cerebellum of Ingvar, Larsell, and Dow are arranged as a rostrocaudal series of zones (both afferent and efferent to the cerebellar cortex) that intersect with the transverse lobules [81]. Obviously, the simple division of the mammalian cerebellum in vestibular, spinal, and corticopontine regions by Ingvar, Marburg, Larsell, and Dow has been revised, as the borders of such regions are located at the bottom of a fissure, but, foremost, run along its sides between the base and the apex of the lobules, dividing them in proximal and distal portions. Therefore, each lobule and sublobule has its own distribution of afferents and represents regional specializations rather than simple expansions of the cerebellar surface [40].

Skeletomotor and visuomotor divisions have been recognized in the mammalian cerebellum. The *skeletomotor* cerebellum includes the anterior lobe with the lobulus simplex, the pyramis, the paramedian lobule, and the lateral crus I; the inputs and the outputs of the skeletomotor cerebellum are somatotopically organized. The *visuomotor* cerebellum includes the flocculus, ventral paraflocculus, nodulus, dorsal paraflocculus, oculomotor vermis, and crus I. A role of the cerebellum in the sensory guidance of movements has been suggested, with skilled visuomotor guidance probably involving the sequential activation of visual and motor areas in the cerebral cortex [82].

In discussing the physiological aspects of cerebellar function, Ingvar made the following interesting remark: “Since my investigations, in agreement with those of earlier authors, showed that the [anterior spinocerebellar] tract of Gowers and the [posterior spinocerebellar] tract of Flechsig do not go to the cerebellar centers of the extremities, one cannot imagine that such signals travel from the spinal cord to these centers directly, but that they are perhaps mediated cerebrally” [14]. Today, the anterior lobe and the pyramis with the paramedian lobule (the copula pyramidis, the region that receives the spinocerebellar tracts) are considered as the motor regions of the cerebellum, while lobule VII with the ansiform lobule as the non-motor regions [83, 84].

The current understanding of the cerebellar operational unit rests with the sagittal microzone, a concept commensurate with the cerebral cortical column [85]. That idea was advanced by the excellent work of physiologist Olov Oscarsson (1931–1996), also at Lund University, following an earlier hypothesis that such zones existed, proven by the afferent and efferent connections of zones using tract-tracing techniques. What Oscarsson showed, with his fine observations, was that climbing fiber potentials, upon stimulation of peripheral nerves, and Purkinje cell complex spikes observe a discrete parasagittal zone pattern [53, 86]. More precisely, these microzones, which reach a maximum width of 200 μm, are oriented perpendicularly to the long axis of the folia and the parallel fibers; their orientation corresponds to the sagittal plane where the folia are arranged transversely [85, 87]. Thus, the organizing principle in the cerebellum, rather than being based on cytoarchitectonics, which is the case in the cerebral cortex, is based on longitudinal subdivisions regarding neurogenetic attributes, molecular identities, afferent and efferent connections, whereby each microzone presumably regulates a particular functional mechanism.

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## Compliance with Ethical Standards

**Conflict of Interest** The author declares that he has no conflict of interest.

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